Evolution of Plant–Pollinator Relationships

What are the evolutionary mechanisms and ecological implications behind a pollinator choosing its favorite flower? Sixty-five million years of evolution have created the complex and integrated system which we see today, and understanding the interactions involved is key to environmental sustainability.

Examining pollination relationships from an evolutionary perspective, this book covers both botanical and zoological aspects. It addresses the puzzling question of co-speciation and co-evolution and the complexity of the relationships between plant and pollinator, the development of which is examined through the fossil record. Additional chapters are dedicated to the evolution of floral displays and signaling, as well as their role in pollination syndromes and the building of pollination networks. Wide ranging in its coverage, the book outlines current knowledge and complex emerging topics, demonstrating how advances in research methods are applied to pollination biology.

SÉBASTIEN PATINY is a scientific collaborator in the Laboratory of Zoology, Université de Mons, Belgium. A large part of his research focuses on desert species of bees, their distribution, and the importance of biogeographical features in some species-level radiations. He is currently developing a series of papers dedicated to the inference of large phylogenetic topologies.

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DAVID J. GOWER

Department of Zoology, The Natural History Museum, London, UK

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EDITED BY

SÉBASTIEN PATINY

University of Mons, Belgium

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Contributors

Nadir Alvarez Department of Ecology and Evolution, University of Lausanne, Switzerland

Bruce Anderson Botany and Zoology Department, Stellenbosch University, South Africa

W. Scott Armbruster School of Biological Sciences, University of Portsmouth, UK

James Cook Philip Lyle Building, School of Biological Sciences, University of Reading, UK

Astrid Cruaud INRA-UMR Centre de Biologie et de Gestion des Populations, CBGP (INRA/IRD/CIRAD/Montpellier SupAgro), Campus international de Baillarguet, France

Amots Dafni Laboratory of Pollination Ecology, Institute of Evolution, Haifa University, Israel

Yang Da-Rong Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China

David L. Dilcher Department of Biology, Indiana University, USA

Achik Dorchin Laboratory of Pollination Ecology, Institute of Evolution, Haifa University, Israel

Anna Dornhaus Center for Insect Science / Department of Ecology and Evolutionary Biology, University of Arizona, USA

Stefan Dötterl Department of Plant Systematics, University of Bayreuth, Germany

Yoko L. Dupont Department of Biological Sciences, Aarhus University, Denmark

Connal D. Eardley Agricultural Research Council, Plant Protection Research Institute, School of Biology and Conservation Science, University of KwaZulu–Natal, South Africa

Allan G. Ellis Botany and Zoology Department, Stellenbosch University, South Africa

Michael S. Engel University of Kansas, Division of Entomology and Department of Ecology and Evolutionary Biology, USA

GWENAËLLE GENSON INRA-UMR Centre de Biologie et de Gestion des Populations, CBGP (INRA/IRD/CIRAD/Montpellier SupAgro), Campus international de Baillarguet, France

ANTOINE GUISAN Department of Ecology and Evolution, University of Lausanne, Switzerland

MELANIE HAGEN Department of Biological Sciences, Aarhus University, Denmark

SHUSHENG HU Division of Paleobotany, Peabody Museum of Natural History, Yale University, USA

ROULA JABBOUR-ZAHAB INRA-UMR Centre de Biologie et de Gestion des Populations, CBGP (INRA/IRD/CIRAD/Montpellier SupAgro), Campus international de Baillarguet, France

TOM J. DE JONG Plant Ecology, Leiden University, The Netherlands

ANDREAS JÜRGENS School of Biological and Conservation Sciences, University of KwaZulu-Natal, South Africa

H. ELIZABETH KIRKPATRICK Biology Department, University of Puget Sound, USA

FINN KJELLBERG CNRS – UMR Centre d'Ecologie Fonctionnelle et Evolutive, CEFE, France

MICHAEL KUHLMANN Department of Entomology, The Natural History Museum, UK

ANNE S. LEONARD Center for Insect Science / Department of Ecology and Evolutionary Biology, University of Arizona, USA

YAEL MANDELIK Department of Entomology, The Robert H. Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, Israel

TALYA MAROM-LEVY Laboratory of Pollination Ecology, Institute of Evolution, Haifa University, Israel

DENIS MICHEZ University of Mons, Laboratory of Zoology, Belgium

SIMON VAN NOORT Natural History Division, South African Museum, Iziko Museums of Cape Town, South Africa

JENS M. OLESEN Department of Biological Sciences Aarhus University Denmark

DANIEL R. PAPAJ Center for Insect Science / Department of Ecology and Evolutionary Biology, University of Arizona, USA

SÉBASTIEN PATINY University of Mons, Laboratory of Zoology, Belgium

LOÏC PELLISSIER Department of Ecology and Evolution, University of Lausanne, Switzerland

RODRIGO AUGUSTO SANTINELO PEREIRA Depto de Biologia/FFCLRP-USP, Brazil

GIDEON PISANTY Department of Entomology, The Robert H. Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, Israel

CLAUS RASMUSSEN Department of Biological Sciences, Aarhus University, Denmark

JEAN-YVES RASPLUS INRA-UMR Centre de Biologie et de Gestion des Populations, CBGP (INRA/IRD/CIRAD/Montpellier SupAgro), Campus international de Baillarguet, France

NINA RØNSTED Department of Medicinal Chemistry, Faculty of Pharmaceutical Sciences, University of Copenhagen, Denmark

OTILENE SANTOS-MATTOS Instituto Nacional de Pesquisa da Amazônia, Brazil

VINCENT SAVOLAINEN Imperial College London, UK

FLORIAN P. SCHIESTL Institute of Systematic Botany, University of Zürich, Switzerland

BORIS O. SCHLUMPBERGER University of Munich, LMU, Germany (Current address: Herrenhausen Gardens, Hannover, Germany)

YUVAL SHIMRAT Laboratory of Pollination Ecology, Institute of Evolution, Haifa University, Israel

DAVID WINSHIP Taylor Department of Biology, Indiana University Southeast, USA

KRISTIAN TRØJELSGAARD Department of Biological Sciences, Aarhus University, Denmark

ROSICHON UBAIDILLAH Entomology Laboratory, Zoology Division (Museum Zoologicum Bogoriense), Center Research for Biology, LIPI, Indonesia

MARYSE VANDERPLANCK University of Mons, Laboratory of Zoology, Belgium

JANA C. VAMOSI Department of Biological Sciences, University of Calgary, Canada

STEVEN M. VAMOSI Department of Biological Sciences, University of Calgary, Canada

PAUL WILSON Department of Biology, California State University, Northridge, USA

TAINA WITT School of Biological and Conservation Sciences, University of KwaZulu-Natal, South Africa

PENG YAN-QIONG Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China

Preface

Pollination has been a source of questioning and fascination as long as there have been naturalists. Aristotle and Herodotus before him were already according a specific interest to the topics of fig and palm pollination. In the eighteenth and nineteenth centuries – adopting a more adaptationist point of view – Kölreuter (1761), Sprengel (1793), and Darwin (1862) authored books that constitute the early stepping stones in development of modern pollination biology. From the time Darwin published the *On the Origin of Species* (1859), the functional relationships of plant and pollinator were cast in evolutionary scenarios in which plants adapted to pollinators and pollinators adapted to flowers.

Over the last decade, many edited volumes have been published on pollination-related topics (Proctor et al. 1997; Chittka and Thomson 2001; Dafni et al. 2005; Waser and Ollerton 2006; Harder and Barrett 2007). The present volume originated in a symposium dedicated to the evolution of plant–pollinators relationships (EPPR), which was organized in the framework of the *SYSTEMATICS 2009* meeting in Leiden in the Netherlands. Given the intense scientific activity in pollination biology (Mitchell et al. 2009), the idea behind this symposium was to provide a forum for authors to pull together recent advances in pollination in the context of systematics. The present book constitutes an outcome of this symposium along with its natural prolongation. It has been developed with an explicit sensitivity for the evolutionary aspects of pollination. It includes contributions from the participants in the symposium and additional authors who joined the book project to round out its evolutionary coverage.

The attention currently given to pollination can be considered as the consequence of the combined importance of the pollination ecological service, plus threats weighing on a continually increasing number of pollinator populations worldwide, and interest in how plant–pollinator relations evolve in the face of environmental change.

(1) The economic value of pollination has focused the interests of numerous research groups (Aizen et al. 2009; Allsopp et al. 2008; Buchmann and

Nabhan, 1996; Gallai et al. 2009). Two very recent reports underscore the economic importance of pollination. Gallai et al. (2009) estimated about €150 billion per year are contributed by insect pollination to crops worldwide. Allsopp et al. (2008) showed that, despite the deep divergences in the methods used and the results tabulated, the varied studies that have been done converge in concluding that pollination constitutes a key component of the world economy.

(2) Echoing the economic importance of pollination services, the observation of continued population regressions and diversity erosions (e.g. Biesmeijer et al. 2006; Kluser and Peduzzi 2007; Potts et al. 2010) is increasing the urgency for better conservation of pollinators. Conservation of pollinators, in turn, demands the development of better supporting science.

(3) In addition to these econocentric and conservation interests, pollination systems emerge as wonderful models for the study of adaptation, cophylogeny and speciation, topics in which a wealth of questions are puzzling the scientific community. This last point constitutes the main focus of the present book, and in the following pages expert authors discuss in detail varied aspects of the evolution of pollinators, pollinated plants, and pollination systems.

Considering the above points, the improvement of the understanding of the evolution of interactions between pollinators and pollinated plants within their ecological webs is highly desirable. Likewise, renewed models of the evolution of pollination in space and time are needed.

Nowadays, understanding of the evolutionary dance between pollinators and pollinated plants remains quite fragmentary. The simple coevolutionary model – envisioned as specialized forms adapting reciprocally to one another – and the basic picture of progress to specialization have been questioned (e.g. Danforth et al. 2006a, 2006b; Cruaud et al. Chapter 4). The scale of pollination processes range from the molecular to the community level, but studies at the various scales seem not to have settled into a coherent model of evolution. The aim of the present book is to embrace an evolutionary point of view, bringing together the contributions from a large panel of research groups that have explored pollination with various approaches. The following chapters address a series of domains within the biology of pollination:

(1) Evolutionary biology of pollination integrating phylogenetic thinking

(2) Evolution of pollination syndromes, floral displays and rewards

(3) Evolution of feature of pollination networks

The contributions in these sections outline both the state of the knowledge in the three domains and novel aspects under development.

Phylogenetics are the new toolkit in studying all aspects of the diversification of life. This is, of course, true when studying examples of coevolution involving distinct groups of living forms, as for instance in the evolution of pollination. The methodological and analytical opportunities to map phylogenies onto one another, to date clades using molecular clocks, and to trace evolution of characters on trees are the operational promises of phylogenetics as applied to pollination biology. However, despite this promise of phylogenetics, very few specific empirical results have been produced so far for the study of pollination as has been the case in biogeography (e.g. Ree and Sanmartin 2009; Salvo et al. 2010). Evolutionary pollination biology has so far mostly benefited from the general progress made in phylogenetics. For example, phylogenetics allow us to recast our conceptual understanding of macroevolution. The first chapters of this book present some of the key phylogenetic insights into pollination biology.

For a long time, attention has been paid to the concordant evolution of plants and their pollinators, notably the evolutionary strategies developed by plants to increase pollination by their best pollinators and the senses used by pollinators to identify and locate food. The conceptual framework of pollination syndromes developed from these two topics (Faegri and van der Pijl 1979; Proctor et al. 1997). With increased ease over the next few years, genomics, transcriptomes, and floral physiology point to a wealth of new directions for investigation. This will open new vistas in pollination biology. Our understanding of the ways in which pollinators perceive flowers and are rewarded by flowers seems to be constantly improving. While all these avenues of research are of interest in and of themselves, they also are providing a fountain of data of a new kind to be used in deciphering the evolutionary relationships between plants and pollinators. Aspects of these topics are developed in the last chapters dedicated to the evolution of pollination syndromes.

Moving out in scale, to the level of communities, we must now recognize that pollination webs evolve. This topic is directly related to conservation, as well as evolution. Pollination webs are fundamental to understanding the general patterns in community context in which the evolution of the pollination systems occurs. Studying pollination webs means considering the interactions of multiple species with distinct levels of respective knowledge and interacting partners that are, at some level, competing for niches and resources within niches. The study of pollination webs is, *par nature*, integrative. The chapters dealing with pollination webs discuss both the theoretical aspects of pollination evolution and several study cases. A particular focus has been set on evolution of the plant sex systems, emergence of unusual floral rewards, and relationships between herbivory and pollination.

This book should become a reference for questions related to the evolution of pollination systems in varied contexts. Secondly, it documents the ways in which

the complexity of pollination ramifies into many areas within biology. Finally, it serves as an example of new research methods applied to pollination systems that give us the opportunity to revisit old problems such as the usefulness of varied species concepts.

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