
Preface

I had been working in the western part of Ecuador for about three months before I got around to heading east, taking the road from Baños, high in the Andes and overshadowed by volcanoes, down through the narrow valley towards Puyo. At the time, this road was famous with backpackers because of a waterfall that fell right onto the middle of the road. Travellers who opted for the open-air option and sat on the roof of the bus would get soaked on the way down. My first stop was in a town called Shell—in the 1930s, it was a frontier oil town, named after the oil company responsible for its establishment. I walked through the dusty streets towards a stream just at the edge of the town, which I had heard was a good place to collect *Heliconius*.

It was getting towards dusk, and sure enough, as I waded along the shallow stream, there was suddenly a gentle fluttering of butterflies all around me. I had come across a roost of *Heliconius erato*, just starting to gather before settling on a twig to sleep together for the night. Even by this stage, early in my PhD, I felt that I was starting to get to know this species fairly well. I had already collected several hundred of them across south-western Ecuador, as part of my PhD project.

But these butterflies were wildly different. For a few moments I was completely confused—I knew the shape, the flight pattern, even the strange habit of gathering in streams at dusk. But the butterfly I knew from western Ecuador, *Heliconius erato cyrba*, was iridescent blue with red patches. These butterflies had pink and white spots. I had seen lots of pictures, so logically I knew that these were *Heliconius erato notabilis*, a geographic race of the same species. But nothing quite prepared me for the dramatic difference in appearance between what I was familiar

with and what was fluttering around my head. It was the moment in which the geographic variation in form that *Heliconius* are famous for came vividly to life. I hope that in this book I can convey some sense of the awe that I felt that day about the unusual biology of these butterflies.

Along the way, I hope to address some current questions in evolutionary biology, and highlight areas in which we remain ignorant. In the first chapter, I outline some of the questions that work on *Heliconius* has helped to address, or in some cases might contribute to in the future. These topics are largely focused on the genetic basis for adaptation and speciation that have been the motivation for my own work on *Heliconius*. However, this brief overview of topics is not meant to be comprehensive, and throughout the book I will also describe many other areas of ongoing and past *Heliconius* research.

The second chapter introduces the butterflies and their relationships, as well as briefly summarizes the history of *Heliconius* research (with not a little trepidation, as I have certainly missed some moments that others would consider critical). The next four chapters review many aspects of the basic biology of *Heliconius*, before moving on to wing pattern evolution and finally speciation.

This book is based on the premise that a complete understanding of any topic in biology—but evolution particularly so—requires an intimate understanding of the natural biology of the organism studied. I therefore review the different aspects of *Heliconius* natural history that have been studied over the years, before coming back to the topics of speciation and the genetic basis of adaptation, which have come to the fore in *Heliconius* research. I hope that readers primarily interested in the latter

will gain a richer understanding of *Heliconius* speciation biology from reading about the ecology and natural history of these butterflies. Conversely, readers interested in the natural history of these brightly coloured butterflies—so common in tropical butterfly displays around the world—will hopefully be pleasantly surprised to learn that they are also the subject of evolutionary studies in genomics and developmental biology.

It has taken me a long time to write this book. Looking back through emails, I found that my first correspondence with Ian Sherman at OUP dates back to November 2005. In the meantime, *Heliconius* research has surged ahead. I had originally planned that the book would summarize the older literature on the natural history of *Heliconius*, and only briefly touch upon later developments. However, the genomic and developmental studies have progressed so much that I now feel compelled to include more of them here than was originally

planned. Undoubtedly, some of these sections will become dated fairly quickly, but I hope that our understanding of wing pattern development and speciation genomics is sufficiently advanced now that the basics will remain relevant for some time to come.

I would also like to acknowledge the fact that two chapters are reworked from earlier publications - Chapter 8 (Jiggins, 2017) and Chapter 9 (Jiggins et al., 2017).

One of the sources of inspiration as I was thinking of writing this book was Peter Grant's *Ecology and Evolution of Darwin's Finches*. In his Preface, Grant mentions a number of other systems that might also be excellent case studies for understanding biological diversification, one of which is *Heliconius* butterflies. Over 30 years after the first publication of the *Ecology and Evolution of Darwin's Finches*, I am hoping that the butterflies can finally catch up with the finches.