

Preface

Observing plant-animal interactions in nature has remained one of the most fascinating aspects of our scientific activity. We recall the unforgettable experience of witnessing frugivorous birds feeding on fruits or hummingbirds pollinating flowers. These are mutually beneficial interactions: animals move the genes of the plants across the landscape, and obtain a food reward for this service. Mutualisms in nature are widespread and have played a major role in the diversification of life on Earth. A persistent challenge is to understand how these mutualistic interactions evolve and coevolve in species-rich communities.

Mutualisms form complex networks of interdependence between dozens or even hundreds of species. Understanding the architecture of these networks is very important for understanding coevolution and network robustness to global change. This monograph reviews research on plant-animal mutualistic networks that brings a community-wide approach to coevolution. It puts the emphasis on the component of biodiversity explained by species interactions, and how these interactions are dismantled through human-induced perturbations. The extinction of interactions leads to the empty forest: species are still there but the whole system loses its functionality. In Daniel Janzen's words, "... the most insidious type of extinction is the extinction of interactions" (Janzen, 1974). Deforestation and defaunation are the main drivers of interaction loss and their effects pervade multiple ecosystem services.

In our tour across the structure and dynamics of mutualistic networks we will be combining a deep enthusiasm for natural history with modern analytic techniques such as network theory and phylogenetically-informed analyses. We begin this book with two introductions, one focussing on the natural history background, the other on the network tools we will be using. Paralleling the development of this young research field, we will follow by describing the architecture of these networks, a task that depends on the analysis of large data sets with appropriate statistical tools. One such a tool is a null model, and we describe the technical aspects in appropriate appendices. This organization of the book aims at allowing interested readers

to explore these details without precluding the reading of the book by a wider audience.

Next, we will review the suite of ecological and evolutionary mechanisms generating mutualistic networks. To achieve this, we will be combining simple build-up models of network formation with phylogenetic analysis and ecological correlates of network structure.

As in food webs and other interaction networks, mutualistic networks represent aggregates through time and space. Space and time are the next frontiers in network research, but fortunately there are a few papers that we will review, showing us the path to follow.

We will proceed by exploring the consequences that the above network patterns have for coevolution and community stability by using mathematical models and computer simulations. Up to a few years ago, there was no theory for mutualistic networks as there was theory for competition or predation. We will summarize the first steps towards such a general theory for mutualistic networks. Finally, we will end up by looking at work that has taken networks a step further, moving this basic research field into a more applied science in the context of some of the most pressing questions such as biological invasions or habitat transformation.

This book is the consequence of more than ten years of close collaboration between the two authors. The move of one of us (JB) to the Estación Biológica de Doñana (Sevilla) in 2000 created a wonderful opportunity to tackle the coevolution of mutually beneficial interactions in species-rich communities. The timing was very good. On one hand, there were large data sets available. On the other hand, network theory was making a splash in the late nineties, providing new tools to shed light to these complex networks of mutual dependence among species.

Our early work immediately benefited from the continuous source of support, inspiration, and keen naturalistic insight of our good friend and co-author Jens M. Olesen. This initial triad is only the core of a larger scientific network where many have played influential roles. Among them, we have been very fortunate to join forces with Thomas Lewinsohn, who independently had reached similar views to the ones we were reaching. Thomas is a renascent man and we have enjoyed his wise comments and ideas. Similarly, a most influential contribution has been provided by the generous insight from John N. Thompson. Few like John have seen the potential of the concept of networks as a way of "dispelling the naive view that mutualisms between free-living species are diffuse assemblages that are intractable for coevolutionary analysis" (quoted from an enthusiastic e-mail written after reading our 2003 PNAS paper).

In turn, our current and former graduate students and postdocs Carlos Melián, Miguel A. Fortuna, Paulo R. Guimarães Jr., Enrico Rezende, Jofre Carnicer, Cristina García, Alfredo Valido, Daniel Stouffer, Luisjo Gilarranz, Franck Jabot, Jelle Lever, Rudolf Rohr, Serguei Saavedra, and Vasilis Dakos have been pivotal in the generation of some of the work on mutualistic networks here discussed. Other members of the Integrative Ecology Group have also contributed very useful suggestions, ideas, and discussions: Pete Buston, Arndt Hampe, Jessica Lavabre, Kimberly Holbrook, Rocío Rodríguez, Cande Rodríguez, and Abhay Krishna. Over the years, the technical support of Manolo Carrión, JuanMi Arroyo, Cristina Rigueiro, María Cabot, and, especially, Javier Escudero and Raúl Ortega have made things much easier for us in the lab.

Outside our lab, we should highlight Bartolo Luque, Ugo Bastolla, Antonio Ferrera, and Alberto Pascual-García for their development of analytical techniques that have advanced the theory for mutualistic networks. Jason Tylianakis, in turn, has championed the use of networks in the conservation arena. Other co-authors in our work on mutualistic networks deserve a special mention since this is their work as well. The list of co-authors expands to include truly outstanding scientists such as Stuart Pimm, Diego Vázquez, Marcus A. de Aguiar, Sergio F. dos Reis, Mauro Galetti, José M. Gómez, Miguel Verdú, Paulo I. Prado, Anders Nielsen, and Victor Rico-Gray. We are also in debt to Roger Guimerà, Marten Scheffer, George Sugihara, Robert May, Robert Paine, Joel Cohen, Eugene Schupp, Louis-Félix Bersier, Scott Armbruster, and Wesley Silva. It has been very rewarding learning from them all.

Over the years, we have enjoyed discussions with students in our courses at the Universities Pablo de Olavide (Sevilla), Alcalá (Madrid), Internacional Menéndez Pelayo, and UNESP, UNICAMP, and USP (all in Brazil). The suggestions, insight, and support obtained in these courses have been instrumental during the writing of this book.

We extend our appreciation to the excellent administrative support provided by the staff at the Estación Biológica de Doñana. Facilities for field work have been generously provided over the years by the Consejería de Medio Ambiente, Junta de Andalucía. The Centro de Supercomputación de Galicia (CESGA) generously allowed us to use their computing resources for some critical simulation work.

We have benefited from the generous help and advice of the technical staff at PUP, especially Sam Elworthy, Alison Kalett, and Dimitri Karetnikov. We are also very thankful to Simon Levin and Henry Horn, for inviting us to write this monograph and their constant encouragement.

Paulo R. Guimarães Jr, Jens Olesen, Rudolf Rohr, Jason Tylianakis, John Thompson, Alfredo Valido, and an anonymous reviewer have read a previous version of this book and provided wonderful suggestions to improve clarity and content.

Financial support has been generously provided by the European Science Foundation through a EURYI (European Young Investigator) Award and a European Research Council's Advanced Grant to JB, and several grants from the Spanish Ministry of Science, the Regional Government of Andalucía, and the Programa Iberoamericano de Ciencia y Tecnología para el Desarrollo (CYTED) to both JB and PJ.