CHAPTER ONE

Biodiversity and Plant-Animal Coevolution

HISTORICAL OVERVIEW

The almost-perfect matching between the morphology of some orchids and that of their insect pollinators fascinated Charles Darwin, who foresaw that the reproduction of these plants was intimately linked to their interaction with the insects (Darwin, 1862). Darwin even predicted that the extinction of one of the species would lead to the extinction of its partner:

If such great moths were to become extinct in Madagascar, assuredly the *Angraecum* would become extinct (Darwin, 1862, p. 202).

Later on, Alfred Russell Wallace would take the examples of plant-animal interactions to illustrate the force and potential of natural selection to shape phenotypic traits. He already noted that the selective pressures derive directly from the interaction itself (Wallace, 1889).

The fascinating experimental work by Darwin on plant sexuality was very influenced by the earlier work of Sprengel (1793) demonstrating the role of insects in plant fertilization (Fig. 1.1a). Similarly, his work on hybridization shows the strong influence by Köllreuter (1761; see Waser 2006, for a historical overview). Köllreuter already documented the diversified pollination service that multiple insect species provide to plants. However, the major advances at that time in documenting the specificity of pollination patterns are due to the monumental work of Müller, Thompson, et al. (1883), providing the list of pollinator species for 400 plant species, and Knuth (1898), reporting records for more than 6000 species. Early researchers on plant-seed disperser interactions (Hill, 1883; Beal, 1898; Sernander, 1906) also emphasized the diversity and subtleties of mutual dependencies among the partners and provided well-grounded evidence for mutual coadaptations between them (Fig. 1.1b). Beal provides an analogy with pollination systems, quoting

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FIGURE 1.1. The work by early botanists and zoologists represented the foundations for later studies on mutualistic interactions. Prominent among them was a series of monographs on different types of interactions (pollination, seed dispersal, ant-plants, etc.) appearing between the late 1700s and early 1900s. (a) The beautifully detailed front page of Sprengel, the author of an important monograph on flowers and pollination (Sprengel, 1793); (b) detailed view of one of the plates illustrating Sernander monograph on seed dispersal by ants (Sernander, 1906), showing the anatomical details of elaiosomes (reward tissue) attached to the seeds.

Darwin's orchid book (Darwin, 1862):

The more we study in detail the methods of plant dispersion, the more we shall come to agree with a statement made by Darwin concerning the devices for securing cross-fertilization of flowers, that they "transcend," in an incomparable degree, the contrivances and adaptations which the most fertile imagination of the most imaginative man could suggest with unlimited time at his disposal (Beal, 1898, p. 88).

The complexity that such interactions could take was already recognized by Darwin in the final paragraphs for the first edition of on the *Origin*:

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect

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that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us (Darwin, 1859, p. 498).

Similarly, in Chapter III, Struggle for Existence, we can read:

I am tempted to give one more instance showing how plants and animals, most remote in the scale of nature, are bound together by a web of complex relations (Darwin, 1859, p. 73).

Darwin also envisioned the mutually reciprocal effects involved in the pollination of red clover by "humble-bees" and the potential effects of declines in pollinator abundance. He foresaw the complexity of mutualistic networks, a complexity that precluded a community-wide approach.

Mutualism and symbiosis became quickly incorporated into the research agenda after de Bary (1879) coined the term *symbiosis* to account for interactions among two or more dissimilar entities living in or on one another in intimate contact. These developments of the study of mutualisms were well grounded on the empirical evidence obtained by botanists documenting every detail of the morphological structures of flowers, fruits and seeds (Fig. 1.1) as well as the intricacies of the interactions with animals. Since then, a myriad of scientific papers have described the mutually beneficial (mutualistic) interactions between plants and their animal pollinators or seed dispersers. But the interest of ecologists and evolutionary biologists in mutualistic interactions has been quite variable in emphasis and prevalence during this period of time.

Work on mutualism, like the analysis by Pound (1893), remained marginal to dominant views in ecology. Antagonistic interactions were at the core of Clements and Tansley's views of plant ecology, which dominated the field in the United States and United Kingdom during the early 20th century. This was paradoxical given the rapid discovery of new major symbiotic interactions like mycorrhizae in the 1880s and 1890s (Schneider, 1897). In fact, a few years after the Lotka-Volterra models were developed for antagonistic interactions, Gause and Witt (1935) proposed dynamic models of mutualism based on very similar formulations. However, mutualistic interactions were ignored in the extensive treatment that Volterra and D'Ancona (1935) dedicated to the dynamics of "biological associations" among multiple species. Up to the early 1970s, mutualism was not at the center of ecological thinking (L. E. Gilbert and Raven, 1975), which was more focused on the dynamics of antagonistic interactions such as predation and competition as the major forces driving community dynamics.

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Most recent textbooks on ecology and evolution just treat mutualisms as iconic representations of amazing interactions among species, lacking a formal conceptual treatment at a similar depth to predation or competition (Sapp, 1994). Boucher (1985a) provides a lucid analysis for the reasons why mutualism had a marginal importance in ecological studies up to the late 1970s and early 1980s, when dynamic and genetic models of mutualistic interactions started to be revisited (May, 1982). Among these reasons, there are the technical difficulties to find stable solutions for dynamic models of mutualism (May, 1973) and the lack of appropriate empirical and theoretical tools to develop a synthesis of the enormous diversity of mutualistic interactions (May, 1976). Also, the association of the idea of mutualism with anarchist thinking related to the 1902 book *Mutual Aid* by Peter Kropotkin most likely had an influential effect on the demise of mutualism in the early 1900s and its marginal consideration (Boucher, 1985a).

Ehrlich and Raven, in their classic paper, emphasized the pivotal role of plant-animal interactions in the generation of biodiversity on Earth (Ehrlich and Raven, 1964). Interestingly enough, insects and flowering plants are among the most diverse groups of living beings, and it is assumed that the appearance of flowering plants opened new niches for insect diversification, which in turn further spurred plant speciation (Farrell, 1998; McKenna, Sequeira, et al., 2009). This scheme has some alternative explanations, such as that one group may have been tracking the previous diversification of the other one without affecting it (Ehrlich and Raven, 1964; Pellmyr, 1992; Ramírez, Eltz, et al., 2011). However, the relevant point is that animal-pollinated angiosperm families are more diverse than their abiotically pollinated sister-clades (Dodd, Silvertown, et al., 1999).

Since the seminal paper by Ehrlich and Raven (1964), there has been a flourishing of studies on plant-animal interactions in general and on mutualisms among free-living species in particular. A significant amount of this work stems from recent advances in the study of coevolutionary processes (Thompson, 1994, 1999a) and the recognition of their importance in generating biodiversity on Earth.

Fortunately, there is ample fossil evidence of the origin of mutualistic interactions. Thus, the first preliminary adaptations to pollination can already be tracked around the mid-Mesozoic, almost 200 million years ago, and became widely observed from the mid-Cretaceous, more than 100 million years ago (Labandeira, 2002). In relation to seed dispersal, the early evolution of animaldispersed fruits in the upper Carboniferous, together with the diversification of small mammals and birds in the Tertiary, allowed the diversification of plant fruit structures and dispersal devices (Tiffney, 2004). Therefore, multi-specific

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interactions among free-living animals and plants have been an important factor in the generation of biodiversity patterns for a very long time.

But mutualisms have been important not only in the past. They remain important in the present. Mutualisms among free-living species are one of the main wireframes of ecosystems, simply because extant ecosystems would collapse in absence of animal-mediated pollination or seed dispersal of the higher plants. Effective pollen transfer among individual plants is required by many higher plants for successful fructification, and active seed dispersal by animal vectors is a key demographic stage for maintaining forest regeneration and dynamics. Both processes depend on the provision by plants of some type of food resource that animals can obtain while foraging. These plant resources (nectar, pollen, fleshy pulp, seeds, or oil) are fundamental in different types of ecosystems for the maintenance of animal diversity through their keystone influence on life histories and annual cycles.

From a conservation point of view, hunting and habitat loss are driving several species of large seed dispersers toward extinction, and these effects cascade towards a general reduction of biodiversity through reductions in seed dispersal (Dirzo and Miranda, 1990; Kearns, Inouye, et al., 1998; S. J. Wright, 2003). Looking back through time, evidence for these effects comes from the fossil record. Episodes of insect diversity decline, such as the ones during the Middle to Late Pennsylvanian extinction, during the Permian event, and at the Cretaceous/Tertiary boundary, have been followed by major extinctions of flowering plants (Labandeira, 2002; Labandeira, Johnson, et al., 2002). All this evidence already suggests that in conservation we cannot treat these species isolated from each other or consider only pairs of interacting species. Rather, we need to have a network perspective.

The first studies on mutualism focused on highly specialized one-to-one interactions between one plant and one animal (Johnson and Steiner, 1997; Nilsson, 1988). Examples of these highly specific pairwise interactions are Darwin's moth and its orchid (Darwin, 1862; Nilsson, Jonsson, et al., 1987), long-tongued flies and monocot plants (Johnson and Steiner, 1997), fig wasps and figs (Galil, 1977; Wiebes, 1979; J. M. Cook and Rasplus, 2003), and yucca moths and yuccas (Pellmyr, 2003). However, their strong emphasis in evolutionary studies probably reflects more the aesthetics of such almost perfect matching than their frequency in nature (Schemske, 1983; Waser, Chittka, et al., 1996). Motivated by this fact, several authors already advocated a community context to address mutualistic interactions (Heithaus, 1974; Feinsinger, 1978; Janzen, 1980; Herrera, 1982; Jordano, 1987; Fox, 1988; Petanidou and Ellis, 1993; Bronstein, 1995; Waser, Chittka, et al., 1996; Iwao and Rausher, 1997; Inouye and Stinchcombe, 2001).

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Waser, Chittka, et al. (1996) made the point that generalism is widespread in nature and advanced conceptual reasons based on fitness maximization in highly fluctuating interaction environments. More recently, and as a consequence of this interest in expanding the pairwise paradigm, there has been significant progress in our understanding of how pairwise interactions are shaped within small groups of species across time and space (Thompson and Pellmyr, 1992; Thompson, 1994; Parchman and Benkman, 2002).

A BIT OF NATURAL HISTORY

Mutualisms are assumed to be among the most omnipresent type of interaction in terrestrial communities (Janzen, 1985). Beyond the mutualistic interactions among conspecific individuals (i.e., the subject of kin-selection and parentoffspring interactions), most of these interactions are allospecific interactions, involving species, or sets of species, completely unrelated. Multispecific interactions involving mutual benefits among partner species are extremely widespread and involve all the terrestrial vertebrates, plants, and arthropods. Many of these mutualisms involve sets of animal species interacting with plant species.

Only five major groups of multispecific mutualisms exist in natural terrestrial ecosystems: (1) pollination and (2) seed-dispersal mutualisms among animals and plants (Jordano, 1987); (3) protective mutualisms among ants (and sometimes other arthropods) that protect plants and homopterans (Rico-Gray and Oliveira, 2007); (4) harvest mutualisms, including the gut flora and fauna of all vertebrate species and many invertebrates, the root rhizosphere occupants, lichens, decomposers, epiphyllae and some epiphytes, and antplants (ant-feeding plants; L. E. Gilbert and Raven 1975; Janzen 1985; Rico-Gray and Oliveira 2007). A fifth type of mutualism is the interaction between humans and plants (agriculture) and animal husbandry (Boucher, 1985b), mediated by the domestication process. Facilitative interactions among plants can also be considered as a type of mutualism with beneficial consequences for both partners (Verdú and Valiente-Banuet, 2008), although in many cases the positive effects occur only during specific stages (e.g., facilitation of seedling establishment).

In this book we focus on pollination and seed dispersal with brief excursions into protective and ant-plant mutualisms (Fig. 1.2). The reason for this choice is because this is where the majority of research on mutualistic networks has focused and is where our expertise lies. Still, there is no evidence to suggest that the same rules do not apply to other mutualistic networks.

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FIGURE 1.2. Examples of plant-animal mutualisms illustrating interactions among free-living species. These mutualisms typically involve the harvesting of plant resources by animal species with outcomes of fitness gain directly derived from the interaction. Clockwise from top right: *Tangara cyanocephala* swallowing a *Campomanesia* (Myrtaceae) berry (Ilha do Cardoso, SE Brazil; photo courtesy of André Guaraldo). Agouti, *Dasyprocta aguti*, feeding on fallen fruits of a Sapotaceae tree (Amazonia, N Brazil; camera-trap photo courtesy of Wilson Spironello). *Eristalis tenax* (Syrphidae) visiting an inflorescence of Allium sp. (Sierra de Cazorla, SE Spain; photo by P. Jordano). *Ectatomma tuberculatum* ants tending the extrafloral nectary of an *Inga* tree (Gamboa, Panama; photo: © Alex Wild, used with permission).

Typically, we might expect the net outcomes of mutualistic interactions among individuals or among species to fall somewhere along a gradient between antagonism (e.g., parasitism or cheating) and legitimate mutualism (Thompson, 1982). For instance, Rico-Gray and Oliveira (2007) document that ant-plant interactions most likely originated from antagonistic interactions, but the most frequent form of their ecological relationships is mutualistic. And this range can be observed in the interaction of two partner species (variation among individual effects) or when multiple species are involved (variation among species effects). For example, consider the diverse assemblage of insects visiting the flowers of a plant species. The whole range of interactions

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in a given population of the plant would be the result of the combined interactions of individual plants with individuals of different flower-visiting insects. Some individual plants will be visited by many insect species, whereas others (e.g., plants growing in isolated patches within the population) would be visited by a restricted set of flower-visitors, presumably with lower visitation frequency. If insect species differ in the effectiveness of pollen transfer, we could imagine that some individual plants receive most visits by legitimate pollinators, whereas other might be visited more frequently by noneffective pollinators (e.g., nectar thieves). Individual fitness variation across individual plants would depend on the relative location of each plant along the gradient of effectiveness defined by its flower-visitor assemblage: plants with reduced fruit set most likely had visits by low-efficiency pollinators, and those with higher seed set were most likely visited by legitimate pollinators. The overall interaction pattern for the plant species would be a composite of the visitation pattern to the different individuals in the population.

The dynamics of mutualistic interactions are surprisingly robust to the presence of cheaters or antagonists (Bronstein, Wilson, et al., 2003), yet they determine ample temporal and spatial variation in the outcomes. Multispecific mutualisms involving plant-animal interactions are harvest-based mutualisms, mostly through the feeding of one species on the other (Janzen, 1985; Holland, Ness et al., 2005). Plants offer a resource (nectar, pulp, pollen, volatile fragrances, resin material to build nests, corolla parts, or other ancillary structures) that are collected by animals. The mutualistic service by animals directly derives from their foraging and movement patterns, resulting in dispersal of the plant propagules (seeds or pollen) or protection for the plant against herbivores or pathogens.

Seed-dispersal mutualisms involve benefits in terms of fitness gain for both the mother plant dispersing its progeny and the progeny itself (individual seeds), largely because the fitness of both the mother plant and the propagule would be lower in the absence of the mutualistic interactions (Janzen, 1983; Jordano, 2000). So, most—if not all—multispecific mutualisms among freeliving plants and animals are resource based, and many involve dispersal events of some type of propagule. Therefore, these multispecific mutualisms play a central role in the population dynamics of plants (Fig. 1.3), where regeneration cycles depend on the successful establishment of new propagules and the successful closing of the dispersal loop (Wang and Smith, 2002). Mutualistic interactions are key at the specific stages (flowering, fruiting) where plant propagules need to be dispersed, and any environmentally driven collapse of such interactions will have far-reaching consequences for the plant population, with a negative feedback on the animal mutualists. Frugivorous

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FIGURE 1.3. The main elements of the population cycle of a higher plant (Harper, 1977). I, the seed bank; II, the early recruitment stage (seedlings); III, the growth phase (saplings); IV, production of flowers and fruits; and V, dispersal of the seeds. Mutualistic animals mediate the dispersal of pollen among flowering individuals and the dispersal of seeds. The entire population demography loop critically depends on the successful outcome of these interactions (Wang and Smith, 2002).

animals can remove large fractions of the fruit crop of maternal plants and move seeds to microsites with high probabilities for progeny establishment. Animals that eat fleshy fruits and disperse seeds have thus potential fitness influences on the plants (Jordano, 2000). Higher fruit-removal rates from mother plants result in more progeny successfully dispersed away from the parent and a lower probability for the seeds to die beneath the canopy of the mother plant. But animal-mediated dispersal also entails delayed effects that depend on the quality of the dissemination site for the survival prospects of newly established individuals. So, ultimately, an efficient disperser is a frugivore able to (1) efficiently consume and remove fruits from the canopy of the fruiting plant and (2) disseminate the seeds to suitable microsites for seed germination and seedling establishment (Schupp, Jordano, et al., 2010). These two aspects determine the *quantity* and *quality* components, allowing ample variation across mutualistic species in seed-dispersal effectiveness.

Now, consider the potential fitness effects and benefits of the fruiting plant on the animal (Jordano, 2000). Most animals that depend on fruit food for their living rely on multiple plant species. A given fruit species, even those

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that contribute the basic diet of a frugivore species, frequently represents only a fraction of the whole diet and daily energy income of the frugivore. There are many reasons for this, but two important ones are that (1) the fruit-ripening period of most plant species is limited to certain periods of the year and (2) most fleshy fruits have pulps limited in a specific major nutrient (e.g., lipids, protein, nonstructural carbohydrates, and minerals) or energy content. The main result of these two important limitations is that frugivores relying largely on fruit food need to diversify their diets by interacting with multiple fruit species that, collectively, supply the daily energy and nutrient budget. Thus, there is ample variation across mutualistic plant species in terms of their effectiveness as food sources for animal frugivores. Plant-frugivore mutualisms, therefore, typically show very low specificity of the interactions (Jordano, 1987).

Turning now to the second major type of mutualism, pollination also involves multiple types of outcomes, illustrating ample variation between the antagonism-mutualism extremes as well as in the specificity of the interaction (Feinsinger, 1983; Waser and Ollerton, 2006; Schemske, 1983; Waser, Chittka, et al., 1996). As with multispecific seed-dispersal mutualisms, pollination conveys dispersal of plant propagules (pollen) to distinct target sites (stigmas) of conspecific individuals. This constitutes a type of plant movement mediated by animals. Pollinators thus determine both the male and female fitness functions for the plants and, together with animal frugivores, mediate gene flow patterns in zoophilous plant species. Visitation frequency, pollen removal, and type of pollen deposition (e.g., on stigmas of the same plantgeitonogamous crosses-or on stigmas of a different individual-xenogamous crosses) influence the effectiveness of pollinator species. Therefore, the fitness effects of interactions with specific pollinators also depend on both the *quantity* and *quality* components of their foraging patterns. Ample variation between the extremes of antagonistic flower visitation and legitimate pollen transfer thus exists in multispecific pollination mutualisms.

Despite the fact that seed dispersal and pollination mutualisms share some analogies, they are very different in many aspects (Wheelwright and Orians, 1982; Table 1.1). These differences mainly relate to the foraging patterns and outcomes involved and to the temporal span of the effects derived from the interaction. Although a specific target (conspecific stigmas) is very clear in pollination mutualisms, potentially advantageous targets for dispersed seeds are much less clear and often unpredictable at the time of seed release by maternal plants. For instance, high-quality microsites for survival to postdispersal seed predators and/or germination generally are poor-quality sites for early seedling establishment (Schupp, 1995). Successful pollination often benefits from high specificity of visitation by flower-visiting insects. This assures effective pollen

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	Pollen Dispersal	Seed Dispersal
Target-site suitability	Stigma of conspecific flower.	Microsite adequate for germination and establishment.
Predictability of target quality	Distinctive. Color, shape, odor apparent at a distance.	Unpredictable.
Temporal suitability	Synchronous with pollen dispersal.	Scarcely predictable; often with delayed effects. Good microsites for seeds are poor for seedlings.
Advantage of interaction specificity	High. Most pollen lost if carried over other species' flowers.	Low. Negative effects of proximity to conspecific adults.
Ability of directed dispersal to suitable sites	High. Plant can "control" directionality of movement.	Low. Movement influenced by multiple foraging choices.

TABLE 1.1. Analogies and differences between pollen and seed dispersal. Modified from Wheelwright and Orians, (1982).

carryover to multiple conspecific stigmas during short foraging bouts and avoidance of stigma clogging by allospecific pollen (Table 1.1). Color, odor, and display clues often signal the receptivity of flowers to foraging flower visitors. In contrast, most frugivores visit a number of fruiting plant species while foraging and maintain switching behaviors to consume alternative food items to fruits (e.g., insects, leaves, etc.). Therefore, multiple natural history details underpin the outcomes of pollination and seed-dispersal mutualisms, ultimately favoring some degree of generalization by a widespread occurrence of variable outcomes of pairwise interactions. Rather than reductionistic approaches that underscore the exceptions, understanding how these fascinating natural history details influence evolution and coevolution requires tools that incorporate these complexities to identify shared patterns.

This tension between reductionistic and synthetic approaches has been a dominant theme in research on plant-animal interactions since the early 1970s, when interest in coevolution of mutualisms reflourished in ecological research (Waser, 2006). Ollerton (1996) describes it as a paradox. On one hand, broad groups of floral and fruit traits seem unequivocally related to visitation patterns by specific subsets of animal mutualists—that is, the interaction syndromes described by Stebbins (1970). Yet looking to the details of interactions, many plant species share a wide array of animal mutualists as pollinators and

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seed dispersers, conjuring up visions of intense reciprocal effects (Schemske, 1983). Understanding complex networks of interaction will be helpful to assess patterns of evolution in generalization–specialization in mutualisms, a subject ultimately related to the issue of niche variation and community assembly processes.

COEVOLUTION IN MULTISPECIFIC MUTUALISMS

Coevolution is evolution of interacting species; therefore, the outcomes of multispecific interactions underpin the evolutionary process of the partner species involved. The coevolutionary process thus involves the joint evolutionary trajectories of two separate gene pools that do not mix (Thompson, 1982, 1994). Coevolution is then one of the many outcomes of plant-animal mutualisms. Strict-sense coevolution (Janzen, 1980) involves specific and reciprocal effects directly derived from the mutualistic interaction. As a consequence, it is difficult to anticipate how coevolution can produce complex webs of interaction involving hundreds of species (Thompson, 2006). Most multispecific interactions in nature are highly diversified, with species that range widely in the net effect of the interaction, from legitimate mutualists to mutualism parasites. This has caused some confusion in the use of the term coevolution, broadly applied to any interaction among species irrespective of the geographic scale, potential outcome, sign and magnitude of the reciprocal effects, and specificity. The catchall term diffuse coevolution has thus been applied to the many circumstances where the complexities of the natural history of mutualisms are well beyond simple pairwise interactions (Herrera, 1982; Fox, 1981, 1988; Strauss, Sahli, et al., 2005). The recent conceptual development of coevolutionary studies has thus been limited by a lack of appropriate frameworks that provide testable hypotheses about how diversified coevolution operates in natural systems.

A recent insight to understand the coevolutionary process has been framed by John N. Thompson around the concept of geographic mosaics of coevolution (Thompson, 1994, 1999b, 2005; Gomulkiewicz, Drown, et al., 2007). This has represented a major advance in our understanding of how coevolution proceeds in complex natural settings, such as the spatially— and temporally variable mutualistic interactions among species. Most mutualisms show marked temporal and spatial changes in their main components: species involved, strength of the interaction, and outcomes of the interaction (Bronstein, 1994; Chamberlain and Holland, 2009). The challenge is to provide robust generalities underlying what may seem a markedly context-dependent process.

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A mosaic pattern of coevolving interactions accommodates the characteristic context dependency that multispecific mutualisms show, based on three premises: (1) interactions occur among species that are themselves distributed in populations; (2) the outcomes of interactions vary across populations; and (3) interacting species do not necessarily have matching geographic ranges. In multispecific mutualisms, a given species typically shows local (amongpopulation) variation in the pollinator or seed-disperser assemblage, and the composition of local plant-animal communities interacting can also vary. Therefore, we might expect (1) a selection mosaic across populations, with variation in selection regimes and outcomes leading to different evolutionary trajectories; (2) actual coevolution occurring in a subset of the populations (coevolutionary hotspots), with no change in others; and (3) remixing of traits resulting from gene flow, genetic drift, and local extinction of populations (Thompson, 2005). Multispecific interactions will be structured in local communities also subjected to this mosaic of interaction outcomes. Few traits will be locally favored given the marked local context dependency of the interaction patterns and the low specificity of the interactions (Thompson, 1994). Local variation in the degree of trait matching among interacting species is expected, as well as local variation in the degree of convergence among species in each of the partner groups (animals and/or plants) (Thompson, 2006).

The next frontier is to extend these multispecific systems to embrace whole networks, to address how these large assemblages of species are organized by ecological and evolutionary processes, and to infer the consequences of network architecture for the persistence of biodiversity. This book is about this frontier. Our ultimate goal is to understand how diversified mutualisms among animals and plants evolve and coevolve into megadiverse assemblages of species. To this aim, we will be looking at multispecific mutualisms as networks of mutual dependences among species. First, though, we need some tools and concepts derived from the study of other types of networks.

Our understanding of community-rich mutualistic interactions has indeed been constrained by the lack of an appropriate conceptual framework. This is a situation that echoes similar limitations in other fields addressing complex systems formed by a large number of different elements interacting among themselves. Traditionally, the reductionistic approach has followed the path of breaking up these complex networks in basic units and studying them in isolation. Given the complexity of these networks, without the appropriate conceptual framework, we could not have advanced our understanding of mutualisms at the community level.

The theory of complex networks, indeed, provides the right framework for addressing entire communities. First, network theory provides a way

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to describe such communities. Second, it brings a set of tools that allows measuring the architecture of these networks. Third, there are dynamical models that exemplify the processes that may be at work in building up these networks. Finally, this framework allows comparing the properties of these ecological networks with those of other networks such as the Internet or protein-regulation networks. Network theory provides a conceptual framework for learning how to tackle mutualisms as integral elements rather than just focusing on their basic components.

As with any such conceptual framework, we have to face some trade-offs between realism and complexity. Thus, we have to leave aside (momentarily; see following chapters) differences across species that are now represented as similar nodes. The hope is that this sacrifice of detail will be compensated by our ability to extract meaningful patterns in what was once thought to be a diffuse and intractable set of dependencies.

We are convinced that the enormous challenge to understand how extremely diversified mutualisms evolve and coevolve in systems such as tropical rainforests requires an integrative approach. This should combine a solid knowledge of the natural history of plant-animal interactions with robust quantitative tools aimed at visualizing, exploring, and analyzing their complexity.

SUMMARY

Plant-animal mutualistic interactions are the wireframe that supports many terrestrial ecosystems. The importance of these interactions and the mutual benefits conveyed to the partner species were recognized since the early times of ecological studies. Yet, the interest in mutualistic interactions and their patterns of evolution and coevolution has been marginal during most of the recent history of ecology, with its central emphasis on antagonistic interactions. A persistent challenge has been to understand how multispecies interactions evolve and coevolve among free-living species. This understanding has been limited by the absence of methodological tools enabling the integrated analysis of the intrinsic complexity of details that make mutualisms so fascinating. Reductionistic approaches have underscored limiting cases such as highly specialized one-on-one interactions, failing to identify the general, shared patterns in multispecies assemblages. This book aims to describe these mutualistic patterns, which can be regarded as the architecture of biodiversity.

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