

EVOLUTIONARY ECOLOGY OF POLLINATION AND REPRODUCTION OF TROPICAL PLANTS

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Keywords: Pollination, tropical plants, diversity, mating systems, gender, conservation.

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Summary

Angiosperms are the most diverse group of living plants. It is in the tropics where the striking diversity of reproductive organs (flowers) and the unparalleled variety of pollination and reproductive systems evolved. The diversification of many groups of animal pollinators such as bees, butterflies, moths, flies, wasps, hummingbirds, and bats occurs also in tropical forest. Indeed the pollination of flowering plants by animals is one of the best examples of co-evolution by natural selection. Besides, among the reproductive systems of tropical angiosperms there is a high incidence of both outcrossing species and dioecious trees. This fact stresses the reproductive dependence of tropical plants on pollinators. Consequently, the reduction and fragmentation of

tropical forests is one of the major threats to the extinction of natural pollinators and the plant populations that depend upon them. Besides the negative consequences on pollinators and plant reproduction, the reduction of populations and their reproductive isolation is predicted to negatively affect the genetic diversity and structure of populations in tropical trees species. The viability and maintenance of tropical forest depends largely on the capacity of tropical trees to reproduce and regenerate under natural conditions. Hence, studies designed to understand the reproduction of tropical plants are critical. On this knowledge depends the possibility to protect biological resources and the subsequent management of tropical forests.

1. Introduction

Imagine a world without flowers, without oranges or bananas, a green planet free of colorful petals, or the aroma of flowers. The planet 120 million years ago was very different from the way it is today, it was a place without flowering plants. This important group of organisms provided us vegetables, cereals, fruits, fibers, material for clothing, and the prime source for medicinal drugs, perfumes, wine, beer and many other drinks. The objective of this chapter is to illustrate the current knowledge of biological diversity of flowering plants in tropical regions and their relationship with pollinators.

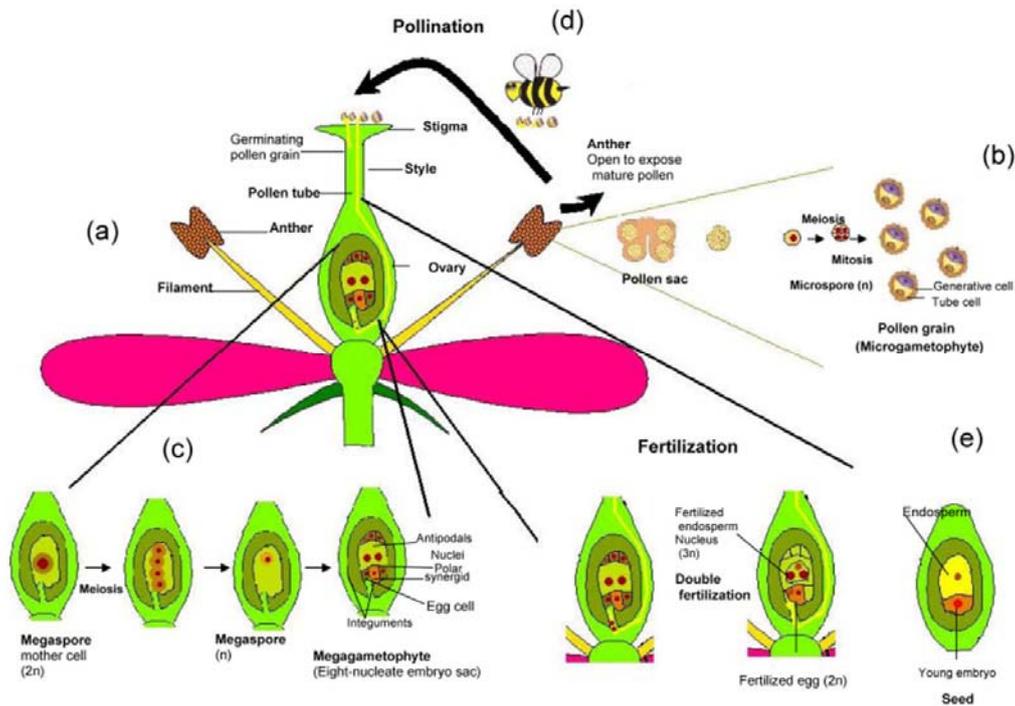


Figure 1. Life cycle of angiosperms. a) Flower with specialized structure that contain reproductive organs. b) Development of microgametophyte or male phase. c) Development of megagametophyte or female phase. d) Pollination by animals e) Fertilization is characterized by the pollen tube development, double fertilization and formation of enclosure seed.

In the Early Cretaceous, the first flowering plants appeared on earth. Ever since, this important group of plants has dominated all terrestrial habitats of the planet. Today, we know that angiosperms are tropical in origin and started as animal pollinated organisms. A brief description of the life cycle of angiosperms could be of utility for visualizing the distinctive characteristics that differentiate angiosperms from other groups of plants. (Figure 1).

1.1. The Life Cycle of Angiosperms

One of the explanations to describe the success of flowering plants in the planet is related to their life history. A complex system of two life phases in one organism is a common characteristic of all these plants. The life cycle of angiosperms is divided in two **alternate generations**: a conspicuous and extended autonomous sporophyte generation and a highly reduced gametophyte generation (Figure 1). The green sterile sporophyte, represented by roots, stems and leaves, constitutes half of the life cycle of the organism. The other half of the life cycle is fertile and it is responsible for the formation of pollen and ovules. The life cycle could start from **the flower**; a specialized and astonishing diversified structure that contains the reproductive organs that characterizes angiosperms. It is a compressed shoot with four whorls of modified leaves. The two internal layers are the gynoecium (group of carpels) and androecium (group of stamens), the female and male reproductive organs, respectively. The two

external and sterile layers are the corolla (group of petals) and the calyx (group of sepals) and together make up for the perianth, a structure that protects the reproductive organs and in many cases it is also a colorful structure that serves to attract pollinators. The stamens have a filament and an anther where male gametophytes develop as pollen grains after both meiotic and mitotic cell divisions. The female structure (carpel) is differentiated into an ovary that contains the ovules, a stigma that receives pollen grains and a style that connects the ovary to the stigma. The mature female gametophyte (or embryo sac) develops within the ovary after meiotic and mitotic cell divisions. In most instances it is reduced to a central cell that remains binucleate (the polar nuclei), an egg apparatus formed by the egg cell and two synergid cells (in the micropylar end of the embryo sac) and three antipodal cells (in the distal side of the embryo sac). Sexual reproduction in angiosperms is achieved by pollination, which is the process of pollen grain transport from anthers to conspecific stigmas and the subsequent pollen tube growth through the style. The pollen tube carries the 2 sperm gametes through the stylar tissue to the ovary; in contrast to the single fertile sperm of gymnosperms, both sperm cells of the male gametophytes are functional, one fertilizes (syngamy) the egg cell to form a $2n$ zygote and the second one fuses with the two polar nuclei to form the $3n$ endosperm. This phenomenon is recognized as ***double fertilization***, a distinctive reproductive feature of angiosperms. After fertilization, the ovary becomes a fruit and the ovules develop into seeds. ***The enclosure of seeds in the fruit*** is also an important trait that differentiates angiosperms from gymnosperms. The cycle ends and starts again when a seed develops into a sporophyte (a green plant) that at maturity produces flowers (Figure 1).

1.2. Overview of Angiosperm Diversity

Angiosperms are the most diverse group of living plants with more than 250,000 species. Such diversity is divided into monocots (70 000 spp) and dicots (180 000 spp) (subclasses Monocotyledoneae and Dicotyledoneae). Monocots include: lilies, orchids, yuccas, palms, grasses, sugar cane and grain crops (corn, wheat etc). Dicots comprise roses, peas, buttercups oaks, etc. The most diversified angiosperm floras in the world occur in tropical regions. For example, in the neotropics alone there are more than 300 families, 5000 genera and 80, 000 species. Two important features characterize the evolution of angiosperms, an extraordinary diversity of reproductive organs (flowers) without equivalence in any other group of organisms, and an unrivaled variety of pollination and reproductive systems mainly expressed in the tropics.

An explanation for the evolution of such extraordinary diversity in flowering plants relies in the necessity to achieve the essential function of mating, predominantly accomplished by sexual reproduction. Because of their sessile habit, plants require vectors (biotic or abiotic) for pollen dispersal. In particular, the greater part of tropical angiosperms are pollinated by animals and has a self incompatibility system (SI) that allows the rejection of own pollen. Therefore, flowering plants of tropical ecosystems are highly dependent on animal vectors to move their pollen to receptive compatible plants of the same species to accomplish sexual reproduction. The pollination of

angiosperms by animals is indeed one of the most common and elaborated examples of adaptation. In general, the evolution of complex and diversified flower morphology, color, scent, size, and type and amount of reward offered to animal pollinators, is largely a result of the selection exerted by the type of vector employed to disperse pollen between plants. In turn, diversification of many animal groups such as bees, butterflies, moths, flies, wasps, hummingbirds, bats and others are coupled with the evolution of flowering plants. Some multicolored scenes of the interaction between flowering plants and their pollinators are used to illustrate textbooks regarding the evolution of biodiversity and coevolution.

2. Degree of Specificity of Pollination System

The degree of specialization of pollination systems has been explored on the basis of two contrasting views. The first perspective proposes that each plant species is mainly visited and pollinated by a particular and specific group of pollinators; therefore, it is assumed that pollination systems are highly specialized. According to the principle of the most effective pollinator, a plant should specialize on the most effective and/or most abundant pollinator when its availability is predictable. A contrary point of view considers pollination systems as being mostly generalized in nature because plant species can be pollinated by several groups of taxonomically different pollinators. It is assumed that generalization is favored when the availability of an effective pollinator is unpredictable for a given reproductive period. Phenotypic selection exerted by pollinators on reproductive traits of plants is the main evidence to assert that most flowers are specialized for pollination by particular animal types. However, it is almost equally evident that plant species are pollinated by several different types of pollinators. Evidence from both viewpoints indicates that the apparent dichotomy between

generalization and specialization represent a simplification of what is really a continuum; from plants being pollinated by a few or a single pollinator to those plants pollinated by several or many animal species. Review studies regarding the degree of specialization in pollination systems reveal that the median number of pollinators per plant species differs among families. For example, the Asteraceae and Ranunculaceae families have 25 and 10 pollinators per specie, respectively, being among the most generalist. Other families such as Polemoniaceae and Asclepiadaceae have four and three respectively, whereas Orchidaceae has a single pollinator per specie, being the most specialized family. It is not clear if such trends are due to phylogenetic constraints in floral structures or due to local adaptations to habitats or geographical regions where these families occur. Regardless of such discrepancy, it is clear that the most diverse and elaborated pollination systems involving bats, hawkmoths, crepuscular beetles, fig wasps, and euglossine bees occur in tropical forests. The orchids, with more than 20 000 species, are an amazing example of both floral complexity and diversity related to very specialized pollination systems.

3. Diversity of Pollination Systems

Traditionally, concurrent flower and pollinator traits have been used as clear examples of evolutionary adaptations. In fact, the bases that developed the theory of *pollination syndromes* assume that the specific combinations of floral traits have adjusted to attract

and exploit specific groups of animals as pollinators. However, there is little empirical evidence showing that such specific floral traits actually reflect selection exerted by a specific type of pollinator through evolutionary time. The idea of pollination syndromes is also criticized because flowers can attract a larger variety of visitors than those predicted by pollination syndromes. Despite these limitations, the concept of pollination syndromes has promoted a discussion in the literature to understand the evolutionary mechanisms responsible for the diversification of floral traits. An idea developed from the concept of pollination syndromes states that pollinators can be clustered into functional groups that behave in similar ways and exert similar selection pressures on the flowers they visit. For example, flowers pollinated by long-tongued moths have been selected to develop long narrow corolla tubes. The overlapping degree of selective pressures exerted by functional groups of pollinators can help explain the evolution of complex floral designs as well as several kinds of rewards produced. Some combinations of floral advertisements, such as specific scents, colors and other morphological attributes that restrict the access to nectar and other rewards are examples of traits selected by particular pollinators. For example, anthophorid and melittid bees that collect oil rewards pollinate hundreds of tropical and subtropical plant species. Male euglossine bees collect fragrances produced by the flowers they pollinate and use the reward to attract female bees. Some species of bees and wasps collect floral resins that are used in nest building. The several hundred species of plants that produce resins as rewards grow mainly in tropical habitats and this reward is used by the pollinators for rearing their nests. Over 900 species of figs distributed largely in tropical forests are pollinated specifically by seed feeding wasps. The following section describes the classical view of pollination syndromes with emphasis in tropical plants.

3.1. Beetle Pollination (Cantharophily)

Originally, beetles were considered primitive pollinators because they were the main pollinators of early angiosperms; however more recent studies indicate that this group also maintains such mutualistic interactions with more derived groups that include palms (family *Arecaceae*) and *Cyclanthaceae*. The main beetle pollinator families include *Chrysomelidae*, *Staphylinidae*, *Cantaridae*, and *Cerambycidae*. In general, flowers pollinated by beetles produce large quantities of pollen, tissues rich in nutrients and nectar or other floral exudates. These flowers usually have diffuse green or dark colors. Beetles are considered rather clumsy pollinators because they do not necessarily touch the entire main fertile flower parts, eat the pollen without moving it from flower to flower and waste a lot of pollen in the process. Beetle pollination has even been associated to parasitism because evidence reveals that these insects feed on pollen and develop their oviposited eggs in the inflorescences they visit. In some cases they even destroy the developing fruits.

An interesting example of this type of pollination has been described in the family *Araceae*. A unified feature of this family of plants is the spadix, an inflorescence with small flowers packed onto a fleshy axis, which is mainly pollinated by beetles. This inflorescence usually heats up for the diffusion of scents from the flower and in some

cases a disagreeable scent is produced for the attraction of carrion insects. Flowers produced in this family are monoecious, unisexual and protogynous (i.e. female flowers are produced before male flowers in the same inflorescence). Therefore, beetles are usually attracted to the female phase of the inflorescence before the male phase. Similarly in the family Magnoliaceae (Magnolia trees), flowers are also protogynous and beetle-pollinated but the insects are mainly attracted by the fragrance of the nectarless flowers. In the case of Annonaceae, beetles are attracted to a fragrant or unpleasant scent and to sweet nectar and sticky exudates usually present in the anthers and stigmas of the flowers.

3.2. Lepidoptera

The principal groups of Lepidopteran pollinators are butterflies (family Rhopalocera), moths (family Noctuidae) and hawkmoths (family Sphingidae). A common characteristic of many of these flowers are the nectaries concealed in narrow tubes. The following sections describe each one of the Lepidopteran groups of pollinators.

3.2.1. Butterfly Pollination (Psychophily)

Butterfly-pollinated flowers tend to be large and showy, pink or lavender in color, frequently have a landing area, and are usually scented. Since butterflies do not digest pollen (with one exception), flowers tend to have more nectar than pollen. These flowers have simple nectar guides with nectaries usually hidden in narrow tubes or spurs that can only be reached by the long tongue of butterflies. These flowers open during the day when butterflies are active. Flowers frequented by butterflies display a wide range of colors ranging from red, yellow, pink and purple. Plant families with butterfly pollination are Verbenaceae, Caesalpinaceae, Zingiberaceae, Liliaceae, Boraginaceae, Nyctaginaceae, Orchidaceae, Rubiaceae, among other families.

3.2.2. Moth Pollination (Phalaenophily)

Hawkmoths (Sphingidae) are among the more important moth pollinators in the tropics. Their behavior is similar to hummingbirds: they hover in front of flowers with rapid wing beats. Most are nocturnal or crepuscular. Moth-pollinated flowers tend to be white, large and showy with tubular corollas and a strong, sweet scent produced during the night or early morning. The nectar produced by hawkmoth flowers has high sugar concentration needed to power the flight of that require high metabolic rates. Examples of hawkmoth plant families are Verbenaceae, Asclepiadaceae, Caesalpinaceae, Apocynaceae, Rubiaceae, Solanaceae, Campanulaceae-Lobeloideae, Liliaceae, Caricaceae, Combretaceae, Nyctaginaceae, Pittosporaceae, Agavaceae, Convolvulaceae and other families.

Other moths (Noctuids, Geometrids, Pyralids, for example) have relatively short proboscides, fly slowly and settle on the flower. They do not require as much nectar as the fast-flying hawk moths, and the flowers tend to be small (though they may be aggregated in heads). Noctuids-pollinated families include Liliaceae, Convolvulaceae and others.

An interesting example is found in the genera *Yucca* (Agavaceae). As in *Yucca*, white

color is typical of moth-pollinated flowers. Each species of yucca is apparently pollinated by a single, highly specialized species of moth. The moth has special appendages that are used to actively pack pollen onto the stigma. It then oviposits its eggs directly into the ovary. The developing larvae eat part of the developing seeds, but the cost for the plant is outweighed by the benefit of having an efficient and reliable pollinator. If a moth oviposits too many eggs on a flower, this flower aborts and drops off the plant, selecting against individuals that overexploit the plant. The yucca-yucca moth system is one of the clearest examples of co-evolution between plants and animals.

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Biographical Sketches

Mauricio Quesada was born in San Jose, Costa Rica. He obtained his B. S. in Biology at the Department of Biology, Universidad de Costa Rica, and M.Sc. and Ph.D. in Ecology at the Department of Biology, The Pennsylvania State University, USA. Dr. Quesada has conducted research on pollination and plant reproductive systems, plant genetics, tree ecophysiology and conservation biology. He has conducted research at La Selva Biological Station and Palo Verde Biological Station, Organization for Tropical Studies, OTS, Costa Rica. He served as Co-Director of Palo Verde Biological Station, Organization for Tropical Studies, OTS, Costa Rica and as Invited Professor at the Department of Biology, University of Costa Rica. He also served as a Research Professor at the Chamela Biological Station, Institute of Biology and Institute of Ecology, Universidad Nacional Autónoma de México. He is currently a Research Professor at the Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México. He has conducted studies in the evolution and genetics of plant reproductive systems. He is currently interested in the effects of forest fragmentation on pollinators, plant reproductive systems and the genetic structure of tropical trees of the dry forest. He is also developing research on the effects of transgenic plants on its wild relatives. He is particularly interested in conservation of tropical dry forests. Finally, he is interested in the relationship between plant functional groups under succession and remote sensing. He has more than 50 publications in international peer review journals and book chapters and edited a book. He has participated in more than 80 international meetings.

Fernando Rosas was born in Mexico city, Mexico. He obtained his B.S. in biology at the Facultad de Ciencias, and his Ph. D. at the Instituto de Ecología, Universidad Nacional Autónoma de México (UNAM) Mexico. He is currently a posdoc researcher at Centro de Investigaciones en Ecosistemas (CIEco), Universidad Nacional Autónoma de México. Dr. Rosas has conducted research on the evolutionary biology of reproductive systems of flowering plants, mainly regarding male sterility as a relevant factor influencing the evolution of gender specialization from cosexuality. He also had worked as professor at the School of Sciences, the Institute of Ecology and at the Centro de Investigaciones en Ecosistemas, UNAM. At present he is conducting studies regarding the effects of forest fragmentation on the patterns of gene flow as well as on the genetic diversity and structure of tropical trees of dry forest. The main interest is to evaluate explicitly the relationship of the reproductive system, the phenological patterns and the type of pollinators with male and female reproductive success and its consequences on the maintenance of populations of endangered tree species in the tropics. His research is being published in peer review international scientific journals.

Yvonne Herrerías-Diego was born in Mexico city, Mexico. She received her B. S in Biology at the Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), and her Ph.D. in Biological Sciences at UNAM. Her general area of research is in plant ecology, particularly focusing on the ecology, ecological genetics, and conservation biology of woody plants. She has worked on the effects of forest

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Gumersindo Sanchez-Montoya was born in Mexico City, Mexico. He obtained his B.S. in biology at the Facultad de Ciencias, Universidad Nacional Autonoma de Mexico (UNAM) Mexico. He is currently a research technician at the Centro de Investigaciones en Ecosistemas, Universidad Nacional Autonoma de Mexico. He has conducted research on pollination biology, plant reproduction and plant population genetics. He has experience on the application of molecular biology techniques to the field of ecology and evolution of plants, specifically on the use of molecular markers such as isozymes, RAPD's, AFLP's, and microsatellites. He has served as teacher of courses in general biology, plant reproductive biology, field ecology and molecular techniques applied to ecology. His research is being published in peer review international scientific journals.