Ecological Research Monographs

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Makoto Kato • Atsushi Kawakita
Editors

Obligate Pollination Mutualism

Springer

Editors
Makoto Kato
Graduate School of Human
and Environmental Studies
Kyoto University
Kyoto, Japan

Atsushi Kawakita
Center for Ecological Research
Kyoto University
Otsu, Shiga
Japan

ISSN 2191-0707 ISSN 2191-0715 (electronic)
Ecological Research Monographs
ISBN 978-4-431-56530-7 ISBN 978-4-431-56532-1 (eBook)
DOI 10.1007/978-4-431-56532-1

Library of Congress Control Number: 2017938280

Front cover: A female *Epicephala anthophilia* moth actively depositing pollen on the pistil of a *Glochidion acuminatum* flower in a subtropical forest of Amami Island, Japan. Note that the proboscis, which the moth uses to pollinate, is coated with numerous pollen grains that the moth collected previously on a male flower. Photo by Atsushi Kawakita.

Printed on acid-free paper

This Springer imprint is published by Springer Nature
The registered company is Springer Japan KK
The registered company address is: Chiyoda First Bldg. East, 3-8-1 Nishi-Kanda, Chiyoda-ku, Tokyo 101-0065, Japan

Preface

Organisms cannot live without interacting with other species of organisms, because each organism sits anywhere in a local food web, and because organisms utilizing similar food resource inevitably compete with each other. Although most interactions between a random pair of species are antagonistic, two intimately interacting species occasionally evolve to reduce the cost of the antagonistic interaction and occasionally become cooperative. Accordingly, we are stunned by the fact that the ecosystem is a network of innumerable mutual interactions.

Life on the earth is believed to have originated somewhere in the sea, and the land has been colonized by diverse lineages in the Paleozoic. All the land plants are descendants of the green plants that first colonized the land in the Ordovician, and the land plants at each geological era have shaped the forest ecosystems since the Carboniferous. In modern terrestrial ecosystems, angiosperms are the predominant large-size sessile primary producers and are involved in four mutualisms, i.e., pollination mutualism, seed-dispersal mutualism, mycorrhizal mutualism, and protection mutualism. The conspicuous diversification of angiosperms is hypothesized to have been driven by these mutualisms.

In contrast with terrestrial ecosystem, the medium of the marine ecosystem is sea water, where diverse microorganisms can live as plankton. Accordingly, planktonic photosynthetic microorganisms are primary producers in the ocean, whereas macrophytes are primary producers only in coastal sea. Because biomineralization especially via calcium carbonate is easy in sea water, the hard substrate in the coastal sea is often colonized heavily by diverse reef-building sessile organisms, which flourish as filter-feeders of plankton. The reef-building sessile organisms are furthermore colonized externally and internally by diverse encrusting or boring organisms, thus these symbiotic organisms form cohabitation mutualism. The exceedingly high biodiversity of coral reefs is associated with the chain of cohabitation and has been created at least partly by the complicated interactions between these symbiotic/parasitic organisms. A coral reef is also characterized by the predominance of photosynthetic mutualisms in which sessile organisms host photosynthetic microorganisms and receive their assimilates.

The origin of eukaryotic cells is endoparasitism by intracellular symbiosis of prokaryotes, which evolved into intracellular mutualism. Moreover, although the interaction between prey and predator is a typical antagonism, even the prey and the predator happened to evolve to be mutual, like crop cultivation or livestock farming by humans.

Among these diverse mutualisms, obligate mutualisms have attracted the attention of evolutionary biologists and naturalists alike because they are models for exploring the evolutionary dynamics between interacting organisms and because humans were originally involved in admiration of altruism. Excluding intracellular symbiosis, obligate mutualisms are rare, and the rare examples are the fig–fig wasp and yucca–yucca moth pollination mutualisms, both of which were discovered more than 100 years ago. In both systems, pollen-bringing adult females actively pollinate and oviposit into the ovary, and the larvae of the pollinators grow only by infesting the growing seeds. These plant–pollinator mutualisms are obligate and highly host-specific and must have accelerated reciprocal diversification of plants and pollinator insects. So far, several hundred papers on these pollination mutualisms have been published, but many hypotheses on the evolution of obligate mutualism have not been fully tested because there are only two known systems. The unanswered hypotheses are (1) obligate pollination mutualism evolved from antagonism between seed and seed-infesting insects, (2) high host specificity is reinforced as the result of coevolution, (3) obligate pollination mutualism is maintained by plant sanctions against uncooperative pollinators, and (4) obligate pollination mutualism causes reciprocal diversification of both the plants and the pollinators.

In this book, we provide the third case of obligate pollination mutualism, i.e., the leafflower–leafflower moth mutualism discovered in the plant genus *Glochidion* (Phyllanthaceae). The flowers of *Glochidion* are minute and far from showy, and their reproductive systems have not been explored until recently. The obviously rewardless inconspicuous flowers, low frequency of anthophilous insects, and the high rate of infested seeds caused us to explore the reproductive system of the plants. By rearing seed-infesting larvae, the seed-parasites proved to be gracillariid moths. However, irrespective of extensive observations of insect visitors on *Glochidion* plants, we could not detect the pollinator for several years. By sweeping insects around the inflorescence, the gracillariid moths were collected. By examining the collected female moths, the proboscises were found to be covered by pollen of the *Glochidion* flower. At last, 8 years after the start of observation, the actual pollination behavior of the moth was observed on a tree of *Glochidion acuminatum* one midnight in May 2001 in a subtropical forest in Amami-Oshima Island in the Ryukyu Archipelago, Japan.

Like figs and yuccas, the adult females of the seed-parasitic insect actively pollinate the female flowers and oviposit to the flowers. Unlike figs and yuccas, however, the plant and insect taxa involved in the mutualism are Phyllanthaceae and Gracillariidae. The mutualism of Phyllanthaceae is widespread throughout tropical regions of the world, and the number of Phyllanthaceae species involved in the obligate pollination mutualism is estimated to exceed 500 species. Since the first report of the mutualism in 2003, much data and information have accumulated, e.g., morphological adaptation in plants and insects, pollination behavior, mechanism maintaining the mutualism, phylogenetics of both the plants and insects, and the origin and diversification process of the mutualism. By exploring the third system following figs and yuccas, now we can examine the abovementioned hypotheses on the evolutionary process of obligate pollination mutualism.

Kyoto, Japan Makoto Kato
Shiga, Japan Atsushi Kawakita

Acknowledgments

We wish to thank Yoh Iwasa who suggested that we write this volume. To Eiji Kuno, Masafumi Matsui, Sadao Sakamoto, the late Tamiji Inoue, and the late Mitsuru Hotta, MK is deeply grateful for their guidance of ecology, zoology, and botany and vital encouragements. We thank Ryohei Terauchi, Toshimitsu Fukiharu, Takayoshi Nishida, and Reiichi Miura for their constructive advice and discussion on wide academic disciplines. We are grateful to Toshio Kumata for his kind guidance on taxonomy and biology of Gracillariidae. Toby Kiers came to our laboratory during the postdoctoral summer program of JSPS in 2004 and gave us several substantive help and comments on our studies since then. Glenn Svensson also visited our laboratory in 2006 and 2008 and made great contribution to our understandings on the moth's olfactory sense and the function of floral odor in *Breynia*. We express our thanks to them. During our field trips in various countries, many researchers helped our study in various ways: Yasuhiro Kosaka in Laos, Takao Itioka in Malaysia, Shi-Xiao Luo in China, Elisett in Madagascar, Akira Wong Sato and Juana Rosa Llacsahuanga Salazar in Peru, and Hervé Vandrot in New Caledonia. We thank them for their kind help in our field works. AK is deeply obliged to Issei Ohshima for his kind guidance to the methodology in lepidopteran taxonomy and for discussion on broad topics in Gracillariidae biology.

We thank Teiji Sota and Hidetoshi Nagamasu for reading and providing many comments on our manuscript. The students, postdocs, and staffs associated with our laboratories often served as a critical sounding board in seminars and field excursions. They contributed in many ways to the development of our research, and we would like to thank Takao Itioka, Shoko Sakai, Atsushi Takimura, Hiroki Hata, Shinji Sugiura, Hiromitsu Samejima, Hirokazu Toju, Chisato Kobayashi, Yudai Okuyama, Yuichi Kameda, Remi Tsubaki, Yuta Nakase, Kenji Suetsugu, Eri Yamasaki, Yoshiko Yamane, Yume Imada, Saori Furukawa, Takayuki Ohgue, Akira Wong Sato, Ko Mochizuki, Momoko Igawa, Luna Yamamori, and Sho Sakurai.

Sincere thanks are also due to John N. Thompson, J. Nathaniel Holland, Laurence Després, Anne-Marie Labouche, and Bo Song who have generously provided their original photographs to be used in this book.

Finally, we thank the contributors of this volume, Ryutaro Goto, Tomoko Okamoto, and David Hembry, who have been wonderful collaborators since the early years of our study of Phyllanthaceae. Their studies have brought about major advances in our understanding of obligate pollination mutualism.

Our research was partly supported by the Ministry of Education, Science, Sports and Culture, Grant-in-Aid for Scientific Research: (B) 2000–2002 (12440217, Makoto Kato), (B) 2003–2006 (15370012, Makoto Kato), (A) 2006–2011 (18207002, Makoto Kato), (A) 2010–2014 (25241024, Makoto Kato), (B) 2010–2014 (22247003, Makoto Kato), (A) 2015–2020 (15H02420, Makoto Kato), (B for young scientists) 2010–2011 (22770017, Atsushi Kawakita), (B for young scientists) 2012–2013 (24770018, Atsushi Kawakita), and (B) 2015–2019 (15H04421, Atsushi Kawakita).

Kyoto, Japan Makoto Kato
Shiga, Japan Atsushi Kawakita

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