

Physical Biology” came out, much attention was paid to oscillating predator–prey systems. About 90 years later, the Lotka–Volterra predator–prey model still holds a prominent place in ecological textbooks as well as in ecological research, the latter ranging from studies of two-species predator–prey systems to complex, multi-species systems (food webs). Given that the Lotka–Volterra model has problematic properties (*e.g.*, neutral stability), a number of ecologists have proposed modifications and/or alternative model formulations – none of which has reached nearly as much attention as the original work by Lotka and Volterra.

In their book “How species interact – Altering the standard view on trophic ecology” Roger Ardit and Lev Ginzburg are now challenging the dominance of the Lotka–Volterra model. Ardit and Ginzburg belong to a number of scientists that oppose the idea that the number of prey consumed by the average predator at time  $t$  (*i.e.* the functional response) does exclusively depend on the number of prey present at that time, as is the case in the Lotka–Volterra model or under Holling’s disc equation. Rather, they argue that at high predator densities, predators interfere with each other and therefore the functional response should depend on the ratio of the number of prey to the number of predators present in the system. With this change, the Ardit–Ginzburg ratio-dependent model of predator–prey population dynamics has several more realistic features than the Lotka–Volterra model. For example, cycles are one possible outcome but for a limited parameter space only, which takes better care of the ecological observation that predator–prey cycles are rather the exception than the rule.

Chapter 1 is a review of the ecological predator–prey models, their assumptions and implications. This chapter also serves as sort of a book summary, as it gives outlooks on all topics that are covered in the following chapters.

Chapter 2 reviews evidence from 22 laboratory and field studies (all the authors could find) for the form of the functional response, with most studies indicating that the truth lies somewhere between prey and ratio-dependence, yet with a pronounced tendency to ratio-dependent functional responses.

Chapter 3 moves from two species predator–prey systems to food chains. Classic prey-dependent models of food chains make rather complex predictions on how perturbations at the bottom or top of the food chain affect populations along the food chain, while ratio-dependent models predict proportional responses at all levels of the food chain. A review of the, again limited number of, available laboratory and field studies is clearly in favor of ratio-dependent models and in disfavor of some highly cited papers based on prey dependence.

My favorite chapter is chapter 4, which shows, based on experiments and theoretical considerations, that the Lotka–Volterra model is appropriate for homogeneous, well-mixed, systems. Most natural systems are heterogeneous and these are better described by ratio-dependent models.

Much of the material covered in this book has previously been published in journal articles. Chapter 5 addresses

criticism of ratio-dependent models and adds some more evidence and philosophical arguments in favor of ratio-dependence. Finally, chapter 6 wraps up the main conclusions of the book with some philosophical considerations.

The entire book is well-organized and very clearly written; it has a comprehensive index. Ardit and Ginzburg make it clear from the onset that the focus of the book lies on their own work. Given their quite comprehensive work, they still cover a lot of ground with this approach. Even though there is no outlook for future work given, the book is an excellent point of departure for further experimental and modeling work alike – so it will be interesting to see which standard view of tropical ecology will have developed by the year 2025, 100 years after Lotka.

Overall, I highly recommend the book to all that teach and/or work on the dynamics of interacting species.

Kerstin Wiegand

Göttingen, Germany

E-mail address: [mail@kerstin-wiegand.de](mailto:mail@kerstin-wiegand.de)

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**The Tragic Sense of Life—Ernst Haeckel and the Struggle Over Evolutionary Thought, R.J. Richards. The University of Chicago Press, Chicago, USA (2008). 551 + XX pp., Price: €21, ISBN: 978-0-226-71216-1**

Ernst Haeckel (\*1834 Potsdam, †1919 Jena) should be Germany’s best-known ecologist – he invented the discipline. He should also be remembered beyond the sphere of protozoan biology as taxonomist and evolutionary biologist. The wonderful Phyletic Museum in Jena, erected to take his collection of specimen and books, drawings and letters, should be a place of pilgrimage for historians in evolution. When Darwin’s reputation rose, in the course of a century, from modest beginnings to the status of a scientific superhero, Haeckel’s sputniked early in his career, only to plummet during the Nazi regime to never be revived. Richards’ book is a biography and an historical approach to Haeckel, providing the reasons for why things are not what they should be with Haeckel.

The reception in Germany of Darwin’s *Origin of Species* and his theory of natural selection was not merely aided by Haeckel, he made it his own cause. He immediately followed Darwin’s reasoning through to the evolution of humans, and did so systematically and comprehensively. When he referred to himself as a Darwinist, Darwin himself was only short of calling himself a Haeckelian, since, for example, his later work “*Descent of Man*” describes Haeckel’s preceding work in that field as “more competent” than his own. Why, then, does the whole academic world know Darwin, and only interested historians (or protozoologists) know Haeckel?

The answer is: modesty (on the side of Darwin, not of Haeckel). The German managed to drench his evolutionary work in anti-clerical, anti-dualist, anti-establishment cynicism; he leapt from his profound knowledge on morphology and taxonomy of marine invertebrates (and humans: he was a physician, after all) to human evolution, solving the world's scientific riddles, entertaining the Wilhelminian Germany with colourful illustrated travel stories, and reviving a new kind of religion, monism. While his scientific credentials are beyond dispute, they are dwarfed by his missionary and outreaching personality, which forcefully and polemically fought against anyone opposing Darwin's idea. Darwin got things wrong, and so did Haeckel (for example, since both were ignorant of DNA as the carrier of hereditary information, they assumed that even phenotypically acquired characteristics could, in principle, be inherited to the next generation). But while neo-Darwinism taints Darwin's name, it does not affect our perception of his scientific ideas. Haeckel, in contrast, was (wrongly) connected to contributing to the "racial theory" of Hitler Germany, a stain that to date could not be removed. His flamboyant and unbridled writing offers an open door for text pickers seeking to depreciate him. For example, the influential, but similarly polemic and debaucherous American palaeontologist Stephen Jay Gould viciously debunked Haeckel's work because he thought him partly responsible for Nazi atrocities committed decades later. Even if Gould was right (which he wasn't, as Richards demonstrates), this would not invalidate Haeckel's scientific work.

Haeckel's personality was certainly very different from that of Darwin. But his mastery of science, his breadth of

knowledge in any area touching evolutionary theory was second to none. Richards' biography traces Haeckel's ferocity to the loss of his adored wife at the age of 30, after only one year of marriage. The depression and devastation, so both Haeckel and Richards argue, led to an attitude so very different from that of Darwin. While such a monocausal, traumatic explanation may be incomplete, Richards' book easily makes up for this minor shortcoming by its enormous competence in embedding Haeckel into the *Zeitgeist*. He traces Darwinian ideas to Goethe, links Haeckel's own mind set to the Romantic period, and follows a wide range of arguments levered against evolution from their conception to their rejection in Haeckel's work.

While we learn little about the "monera" Haeckel discovered as a phylum, or the ecology of jellyfish, or the embryological work of his students, Richards masterly dissects prejudices in previous treatments of Haeckel's life and work, and transparently and explicitly develops a historically justified view. This biography of Haeckel has the capacity to show "the German Darwin" in a light more truthful to Haeckel's real beliefs and achievements, and maybe to reconcile in particular German ecologists with the founder of their trade.

Carsten F. Dormann

*University of Freiburg, Germany*

*E-mail address: carsten.dormann@biom.uni-freiburg.de*

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