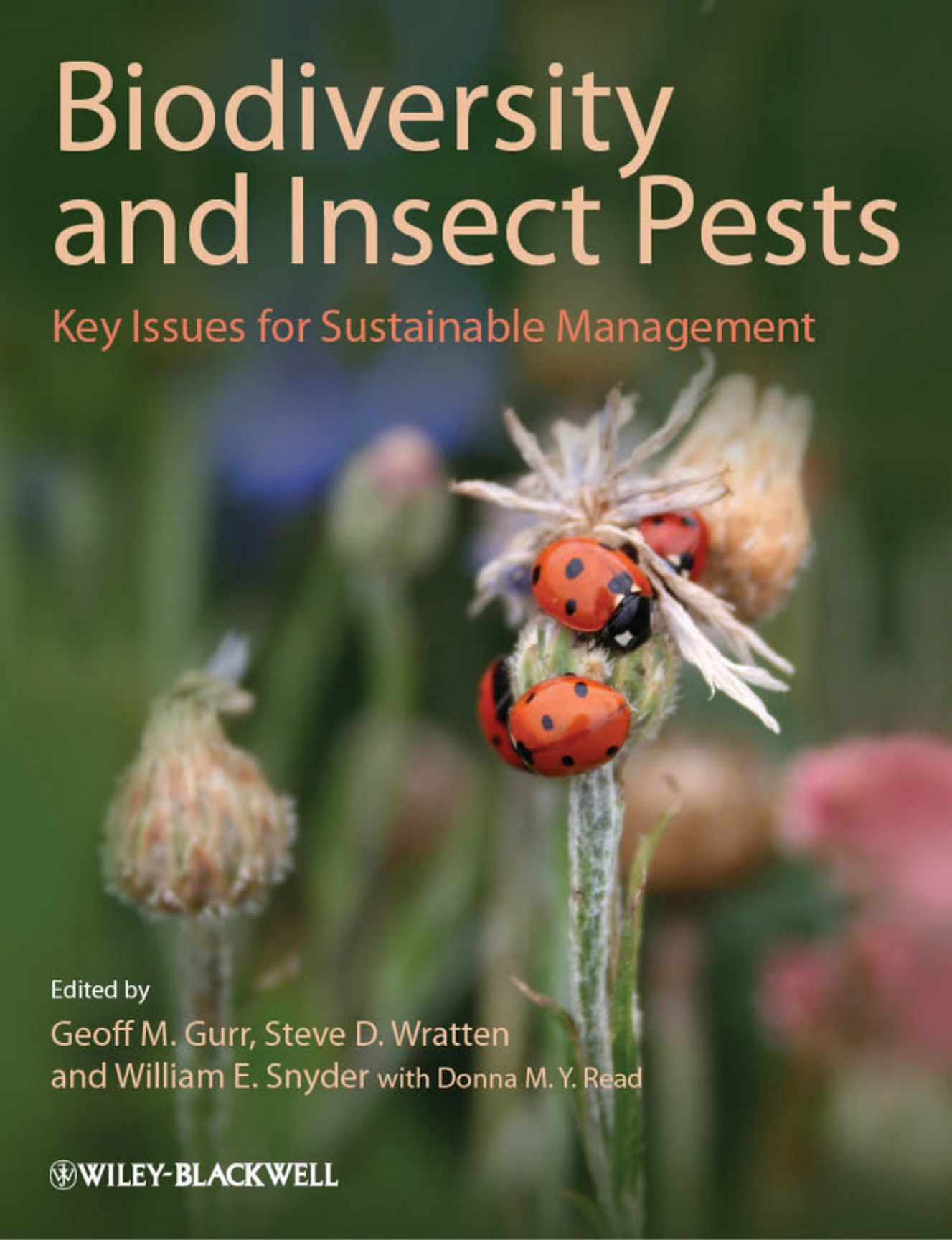
Biodiversity and Insect Pests

Key Issues for Sustainable Management



Edited by
Geoff M. Gurr, Steve D. Wratten
and William E. Snyder with Donna M. Y. Read

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PREFACE

Agriculture accounts for approximately 40% of the land area on planet Earth and has been a major factor in global biodiversity decline. It is ironic, then, that agriculture is now showing conspicuous signs of faltering because of a breakdown in the services provided by nature. Pest control, soil fertility and nutrient cycling are amongst the most important of these. Industrialised agriculture, in striving for greater levels of productivity, uses inputs such as millions of tons of pesticides and fertilisers to replace natural processes. Reliance on technologies based on non-renewable resources has widely acknowledged problems including pollution, human safety and – in the case of pesticides – reduced efficacy as a result of resistance developing in pest populations.

It is time to consider how agriculture worked in such a sustainable manner for thousands of years before the rise of industrialised agriculture. Much is to be learned from traditional practices of diverse crop systems in which biodiversity is maintained. But if agriculture is also to meet the future needs of an increasing human population, ecological science must rise to the challenge of providing more than theoretical understanding and ingenious new research methods. Practicable methods are also required that will permit highly productive farming systems which, by virtue of their ecological foundation, are more sustainable.

The chapters in this book address this challenge from the perspective of insect pest management. Insect pests continue to cause severe crop losses worldwide but novel pesticides and genetically modified plants are not the only technologies available for their control. This book explores ways in which biodiversity can be harnessed to achieve sustainable pest management. Vegetation diversification at scales ranging from the field up to the landscape can reduce pests either directly or by enhancing the activity of predators and parasites. Biodiversity is also a source of genes for better crop varieties and of compounds that can be used as botanical insecticides or that work by more subtle chemical ecology mechanisms.

The role of biodiversity in pest management is a burgeoning area of research and novel pest management strategies are now being implemented successfully in many countries. Forms of ecologically based pest suppression are important examples of the ecosystem services that can be provided by biodiversity. Moreover, pest suppression can be achieved concurrently with providing other benefits such as pollinator enhancement, wildlife conservation, dual crop production and even carbon sequestration.

Our aim as editors as we planned this book in 2010, the United Nations International Year of Biodiversity, was to achieve a comprehensive synthesis of this exciting and important field of applied science. To this end we recruited authors who include leading researchers and practitioners and combined their wide experience with that of carefully selected younger scientists with innovative thinking. With wide international coverage including Africa, America, Asia, Australasia and Europe, our treatment of the subject is significantly broader that that available from mainstream, English-language journals.

We have strived to make the material in this book accessible to advanced undergraduates and newcomers to the field, with plenty of illustrative features, while still offering the specialist reader a current synthesis and stimulating new ideas. Chapters are arranged under a series of headings (Introduction, Fundamentals, Methods, Application and Synthesis), but these should not be viewed too rigidly. Many of the chapters include a blend of material; especially when stressing the link between aspects of theory and the success of real-world use. Ultimately, we hope that the book will prove useful in placing pest management on a more sustainable footing.

We thank the chapter authors for their generous contribution of ideas, attention to detail and (nearly always) keeping to schedule. Many also served as reviewers for other chapters. We very much appreciate the assistance of the many colleagues who acted as reviewers for chapters: Helmut van Emden, Daniel Karp, Myron Zalucki, Sarah Wheeler, Debbie Finke, Gary Chang, Cory Straub, Deborah Letourneau, Stephen Duke, James Hagler, Wopke van der Werf, Nuria Agusti, Matt Greenstone, Mark Jervis, Jana Lee, Marcel Dicke, Liu Shu Sheng, A. Raman, Bob Bugg, Samantha Cook, Norman Arancon and Katja Poveda. This book would not have been possible without Donna Read, whose input went way beyond proofreading and formatting.

Geoff M. Gurr
Steve D. Wratten
William E. Snyder
August 2011

FOREWORD

Agriculture has been practised for several thousand years but it is only in the past few generations that the traditional practices that sustained agriculture have come to be replaced by modern and largely industrialised systems. Despite dramatic increases in food production, it is now recognised that agriculture can negatively affect the environment through overuse of natural resources as inputs or through their use as a sink for waste and pollution. Such effects are called negative externalities because they impose costs that are not reflected in market prices. What has also become clear in recent years is that the apparent success of some modern agricultural systems has masked significant negative externalities, with environmental and health problems widely documented. These environmental costs shift conclusions about which agricultural systems are the most efficient, and suggest that alternative practices and systems which reduce negative and increase positive externalities should be sought.

The growing human population and rapidly changing consumption patterns will bring increasing demands for food, fuel and fibre. It is estimated that world population will reach some nine billion by the middle of the twenty-first century. This will require agricultural production to increase by at least two-thirds; perhaps doubled if those in developing countries are to approach levels of animal protein intake that are taken for granted in industrialised countries. The scale of this challenge is daunting but studies of agricultural sustainability in developing countries suggest overall yield increases of 80–100% are possible in many countries and systems. One analysis of 286 projects in 57 countries showed improvements had been made by 12 million farmers on 37 million hectares of farmland (Pretty et al., 2006, *Environmental Science and Technology*, 4, 1114–1119); a recent study of African agriculture found that 10 million farmers and their families had more than doubled yields on another 13 million hectares (Pretty et al., 2011, *International Journal of Agricultural Sustainability*, 9, 5–24). Food outputs by such sustainable intensification have been multiplicative – by which yields per hectare increased by combinations of the use of new and improved varieties and new agronomic-agroecological management, and additive – by which diversification resulted in the emergence of a range of new crops, livestock or fish that added to the existing staples or vegetables already being cultivated.

Realising the promise of ecologically based agriculture will require a massive and coordinated effort. A key component is the role of science to both provide a better understanding of the natural resource base and develop new technologies. The significance of this book is that it amply demonstrates the power of biodiversity to combat one of the major causes of crop loss: insect pests. Methods such as growing secondary crops on the embankments around rice fields, incorporating agroforestry into farming systems, using locally appropriate crop varieties and adopting integrated pest management were widely used in these agricultural sustainability studies. Much of what is now happening on farms has drawn from the work of the authors and editors of this book. Each of these methods, and many other biodiversity-based approaches, are detailed in chapters that span the full spectrum from underlying theory, to methods for research and implementation and, ultimately, to cases of successful application and use. This book compellingly shows that biodiversity on farms and across landscapes can provide a range of benefits to humans at the same time as contributing to suppressing pests.

Understanding, protecting and harnessing biodiversity is a key to the agricultural and food challenge before us.

Professor Jules Pretty OBE, University of Essex
August, 2011

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Introduction

Chapter 1

BIODIVERSITY AND INSECT PESTS

Geoff M. Gurr, Steve D. Wratten and William E. Snyder

Biodiversity and Insect Pests: Key Issues for Sustainable Management, First Edition. Edited by Geoff M. Gurr, Steve D. Wratten, William E. Snyder, Donna M.Y. Read.

INTRODUCTION: INSECTS, PLANTS AND HUMANS

This book is essentially about interactions between the three most important life forms on planet Earth: insects, plants and humans, and the ways in which they are affected by biodiversity, the complex web of life. Over a million species of insect have been formally described (20 times the number of all vertebrates), with just one insect order, the beetles (Coleoptera), representing 25% of all described species of all forms of life (Hunt *et al.*, 2007). It has been estimated that the biomass of insects in temperate terrestrial ecosystems is 10 times that of the usually more conspicuous vertebrates, and that for each human there are 1,000,000,000,000,000,000 living insects (Meyer, 2009).

Insect and plant biodiversity are tightly linked, and it is generally accepted that the rise of angiosperm plants during the Cretaceous period (145–65 million years ago) was accompanied by the development of many intricate coadaptations between plants and insects. These included pollination and seed dispersal (Ehrlich and Raven, 1964; Scriber, 2010), such that many insects benefit plants. However, many other insect species are herbivores harmful to plants, and there is compelling evidence for coevolution between plant defences and the ability of insect herbivores to overcome them. An example of great relevance to agricultural pest management is the phenomenon of 'resistance breakdown'. This occurs when a pest population responds to the resistance genes bred into into a widely used crop variety by the development of increased virulence over successive generations of the adapting pest (e.g. McMenemy *et al.*, 2009). This renders the host plant's resistance mechanism(s) ineffective.

In contrast to the two 'mega taxa' sketched out above, *Homo sapiens* is an evolutionary newcomer, as anatomically modern humans have existed for much less than a million years. Of course it is only in the last few centuries that technological advances have allowed numbers of this single species to escalate, approaching seven billion as of June 2011 (US Census Bureau, 2011). The impacts of this rise are such that we are now said to be living in the Anthropocene era (Crutzen, 2006), characterised by very high rates of species extinctions, pollution (including elevated atmospheric carbon dioxide levels) affecting every corner of the globe, destruction of natural ecosystems and high levels of land use for urban and agricultural purposes. Amongst the most important technological advances that have allowed this dramatic success ('success' at least in terms of the population size of *H. sapiens*) is agriculture.

The concept of 'pests' has arisen out of human agricultural practice and the desire to preserve food security by protecting crops from ubiquitous insects. Some, such as the locust (most likely desert locust, *Schistocerca gregaria* Forsk. (Orthoptera, Acridiidae)), are mentioned in the Bible and in other early written works (Nevo, 1996). For many centuries, farmers combated pests with cultural techniques ranging from hand removal of pests to the use of crop rotations. Saving the best seeds from each year's crop to sow in the following season led to the development of many landraces (locally adapted varieties) of major crop species, some of which persist to the present day (Thomson *et al.*, 2009). These landraces often had useful levels of broadly based resistance to various pests to which they were exposed for hundreds of generations. More recently, other technologies were brought to bear against pests including chemistry to produce ever more sophisticated insecticides (Casida and Quistad, 1998), radiation technology to allow the development of the sterile insect technique (Dyck *et al.*, 2005) and molecular biology to support plant breeding efforts (Sanchis and Bourguet, 2008). Many pest management technologies, however, are beset with problems of a technical nature (e.g. pollution, resistance breakdown, cost, etc. (van Emden and Peakall, 1996)) or a social nature (e.g. public acceptance of biotechnology in agriculture, deregistration of insecticides because of safety concerns (Cullen *et al.*, 2008; Lemaux, 2009)).

Although the term 'pest' is a human construct, and pest management involves humans modifying natural processes, there is much to be learned from nature. For more than 100 million years plants have been developing strategies to defend themselves from insect herbivores. In addition to familiar morphological adaptations such as hairs and thickened cuticles, plants have also evolved a powerful arsenal of chemical defences. Insecticide scientists and plant breeders are learning much from nature about new compounds that might be used in future insecticides (Isman, 2006) and about plant genetics that might be manipulated through molecular biology (Yencho *et al.*, 2000). The value of plant biodiversity as a resource from which botanical insecticides may be discovered is another important field, and is covered in chapter 6 of this book. Biological control

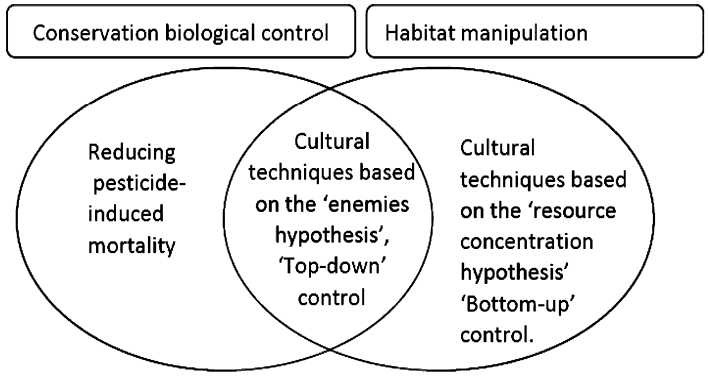

Figure 1.1 The relationship between conservation biological control and habitat manipulation approaches to arthropod pest management. Enemies hypothesis and resource concentration hypotheses are as described by Root (1973).

workers, too, have developed a very active interest in plant defences. Morphology such as glandular trichomes can directly impede natural enemies (Simmons and Gurr, 2005) and chemical defences can be exploited to make plants more attractive to predators and parasitoids (Kvedaras *et al.*, 2010; Simpson *et al.*, 2011). Chapter 11 of this volume explores the latter aspect, offering scope to manipulate or mimic the chemical ecology of plants to rapidly recruit natural enemies from nearby source habitats.

Aside from the various direct interactions that occur between plant and herbivore species, interactions involving other trophic levels are increasingly understood to be important in determining the magnitude of herbivore impact on plants and offer promise to pest management scientists. Indeed, for well over 100 years the action of predators, parasites and pathogens on pests has been exploited to provide biological control for pest management (Gurr *et al.*, 2000). Pesticides, too, have a long history, although for much of this time they were broad-spectrum and used in a manner that was dangerous to non-target species including biological control agents. The human health and environmental negatives of widespread use of broad-spectrum pesticides are well documented. In the 1950s, Californian entomologists created the 'integrated control concept' (Stern *et al.*, 1959), which included pesticides applied on the basis of crop scouting rather than prophylactic calendar spraying. This concept acknowledged that 'background' populations and communities of natural enemies had a key role in suppressing pests. This landmark work paved the way for modern integrated pest management (IPM).

There are three common approaches to biological control – conservation, classical and inundative – all of which might be harnessed to improve natural pest control. In the early days of IPM, there was little explicit emphasis on conservation biological control, achieved by enhancing food, shelter and other resources needed by natural enemies (Figure 1.1) (Barbosa, 1998). IPM practices initially focused on enemies imported from overseas, ideally to target one particular pest species (classical biological control). These enemies were also more likely to be effective under a regime of insecticides that were target-specific for pests but again the ecological needs of these enemies were not researched. Inundative releases of natural enemies reared in very large numbers pre-dates conservation biological control, having taken place since the 1930s, especially in commercial glasshouse crops (van Lenteren and Woets, 1988; Albajes *et al.*, 2000).

Classical biological control of arthropods by arthropods has been practised worldwide since the 1880s but this approach has had at least three problems associated with it. The first is that for a period of at least 100 years, successful suppression of the target species remained at around 10% (Gurr *et al.*, 2000). Failure to establish biological control agents was the major cause of this low success rate. Secondly, some introduced classical biological control agents attacked arthropods other than the 'target' species (Howarth, 1991) and work on how to manage this risk has

become an important strand in the biological control literature (Barratt *et al.*, 2010). Thirdly, the introduced agent may become a pest in its own right. For example, the cane toad (*Bufo marinus* L.) has devoured and poisoned non-target native species and caused other adverse ecological effects in Australia (Shine, 2010). Despite its problems, however, classical biological control is considered by most practitioners as 'risky but necessary' (Thomas and Willis, 1998).

We have briefly reviewed so far patterns of insect and plant biodiversity, the growing global impacts of agriculture, and the development of IPM and biological control; but how might biodiversity itself be exploited to improve pest management? Indeed, why might Schoonhoven *et al.* (2005), at the end of a detailed treatise on insect–plant interactions, conclude that 'diversification holds the clue to control of pestiferous insects'? In seeking to answer these questions it is necessary to explore the nature of biodiversity.

BIODIVERSITY

The much-used term 'biodiversity' is a contraction of 'biological diversity'. In popular usage is often taken to refer casually to the plants and animals that humans cannot directly eat or otherwise use and, for often poorly defined reasons, 'good stuff' that needs to be valued and protected. Various technical definitions have been proposed and a significant volume of literature exists on this subject (Gaston, 1996). Generally, definitions refer to biodiversity encompassing the variety of life on Earth at organisational scales ranging from genes, through species, to entire ecosystems. Genetic diversity covers the genes found within a given population of a single species, and the pattern of variation across different populations of that species. For example, genes in rice might provide useful traits such as insect resistance and salt tolerance. Species diversity is the more familiar level of biodiversity, referring to the assemblage of species in a given area. An example is the insects present in a cotton crop. At the higher organisational level, ecosystem diversity is the variety of habitats that occur within a region, or the mosaic of patches found within a landscape. This might include the crops, woodland, built environment, aquatic and wetland habitats found on a farm.

Species diversity and its relationship to ecological functions and their provision of ecosystem services has been the subject of intense study, reflecting its significance in ecology and the future of man's management of the environment. Of particular importance is the distinction between alpha, beta and gamma diversity (Whittaker, 1972). This is best explained by a hypothetical example addressing the issue of whether woodland vegetation is valuable in conserving spider species that might colonise wheat fields via a network of hedgerows (Table 1.1). Spiders can be captured by pitfall traps or vacuum sampling and identified to species. Alpha diversity is the resulting measure of species diversity for each of the above three habitats: 10 in the woodland, 7 in hedgerows and 3 in the wheat fields. Beta diversity, in contrast, is a comparison of habitats that provides an index of the number of species that are not common to both habitats. Thus, there is a different beta diversity statistic for each of the permutations of two-way habitat comparison. In this case, the beta diversity value for woodland versus hedgerows is 7, a relatively low value (given the alpha diversity in each) because many of the species are common to both habitats. In contrast, the woodland to field beta diversity value is 13 because none of the species is common to both habitats. Finally, the gamma diversity value of 14 is an index of spider species richness over all of the farm's three habitats. As is evident from this hypothetical example, species richness is amongst the aspects of biodiversity of direct relevance to pest management and the landscape-level effects are particularly important. Reflecting this, much of the remainder of this chapter discusses how natural enemy diversity can suppress pest populations, and how it might be managed to improve these benefits. For example, intensification of the landscape that comprises crop fields only (each with associated high levels of disturbance) (Figure 1.2, left) or agricultural areas in a naturally inhospitable matrix (Figure 1.2, right) can deprive natural enemies of refuges and important non-crop resources such as plant foods. Reflecting the importance of landscape-scale effects and associated gamma diversity, one chapter in this volume explores this area from a theoretical perspective (Gamez-Virues *et al.*, chapter 7) and one explores it from a methodological perspective (Scherber *et al.*, chapter 8).

Manipulating plant biodiversity to control pests

The notion that plant biodiversity could help suppress pests has origins dating back to the polycultures that

Table 1.1 Example of alpha, beta and gamma diversity of spider species in adjacent habitats of a farm landscape (based on the hypothetical example given by Meffe *et al.* (2002)).

Spider species	Woodland	Hedgerow	Wheat field
1	present		
2	present		
3	present		
4	present		
5	present		
6	present	present	
7	present	present	
8	present	present	
9	present	present	
10	present	present	
11		present	
12		present	present
13			present
14			present
Alpha diversity	10	7	3
Beta diversity	Woodland vs. hedgerow: 7	Hedgerow vs. field: 8	Woodland vs. field: 13
Gamma diversity		14	

Figure 1.2 Challenging habitats for natural enemies: landscape composed entirely of arable fields and towns in Western Europe (left) and isolated patches of irrigated agriculture in the arid landscape of the US Midwest (right) (photos by G.M. Gurr).

were the norm in pre-industrialised agriculture and persist in the concept termed 'companion planting'. This practice recommends, for example, that aromatic plants such as basil (*Ocimum basilicum* L.) or *Allium* spp. be inter-sown with pest-prone vegetables. These aromatic plants supposedly repel pests or interfere with their location of a suitable host plant (Cunningham, 1998), but rigorous testing of the approach does not always yield encouraging findings (Held *et al.*, 2003). More sound ecological support for the significance of

non-crop vegetation came from early work suggesting the importance of nectar availability to predatory insects such as parasitoid adults (Thorpe and Caudle, 1938). In that study, newly emerged *Pimpla ruficollis* Gravenhorst, an ichneumonid parasitoid of the pine shoot moth (*Rhyacionia (Evetria) buoliana* Schiff. (Eucosmidae)) demonstrated repellency to the pine oil volatiles from *Pinus sylvestris* L. trees. This led young adult parasitoids to leave areas with trees where the dense shade was likely to mean an absence of an under-storey. Outside the forest they were presumed to feed on nectar, including that of plants in the family Apiaceae, returning to the trees 3–4 weeks later when suitable larval hosts were available.

Another important early example, and one that demonstrates a separate ecological mechanism by which plant biodiversity may benefit natural enemies, is the study by Cate (1975) on the ecology of the western grape leafhopper *Erythroneura elegantula* Osborn (Homoptera: Cicadellidae). That, and subsequent studies, showed that the presence of blackberry bushes (*Rubus* spp.) in riparian habitats close to vineyards could improve biological control of this pest by the parasitoid *Anagrus epos* Girault. The mechanism for this is that the blackberry bushes fill the temporal absence of *E. elegantula* eggs which are the host of the parasitoids. The leafhopper overwinters as adults but these are unsuitable as hosts because the parasitoids can overwinter only as eggs inside host eggs. Clearly, parasitoids are unable to overwinter within the vineyard itself. The presence of a suitable overwintering host, the blackberry leafhopper *Dikrella californica* Osborn, on non-crop vegetation throughout the year allows populations of *A. epos* to persist in the region. If these overwintering sites are close to vineyards the parasitoid is better able to colonise those vineyards and help check development of pest leafhoppers (Murphy *et al.*, 1998).

Pivotal work by Root (1973) suggested two ways that greater plant diversity within crops might improve pest suppression. The first was the 'enemies hypothesis', which postulated that diverse plantings would encourage greater prey, nectar and pollen resources for natural enemies, building their densities and encouraging stronger impacts on pests. The second was the 'resource concentration hypothesis', which holds that herbivorous insects (at least specialists) should more easily find, and choose to remain within, large monoculture plantings of suitable host plants. Testing the relative importance of these two hypotheses has remained a research-rich challenge amongst insect ecologists (e.g. Grez and González, 1995) and has led to the concept of 'top-down, bottom-up' trophic effects. The former refers to the action of predators and other natural-enemy species in the third trophic level, while the latter emphasises plant defences and benefits of plant biodiversity such as disruption of herbivore visual and olfactory cues (as well as other mechanisms reviewed below). The complexity of analysing and separating these effects was discussed by Lawton and McNeill (1979) under the compelling title 'Between the devil and the deep blue sea: on the problems of being a herbivore'.

BIOTIC FORCES SHAPING PESTS: BETWEEN THE DEVIL AND THE DEEP BLUE SEA REPRISE

Just as the design of a coin is derived from pressure to each face, so too may a pest population be viewed as taking shape by pressure from opposing forces (Figure 1.3). First, plants are far from passive players in the game of herbivory. Millions of years of evolution have given plants a formidable arsenal of defences to which the animals seeking to feed upon them have had to adapt. Plant defences include conspicuous morphological features such as spines, hairs (including trichomes that poison and entrap pests (Figure 1.3, bottom insert), thickened cuticles and protected growing points as well as sophisticated metabolic defences that give constitutive and induced defences designed to poison or otherwise impede herbivores (Wu and Baldwin, 2010). In addition to this 'bottom-up' pressure from the first trophic level, herbivorous arthropods also have to contend with the action of 'top-down' forces from the third trophic level. Predators and parasitoids have forced insect herbivores to evolve adaptations ranging from morphological (e.g. hairs (Figure 1.3, centre)), physiological (e.g. encapsulation of parasitoid eggs (Namba *et al.*, 2008)) to behavioural (e.g caterpillars dropping from plants when sensing a predator (Steffan and Snyder, 2010)).

Of course, factors other than top-down and bottom-up forces will also shape pest adaptations. Competition and the abiotic environment are two of the most important. In agriculture, however, the importance of competition is reduced by the usual super-abundance of food resources for pests of the relevant crop. Aspects of the physical environment that are of particular

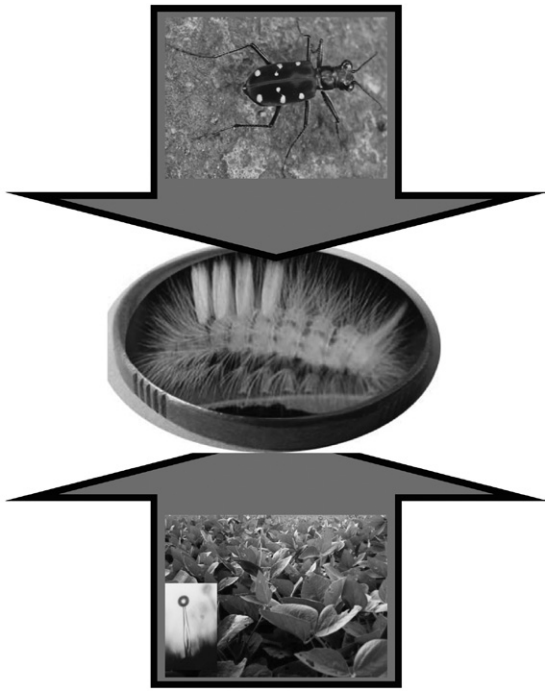

Figure 1.3 The pest as a coin: shaped by pressures from top-down trophic force of natural enemies (e.g. tiger beetle) and the bottom-up force of plant defences (e.g. glandular trichomes) (centre photo by J. Liu, other photos by G.M. Gurr).

importance in agricultural systems include the weather (frosts, flood, etc.) but often these effects are ameliorated for the sake of efficient crop production, by protected cropping (greenhouses, cloches, etc.), site selection or by a carefully selected sowing date. Then, human imposed disturbance becomes the most important form of abiotic mortality factor for pests (e.g. irrigation, harvest, tillage).

Bottom-up trophic effects of biodiversity on pests

Host accessibility for herbivores is unrestricted in large monocultures (assuming the host is suitable for the herbivore in question) and two ecological mechanisms can be at play. First, insect herbivores tend to locate suitable hosts and remain upon them more readily in monocultures (Root, 1973). Baliddawa (1985) reviewed 36 papers and found that 24 provided evidence that suitable hosts were less apparent in polycultures. Cases where this applied included herbivores that located hosts by random landings and which were not directed by host cues. These insects – such as wind-dispersed aphids – may have limited opportunity to leave unsuitable host plants or patches of plants so are unable to make repeated attempts to land on a host. Second, herbivores can be expected to be more numerous in large patches of suitable habitat (Kareiva, 1983). An example of how such an effect may operate is provided by bark beetles (*Ips* spp.). Generally, these herbivores are repelled by plant defences so they are usually unable to overcome the defences of a healthy tree. Therefore their fitness is greater on stressed hosts with weakened defences. Normally these poorly defended trees are scarce and widely dispersed so the herbivore population increase is prevented. Only after a storm event that weakens sufficient host trees will the pest population build up to high enough numbers to successfully attack and overwhelm the defences of healthy trees (Speight and Wainhouse, 1989).

For both of the above cases, any spatial or temporal break in availability of susceptible hosts can reduce pest build-up (Jactel *et al.*, 2005). Temporal barriers may result in cases where the herbivore is able to feed only on a certain phenological stage of the host plant; on young leaves, for example (Wratten, 1974). In such cases egg hatch must coincide with bud burst. In a polyculture forest system, bud burst is staggered across tree species so many trees, although potentially suitable hosts, will not be available to neonate larvae, thus restricting food resources available to the pest population. Plant diversity might also lead to physical barriers that protect crop plants from herbivores. For example, understorey plants may be protected by the presence of an overstorey that impedes host plant detection. Chemical barriers, too, are important because many insect species use the volatiles produced by plants as host location cues. Mixed species vegetation will provide a more complex chemical environment in which it is more difficult for a specialist herbivore to locate and settle on suitable plants. Chapter 19 of this volume, on cover crops, provides examples where the close proximity of the primary crop to the secondary (cover) crop can evoke bottom-up effects.

The other way in which insect pests may be suppressed in a plant stand with more than two species

is through 'trap cropping' (Rea *et al.*, 2002). At its simplest, one plant might be a preferred site for egg laying so might be sown alongside the main crop to divert pests. There are cases of such 'trap crops' being attractive to egg-laying pest females but providing poor support for the development of their larvae (Khan *et al.*, 2006). In a further example, females of the cerambycid stalk boring beetle *Dectes texanus* LeConte prefer to oviposit on sunflower (*Helianthus annuus* L.) over soybean (*Glycine max* L. Merr.), to the extent that an individual host plant may accumulate multiple eggs. Larvae subsequently fight, typically leading to the death of all but one individual per plant. Even where such biological mechanisms do not operate to kill pests, 'trap crops' may be established and methods such as targeted insecticide application or mechanical destruction used to prevent pest development. A particularly elegant form of trap cropping is the 'push–pull' strategy (Cook *et al.*, 2007) whereby a synergistic behavioural manipulation of pests is brought about. This usually uses non-host volatiles, anti-aggregation or alarm pheromones, oviposition deterrents or antifeedants on the focal crop to 'push' the pest away from it. Visual distractions might also be involved. Simultaneously, pests are 'pulled' to a trap crop using visual oviposition or gustatory stimulants, pheromones or host volatiles. The most successful example of the push–pull strategy is for control of stem borers in African maize and sorghum using the trap plants Napier grass, *Pennisetum purpureum* Schumach and Sudan grass, *Sorghum sudanensis* Stapf (Khan *et al.*, 2000). Chapter 16 of this volume provides an analysis of reasons for the outstanding success of this push–pull approach.

Meta-analyses of plant-biodiversity benefits for pest control

As well as the mechanisms and associated pest management approaches summarised above, several meta-analyses have been conducted over many experimental studies on the effects of plant diversity on herbivores. For example, such an analysis of 21 studies of the effects of diversified crops on insects pests found a 60% reduction in mean insect density in diverse compared with simple crop situations (Tonhasca and Byrne, 1994). In a non-agricultural context, Hillebrand and Cardinale (2004) examined effects of grazers on the biomass of periphytic algae and found a robust trend whereby the impact of grazing tended to decrease as the diversity of algae increased. Similarly, in a particularly comprehensive meta-analysis of the biodiversity effects on ecosystem functioning and services, Balvanera *et al.* (2006) found evidence for positive effects of biodiversity on pest control whereby higher plant diversity was associated with reduced plant damage. Allied to this there was also evidence of benefit against an important category of pests: invasive species. Under conditions of higher plant diversity, invader abundance, survival, fertility and diversity were all reduced. Most recently, Jactel and Brockerhoff (2007) also found that diverse plant communities were less affected by pests. Their meta-analysis covered 119 forest-related studies of 47 different tree:pest systems and found overall a significant reduction of herbivory in more diverse forests. Importantly, however, in terms of formulating any specific recommendations, the response varied with host specificity of the pest species. In diverse forests, herbivory by oligophagous species was generally reduced but the response of polyphagous pests varied. An important effect that explains instances of oligophagous species sometimes being favoured by tree diversity is 'associational susceptibility'. This operates when a herbivore develops high population densities on a palatable host and then spills over to the other, less preferred plant species. An example is the gypsy moth (*Lymantria dispar* L.) which feeds on conifers once it has defoliated its preferred broadleaved hosts, such that white pine (*Pinus strobes* (L.) growing in mixed stands with oaks (*Quercus* spp.) is more likely to be attacked than when in monoculture (Brown *et al.*, 1988). Another finding from the meta-study by Jactel and Brockerhoff (2007) was that, as might be expected, the effects on herbivory were greater when the diverse tree species were more distantly related. The authors claimed that this finding lends support for the action of bottom-up effects based on the notion that trees from taxonomically distant groups would be more likely to have dissimilar volatiles, so impeding host location by pests. The same trend could, however, result from natural enemy activity if the diversity of trees (e.g. nectar-producing angiosperms with conifers) enhanced the top-down effects. Indeed, it is very likely that the effects in many of the publications covered by the foregoing meta-studies include a mixture of bottom-up and top-down effects, even where the original authors did not specifically seek evidence of enhanced natural enemy activity.

Top-down trophic effects

The second suite of hypotheses that may account for the suppressive effects of biodiversity on pests involves the third trophic level: natural enemies attacking herbivores. Pest control by natural enemies is now widely acknowledged as an important ecosystem service with annual values estimated at US$2, $23 and $24 per hectare in forests, grassland and cropland, respectively (Costanza *et al.*, 1997). More recent work using in-field experimental approaches, has put the value of 'background' biological control of pests at over US$100/ha/year even though the effects of only one pest were explored (Sandhu *et al.*, 2008). Partly because of these recent results, the influence of natural enemies on pests has emerged as an important aspect of the wider field of biodiversity and ecosystem function (Wilby and Thomas, 2002). Cardinale *et al.* (2006) performed a meta-analysis of 111 field, greenhouse and laboratory studies that manipulated species diversity to examine its effect on ecosystem function in a range of trophic groups and ecosystems. On average, decreasing species richness led to a decrease in the abundance or biomass of the relevant trophic group and reduced ecological process rate (e.g. predation).

BIODIVERSITY AND ECOSYSTEM FUNCTION

An intuitive view is that a more diverse community of natural enemies should yield higher consumption rates across the entire community of natural enemies (Wilby and Thomas, 2002). This would be expected when different species occupy different feeding niches, so that more unique niches are filled when more species are present (e.g. Finke and Snyder, 2008). Yet increasing amounts of empirical research and modelling (Casula *et al.*, 2006) indicate that this relationship is more complex than a simple additive one where each new enemy species provides incrementally more ecosystem function. Indeed, the addition of more enemy species can lead to an overall reduced consumption of pests when predator species interfere strongly with one another (e.g. Finke and Denno, 2004). On the other hand, the addition of enemy species may lead to the opposite effect: synergy (e.g. Cardinale *et al.*, 2006). Synergy among natural enemies occurs when one predator species enhances prey capture by another (e.g. Losey and Denno, 1998). In still other cases, predator species fill similar niches (that is, are functionally redundant) such that adding new species to a community is neither beneficial nor harmful to pest control (e.g. Straub and Snyder, 2006). Thus, positive, negative, and neutral enemy-diversity effects can result from niche or functional complementarity, predator interference, and functional redundancy, respectively (Straub *et al.*, 2008).

A recent review of the effects of natural enemy biodiversity on suppression of arthropod herbivores in terrestrial systems (Letourneau *et al.*, 2009) is important in distilling the now considerable volume of experimental work in this field. The meta-analysis of 62 published studies covering 266 comparisons of herbivore and natural enemy communities revealed a significant overall strengthening of herbivore suppression with greater natural enemy species richness (Plate 1.1). The analysis of these comparisons revealed herbivore suppression from increased enemy richness in 185 cases, one instance of no effect and 80 where herbivores were favoured by enemy richness. The overall significant effect of natural enemy richness on herbivores was consistent for studies conducted in tropical and temperate agriculture. Indicative of the robustness of predator biodiversity's benefit, this effect was also significant across both of the common approaches for conducting such work: cages with artificially manipulated arthropod community structure and insect numbers and open-field investigations of systems where natural enemy communities differed in response to an aspect of the local environment. The overall finding of Letourneau *et al.* (2009) is consistent with an earlier meta-analysis of predator removal studies (Halaj and Wise, 2001) which concluded that herbivore abundance increased as predation pressure decreased in 77% of cases, with the opposite occurring in only 20% of studies. These meta-analyses are powerful evidence for the influence of natural enemy diversity on pests but it is clear that the outcome of enhancing the enemy community in any particular system is still unpredictable.

An important complement to biodiversity:ecosystem function (BEF) studies that has undergone rapid advances in the past decade is the use of molecular techniques to analyse the diet of predators. These approaches have the potential to firmly define feeding-niche overlap among predator species, and the frequency with which predators feed upon one another (intraguild predation). Chapter 10 of this volume provides a state-of-the-art view of how newly available

methods can be used to move from a general understanding of the effect of predators on pests to a quantified understanding of 'who eats whom'. At this level, however, assessing the effects of predators on prey populations, using other methods, may still be needed. The relatively new technique of pyrosequencing can help in this regard, as shown by work in New Zealand by Boyer and Wratten (2004).

Specialist and generalist natural enemies: the importance of partitioning

A good generalisation that helps understand the results of the meta-analyses by Letourneau *et al*. (2009) and Halaj and Wise (2001), is that suppression of pests by enemies is reduced when intraguild predation takes place (Finke and Denno 2003). Conversely, pest suppression is enhanced when enemy species are able to partition prey by life stage, size or microhabitat use effects (Wilby *et al*., 2005). This partitioning might also result from enemy species having some kind of synergy such as 'predator facilitation' (Charnov *et al*., 1976) whereby prey is more readily captured by one predator after being disturbed by another. Although the classical example of this phenomenon (Soluk and Collins, 1988) concerns trout and stoneflies there is also evidence for predator facilitation effects amongst arthropod natural enemies of pests (Losey and Denno, 1998). Certainly there is an important difference between the way that generalist and specialist enemies interact to drive effects on pest populations. In the study by Finke and Snyder (2008), a model system with radish (*Raphanus sativus* L.), aphids (green peach aphid (*Myzus persicae* Sulzer)), cabbage aphid (*Brevicoryne brassicae* L.) and turnip aphid (*Lipaphis erysimi* Kaltenbach) and parasitoids (*Diaeretiella rapae* McIntosh, *Aphidius colemani* Viereck, *and Aphidius matricariae* Haliday (Braconidae)) was used to tease apart the relative effects of resource partitioning and diversity *per se*. That study exploited the phenonenom of natal fidelity whereby a given wasp individual will prefer to attack a host of the same species from which it emerged. This is despite the fact that each of the three wasp species is potentially able to parasitise all three of the aphid species. The experimentation involved rearing batches of each wasp species on each aphid species (nine permutations). This then allowed arenas to be set up in which parasitoids were confined with aphids such that the wasps either fully partitioned the available hosts or were generalists that overlapped in terms of resource use. At the same time, parasitoid species richness was varied from one to three species. Increasing the number of resource partitioning parasitoids from one to three species markedly increased the parasitism rate and reduced aphid abundance. In contrast, when the parasitoids were effectively generalists (i.e. they were competing for hosts rather than each searching for one species in a specialist manner) there was no effect of increasing species diversity. The increase in aphid use by specialist parasitoids but not generalists demonstrated that the extent to which enemies partitioned the resource was the dominant factor.

Remarkably, such positive influences of enemy diversity can be mediated even independently of actual predation events. This is because, rather than simply staying put and waiting to be killed, herbivores often deploy a wide range of chemical, physical and behavioural defences. These defences often are energetically costly, however, such that herbivores bear a cost in their deployment. For example, in work with lepidopteran pests of *Brassica oleracea* L., Steffan and Snyder (2010) examined the effects of predator diversity. The pest in that system, *Plutella xylostella* L., drops from the host plant when disturbed by a predator but remains suspended by a silken thread, presumably to avoid falling to the ground where it is likely to be vulnerable to soil-associated natural enemies (such as those covered by Altieri *et al*.; see chapter 5 of this volume). Only after some minutes does the larva return to the leaf and resume feeding, so the defence strategy carries an opportunity (i.e. feeding) cost. The manipulative experiment replaced caterpillars predated by *Diadegma* and *Hippodamia* enemies to ascertain the effects of the different enemy communities on pests via behavioural mechanisms independent of the actual predation. Another treatment was predator-free but caterpillars were carefully removed to simulate predation free of the induction of larval defence reactions. This study demonstrated that plant production was increased by enemy diversity-induced anti-predation behaviour by the caterpillars in the absence of any actual predation. These 'predation-free' effects are considered in more detail in chapter 2 of this volume.

Functional redundancy and complementarity

Several factors influence the relationship between the number of natural enemy species in a system and the

Box 1.1 Examples of functional redundancy and functional complementarity of natural enemies

Several egg parasitoid species of a pest species that forage in the same microhabitat and season exhibit *functional redundancy*. This means that the loss of one species is unlikely to result in a pest population growth.

Several spider species that attack the eggs, small nymphs and adults of a pest species with different hunting strategies in different microhabitats exhibit *functional complementarity*. This means that the loss of a single species is more likely to result in pest population growth.

resulting rate of prey consumption. An important aspect is the distinction between functional redundancy and functional complementarity (Box 1.1; Rosenfeld, 2002). Species of natural enemies that exhibit functional redundancy are similar to one another in terms of the life state of the pest attacked, the microhabitat used, the season of the year in which they are active and so on. In contrast, enemies with functional complementarity differ markedly in terms of their niche characteristics (Bográn *et al.*, 2002).

Although the characteristics of a given species will be profoundly influenced by its genotype – a spider is unable to parasitise a pest egg, for example – phenotypic plasticity can also allow the members of an enemy species to respond to the availability of prey. For example, Tahir and Butt (2009) showed in a study of spiders of Pakistani rice systems that Diptera were the dominant prey early in the season. Only later, when planthopper numbers in the crop began to increase, did this prey become dominant in the diet. Such plasticity – in this case responding to temporal shifts in prey availability – has clear importance in pest suppression. The availability of dipteran prey early in the season allowed spider numbers to increase to high levels and thereby provided effective control of pest planthoppers. In a situation where diet plasticity was not exhibited by the predator this would not be possible. Clearly the early season build-up of the spider community also depends on the availability of prey species and this in turn is dependent largely on the use of inputs of organic matter such as animal manure (Settle *et al.*, 1996). A similar idea comes from the use of nectar by natural enemies. Lacewings (Hemerobiidae in this case) use and benefit from nectar when aphid prey numbers are low, but nectar does not contribute significantly to their fitness at high prey densities (Robinson *et al.*, 2008).

NATURAL ENEMY EVENNESS

Considerable research attention has been given to increasing overall numbers of natural enemies or the numbers of species (species richness). However, recent work has shown that relative evenness of the numbers of individuals across the species in an enemy community is also important (Crowder *et al.*, 2010). In that study, field enclosures were used to test the effect of relatively even versus less even communities of enemies. Pest population reduction and plant productivity were higher when enemy evenness was high; an effect that was independent of which enemy species was numerically dominant.

Unevenness can leave niches under-exploited and the common enemies are likely to be competing for prey as a result of low levels of resource partitioning. This difference between species diversity and species evenness can be important but, perhaps surprisingly, many studies of biodiversity in agricultural systems measure diversity alone and ignore evenness (Bengtsson *et al.*, 2005).

From theory to practice: exploiting top-down effects with agri-environmental schemes, 'SNAP' and ecological engineering

As awareness of the potential of natural enemies as biological control agents increased, a great deal of modelling work was undertaken to understand the ecological mechanisms that would lead to density-dependent population regulation and therefore persistence of the parasitoid–host relationship (Nicholson and Bailey, 1935). This work brought about a realisation that density-dependent regulation was not required for population reduction to take place, and that parasitoid– and predator–host communities do not exist as single, homogeneous units. Rather, such communities exist in patchy environments (Hassell *et al.*, 1991) that require models to take into account

meta-population effects (Hanski and Simberloff, 1997). Further, although concepts such as the area of discovery (a) and instantaneous attack rate (a′) of the natural enemy were crucial components of these models, there was no recognition that these two key parameters could change substantially if non-host/prey resources such as nectar were part of the system. Kean *et al.* (2003) showed the profound effect on these parameters of nectar provision by using a development of the models produced by Hassell *et al.* (1991). The awareness that biological control effectiveness in monocultures is almost always operating at a sub-optimal level grew along with knowledge of the value of uncultivated land as a refuge and as a source of non-prey food (van Emden, 1965) and the emergence of conservation biological control began to develop as a science in its own right (Barbosa, 1998). This awareness began to be reflected in farm environmental policies within the European Union and elsewhere by the use of approaches such as unsprayed crop strips ('conservation headlands'), areas taken out of crop production ('set aside'), and the broader 'Countryside Stewardship Scheme' set up in 1991 and now replaced by the 'Environmental Stewardship Scheme' (Natural England, undated). These agri-environmental schemes have a broad public good and environmental protection and remediation mission rather than being focused on the management of farm biodiversity for any specific ecosystem service such as pest control (Wade *et al.*, 2008a). Accordingly, they are not informed by appropriate ecological research addressing aspects such as which plant species are best to sow or conserve, the optimal layout of non-crop features such as 'weed strips', the nature of effects on pest and natural enemy species and the ecological mechanisms at play. Notwithstanding these potential problems, some land use practices such as cover crops to enhance breakdown of prunings or tree strips to shelter crops and livestock offer scope to promote natural enemy biodiversity (Plate 1.2). A caution was provided, however, by an assessment of agri-environment schemes in the Netherlands that showed no positive effects on plant and bird species diversity (Kleijn *et al.*, 2001). Nevertheless, of some relevance to pest management, the hoverfly (Syrphidae) fauna was slightly more diverse (Kleijn *et al.*, 2001). This is, however, a minor gain from the major funding allocated to these schemes.

As the science of conservation biological control grew, the freshwater ecology concept of 'resource subsidies' (inputs from external habitats to support the food web in a focal habitat) (Takimoto *et al.*, 2002) became increasingly used to stress the significance to natural enemies of external habitats and the resources available therein (Tylianakis *et al.*, 2004). The role of plant-provided foods for predators and parasitoids is now well understood and actively exploited for pest management (Wäckers *et al.*, 2007). A simple acronym, 'SNAP', is used to summarise the ways in which non-crop resources can help natural enemies. The letters stand for shelter, nectar, alternative prey and pollen. The value of shelter is apparent in a British research programme that led to the development of grassy, overwintering strips ('beetle banks', Plate 1.2) in arable farmland (Thomas *et al.*, 1991; 1992; 2001). These raised earth banks, sown with cocksfoot grass (orchard grass), *Dactylis glomerata* L., are established across fields. Large numbers of predatory carabid and staphylinid beetles as well as spiders overwinter in the shelter provided. Many of these emigrate into the crop in spring, leading to reductions in aphid pest numbers (Collins *et al.*, 2002). Subsequently, other ecosystem services have been demonstrated for these refuges, including breeding populations of the harvest mouse (*Micromys minutus* Pallas) (Bence *et al.*, 2003), a species of conservation relevance, and gamebirds such as the grey partridge (*Perdix perdix* L.), a species of cultural and economic significance for recreational shooters. The extent to which features such as beetle banks can support wildlife is greatly influenced by the level of use of native as opposed to exotic plant species; a subject explored in chapter 17 of this volume. Beetle banks are effectively a 'service providing unit' (Kontogianni *et al.*, 2010) in that the protocol for improved ecosystem services is clear and emphasises to farmers how, where and why these enhancements should be made. The use of biodiversity as a pest management tool is explored from the perspective of ecological economics in chapter 4 of this volume.

Other examples of research and uptake of conservation biological control have concerned the other three components of SNAP, especially the provision of nectar (N) and pollen (P) for natural enemies such as parasitoid wasps, hoverflies, lacewings, ladybirds (Wäckers *et al.*, 2007). Nectar provides the carbohydrates for energy, as well as amino acids and minerals, while pollen provides much of the protein required by these insects for egg maturation. Plant species commonly used include buckwheat (*Fagopyron esculentum*

Moench) (e.g. Berndt *et al.*, 2002), phacelia (*Phacelia tanacetifolia* Benth.) (e.g. Hickman and Wratten, 1996), alyssum (*Lobularia maritima* L.) (Begum *et al.*, 2004) and, sometimes plants in the Apiaceae (e.g. Idris and Grafius, 1995). The majority of studies tend to focus on nectar use by hymenopteran parasitoids but the Hickman and Wratten (1996) study is an example of one on pollen use by adult hoverflies.

As pointed out by Wade *et al.* (2008b), a hierarchy of effects of floral provision is usually expected. This hierarchy is:

1. Natural enemies aggregate on the flowers
2. The ecological fitness of natural enemies increases
3. Searching behaviour of the insects changes
4. The proportion of pests killed increases
5. Pest populations are reduced
6. Pest populations are brought below the economic threshold.

For conservation biological control practitioners, achieving the effects in the above hierarchy becomes more difficult as the steps in the hierarchy are progressed. One way in which the science has risen to this challenge of increasing efficacy whilst avoiding possible negative effects has become known as 'ecological engineering' for pest management (Gurr *et al.*, 2004). Essentially, ecological engineering aimed to place conservation biological control on a more rigorous theoretical foundation with an experimental framework informing decisions such as the choice of nectar plant species. This was an advance because many previous attempts at CBC were not well targeted, consisting of seed mixes for example. The species in these were not generally tested for efficacy for any particular natural enemies, or to deny benefit to pests (e.g. moths taking nectar (Lavandero *et al.*, 2006)). In tropical rice, in particular, the need for ecological engineering has been stressed (Settele *et al.* 2008) and is now the focus of significant research in Asia (Gurr *et al.*, 2011). The broader state of research on the use of biodiversity to increase availability to natural enemies of important plant foods is explored in chapter 9 of this volume.

The least actively researched aspect of the SNAP acronym is provision of alternative hosts and prey. The pioneering work by Cate (1975) which identified non-crop plants that support alternative hosts of *E. elegantula* parasitoids has led to only sporadic work to look at similar relationships in other systems (e.g. in pome (pip) fruit (Pfannenstiel *et al.*, 2010)). The availability of alternative prey has received more research attention by virtue of a growing interest in the importance of generalist natural enemies. Chapter 3 of this volume explores this phenomenon whilst chapter 13 provides a detailed example of how detritivores can be enhanced in rice systems as alternative prey to support early season build-up of generalist predators.

CONCLUSION: BIODIVERSITY FOR PEST MANAGEMENT

Irrespective of whether bottom-up or top-down ecological effects are being exploited, and whichever aspect of the SNAP acronym is targeted, an advantage of manipulating biodiversity for pest management is that it can be initiated and carried out by individual landowners. This is in direct contrast to classical biological control where phytosanitary-related quarantine regulations restrict the introduction of exotic agents, making it the realm of government agencies. Only these and large research providers are able to conduct the necessary host specificity testing to clear regulatory hurdles. In contrast conservation biological control is much more in the hands of the individual farmer. Further, the implementation tends to lead to intensely visual improvements in landscape features, making it easier for the growers to demonstrate that they are making a tangible, biodiversity-based attempt to improve pest suppression on their land. Demonstrating this can have benefits in terms of farm tourism and sales of 'branded' products as well as qualifying for government payments under agri-environmental schemes. Several reviews of this biological control approach analyse the ecology and utility of this method (Landis *et al.*, 2000; Zehnder *et al.*, 2007; Jonsson *et al.*, 2008 and other papers in that special issue of *Biological Control*). Uptake of biodiversity-based strategies by farmers and other land managers is, however, contingent on effectively communicating to them the need to implement new approaches, and the means by which such approaches can be implemented. This is an area often overlooked in research on pest, disease and weed management and several chapters in this volume seek to redress this. Chapter 12 examines the sociological dimension of effective communication with farmers, drawing on a successful project that is persuading Asian rice farmers to reduce dependence on insecticides. Also, chapter 14 examines the importance of

policy in driving change in pest management, reporting on a national 'Green Plant Protection' initiative being implemented in China. Finally, chapter 18 considers the use of biodiversity-based strategies in the urban environment; an important arena given that an increasingly large proportion of the world's population live in cities and are potentially exposed to the detrimental effects of insecticide use in ornamental and amenity areas.

It is critical for the successful use of biodiversity in pest management that farmers and other practitioners, as well as policy-makers responsible for incorporating this ecosystem service into agri-environmental schemes, are well served by the research community. Readers of this book will need to rise to this challenge and ensure that research and conventional 'outputs' (e.g. scientific publications) are converted into 'outcomes' (i.e. changed practices) that enhance the three pillars of sustainability: economy, society and the environment. However, too great a role for Gross Domestic Product as an indicator of improvement is unwise, as GDP is increasingly recognised as a poor measure of human wellbeing (Costanza *et al.*, 2009). This will demand ongoing work to more completely understand the ecology of the mechanisms that drive the effects of biodiversity on pests and their natural enemies. Important also is the need to convert such knowledge into practicable technologies that are compatible with modern and future farming systems. Fortunately for this mission, it seems likely that future farmers will significantly broaden their enterprises beyond food, fibre and fuel production. The expansion of agri-environmental schemes will increasingly provide revenue streams to farmers for providing 'public good' services such as conserving biodiversity, and for practices that help capture atmospheric carbon dioxide. These practices will include planting farm trees, perennial forages and green manure crops to increase soil carbon. With careful planning these practices might simultaneously harness the power of biodiversity to reduce the impact of pests (i.e. multiple ecosystem services on farmland), and developing a structure to pay for them must be tackled in future agricultural policies.

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