FOREST OF GRASS

DISCOVERING BIODIVERSITY IN THE AMAZON'S BAMBOO JUNGLES

BY JENNIFER M. JACOBS AND RUDOLF VON MAY

When people visit the Amazon River basin—at least the parts of Amazonia that no one has cleared of rain forest—they usually expect to find a dense habitat with many different kinds of big trees, shrubs, and vines—something that looks like . . . well . . . a rain forest! But if you are traveling to southwestern Amazonia, you may literally bump into a large and nearly impenetrable thicket of bamboo. If you are adventurous and decide to proceed, you might make your way through a small patch within a few minutes, but negotiating a larger tract might take you several hours or days of wielding a machete. Because bamboo stems grow very fast, reaching for the light, they often become top-heavy, bend over, and collapse. To encounter a collapsed portion is practically like running into a wall. The only option may be to crawl underneath fallen stems, dodging their spines and trying to avoid stinging and biting rain forest creatures that dwell on the ground or in low-lying vegetation. Sound like fun? Maybe not initially; but we've become hooked on this unique environment.

The bamboo forests of southwestern Amazonia cover a large area, but until recently the extent of their range was "unknown to science." According to research primarily conducted by Bruce W. Nelson of Brazil's National Institute of Amazonian Research (INPA), bamboo forests cover approximately 70,000 square miles in this part of the Amazon basin. Primarily distributed in southeastern Peru, in the neighboring states of Acre and Amazonas in Brazil, and in northern Bolivia, bamboo forests have been an important part of the landscape for a long time. A recent study published by Jean Olivier, of the University of Toulouse–CNRS, and his colleagues presented fossil evidence that *Guadua,* a prominent bamboo genus, existed in the region at least 45,000 years ago.

Looking further back in time, Mariana Brea and Alejandro F. Zucol, of the Center of Scientific Investigations in Diamante, Argentina, have described a fossilized piece of *Guadua* bamboo stem from northeastern Argentina dating from the Pliocene epoch (between 5.3 million and 2.6 million years ago). This suggests a warmer and more humid climate in that

View up through a canopy of Guadua bamboo: The genus has been present in the southwestern Amazon basin for at least 45,000 years. Bamboo plants may grow on land inhospitable to trees as well as colonize forested areas that open up when trees fall.

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area at the time: members of the genus today do not grow so far south. Probing still deeper into the past, recent phylogenetic studies by evolutionary biologist Eduardo Ruiz-Sanchez of the Institute of Ecology (INECOL) in Xalapa, Mexico, indicate that bamboo species of the subtribe Guaduinae, of which *Guadua* is a member, began to diversify in South America about 8.8 million years ago.

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At the entrance to its underground tunnel, a male scarab beetle perches on the mound it has built at the base of a Guadua *bamboo plant. The beetle species,* Enema pan, *feeds on the plant's sap.*

Guaduinae is one of three neotropical subtribes of woody species in the Bambusoideae, the bamboo subfamily. Woody bamboos are the hard-stemmed plants most people think of when they hear the word "bamboo," but the subfamily also includes herbaceous species, and in fact

DANIEL J. LEBBIN

*A female white-lined antbird: The species (*Percnostola lophotes*) nests within bamboo forest, in dead bamboo debris on the ground.*

falls within the larger grass family. The three neotropical subtribes of woody bamboos most likely radiated into Mesoamerica and Amazonia from an ancestor in Andean South America. How they are related to woody bamboos in other parts of the world is still unclear, although ultimately all bamboo is believed to have had a common ancestor in the Southern Hemisphere, either in Africa or in South America before those continents separated.

Not surprisingly, bamboo forests provide distinct vegetative surroundings for rain forest invertebrate and vertebrate species, such as ants, beetles, birds, frogs, and rodents. The degree of association between those organisms and the bamboo forests varies depending on whether they use the plants for shelter, foraging, or reproduction—or a combination of purposes. Each culm, or stem, of a woody bamboo plant is like a hollow tube, with solid nodes dividing it into a series of chambers, called internodes. The pumping action of the bamboo plant assures that the internodes are partly or completely filled with water. Those aquatic microhabitats often become home to invertebrate larvae, such as those of mosquitoes, which may dine on microorganisms that live there. Other organisms, such as ants, katydids, and weevils, find that dry walls above the water inside the internodes are ideal places on which to deposit their eggs. Ants live inside live or dead bamboo stems, while beetles, rats, and monkeys eat the leaves, shoots, or sap. And many birds use the bamboo forest for nesting, feeding, and shelter.

Although the water-bearing feature of neotropical bamboo stems was described long ago by the German naturalist and explorer Alexander von Humboldt, little research has been conducted on bamboo forest ecology. Indeed, until relatively recently bamboo forests have been thought of as species-poor, weedy habitats. Upland (terra firme) forests and floodplain rain forests seemed more worthy of attention. Some early investigators thought that the expansion of bamboo forests in southwestern Amazonia might even be threatening to plants and other organisms inhabiting other forest types. With the exception of a few notable studies, biologists have just begun to discover this important component of the region's greater ecosystem.

THE MOST COMMON BAMBOOS IN SOUTHWESTern Amazonia are *Guadua angustifolia, G. sarcocarpa,* and *G. weberbaueri*. They are spiny species that grow in dense stands and that can reproduce clonally with rhizomes or sexually with seeds. As pointed out initially by Nelson and collaborators, and in subsequent research by Bronson W. Griscom and P. Mark S. Ashton of the Yale School of Forestry & Environmental Studies, most bamboo in the region grows in patches, from a few acres up to tens or even thousands of square miles in size. Those patches are often surrounded by upland forest or floodplain rain forest. Griscom and Ashton determined that the basic composition of soil does not differ between bamboo-dominated forest and neighboring forest without bamboo, but the topsoil in bamboo forest is either wetter or drier than in the surrounding forest—bamboo can tolerate a wide range of soil conditions. Bamboo grows fast and aggressively and will colonize small gaps created by treefalls or large gaps created by blowdowns from convective storms, characteristic of the Amazonian climate. Large bamboo patches are also common along roadsides or in pastureland cleared by humans, which gives the impression that bamboo is an invasive, alien plant—but it is not.

MARCOS RIOS

A female weevil (genus Rhinastus*) uses its snout to drill holes in* Guadua *bamboo. She will then deposit eggs onto the inner walls of the bamboo stem.*

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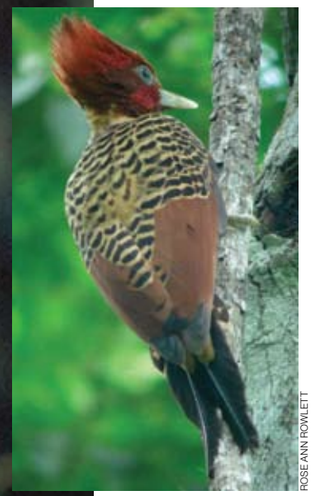
Cutaway view of the "internode" space in a dead Guadua *bamboo stem reveals an old wasp nest.*

Whereas rain forests typically have many large trees that create a dense canopy, bamboo forests primarily comprise plants with relatively thin stems, small leaves, and a lower canopy—which allows more light to enter. In addition, bamboo forests have layers of fallen or bent branches and stems. Griscom and Ashton have seen evidence that the piling up of bamboo may actually damage and suppress the growth of tree species. Yet bamboo forests are ephemeral, because many patches flower synchronously and then die over large areas. Nelson and other researchers who have studied bamboo on large spatial scales with remote sensing (among them Sassan Saatchi of the Institute of the Environment and Sustainability at the University of California, Los Angeles, and Miles R. Silman of Wake Forest University in Winston-Salem, North Carolina) suggest that the plants may recolonize the same areas if they successfully set seed. Thus large patches of bamboo may blink in and out of existence over time and space, presenting a dynamic, relatively short-lived resource for other organisms.

Some of the questions that have puzzled scientists studying long-term forest cycles in Amazonia are how often bamboo forests experience massive die-offs, how much reduction or expansion bamboo-dominated forests have experienced through time, and whether bamboo will take over large areas by displacing other types of forest. Nelson and his colleague Milton C. Bianchini, who along with other researchers have been studying forest dynamics, have addressed some of those questions. Using images obtained by satellites (Landsat and MODIS), they analyzed specific optical bands and compared the reflectance of canopy in forest dominated by live bamboo, forest with no bamboo, and areas with recently dead bamboo—that is, those that had experienced synchronous bamboo die-off. Studying images collected over nearly three decades, they concluded that stands of *Guadua* bamboo distributed around the Peru-Brazil border in western Amazonia undergo life cycles of twenty-eight to thirty years.

Because the image coverage barely spanned the bamboo's estimated life cycle, Nelson and Bianchini could not observe any mature bamboo stand dying off twice in the same area. They did, however, discover that some areas exhibited a pattern of semi-synchronous mortality, with most, but not all, bamboo populations distributed close to one another dying off relatively close in time. They compared that phenomenon to falling dominoes.

Other, less extensive bamboo forests also exist in the region and are composed of species in the non-spiny, woody bamboo genera *Aulonemia* (in the subtribe Arthrostylidiinae) and *Chusquea* (subtribe Chusqueinae), and in the herbaceous (non-woody) genus *Olyra*. According to research by Glenn H. Shepard Jr. of INPA and colleagues (including Nelson), members of the Matsigenka indigenous group in southwestern Amazonia are



ROSE ANN ROWLETT

RUDOLF VON MAY

Square holes in a Guadua *bamboo stem, above, were drilled by a rufous-headed woodpecker—shown above right, on a tree.*

able to identify and name up to six forest types dominated by bamboo, out of the total of sixty-nine habitat types that they recognize based on vegetation characteristics. For example, patches of *Chusquea* appear on mountain slopes in the Andean foothills, whereas large areas covered by *Guadua* species occur in upland and floodplain forests.

For the Matsigenka, Yora, and other indigenous groups, *Guadua* species are economically important because the stems are used to make arrow points for hunting, raiding, and defense. Other locals in various settlements and urban areas use bamboo stems for constructing walls, manufacturing household objects (such as candle holders and vases), and even in cooking (*pacamoto,* a local delicacy in southeastern Peru, is fish or meat steamed inside a piece of bamboo). It is also common knowledge that bamboo holds water and thus provides a source of drinking water for thirsty humans.

ANIMAL LIFE ASSOCIATED WITH BAMBOO HAS been investigated by various biologists, usually based in one of three prominent study areas in southeastern Peru: Tambopata National Reserve, Los Amigos Conservation Concession, and Manu National Park. In 1996, for instance, entomologist Jerry A. Louton of the National Museum of Natural History (NMNH) at the Smithsonian Institution in Washington, D.C., and his colleagues described the aquatic microhabitat inside bamboo internodes. They documented twenty-nine insects using this resource, including a huge damselfly, a katydid, and various mosquitos and flies. Regarding the katydid (*Leiobliastes laevis*), they hypothesized that the female uses her blade-like ovipositor to slice into the bamboo, leaving a characteristic "slot" in the stem, and then deposits her eggs on the inner walls of an internode. They concluded that the area around such slots would decompose and produce a larger entryway for other organisms making use of the internode. Some, whose larvae require aquatic habitat for rearing and development, use the miniature pools. Others use the inner walls of the bamboo as a retreat site or a protected place to lay their eggs.

In spite of their many contributions, Louton and his colleagues overlooked two Brazilian studies, published in 1916 and 1928, that describe an Amazonian weevil puncturing the stems of various bamboo species and laying its eggs inside. In Brazil, this weevil, in the genus *Rhinastus,* was even considered a plague to bamboo plants. Louton may have missed those studies because the Brazilian researchers didn't describe the weevil specifically using *Guadua* bamboo, but photographs and observations have confirmed that this weevil is responsible for the damage described by Louton. Entomologist Terry Erwin of NMNH has studied insects found with bamboo in South America, and has also observed this weevil ovipositing in bamboo. In fact, we have observed katydids ovipositing in the soft shoot (tip) of a bamboo stem, but not in the region of the bamboo stem that contains water-filled chambers.

Once the aquatic microhabitat is colonized, an entire food web develops, with voracious mosquito and damselfly larvae as top predators, along with carnivorous tadpoles. The tadpoles belong to the poison frog *Ranitomeya sirensis*, which takes advantage of internodes that have been opened by other organisms. Even though this species is not a bamboo specialist—it may breed in tree holes and other water-filled plant structures—it is frequently found in close association with bamboo throughout its range. When using bamboo, a mating pair deposit and fertilize their egg clutch on the inner wall of the internode, above the water. When newly hatched, tadpoles may drop into the water or, more commonly, be transported by the father to other individual pools to complete their development. If two or more tadpoles remain in the internode or are deposited in the same pool, which sometimes occurs, then one tadpole will cannibalize the others.

DIANE W. DAVIDSON

Nest entrance of* Camponotus *mirabilis, an ant species that exclusively inhabits bamboo forest

MARGARITA MEDINA-MULLER

Bullet ants on a* Guadua *bamboo stem: The predatory species (*Paraponera clavata*) is noted for its fierce sting.

Although the tadpoles prey upon many aquatic insect larvae living in bamboo internodes, they can easily be prey for large mosquito larvae in the genus *Toxorhynchites*. It's a rough world inside the seemingly peaceful bamboo stems. If it is lucky, a larva that successfully completes the aquatic phase of its life cycle inside bamboo will exit through the same hole it entered as an egg, and the cycle continues.

In our surveys of bamboo internodes in southeastern Peru, we also found that five species of tree frogs, one lungless salamander, and two species of arboreal snakes use the bamboo internodes as retreat sites. We observed none of those species, however, breeding in bamboo.

BAMBOO IS ALSO USED IN A COMPLETELY different way by a large, beautiful scarab beetle with the unfortunate name *Enema pan*. We have observed that this beetle builds a mound of soil at the base of a bamboo stem. Beneath the mound, the beetle shreds open the bamboo stem to obtain sap from the plant tissue. Though the entire life cycle of the species has not been described, we know, based on our own observations and excavations of a few mounds, that the beetle digs one tunnel, sometimes with small offshoots, more than three feet deep beneath the base of the bamboo plant. Presumably it lives in the tunnel, coming up to feed at night from the bamboo.

MARGARITA MEDINA-MULLER

*A male poison frog (*Ranitomeya sirensis*) carries one of its newly hatched offspring on its back. The frog distributes the tadpoles to individual pools, such as water-filled bamboo internodes.*

Also at night, the beetles open their soil mounds and perch at the entrance, possibly to attract mates. While the mounds are open, the shredded bamboo stem attracts a variety of beetles, flies, spiders, sweat bees, and wasps. Like the weevil's ovipositing behavior, *Enema pan*'s feeding on the bamboo stem makes a new resource or microhabitat accessible to many other organisms.

ACCORDING TO RESEARCH BY UNIVERSITY OF UTAH BIOLOGIST Diane W. Davidson and her colleagues, several species of ants in the genus *Camponotus*—commonly known as carpenter ants or sugar ants—make use of bamboo internodes. Some inhabit live or dead bamboo stems, but not exclusively, since they also form colonies in other settings. But two species (*C. mirabilis* and *C. longipilis*) are considered bamboo specialists, because they establish colonies inside the live stems and are absent from surrounding forest that lacks bamboo. They build paper-like layers of organic material, where they maintain their eggs and larvae. Inside the nest, the larvae are typically positioned near scale insects—also known as coccids—which in turn are attached to the internal wall of the bamboo internodes. These scale insects (*Cryptostigma guaduai*) produce honeydew that supplements the nutrition of ant workers and larvae, and in exchange, the scales are protected by ants.

At night, the bamboo stems and their immediate surroundings may experience busy traffic as worker ants shuttle the brood (eggs, larvae, and pupae) and scale insects here or there among neighboring stems. The ants also forage for leaf-litter arthropods and collect decaying wood, all of which is brought back to the nests. The ants' nocturnal activity protects them from diurnal predators and from phorid flies, which parasitize various species of ants. Occasionally, the ants have to defend their colonies from attacks by army ants. *C. mirabilis* and other bamboo-inhabiting ants also have to face much larger predators, even during daytime hours. According to Davidson and her collaborators, the brown capuchin monkey

Trail through a dense bamboo patch: Weighed down by water, bamboo stems often fall over, taking down competing vegetation, such as tree seedlings. After years of growth, however, a stand of a particular bamboo species may vanish, when the plants flower and die synchronously.

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Boa constrictor is one of the many Amazonian organisms that are not specifically associated with bamboo forest but do frequent the habitat.

may feed on adult ants and their brood. We, in addition to other researchers, have observed the monkeys biting on bamboo stems, cracking them open, and retrieving and eating insect adults and larvae. We have also observed rufous-headed woodpeckers (*Celeus spectabilis*) drilling into bamboo stems in search of insects.

Several other mammals, including other monkey species as well as peccaries and rodents, benefit from the resources of bamboo patches. Bolivian squirrel monkeys search through curled up bamboo leaves during the day and regularly find arthropods hiding there. Peruvian night monkeys forage in bamboo at night and may use dense bamboo patches as a daytime retreat. White-lipped peccaries feed on new bamboo shoots and the underground rhizomes, causing damage to multiple stems at a time. Bolivian bamboo rats, which in southeastern Peru mostly inhabit bamboo stands, use them as a retreat during the day and night, and feed on the fresh leaves and sprouts at night. These arboreal rats can be detected hundreds of yards away because both males and females advertise their presence with a series of loud staccato calls that resemble a toad's croaking.

Mammalogists James L. Patton, of the University of California, Berkeley, Louise H. Emmons, from NMNH, and their collaborators, who have extensively investigated the ecology, behavior, and distribution of some mammals that use bamboo habitat, recognize that they are often present in other forest types. But mammals such as the Bolivian bamboo rat thrive in bamboo throughout their ranges. And Karim J. Ledesma, a Peruvian researcher who conducted her master's research on the assortment of small mammals in southeastern Peru, documented more species and a higher abundance of terrestrial mammals in the bamboo forest than in adjacent old-growth forest.

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Brown capuchin monkeys, here in a non-bamboo setting, also frequent bamboo patches, where they have been observed biting on stems, cracking them open, and retrieving and eating insect adults and larvae.

MANY BIRD SPECIES, INCLUDING the rufous-headed woodpecker, are considered to be bamboo specialists, or at least to be associated with bamboo habitat. That woodpecker, and some of its close relatives, drill square holes in bamboo stems in search of ants living inside. It is possible that woodpecker-induced holes may also initiate the colonization of the water inside bamboo stems, though it is unclear whether the woodpecker drills holes into water-filled stems while searching for ants, or can detect which stems don't have water and only targets those.

A 1997 study by Andrew W. Kratter of the Florida Museum of Natural History in Gainesville (then at Louisiana State University in Baton Rouge) recorded nineteen bird species, in four families, connected with bamboo. These bird species range from those that specialize in bamboo throughout their entire ranges to those that prefer bamboo forest when present but which are also capable of using other habitats. Another ornithologist, Daniel J. Lebbin of Cornell University in Ithaca, New York, who conducted his dissertation research on birds in bamboo forests of southeastern Peru, has, with colleagues, described nest architecture and breeding biology for nine species of birds that use bamboo forests. In addition he has recorded seven species feeding on *Guadua* seeds after a mass flowering event. When bamboo plants flower synchronously, a large resource becomes available to many animals, and especially to seed-eating birds. Some, but not all of the birds in Lebbin's studies were previously documented by Kratter or by the late Theodore A. Parker III, who conducted extensive ornithological research in South America. Given the small number of studies conducted on birds in bamboo forest, it is highly probable that additional birds use this habitat but haven't yet been observed.

Many human activities, such as clearing forest for agriculture or pasture, are destructive of Amazonian environments and imperil their wildlife. Climate change is also likely to affect the region. How both may alter the distribution of bamboo forests is uncertain. One recent, experimental study by Maira Smith and Bruce W. Nelson of INPA suggests that fires may favor bamboo expansion over tree species in southwestern Amazonia. With many climate change predictions indicating a drying-out of the Amazon, more frequent and intense blowdowns, and increased deforestation and subsequent drying directly caused by human activities, bamboo may become too common—at the expense of other forest types.

If you are familiar with planting exotic bamboos for landscaping, you may know that they can aggressively take over an entire backyard. Does this mean that the Amazon will one day be covered by a giant grass? Probably not, but understanding how species coexist with other species in their native ranges, and under specific climatic conditions, will allow people to predict and mitigate irreversible changes. It is also possible that one disease could wipe out huge swaths of bamboo forest, especially because they are clonal organisms and their limited genetic diversity puts them more at risk from plagues. All we know is that as long as bamboo forests are around, they will continue to support a great diversity of life. It's time to sharpen your machete!

Jennifer M. Jacobs, a native Californian, is a graduate student of ecology in the Department of Integrative Biology, University of California, Berkeley. She enjoys exploring nature and participating in environmental education. Her husband, **Rudolf von May,** grew up in a rainforest region of central Peru and is now a postdoctoral research fellow in the Museum of Vertebrate Zoology, University of California, Berkeley, with a special interest in tropical amphibians.