Preface

Communication is ubiquitous, and a key feature of life on every organizational level, from intracellular signalling to communication between individuals of the same and of different species. It has most likely evolved independently many, many times between vastly different partners. Although communication is central for the organization of life, communication theory is a concept that has been predominately developed in fields other than biology: namely economics, mathematics, and social sciences. Within biology, evolutionary biology has been the discipline that has contributed most to the conceptual growth of communication theory.

Given that communication often represents the first interaction among organisms, it can structure these interactions and thereby contribute to the organization of biodiversity. It is therefore perhaps surprising that communication theory has been less influential in ecology. In an elegant editorial to a special feature on flower volatiles in *Functional Ecology*, Robert Raguso (2009) laid out why he felt that sensory ecology is now deemed less important in mediating the ecology of pollination than it was one or two decades ago. The main reason for this perspective is that pollinator-driven selection may be overridden by that of herbivores or other selective agents, and that these selective pressures constrain the adaptations of floral phenotypes to communication. Is writing a book on plant–animal communication in 2011 then a day late and a dollar short?

We feel that communication between plants and animals is currently a particularly exciting topic. Plant–animal communication is fascinating because it provides a particularly compelling example of the hidden complexity of seemingly simple questions. If we ask how and why communication evolves, the answers are often far from obvious because evolution works economically on a limited number of traits. The same traits may be adapted for multiple purposes, both within a species and between species. The traits that plants use to communicate with animals provide wonderful examples for the economic nature of evolution. Anthocyanins, for example, are versatile pigments that serve various functions in plants. In fruits and flowers the adaptive significance of anthocyanins is traditionally attributed to the attraction of pollinators and seed dispersers, but these pigments are also involved in defence against abiotic factors and pathogens (Strauss and Whitall 2006, Schaefer et al. 2008a). In vegetative parts, the adaptive significance of anthocyanins is generally attributed to their function as antioxidants directly reducing oxidative stress (Gould et al. 2002); as sunscreens protecting photolabile defensive compounds (Page et a. 1999) and the photosynthetic apparatus against excess light, and thereby reducing the risk of free radical production under unfavourable conditions (Gould and Lee 2002, Gould 2004); to increase cold hardiness (Chalker-Scott 1999); and as defence against herbivorous insects (Archetti 2000, Hamilton and Brown 2001, Hagen et al. 2003). Anthocyanins can thus be involved in the amelioration of plants' responses to various environmental stressors, as well as with the attraction of animal mutualists and the defence against various plant antagonists both in vegetative and reproductive organs.

Coming back to our question on how communication evolves, it is not a trivial task to trace the evolution and original function of anthocyanins. From a purely adaptionist perspective, we might assume that anthocyanins evolved for fulfilling the functions that they currently perform in each organ.

This is unlikely, however, as this view neglects developmental, morphological, physiological, and genetic constraints. Gould and Lewontin (1979) summed up this view as the adaptationist programme or the Panglossian paradigm – where natural selection is assumed to be near omnipotent in fashioning the best of all possible worlds. Moreover, assuming that traits such as anthocyanins evolved to fulfil their current function requires multiple independent origins of these pigments even within the same organs where they fulfil various purposes at the same time. Despite a natural human tendency to want to believe in simple and often beautifully elegant answers for the evolution of complex traits, we are faced with a more difficult but also a more rewarding task: disentangling cause and effect throughout the evolution of these and many other plant traits. Thus, if we ask whether anthocyanins in fruits primarily fulfil a signalling role (i.e., they evolved for attracting mutualists) or whether anthocyanins in leaves evolved as *signals* to deter antagonists, we have to evaluate the fitness effects of one function (say, signalling to animals) relative to the fitness effects of other functions (*photoprotection*, anti-oxidation). Though challenging, this pluralistic approach, encompassing different fields in biology, is more rewarding and gives a more realistic view on the evolution of complex traits than a purely adaptionist perspective.

To exemplify this situation, suppose that anthocyanins evolved first to ameliorate plants' stress responses to abiotic factors and are later used to communicate to animals. In this case anthocyanins are an *exaptation* that evolved for one reason and that has been co-opted throughout evolutionary history to serve a different function, signalling. Similarly, anthocyanins might predominantly function in stress response against an abiotic factor while, at the same time, communicating to animals. In this case, anthocyanins might best be described as a *cue*, not a signal. As we discuss in Chapter 1, the term 'signalling' can usefully be reserved for situations where a trait predominantly functions to communicate to animals.

However, the example of anthocyanins highlights that – in order to understand how plants communicate to animals – we need to evaluate the significance of communication *relative* to the significance of other, non-communicative functions. Only such an integrative approach will allow us to examine questions as to whether (and which) plant traits communicate to animals and benefit both parties (and are thus signals) or whether animals often attend to cues provided by plants. Focussing on the distinction between signalling and cues is a rewarding research avenue for students of communication. However, we feel that the study of plant–animal communication is even more broadly interesting, because it elucidates a central problem: the evolution of complex traits by multiple, often varying or even opposing, selective pressures.

We therefore view the question of how communication arises in the context of multiple selective pressures as an intellectually stimulating question that has not lost its appeal by the insight that non-sensory interactions are important and can often be predominant. On the contrary, as we will lay out in the book, information sometimes arises in plant–animal interactions without being selected for. It is quite likely that 'unintentional' information is more reliable than 'intentional' signalling; a situation that seems counterintuitive at first. We therefore advocate a broad approach to the study of communication.

Based on the above, we conclude that the study of plant communication is not only an ecological and evolutionary endeavour, but one that also involves plant physiology, development, and biochemistry as well as biophysics and considerable knowledge of animal behaviour, their sensory physiology and *perception*. The integrative nature of plant communication originates from two facts. First, the study of communication is always truly integrative, primarily because communication is *per se* a topic concerned with the actions of different partners. Second, the integrative nature of communication is even more apparent when studying how disparate partners, such as plants and animals, interact with distinct physiological processes and pathways involved in the communication system from stimuli production to stimuli perception. The study of communication and signalling has been fraught with problems involving the definition of terms. You might reasonably be concerned that we might not define 'communication' or 'signal' in the same way that you would, or in the way that other texts use these terms. Hence we will begin Chapter 1 by explaining how we define these terms, and thus how they will be used throughout the book.

We should be clear from the start about what this book covers, and what it does not. We adopt a very wide definition of communication, but we are interested in communication (involving stimulation of the sensory systems of animals) rather than the broader subject of 'interactions' between plants and animals. For example, we are interested in questions of how squirrels detect nuts in their local environment, and how they can use their senses to gain information on the relative qualities of different nuts as food. We will not cover how squirrels digest nuts, or how the availability of nuts structures squirrel populations. We are interested in the evolutionary ecology of how traits of plants differentially stimulate animal sensory systems. We touch only very briefly on plant responses to neighbouring plants, which may sometimes usefully be described as plant–plant communication. We similarly do not consider in full the many plastic responses that plants can show to damage by herbivores, some of which could be described as involving within-plant communication. However, we do consider a broad range of ecological processes that involve flexible animal behaviour in response to excitation of their senses by plant traits. These include pollination and seed dispersal by animals, trophic exploitation of plants by animals, and (less usually) trophic exploitation of animals by plants. Of these processes, the most intensely studied has been pollination. Because there have been several excellent, recent books on pollination we have sought to avoid simple repetition of these works. Thus, we do not attempt a comprehensive review of the evolutionary ecology of pollination, but rather take a more comparative approach and look for general points of similarity and difference between how communication influences pollination and how it influences the other plant–animal interactions that we consider here, particularly seed dispersal. Another area where we admit to failing to provide detailed treatment is in below-ground influences of plants on subterranean animals and mycorrhiza. We likewise do not cover how plants interact with viruses and bacteria even though these may sometimes influence traits that interact with the senses of animals. The reason here is the opposite of the situation regarding pollination, below-ground plant–animal communication is very poorly known.

Although we are primarily interested in the evolutionary ecology of plant–animal communication, we must sometimes briefly consider selection pressures on plant traits that may restrict or dominate selection pressures related to communication to animals. This will involve brief consideration of plant biochemistry and physiology, but these fields are very much not the focus of this book.

The diversity of fields involved in communication does not require complete mastery in each. Instead, depending on which step in communication is under study, different aspects might become more important than others. To facilitate an encompassing view on plant–animal communication, we first use communication theory to explore whether (and, if so, how) communication structures the interactions between plants and animals. To attain an evolutionary perspective, we will elucidate how interactions among multiple species affect evolutionary dynamics in plant–animal interactions in general, and those of plant–animal communication in particular, in Chapter 1. We then present basic information on plant biochemistry and the sensory world of animals that commonly interact with plants in Chapter 2. In subsequent chapters, we will be mainly concerned with two types of questions. The proximate question: *how does communication between plants and animals work?* and the ultimate question: *did the sensory interactions between plants and animals shape plant traits?* In other words, we ask whether communication between plants and animals is primarily adaptive or whether it is a by-product of other selective pressures. We address both questions by discussing how plants and animals interact in various communication systems: ranging from plants eating animals (carnivory, Chapter 10), to the more common phenomenon of animals eating plants (herbivory, Chapter 9), to animals eating plant rewards (pollination and seed dispersal, in exchange for dispersing their genes (Chapters 3–6)). Chapter 7 discusses the various selective pressures shaping non-green-leaf colouration (including communication), whereas Chapter 8 considers camouflage, *aposematism,* and *mimicry* in the plant kingdom.

As mentioned above, pollination is only the focus of a single chapter because it has already been effectively reviewed from several perspectives in recent years (e.g., Chittka and Thompson 2001, Harder and Barrett 2006, Raguso 2008, Rausher 2008). The reason for our disproportionate focus on communication in herbivory, seed dispersal, and carnivory is that we view our book not as providing definitive and all-encompassing answers to the proximate and ultimate questions we pose. Instead the chapters aim to delineate the unknown and propose research activities that might help reduce the gaps in current knowledge. Also, we agree with Raguso (2009) that our understanding of pollination biology will be enhanced by increased emphasis on other plant–animal interactions. A key theme that emerges in this book is the shaping of plant traits by simultaneous selection pressures from both mutualists and antagonists. In order to develop our arguments, we must be very clear about what we mean by particular key concepts and terms that we use when laying out our arguments. Defining these key concepts is the first task of our introductory chapter.