
10 The Conservation of Ecological Interactions

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1 Introduction

The need to give the conservation of ecological processes an equal weighting to the conservation of patterns is repeatedly stressed but rarely implemented. Instead, conservation research tends to focus on the species as the unit of study, looking at the impact of habitat destruction on individual species, or assemblages of species from particular habitats. There is, however, increasing recognition that species and species lists are not the best units for study by conservation biologists, and that species interactions may be much more important. Although this issue was raised more than 30 years ago by Daniel Janzen (1974) stating that ‘what escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions’, it is only recently that we have developed the empirical and analytical tools needed to study interactions at the appropriate scale: that of the whole community. All organisms are linked to at least one other species in a variety of critical ways, for example, as predators or prey, or as pollinators or seed dispersers with the result that each species is embedded in a complex network of interactions. Consequently, the extinction of one species can lead to a cascade of secondary extinctions in ecological networks in ways that we are only just beginning to understand (Sole and Montoya, 2001; Dunne *et al.*, 2002; Ives and Cardinale, 2004; Memmott *et al.*, 2004). Moreover, interactions between species can lead to ‘community closure’ after the loss of a species, with the result that a locally extinct species cannot re-establish itself if it is reintroduced (Lundberg *et al.*, 2000).

Ecosystem services are those ecological processes of use to mankind, with insects being key components of ecosystem services such as pollination, seed dispersal and pest control. The utilization and exploitation of ecosystem services by mankind is likely to be detrimentally affected by the loss of ecological interactions. This will impact, for example, upon biological control

using indigenous natural enemies and upon crop yields via altered pollination rates. However, mammals and birds collectively still receive the majority of attention in terms of conservation efforts and remain flagship species for numerous conservation and agro-environmental programmes. While perhaps more charismatic than the average earwig, vertebrates contribute to far fewer ecosystem services than insects; indeed, Wilson (1987) succinctly described insects as 'the little things that run the world'.

The aim of this chapter is to review insect interactions and consider both their need for conservation and conservation's need for them. We begin by briefly reviewing three key categories of insect interactions and by describing a relatively new method of analysing the interactions between species. We then consider desirable interactions, i.e. those which can be exploited by man, undesirable interactions, such as those with alien species, and consider how best to restore lost interactions. As a measure of how seriously insect interactions are taken in conservation, we ask how many studies of rare plants consider the conservation of their insect pollinators. We end by outlining four areas we consider to merit particular attention for future work on ecological interactions.

2 Types of Ecological Interactions Involving Insects

Although food webs are the most commonly described ecological network, other types of interaction webs are investigated that include a variety of trophic and non-trophic interactions, such as pollination, seed dispersal, interference competition, habitat or shelter provisioning, recruitment facilitation or inhibition (Memmott *et al.*, 2006). For the purposes of this chapter we restrict ourselves to trophic and reproductive mutualisms, mentioning decomposition briefly to bemoan its status as the ugly sister of interaction networks, especially with respect to insects. We limit ourselves to trophic networks and reproductive mutualisms for ecological and methodological reasons. Ecologically, food webs are a fundamental component of any attempt to describe how complexes of species interact, and because reproductive mutualisms are essential for the survival of most plant species. Methodologically, these interactions have made the transition from the study of pairwise interactions to the study of networks of interactions.

2.1 Trophic interactions

Insects form an important component of many food webs, with food chains comprising green plants, insect herbivores and parasitoids including over half of all known species of metazoa (Strong *et al.*, 1984). Memmott and Godfray (1993) list eight insect food webs and since then there has been a veritable, albeit small, industry in producing these networks with the result that many of the problems with earlier food web studies (Cohen *et al.*, 1993) have been addressed. These new networks all focus on insect herbivores, their food

plants and their natural enemies and they encompass a variety of habitats, from tropical rainforest to English meadow to Hawaiian swamp (Table 10.1). These webs have documented patterns and generated hypotheses concerning the underlying processes that structure communities, and in some cases, have led to tests of these hypotheses using manipulative field experiments. For example, Memmott *et al.* (1994) constructed a plant–leafminer–parasitoid

Table 10.1. Quantitative trophic networks, describing plant–herbivore–parasitoid communities.

Reference	Habitat	Location	Aims	Host herbivore
Clarke (2000)	Ancient woodlands	England	1. Effect of habitat fragmentation on food web structure 2. Effect of fragment size	Leaf-mining insects
Henneman and Memmott (2001)	Swamp forest	Hawaii	1. Community-wide effects of introduced bicontrol agents	Lepidoptera
Lewis <i>et al.</i> (2002)	Moist tropical forest	Belize	1. Diversity of interactions 2. Compartmentalization 3. Seasonal variation 4. Indirect interactions (apparent competition)	Leaf-mining insects
Memmott <i>et al.</i> (1994)	Tropical dry forest	Costa Rica	1. Identify factors influencing diversity 2. Identify factors influencing diet breadth at two trophic levels 3. Identify species with a strong function in the community	Leaf-mining insects
Muller <i>et al.</i> (1999)	Meadow	England	1. Identify changes in food web over time 2. Apparent competition 3. Compartmentalization	Aphids
Schönrogge and Crawley (2000)	Oak stands	England	1. Impact of invasion on structure and function of native communities 2. Apparent competition	Cynipid gall wasps
Rott and Godfray (2000)	Woodland	England	1. Variations between generations 2. Recruitment webs 3. Importance of host plant 4. Apparent competition	Phyllonorycter leaf miners
Valladares <i>et al.</i> (2001)	Native vegetation and zoological park	Argentina	1. Analyse the structure 2. Compartmentalization 3. Indirect interactions (apparent competition)	Dipteran leaf miners

web that described the trophic interactions in a Costa Rican tropical dry forest. On the basis of this web, a field experiment was used to investigate interactions between two groups of natural enemies (Memmott *et al.*, 1993). Similarly, Lewis *et al.* (2002) used a food web to characterize the structure of a leaf miner–parasitoid community in Belize and a field experiment was then used to test for the presence of indirect interactions (Morris *et al.*, 2004). New analytical techniques for dealing with the impact of extinction on networks (Sole and Montoya, 2001; Dunne *et al.*, 2002; Ives and Cardinale, 2004; Memmott *et al.*, 2004) bode well for giving food webs a predictive role in conservation biology, and these will be discussed in Section 3.

2.2 Pollination

Most higher plant species – up to 90% by some estimates (Nabhan and Buchmann, 1997) – rely on animals to pollinate their flowers. Although vertebrates such as birds, bats and marsupials can all act as pollinators, ‘insects are undoubtedly the most important animal pollinators’ (Proctor *et al.*, 1996). Insects visit flowers to obtain food, usually in the form of pollen or nectar. This is one side of a mutually beneficial relationship; the plants, in return, obtain the services of the pollinators in carrying pollen from one flower to another (Proctor *et al.*, 1996). Although plant–pollinator interactions have a long history of research, a community level network approach has only recently become popular. The study of pollination networks was, if not born, at least baptized by a seminal paper in 1996 by Nick Waser and colleagues and the first quantitative visitation web followed soon after (Memmott, 1999). Waser *et al.* (1996) assessed the evidence for generalization within plant–pollinator communities. Using a broad review drawing on studies of two American floras, and several surveys of pollinators of particular plants (e.g. of buttercups and orchids) and the plants used by particular pollinators (e.g. solitary bees), they deduced that moderate to substantial generalization is widespread. At the time of publication of this chapter, the paper by Waser *et al.* (1996) had been cited 296 times reflecting the huge surge of interest in this field. Since the publication of that paper, there has been a change in data quality, similar to that seen with trophic webs, as connectance webs have been replaced by webs that incorporate quantitative as well as qualitative information (Table 10.2).

2.3 Seed dispersal

Seed dispersal is the removal of seeds from a plant to another location, and plays a key role in regenerating natural communities (Christian, 2001). Ants are most commonly involved in seed dispersal, especially in drier habitats such as deserts, grassland and fynbos vegetation (Hölldobler and Wilson, 1990). They are especially attracted to seeds that offer food bodies known as elaiosomes, which are rich in amino acids, fatty acids and sugars (Hölldobler

Table 10.2. Quantitative pollination networks describing the frequency of interactions between plants and pollinators.

Reference	Habitat	Location	Aims
Dicks <i>et al.</i> (2002)	Meadow	England	1. Are plant–pollinator networks compartmentalized?
Forup and Memmott (2005)	Meadow	England	1. Does habitat restoration restore ecological interactions? 2. Pollen transport webs
Gibson <i>et al.</i> (2006)	Arable fields	England	1. What are the pollinator requirements of rare plants? 2. How to identify pollinators in visitation networks 3. Spatial and temporal variation in network structure
Memmott (1999)	Meadow	England	1. The structure of a plant–pollinator network
Olesen <i>et al.</i> (2002)	Oceanic islands	Azores and Mauritius	1. Testing for presence of invader complexes
Vazquez and Simberloff (2002)	Temperate forest	Argentina	1. Niche breadth in a disturbed habitat 2. Asymmetry in interactions

and Wilson, 1990). To date, published seed dispersal networks are dominated by bird dispersal (see references cited in Bascompte *et al.* 2003); indeed, we are not aware of a single published seed dispersal network dominated by ants, despite the popularity of research on granivorous ants.

3 Using Networks to Study the Conservation of Ecological Interactions

Using food webs such as those listed in Tables 10.1 and 10.2 as predictive tools in conservation biology has until recently been an unattainable goal. At first sight, webs appear labour-intensive to make, statistically intractable to analyse and of limited use to conservation ecologists. If, however, ecological webs are considered as networks, a suite of new analytical tools becomes available. A network is simply a set of nodes with connections between them, such as food webs, neural networks, social networks, the World Wide Web and co-authorship networks. Whilst ecologists have not yet used network techniques to study conservation, they have started to study its opposite: extinction. Species extinction is obviously what conservation ecologists are trying to avoid, but an understanding of the community-level impact of extinction is highly desirable. A complex systems approach simply involves asking what happens to the network when nodes (species in this context) are removed. This method allows ecologists to predict what happens to an ecological network when species go extinct. For example, does it have little effect on web structure or does it lead to a cascade of secondary extinctions?

Many complex systems, food webs included, display a surprising degree of tolerance against the loss of nodes. However, this tolerance comes at a high price, as these networks are then highly vulnerable to the removal of a few key nodes that play a vital role in maintaining the network's connectivity (Sole and Montoya, 2001; Dunne *et al.*, 2002). In particular, 'food webs show rivet-like thresholds past which they display extreme sensitivity to the removal of highly connected species' (Dunne *et al.*, 2002). This sensitivity is seen as a collapse of the entire network (i.e. 100% extinction). Thus, removing just a handful of well-connected species could, in theory at least, cause a cascade of secondary extinctions. This cascade cannot be predicted by independent data on the abundance and distribution of individual species. Memmott *et al.* (2004) developed this technique one step further by assigning different trophic groups differing risks of extinction. Combining computer models with a large plant-pollinator data set describing the interactions between 456 plants and 1428 pollinators they explored the vulnerability of plants to extinction of their pollinators. They found that many plants are pollinated by a diversity of insect species, whilst those that are specialized (i.e. visited by few pollinators) tend to use pollinators that are themselves generalists. By incorporating variation in extinction risk (i.e. increasing trophic rank leads to increasing risk of extinction) known from empirical work (e.g. Gilbert *et al.*, 1998), there was a profound effect on the extinction dynamics and the network became far more robust in terms of secondary extinctions. These features confer relative tolerance to extinction for plant species. However, as Memmott *et al.* (2004) point out, tolerance is not immunity and it is essential to conserve pollinators that are generalized, including bumblebees and some other types of bees.

4 Desirable Interactions and Their Utilization

Ecological interactions are effectively the currency of ecosystem services and these services provide gratis products, such as pest control, pollination and decomposition. The collection of data on interactions in applied systems usually involves data on simple food chains (e.g. crop-herbivore-predator and crop-herbivore-parasitoid) in which a pest herbivore is the focus of the study. This approach is used for the practical reason that it is relatively quick to use. However, by ignoring the community in which a pest herbivore operates, ecologists are likely to miss interactions that limit pest abundance or mitigate the impact of beneficial arthropods. Numerous reports list the major pest, predator and parasitoid species collected in different crop types, but only rarely is this information presented in the form of a food web illustrating the interactions between trophic levels (exceptions include Schoenly *et al.*, 1996 in rice and Mayse and Price, 1978 in soybean). Often a link between trophic levels is based only on previous studies in other systems and rarely quantified. This is disappointing given the potential of food webs not only in clarifying the links and importance of interactions between trophic levels, but also for evaluating the effects and sustainability of management strategies (Cohen *et al.*, 1994). It

seems clear that the simple food chain (plant–herbivore–predator) on which most pest control theory is based is unrealistic (Rosenheim *et al.*, 1999). The good news is that food web science has developed to a stage where we are capable of sampling, visualizing and analysing complex interactions, although this technique is only just beginning to be applied to agroecosystems.

It is relatively straightforward, if time-consuming, to determine the parasitoids of a given host species. The host insect is reared in isolation until either an adult host or a parasitoid emerges (Memmott and Godfray, 1994; Memmott, 1999). However, in spite of the relative lack of obstacles (in comparison to predators, see below) only eight quantitative host–parasitoid webs have been published (Table 10.1), and none are from agricultural systems. Most are descriptive in nature (utilizing a single field site), and have general aims (e.g. to identify species with a strong function in the community) or seek to understand theoretical aspects of community ecology (e.g. compartmentalization). The use of trophic webs to investigate applied questions has so far been limited. One example is Henneman and Memmott (2001), who investigated the community-wide effects of introduced biocontrol agents in native Hawaiian habitats, these parasitoids having originally come from agricultural cane fields. They constructed quantitative food webs of interactions among plants, moths and their parasitoids in a native forest in order to examine the community-wide effects of introduced biocontrol agents on Kaua'i Island, Hawaii. About 83% of parasitoids reared from native moths were biological control agents, 14% were accidental immigrants and 3% were native species. On the positive side, all the biological agents reared were released before 1945 and there was no evidence that biocontrol agents released recently were attacking native moths. Their study highlights the importance of considering the potential damage caused by an introduced control agent, in addition to that being caused by the target alien species.

Even without food webs, though, parasitoids and their interactions with their host insects can be used as good indicators of ecological change at a variety of spatial scales (Tschardt and Brandl, 2004). Thies and Tschardt (1999) showed that in structurally complex agricultural landscapes (i.e. high percentage non-crop area), parasitism of the rape pollen beetle (*Meligethes aeneus*) was higher and crop damage lower than in simple landscapes. In a later study in wheat fields, Thies *et al.* (2005) found that complex landscapes were not only associated with increased aphid parasitism, but also higher rates of aphid colonization.

Whilst the action of parasitoids can be easily seen and studied in the field, the activity of predators is considerably harder to quantify. The 'hit-and-run style' of insect predation makes it very easy to miss predator–prey interactions when sampling. It is also uncommon for clear evidence to remain of who ate whom after predation occurs, further compounding the problem (Memmott *et al.*, 2000). However, molecular and immunological methods are increasingly used to detect prey in predator guts. For example, Symondson *et al.* (1996) used molecular probes to detect slugs in the diet of carabids; Harwood *et al.* (2005) used them to detect aphids in spider guts; and Sheppard *et al.* (2004) used them to detect non-target prey in the guts of

predatory biocontrol agents. Techniques that can scan for multiple prey in a host in a single test have recently been developed (Harper *et al.*, 2005) and could revolutionize the way food webs are constructed.

In addition to biological control, insects provide a range of other ecosystem services and useful interactions. For example, without the services of dung beetles and dung flies the world would become a rather unsavoury place. The insects that act as decomposers, along with their predators and parasitoids, form a large component of soil food webs, and these webs drive ecosystem level processes such as energy flow and nutrient cycling (Wardle *et al.*, 1998). Pollination is obviously another key ecosystem service (Kremen *et al.*, 2002) and is discussed in more detail by Kremen and Chaplin-Kramer (Chapter 15, this volume).

5 Undesirable Interactions and Their Control

Not all ecological interactions are desirable. Many authors have stated that the introduction of alien species, and their interactions with native species, are one of the major threats to biodiversity (e.g. Schmitz and Simberloff, 1997; Mack and D'Antonio, 1998; Chittka and Schurkens, 2001). Aliens have been introduced at all trophic levels into both trophic and mutualistic networks. Their interactions with native species can occasionally be positive, for example, in Hawaii the pollinators of a native vine, *Freycinetia arborea*, are all extinct, but it is probably pollinated now by an alien bird, the Japanese white eye (Buchmann and Nabhan, 1996). Rather more frequently though, native-alien interactions are negative, for example, the disruption of native seed dispersal by Argentine ants in the South African fynbos (Christian, 2001). Most often ecologists simply do not know what most alien species are doing at the community level. Although extensive data exist on the distributions of alien species, their impact on native species as competitors, prey species, predators, pollinators and parasites, and even their impact upon ecosystem properties, there are rather little data on how aliens are accommodated into ecological networks. Five exceptions to this rule are Schönrogge and Crawley (2000) working on an alien cynipid wasp in the UK, Henneman and Memmott (2001) working on alien parasitoids in Hawaii, Munro and Henderson (2002) working on alien parasitoids in New Zealand, Memmott and Waser (2002) working on alien pollinators in the USA and Olesen *et al.* (2002) working on alien pollinators on two tropical islands.

Classical biological control involves the deliberate introduction of an alien species. For many years this was viewed as a sustainable, environmentally friendly form of pest control. However, over the last decade the environmental safety of biological control has become rather contentious with particular concerns about the potential interactions between biocontrol agents and 'non-target' species (Louda *et al.*, 1997; Thomas and Willis, 1998; Boettner *et al.*, 2000; Pemberton and Strong, 2000). A parasitoid maintained at high densities on a common pest insect can potentially drive a rare non-target species to extinction. Density dependence, which would ameliorate such an effect

in a simple two-species interaction, is lacking in such cases (Simberloff and Stiling, 1996). There is a firm theoretical basis for this phenomenon, known as apparent competition (Holt, 1977). Non-target interactions can occur either directly, if an agent attacks a non-target host, or indirectly, when the agent affects non-target species via shared natural enemies. Food webs have been suggested as the appropriate model for research on non-target interactions in biological pest control (Strong, 1997; Pemberton and Strong, 2000; Henneman and Memmott, 2001). As described earlier, Henneman and Memmott (2001) successfully used this approach to quantify non-target effects in Hawaii.

The role of plant–pollinator interactions in promoting or constraining invasions is likely to vary considerably among invaded communities (Parker and Haubensak, 2002). Nevertheless, only a small proportion of possible invaders are known to have been restrained by lack of pollinators (Richardson *et al.*, 2000). Alien plants have the potential to influence native plants via shared pollinators. Alien and native plant species interact for pollinators in the same three ways that native plant species interact with other native plants: an alien plant species can compete for pollinators with a native plant species (Chittka and Schurkens, 2001; Ghazoul, 2002), facilitate attraction of pollinators (Moragues and Traveset, 2005) or even have no effect on visitation rates (Aigner, 2004). The extent to which the alien interaction affects the population of the native plant species will depend on whether seed set is pollen-limited and whether population size is limited by seed recruitment (Palmer *et al.*, 1997). Therefore, changes in pollination quantity (i.e. visitation rates), and even in pollination quality (i.e. reduction of conspecific pollen on stigmas or deposition of exotic pollen), will not necessarily affect seed set. In Thailand, Ghazoul (2002) reported that only one group of visitors, the butterflies, switched their diet from native *Dipterocarpus obtusifolius* to the alien *Chromolaena odorata*. This reduced visitation rates to *Dipterocarpus* along with the number of flowers receiving conspecific pollen. Moreover, it increased heterospecific pollen on stigmas. However, none of these factors influenced *Dipterocarpus* seed set. In comparison, Chittka and Schurkens (2001) found that the introduced *Impatiens grandulifera* (Himalayan Balsam) reduced visitation rates and seed set of the native *Stachys palustris* (Marsh Woundwort), this effect being mediated by shared bees. In summary, the effect of alien species on other plant species is species-specific and variable, depending on many ecological variables (Moragues and Traveset, 2005).

Several bee species (*Apis mellifera*, *Bombus* spp., *Megachile* spp. and *Osmia* spp.) have been deliberately introduced around the world, particularly for crop pollination, and in the case of the honeybee, also for its honey. *A. mellifera* and *Bombus terrestris* stand out for being widespread and very abundant. In general, these species tend to have a much wider diet than native bees, forage earlier and later in the day than native bees, outnumber any native species and use a large amount of the floral resources available (Goulson, 2003 and references therein; Potts *et al.*, 2001). Although there is no direct evidence at the population level, there are many indications that these bees compete with native species. For example, declines in native bee abundance are reported where exotic bees are present or most abundant (Aizen and Feinsinger, 1994; Dafni and Shmida, 1996; Kato *et al.*, 1999).

Although usually considered detrimental to local species, alien insect pollinators may successfully pollinate native plant species (e.g. Percival, 1974; Butz Huryn, 1997; Freitas and Paxton, 1998). However, there are also reports of reduction of pollination of native flora (e.g. Aizen and Feinsinger, 1994; Roubik, 1996). Nectar robbing by alien pollinators, e.g. *Bombus* spp., can potentially reduce visitation rates (McDade and Kinsman, 1980) and seed set (e.g. Irwin and Brody, 1999) of native plants. Moreover, *Apis* and *Bombus*, although having large flight ranges when compared with other visitor species, engage in few long flights while they are foraging, altering patterns of cross-pollination, which consequently may change the genetic structure of plant populations (Goulson, 2003 and references therein).

Field evidence for the community-level impacts of alien seed dispersers was anecdotal until recently. Christian (2001) reported that the invasion of South African shrublands by the Argentine ant, *Linepithema humile*, led to changes in plant community composition and the near extinction of two native ant species. The changes in plant community composition were due to a disproportionate reduction in large-seeded plant dispersal, as these rely on fewer more specialized dispersers for which services are not replaced. Whether parasitoids, pollinators or seed dispersers, all these community studies exemplify Simberloff's (2004) statement that 'most key issues in invasion biology ... fall squarely at the community level', and that to answer how an invader affects a community 'often entails ingenious, detailed research on complicated systems because many impacts...are subtle even if devastating'.

6 The Restoration of Ecological Interactions

Restoration ecology can be viewed as the study of how to repair anthropogenic damage to the integrity of ecological systems (Cairns and Heckman, 1996) and one of the greatest challenges facing mankind will be maintaining ecological systems in working order as the human population rises towards 9 billion (UN, 2003). The São Paulo Declaration on Pollinators (Dias *et al.*, 1999) revealed serious declines in the number of native pollinator species in Central and North America and six European countries. It has been estimated that over the next 300 years, up to half a million insect species may become extinct (Mawdsley and Stork, 1995). Furthermore, the International Union for Conservation of Nature (IUCN) predicts a global loss of 20,000 flowering plant species over the next few decades, with inevitable consequences for the survival of their co-dependent pollinators. Such losses are likely to involve keystone plants or pollinators, affecting community structure and potentially exacerbating biodiversity degradation and losses of ecosystem services (Bronstein *et al.*, 1990; Cox *et al.*, 1991; Walker, 1992; Grime, 1997; Allen-Wardell *et al.*, 1998; Kearns *et al.*, 1998).

As succinctly described by Simberloff (1990), 'restoration is a game with a moving target whose trajectory cannot be accurately predicted, and the target in any event cannot quite be seen or characterised'. He refers to restoration as

having a 'fuzzy target', as restoration practitioners often do not know exactly what they are hoping to restore, and indeed the resolution of the target itself has raised much debate. Furthermore, economic and social constraints have dictated the degree of partial restoration in order to minimize costs, resulting in managers focusing on restoring the 'superficial' vegetative structure of the system (Handel, 1997; Palmer *et al.*, 1997). Through reinstating the basic community structure, organisms associated with such habitats would be expected to arrive and establish themselves with time (Anderson, 1995; Handel, 1997; Palmer *et al.*, 1997; Hilderbrand *et al.*, 2005). Referred to as the 'field of dreams hypothesis' (Palmer *et al.*, 1997), this remains poorly tested, but relies on the redundancy of species present, particularly pollinator redundancy (the ability of other species to act as back-up pollinators in the absence of the main pollinator(s)), to restore ecosystem function (Zamora, 2000; Kearns, 2001). If this inherent functional redundancy is high, it is possible to set a minimum level of species diversity to be restored, which would ensure the gradual re-establishment of ecosystem function (Palmer *et al.*, 1997). Such thresholds have been tested through modelling (Lundberg and Ingvarsson, 1998), although in reality data to determine this baseline are either scarce or incomplete (Lambeck, 1997). Moreover, effective surrogate pollinators may also disperse pollen differently (Thomson and Thomson, 1992; Montalvo *et al.*, 1997; Aigner, 2001).

7 The Conservation of Interactions: Theory or Practice?

Insects form a large component of global biodiversity and as reviewed above form many links with other organisms. To determine the extent to which entomological interactions are considered in conservation ecology, we considered the case of pollination, asking how often this key link was investigated when conserving a rare plant species. To do this we searched the Web of Science for studies of named rare plant species between 2000 and 2005, and found 139 published studies. Although 113 of these had a conservation focus, we found that only 18 mentioned the importance of pollinators for the plant's survival, 14 went on to name the types of insects visiting the plant in question (e.g. bees or flies) and only 4 (Kang *et al.*, 2000; Peterson *et al.*, 2002; Evans *et al.*, 2003; Rodriguez-Perez, 2005) gave a full list of the insect species visiting the rare plant's flowers. Visitation does not equate to pollination, however, and none of the papers definitively identified the pollinator(s). From our survey of these 139 papers it is apparent that interactions are still not given the attention they deserve, at least by people working on plants. Without the conservation of interactions with pollinators, the conservation of a plant species is unlikely to be sustainable in the long term. In an effort to redress the balance, and using a community-level network approach we ran a project specifically designed to identify the pollinators of rare plants (Gibson *et al.*, 2006). One of the rare plants, *Galeopsis angustifolia* (Red Hemp Nettle) was visited by 22 insect species, but assessing the quantity and quality of the pollen on the flower visitors allowed us to uncover hidden links in the network, where the pollen carried on an insect's body acts as a record of its

previous movements between flowers of different species. In addition, pollen transport data allowed us to eliminate 18 visitors which did not carry *G. angustifolia*'s pollen from the list of its potential pollinators (Fig. 10.1). Using a similar approach, Forup and Memmott (2005) asked whether a meadow restoration scheme had been successful. Working on plant–pollinator interactions on two old and two restored hay meadows, they found no difference in the proportion of plant species visited by potential pollinators, whilst all the



Fig. 10.1. (a) Visitation web for *Galeopsis angustifolia*. Each species of plant and insect is represented by a rectangle: the lower line represents flower abundance; the upper line represents insect abundance. The widths of the rectangles are proportional to their abundance at the field site, and the size of the lines connecting them represents the recorded frequency of the interaction. The target plant and the species it interacts with are shown in black. The scale bar represents number of floral units (1000) and number of insects (100). (b) Pollen transport web for *G. angustifolia* at GA1. The lower line represents pollen abundance; the upper line represents insect abundance. The scale bar represents the number of pollen grains (1000) and the number of insects (100). Note that in the visitation web, all interactions are shown, not just those involving insects identified to species. Consequently, (a) actually shows 25 insects visiting *G. angustifolia* (rather than 22 as stated in the text). (Reprinted from Gibson *et al.*, 2006, with permission from Blackwell Publishing.)

visited plant species were generalized, each having more than a single species of insect visitor. With regard to the restoration of interactions, as opposed to the restoration of species, is a field of research with very little data, but with considerable potential to make restoration more sustainable.

8 Conclusions

Insects form numerous key links with other species leading to complex networks of interactions. These links can take numerous forms: they may be critical to the survival of another species, e.g. pollination; they may form part of an ecosystem service and be of direct use to mankind, e.g. pest control; they may be undesirable links with alien species. However, as is apparent from our survey, considering the restoration of interactions is not a widespread practice. In this final section we will discuss potential future directions in the study of the conservation of ecological interactions, highlighting four fields in need of further attention and discussing some barriers impeding progress in these fields.

8.1 Interdisciplinary networks

Researcher comfort zones are a divisive force in ecology. Thus, while tropical pollinators are well studied at the levels of bees (by entomologists), hummingbirds (by ornithologists) and bats (by mammologists), there are no published data at the level of an entire tropical pollinator community. From the plant's point of view, insects, birds and bats are all simply pollen transporters and the taxonomic distinctions used by biologists are indiscernible. Similarly, ecosystem services are divided into different research fields, with pest control studied by agroecologists, pollination studied by pollination biologists and seed dispersal studied by ant ecologists and ornithologists. However, there are almost no data to say whether these services are actually independent of each other and the links between them could be of considerable importance (but see Larsen *et al.*, 2005 for a notable exception). A more interdisciplinary approach to the study of interactions would be very revealing. A handful of fascinating papers have been published: Bailey and Whitham (2003) link elk, aspen, sawflies and insectivorous birds; Knight *et al.* (2005) demonstrate that fish indirectly affect pollinators. These types of cascading interactions across very different groups of species (Bailey and Whitham, 2003) and across ecosystems (Knight *et al.*, 2005) are probably not uncommon, but just go unrecorded.

8.2 Clarity of measurements

With some interactions, ecologists do not measure what is assumed; for example, 'pollination networks' are without exception visitation networks. Nobody has yet unambiguously identified all the pollinators in a pollinator web (though see Gibson *et al.*, 2006 and Dicks, 2002 for identifying a few of

the pollinators in their networks). Similarly, when working with birds, to be confident that seed dispersal is real dispersal, more than seed intake needs to be measured; intact seed also must be recovered from bird droppings.

8.3 Quantification

Quantitative data are needed for some types of networks, while others such as decomposition networks have received little study at all. Seed dispersal networks remain undeveloped in contrast to the publishing boom in high quality, quantitative pollination and trophic webs. Published bird networks are largely connectance webs and we are not aware of any published ant dispersal networks. Similarly, decomposition networks remain deeply unattractive as study systems, despite the decay of plant and animal remains being essential to the nutrient cycle, and indeed to life itself. Finally, while parasitoids are seen in food webs, parasites and diseases are not commonly represented, despite the fact that they are both diverse and abundant (e.g. Huxham and Raffaelli, 1995) and are ubiquitous in terrestrial, marine and aquatic systems.

8.4 Reality and validation of models

Considerable progress has been made using complex systems approaches to study the extinction of interactions at the community level. However, this approach needs to become more realistic and the models require validation in the field. Recent work by Ives and Cardinale (2004) that incorporates environmental stress into a network, making the species that survive more resilient to this stress, is an excellent example of how more realism can be introduced. Despite being computationally (relatively) straightforward, a complex systems approach has to date been largely used by theoretical ecologists. To validate these models in the field will require greater collaboration between field ecologists and theoretical biologists, or for field ecologists or theoreticians to master new techniques.

In summary, food webs, pollination webs and other ecological networks have not been widely applied to the field of conservation biology (but see Corbet, 2000 for a notable exception). Given the recent practical advances made in food web construction (e.g. ecoinformatics), the theoretical advances (e.g. models of extinction dynamics) and the ongoing loss of biodiversity, this is a very exciting time to begin to use the study of ecological interactions as a tool in conservation biology.

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