On the Snails' Trail

Evolution and Speciation Among a Vanishing Tribe

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Dr. Guy Coppois is a malacologist. He started investigations on Galápagos terrestrial malacofauna in 1973, focusing on systematics, distribution, ecology and adaptation. A member of the Charles Darwin Foundation (CDF) General Assembly, he served on its Board of Directors (Belgian representative) from 1987–2003. He is Professor of Biology at Brussels's Free University.

Christine's experience 1999–2005

FOR OVER EIGHT YEARS now I have been studying the endemic land snails of Galápagos, during which time these creatures have truly 'grown on me.' I first came across their trail in 1999, when I spent five months on Galápagos doing research on two introduced predatory wasps. Toward the end of my field season, in the arid zone of Santa Cruz Island, I was sitting on a lava rock observing *Polistes versicolor* wasp nests when I noticed tiny white shells littered about. It was the first time they had caught my eye, but soon I began to see them almost everywhere. The shells were quite small, at most 1 cm (0.4 in), so it was no surprise that I hadn't seen them earlier. As I would learn later, not many people had noticed them before either. Now that I had a few in my hand, I could tell that these were old shells left behind by their builders a long time ago. They were pure white, bleached through long hours lying in the sun; a light pressure of my fingers would easily crush their fragile whorls — they were simply beautiful.

Later, at the Charles Darwin Research Station (CDRS) library, I came across a revealing paper published in 1966 by Allyn Smith describing the 'Galápagos land-snail fauna [as] unique in many respects.' According to Smith, there were over 50 species in one genus alone, known as *Bulimulus*. Over 50 species?! Among the famous examples of adaptive radiation in Galápagos, Darwin's finches are the most celebrated yet consist of *only* 13 species. The largest other group I knew of were beetles, with 20 species or so. I was shocked — how was it possible that I never noticed the snails before? But I was also very excited: maybe this *Bulimulus* genus could be a great topic for the study of evolutionary diversification, my main scientific interest.

After I returned to Carleton University in Canada to finish my Master's thesis on wasps, I started thinking about pursuing a Ph.D. in evolutionary ecology, and, with my supervisor's encouragement, decided to study the Galápagos bulimulid land snails. But remembering the empty shells on Santa Cruz, I became concerned upon reading that a lot of the species were now possibly extinct. Dr. Guy Coppois had done extensive work on these snails in the 1970s and 1980s and stated 'land snails are endangered, and many species are already extinct.' But other reports were claiming that not all had so far been discovered, as every single scientific expedition that looked for snails had returned with additional undescribed forms. Even while they were going extinct, I hoped that enough snails were left to study the most species-rich radiation known on Galápagos.

RIGHT: Typically clinging to low plants, live *Bulimulus* snails are still fairly common on the rain-drenched slopes of Isabela's southern volcanoes.

In November 2000, I was back on Santa Cruz Island with a simple goal: I had 10 days to find samples of as many species of bulimulid land snails as possible to bring back to Simon Fraser University in Canada, where I had started my Ph.D. a couple of months earlier. I needed live specimens to be able to extract DNA from their fresh tissues. The same strand of DNA for each specimen would then be amplified and sequenced so that I could read a small part of the genome of every individual I collected. Comparing the DNA, I would determine the evolutionary relationship among the different species, in the same way you can determine how closely related individuals are based on morphological resemblance. Once a phylogeny (a tree representing the sequence of species formation in a group) based on the DNA sequences is obtained, it becomes possible to look back in time and infer their evolutionary history: what is the sequence of species formation in this lineage? Does it match the geological sequence of island formation? Are species often formed within an island or do they always need to colonize a new island to split definitively from an ancestor? Those were among the many evolutionary questions I was hoping to solve. In addition, my goal was to gather enough information about bulimulid populations to help protect this unique island fauna.

By this time, I had learned that there are over 80 species and subspecies described in the genus. On Santa Cruz Island, this diversification had reached such extremes that almost every hill or valley might harbour a separate type. I also knew that the snails could potentially be found at all elevations (except in the littoral zone along the shore) and on all major islands. According to early reports, the difficulty of finding these small, dull-coloured species leading cryptic lifestyles should be compensated by their omnipresence. I figured that the best chances to find snails alive were in the moister environments, so with the help of the Invertebrate Department staff at the CDRS, I started my search on Santa Cruz Island, walking through the *Scalesia* forest in the humid zone. I knew that Guy Coppois had found up to 11 species at a single locality in this forest. However, after spending three entire days in the highlands, walking around and searching everywhere I could imagine, I found plenty of empty shells but not a single live snail.

Once again I worried that working on these snails might not have been such a great idea after all. With the major declines already reported by Guy, maybe I was just too late. He had noted that introduced species such as rats and little fire ants (*Wasmannia*

ABOVE: The lush *Scalesia* forest floor on the northern slope of the Santa Cruz highlands once harboured up to seven species bulimulid snail, all of which have mysteriously disappeared in recent years.
BELOW: A *Bulimulus ochsneri*, once extremely common around the village of Bellavista and throughout the Santa Cruz highlands.

DEEP-SEA DISCOVERIES

Strombina deroyae

Paziella galapagana

Pteropurpura deroyana

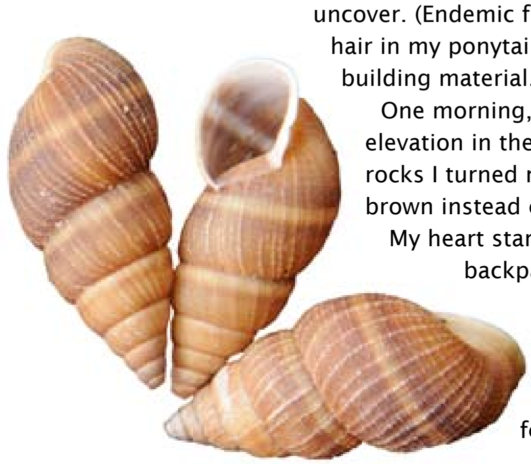
Latiaxis santacruzensis

Fusinus allyni, named after Allyn G. Smith of land snail fame.

The marine molluscs of Galápagos, though more varied than their terrestrial counterparts, are in many ways just as fascinating and unique. In the late 1960s and 1970s, the De Roy family conducted extensive dredging explorations of the deep-sea floor between the central islands, using a lightweight rig entirely designed and hand-crafted by André (fishnet dredge and hand-crank winch with 1200 m, or 3900 ft, of cable mounted on the stern of their small boat). Reaching depths of 600 m (1970 ft), numerous unknown gastropods were revealed, many of them extremely delicate in form. Jacqueline corresponded with various museum specialists who eventually described dozens of species new to science. Even though the De Roys advocated the use of descriptive or location names, which they felt would have more enduring significance in the nomenclature, several are nonetheless named in their discoverers' honour. No such dredging has ever been repeated since.

Tui De Roy

BELOW: Some of the most exquisite *Bulimulus* shapes and colours could be found on Floreana.



auropunctata) were preying on the snails and, at the same time, goats, donkeys and pigs were destroying their preferred habitats. I developed a routine of turning over lava rocks, lifting the bark of trees, rolling dead trunks, scratching in the leaf litter and even digging the soil. Usually after a few minutes I would have one or two mockingbirds join me, intent on snatching the tiniest moving creatures I might uncover. (Endemic flycatchers would come after the hair in my ponytail, I suspect looking for exotic nest-building material.)

One morning, I started my search at low elevation in the arid zone near town. The first rocks I turned revealed shells that were dark brown instead of the usually bleached white. My heart started pounding. I dropped my backpack, as well as my GPS and my notebook, and started frenetically lifting every lava rock I could find in the area. And there they were! Finally, I had found a few live specimens. In my head everything was going very fast: I could now return with some samples, get DNA from them, convince my supervisor that this project would work, return for several complete field seasons to Galápagos, and do my Ph.D. on a subject that I now truly loved! When I left Galápagos at the end of those 10 days, I had specimens of seven species from three different islands. This was all I needed to start developing methods towards a robust phylogeny to eventually describe the relationship among species in this spectacular group.

In January 2001, I resumed snail hunting on Galápagos, and this time stayed for three months. I went back successively in 2002, 2003 and 2005, spending overall more than two years looking for bulimulid snails. During that time, I visited most of the major islands and some smaller islets, collecting over 40 species. Along with the snails, I brought back fond memories of the unique fieldwork on Galápagos. Although the fauna is reputed to be inoffensive and tame, I managed to get bulldozed by a marine turtle while sleeping in my tent on the beach, have a Galápagos hawk, who felt that I was trespassing its territory, hit my head with his claws, and be stung and bitten by mosquitoes, wasps, scorpions and centipedes. However, these 'little' inconveniences, together with the difficulties of doing fieldwork in a place where water is scarce and the sun is unforgiving, have not spoiled my unique experience on these 'Enchanted Islands.'

Guy's experience 1973–2003

If Christine had such a hard time finding live snails, this situation was not always the case. Although scant attention was directed toward invertebrates during early expeditions, museum collections nonetheless testify that collectors picked up live specimens easily, mainly on San Cristóbal and Floreana islands. During the 19th century, human settlements and invasive introduced mammals brought deep modification to the natural habitat, and one can assume this to be the main reason for gastropod disappearance. Santa Cruz Island was colonized much later, with critical habitat destruction only beginning early in the 20th century. Populations of live bulimulids were still common when the CDRS was established and even when I initiated my work.

My field investigation on Galápagos snails started with an intensive three-year stint in September 1973, occupying the government-sponsored 'Belgian seat' at the CDRS, complemented by shorter trips up to 2003. The focus of the study, initiated by Professor Van Mol, was on species distribution, comparative ecology and systematics, with the final aim of gathering enough elements to build a clear picture of the adaptations and evolution of this complex group.

Part of my plan was also to work with the collections of Allyn G. Smith of the California Academy of Sciences who, as Christine mentioned, had already accomplished a major taxonomic revision of Galápagos terrestrial gastropods. Unhappily, this never happened, as he died just days before I arrived in San Francisco to meet him in September 1976. But Allyn had received much prior information on collecting sites and bulimulid ecology from a long-time Galápagos resident André De Roy, with whom I was lucky enough to collaborate.

André was an accomplished naturalist and an excellent observer of tiny details. He had an artist's eye and the skills that go with practical imagination. His wife Jacqueline also made major contributions by networking with experts around the world. Together with their children, Gil and Tui, the De Roy family assembled an incredible bank of observations on Galápagos flora and fauna when exploring the islands. André was fascinated by bulimulid land snails, and noted many details I was able to confirm in my own findings later. His experiences and observations on Galápagos land snails were exceptional, and we had unforgettable hours of discussions.

I first started work in the arid zone on CDRS territory. Even in the dry season, I soon found live specimens of pale brown *Bulimulus akamatus* hiding in cavities under lava blocks, while *B. reibischi*, slender white with a wrinkled surface, was aestivating (dormancy similar to hibernation, but induced by drought rather than cold temperatures) usually on, or under, tree bark. Every month, I collected in this area over a full year, using quadrate sampling techniques for comparison with other sites chosen in the various vegetation zones at different elevations. Today, this original sampling spot sits partially beneath the CDRS meeting hall and, as far as I know, living snails have vanished from the whole area. It is sad to recall, too, that in this same place I also found the well-preserved remains of another extinct species, the giant rat *Megaoryzomys curioi* [Lenglet & Coppois 1980]. Such experiences remain in your mind forever.

In the seventies, the variety of bulimulid land snails on Santa Cruz was extraordinary. It was so much more complex than what was observed on the other islands, though it is possible that San Cristóbal and Floreana may have been comparable before human settlement, but this we will never know. On Santa Cruz, many species were still abundant, some distributed over huge areas, others limited to tiny ranges, such as a single valley or one side of a hill characterized by a local microclimate or habitat. For this reason, I spent a lot of time crisscrossing the island, analyzing distribution patterns along altitudinal transects and taking monthly samplings to be able to compare populations. GPS was not available at the time, so

ABOVE: Many *Bulimulus* species evolved among Floreana's numerous volcanic cones.
FAR LEFT: Old, bleached shells reveal that even minute islets, such as Devil's Crown near Floreana, once harboured thriving land snail populations.
BELOW: From luxuriant highland habitat to arid lowlands, dozens of species adapted to tiny microhabitats on Santa Cruz.

ABOVE: A live *Bulimulus* clings to a fern frond on Cerro Azul, southern Isabela.
BELOW: As young volcanoes continue to grow, a quiltwork of lava flows such as the slope of Wolf Volcano, represent insurmountable barriers dividing populations and driving evolution.

I relied mainly on a compass. For precise transects or quadrate positioning, I used Topofil, a measuring string in 5-km (16,400 ft) spools (precision 10 cm, or 3.9 in), much to the delight of my helper who recycled the strong cotton thread once the measurements were done. But I did not forget the younger islands, and, as a final result, I was able to gather over 80 *Bulimulus* taxa from the whole archipelago.

In 1973, the road crossing Santa Cruz was still under construction as I started surveying the Cerro Maternidad area near the Gemelos craters. From this hill, I could hear dynamite blasts as a straight line was being carved through the *Scalesia* forest — the future connection to Baltra airport. This hill, or at least its southern slope, was very interesting to me, harbouring a healthy refuge population of *Bulimulus. cavagnaroi* at the western limit of its range, as indicated by bleached shells elsewhere in the *Scalesia* forest. Another population lived in a small central valley near Cerro Coralon, mixed with *B. gilderoyi*, a species named in 1972 by Van Mol after its discoverer (André De Roy's son). This species was only ever encountered in this tiny lush depression and has since vanished. I was often alone when working in those remote places (this was still permitted in those times), and I enjoyed the little Galápagos rails (*Laterallus spilonotus*) that often came to take a closer look at me crawling through the undergrowth. Sometimes, they were as close as half a metre from my face.

On the leeward side of Cerro Crocker and Puntudo (north slope), snail distribution followed fast-changing vegetation gradients, with many species restricted to horizontal bands characterized by precise local climatic conditions. For example, at its upper limit the humid *Scalesia* forest gave shelter to species like the common *Bulimulus ochsneri*, with up to seven sympatric species (species with a common or overlapping range) out of a total of 11 in the region. Further down, *B. tanneri* enjoyed a much wider distribution in the northern transition and arid zones.

But already there were early signs of human-induced destruction. In the rolling fern/sedge zone, I located only a few bleached shells along with charcoal, telltales from uncontrolled fires set across the highlands in the 1960s. On the south slope where National Park land is replaced by farms, in my first year I observed one of the last populations of *Bulimulus blombergi* still alive, one of the largest species at 20 mm (0.8 in). A small strip of *Scalesia* forest survived at El Occidente along the rough road to the western farmlands. Here, the conspicuous white crinkle-shelled snails hung from trunks and low branches. All around, original native vegetation was already replaced by grassland for cattle. Less than a year later, the forest was still there but the undergrowth was drier and the ground littered with empty shells. Sadly for these endemic gastropods, what had become farmland was, for them, probably the most richly adaptive area in the whole archipelago.

Habitat destruction and the negative impact of introduced predators such as little fire ants (*Wasmannia auropunctata*), rats, and possibly mice, plus competitors like the recently introduced slug pest *Vaginulus plebeius* (Veronicellidae) have all taken their lethal toll. In my view, these are the main reasons explaining most extinctions in this group, although for some species other causes are still to be found, especially where the above doesn't appear to apply, such as the small islets off Floreana. The process of speciation within each island was possible because of the complexity of available habitats and inter-island colonization events, probably also aided by volcanic activity periodically redefining natural boundaries. But there are many challenging dilemmas that remain unsolved regarding this extraordinary level of adaptive radiation. Unhappily, present conditions have outpaced the survival ability of many *Bulimulus* species, and perhaps it will be too late to answer those questions.

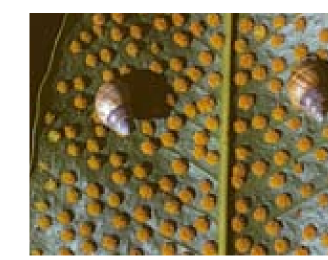
How many species are extinct in this endemic group of gastropods? It is difficult to declare when a species is extinct, and one should always keep in mind that perhaps somewhere a few specimens are still alive… for a while. I discovered this in my search for one particularly emblematic species, *Bulimulus achatellinus*, known only from a few shells. Hugh Cumming visited Galápagos on the yacht *Discoverer* in1829–30 and collected one live specimen on San Cristóbal Island, most probably inland from Fresh Water Bay (no precise location was given). Another live specimen was collected in 1890, and five shells were found in the 1930s, all in the same area. After almost a century with no live *B. achatellinus* seen, I made two expeditions to carefully search the site, without success. But on my third attempt, in 1987, I hit gold. I had not much time, riding an old motorcycle on a day trip, which was not easy as it had rained in the highlands and the trail was slippery and muddy. Coming out of Cerro Verde village, the trail was narrower and I intended to take samples a little further along, when suddenly I saw it. No mistake was possible — I recognized its characteristic shell from a distance, attached to the leaf of a vine covering the bushes. Unbelievable! I almost fell from the motorcycle, stopped the engine and after calming down searched all surrounding vegetation and ground: only two live specimens were found… not even old shells on the ground.

The best part of any study is often the field time, but this must be followed by analyses in the laboratory. These showed that vegetation structure and composition in microhabitats are determining factors in the local distribution of sympatric species, and that climate-driven zonation is also important on a bigger scale. Comparisons between taxa were made using biometric methods including multivariate analyses of the shells and anatomical data (factor and discriminant analyses). With no X-ray available, I had to draw each shell to scale, using a WILD binocular microscope fitted with a *camera lucida*, complemented by anatomical data mainly concerning the genital tracts. These analyses lead to an intra-generic pattern of relationships between the species that show similarities with the results Christine found later using DNA analysis. But this is another story.

From exhilarating discoveries to sobering conclusions — a joint view

Phylogenetic analyses were used to elucidate the relationship between species within this group, and to determine their sequence of colonization and

ABOVE: A tiny islet inside Beagle Crater on Isabela could become on opportunity for speciation.



BELOW: Land snails among fern spores, Alcedo Volcano, Isabela.

Floreana (middle), and greatest variety on Santa Cruz (left).

LEFT: André De Roy's collections show general characters unique to each of three islands, whereas species diversification reflects the islands' age and habitat opportunities: least diverse on young Isabela (opposite page), most colourful trend on

ABOVE: *Bulimulus gilderoyi* was restricted to a small valley near Cerro Coralón (top), Santa Cruz.
BELOW: *B. nov.* sp. *tuideroyi* (above) disappeared before being formally described; *B. blomberhi* (below) vanished in the 1970s.

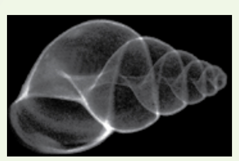
speciation on Galápagos. Results show that bulimulids arrived first on Española or San Cristóbal (the oldest currently existing islands). The lineage then colonized younger islands successively, as shown by the younger species found there. The total number of species found on a given island is determined by a combination of biogeographical factors such as island area, elevation and habitat diversity, all of which have a positive effect on bulimulid species diversity. However, it is striking to note that the young islands of Fernandina and Isabela together form over 60% of Galápagos total land area, but only 12 (about 17%) of the 71 total described species in the genus *Bulimulus*. Although the relationship between species diversity and island age is marginally non-significant, this pattern suggests that at least some of the youngest islands have not reached equilibrium in species diversity.

A surprise was to discover that interisland colonization is not such a rare event, and although some island assemblages consist exclusively of taxa formed within-island, most stem from the combination of at least two to three colonization events followed by further speciation. Interestingly, by separating island diversity into species coming from other islands and species formed *in situ*, a clear biogeographical pattern emerges. Species diversity resulting from colonizers is mostly determined by geographical distance between islands, along with island size. In other words, it is dictated by how far and how big the target islands are. Conversely, for species resulting from within-island speciation, the only determinant factor is plant diversity. In a sense, for bulimulid species to form within islands, it doesn't matter how large, how old, how far, how high an island is, the key is habitat diversity for new species to exploit. This finding is significant because it highlights the importance of considering the process of species diversification when trying to understand what factors promote and maintain biodiversity, with broad implications for many island-like systems and fragmented habitats. Such systems are becoming the norm in our modern world.

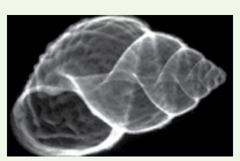
Between us, we also unravelled some of the mysteries of the amazing morphological diversity amongst bulimulids. Although generally small (under 3 cm, 1.2 in) and dull (ranging from white to dark brown), their shapes often vary widely, even in the same location, though certain types seem to prevail at some elevations. After detailed morphometric analyses, and later by taking radiographs of over 2000 shells belonging to some 40 species (using an X-ray instrument to measure each shell inside and out), a pattern emerged. Species with 'slender' shells are more likely to be found at lower elevations in the arid zone, whereas those with 'fatter' shells tend to occur in the humid highlands. One hypothesis is that even though the least 'costly' shell to build (in terms of material required versus living space within) is a blunt conical shape, in the very harsh environment of the arid zone a slender shell allows the skinless mollusc to maintain its shell opening as small as possible thus reducing moisture loss. When testing for this shape-elevation relationship further *within* individual species, these patterns paralleled the morphological trend across the entire radiated group, providing evidence for the continuity between the micro and macro evolutionary scales, a concept still sometimes debated.

STORYTELLING SHAPES

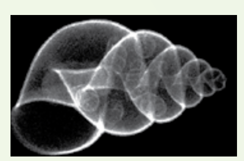
X-ray reveals adaptations to climate zones, with taller spires and smaller apertures prevailing in arid coastal areas, and wide-bodied shells in humid highlands. The bubble-like shapes sheltering inside the empty *B. olla* are minute *Tornatelides* land snails, a group distributed on widely dispersed Pacific islands, probably carried by birds.
Tui De Roy



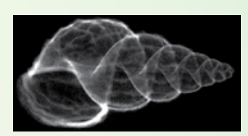
Bulimulus ustulatus, Floreana



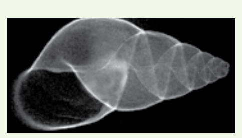
Bulimulus darwini, Santiago



Bulimulus olla, Santiago

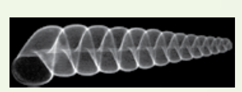


Bulimulus sculpturatus, Santiago

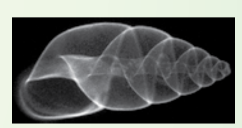


Bulimulus eos, Santa Cruz

Bulimulus reibischi, Santa Cruz



Bulimulus chemnitzioïdes, San Cristobal



Bulimulus planospira, San Cristobal

Photos courtesy Christine Parent

Because of our jointly acquired knowledge of bulimulid snails, we are now in a better position to assess the overall health of the different populations. Our work has led to the update of their endangered status, with a total of 57 species now on the IUCN Red List of Threatened Species. On Santa Cruz Island in particular — the hub of tourism and concurrent resident human population expansion — the rich bulimulid fauna has largely disappeared during the past 30 years. Twenty-seven taxa were studied on this island in the early 1970s, and just a decade later no live populations could be found of all but a few. In highland areas in particular, both in the farmland and native habitats where numerous species were once extremely abundant, no live snails can now be found.

Another striking observation is that Santa Cruz, San Cristóbal and Floreana islands, where human settlements have been established longest, are the most seriously affected, with 32 species either categorized as endangered or critically endangered among the 43 species that have been assessed for these islands (another 17 remain to be assessed). Extensive defoliation by goats can have a severe impact too, as noted on Alcedo Volcano on Isabela, where at least four species were rapidly reduced to remnant patches. But there are hopes for their recovery in the wake of recent goat eradication. On Santiago Island, snail species composition appears to be relatively intact, despite the extensive past habitat destruction due to introduced goats and pigs, now reversed through eradication over the last decade. Similar efforts may have come too late on dry islands such as Española and Santa Fe, where few, if any, live snails are present even after goat removal and subsequent spectacular vegetation recovery.

Habitat loss is clearly a continuing threat. On Floreana and San Cristóbal, while farmed areas have become devoid of live bulimulids, remnant patches of forest still host populations of a number of species endemic to these islands, and there remains the opportunity to protect them at these sites. Land snails can be directly impacted by many invaders, especially potential predators, or indirectly due to habitat transformation by introduced plants. In one study, we found that the number of introduced plant species on a given island was a significant predictor of the proportion of endangered and critically endangered bulimulid species, though it is unclear whether this is a causal relationship or if another independent factor is responsible for the correlation. Indeed, live snails are almost extirpated from the remnant *Scalesia* forests and other areas on Santa Cruz that appear to be otherwise intact, the wave of extinction having swept across the island with little regard to apparent human disturbance. With scant direct evidence at this point to implicate specific causes, the remarkable disappearance of the bulimulid fauna remains largely a mystery.

Like many other land snails, bulimulids probably |do not need large patches of habitat to survive. However, species with greater density and wider distribution have higher chances of long-term survival. We are now using a combination of population genetics and biogeographical analyses to better understand the potential impact of reduction and partitioning of suitable habitat on the genetic diversity and structure of different populations. Ultimately, we hope to be able to better define the habitat needs of the different species in this remarkable group so that more informed decisions can be made towards their protection.

On a few islands, there is still a chance that this fascinating mollusc fauna may be preserved, but continued efforts to understand the causes of their demise on islands such as Santa Cruz is necessary. Until those causes are better understood, habitat protection is all that can be accomplished, and it may not be enough.

ABOVE: We may never know how many species once inhabited the tranquil landscape of San Cristóbal, one of the oldest islands but also the most affected by human colonization. Of 57 known Galápagos *Bulimulus*, the majority have not been seen for years, with 26 species considered Critically Endangered, 22 either Vulnerable or Endangered, and the remainder awaiting assessment.
BELOW: *Bulimulus achatellinus* of San Cristóbal was only ever known from a total of nine specimens, one collected in 1829–30, one in 1890, five during the 1930s and the final two found by the author in 1987, offering a glimmer of hope for other 'lost' species.