

Bibliophilia: The Father of Modern Ecology*

Raghavendra Gadagkar

“A scholar is just a library’s way of making another library.”

– Daniel Dennett, Philosopher, Writer, and Professor (1942–)

In this new series, I will muse about books I love and reflect on the authors, the content, the style, the context in which the books were written, and what they mean for us today. My goal will be less to convey the book’s subject matter and more to inspire my readers to read the book under discussion and books more generally and reflect on the process of reading and writing. Today most scientists live and run in the fast lane, writing large grant proposals and short papers with no time to read or write anything more than a few pages; we live in a world where short-term performance is rewarded and not sustained scholarship. Indeed, it has become fashionable to look down upon reading and writing books as old fashioned. My goal is to reverse this trend and put the mojo back into reading and writing books in science.

I am embarrassed to say how little I knew about G. Evelyn Hutchinson’s life and even his work until I read *G. Evelyn Hutchinson and the Invention of Modern Ecology*, an inspiring biography by Nancy Slack. I knew, of course, that Hutchinson is widely considered the father of modern ecology. Still, for me, he was a kind of mythical figure, known for his work in limnology and famous for his 1959 paper ‘Homage to Santa Rosalia or Why Are There So Many Kinds of Animals?’ [1]. I knew that this classic paper, which I had read and re-read, had spawned the interest of generations of ecologists in biodiversity. Hutchinson was one of the early minds to go beyond marvelling at the magnitude of biodi-



Raghavendra Gadagkar is DST Year of Science Chair Professor at the Centre for Ecological Sciences, Indian Institute of Science, Bangalore, Honorary Professor at JNCASR, and Non-Resident Permanent Fellow of the

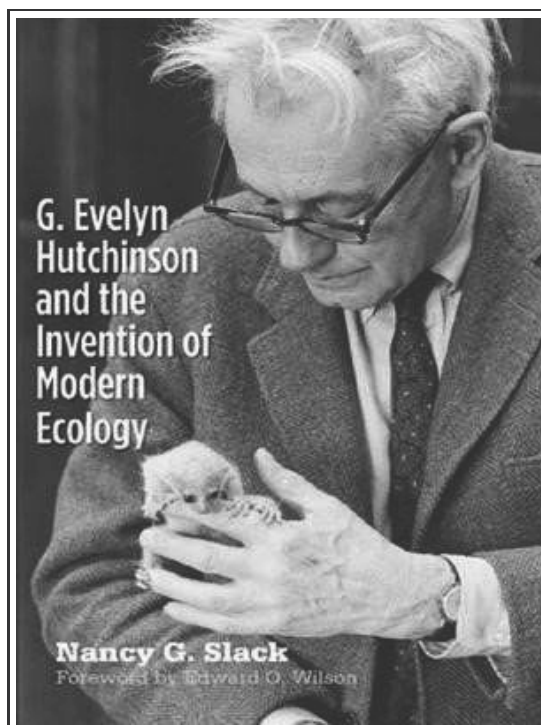
Wissenschaftskolleg (Institute for Advanced Study), Berlin.

During the past 40 years he has established an active school of research in the area of animal behaviour, ecology and evolution. The origin and evolution of cooperation in animals, especially in social insects, such as ants, bees and wasps, is a major goal of his research.

<http://ces.iisc.ac.in/hpg/ragh>.

https://www.researchgate.net/profile/Raghavendra_Gadagkar

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versity and wonder about its causes.

Nancy Slack's biography [2] taught me so much about the man and his work. Like a good biographer, she not only marvels at the magnitude of her protagonist's work and scholarship but asks how he came to become the polymath and colossus he was.

Hutchinson the Mentor

Hutchinson had a sign on his office door that read: 'Do not discourage students. You are almost certain to succeed'.

Even more important, Nancy Slack movingly brings out the teacher and mentor in Hutchinson.

She tells us that "Hutchinson had a sign on his office door that read: 'Do not discourage students. You are almost certain to succeed'."

And that he believed that "One should always recognize the 'good



things in bad papers’—or in poor seminars.”

What I like most about these sentiments is that they are entirely consistent with any philosophical worldview about the relative roles of merit, diversity, inclusivity, equity and empathy.

In response to a letter from a graduate student, Hutchinson replied, Slack tells us,

“I have thought a lot about your project. First a piece of general observation. Practically nobody has ever done any good work by setting up a detailed project ahead of time and then carrying out all the projected details in order. One can start out and get a lot of data; when it has become familiar [,] the new and exciting implications appear while drying a cup or getting into a car, in a quite unpredictable way. This I fancy only happens if one really knows a lot of factual material got with our own hands and allowed to dance around in our unconscious... If you really get started and are as good as I think you are... the original ideas will come. Until you get them you don’t have any idea what they will be.”

There is so much wisdom in this passage—about the futility of too much advance planning in research, the importance of discovering facts first hand, the unpredictability of the outcome... Will funders and evaluators of people and projects ever take note?

Nancy Slack, the Biographer

It gives me particular pleasure that Hutchinson’s biographer Nancy Slack is a fellow scientist. She tells us:

“I was one of many graduate students in ecology who did not study at Yale but were much influenced by Hutchinson’s writings. My research concerned community and evolutionary ecology, and I read many of Hutchinson’s papers and books, including my favorite one, *The Ecological Theater and the Evolutionary Play* [3]. I dedicated my dissertation, and its subsequent publication, to Hutchinson...When I was offered a sabbatical year at Yale working in the Section of the History of Medicine and Life Sciences, I wrote to Hutchinson and then visited him to discuss writing an

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– G E Hutchinson

article about his life and work...There was too much material for one article. I worked in additional archives and recorded interviews, now at the Smithsonian Institution, with more than fifty Hutchinson students, scientific associates, and family members in several countries, much of which went into writing this book.”

I have often heard historians of science express skepticism about scientists’ foray into history. Nancy Slack proves them wrong.

Gandhi and India

I was pleased to see a photo of Gandhi with Hutchinson’s distinguished parents, Arthur and Evaline Hutchinson, at Pembroke College, Cambridge University, when “Mr Gandhi paid a visit to Cambridge...to hold a conference with a select group of Cambridge thinkers, both men and women, with regards to important issues which were being worked out at the Indian Round Table Conference in London.” [4]. But I must confess I felt a bit sad that Gandhi’s name is carelessly misspelt.

Hutchinson’s book *The Clear Mirror* describes the colors, organisms, and ecology of the high-elevation lakes as well as the lives, religion, and art of the people of Ladakh.

A fact (among many) that warmed my heart is that Hutchinson made a study trip to India early in his career. Slack tells us that:

“This trip also marked the beginning of Hutchinson’s literary career. His often lyrical book *The Clear Mirror* [5] describes the colors, organisms, and ecology of the high-elevation lakes as well as the lives, religion, and art of the people of Ladakh. Few scientists can write well, but Hutchinson could; his many subsequent essays and books were read by a wide audience. His *The Ecological Theater and the Evolutionary Play* [3] captivated this author early in her ecological career.”

Hutchinson, the Writer

Indeed, Hutchinson wrote well and wrote for a broad audience. These, of course, were in addition to his many scholarly tomes, such as the four-volume *A Treatise on Limnology*, published by Yale University Press in 1956, 1967, 1975 and the last, published



posthumously in 1993. Apart from his many books that I have just begun to read, he wrote a column that he called ‘Marginalia’, which appeared in *The American Scientist* starting in 1943 [6] and went on for several decades.

In 1983 *The American Scientist* introduced the second series of Hutchinson’s ‘Marginalia’ in the following words [7]:

“In 1943, G. Evelyn Hutchinson, then an associate professor of zoology at Yale University, began what was to become a notable series of musings, ostensibly on current scientific research but actually taking in the entire universe, past, present, and future. Called “Marginalia”, the column continued for twelve years, ranging over dodos and bowerbirds, the colors of the planets, Linear B, the nature of mathematics, the mating habits of bacteria, and the fleeting geometry of the human face. Its author became, in addition to a beloved contributor to *American Scientist*, one of the founders of population ecology, and, among his many other honors, a Foreign Member of the Royal Society.”

Nancy Slack tells us that one of Hutchinson’s ‘Marginalia’ columns so impressed the English novelist Dame Rebecca West that she went to meet him, and that meeting led to an intense friendship and correspondence that lasted 35 years. We are also told that Hutchinson had a long-standing friendship with the famous anthropologist Margaret Mead and regularly read, commented, and even copy-edited her books.

Incidentally, the title of my own column ‘Bibliophilia’ is inspired in part by Hutchinson’s ‘Marginalia’ and in part by E.O. Wilson’s book title *Biophilia* [8].

I have developed a great admiration for Nancy Slack on account of her accurate and inspiring description of Hutchinson’s science and much respect for her sensitive, non-judgemental account (so rare these days!) of Hutchinson’s personal life and those of many others in his unusually large circle of family, friends, students and colleagues.

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‘The Paradox of the Plankton’

Hutchinson began as a classical zoologist, describing and classifying aquatic insects, especially water striders. He spent a major portion of his life studying biogeochemical cycles, focusing mainly on the aquatic environment.

Nancy Slack’s biography inspired me to read some of Hutchinson’s lesser-known papers. I particularly enjoyed Hutchinson’s “Contribution to a Symposium on Modern Aspects of Population Biology” in 1960. I enjoyed everything about it, especially the Title, the Introduction and the Conclusion. Entitled ‘The Paradox of the Plankton’ [9], it begins thus:

“The problem that I wish to discuss in the present contribution is raised by the very paradoxical situation of the plankton, particularly the phytoplankton, of relatively large bodies of water...The problem that is presented by the phytoplankton is essentially how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials.”

And concludes with:

“Apart from providing a few thoughts on what is to me a fascinating, if somewhat specialized subject, my main purpose has been to show how a certain theory, namely, that of competitive exclusion, can be used to examine a situation where its main conclusions seems to be empirically false. Just because the theory is analytically true and in a certain sense tautological, we can trust it in the work of trying to find out what has happened to cause its empirical falsification.”

Why don’t we write papers like this anymore? I think part of the problem is the overzealous policing by reviewers and editors to conform to a stereotype. Unsurprisingly, the editorial axe falls more heavily on the younger scientists who accept it for the sake of survival and promptly impose it down the ladder when they become seniors! We need to find a way to break this cycle; We need some rebels.



The Mathematics Wars

Another major concern of Hutchinson was population ecology, and that is where he became famous for the ‘colonization of ecology by mathematics’. I had not realised how important a figure Hutchinson was in nurturing the field of mathematical ecology and being a bridge between the Lotka–Volterra era and the modern era of the likes of Robert MacArthur and Robert May, both of whom were his intellectual descendants (See *Box*).

Nancy Slack provides a most interesting account of the resistance Hutchinson faced for bringing mathematics into ecology, some of his papers being rejected for the sole ‘sin’ of being mathematical. A colleague Robert Pennak told his students that “[Hutchinson] is writing a book on Limnology, and it is to be chiefly mathematical. So you can look forward to the worst.” As it happens so often, resistance to mathematics disguises opposition to theory more generally, and that is far more dangerous. The same Robert Pennak wrote sarcastically that “In a short time I shall expect them to tell all about a lake thermally and chemically just by sticking one, perhaps two, fingers into the water, then go into a mathematical trance and figure out all its biological characteristics.” This attitude was not just plain wrong but also quite unfair. Hutchinson and Robert MacArthur always maintained that:

“Scientists are perennially aware that it is best not to trust theory until it is confirmed by evidence. It is equally true...that it is best not to put much stock in facts until they have been confirmed by theory.”

Criticism of Hutchinson’s penchant for theoretical generalisations erupted again and even more strongly in the ‘competition wars’ in the 1980s. I especially enjoyed Slack’s description of this episode as I have myself lived through it, following all the arguments and counterarguments, not to mention mudslinging, that appeared in the pages of high-profile journals on a regular basis. In hindsight, such controversies serve a useful purpose, showing that much of what we thought was black and white is actually grey. I also often find controversies illuminating as they bring out people’s

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creativity in the use of metaphors (see *Box*).

One of Hutchinson's best-known contributions is the so-called 'Multidimensional niche model'—the idea that competition leads to partitioning of the environment into individual ecological niches to accommodate different co-existing species. Such competition induced niche partitioning was the backbone of Hutchinson's answer to the question "Why are there so many kinds of animals" in his 'Homage to Santa Rosalia' paper.

Homage to Santa Rosalia

In the 'Santa Rosalia' paper, which was based on the Presidential address he gave at the annual meeting of the American Society of Naturalists in 1958, Hutchinson tells us the back story which took place when he was visiting Sicily.

"Fortunately, I was driven up Monte Pellegrino, the hill that rises to the west of the city, to admire the view. A little below the summit, a church with a simple baroque facade stands in front of a cave in the limestone of the hill. Here in the 16th century a stalactite encrusted skeleton associated with a cross and twelve beads was discovered. Of this skeleton nothing is certainly known save that it is that of Santa Rosalia, a saint of whom little is reliably reported save that she seems to have lived in the 12th century, that her skeleton was found in this cave, and that she has been the chief patroness of Palermo ever since...Nothing in her history being known to the contrary, perhaps for the moment we may take Santa Rosalia as the patroness of evolutionary studies, for just below the sanctuary, fed no doubt by the water that percolates through the limestone cracks of the mountain, and which formed the sacred cave, lies a small artificial pond, and when I could get to the pond a few weeks later, I got from it a hint of what I was looking for."

Hutchinson was ostensibly looking for water bugs, which he got, of course, but he got much more—the wisdom that prompted his Presidential address and the resulting paper. Hutchinson found two species of water striders, a large one at the end of its breeding



season and a smaller one at the beginning of its breeding season. Hutchinson goes on to say:

“This is the sort of observation that any naturalist can and does make all the time. It was not until I asked myself why the larger species should breed first, and then the more general question as to why there should be two and not 20 or 200 species of the genus in the pond, that ideas suitable to present to you began to emerge. These ideas finally prompted the very general question as to why there are such an enormous number of animal species.”

Hutchinson tells us that ideally, he would like to construct a theory that predicted the existing 10^6 species rather than 10^8 or 10^4 but confesses that he cannot. The best he says he can do is “to point out some of the factors which would have to be considered if such a theory was ever to be constructed.” And before proceeding, he declares upfront that he subscribes to “the view that the process of natural selection, coupled with isolation and later mutual invasion of ranges leads to the evolution of sympatric species, which at equilibrium occupy distinct niches...”. And then, he confesses that “the empirical reasons for adopting this view and the correlative view that the boundaries of realized niches are set by competition are mainly indirect.”

These were the heady times when Hutchinson was developing his ideas of competition and niche partitioning, which he published at about the same time in what is perhaps his other most influential paper. This paper, too, has its own interesting back story! For one thing, the paper is simply called ‘Concluding Remarks’! [10]. Not only did Hutchinson present some of his life’s most important ideas under such a non-explicit title, but he did so with no fanfare at all. It was a part of his concluding remarks at the end of a symposium on demography at the Cold Spring Harbour Laboratory. More remarkable still is that his ‘Concluding Remarks’ begins with a footnote that says, “Anything that is new in the present paper emerged from this seminar that is not to be regarded specifically as an original contribution of the author.”

Hutchinson’s ideas contained in his ‘Concluding Remarks’ in-

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– G E Hutchinson



spired a whole generation of young ecologists who developed the theoretical foundations of community ecology (see *Box*).

The Competition Wars

But controversy erupted in the 1970s and early 1980s. Daniel Simberloff led the attack from the front claiming that Hutchinson's emphasis on competition "has cost a generation of ecologists to waste a monumental amount of time". Simberloff and William Boecklen began their paper, with the reasonable enough title 'Santa Rosalia Reconsidered' [11], with a sarcastic quote:

"When Prof. Buckland, the eminent osteologist and geologist, discovered that the relics of St. Rosalia at Palermo, which had for ages cured diseases and warded off epidemics, were the bones of a goat, this fact caused not the slightest diminution in their miraculous power.",

but ended it rather tamely conceding that:

"We do not claim that sizes are not partly determined by competition... But we do feel that the evidence presented to date that sizes are competitively determined is weak...".

Of course, the opening sarcastic quote was more newsworthy than the more cautious ending of the paper, so Roger Lewin published a paper in *Science*, summarising the controversy, with the title 'Santa Rosalia Was a Goat' [12].

Like most controversies, this one was also never fully resolved, because, as it so happens, the truth lies somewhere in between. I think good science is one that generates a lot of new research and creates much new knowledge, even if the original idea eventually turns out to be wrong. So I disagree with Simberloff's claim that "[Hutchinson's] theory has cost a generation of ecologists to waste a monumental amount of time."

Interestingly, the "anticompetitionists" tried to gain sympathy by posing as underdogs, calling themselves the 'Florida mafia' at war with the "competitionists" who were "devout MacArthur-



ans...in powerful positions in powerful universities”. Biographies often throw light on the process of science as humans practise it with all their fragilities, as opposed to the sanitised, false impression one gets from reading peer-reviewed technical papers.

The Nobel Prize Craze

I also liked very much Slack’s discussion of why Hutchinson did not get the Nobel Prize. As she says, the easy answers are that there is no Nobel Prize in ecology and that Hutchinson won the Kyoto Prize, “a sort of Japanese Nobel Prize”, not so different in fame and money. But she prefers the more philosophical answer and quotes Dan Livingston:

“Hutchinson had a first order knowledge of everything that seemed important in the world. That was very wonderful, in an age when most people thought that sort of mastery had gone out with Leonardo and the Renaissance. . . . It is vital that a few people in each generation should hold up the waving banner of ideas, and that the ability to do so is even scarcer than the ability that will, in a few fields, lead to the sort of recognition that a Nobel Prize confers.”

This is so refreshing compared to the perennial, tasteless discussion we have in India every October/November!

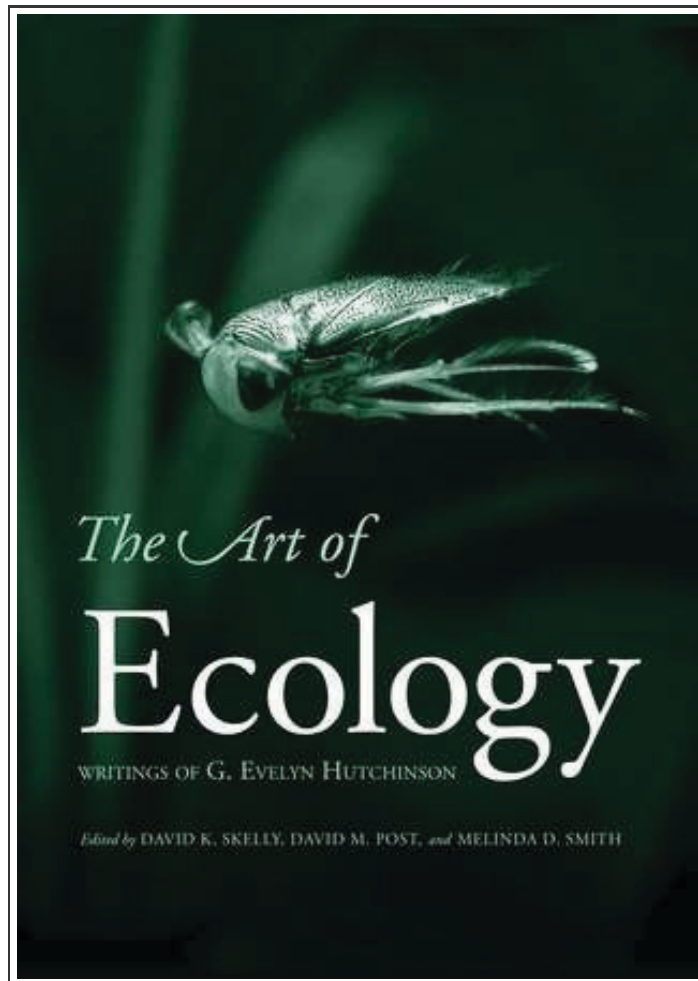
Be Inspired, the Young and the Old

“Be blessed”, people often say, on your birthday or other occasions when they want to wish you well. I have never understood what that means and how to go about being blessed. I would rather say, “Be inspired”. And there are many transparent mechanisms to achieve this state.

It is hard to overemphasize the inspirational value of biographies and autobiographies of scientists. What a shame then that we often believe that we have no time to read them when they are most likely to inspire us formatively and wait until we retire! Young ecologists and young scientists of any description, go read Nancy

Be inspired!

Slacks' story of Hutchinson—it may be more important than any research papers that you might read in the time spent.



The Art of Ecology published by Yale University Press (2010) is a treasure house of the writings of and about G. Evelyn Hutchinson, with a Foreword by Thomas Lovejoy. Highly recommended.



Box 1. Competition in Ecology and Evolution

It is easy to see that competition is the cornerstone of evolution by natural selection. The subtitle of Darwin's book was *Preservation of Favoured Races in the Struggle for Life* [13]. The struggle is, of course, for limited resources. If resources are unlimited, there will be less scope for natural selection. Darwin argued that if unchecked, populations will grow so large that resources will inevitably become exhausted. There can be competition both within and between species, and there can be competition for different kinds of resources such as food, space or mates. Therefore, the study of ecology and evolution has been greatly concerned with the study of competition and understanding how competition of different kinds will influence living organisms.

Alfred J Lotka (1880–1949), a US mathematician and Vitto Volterra (1860–1940), an Italian mathematician, independently developed a pair of non-linear differential equations that help model the rates of growth of two species that competitively interact with each other. The Lotka–Volterra equations have greatly influenced the study of competition. Although the equations are very simplistic and rarely capture the richness of competitive interactions in nature, they have led to the development and/or elaboration of a number of concepts that can be investigated in nature and the laboratory.

One such concept is the “Competitive Exclusion Principle” proposed by Joseph Grinnell in 1904, which states that if two species have exactly the same ecological requirements, they cannot co-exist because even the slightest difference in their growth rates will result in one species driving the other to extinction. Such competitive exclusion was first demonstrated in the simplified environment of the laboratory in classic experiments of G. E. Gause with two species of protozoa, *Paramecium caudatum* and *Paramecium aurelia*. But a more useful implication of the competitive exclusion principle is that if two species coexist, they must be different in some way. This can then pave the way to understanding those differences. Robert MacArthur, a student of Hutchinson, for example, investigated how five species of warblers manage to coexist by spending different amounts of time in different heights on the same trees.

Another useful concept is “Character Displacement”, an idea credited to the famous myrmecologists William L. Brown and Edward O. Wilson [14]. Peter Grant redefined the concept as follows: “character displacement is the process by which a morphological character state of a species changes under Natural Selection arising from the presence, in the same environment, of one or more species similar to it ecologically and/or reproductively” [15]. It is the idea that two species can be very similar in habitats where they occur separately but must diverge from each other when they coexist. Perhaps the most famous example of character displacement is the divergence in beak size in the Galapagos finches studied by Rosemary and Peter Grant, not the least because they witnessed the character displacement happening in real-time [16, 17].

Contd.



Box 1. Contd.

A related concept also first developed by Joseph Grinnell is the “Ecological Niche”, defined as the ecological space occupied by a species. Thus the competitive exclusion principle can be restated as, no two species with exactly the same niche can coexist in the same habitat. When two species do coexist, we can speak of the extent to which their niches overlap and how that overlap is minimised due to character displacement.

Evelyn G. Hutchinson is one of the most prominent names in the study of competition and niche. Using set theory and n-dimensional geometry, Hutchinson and his students developed formal models of the niche so that the niche came to be defined as an organism’s n-dimensional hypervolume. Hutchinson famously set out these concepts in great detail in his cryptically labelled ‘Concluding Remarks’ paper (see the main text).

Hutchinson is also famous and controversial for his concept of the so-called Hutchinson Ratios, which define how much niche overlap can be tolerated when two species co-exist. Hutchinson empirically found a ratio of 1.3, i.e., when two species co-exist, one of them should be at least 1.3 times the other in body length or mouthpart length.

Hutchinson’s emphasis (some would say over-emphasis) on competition and especially his 1.3 ratio came under attack in the 1970s and 1980s. By examining larger data sets and subjecting them to statistical analysis, some authors cast doubts on the universality of the 1.3 ratio. Others tried to measure competition in the field, which is very hard to do and failed to find good evidence (see the main text). Unfortunately, there was more heat than light during these often vitriolic debates, and no really credible alternative ideas and mechanisms were put forward. As Hutchinson says, the simplified models of competition serve a useful purpose, even if only to understand why they fail when put to the test with real data.

In addition to the Readings already suggested in the main text, a valuable overview of the role of competition in ecology and evolution can be got from the 12th and 13th chapters of the 7th edition of *Evolutionary Ecology* by Eric R. Pianka [18]; Pianka himself has made significant contributions to this field.

Suggested Reading

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Address for Correspondence
Raghavendra Gadagkar
Centre for Ecological Sciences
Indian Institute of Science
Bangalore 560 012, India.
Email: ragh@iisc.ac.in

