



The Biogeography of Host—Parasite Interactions

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Parasitology and Recent Developments in Biogeography

The Biogeography of Host–Parasite Interactions. Serge Morand and Boris R. Krasnov, eds. Oxford University Press, 2010. 288 pp., illus. \$65.00 (ISBN 9780199561353 paper).

Ecological biogeography has experienced a burst of activity with the advent in 1989 of macroecology, the search for patterns in the geographic distributions of organisms over enormous spatial scales. In addition, the development of molecular methods beginning in the 1960s has led to interaction between historical biogeographers and evolutionists, with many advances in phylogenetic reconstruction and the invention of an entire new subdiscipline—phylogeography. The rapid growth of modern invasion biology, beginning in the 1980s, is also linked to biogeography, because invasion biologists track and predict spatially spreading introduced species. Finally, the explosion of interest in predicting the potential ranges of invaders, as well as geographic range changes of species in response to global climate change, has produced a burgeoning branch of biogeography called *environmental niche modeling*.

Parasites have played a rather minor role in these developments, probably because their geographic distributions are, on average, poorly known relative to those of many free-living species, but perhaps also because there are simply far fewer parasitologists (at least those not primarily working in medicine) than ecologists and evolutionists. *The Biogeography of Host–Parasite Interactions* aims to remedy this shortcoming with 18 contributions by 38 leading parasitologists. The book's success is varied, although most of the chapters detail interesting, specific cases of parasite–host interaction that will be new and intriguing to most biologists who are not parasitologists.

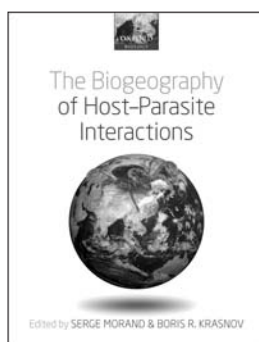
Five chapters pertain to historical biogeography. In the most straightforward of these, Katharina Dittmar recounts the status of parasite biogeography in the paleontological record and describes several remarkable finds (e.g., molecular evidence for a trypanosome in 4500–7000-year-old Brazilian human remains) and a general dearth of data so pervasive that it is premature to draw patterns. However, she is optimistic that further fossil and archeological records will

which ecological traits determine this degree. (This chapter's contents are entirely theoretical and are dry reading for nonparasitologists.)

In the most complicated historical chapter, Eric P. Hoberg and Daniel R. Brooks develop a complex framework involving taxon pulses and ecological fitting to try to explain several patterns of host–parasite association. Although they fit the framework convincingly to an example of nematodes and mustelids across Beringia, so many factors are included that it is difficult to envision generalizations. Perhaps this is the main message of the chapter: The details of particular hosts, parasites, and their physical environment are paramount in explaining biogeographic patterns.

Many chapters delve into the details of interactions between particular parasites and their hosts as manifested by geographic data. The chapter by Kevin D. Lafferty and colleagues on invasions and that by Kevin D. Matson and Jon S. Beadell on parasites in island birds overlap to an extent. The former is largely a restatement of the enemy release hypothesis; unsurprisingly, introduced populations tend to have fewer parasite species than corresponding native populations. The latter includes a thorough description and update on the biology of a paradigmatic case, avian pox and malaria in native Hawaiian birds, and especially on the role of immune function.

Another interesting and large section of *The Biogeography of Host–Parasite Interactions* is on the birds of the Galápagos, although the focus on endoparasites has led editors Serge Morand and Boris R. Krasnov to omit any mention of the ectoparasitic fly *Philornis downsi*, whose recent arrival and impact in the Galápagos have alarmed conservation biologists. Overlapping content includes that of



allow stronger inference about parasite dispersal and geographic spread. Pascal Perrin and coauthors explore geographic patterns in parasites of the best-studied host—humans. Some patterns are clear, such as a correlation between the number of parasite species shared between humans and various domesticated or commensal animals and the length of time since the species was first associated with humans. An interesting development is the increasing availability of phylogeographies of human parasites, which reflect ancient human migrations. Nadir Alvarez and colleagues explore the phylogeographies of mutualists, showing striking topological congruence in such mutualisms as figs and their pollinating wasps or ants and lycaenid butterflies. Caroline Nieberding and coauthors describe the use of the computer program ParaFit to determine the degree of phylogeographic congruence between host and parasite and

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Morand and his colleagues on the geography of defense, which adduces many data on the parasites of island populations, including rodents recently introduced to islands, and is particularly focused on immune defense as a key force underlying geographic patterns. Anders P. Møller and László Z. Garamszegi also emphasize the role of immune defense in biological invasions, having found that several measures of immune function in young birds correlate with success—that is, survival—of introduced populations.

The forays of the book into macroecology are less compelling, probably because macroecologists seek “big picture” patterns by graphing masses of data derived from huge areas and usually find tremendous variance—clouds of points rather than clear lines.

Julie Deter and coauthors derive novel insights on the evolution of parasite virulence and host resistance from the details of geographic intraspecific variation in these features, especially in pathogens causing emerging diseases. Jan Slingenbergh and colleagues use biogeographic data to elucidate how such diseases emerge and extensively explore highly pathogenic avian influenza (HPAI H5N1) as an example. Vincent Herbreteau takes a parasitological perspective on the field of ecosystem health, relating human health problems—such as the emergence of swine flu (H1N1) as a human threat—to various phenomena lamented by conservationists and environmentalists—such as deforestation and species introductions.

The forays of the book into macroecology are less compelling, probably because macroecologists seek “big picture” patterns by graphing masses of data derived from huge areas and usually find tremendous variance—clouds

of points rather than clear lines. Then they present overarching explanations for these fuzzy patterns. To be fair, the paucity of accurate biogeographic data for so many parasites, lamented by many of the authors, is debilitating. To the extent that parasites are tied to their hosts, knowing which parasites are where requires extensive collections of host species, followed by a search for parasites within those collected individuals. Because this is not always possible, any lacunae of host distributional information are magnified in seeking to characterize parasite distributions. The chapter by Mariah E. Hopkins and Charles L. Nunn addresses this problem by advocating gap analysis, which is used in conservation reserve design, to prioritize sites to be sampled for possible hosts.

Probably the most fundamental macroecological pattern is that of latitudinal gradients in species diversity. Several chapters refer to such gradients for parasites, and two chapters (that by Klaus Rohde on marine parasites and that by Frédéric Bordes and colleagues on the parasites of terrestrial mammals) highlight them. The authors of both of these chapters find latitudinal gradients for some parasite groups but not for others, and both chapters emphasize the need for more data in order to determine the frequency of such gradients and to test hypotheses for the gradients or their absence. Rohde's chapter includes an excellent, concise review of the currently popular explanations for latitudinal gradients (i.e., greater area in the tropics, the mid-domain effect, and species–energy relationships) but does not implicate any of them in marine parasite gradients. The chapter by Bordes and his coauthors depicts a strong latitudinal gradient for human pathogens, but the authors fail to find one for helminths in mammals generally. This chapter interestingly points to the details of parasite transmission as potentially important determinants of parasite richness, suggesting that low temperatures or greater climatic temporal variation in high latitudes

should lower the probability of successful transmission and should therefore reduce parasite richness.

In a chapter documenting patterns of distance decay of species similarity in parasites, Robert Poulin and Boris R. Krasnov raise the surprising prospect that such patterns may explain a substantial fraction of latitudinal gradients, but their data do not directly address this hypothesis. The most striking pattern recurring throughout their chapter is one of tremendous variation, and most of their graphs on similarity versus distance are diffuse. Another chapter by the same authors explores the stability across geographic gradients of various parasite species traits but similarly depicts enormous variation. (In one case, a pattern rested on the meta-analysis of individually insignificant results.) Eric Waltari and Susan L. Perkins provide an excellent overview of environmental niche modeling and consider the idea of modeling the potential geographic range of a host–parasite complex. It is surprising, however, that in their thorough example (the red imported fire ant and potential biocontrol agents) they fail to note that the current northernmost US populations are actually hybrids of the red and black imported fire ants, and no one has modeled the potential geographic range of such hybrids.

In summary, *The Biogeography of Host–Parasite Interactions* depicts the extent to which parasites are integrated into modern biogeographical research, and it suggests how parasitologists and biogeographers can aid one another to advance their respective fields. The target audience is unclear, however. Some chapters appear to be aimed at biologists in general, whereas others are so jargon-laden as to challenge even readers familiar with the two fields. Differences also exist among the chapters as to which organisms should be counted as parasites; some chapters omit such pathogens as bacteria and viruses, whereas others focus on them. However, most chapters contain interesting examples of parasite distributions and their relationships with

host distributions as well as intriguing aspects of parasite biology.

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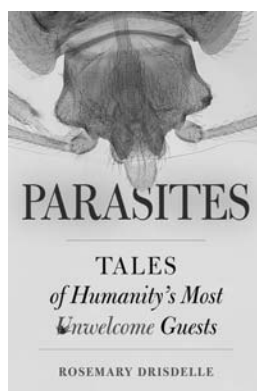
STRANGERS AT THE TABLE

Parasites: Tales of Humanity's Most Unwelcome Guests. Rosemary Drisdelle. University of California Press, 2011. 280 pp., illus. \$18.95 (ISBN 9780520269774 paper).

In her introduction to *Parasites: Tales of Humanity's Most Unwelcome Guests*, author Rosemary Drisdelle, a clinical parasitologist living in Nova Scotia, begins by saying what we all know: that parasites and their influences are often unknown, hidden, ignored, and otherwise unrecognized. Indeed, join two parasitologists for coffee or beer, and you are likely to hear a similar tale of fascinating animals that have somehow escaped recognition. But the author is clearly not content with this state of ignorance, and she uses it as a springboard to launch her mission in this book: "In the pages that follow, I seize the parasites one by one, drag them into the light, and ask, 'What are you and what are you up to?'" Right there, on page 3, is the last time she says much of anything that we all know. This is a book of surprises.

Drisdelle introduces many, if not most, parasites of humans in this book, but she does much more than commandeer a march through medical parasitology. Instead, she is an expert tour guide, sharing her excitement at finding the next unexpected view, the next little-known connection, the next worm, flea, tick, or protist set to make its living on humans—all the while regaling her readers with the stories that swirl around parasites but that are

often left out of textbooks. Therefore, we not only learn about *Trichinella spiralis*, we learn about the prolonged effect of *T. spiralis* on one person who consumed uncooked pork, and we learn about the broader effect of *T. spiralis* on food-safety regulations. We not only learn about the deadly tapeworm *Echinococcus multilocularis*, we learn about how parasites travel, sometimes as stowaways in animals that are themselves smuggled into a country. We learn about the role of



parasites in crime—or in preventing crime—and about their role in world affairs. And we are introduced to that most far-flung group of parasites, sometimes the most devastating of all: those that inhabit the imagination.

Committed to this layered approach, Drisdelle resists the temptation to organize the book along taxonomic or even diagnostic lines. Instead, the themes of her nine central chapters, bookended by an introduction and an epilogue, reflect the stories she tells. One chapter is devoted to the effects of parasites on history, another to parasite immigrants, yet others to parasite emergence and extinction. Not surprisingly, there is one chapter focusing on food and another on water. Within each of these chapters, Drisdelle weaves stories together with remarkable skill. For instance, she begins the chapter on immigrant parasites with hookworms arriving in Jamestown, Virginia, in 1694, carried by slaves. She detours into the pathology associated with *Necator americanus*, which leads to a discussion of its role in the American Civil War. From there, we

are introduced to a broader swath of immigrants and their parasites, ranging from honeybees with mites to reindeer with worms. The flow of her writing reminds us that these parasite–host associations do not exist in a vacuum but are part of a much larger network, and Drisdelle takes care to demonstrate that not all of the connections and outcomes are bad.

From St. Thomas à Becket's lice (impressive even to his "lousy" medieval contemporaries) to modern terrorists who are stopped in their tracks by parasites, Drisdelle's subject matter is interesting enough, but her writing style makes the book even more engaging. She writes humorously, sharing advice that one is not likely to pick up on any street corner (e.g., "If you don't want your intestinal contents analyzed thousands of years after your death, do not defecate in caves." p. 6). In addition, her use of imagery is creative and instructional. For instance, in chapter 3, she asks us to imagine that we are touring a watershed (and a water treatment facility) while perched on an oocyst of *Cryptosporidium*, which evades centrifugation and rises "like a shimmery hot air balloon." She informs us that because of our very small size, we can clear the filtration system—we are "veteran whitewater rafter[s] on a giant [oocyst] beachball" moving through "boulders" of anthracite and sand. If we peer inside the oocyst, we see the sporozoites, which look "like fat sleeping maggots."

In the chapter on food-borne parasites, Drisdelle asks us to examine a fly that has been stopped in mid-air and magnified 500 times. Amid spines and eyes "like the surface of a ripe raspberry," there are "glittering balls," "slightly flattened grains of cooked tapioca"—*Toxoplasma gondii* oocysts. We find all manner of hitchhikers inhabiting the surface of a fly; Drisdelle's narrative is at once disconcerting and skillful, flowing between tapeworm eggs that resemble golden-brown marbles and the biological backstory that reminds us of fecal

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