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CLIMATE CHANGE AND INVERTEBRATE GENETIC RESOURCES FOR FOOD AND AGRICULTURE: STATE OF KNOWLEDGE, RISKS AND OPPORTUNITIES

by

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LIST OF ABBREVIATIONS

BCA	biological control agent
eCO_2	elevated carbon dioxide (CO_2)
EPN	entomopathogenic nematode
FACE	Free-Air Carbon dioxide Enrichment programme (USA)
FAO	Food and Agriculture Organization of the United Nations
FBO	Fertilization Bio-Organique
GTR	generation time ratio
HIPV	herbivore induced plant volatiles
IPCC	International Panel on Climate Change
IPM	integrated pest management
IPPC	International Plant Protection Convention
ISPM	International Standards for Phytosanitary Measures (of the IPPC)
NTZF	northern temperate zone forests
OIE	World Organisation for Animal Health
TLRF	tropical lowland rainforests
UN	United Nations

GLOSSARY

This glossary is intended to explain most of the technical terms relating to invertebrates, and their evolution and ecology, used in this study. Words or terms only used once are explained where they occur. Many entries have been taken from Wikipedia (http://en.wikipedia.org/); others from a variety of sources or defined by the authors.

Term	**Definition/explanation**
Adaptation (ecosystems)	Those activities that will enable ecosystems to adjust to climate change and, via such alterations, to decrease their vulnerability to its impacts.
Adaptation (organisms)	The evolutionary process whereby a population becomes better suited to its environment via natural selection. Adaptation can also occur as a result of physiological or morphological modifications, usually referred to as acclimatization, acclimation or plasticity.
Alien species	A species living outside its native distributional range.
Anecic	Soil-dwelling and surface-feeding habits (e.g. anecic earthworms construct deep permanent burrows and visit the surface to obtain plant leaf litter).
Arthropoda	The phylum Arthropoda or arthropods are invertebrates with segmented bodies and jointed limbs. They include chelicerates (spiders, mites, scorpions, etc.), myriapods (millipedes, centipedes, etc.), hexapods (insects and closely related groups), and crustaceans (lobsters, crabs, barnacles, crayfish, shrimp and many others including woodlice).
Assemblage(s)	All of the various groups of species that coexist in a particular habitat.
Assembly rules	Rules for why a particular type of community of organisms/species

(communities or species)	developed when other stable community types were possible. These can be generated by species interactions or random processes.
Augmentative biological control	The release of a biological control agent (BCA), usually directly onto the crop to be protected, once or several times in a cropping cycle (see p. 19).
Biogenic structures	A physical structure of biological origin, e.g. termite mounds, earthworm casts.
Biological control agent (BCA)	A natural enemy of a pest.
Broad-spectrum pesticide	A pesticide that kills a broad range of organisms, both pests and beneficial organisms (including naturally occurring predators and parasites).
Carbon sequestration	The process of removing carbon from the atmosphere through photosynthesis and depositing it in a reservoir.
Classical biological control	The introduction of natural enemies to a new locale where they did not originate or do not occur naturally (see p. 19).
Co-evolution (co-evolved)	Evolution in a one-on-one interaction, such as that between plant and herbivore, predator and prey, host-symbiont or host-parasitic pair, where adaptations by one species in the pair act upon the other.
Coleoptera	Beetles (an order of insects).
Collembola (collembolans)	Springtails (an order of insects).
Comminution	Breaking up of (soil) particles.
Cosmopolitan	Found almost anywhere around the world – at least in the Old and New Worlds.
Cryptic species	Species that look very similar morphologically to each other and may be misidentified (and hence overlooked).
Decomposition	The process by which organic material is broken down into simpler forms of matter resulting in CO_2 production.
Detritivore	An organism that obtains nutrients by consuming detritus (decomposing organic matter).
Diapause	A period of suspended development and growth accompanied by decreased metabolism in insects and some other animals (e.g. earthworms); usually over winter (hibernation), over summer (aestivation) or during dry periods.
Diptera	Flies (an order of insects).
Dispersal	Movement of individuals of a species away from an existing population or away from the parent organism.
Ecoregion	A relatively large unit of land or water that is characterized by a distinctive climate, ecological features and plant and animal communities, e.g. East African coastal forest, the llanos of Colombia.
Ecosystem engineer	An organism that creates or modifies physically the environment it lives in; sometimes their activities may result in complete alteration of habitats.
Ecosystem service	Any of the many benefits that humans obtain from (usually natural) ecosystems, including products such as harvestable invertebrates and processes such as the decomposition of wastes and natural biological control.
Ectoparasite	A parasite that lives on the outside of its host’s body.
Enchytraeidae (enchytraeids)	A family of oligochaete worms, resembling small earthworms and including species known as potworms that live in highly organic terrestrial

	environments.
Endogeic	A species that lives and feeds in the soil (e.g. some earthworms).
Endosymbiont	Any organism that lives within the body or cells of another organism.
Entomopathogenic nematodes (EPNs)	Soil-inhabiting, lethal insect parasitoids that belong to the phylum Nematoda.
Epigeic	A species that lives and feeds in the soil litter layer (e.g. some earthworms).
Fitness	The ability to both survive and reproduce. In classic Darwinian natural selection, the ability of a female to produce grand-daughters.
Flow-on effects	Effects that happen as a consequence of a preceding event.
Food web	A diagram showing the connections among everything that organisms in a location eat and are eaten by. A food web is more complex than a food chain because it has more connections.
Functional domain (soil)	Soil is influenced by biotic regulators (e.g. an ecosystem engineer or plant roots) and abiotic regulators (e.g. dry and wet periods), and characterized by its organic resources (litter, organic matter) and biogenic structures where there is a biotic regulator. The sum of structures produced by a population or community of invertebrate engineers creates a specific environment defined as a functional domain.
Functional group	A set of species that have similar effects on a specific ecosystem-level biogeochemical process.
Generalist natural enemy	A natural enemy that can use a wide variety of hosts/prey, e.g. more than one order.
Genetic bottleneck	A temporary reduction in population size that causes the loss of genetic variation.
Guild	A guild (or ecological guild) is any group of species that exploit the same resources in a similar way, therefore sharing a similar ecological niche.
Herbivore	An animal that feeds chiefly on plants.
Hymenoptera	Ants, bees and wasps (an order of insects).
Hyperparasitoid	A parasitoid which develops on another parasitoid.
Insecta	The class insects.
Integrated pest management (IPM)	"a strategy of pest containment which seeks to maximise natural control forces such as predators and parasites [i.e. parasitoids] and to utilise other tactics only as needed and with a minimum of environmental disturbance" (Glass in Davis and McMurtry, 1979) (see p. 19)
Invasive alien species	Species that are (i) outside their natural distribution area, and (ii) threaten biological diversity.
Invertebrate	An animal without a backbone (all animals except the vertebrates: mammals, birds, reptiles, amphibians and fish).
IPCC scenario	The IPCC considered several possible scenarios for climate change depending upon different assumptions (IPCC, 2007a, 2007b) (see p. 29).
Isopoda (isopods)	Various small terrestrial or aquatic crustaceans with seven pairs of legs adapted for crawling, e.g. wood louse.
Keystone species	A species whose presence and role within an ecosystem has a disproportionate effect on other organisms within the system; a species that plays a fundamental role in maintaining the plants and animals in an ecosystem.
Micro-organism	An organism of microscopic size; used here to include bacteria, protozoans,

	yeast, fungi, viruses and algae; all living organisms except plants and animals.
Mitigation (in the context of climate change)	Mitigation involves reducing the actual level of CO_2 (and other greenhouse gases) or reducing the rate of increase in CO_2 levels. There are two main strategies available to mitigate CO_2 increases: reduce emissions (i.e. the source) or increase the photosynthetic biomass (i.e. the sink)
Mutualism (mutualist)	The way two organisms biologically interact where each individual derives a fitness benefit (i.e. increased reproductive output).
Natural biological control	The role of indigenous naturally occurring natural enemies in controlling pests (see p. 19).
Natural enemies	The organisms that cause mortality or reduced fitness of another (usually a pest).
Nematoda and nematode	A large phylum of diverse, usually small or very small, round, worm-shaped animals.
Oligophagous	Feeding on a restricted range of food substances, especially a limited number of plants; as opposed to polyphagous (many food substances) or monophagous (one food substance).
Omnivores	Animals that consume resources from two or more trophic levels. “True omnivores” feed on both plants and animal prey, whereas “trophic omnivores” feed on animals at two different trophic levels (e.g. herbivores and predators).
Parasites	An organism that lives on or inside another organism to the detriment of the host organism.
Parasitoid	An organism that spends a significant portion of its life history attached to or within a single host organism, which it ultimately kills (and often consumes) in the process.
Phenolic(s)	Organic compounds with one or more phenolic groups: i.e. a phenyl ($-C_6H_5$) group bonded to a hydroxyl (-OH) group. They are the most widely distributed class of plant secondary metabolites and several thousand different compounds have been identified.
Phenology	(The study of) periodic plant and animal life cycle events and how these are influenced by seasonal and inter-annual variations in climate.
Photoperiod (photoperiodism)	The relative length of day and night. (Photoperiodism is the physiological reaction of organisms to the length of day or night.)
Plasticity	The ability of an organism to change its phenotype in response to changes in the environment.
Predator	An organism that attacks and feeds on its prey (the organism that is attacked).
Primary consumers	Animals that eat plants; herbivores.
Protists	A diverse group of eukaryotic micro-organisms.
Quaternary (Period)	The most recent period in the geological time scale, spanning the last 2.6 million years; it includes two geological epochs: the Pleistocene and the Holocene.
Refugium (plural refugia)	Location of an isolated or relict population of one or more once widespread animal or plant species.
Saprophyte	A species that obtains its nutrition from the processing of dead or decayed organic matter.
Secondary consumers	Animals that eat other animals.

Self-organized system	An (ecological) system in which the overall pattern emerges from numerous interactions among the lower-level components of the system. The rules specifying interactions among the system's components are executed using only local information, without reference to the overall pattern.
Sericulture	The rearing of silkworms for the production of raw silk; silk farming.
Soil aggregate	A broad category of coarse particulate material of varied organic and mineral origins.
Soil compaction	The effect that occurs when something compresses the soil, causing it to lose pore space. It may be due to the weight of heavy machinery, lack of water in the soil, or changes in invertebrate fauna. Affected soils become less able to absorb rainfall, thus increasing runoff and erosion. Plants have difficulty in compacted soil because the mineral grains are pressed together, leaving little space for air and water, which are essential for root growth. Burrowing animals also find it a hostile environment, because the denser soil is more difficult to penetrate.
Soil profile	The vertical sequence and thickness of soil horizons; a soil horizon is a specific layer that possesses physical characteristics that differ from the layers above and beneath.
Specialist natural enemy	A natural enemy with a limited range of host/prey species, e.g. a few, usually related, genera or species.
Sub-fossil	Organism remains whose fossilization process is not complete, either for lack of time or because the conditions in which they were buried were not optimal for fossilization. Sub-fossils are often found in depositionary environments, such as lake sediments and soils.
Successional stages	A stage in the series of changes in an ecological community that occur over time after a disturbance.
Top predator	Predators that have no predators of their own, residing at the top of their food chain.
Trophic level	The position an organism occupies on the food web or in a food chain. A food chain represents a succession of organisms that eat other organisms and are, in turn, eaten themselves. The number of steps an organism is from the start of the chain is a measure of its trophic level. Food chains start at trophic level 1 with primary producers such as plants, move to herbivores at level 2, predators at level 3 and typically finish with carnivores or top predators at levels 4 or 5.
Voltinism	The number of broods or generations of an organism in a year.

EXECUTIVE SUMMARY

Invertebrate species are predominant in the food webs and among the ecosystem engineers associated with agriculture. They have a major influence on productivity and therefore play a key role in food security. From an ecological perspective, invertebrates play important primary roles in food webs as primary consumers (herbivores); higher-order consumers (predators, parasitoids, hyperparasitoids); mutualists (facultative and obligate pollinators); parasites of plants, invertebrates and vertebrates; and saprophytes (mediators of decomposition, and energy and nutrient flows into and out of agricultural ecosystems). As ecosystem engineers, invertebrates perform vital physical roles in maintaining soil structure and processes. The different roles that invertebrate species play in an agricultural ecosystem are responsible for a complex web of direct and indirect interactions with each other and with the broader landscape, including natural ecosystems. Subtle changes in interactions between species can dramatically affect the impact that arthropods have on plant productivity in agricultural systems. Therefore, predicting how climate change will influence the effects of invertebrates on crop productivity is not straightforward. Complex and non-linear responses are expected among the interactions between invertebrates, plants and ecological processes.

This study focuses on three main groups of organisms: soil invertebrates, biological control agents (BCAs) and pollinators. Invertebrates as food and as a source of products are also briefly considered. In broad terms, invertebrate genetic resources can be considered to include all material that contains genetic information of, or derived from, invertebrates. However, this study focuses on whole organisms, as it is these, rather than their genetic information, that play key roles in agricultural systems, and have the potential to be used, moved or manipulated to the benefit of agriculture.

Soil invertebrates are a key component of agricultural landscapes. They participate in essential soil processes that maintain healthy productive soils in the face of changing environmental conditions. Reducing the diversity of a community of soil invertebrates reduces its beneficial functions and services, with drastic ecological effects such as long-term deterioration of soil fertility and agricultural productive capacity. The introduction of a keystone species may have detrimental or beneficial effects depending on the context. The interaction between soil invertebrates and soil micro-organisms is critical; the activities of soil invertebrates regulate microbial activity in soils, and micro-organisms enter into intimate relationships with soil invertebrates to help them degrade highly complex compounds such as cellulose.

Different groups of invertebrates provide biological control of crop pests. In many situations they form the basis of, and tools for, the integrated pest management (IPM) approach. Given that the losses caused by pre- and post-harvest pests can be very substantial, and are likely to increase as a consequence of climate change, the potential benefits of using invertebrates as BCAs are vast, but as yet only partially tapped. The potential of soil invertebrates to assist in this function is still largely unknown.

Pollination services by animals, especially by insects, are among the most widespread and important processes that structure ecological communities in both natural and agricultural landscapes. An estimated 60–90 percent of the world’s flowering plants – including a range of economically important species – depend on insects for pollination. Crop pollination used to be (and often still is) provided by wild pollinators spilling over from natural and semi-natural habitats close to crop fields. This service has generally been free and therefore has received little attention in agricultural management. If wild pollinators are lacking or additional pollination is required, as is the case in many intensive agricultural production systems, farmers in some developed countries can buy or rent managed honeybees or sometimes other species (e.g. bumblebees, alfalfa leafcutter bees, alkali bees). Both options – i.e. use of wild species and managed bees – have recently come under pressure, a development that is sometimes referred to as the “pollination crisis”.

Some invertebrates are important food items in their own right, and several other sectors rely on products from insects (e.g. honey and silk production). In groups with little access to other sources of protein, insects can be a relatively important component of the diet. They are already widely used as a wild food resource in the developing world, particularly when other foods are scarce. The cultivation of invertebrates for human food may emerge as an ecologically sound source of animal protein.

One of the pathways through which food security and agricultural production will be influenced by climate change is via its impact on invertebrates. The pests that affect crop production, quality and storage; the beneficial species that pollinate and protect crops by predation and parasitism of pests; the decomposers that aid maintenance and nutrient cycling within managed ecosystems; the ecosystem engineers that sustain the ability of soil to provide ecosystem services; and the vectors that spread animal and plant diseases all respond to regional and seasonal changes in climate. The key climate projections and impacts on agriculture are based on the latest Intergovernmental Panel on Climate Change (IPCC) assessment and the potential direct and indirect impacts on invertebrates relevant to food and agriculture are reviewed. Single and combined effects are expected, and the responses of invertebrate species and food webs will be context dependent. Most studies have dealt only with a single factor such as elevated CO_2 (eCO_2), warming or changes in rainfall patterns; there are few data on the likely interactions among these climate change-related factors. The interaction of these factors with land-use change also needs to be considered.

Invertebrates have limited ability to regulate their body temperature and are directly under the control of temperature for development, reproduction and activity. Therefore, although some groups such as soil invertebrates and animal ectoparasites may be buffered by the niches they occupy, the interaction between a species' thermal sensitivities and the abiotic factors determined by climate largely explains its observed distribution and abundance. Within this distribution, climate change will have further indirect effects through its influence on host availability and the other resources that plant communities provide.

The crops produced in most regions are expected to change over time with climate change as growers select and develop species and varieties that optimize yield and/or economic returns under the prevailing conditions. Aided by transfer through human activities, the majority of invertebrate pollinators, pests and their natural enemies can be expected to move with their host plants as crop and forage distributions change. Sub-fossil evidence from the Quaternary Ice Ages suggests that in times of rapid climate change, insects track acceptable conditions rather than evolving *in situ*.

Extreme weather events such as droughts, floods and unseasonal frosts are followed frequently by pest population explosions. Temperate geographically isolated islands and regions will become more vulnerable to colonization through wind dispersal with the intensification of weather systems and/or absence of frosts. Increases in CO_2, changes in water availability and increases in temperature will alter plant chemistry, phenology, growth and distribution. In turn, changes in the physiology, form and biomass of plants will alter the quality and composition of the leaves, which may affect the growth and development of plant herbivores and the animals that prey on them. Natural enemies with narrow host ranges may be more sensitive to climate change than generalist herbivores and predators because they are, of necessity, precisely synchronized with the development of their hosts. They may become locally extinct if these interactions become decoupled. Even in simplified agricultural ecosystems, the large number of potential interactions makes predicting the impact of climate change on invertebrates daunting.

The role of invertebrates in mitigating climate change is limited. However, the amount of carbon in the soil is affected by the action of soil invertebrates and micro-organisms. If these actions could be managed, they might provide a means of reducing atmospheric CO_2. Understanding the role of invertebrates and micro-organisms in soil aggregation processes and dynamics will help in predicting future impacts and designing targeted management options, as these processes determine the residence time of carbon in soil. The action of soil invertebrates, BCAs and pollinators will all affect plant biomass and, hence, the amount of carbon fixed in crop plants, but this is only a temporary effect during the cropping cycle.

There is little or no scope to use genetically modified invertebrates in agriculture and food. Indeed, as yet very little is known about the natural genetic diversity in the invertebrate groups relevant to agriculture.

Conservation of invertebrate genetic resources useful to agriculture and food is necessarily based on whole organisms *in situ*. Healthy agro-ecosystems will provide much of this, but natural habitats as a source of soil invertebrates, BCAs and pollinators will also be important, in as yet unpredictable ways.

Because of the risk of introducing invasive species that may put some soils at risk, the movement of soil invertebrates between countries is not recommended, and there are no suitable guidelines and protocols for this. We anticipate an increasing demand for the movement of BCAs between countries to address new pest problems. There are guidelines and protocols in place, but it will be important that national regulations implementing the Nagoya Protocol facilitate this exchange. Specialist pollinators, such as the oil palm weevil (*Elaeidobius kamerunicus* (Faust); Coleoptera, Curculionidae), have only been moved between countries to a very limited extent, and in this case the procedures and protocols of weed biological control have been used. The movement of social bees, such as honeybees and bumblebees, between countries has been implicated in the spread of pests and diseases, and improved guidelines and protocols may be needed, especially in the light of anticipated demand. Domestication of wild pollinators is likely to lead to increased movement of new species between countries, and guidelines and protocols for this will be needed.

In this report, we find that there are many gaps in our knowledge of how invertebrate genetic resources are affected by climate change, and how to use them in response to climate change. Specific conclusions regarding the impact of climate change on particular elements of invertebrate genetic resources are not possible yet. However, three general conclusions are evident.

- It is likely that climate change will disrupt the use of invertebrates in agriculture, although the precise nature of the disruptions is not yet known.
- Without intervention, these disruptions will result in production losses, although the scale and extent of the losses is not yet known.
- The extent of some of the losses will require intervention to facilitate adaptations of the relevant invertebrates. The methods for these interventions have not yet been developed, and policies to facilitate them are not yet in place.

Below we identify the priority actions needed in the context of these conclusions.

Scientific knowledge

- Improvement to knowledge and understanding of (i) wild pollinators of major crops, (ii) soil invertebrates, (iii) natural BCAs, and (iv) their contribution to crop production in developed and developing countries.
- Quantification of the responses of invertebrate species, communities, food webs and their various interactions to climate change-related factors.
- Further investigation of past climate change in tropical areas, and assessment of how invertebrate species have responded in terms of distribution (based on sub-fossil records).
- Taxonomy and genetic characterization of the invertebrates of agro-ecosystems, especially critical BCAs and soil invertebrate faunal groups.
- More studies on the rates of movement of selected key species, especially soil invertebrates without a motile stage.

Conservation, use and access

- Improvement of rearing technologies to shift selected wild bee and other pollinator species to domestication.
- Improvement of technologies and approaches to ensure the conservation and promotion of generalist natural enemies in agricultural landscapes.
- Identification and conservation of the source habitats of pests and associated BCAs.
- Development of mass production methods for some important soil ecosystem engineers so as to facilitate experimental evaluation of their use in soil management practices.
- Further research on the sustainable exploitation and domestication of edible invertebrates.

Facilitating policy environment

- Development of an overarching holistic strategy that integrates invertebrates with other ecosystem components to better design and manage agro-ecosystems for food security in the face of climate change.
- Development of guidelines for facilitating and regulating the movement of invertebrate genetic resources between countries that build on what is already available for BCAs and include emergency responses and pest risk assessment protocols.
- Recognition that in implementing the Nagoya Protocol, countries need to take into consideration the need for invertebrate genetic resources to sustain agriculture, food production and world food security when drafting national strategies (e.g. producing guidelines and procedures).
- Further development and implementation of existing national biodiversity programmes.

Islands versus continental areas

- Policy support for island states, which will probably not be original sources of BCAs (or pests) but will need new BCAs.

Temperate versus tropical areas

- Attention to the question of how species ranges will change in tropical regions in response to climate change.
- Testing the hypothesis that tropical species may be more sensitive to climate change as a result of narrower biotic ranges and lack of exposure to climatic variation.

CHAPTER I. INTRODUCTION

1.1 ROLES OF INVERTEBRATES IN SUSTAINABLE AGRICULTURE AND FOOD SECURITY

Invertebrate species are predominant in the foodwebs and among the ecosystem engineers associated with agriculture. They have a major influence on productivity and therefore play a key role in food security. The vast majority of the invertebrate species in agro-ecosystems belong to the phyla Arthropoda (especially the Insecta), Annelida (segmented worms) and Nematoda. From an ecological perspective, these animals play important roles in food webs as primary consumers (herbivores); higher-order consumers (predators, parasitoids, hyperparasitoids); mutualists (facultative and obligate pollinators); parasites of plants, invertebrates and vertebrates; and saprophytes (mediators of decomposition, and energy and nutrient flows into and out of agricultural ecosystems). Soil invertebrates include ecosystem engineers that are powerful drivers of soil physical functions (water dynamics, aeration, protection from erosion hazards). They play an important role in carbon cycling, as they control the carbon sequestration process and influence greenhouse gas emissions. The different roles that invertebrate species play in an agricultural ecosystem are responsible for a complex web of direct and indirect interactions, which in soils manifests as self-organized systems of different sizes and functions. Subtle changes in the interactions between species at different trophic levels within food webs can dramatically modify the impacts of arthropods on plant productivity in agricultural systems. However, the disappearance of earthworms and ecosystem engineers generally impedes the formation of their functional domains in soils (see 3. Ecosystem Engineers in Section 2.1.1). Given the number and complexity of the processes involved, predicting how the contributions of invertebrates to plant productivity will be affected by climate change is far from straightforward.

For this study, we focus on three main functional groups which act in a positive way on agriculture, and so may be used, manipulated or moved to benefit agriculture: soil invertebrates, biological control agents (BCAs) and pollinators (Chapter II).

1.2 THE EXPECTED IMPACT OF CLIMATE CHANGE ON AGRICULTURAL PRODUCTION SYSTEMS AND INVERTEBRATES RELEVANT TO FOOD AND AGRICULTURE

As areas become more favourable for growing a particular crop, they also become more favourable for a suite of associated crop pests. Pest management practices will therefore need to adapt to such changes. As regions further from the equator become warmer, they may be able to learn from past experiences of pest management in regions closer to the equator.

Land-use changes, whether as responses to climate change, or other (socio-economic) factors, are expected to have a greater impact on the occurrence of invertebrate pests than the direct effects of climate change alone. At one extreme, conversion of natural or semi-natural habitat to agricultural land will destroy most of the associated food webs and eliminate most ecosystem services, until a new balance is established that will partially fill this gap. A plethora of indirect effects can result from land-use changes. For example, simplified agricultural ecosystems are much more prone to invasion by, and outbreaks of, invertebrate and other pests, and changes in vegetation cover can modify the climate via alterations in the surface albedo and the roughness of the land (Peñuelas *et al*., 2009). **Crop choice and soil and pest management practices will be very important in terms of mitigating the effects of climate change.**

Despite many uncertainties and unknowns, **there is a growing consensus that climate change could lead to an overall increase in the abundance and diversity of invertebrate pests – and pest pressure – as habitats become more favourable for their establishment and development, new niches appear, stabilizing interactions are decoupled, and invasive species arrive as a result of range expansions** (e.g. Cannon, 1998; Patterson *et al*., 1999; Rosenzweig *et al*., 2001; Fuhrer, 2003; Luedeling *et al*., 2011). This is not to deny that some impacts of climate change may be beneficial, but the detrimental effects referred to above suggest that, at the very least, “pest and pathogen attacks are likely to be more unpredictable and the amplitude larger” (Gregory *et al*., 2009). The impact of increased temperatures on pest status can be crudely assessed in terms of the number of sprays required to control a given type of pest along a latitudinal transect. For example, sweetcorn farmers in Florida make considerably more insecticide applications against Lepidoptera pests than those located further north in the United States of America (Petzold and Seaman, 2006).

The impact of climate change on agriculture, and especially on invertebrates associated with agricultural systems, is discussed in Chapter III.

1.3 POTENTIAL OF INVERTEBRATE GENETIC RESOURCES TO ADAPT TO AND MITIGATE CLIMATE CHANGE

Biotic responses to climate change include persistence *in situ* (if species have the physiological capacity to tolerate the change), range shifts to more tolerable climes or, failing these, extinction (Davis *et al*., 2005). In other words, **organisms will have to adapt, move or die**. Their inherent “flexibility” – in terms of both their genotype (i.e. genetic makeup) and the plasticity of their phenotype – will determine their survival (Hodkinson and Bird, 2006).

As we shall discuss, **most invertebrates are expected to change their geographical distribution in response to climate change so as to remain in areas to which they are well adapted.** This view is strongly supported by sub-fossil evidence of insect distribution during glaciations and interglacial periods of the Quaternary Period. Even so, we recognize that the current landscape is very different from any that existed during the Quaternary Period, being divided by barriers created by human activities. However, these barriers are likely to affect species in natural ecosystems rather more than those associated with agro-ecosystems, and the movement of the latter is likely to be facilitated rather than hindered by human-induced landscape changes. There will also be some *in situ* adaptation. This is expected to be more marked where movement is not an option (e.g. low, isolated islands). Hence, many of the challenges associated with the management of invertebrate genetic resources in agriculture in the context of climate change will relate to climate-driven or human-assisted movement of invertebrate species.

Experiments, as well as observations of natural above-ground systems, suggest that species higher up the food web – including top predators as well as herbivores – are more likely to be affected by global warming than species lower in the food web(Petchey *et al*., 1999). It is generally assumed that species will not have sufficient time for evolutionary adaptations to the changing climate, although all of the available responses – acclimation (i.e. physiological adaptation), adaptation and dispersal – involve adaptive responses of some sort (Davis *et al*., 2005). The extent to which species are able to adapt to the changing climate will, in the absence of human intervention, determine which response they exhibit.

Where self-organization and mutualism predominate, such as in soils, there is a possibility that systems will adapt more rapidly to the effects of climate change as invertebrates may not be so reliant on their own ability to change. For example, earthworms and termites depend on soil microflora for their digestion, and as the microflora is likely to adapt relatively rapidly to new conditions associated with climate change, the invertebrates may profit.

The potential of invertebrate genetic resources to adapt to climate change and its effects are considered in Chapter IV. We do not see much immediate scope for invertebrate genetic resources to mitigate climate change, but the few possibilities are also discussed in Chapter IV.

1.4 SCOPE OF THE STUDY

The scope of this study is restricted to terrestrial agriculture, and excludes marine and aquatic production systems. All terrestrial agricultural systems are considered, including forestry and pasture, but the main focus is on crop production systems. We recognize that in addition to their role in crop production, biological control agents (BCAs) play a role in the protection of stored crops. However, the latter role is not treated as a separate topic.

Invertebrate genetic resources may be considered to include all material that contains genetic information of, or derived from, invertebrates. However, the study focuses on whole organisms (as opposed to genetic material or genetic information), which play key roles in agricultural systems and have the potential to be manipulated to the benefit of agriculture.

Recognizing the great invertebrate biodiversity associated with agro-ecosystems, the study focuses on three key functional groups – BCAs, pollinators and soil invertebrates – each of which is treated separately in the following chapters. Between them, these three groups cover the most important ecosystem services that invertebrates provide to agriculture. However, many invertebrates are also important food items in their own right, and have the potential to make a much greater contribution in the future. In addition, several sectors (e.g. honey and silk) rely on products produced by invertebrates. Accordingly, invertebrates as food and as providers of products are briefly discussed in Chapters II and IV.

CHAPTER II. ROLES OF INVERTEBRATES IN SUSTAINABLE AGRICULTURE AND FOOD SECURITY

All ecosystems and human societies depend on a healthy and productive natural environment. If the capacity of ecosystems to produce goods and services is diminished, it is normally the poor who are most seriously affected. They often depend directly on forests, fisheries and agriculture, and tend to be most vulnerable to environmental problems, such as floods or crop failures, that result from ecosystem or land degradation. Given that terrestrial ecosystems provide roughly 99 percent of the world’s food supply, and that the world’s population is close to 7 billion (10^9) and increasing at a rate of 1 percent per year, viable agricultural systems are critical to food security and poverty alleviation. The question is whether it will be possible to develop a sustainable agriculture that is able to feed these numbers and meet increasing consumption patterns in an ecologically compatible way? This question is even more critical given that other human needs – biofuels, urbanization, not to mention biodiversity conservation and climate regulation – also place increasing demands on soils, 30 percent of which are at some stage of degradation (Lal, 2004). Assessing the sustainability of agriculture, and thereby predicting the future state of food security, requires prior understanding of the functioning of agricultural systems and the intricate relationships that exist between below- and above-ground biodiversity.

Losses of biodiversity have been escalating with the growing encroachment of human activities on ecosystems and increasing intensification of land use to meet demographic and socio-economic pressures. The multitude of small organisms associated with production systems, from pollinators to beneficial predators and soil organisms, has been overlooked. Reduction in the use of biodiversity in agriculture is driven by the increasing pressures and demands of urban and rural populations, by the global development paradigm, and by market forces which are favouring specialization and intensification but do not, as yet, internalize the cost of land degradation.

2.1 SOIL INVERTEBRATES

Soil invertebrates are a very important component of agricultural biodiversity, and largely determine the structure and the basic functions of natural ecosystems. They are an integral part of agricultural ecosystems and are key actors in maintaining soil health, ecosystem functions and production. The presence of a range of species and organisms capable of supporting critical soil processes is essential for the maintenance of healthy productive soils in the face of changing environmental conditions. **The decline of these soil communities and the fact that their beneficial functions in agricultural ecosystems have been overlooked have certainly contributed to increased rates of land degradation, nutrient depletion, fertility decline, water scarcity, loss of crop productivity and yield reductions, although this has yet to be quantified.** The loss of species with unique roles can have very drastic ecological effects that lead to long-term deterioration of soil fertility and agricultural productive capacity. **The deliberate or accidental introduction of a keystone species may have detrimental or beneficial effects, depending on the context.**

Soil invertebrates interact with one another and with the various plants and other animals in the ecosystem, forming a hierarchy of self-organized systems that span at least three scales of organization: microfoodwebs that operate in aggregates (c. 50 to 100 µm in size) and interaggregate spaces; functional domains of ecosystem engineers that extend over scales of centimetres to metres; and mosaics of functional domains that cover several square metres (Lavelle *et al*., 2006). **We still do not know how many soil invertebrate species exist worldwide, and there is almost no soil where we are able to identify or even quantify all the resident invertebrate species** (Wall *et al*., 2005, but see Schaefer, 1990). Soil fauna is relatively poorly represented in the scientific literature and relevant web sites compared to above-ground communities. The less-charismatic soil organisms receive less scientific attention than the high-profile above-ground animals. An overview of the number of described species vs. the estimated number of species that remains undiscovered for the major taxa of soil animals (modified from Wall *et al*., 2001) indicates that the smaller the taxa are, the more they are disregarded in biodiversity surveys. Correspondingly, the taxonomic deficit (ratio between the estimated diversity and the number of described species) tends to be higher for small body-sized invertebrates (Decaëns, 2010). Gaps in taxonomic knowledge make it difficult to generalize about the diversity of soil organisms. **Even in the most intensively studied groups such as Lumbricidae (earthworms), the use of molecular identification tools (DNA barcoding) has revealed an unsuspected number of cryptic species that cannot be distinguished on a morphological basis (James *et al*., 2010).**

Environmental factors shape the structure of communities across spatial scales, from patches to landscapes and biosphere. A series of abiotic and biotic filters sift species out of a regional pool (Weiher and Keddy, 1999). Following this idea, the “species pool hypothesis” considers local species diversity as part of a larger species pool at the regional level, i.e. the number of species potentially present in a given region (Belyea and Lancaster, 1999). The impact of anthropic activities on community diversity may thus be considered a result of modifications to the natural filters or the creation of new filters. This process occurs at various scales, ranging from the local (changes in biotic interactions to modification of the vegetation or introduction of exotics), to the ecosystem (ecosystem alteration or conversion to agro-ecosystems) and the landscape (habitat fragmentation or global change).

2.1.1 Classification of soil invertebrates

Soil biodiversity has generally been classified by size (Swift *et al*., 1979) or by the functions and processes that the organisms mediate (Lavelle *et al*., 2004). Three main groups are distinguished according to body size (Swift *et al*., 1979): macro-invertebrates or macrofauna (body length > 2 mm), meso-invertebrates or mesofauna (body length ranging between 0.2 and 2 mm) and micro-invertebrates or microfauna (body length < 0.2 mm). Soil invertebrates include “full-time inhabitants” – such as many micro- and meso-arthropods, earthworms and macro-invertebrates – and “part-time inhabitants” such as soil-dwelling insect larvae or mound-building insects (Wolters, 2001).

Functional classification of soil invertebrates

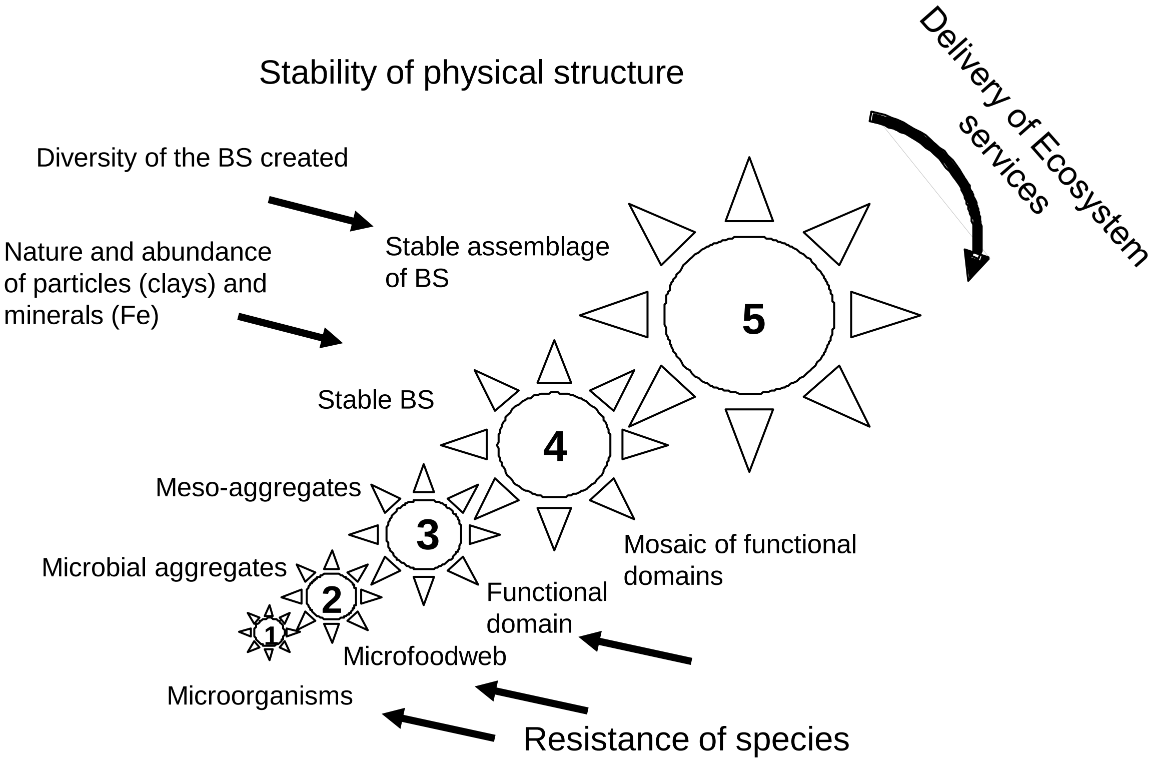
As Wolters and Schaefer (1994) state, soil invertebrates contribute significantly to many ecosystem functions including decomposition, nutrient cycling and maintenance of soil physico-chemical properties. They define a functional group as “a set of species that have similar effects on a specific ecosystem-level biogeochemical process”. No single classification exists, as the criteria used in classifying organisms and the degree of subdivision applied are functions of the question being addressed (see Decaëns *et al*., 2006). **The functions that soil biota carry out depend largely on the efficiency of their digestive systems (which themselves depend on the organisms’ interactions with soil micro-organisms, such as bacteria) and on the occurrence and abundance of the biogenic structures they produce in the soil.** Using these two criteria, three large functional groups of invertebrates can be distinguished (Lavelle, 1997):

1. **Micropredators** – within this group are the smallest invertebrates, including nematodes. Their main role in soil is to stimulate the mineralization of soil organic matter by preying upon micro-organisms inside soil microfoodwebs (Coûteaux *et al*., 1991), but they also feed on larger organisms. They do not produce biogenic structures (Lavelle, 1997). However, this does not provide a complete view of the spatial and temporal relationships between soil invertebrates and the production of biogenic structures. Microfoodwebs play an important role in ecosystems where soil ecosystem engineers have been depleted, such as intensive high-input agricultural systems and some deserts.

2. **Litter transformers** – some members of the mesofauna and macrofauna live in the leaf-litter layer and participate in the decomposition of plant litter (Lavelle, 1997) through comminution (breaking up particles) and digestion. They rely on micro-organisms for their digestion, mainly using the external rumen strategy: their faecal pellets act as incubators and they re-ingest them after some period of incubation to take advantage of the assimilable organic compounds released, and probably also the microbial biomass accumulated (Swift *et al*., 1979). They produce structures in the litter soil environment, which being mostly organic are usually fragile and short lasting. Some litter transformers, as they change resources from one physical state to another, also carry out some soil ecosystem engineering activity; for example, Diplopoda (millipedes) ingest leaf litter and produce faecal pellets with structure and physical properties that are different from the previously ingested plant litter.

3. **Ecosystem engineers** (*sensu* Jones *et al*., 1994) – This functional group comprises organisms that produce solid organo-mineral physical structures through which they are able to modify the availability or accessibility of water, trophic and spatial resources for other organisms. They include earthworms, ants and termites and a few other animals that can excavate soil and produce a wide variety of aggregated structures that have physical and chemical properties different from the surrounding soil. Their activities and production of biogenic structures can modify the abundance of organisms and the structure of their communities. The accumulation of the structures produced by ecosystem engineers forms functional domains in soil: the "drilosphere" of earthworms, "termitosphere" of termites or "myrmecosphere" of ants. These provide habitats for rather specific communities of smaller invertebrates and micro-organisms (Figure 1). Soil ecosystem engineers also play important roles in the basic soil processes: hydric functions (water infiltration, storage at different tensions and release), organic-matter dynamics (sequestration in stable aggregates), soil chemical fertility and plant growth (Anderson, 1995; Lavelle, 1997). Dung beetles, soil-nesting bees, solitary predatory wasps, cicada nymphs and desert isopods, among other invertebrates, also dig small holes and burrows in the soil. However, the effects of these invertebrates in soil ecosystems are more localized and, with some exceptions, their roles have barely been assessed.

Figure 1. Self-organizing systems in soils at different scales



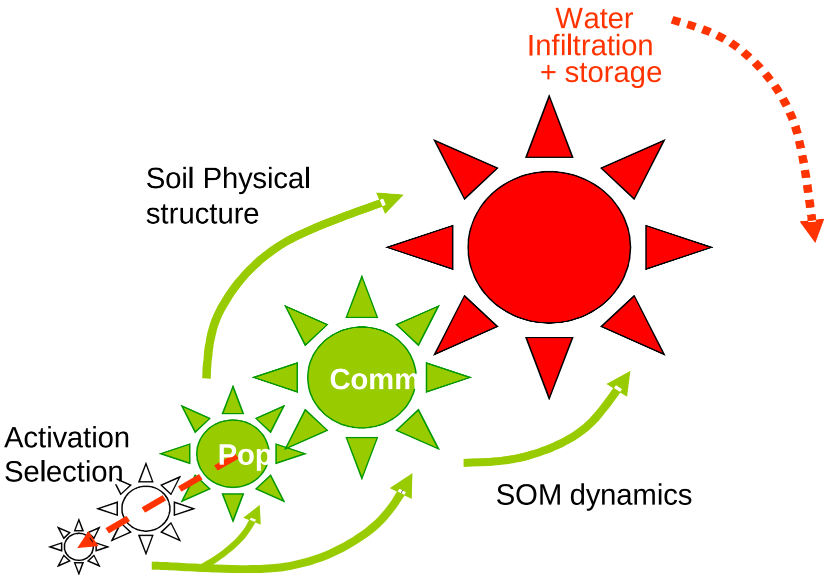
Note: Scales are indicated by the numbers 1 to 5: from microbial films (1) – where most microbial transformations occur – to the landscape (5) where ecosystems services are delivered. The stability of the delivery of ecosystem services at scales larger than 5 is supported by the resistance of species to disturbances and/or the stability of physical structures, and other effects of invertebrates, that may extend their effects when they are temporarily absent. BS = biogenic structures.
Source: Modified from Lavelle *et al*. (2006).

2.1.2 The role of soil invertebrates in key functions relevant for agriculture

The presence of a range of species and organisms capable of supporting critical soil processes is essential for sustaining healthy productive soils in the face of changing environmental conditions. Ecosystem services such as decomposition, organic-matter dynamics, nutrient cycling, carbon storage, energy flow, water infiltration and storage in soil and (to some extent) plant growth are mediated by soil biota, which therefore contribute to the maintenance of ecosystem integrity (Lavelle, 1997; Brussaard, 1998). Decomposition, a key function in soil, is a biological “cascade” process during which resources are progressively transformed into different components. The resources in question may originate above or below ground, and include plant litter, faecal pellets of invertebrates, live and dead micro-organisms, invertebrates and other materials – down to the amorphous soil organic matter composed of fractions of different ages and chemical composition. Decomposition is determined by interactions among three components: soil organisms, physical environment (particularly climate and mineralogy of the parent material) and the quality of the decomposing resources (Swift *et al.*, 1979). The three components are not of equal importance, and they act at different scales of space and time. Consequently, it seems more appropriate to use a hierarchical model. Lavelle *et al*. (1993) proposed a set of hierarchically organized factors that determine microbial decomposition activities in terrestrial ecosystems at decreasing scales of time and space: climate > clay mineralogy + nutrient status of soil > quality of decomposing resources > effect of macro-organisms (i.e. roots and soil invertebrates). Across this hierarchy, factors acting at higher scales of time and space tend to be dominant over those acting at smaller scales (Allen and Hoekstra, 1992).

Many of the functions performed by soil animals contribute to the provision of important ecosystem services (Figure 2) at scales that are orders of magnitude larger than those of the organisms and their functional domains (Lavelle *et al*., 2004). **The loss of beneficial functional groups of soil invertebrates may result in the loss of key ecosystem processes, such as decomposition, nutrient cycling and soil structure, with important consequences in terms of land degradation, declines in crop productivity and greater food insecurity. There may also be wider consequences, such as increased poverty and the expansion of cultivated land for agricultural production.** The maintenance of soil biological function is a key factor underpinning sustainable land-management practices.

Figure 2. Effects of soil ecosystem engineers on the provision of ecosystem services at different spatial scales (cf. Figure 1)



Note: Individual populations (Pop) interact with microbial communities (red dotted line to level 1) which allow them to digest soil organic matter (SOM) and litter, thus activating SOM dynamics (lower green arrows). Populations also accumulate biogenic structures that influence soil physical structure (upper green arrow). Accumulation of these activities at the community level (Comm), results in the provision of ecosystem services at the landscape level (red level 5): water infiltration and storage and climate regulation via carbon cycling. Modified from Lavelle *et al*. (2004).

Invertebrates create structures called functional domains in soil as they interact with other organisms (micro-organisms and plants) at discrete spatial scales. These structures are characterized by the composition of the associated communities (invertebrates, micro-organisms), the physical structures created (aggregates, pores) and their corresponding species assemblages.

Agricultural intensification normally has detrimental effects on biodiversity. It leads to an accelerating loss of biological diversity, both above and below ground. There are many reasons for this loss, including increasing homogenization of agricultural systems, monocultures, use of agrochemicals, and excessive soil disturbance caused by continuous tillage**. Soil biological communities are very responsive to land-use practices that directly modify the availability of trophic resources for soil organisms and hence affect the functions performed in the soil** (Swift *et al*., 1996; Decaëns and Jiménez, 2002). The number of species in a given community is usually lower after replacement of the original ecosystem. Exotic species tend to colonize these new habitats and eliminate endemic species that are poorly adapted to such disturbances. For example, in many tropical American pastures that have been established in place of primary rainforest, earthworm communities are dominated by one exotic neotropical species, *Pontoscolex corethrurus* (Müller) (Glossoscolecidae) (Lavelle and Pashanasi, 1989; Fragoso and Lavelle, 1992). In some areas, however, the opposite has been reported and pastures derived from natural savannas, alone or associated with legumes, are more likely to conserve the native earthworm community than those established on original rainforest sites, although there can be specific responses to the perturbation, such as increases in biomass for some species (Jiménez *et al*., 1998; Decaëns and Jiménez, 2002). **Sustainable management practices can reduce the negative impacts on soil invertebrates with beneficial functions and maximize the positive (synergistic) effects in agricultural lands.** Management options should address plot and landscape scales. At the plot scale, maintenance of permanent plant cover, management of organic inputs and minimum tillage have proved to be efficient means of maintaining active invertebrate communities of all the different functional groups (Hendrix *et al*., 1990; Jiménez and Thomas, 2001). At the landscape scale, mixing agro-ecosystems and natural ecosystems facilitates the recolonization of cropped soils through the movement of invertebrates from “source” plots to “sink” plots (Decaëns and Jiménez, 2002).

Physical engineering: the role of biogenic structures

Soil aggregation is a process whereby soil organisms perform essential soil ecosystem services such as carbon sequestration and water infiltration. Aggregation is the binding of soil particles in solid assemblages of different sizes (micro < 50 µm, meso 50–1 000 µm and macro > 1 000 µm). It results from the accumulation, over long periods of time, of biogenic structures (earthworm casts and burrows, termite faecal pellets and constructs, ant galleries and macrostructures) produced by aggregate-forming invertebrates and roots, their interactions with microbial communities, and physical interactions among soil particles. In fact, **most of the macro-aggregate structure of soils is of biogenic origin and has been formed by the activities of soil invertebrates and roots, sometimes over many years.** The organisms operate at small spatial and temporal scales, but biologically formed aggregates may persist for several years or more, depending on conditions (Blanchart *et al*., 1999). The remarkable microstructure of some soils (oxisols) of the Brazilian Cerrado (savanna) that confers a very porous structure in spite of a mostly clayey texture is said to be the result of several centuries of accumulation of termite pellets, 50–100 µm in size (Eschenbrenner, 1986). The Colombian Llanos (plains) have soil with similar textures, but the lack of such termite activities has resulted in very compact soils with average bulk densities of 1.6–1.8 g/cm^3 (Lilienfein *et al*., 1999) compared to 0.8 in the Brazilian Cerrados. **Practices that eliminate soil ecosystem engineers may not immediately impair soil conditions and the resulting ecosystem services, as biogenic structures do not immediately cease performing their functions. This characteristic gives soils their capability to resist disturbances.** It also masks, for a time, the negative effect of practices that impair soil invertebrate communities because the beneficial effects produced by these communities may last several years or decades after they have been eliminated.

Chemical engineering: the formation of natural compost and nutrient release

Litter transformers are the main actors in the process that – via comminution and chemical transformation (mainly operated by associated micro-organisms) – progressively transforms freshly dead organic matter into humus while nutrients are progressively released. This process involves a wide range of invertebrates, ranging from the tiniest detritivorous nematodes or protists through the highly diverse and abundant micro-arthropods and enchytraeid worms to the largest litter transformers found in litter systems (Isopoda, millipedes, centipedes, epigeic litter-dwelling earthworms) and their respective predators.

Nutrient release is the other important chemical engineering function controlled by invertebrate activities. One pathway through which this occurs is the well-documented process whereby nutrients accumulated by bacteria and fungi in their biomass are further released as nitrogen and phosphorus excretion, in mineral forms, by their micropredators (Coleman, 1983; Clarholm, 1984; Osler and Sommerkorn, 2007). Another pathway is release in fresh faecal pellets by earthworms and termites. Earthworm casts contain quite high concentrations of mineral nitrogen (as ammonium, NH_4+) and assimilable phosphorus, a product of the metabolism of the animals and enhanced microbial activities in their guts (Lavelle *et al*., 1992; Lavelle and Spain, 2001 and references therein).

Biological engineering: foodweb effects and plant health

Soil ecosystem engineers have very close relationships with microbial communities, which they selectively stimulate at different scales according to rules that are still poorly understood. Foodweb controls are known to play a role in the release of mineral nutrients from bacteria and fungal grazing by micropredators (Wardle, 2002; Lavelle *et al*., 2006). These effects are generally embedded in a more general control operated by an ecosystem engineer in its functional domain (e.g. the rhizosphere of roots or drilosphere of earthworms) (Clarholm, 1984). The most efficient organisms in this process are nematodes and protists, which maintain high densities in many soils and are the most resistant part of soil faunal communities.

Biological engineering also produces robust benefits for plant growth and plant protection. These effects have been fairly well documented for earthworms. Plants generally grow much better in the presence of earthworms than in their absence (Section 4.1.2).

2.1.3 Management of soil invertebrate activities

Direct management practices

These practices involve intervening in the production system in an attempt to alter the abundance or activity of specific groups of organisms (Hendrix *et al*., 1990). Examples of direct interventions include: (i) inoculation of seeds or roots with rhizobia, mycorrhizae, fungi and rhizobacteria to enhance soil fertility; and (ii) inoculation of soil or the environment with BCAs (for pests or diseases), antagonists or beneficial fauna (e.g. earthworms).

For example, in southern India, the long-term exploitation of soil under tea gardens has led to impoverishment of soil fertility and stabilization of yields despite increasing use of external inputs such as fertilizers and pesticides. Fertilization Bio-Organique (FBO) technology, i.e. the application of high-quality organic matter and earthworms, has been very effective in increasing tea yields – which have risen by 79.5–276 percent (more than achieved by the application of fertilizers alone) – owing to their favourable effects on physical and biological soil properties (Senapati *et al*., 1999). More research is needed on the production and application of beneficial soil invertebrates in this way.

Indirect management practices

Indirect interventions mean the management of soil biotic processes through manipulation of factors that control biotic activity such as habitat structure, microclimate, nutrients and energy resources, rather than the soil invertebrates themselves (Hendrix *et al*., 1990). Examples include the application of organic materials to soil, reduced tillage, fertilization, irrigation, green manuring and liming, as well as cropping-system design and management.

Examples from Carimagua (Colombia) suggest that the spatial and temporal array of experimental plots allocated to different crops may favour the conservation of locally high densities of earthworms and soil biodiversity. The spatial arrangement of pastures alongside cropped plots can accelerate the recovery of earthworm populations in the cropped plots. These spots may serve as reservoirs and refuges for the colonization of depopulated areas (Lavelle *et al*., 1999). Through such practices, earthworms can be harnessed to improve ecosystem health (Jiménez and Thomas, 2001). Other agricultural practices in tropical countries in Africa (Case study 1), Asia and South America take advantage of the beneficial functions provided by soil invertebrates in a variety of ways.

2.1.4 Conclusion

Soil invertebrates are a key component of agricultural landscapes. They participate in essential soil processes for the maintenance of healthy, productive, soils in the face of changing environmental conditions. In general, agricultural practices have a negative impact on soil invertebrate communities, causing the disappearance of some species. **Such effects disrupt the provision of beneficial soil functions and ecosystem services.**

The importance of interaction between soil invertebrates and soil micro-organisms is worth reiterating. The activities of soil invertebrates stimulate microbial activity in soils, and micro-organisms are in intimate relationships with soil invertebrates, helping them degrade highly complex compounds such as cellulose.

2.2 BIOLOGICAL CONTROL AGENTS

Biological control is defined here as the use of natural enemies to regulate pest populations. Natural enemies of pests are BCAs and provide an ecosystem service (Costanza *et al*., 1997; MEA, 2005). Integrated pest management (IPM) is "a strategy of pest containment which seeks to maximise natural control forces such as predators and parasites [i.e. parasitoids] and to utilise other tactics only as needed and with a minimum of environmental disturbance" (Glass in Davis and McMurtry, 1979). Thus, **biological control, particularly natural biological control, underlies all IPM programmes.**

BCAs are generally present in and around agricultural ecosystems, where they feed on pests and regulate their numbers. Where BCAs are absent, or are not present in sufficient numbers to regulate pest populations, they may be introduced into the cropping system. Pests are generally considered to include all species (invertebrate, vertebrate, weeds and diseases) causing harm to human interests (food, fibre, other agricultural products, environment, health). In this report we refer to invertebrate pests (or subgroups such as arthropod pests or insect pests), vertebrate pests, weeds and diseases. We explicitly exclude diseases and parasites of humans and their invertebrate vectors, as well as diseases of livestock. However, we do include ectoparasites of livestock and pests arising from agricultural practices (e.g. nuisance flies).

Implicit reliance on "natural biological control" is a feature of almost all production systems. For example, the majority of the species that infect, feed on or compete with any given crop do not cause sufficient damage to warrant treating them as pests, and thus it can be assumed that they are regulated by a combination of BCAs, crop resistance (and tolerance) and abiotic factors. The value of this regulatory service has been estimated worldwide at US$400 billion ($10^9$) annually (Costanza *et al*., 1997), although these figures have been criticized on methodological grounds. Losey and Vaughan (2006) estimate that the biological control regulatory service has a value of US$450 million annually in the United States of America alone. Natural biological control encompasses both unconsidered or implicit reliance on this ecosystem service, and manipulation of the service through conservation biological control methods. In the latter form of natural biological control, habitat and practices within and around agricultural land are manipulated to expressly favour the presence of desired natural enemy species (Barbosa, 1998; Case study 2). Overall, natural biological control and conservation biological control are highly dependent on landscape-level processes and can be negatively affected by disturbance, landscape fragmentation and loss of biodiversity (Letourneau, 1998).

Classical biological control is the introduction of an exotic BCA of an exotic pest or weed into a new ecoregion (or a new country in the same ecoregion) with the purpose of regulating the pest's numbers (Case study 3). This strategy is a long-term approach to the regulation of invasive pests. Also known as introduction or importation biological control, it requires the selection, introduction and establishment of one, or a very small number of, BCA(s) that is/are likely to regulate the pest, while not causing any adverse impacts on other species in the new habitat. **Classical BCAs, once established, become part of the natural biological control ecosystem service.** Van Lenteren (2007) estimates that classical biological control is applied on 350 million hectares worldwide.

Augmentative biological control differs considerably from the preceding two strategies. The BCA is introduced, usually directly onto the crop to be protected, once or several times in a cropping cycle (Case study 4). The purpose is to induce sufficient mortality in the target pest or pests to ensure that economic injury thresholds (levels at which damage costs more than the cost of control) are not exceeded during the current cropping season. The BCAs are generally purchased from suppliers, or produced by a growers' cooperative, and are mass reared on natural or factitious hosts or prey. Van Lenteren (2007) estimates that augmentative BCAs are applied on 16 million hectares annually.

Because classical biological control and augmentative biological control using exotic BCAs involve the deliberate introduction of alien species, these processes are carefully regulated according to national legislation, which varies from country to country (e.g. Hunt *et al*., 2008), and international standards, such as the *International Standards for Phytosanitary Measures No. 3. Guidelines for the Export, Shipment, Import and Release of Biological Control Agents and Other Beneficial Organisms* (ISPM3) (IPPC, 2005). Furthermore, because BCAs are genetic resources, their international use is covered by the *Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization to the Convention on Biological Diversity* (UN, 2010), in anticipation of which, Cock *et al*. (2010) have argued that the biological control approach should be treated as non-commercial research, and that since the benefits are in the form of common goods, the benefit sharing with the source country might be best based on joint scientific research.

2.2.1 Types of biological control agents

BCAs are all those species that are natural enemies of pests. They include invertebrates, vertebrates and micro-organisms, although only invertebrates are considered here. BCAs are primarily predators, parasitoids and diseases of arthropod pests, and herbivores that feed on weed pests.

Almost all classes and orders of Arthropoda contain species with predatory lifestyles, and arthropods dominate this guild in and around sustainable cropping systems. Predators consume more than one prey item, and generally many prey items, to complete development of the immature stages; and they often must feed as adults in order to reproduce. The Acari, Arachnida, Opiliones – mites, spiders and harvestmen, respectively – are common predators, and among insects, the orders Odonata (dragonflies), Hemiptera (true bugs), Neuroptera (including lacewings), Coleoptera (beetles), Diptera (flies) and Hymenoptera (bees, ants, wasps) contain predator species of key importance in sustainable cropping systems. Although there are exceptions, most predators are generalist or oligophagous feeders – i.e. they consume more than one prey species, and often feed at more than one trophic level: eating herbivores, other predators, and, in the case of true omnivores, plants.

Parasitoid lifestyles are considerably more specialized, and are common only in the insect orders Diptera and Hymenoptera. Parasitoid females lay one or more eggs in or on a single host individual. As a result, a parasitoid individual normally kills only one host individual during its development. Because the host is killed during parasitoid development, these species cannot be considered parasites; although they must overcome host defences, and form intimate physiological and biochemical relationships with their hosts, in much the same way that parasites do. As a general rule, parasitoids specialize on a few host species, and the life history of most parasitoid species is tied closely to that of the host or hosts, although some species are fairly broad generalists.

Diseases that act as BCAs are not specifically addressed in this study, although many points relating to invertebrate BCAs also apply to diseases. Nematoda include some true parasites that do not kill their hosts. The entomopathogenic nematodes (EPNs), some of which are used in augmentative biological control, occupy a niche that is generally considered to be a disease functionally – mainly because reproduction in the dying host leads to a large number of individual nematodes being produced by a single dead host. *Steinernema* spp. (Steinernematidae) and *Heterorhabditis* spp. (Heterorhabditidae) are produced for use as augmentative biological control products. Infective nematodes are suspended in water and are applied as a spray or a drench, in much the same way as a microbial pesticide. Approximately ten commercially produced species in these two genera are applied against a wide array of pests including Lepidoptera (caterpillars), Coleoptera, Diptera, Siphonaptera (fleas) and Orthoptera (e.g. mole crickets and mormon crickets).

Natural biological control is based on all the above-described types of BCAs. The key species vary depending on the pest species and the location. In general, natural biological control relies on a community of generalist and specialist invertebrate predators and parasitoids, as well as diseases.

In contrast, classical biological control of arthropods uses only the specialized natural enemies that are deemed least likely to have undesirable non-target effects. This means an emphasis on specialized parasitoids (Hymenoptera and Diptera) and a few specialized predators, such as some Coccinellidae (ladybird beetles or ladybugs) and Diptera.

Augmentative biological control mostly uses a mixture of specialist parasitoids which target an individual pest, oligophagous predators and EPNs (usually indigenous) which will eat or attack several species of pest. Most new BCAs being developed for use in augmentative programmes are either specialized parasitoids or indigenous species. This strategy minimizes the risks that BCAs will have undesirable impacts on biodiversity. If an augmentative BCA is exotic to an ecoregion, its first release must be reviewed with as much rigour as is applied to classical BCAs, in accordance with national regulations or international standards such as ISPM3 (IPPC, 2005).

Biological control of weeds with invertebrates is, at present, mostly tackled using classical biological control. There is, however, some potential for augmentative releases of classical arthropod BCAs of weeds (Smith *et al*., 2009). Any herbivore that is suitably host-specific and likely to be damaging can be used. Among invertebrates, these are almost all insects, with an increasing preponderance of beetles, particularly Curculionidae or weevils and Chrysomelidae or leaf beetles, being used as classical BCAs against weeds.

2.2.2 Main targets of biological control

The main targets of biological control used in agriculture have been invertebrate pests of crops (including forestry) and weeds of crops (including pasture). The invertebrate pests of stored products are also valid targets for biological control, but the acceptable thresholds for damage are usually lower than can, at present, be reliably achieved with biological control. Parasitoids are used against fly pests in high-intensity animal-production units such as feedlots and poultry barns. Dung beetles have been introduced in various parts of the world to aid in the decomposition of dung in pasture and rangeland. Ectoparasites of domestic animals (e.g. mites, ticks, mosquitoes, tsetse flies) are also a potential target for biological control, but research is focused on the use of micro-organisms as BCAs in this niche. Environmental pests (i.e. pests of natural, amenity and built ecosystems) and pests of medical importance are also valid targets – with significant successes having been achieved against the former – but beyond the scope of this study.

Classical biological control is mostly used against exotic targets. Although indigenous pests have been targeted using exotic BCAs in the past, this practice has declined because of the increased risk of non-target effects. **All exotic pests are potential targets for classical biological control**, but in practice it is usually those that cause most damage, or prove intractable to other control measures, that are prioritized in much of the world. In some countries (e.g. Australia and New Zealand), all new pests (especially weeds) are considered first as potential targets for classical biological control. Classical biological control has worked in many different situations, but it is more likely to be effective in stable agro-ecosystems (e.g. forestry, plantations, pasture), where there are no indigenous species closely related to the target (less chance of non-target effects, so more choice of agents), and on islands (where the less-diverse indigenous natural enemies are likely to be less effective).

Augmentative biological control using invertebrates has been used almost exclusively against invertebrate pests. Until recently, the majority of the targets of augmentative biological control were exotic, cosmopolitan, pests of crops grown under cover. These pests are easily moved in trade of live plants and plant parts. In general, the pests that are successfully targeted with augmentative BCAs have a predictable seasonal occurrence, and a reasonably large potential market.

This is because augmentative BCAs are produced for sale. Most augmentative BCAs cannot be stored, and production must be planned several weeks in advance to meet anticipated demand. There are roughly 13 targets of augmentative BCAs in covered crops (depending on how one lumps and splits target groups and species). Egg parasitoids, *Trichogramma* spp. (Hymenoptera: Trichogrammatidae), have been used against the eggs of caterpillar pests of forest crops, and indigenous species of *Trichogramma* and other egg-parasitoid species are increasingly being used against important exotic Lepidoptera pests of food crops, such as the diamondback moth (*Plutella* *xylostella* (L.); Lepidoptera: Plutellidae) and European and Asian corn borers (*Ostrinia nubilalis* (Hübner) and *O. furnacalis* Guenée; Lepidoptera: Crambidae). **The application of indigenous, augmentative BCAs against both exotic and indigenous targets has significant potential for growth.**

2.2.3 Scale of use of biological control agents

The application of biological control is widespread in forests, grasslands and rangelands, and in sustainable cropping systems. BCAs contribute to the regulation of pests that are present in these systems and to the regulation of populations that could potentially invade croplands. Even highly industrialized factory farms receive some benefit from the actions of natural BCAs in regulating populations of invading pests. Costanza *et al*. (1997) estimate a value of US$25/ha/year and US$24/ha/year for biological control services in the world's grasslands and croplands, respectively (US dollars, 1994). Based on values provided by Losey and Vaughan (2006) and the area of agricultural land, biological control services have a value of approximately US$11/ha/year in the United States of America. **For world croplands, the value of natural biological control ecosystem services is almost half the value of food production.**

Use of natural biological control is facilitated through development of IPM programmes, farmer field schools and grower participation workshops. In particular, farmers are encouraged to reduce the application of chemical insecticides, which encourages survival of BCAs on and around farms. Because natural BCA communities are location-specific, development of natural biological control programmes is highly dependent on education and local knowledge.

At least 7 000 introductions of BCAs involving almost 2 700 BCA species have been made. The most widely used BCAs have been introduced into more than 50 countries. BCAs from 119 different countries have been introduced into 146 different countries (Table 1). High-income countries have made the most use of classical biological control, and have also been the main source of BCAs. Low-income countries have contributed slightly more BCAs than they have received. For a more detailed summary see Cock *et al*. (2009, 2010).

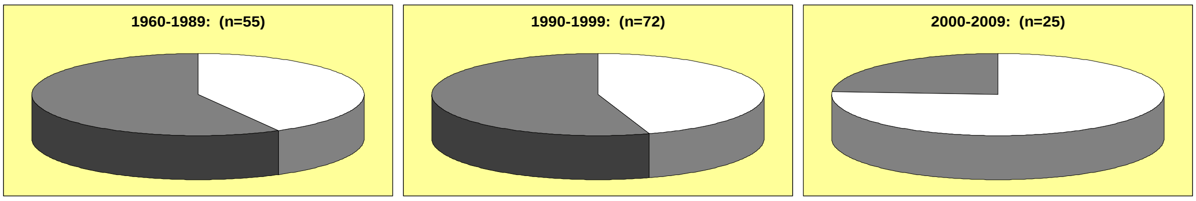
Table 1. The numbers of classical biological control introductions made in different countries

Number of releases per country	Number of countries	Total number of releases in these countries	% of total releases
>100	12[1]	4231	61.6%
50–100	14[2]	997	14.5%
10–49	55	1399	20.4%
1–9	65	245	3.6%
	146	6872	

1. In order: United States of America, Australia, Canada, New Zealand, South Africa, United Kingdom (almost entirely overseas territories), Fiji, Mauritius, India, France (mostly overseas territories), Israel, Guam.
2. In order: Russian Federation, Italy, Barbados, Chile, Trinidad and Tobago, Ghana, Kenya, Philippines, Mexico, St Kitts and Nevis, Papua New Guinea, Greece, Peru, Bahamas.

Augmentative biological control against arthropod pests, using arthropod and nematode agents, takes place on approximately 1.6×10^6 ha of land (van Lenteren and Bueno, 2003; Bale *et al*., 2008). Egg parasitoids, mainly *Trichogramma* spp., are released against a number of pest Lepidoptera, five species of natural enemies are released against pests in orchards in Europe, and more than 30 agents are released against pests in greenhouse production systems worldwide (Bale *et al*., 2008). Most of these programmes are directed against invasive exotic pests. Once established, and therefore endemic to a region, classical BCAs may be used as augmentative BCAs, as in the case of *Cotesia flavipes* (Cameron) (Hymenoptera: Braconidae) used in Latin America for augmentative biological control of sugarcane stem borer, *Diatraea saccharalis* (F.) (Lepidoptera: Crambidae) (summarized in van Lenteren and Bueno, 2003). In the augmentative biological control sector, more than 170 species of natural enemies are produced and sold, but some 30 species make up more than 90 percent of the market worldwide. The trend in augmentative biological control is towards looking first for indigenous natural enemies when a new, even exotic, pest develops (Figure 3, Case study 5).

Figure 3. The changing proportions of first use of exotic (grey) and indigenous (white) natural enemies in augmentative biological control in Europe over time



Source: Cock *et al*. (2009).

Costanza *et al*. (1997) estimated the world’s croplands at 1.4×10^9 ha. Given that augmentative biological control takes place on a very small fraction of this area, the potential market for augmentative programmes is enormous. Van Lenteren (2006) estimated the area under biological control in greenhouses worldwide to be approximately 32 000 ha, which is a very small fraction of the world greenhouse area: approximately 2 400 000 ha (2 280 000 in vegetables, 120 000 in ornamentals). Given current trends in markets, and uptake of new agents by farmers, Pilkington *et al.* (2010) predicted continuing increases in use of biological control in greenhouses.

2.2.4 Advantages and disadvantages of biological control

Biological control has some distinct advantages and disadvantages that set this method of pest containment apart from all others. BCAs exhibit no toxicity to humans or livestock. The vast majority of BCAs exhibit moderate to high specificity to targets. Unlike the long-lasting chemical insecticides, BCAs do not bioaccumulate (i.e. accumulate substances, such as pesticides, in organisms), and they do not contaminate ground and surface waters. BCAs are either naturally present (natural biological control) or, once introduced, establish and spread so that they attack the target pest throughout its range (classical biological control).

Natural biological control has the key benefit that it is naturally present in all agricultural situations and so is free to farmers. In many cases, it can provide adequate control of pests. In many others simple manipulations may allow natural biological control to keep pests at acceptably low levels. The use of broad-spectrum pesticides is incompatible with natural biological control. In many situations, natural biological control can provide substantial control of many pests and therefore should form the foundation of IPM. Further interventions should be selected and implemented so as to minimize the adverse effects on existing natural biological control. Classical and augmentative biological control are two such examples.

Classical biological control is primarily used to control introduced pests which may not be effectively controlled by indigenous BCAs. The introduction and establishment of a classical BCA leads to reproduction and spread of the introduced BCA so that it becomes part of the ongoing natural biological control. This process brings public good benefits to the country and its farmers, but does not generate income or profits for the implementing agency. **The introduction of BCAs normally requires access to genetic resources (i.e. the BCAs) from another country and non-monetary mechanisms for sharing the benefits of what is basically non-commercial research** (Cock *et al*., 2009, 2010).

When neither natural nor classical biological control can solve a pest problem, augmentative biological control may be a good option. It is fully compatible with natural biological control, although conflicts may arise (e.g. with BCAs of weeds present in the same habitat). Because, in most production systems, growers must purchase augmentative BCAs, these agents must be competitive with insecticides with respect to efficacy, predictability and cost. **Augmentative biological control uses indigenous BCAs for preference, but – particularly when dealing with an introduced pest – BCAs may need to be introduced, and so access and benefit sharing will need to be addressed**.

Integrating these different aspects of biological control in an IPM system can provide effective pest management, that minimizes or obviates the need for pesticides: to the benefit of farm workers, the public who consume or use the agricultural products, and the environment. However, if growers are locked into an IPM system based on biological control and a new pest appears, there is a risk of significant losses and reversion to the use of pesticides if an effective BCA is not quickly available (Case study 6).

2.2.5 Conclusion

Losses to agricultural production due to pre-harvest and post-harvest pests can be very substantial, and are likely to increase as a consequence of climate change. Different types of invertebrates provide biological control of pests. They form the basis of, and tools for, the IPM approach to crop pest management in many situations. A large fraction of the biological control ecosystem service relies on natural biological control. This is generally unmanaged, and vulnerable to disruption from disturbance, habitat fragmentation and loss of biodiversity. Classical and augmentative biological control are less widely used on a per-area basis, but have been more widely studied. All forms of biological control are critical components of IPM in sustainable production systems. Their potential is only partially tapped. **Management and conservation of invertebrates that provide biological control of pests in crops is critical for food production and food security.**

2.3 POLLINATORS

A pollinator is a biotic agent (vector) that moves pollen from the male anthers of a flower to the female stigma of a flower to accomplish fertilization and seed setting (Faegri and van der Pijl, 1979). Pollination services by animals, especially insects, are one of the most widespread and important processes that structure ecological communities in both natural and agricultural landscapes (Kevan, 1999). An estimated 60–90 percent of the world’s flowering plants depend on insects for pollination (Buchmann and Nabhan, 1996) and these include a range of economically important plant species (Free, 1993).

Crop pollination used to be (and often still is) provided by wild pollinators spilling over from natural and semi-natural habitats close to crop fields. This service has generally been free and therefore has received little attention in agricultural management. If wild pollinators are lacking or additional pollination is required, as is the case in many intensive agricultural production systems, farmers can buy or rent managed honeybees (*Apis mellifera* L.; Hymenoptera: Apidae) or sometimes other species (e.g. bumblebees, alfalfa leafcutter bees, alkali bees). Both options for pollination service provision – i.e. use of wild species and managed bees – have recently come under pressure, a development which is sometimes referred to as the “pollination crisis” (e.g. Buchmann and Nabhan, 1996).

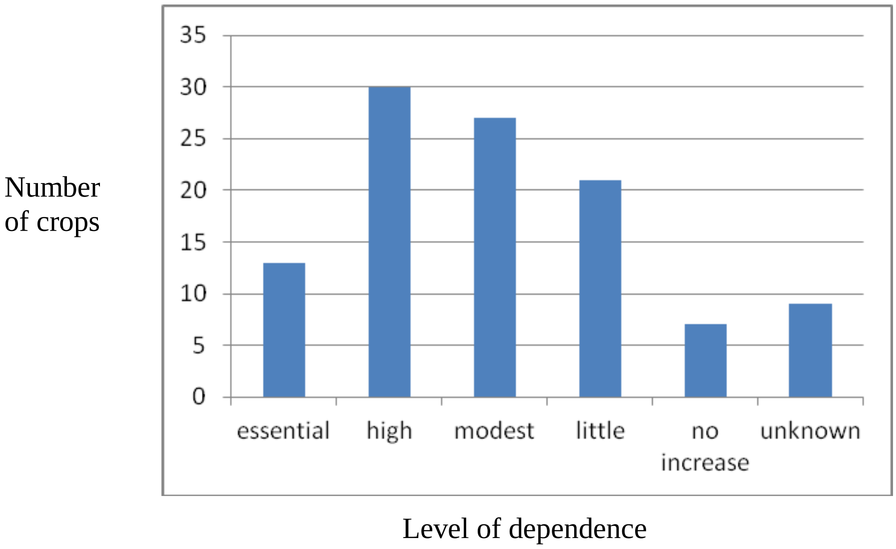
Here we provide a short review of current knowledge on, and estimates for the value of, crop pollination in global agriculture, the insect species providing the pollination services and the threats to the sustainability of these services.

2.3.1 Crop pollination as an ecosystem service: importance and value

Crop pollination is a key ecosystem service vital to the maintenance of agricultural productivity. Using primary data sources from 200 countries, Klein *et al*. (2007) concluded that **fruit, vegetable or seed production from 87 of the leading global food crops is dependent upon animal pollination**, while 28 of these leading crops are self- or wind-pollinated (Case study 7). Global production volumes give a contrasting perspective, as 60 percent of global production comes from crops that do not depend on animal pollination (e.g. most cereals and root crops), 35 percent from crops that depend on pollinators (most fruits, stimulants such as coffee and cocoa, and many vegetables), and 5 percent are unevaluated. Note that these estimates do not take into account the contribution of pollination to the production of animal forage, ornamental plants and seeds, fibres, non-timber forest products or subsistence crops that are not marketed.

Not all insect-pollinated crops depend 100 percent on insect pollination, and many crops can partially self- or wind-pollinate (Figure 4). Taking into account the level of insect-pollinator dependence and the production area for each crop, Aizen *et al*. (2009) calculated the actual volume of crop production that directly results from the contribution of insects to pollination and concluded that 5 percent (developed countries) to 8 percent (developing countries) of food production would be lost if all pollinators disappeared. **The percentage of pollinator-dependent agricultural crops has increased considerably over the last 40 years from 18.2 percent to 34.9 percent in developed countries and from 23.4 percent to 32.8 percent in the developing world** (Aizen *et al*., 2009). These findings suggest that the higher rate of increase in pollinator dependence in developing countries compared to developed countries might well continue into the future, which would warrant specific focus on those parts of the world.

Figure 4. Level of dependence on animal-mediated pollination



Source: Klein *et al*. (2007).

Production volume does not necessarily represent value, because of the disproportionate nutritional or consumer value of specific crops. In fact, insect-dependent crops have on average a five times higher economic value than insect-independent crops (Gallai *et al*., 2009). For the subset of crops that is marketed, it is possible to calculate the actual market value of insect pollinators' contribution. Gallai *et al*. (2009) estimated **that the total value of insect pollination to global agriculture is €153 billion per year, which represented 9.5 percent of the value of the world agricultural production used for human food in 2005.** This may not seem a high proportion, but the figure is much higher for specific groups of products (e.g. 39 percent for stimulant crops including coffee and cocoa, 31 percent for nuts and 23 percent for fruits) and can thus be very high for countries with a strong economic dependence on such crops. Clearly, insect pollination is an important agricultural input.

The value of crop pollination can be estimated to be much higher (5–100 times) when calculated as the investment needed to fully replace the pollination services (Allsopp *et al*., 2008), for example by hand pollination or large-scale dusting of pollen in crop fields (e.g. manually or by helicopter). In some cases the replacement value of the pollination services may be significantly higher than current market prices for commercial pollination. In many cases, loss of wild pollinators can potentially be replaced by introducing managed pollinators. This has been done for centuries using managed honeybees, but recent declines in managed honeybees may lead to much higher prices for hiring colonies or even a shortage of hives for crop pollination. Decreases in honeybee pollination services have already caused problems for some crops. For example, Californian almond growers now pay more than US$100/hive, up from US$40 less than seven or eight years ago as a result of honeybee shortages and have even started to import honeybee colonies from Australia in order to save their US$250 million crop (Losey and Vaughan, 2006; Sumner and Boriss, 2006).

2.3.2 Crop-pollinating insects

Insects are the main crop pollinators among animals. Bees often contribute the most, but in some specific crops most pollination is performed by other groups (e.g. midges for cocoa pollination, moths for pawpaw (papaya) pollination, and weevils for oil palm – see Case study 8). Moreover, in many other crops some pollination is carried out by insects other than bees. Bees are generally good pollinators because of their obligate dependence on flowers (pollen is fed to their offspring), their hairy bodies to which pollen grains easily adhere, and their central-place foraging strategies (i.e. the need to go back and forth to their nest). Flies, beetles, ants, butterflies and moths are among the other flower-visitor groups.

The contribution of most of these species is restricted to the members of their wild populations, because they are not managed. In such cases, the crop requiring pollination needs to be within the foraging range of the pollinator, which can be as little as tens of metres for small insects. This limits the use of wild pollinators in intensive monocultures of annual crops, with more chance of success in perennial crops, mixed cropping systems and more heterogeneous landscapes where there are adequate nesting and living conditions for the pollinators. When wild pollinators are not present in sufficient numbers, farmers can introduce managed pollinators to their fields.

Honeybees are the main managed pollinator and they are potential pollinators of most crops (Klein *et al*., 2007). If a beekeeping industry is present, farmers can set up contracts with beekeepers to hire colonies for pollination purposes, with the beekeepers then maintaining their hives during the period of the contract. Over the last century, the growth in managed honeybee colonies (up 50 percent) has not been able to track the 300 percent increase in demand for pollination of insect-dependent crops (Aizen and Harder, 2009). In addition, managed honeybee populations have recently come under severe pressure, with large local die-offs of 50–80 percent (see also Section 2.3.3). Together, this clearly creates uncertainty as to whether future demand for managed honeybees can be met by beekeepers' supply of colonies.

Even though a single species, such as the managed honeybee, can often do an excellent job as a service provider, **pollination service tends to increase or be more stable where a larger diversity of potential pollinators is present in the system** (Hoehn *et al*., 2008; Winfree and Kremen, 2009). There can even be indirect benefits to pollination as a result of species interactions, as in the case of sunflower pollination in the United States of America where the behaviour of native bees caused a change in honeybee behaviour enhancing their pollination contribution (Greenleaf and Kremen, 2006).

2.3.3 Threats to crop pollinator populations

There is now evidence of a decline in individual species abundance and species richness among wild bees and other pollinators in Europe (Rasmont *et al*., 2005; Biesmeijer *et al*., 2006) and North America (NRC, 2007; Cameron, 2011) probably as a result of multiple, interacting causes (Potts *et al*., 2010a). Pollinator losses seem biased towards species with particular traits, such as diet and habitat specialization (Biesmeijer *et al*., 2006; Kleijn and Raemakers, 2008). Losing specific traits from pollinator communities might lead to loss of specific ecological functions, such as long-distance pollen dispersal if large-bodied bees disappear or pollination of deep flowers if long-tongued species are lost.

A multitude of drivers potentially affect pollinator abundance and diversity, and they are probably interacting in non-linear and unpredictable ways. Our knowledge on how individual drivers act is increasing, but interaction effects have rarely been studied, because of the practical difficulty involved in large-scale experimentation. An important set of drivers stems from land-use change, which results in agricultural intensification (Winfree and Kremen, 2009), loss of flower-rich meadows (Rasmont *et al*., 2005), increased pesticide use (Kevan *et al*., 1997; Brittain *et al*., 2010) and habitat loss, degradation and fragmentation (Winfree and Kremen, 2009; Bommarco *et al*., 2010). All have led to loss of pollinators' foraging and nesting habitats. These problems are further exacerbated by the arrival of invasive species, including new diseases and parasites (Neumann and Carreck, 2010) and, increasingly, by climate change (P.H. Williams *et al*., 2007; Dormann *et al*., 2008). As most natural landscapes around the world are human-dominated, it is likely that pollinator populations have changed, and possibly declined, in most parts of the world, although the responses of individual species to these drivers can range from increases in population, via indifference, to complete local extinction. This can be illustrated with the example of British bumblebees. As a group they have declined considerably (i.e. lower species richness) with several species now restricted to small local populations or virtually extinct. Other species, however, seem to persist in low numbers and 6–7 species occur in most urban gardens and seem to be thriving.

In addition to declines in wild pollinators, **there is mounting evidence that managed honeybees are declining around the world**. Domestic honeybee stocks declined by 59 percent between 1947 and 2005 in the United States of America (NRC, 2007; vanEngelsdorp *et al*., 2008) and by about 25 percent in central Europe between 1985 and 2005 (Potts *et al*., 2010b). In addition to socio-economic factors that are making beekeeping less attractive as a commercial venture or hobby, these declines are a result of the introduction of *Varroa destructor* Anderson and Trueman (Acari: Varroidae), an ectoparasitic mite of honeybees, from Asia (Case study 9). This mite has resulted in the disappearance of most wild and feral honeybee colonies in Europe and the United States of America, leaving only those kept by beekeepers (Kraus and Page, 1995; Moritz *et al*., 2007; Jaffé *et al*., 2010). However, in recent decades the beekeeping industry has diminished considerably in the United States of America and Europe – see figures above – despite having increased globally by about 45 percent since 1961 (Aizen *et al*., 2009).

The observed and expected declines in wild pollinators, combined with steep regional declines in managed honeybees (the only "back-up" option), seem to suggest that **the demand for crop pollination could outstrip the supply of wild and managed pollinators**, particularly with respect to the ongoing increase in the proportion of pollinator-dependent agricultural crops (> 300 percent increase since the 1960s; Aizen and Harder, 2009).

2.4 INVERTEBRATES AS A SOURCE OF PRODUCTS AND FOOD

Some invertebrates are important food items in their own right. Others produce products that are used by humans.

Products from insects

The most important and economically significant products obtained from insects are honey from domesticated and wild bees, and silk from sericulture based on the silkworm, *Bombyx mori* (L.) (Lepidoptera: Bombycidae). However, there are many smaller niche markets, which can be locally very important. For example, the fungus *Ophiocordyceps sinensis*, which grows on the caterpillars of certain ghost moths (Hepialidae) in the high pastures of the Himalayas, commands very high prices in the traditional Chinese medicine market (Case study 10).

The honeybee, discussed above in terms of its pollinator function, plays by far the largest role in honey production. Sericulture is based mostly on a single domesticated species, which is now found throughout the world. There have been trials using various species of Saturniidae (silk moths), but none have yet proved as satisfactory as the silkworm.

Harvesting edible invertebrates

Invertebrates are a good source of protein, fats, vitamins and minerals. **In groups with little access to other sources of protein, invertebrates can be an important component of the diet, and are often available when other food sources are not.** For example, among the Guajivos Amerindians of the Bolivarian Republic of Venezuela, soil invertebrates make up 60 percent of the animal protein consumed during the rainy season (Paoletti *et al*., 2000).

Eating terrestrial invertebrates is common in indigenous cultures in many parts of the world, including North, Central and South America, Africa, Asia, the Middle East, Australia and New Zealand. Although, today, the practice is rare in the developed Western world, insects remain a popular food in many developing regions of Latin America, Africa, Asia and Oceania. In Western culture, marine and freshwater Crustacea (including shrimps, prawns, lobster, crayfish and crabs) and marine molluscs (squid, octopus, oysters, mussels and a wide variety of shellfish) are widely eaten and highly valued. However, of the many edible terrestrial invertebrates, only snails are widely eaten, and then mainly in cultures with a strong French influence.

While insects are not usually considered food in Western culture, elsewhere in the world, most large, easily gathered, non-poisonous invertebrates will be eaten, including grasshoppers and locusts, crickets, cicadas, ants, termites, immature stages of beetles and moths, scorpions, spiders and worms (Defoliart, 1999; Paoletti *et al*., 2000; Decaëns *et al*., 2006). At present, these invertebrates are mostly gathered from the wild, rather than farmed (Case study 11). This strategy takes advantage of a highly abundant and renewable resource. Wild invertebrates are available to all sections of the population, particularly the rural poor, and collecting them for consumption or sale in local markets involves minimal inputs (Case study 12).

Production of invertebrates for food

The cultivation of invertebrates for human food is now emerging in animal husbandry as an ecologically sound concept. Just as the production of marine shellfish has switched to aquaculture, methods for culturing terrestrial invertebrates as food deserve attention.

Compared to traditional livestock (mammals and birds), it has been suggested that production of invertebrates will not utilize crops as a source of feed – although as production is scaled up, feed sources will need to be established and this could involve crops. Insects generally are more efficient than vertebrates at converting food to body mass, do not need to use food to keep warm (being poikilothermic, or cold blooded), reproduce much more rapidly, occupy less space, use less water and produce less greenhouse gas (Paoletti, 2005; Oonincx *et al*., 2010). However, the mass production of invertebrates as food is still only a possibility. Research, testing, market development, supply chains, storage, preparation, promotion and human preferences would all need to be addressed in order to further develop this option (Sileshi and Kenis, 2010).

CHAPTER III. EFFECTS OF CLIMATE CHANGE ON INVERTEBRATES RELEVANT TO FOOD AND AGRICULTURE

3.1 INTRODUCTION

One of the pathways through which food security and agricultural production will be influenced by climate change is through its effects on invertebrates. The pests that affect production, quality and storage of yield, the beneficial species that pollinate crops, those that protect crops by predation and parasitism of pests, the decomposers that aid the maintenance of – and nutrient cycling within – managed ecosystems, and the vectors that spread animal and plant diseases all respond to regional and seasonal changes in climate. This chapter summarizes briefly the key climate projections and impacts on agriculture from the latest Intergovernmental Panel on Climate Change (IPCC) assessment and reviews the potential direct and indirect impacts on invertebrates relevant to food and agriculture.

3.2 CLIMATE CHANGE PREDICTIONS

In 2007, the IPCC completed the Fourth Assessment Report of current scientific understanding of climate change (IPCC, 2007a), which included scenarios projecting future climatic changes and their likely impacts on natural and managed systems, the vulnerability of these systems and their capacity to adapt (IPCC, 2007b).

The projections of future changes in climate included:

- Over the next two decades, a warming of 0.2–0.4°C per decade.
- Warming and sea-level rise to continue for centuries even if greenhouse-gas concentrations are stabilized.
- A 1.8°C rise above 1980–1999 levels in global average surface air temperatures by the end of the twenty-first century for a low emission scenario (IPCC B1).
- A 4.0°C rise above 1980–1999 levels in global average surface air temperatures by the end of the twenty-first century for a high emission fossil-fuel intensive scenario (IPCC A1Fl).
- Warming expected to be greatest over land and at most high northern latitudes.
- By the end of the twenty-first century, rainfall very likely to have increased in high latitudes and East Africa and decreased in most subtropical regions (Central America, the Mediterranean basin and the subtropical regions of Africa, Australia and Central Asia); increases in tropical precipitation projected during rainy seasons, and over the tropical Pacific in particular.
- Increase in extreme weather events (droughts, heat waves, heavy precipitation, intense tropical cyclones).

Elevated levels of CO_2 (eCO_2), the most important anthropogenic greenhouse gas, have positive effects on plant growth and yield. Levels have increased from a pre-industrial level of about 280 ppm CO_2 to 379 ppm in 2005. On its present trajectory, atmospheric CO_2 will pass 550 ppm by 2050. However, the benefits to plant growth and yield will be restricted by many limiting factors. The major projected impacts of climate change on agriculture (and their probability) include:

- Increased crop and pasture yields in colder environments and decreased yields in warmer and seasonally dry environments (virtually certain).
- Increased insect outbreaks (virtually certain).
- Reduction in yields in warmer regions due to heat stress (very likely).
- Increased heavy precipitation events, causing damage to crops, soil erosion and difficulty in land cultivation (very likely).
- Increased area affected by drought, leading to land degradation, lower yields/crop damage and failure, and more livestock deaths (likely).
- Storm intensity increased, leading to damaged crops and uprooting of trees (likely).
- Increased incidence of extreme high seas, causing salinization of irrigation water and freshwater systems (likely).

Agriculture has historically shown high levels of adaptability to climate variations, and trade has the capacity to reduce regional and global impacts. The dependence of developing countries on food imports is likely to increase as even slight warming reduces yield in seasonally dry and tropical regions, and the farmers in these countries may not have the resources or ability to respond.

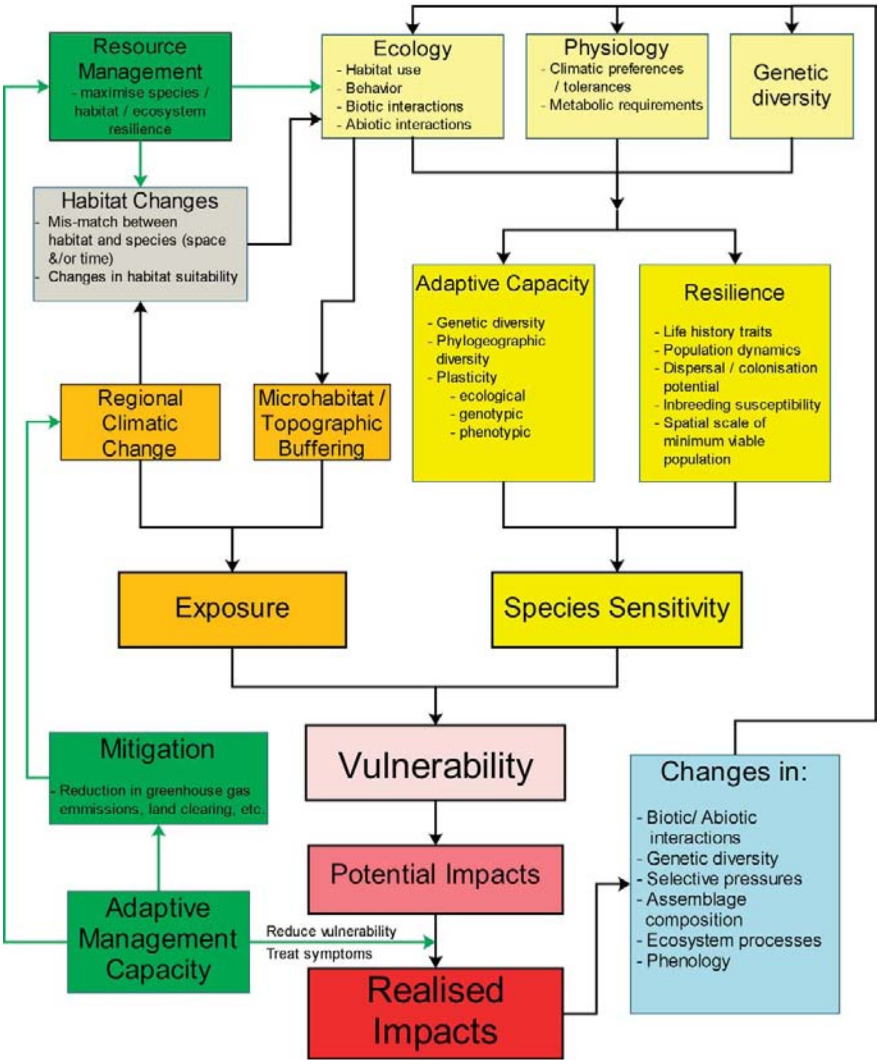
Management options to optimize yield and/or economic returns listed by Easterling *et al.* (2007) include:

- altering timing, location, variety or species of crop planted to better match prevailing conditions and markets;
- wider use and better timing of water conservation/management technologies;
- diversifying income by integrating other farming activities; and
- improving pest, disease and weed management practices.

3.3 IMPACT OF CLIMATE CHANGE ON INVERTEBRATES RELEVANT TO FOOD AND AGRICULTURE

Even in simplified agricultural ecosystems, the sheer number of potential interactions makes predicting the impact of climate change on invertebrates daunting (Figure 5).

Figure 5. A general framework showing factors influencing the vulnerability of species to climate change



Note: Much more detail could be added for most boxes, for example under “Ecology”, food web interactions and more than 80 types of indirect effects could be mentioned.
Source Williams *et al*. (2008).

Single and combined effects are expected, and their responses will be context dependent. Most studies have dealt with only single factors such as eCO_2, warming or changes in rainfall patterns. There is a paucity of data on the likely interactions of such climate change-related factors (Kardol *et al*., 2011; Case study 13).

Invertebrates have limited ability to regulate their body temperature and are directly under the control of temperature for development, reproduction and activity. Therefore, although some groups such as soil invertebrates (Staley and Johnson, 2008) and animal ectoparasites (Estrada-Pena, 2008) may be buffered by the niches they occupy, the interaction between a species' thermal sensitivities and the abiotic factors determined by climate largely explains its observed distribution and abundance (Araújo and Luoto, 2007). Within this distribution, climate change will have further indirect effects on invertebrates through its effects on host availability and the other resources plant communities provide (Kardol *et al*., 2010).

Invertebrates show very wide variations in sensitivity to temperature, depending on their environment. Berg *et al.* (2010) analysed 50 years of published literature and found pronounced and consistent differences between trophic groups. Species living in habitats with relatively constant temperatures, such as in soil, are less sensitive to changes in temperature than above-ground species, which live under more fluctuating temperature regimes. Vulnerability to temperature increases with trophic rank: herbivores respond more strongly to temperature than plants, and warming leads to a disproportionate loss of top predators. There was little evidence for changes in the absolute climate tolerance of species. Sub-fossil evidence from the Quaternary Ice Ages suggests that **in times of rapid climate change, insects track acceptable conditions rather than evolving *in situ*** (Coope, 2004; Case study 14).

The following sections summarize current knowledge on the predicted impacts – either direct or mediated by agriculture – of climate change on invertebrates in agro-ecosystems (Drake, 1994; Cannon, 1998; Harrington *et al*., 2001; Hance *et al*., 2007; Parmesan, 2007; DeLucia *et al*., 2008; Canto *et al*., 2009; Berg *et al*., 2010; Schweiger *et al*., 2010; Thomson *et al*., 2010).

3.3.1 Geographical range shifts

With climate change. the crops produced in most regions are expected to change over time as growers select and develop species and varieties that optimize yield and/or economic returns under the prevailing conditions. There have been abrupt periods of warming in our planet's recent glacial history: temperatures rose from glacial to interglacial values in less than one century, at a rate of about 1°C per decade, about 12 800 BP and about 10 000 BP (Coope, 2004). Thus far, anthropogenic climate change has been a relatively gradual process. Aided by accidental transfer through human activities, the majority of invertebrate pollinators and pests and their natural enemies can be expected to move with their host plants as crop and forage distributions change. The planet has already warmed by about 0.75ºC in the twentieth century (Easterling, 2007) and **there is compelling evidence for a general poleward shift in the breeding distributions of a large number of invertebrates** (e.g. Hickling *et al*., 2006; Musolin and Fujisaki, 2006). Range boundaries are shifting latitudinally (i.e. towards the poles) at an average rate of about 6 km per decade (Parmesan and Yobe, 2003), and altitudinally – assuming a lapse rate of 6.5°C per 1 000 m and 3.5°C rise for the next century – at a rate of at least 50 m per decade (Whittaker and Tribe, 1996; Menéndez, 2007; Colwell *et al*., 2008); rates that most mobile pest and pollinator species are capable of tracking providing there are no major ecological or physical barriers (Case study 15). As range boundaries shift, existing species composition will shift based on temperature sensitivities. For example, the cold-adapted bumblebee *Bombus bellicosus* Smith (Hymenoptera: Apidae) has become extinct in the former northern portion of its distribution range in Brazil whereas two co-occurring species with wider tolerances have become more abundant (Martins and Melo, 2010).

The extent to which invertebrates will be able to track climate change will probably vary enormously. Some species will be tied to specific latitudes because of direct or indirect photoperiod requirements. Just as Coope (2004) observed that any thermally sensitive species that were tied to a specific latitude were unlikely to survive the onslaught of the first glacial cooling, so will such species be vulnerable to climate change unless they can shift to higher altitudes or adapt *in situ*. Those on oceanic islands have similarly limited options. In general, habitat specialists, especially those with poor dispersal ability, will be least able to keep pace with climate change (Travis, 2003). Some species, such as some predatory mites and many soil invertebrates, have low dispersal rates and the time taken for beneficial species to integrate into a new area will be influenced particularly by the supplementary resources needed (e.g. nectar and pollen, and winter or summer diapause sites). Also, the potential distribution of species is mostly constrained by their physiological level of tolerance to extremes (e.g. droughts and frosts) and an increase in the frequency of such extremes may limit species persistence. Therefore current **communities, especially those based on exotic crop species with specialist invertebrate assemblages, are unlikely to move intact under climate change and there could be some beneficial (absence of pest) or negative (absence of beneficial invertebrates) effects on yield as well as possible destabilization of agro-ecosystems**. The evidence from the geological past also suggests that species are unlikely to respond as intact communities (Russell and Grimm, 1990; Lawton, 1998; Colinvaux, 2005).

It has been suggested that **future climates may consist of novel temperature and precipitation regimes, which have no current climatic equivalent, resulting in new species associations** (J.W. Williams *et al*., 2007).

Responses of invertebrates to climate change may be inhibited or hampered by human activities, through habitat loss and fragmentation, land-use changes and reduction of genetic diversity (Thomas *et al*., 2004). How a landscape is managed and changes over time is known to affect the composition and abundance of the invertebrate species present. Butterfly studies have documented the decrease in species diversity that occurred during the rapid industrialization of Europe at the end of the nineteenth century and when intensive large-scale farming was propagated from the middle of the twentieth century (e.g. Laussmann *et al*., 2010). The grain industry in Australia has seen major shifts in invertebrate pest challenges over a 30-year period as a consequence of climate change, altered patterns of crop and pesticide use, and farm management responses (Hoffmann *et al*., 2008). Similarly, 50 years of research on the effects of agricultural landscape management in western Poland has shown a progressive increase in heat-loving (thermophilic) insects related to grasslands, probably connected with climate change, as well as with an increasing share of cereals in crop rotations (Karg and Balazy, 2009). However, responses may be unpredictable, and existing interdependencies between species may only become apparent when they become uncoupled as a result of asynchronous responses to climate change (Parmesan, 2007). Groffman and Jones (2000) concluded that there have been too few ecosystem-scale experiments on the role of invertebrates and suggested that if their importance can be demonstrated at the ecosystem scale, then importance at landscape, regional and global scales is likely.

3.3.2 Increased risk of outbreaks

Extreme weather events such as droughts, floods and unseasonal frosts are followed frequently by pest population explosions. These may be indirectly mediated by factors such as improved food quality and quantity due to seasonal rainfall (Branson, 2008; Case study 16) and physical damage such as gaps left when trees are blown down (Bouget and Duelli, 2004). Effects may also be mediated through impact on natural enemies, particularly the reduction or elimination of specialist natural enemies due to weather fluctuations (Stireman *et al*., 2005). While many invertebrates have mechanisms for coping with extremes, they require time to acclimatize and/or enter the resistant state. Field data indicate that parasitoids are generally more sensitive than their hosts, and lag behind in population recovery (Thomson *et al*., 2010 and references therein). Sequential extremes (e.g. prolonged drought followed by intense precipitation) can decouple long-evolved relationships between species that are essential for controlling pests (Rosenzweig *et al*., 2001). Therefore, **regions that are likely to have an increased frequency and severity of droughts (and deluges) because of climate change may not be able to depend solely on biological control as a pest management method in either environmental or production sectors**. For some invertebrates, infrequent extreme weather events may be more important in determining distribution than long-term gradual changes in climate (Gutschick and Bassirirad, 2003).

The evidence associating insect outbreaks and drought is more circumstantial than that for plant diseases – consisting largely of observations that outbreaks of insects such as bark beetles and leaf feeders are typically preceded by unusually warm, dry weather – although there is also a consistent, positive correlation between insect outbreaks and dry, nutrient-poor sites (Mattson and Haack, 1987). The impact of drought is likely to be mediated through different effects on pests and their natural enemies. In New Zealand pastures, grass grub *Costelytra zealandica* (White) (Coleoptera: Scarabaeidae) outbreaks often occur two to four years after severe summer droughts because of the suppression of protozoan and bacterial pathogens in the soil (Popay, 1992). English-Loeb (1990) demonstrated that extreme drought stress in beans generated increases in spider mite populations, and extreme drought stress also impaired the effects of predatory mites on the pest populations. Stavrinides *et al*. (2010) showed that outbreaks of spider mites in vineyards were associated with leaf temperatures and plant water stress, due in part to effects of extreme leaf temperatures on key predatory mites. Drought may eliminate natural enemies such as small parasitic wasps by eliminating the nectar plants they depend upon, or killing parasitized hosts which are likely to be more susceptable to drought stress. Equally, if droughts reduce pests to a very low level, then associated specialized biological control agents (BCAs) are in turn reduced due to host rarity, resulting in a pest outbreak until the BCA population recovers.

Host-specific parasitoids may suffer disproportionately as a result of increases in climatic variability. Exposure to temperature extremes induces lethal and sublethal damage in parasitoids (Hance *et al*., 2007). It generally decreases their longevity, fecundity and mobility, along with their ability to orient themselves toward attractive odours and their learning capacities. Other consequences of extreme temperatures may include increased efficacy of the host’s immune system in resisting and killing the parasitoids, and decreased host-location ability as a result of changes in plant volatiles (Hance *et al*., 2007).

Temperature extremes can also affect the maintenance of diversity (both species and genetic) of the bacterial endosymbiont community within BCAs. These endosymbiont species mediate many processes in invertebrates, for example defence against parasitoids and pathogens, tolerance of heat and cold stress, host range, and production of essential amino acids (Werren, 1997; Douglas, 1998; Enigl and Shausberger, 2007). In many parasitoid Hymenoptera, the endosymbiont bacterium *Wolbachia* is a sex ratio distorter, and is responsible for female-biased, or even fully thelytokous (female-only) strains and species (Engelstädter and Hurst, 2009). These insect–endosymbiont associations may be impaired, or even eliminated, by exposure to high temperatures (Pintureau *et al*., 1999; Pintureau and Bolland, 2001; Thomas and Blanford; 2003, Guay *et al*., 2009). Where its presence generates female-biased reproduction in parasitoids, the elimination of *Wolbachia* by heat stress may disrupt the population dynamics of the BCA and cause outbreaks of the pest host (Zhou and Zhang, 2009).

3.3.3 New pest and plant species

Temperate geographically isolated islands and regions will become more vulnerable to colonization through wind dispersal with the intensification of weather systems and/or absence of frosts. For instance, New Zealand, as a temperate island nation, has been exposed to airborne invertebrate species from Australia for millions of years, but most have not established (Phillips *et al*., 2006; Case study 17). With increasing temperatures, however, there will be increased use of subtropical plants in production systems and invasive subtropical weed species are likely to become more prevalent. These plants may thrive in the absence of their co-evolved herbivores. Some alien weed species originally introduced for floral displays may benefit pollinators. **It is inevitable that establishment events will increase in frequency, as climate change has the potential to affect the introduction, spread and establishment of invasive alien species** (Weltzin *et al*., 2003; Case study 18). Without specific natural enemies, some of these species will become pests and may be more responsive to eCO_2 than native species (Song *et al*., 2009), with implications for control measures.

3.3.4 Changes in invertebrate development, survival and behaviour

Warmer and shorter winters will mean that many invertebrates will commence activity and reproduction earlier in the year (Bale *et al*., 2002**), and there is already overwhelming evidence of this for some herbivores and their host plants** (e.g. Root *et al*., 2003).

Species with long life cycles, especially if controlled by photoperiod, may show little change, whereas species characterized by high growth potential, multivoltinism (Case study 19) and absence of diapause may expand. Under climate change, multivoltine species may be able to produce additional generations, relative to current conditions in a given locale, with a potentially greater impact on their host plants (Tobin *et al*., 2008). Species that are frost sensitive will benefit from warm winters through increased survival and may increase in pest status. Expansions in the ranges of many pests are already evident as a result of reduced winter mortality (e.g. Yukawa *et al*., 2007). In contrast, species normally in diapause in winter may decrease in pest status by being disadvantaged as a result of high energy losses, development of pathogens and greater availability to predators (Lastuvka, 2009). In many cases, the extrinsic factors controlling diapause are complex, often involving interactions between day length, temperature, and other factors such as moisture, nutrition, crowding and maternal effects. **The effects of climate change on the abundance and status of a pest species will vary with region, ecosystem and the fitness of the individuals in the population.**

There is consensus that climate change will have a profound effect on soil-organism performance and the functions they provide (Klironomos *et al*., 1996; Schröter *et al*., 2004; Kardol *et al*., 2010). Elevated CO_2 can change the abundance and species composition of soil organisms (Jones *et al*., 1998). Yeates *et al.* (1997) reported significant responses in the soil fauna to eCO_2 (750 parts per million by volume): eight out of ten nematode taxa (mainly omnivore and predator species) reacted positively to increased CO_2 levels, while the bacteria-feeding *Rhabditis* spp. showed a marked decrease. Loranger *et al*. (2004) found that collembolan abundance decreased greatly under eCO_2 and O_3 in a Free-Air Carbon Dioxide Enrichment (FACE) experiment in northern Wisconsin. Temperature is a key factor regulating many biogeochemical processes such as soil respiration (the emission of CO_2 due to producers or consumers), litter decomposition, nitrogen mineralization (the biological transformation of organically combined nitrogen to ammonium nitrogen during organic matter degradation) and denitrification (the microbially facilitated process of nitrate reduction that may ultimately produce molecular nitrogen, N_2) (Norby *et al*., 2007). Not all soil fauna will respond in the same way (Roy *et al*., 2004), with flow-on effects on the abundance and community composition of soil invertebrates. For some, the ability to migrate down the soil profile to cooler and moister levels will remain an important survival strategy. Laboratory experiments have shown that a 3.3°C warming had a positive effect on abundance of saprophagous macro-arthropods (i.e. those feeding on dead organisms) such as millipedes, possibly as a result of increased microbial development in the leaf litter and/or increased food utilization (David and Gillon, 2009). Sohlenius and Boström (1999) moved soil cores from cooler to warmer sites in Sweden and found that total nematode populations and the ratio of fungus-feeding to bacteria-feeding nematodes increased. Similarly, Diptera larvae densities fell and enchytraeid worm densities increased when soil cores were transplanted from high-elevation sites to a lower area with an associated mean annual temperature increase of 2.5ºC and drier conditions (Briones *et al*., 2009). Harte *et al*. (1996) showed that experimental heating of field plots in a subalpine meadow in Colorado reduced biomass of soil mesofauna and macrofauna in dry zones but enhanced biomass in moist zones. Soil invertebrate responses to warming are crucial in controlling carbon fluxes in peat soils (Carrera *et al*., 2009) and have the potential to speed up the decomposition of organic matter with important implications for the global carbon cycle. Expected increases in temperature will also favour humivorous (humus-feeding) termites and endogeic earthworm species that feed in the soil (Lavelle *et al*., 1997).

Warmer temperatures are likely to alter invertebrate behaviour. For instance, “sit and wait” spiders will move to cooler niches in the habitat while active hunting species cover larger territories (Barton and Schmitz, 2009). Such behavioural changes by predators may have flow-on effects. In a field food web, increased temperature intensified the behavioural shift by grasshoppers to feed preferentially on herbs rather than grasses in the presence of hunting spiders (Barton *et al*., 2009).

Temperature has a direct effect on the pathogenicity of fungi that attack invertebrates, such as *Beauveria bassiana* and *Metarhizium anisopliae*, which can either be very virulent, causing extensive and rapid mortality in days, or virtually benign, with the same hosts surviving for weeks or even months (Thomas and Blanford, 2003). Temperature can also have considerable effects on host susceptibility to parasitoids with multiple observations that high temperatures can enhance the survival of parasitized hosts (Thomas and Blanford, 2003).

Atmospheric CO_2 levels could have direct effects on invertebrates, but there are few examples (Case study 13). Elevated CO_2 has been reported to affect negatively the avoidance behaviour of invertebrates, such as alarm signalling by aphids in response to a predator (Mondor *et al*., 2004). While some pests, such as mosquitoes and some plant pests, use CO_2 directly in host location (Johnson *et al*., 2006; Guerestein and Hildebrand, 2008), there is no evidence for similar behaviours among predators and parasitoid BCAs to date. However, this is likely to occur in at least some species, and host and prey location, and attack and predation rates, might be compromised in future eCO_2 atmospheres. For some plant pests and weed BCAs, response cells saturate under high CO_2 (400 ppm or higher, depending on species) (Guerenstein and Hildebrand, 2008). *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), an important BCA of prickly pear cactus (*Opuntia* spp.) in some parts of the world, is an example of a BCA in which host location could be impaired by eCO_2 (Stange, 1997).

Interactions between the effects of different elements of climate change will almost certainly be important, and likely to confound some of the expectations based on a single factor. Soil temperature covaries with soil moisture, and global climate change is likely to involve shifts in rainfall patterns, while elevated temperature would lead to increased evaporation and plant transpiration and affect the frequency of wetting–drying cycles. Therefore, **generalizations about the effects of climate change on soil micro-arthropods – and perhaps on all soil invertebrates – must be made with caution.** For example, contrary to their expectations, Kardol *et al*. (2011) found no significant direct effect of warming and eCO_2 on abundance of soil mites; instead, abundance and richness were positively related to soil moisture content (Case study 13). They observed that climate change treatments altered the community structure of soil micro-arthropods, although the combination of climate-related factors only explained about 33 percent of total variation. Other experimental studies have shown that increased temperature would be unlikely to provoke important changes in micro-arthropod populations, although significant increases were observed in an experiment on bacteria- and fungus-feeding nematodes (Ruess *et al*., 1999).

3.3.5 Plant-mediated effects

Increases in CO_2, changes in water availability and increases in temperature will alter plant chemistry, phenology, growth and distribution, and these changes in the physiology, form and biomass of plants, will in turn alter the quality and composition of the leaves, which can affect the growth and development of plant herbivores and those that prey on them. Increases in the concentration of chemicals that act as defences against insects (such as soluble phenolics and condensed tannins) under eCO_2 can have significant consequences for herbivores (Peñuelas and Estiarte, 1998).

Much of the increased plant biomass produced in response to eCO_2 is invested below ground in the root systems (Curtis and Wang, 1998; Lukac *et al*., 2003). Stiling *et al*. (2010) found that under eCO_2, herbivore guilds increased in abundance, but the effect was not passed on to decomposers such as collembolans, beetles and cockroaches. Increased abundance and performance of herbivores under eCO_2 is most like to occur when nitrogen is not limited, e.g. in the case of clover root weevil, *Sitona lepidus* Gyllenhal (Coleoptera: Curculionidae), feeding on underground root nodules (Johnson and McNicol, 2010).

The effects of eCO_2 on BCAs are also likely to be mediated through flow-on effects of CO_2 on plants. Plants grown under eCO_2 exhibit increased growth, but reduced carbon/nitrogen ratios, and hence lower nutritional quality for herbivores, per gram of plant material (DeLucia *et al*., 2008). Thus, in general, eCO_2 is associated with increased damage through compensatory insect herbivory in response to decreased nutritional value of plants. Production of phenolic compounds associated with herbivore defence increases under eCO_2 (Bidart-Bouzat and Imeh-Nathaniel, 2008). The net result is either reduced fitness (e.g. size, reproduction) or longer development times in pests (Ode, 2006). The former will tend to decrease performance of natural enemies, as BCA fitness is correlated with host/prey fitness, or may affect natural enemies through the direct effects (toxicity) of secondary plant compounds (organic compounds in plants that are not directly involved in normal growth, development, or reproduction, but often linked to defences against herbivores) (Ode, 2006). Increased development times will tend to increase the impact of natural enemies, especially those that attack feeding stages, as these stages would remain vulnerable longer under eCO_2. Because prey could be smaller under eCO_2, predators may find them easier to handle, and may have a greater impact on prey populations as a result (Coll and Hughes, 2008). Other species may have better survival. For instance, under eCO_2, cotton aphid (*Aphis gossypii* Glover) survival significantly increased but ladybird larval development took significantly longer, increasing the likelihood that these aphids may become pests in the future (Gao *et al*., 2008).

Plants that are under attack by pests produce a wide array of compounds (herbivore-induced plant volatiles or HIPV) that assist generalist and specialist BCAs in finding the prey (De Moraes *et al*., 1998; Hare, 2011). The production of these compounds is influenced to a great extent by environment (Hare, 2011 and references therein), and it is possible that factors associated with climate change will affect quantity and quality of HIPV. Pinto *et al*. (2007) found that increased O_3 reduced HIPV production in some plants, but not all, but changes in HIPV production did not affect predator–prey associations in their experiments. Volatile emissions from plants generally increase under increased temperatures, but the effects of eCO_2 seem to be variable (Bidart-Bouzat and Imeh-Nathaniel, 2008 and references therein).

It is not possible to generalize about the effects that drought stress in plants has on invertebrates, but droughts can have major effects on ecosystems and can change and disrupt plant-mediated competitive interactions between invertebrates feeding on different parts (sites) of the plant. Species within the same guild can vary in response (Staley *et al*., 2006) and existing plant-mediated interactions between above- and below-ground herbivores can be changed (Staley *et al*., 2007).

Changes in temperature and moisture stress can influence levels of many insect-resistance allelochemicals (substances that affect growth of other organisms) and the intensity and rate of release of volatiles. However, herbivore detoxification systems and immune responses may also be enhanced (Mattson and Haack, 1987) and there can be flow-on effects to parasitoids (Kauffman and Kennedy, 1989). Weed BCAs and parasitoids often depend on volatile organic compounds to locate hosts (Micha *et al*., 2000). Each is likely to have its own optimal temperatures for signal perception; thus, extreme temperatures or large fluctuations can strongly affect the capacity of BCAs to locate hosts and host habitats (Hance *et al*., 2007 and references therein).

3.3.6 Effects on natural enemies

The interactions between plants, herbivorous insects and parasitoids result from a long period of co-evolution in a particular environment. **Species at the higher trophic level (parasitoids and predators) are more likely to be affected by climate change than herbivores because they depend on the capacity of the lower trophic levels to adapt to these changes** (Petchey *et al*., 1999). In other words, climate change effects may be amplified by trophic responses transmitted through natural enemies (Gao *et al*., 2008) or competitors (Stacey and Fellows, 2002). Natural enemies with very narrow and specific host ranges – a highly desirable attribute for classical biological control programmes – may be more sensitive to climate change than generalist herbivores and predators because they are of necessity precisely synchronized with the development of their hosts, and could become extinct if their interactions become decoupled (Hance *et al*., 2007). Those that rely on their hosts remaining alive throughout their development are particularly vulnerable. Accordingly, to ensure effective pest management in the future, increased effort is needed now to better understand and support generalist predators, taking into consideration landscape-level movements, refugia in time and space, alternative food sources and other aspects of conservation biological control.

Contrasting outcomes have been observed in model aphid biological control systems. The abundance of peach potato aphid *Myzus persicae* (Sulzer) was enhanced by both eCO_2 and a temperature increase of 2°C, whereas parasitism rates by its parasitoid, *Aphidius matricariae* Haliday (Hymenoptera: Braconidae), only trended upwards in elevated temperature (Bezemer *et al*., 1998). In contrast, both predator and parasitoid increased attack rate against the grain aphid *Sitobion avenae* (F.) in eCO_2 and as a consequence substantially suppressed aphid abundance (Chen *et al*., 2007). Population dynamics theory predicts that the extent to which a predator population suppresses its prey population is determined by the ratio of the predator's generation time to that of its prey (Godfray *et al*., 1994). When the generation time ratio (GTR) is low, a predator population can increase rapidly compared to its prey, and greater suppression is possible. Conversely, a high GTR leads to poor control. Climate change may influence the GTR of biological control systems if the minimum temperature required for development differs between a BCA and its host, or one of the species is in diapause when the other is active.

3.3.7 Phenology and synchrony

Hance *et al*. (2007) state that “a key factor determining how climate change may affect the range and abundance of insect populations is the extent to which individual species react independently of the community of which they are a component.” Aspects of plant life cycle events controlled by temperature, such as the timing and duration of seed germination, bud burst and flowering, are likely to change with warmer temperatures, subject to photoperiod and water availability. So warmer temperatures should encourage many temperate plant species to flower earlier, and this has already been documented in many crop plants and natural ecosystems (Craufurd and Wheeler, 2009 and references therein). Cues in subtropical and tropical areas may differ: delayed seasonal flowering has been observed in Florida (Von Holle *et al*., 2010). The extent to which an invertebrate is affected by these changes, whether it is a herbivore, predator or parasitoid, will depend on how well its life cycle events are synchronized with its host to ensure optimum survival. Rapid changes in the degree of synchrony between species “seems inevitable” (Singer and Parmesan, 2010) and even small changes between host and parasitoid may change the efficacy of a BCA system locally (Case study 20). An example of an increasing mismatch is provided by egg hatching of the winter moth (*Operophtera brumata* (L.); Lepidoptera: Geometridae) compared to bud burst of its oak tree host (*Quercus robur*; Fagaceae) (van Asch and Visser, 2007). The poor synchrony is due to an increase in spring temperatures (in particular a decrease in the number of frost days and an increase in temperatures above a baseline of 3.9°C) without a corresponding decrease in the incidence of freezing spells in the winter (Visser and Holleman, 2001). The former provides the temperature cues for the moth, the latter for the tree (Harrington *et al*., 1999).

Episodic extreme temperature (heat waves and unseasonal cold) has the potential to disrupt biological control food webs independently of the disruption of cropping systems. Almost all invertebrates are poikilothermic, or cold blooded, and the rates of biological processes are determined by ambient temperature, between an upper and lower threshold. The relationship between temperature and rates of processes follows an asymmetric parabola with an abrupt drop to an upper threshold. Above the upper threshold and below the lower threshold, the process does not occur (Case study 21). Differential responses to extreme temperatures by BCAs, target pests and plants, have the potential to change biological control food webs, but there is, at present, insufficient evidence to determine the extent to which this might occur. The growth of pea aphid (*Acyrthosiphon pisum* (Harris)) populations is impaired under heat stress and the degree of this impairment is different for two different species of ladybird beetle predators (Harmon *et al*., 2009). Exposure to thermal stress can have subsequent effects on longevity and fitness of surviving female parasitoids (Roux *et al*., 2010).

This synchronization between species need not be perfect. In a stable biological control system, the level of regulation is such that sufficient hosts and natural enemies survive to the next growing season to allow similar ongoing regulation in the next. In populations where host and natural enemy have multiple discrete generations a year, imperfect synchronization, allowing some hosts to escape, can stabilize an otherwise unstable interaction (Godfray *et al*., 1994).

Where pests and their natural enemies occur in overlapping generations, an extreme weather event may eliminate only vulnerable pest stages, leaving a synchronized population derived from the life cycle stage that was not adversely affected. This can lead to breakdown of natural control, as many parasitoids will emerge and find no hosts of a suitable stage of development available, and so die out and not be available to control the pest when the suitable life stage is available again (Case study 22).

However, in some circumstances climate change may favour the parasitoid: increased winter temperatures may promote parasitism in regulating populations of the European pine sawfly, *Neodiprion sertifer* (Geoffroy) (Hymenoptera: Diprionidae), due to the lower mortality of parasitized eggs in the winter (Veteli *et al.*, 2005). Similarly, increased summer temperatures can favour increased parasitoid and predator activities (Virtanen and Neuvonen, 1999). Conversely, insects which overwinter as non-feeding, diapausing adults (e.g. the solitary bees *Osmia lignaria* Say; Hymenoptera: Megachilidae) will be negatively affected by extended summers under climate change, as few can survive short winter conditions (Bosch *et al.*, 2010).

Climate change can disrupt the stability of biological control systems in several ways:

- Increased temperature may cause one species to come out of diapause earlier than another. Should the species in a biological control system have contrasting factors regulating diapause, then it is possible for a large mismatch, control failure and local extinction.
- Increased variability between years. Modelling of a simple host–parasitoid system showed that an abnormally warm spring once in 25 years did not affect long-term stability, but the system failed when it occurred more frequently than one in 20 years (Godfray *et al.*, 1994).
- Increased number of generations per year. If either the host or the natural enemy has an additional generation in a season that is not similarly reflected by the other, then the stability of the biological control system may be at risk (Case study 23).
- Loss of synchrony between plant and natural enemy; e.g. if the adult activity of seed-feeding weed BCAs is not synchronized with flowering and seed formation, control will fail.
- Floral or pollen resources may not be present at the right time; e.g. most Diptera natural enemies require pollen in order to produce eggs.

Poor synchronization between flowering and pollinators in early season has been documented, but while this may affect individual species, the heterogeneity of pollinator communities should buffer against impacts on crop yield (Hegland *et al.*, 2009).

3.4 BIOGEOGRAPHICAL DIFFERENCES – TEMPERATE, SUBTROPICAL AND TROPICAL ZONE VULNERABILITIES

While, in most temperate regions, an increase in the capacity to support increased plant diversity is expected, a strong decline in most tropical and subtropical regions is projected (Sommer *et al.*, 2010), although this is at variance with predictions based on the Quaternary pollen record (Colinvaux, 2005). Therefore, land managers in temperate regions will have more options in terms of crops and how to manage ecosystem services supporting pollinators and other beneficial invertebrates compared to those in most tropical and subtropical regions. However, just as temperate regions are most vulnerable to invasion by cosmopolitan weeds (Woodward and Kelly, 2008), so will they be most vulnerable to invasive invertebrates (Case study 15).

Under climate change, the tropical monsoon belt is widening (Seidel *et al.*, 2008). For example, Australian monsoon rainforests have expanded within the savanna matrix (Bowman *et al.*, 2010). However, not all species will alter their distribution. Coffee, a tropical crop, is predicted to be severely affected by climate change: *Coffea arabica* and *C. canephora* (Rubiaceae) are not expected to move latitudinally because both species are highly susceptible to changes in photoperiod, while rising temperatures are increasing the number of generations of the principle pest (Jaramillo *et al.*, 2009).

Tropical plant–herbivore interactions are considered to be more susceptible to the perturbations of climate change than those in temperate zones because of tight ecological and evolutionary linkages. Tropical plants are better defended and, unlike in temperate forests where most herbivory (about 75 percent) occurs on mature leaves, in the tropics most is on young leaves (> 70 percent), an ephemeral resource (Coley, 1998).

CHAPTER IV. POTENTIAL ROLE OF INVERTEBRATES IN THE FACE OF CLIMATE CHANGE

4.1 SOIL INVERTEBRATES

4.1.1 Possible adaptation by invertebrate genetic resources to the challenges identified

Adaptation involves activities that enable ecosystems – and the people that rely on them – to adjust to climate change, for example, by buffering the effects of extreme weather events or decreasing the vulnerability of agro-ecosystems to their impacts (Burgiel and Muir, 2010). In this respect, **soil invertebrates have a major role to play in mitigating the negative effects of climate change** and the presence of a diverse community of soil organisms is crucial to the maintenance of beneficial and complementary functions in agro-ecosystems (Jiménez and Thomas, 2001).

Generalizations about the effect of extreme events on soil invertebrates and decomposers are difficult, as these have seldom been addressed in investigations. We can infer that soil invertebrate populations would probably recover quickly, due to their inherent resilience, although indirect effects – occurring via changes in the productivity and functional composition of above-ground vegetation – would alter associated soil organism dynamics and processes in the longer term, due to changes in sources of detritus (fragments of organic material) and resources entering the decomposer subsystem (Wolters *et al*., 2000; Wardle, 2002). In other words, above- and below-ground communities and processes are intrinsically linked (van der Putten *et al*., 2009)**.**

Microfauna (< 0.1 mm) can tolerate drying events through cryptobiosis (reducing metabolism to imperceptible levels) (Freckman, 1978); micro-arthropods show adaptive strategies that enable them to tolerate or avoid desiccation; and larger soil macrofauna (especially soft bodied taxa) exhibit effective strategies to conserve moisture under dry conditions (Jiménez *et al*., 2000). Although eCO_2 may affect soil ecosystem engineers (such as earthworms, see below) through direct fertilization effects on plant growth, notably an increase in carbon/nitrogen ratios, land-use intensification is of more immediate concern as changes in the functional-group balance within such engineers' communities has been demonstrated (Lavelle *et al*., 1997).

In the case of soil beneficial invertebrates such as earthworms, their maintenance in agro-ecosystems under perturbation seems to be determined by (i) their motile potential and (ii) their adaptive strategies, which together determine their population growth rate. The survival of some soil invertebrates – such as nematodes – is firmly dependent on the maintenance of moisture films around soil aggregates. Micro-arthropods are, however, more resilient to desiccation and not so dependent on soil moisture (Wardle, 2002). **A full understanding of how biotic and abiotic factors determine soil invertebrate distribution across different spatial and temporal scales is essential, if we wish to predict the response of such communities to climate change, as well as the impact it will have on the delivery of ecosystem services.**

Adaptive responses by soil invertebrates to the effects of climate change depend on their limited dispersal abilities. In terms of vertical redistributions within soil horizons, only those invertebrates that are able to move vertically within the soil would be able to counteract the negative effects of climate change, such as increased soil temperature and desiccation. Such **shifts in soil invertebrate species distributions might have a substantial effect on the decomposition process because their functional role depends on the species' vertical position within soils.** Krab *et al*. (2010) found that springtail (collembolan) species differed in their responses to changes in climate or substrate quality, identifying two types of groups: i.e. “movers” and “stayers”. They also suggested that interspecific faunal trait variation may provide a useful tool to predict animal responses to climatic changes. Larger soil invertebrates, such as earthworms, show different adaptive strategies and show different vertical stratification in the face of seasonal changes in tropical areas (Jiménez and Decaëns, 2000). However, the temperature changes required to cause significant shifts in major groups of decomposer biota are probably likely to be much greater than those predicted to result from global warming, particularly in the deeper, temperature-buffered, layers of soil.

Active dispersal involves movement through the soil, while passive dispersal includes transport with eroded soil. The latter has a major influence on the rate of population expansion. In earthworms, for example, the velocity of dispersal has been estimated at less than 10 m per year (Marinissen and van den Bosch, 1992), but this is specific to ecological category, with anecic earthworms having more rapid dispersal rates than endogeic species in both temperate and tropical situations.

At larger scales, there are still knowledge gaps in terms of the biogeographical distribution of soil invertebrates, which need to be filled in order to help us to predict shifts in ranges under climate change scenarios. A recent review by Decaëns (2010) reports that **the few studies currently available on large-scale patterns of soil invertebrate biodiversity suggest a correspondence between soil biodiversity gradients and those classically described for above-ground organisms** (Gaston, 2000). Although major differences among taxa of contrasting body size can be explained by differences in the adaptive strategies and dispersal abilities of species, the paucity of available studies prompts caution in making generalizations.

It is necessary, therefore, to ensure that whatever the effects of climate change may be (and these will vary according to crop and region) soil invertebrates must be preserved and maintained in order to carry out their important role in maintaining the vitality of soils and assuring the continued delivery of important ecosystem services. **The loss of keystone species from the system can result in dramatic changes and impaired provision of ecosystem services by soil invertebrates.** For instance, the removal of just one species of earthworm from the soil led to higher soil compaction, lower plant biomass, lower soil carbon content and higher weed biomass compared to areas where this species was present (Decaëns *et al*., 1999a). In this case, the loss of one key species in an earthworm community resulted in a significant loss in soil ecosystem function.

4.1.2 Potential of invertebrate genetic resources in mitigating climate change

Soil invertebrates play an important role in the sequestration of carbon in soil, but in most cases the mechanisms and scope for manipulation are not adequately understood to use invertebrates in this way. Hence what follows indicates possibilities rather than practice.

Earthworms ameliorate the effects of climate change

The effects of climate change on the interactions between soil invertebrates, plants and above-ground invertebrates are not fully understood. Better models need to be developed to provide guidance to the empirical studies that are required to enhance our capacity to predict the effect of climate change on soil ecosystems (van der Putten *et al*., 2009). The fact that there have been only a limited number of studies on the responses of soil invertebrates to interactive effects of climate change-related factors, such as warming, eCO_2 and precipitation patterns, makes generalizations difficult, but it is foreseen that the responses will be context dependent (Case study 13). However, it is known that **invertebrates (e.g. earthworms) have the potential to mitigate climate change in a number of ways**. For example, Johnson *et al.* (2011) found that earthworms ameliorated the effects of summer drought on a plant (*Capsella bursa-pastoris*) and exacerbated the effects of drought (i.e. a decline in numbers) on above-ground aphids (*Rhopalosiphum padi* (L.)). A similar mitigating effect was found by Blouin *et al.* (2005), who showed that remarkably – and for reasons that are not fully understood – the presence of earthworms helped to mitigate the negative effects of plant-parasitic nematodes on rice plants (Case study 24). Although the earthworms had no direct effect on the nematodes, their presence in the soil somehow reduced nematode feeding damage. So, in both cases, the presence of earthworms reduced the harmful effects of the plant pests (above and below ground); in other words, they have the potential to reduce the loss of biomass (= yield) under climate change (Case study 25).

Ecosystem engineers help preserve soil vitality

Soil invertebrates have the potential to enhance carbon storage via its inclusion in soil aggregates, i.e. the production of biogenic structures within the soil matrix by ecosystem engineers. The effects of large soil invertebrates, the so-called ecosystem engineers or bioturbators (soil removers – mainly ants, termites and earthworms), can have an important role in terms of soil structure, soil porosity and compaction, affecting positively soil water regimes and the availability of water throughout the soil profile. Thus, their role in mitigating the effects of climate change is intimately related to their role in maintaining the water balance of soils to the direct benefit of agriculture. The probable indirect effects of climate change on engineers will also be driven by changes in above-ground plant communities, as vegetation affects both the abundance and diversity of engineers, via the quantity and quality of leaf litter (Lavelle *et al*., 1997).

The activity of soil ecosystem engineers contributes to the build-up of a physically active carbon pool, for example, earthworm-induced accumulation in a stable soil aggregate can be considerable due to the enormous quantities of soil egested as casts. These have been estimated to be as high as 8.6 tonnes of carbon per hectare per year in a tropical grassland (Decaëns *et al*., 1999b). This carbon pool represents 30 percent of the total soil carbon in the topsoil. **It is essential to try and understand and predict how this soil carbon pool will respond or be affected by climate change** (and agricultural adaptation measures).

4.1.3 Analysis of present role and potential use of soil invertebrates relevant to food and agriculture

Increased litter production as a result of the fertilization effect of eCO_2 can increase the resources available for detritivores – potentially resulting in increased abundance of detritivores (Hall *et al*., 2006) and generalist predators (Settle *et al*., 1996). Epigeic and anecic earthworms – and some micro-arthropods – have a vital role in incorporating leaf litter and others forms of plant debris into the soil. In light of the potential increases in plant biomass under climate change, this role will become even more important.

Global change factors such as land use and climate change and atmospheric inputs, whether acting individually or in combination, may lead to non-linear changes in above- and below-ground relationships, with effects that vary geographically throughout the world (Heal, 1997). This limits our ability to make predictions regarding the effects of global change on these above- and below-ground interactions. **Complex and non-linear responses are expected in the interactions between soil invertebrates, plants and ecological processes.** Recent studies have indicated that many different groups of soil fauna (e.g. isopods, mites, collembolans, centipedes, snails, slugs, etc.) obtain carbon directly from plants' roots (Uvarov *et al*., 2011) as well as from leaf litter. This might help maintain the community food web, as higher plant biomass production could result in more resources available to soil decomposer communities, although leading to higher CO_2 emissions from soils. Decomposition is driven not only by temperature-induced changes in substrate quality, and/or physico-chemical conditions, but through the interaction of different levels of soil disturbance with animal assemblages mediating ecosystem processes. Increased decomposition rates of organic substrates due to global warming are expected to result in larger net soil CO_2 emission and less carbon storage in the soil (Jenkinson *et al*., 1991; Seastedt, 2000). However, a global analysis demonstrated that decomposition rates in forest soils were not temperature dependent, meaning that global warming may not necessarily accelerate soil carbon losses. Will higher temperatures move decomposition to deeper layers? In a more recent study, Fontaine *et al*. (2007) demonstrated that the stability of old soil carbon in the subsoil is maintained unless fresh residues are incorporated in deep soil layers. Any change in land use and agricultural practice (e.g. ploughing) that increases the distribution of fresh carbon along the soil profile could, however, stimulate the loss of ancient buried carbon (Fontaine *et al*., 2007).

Moreover, under climate change soil invertebrate assemblages might change and hence soil processes also. Soil invertebrate communities and decomposition rates are responsive to warming (Aerts, 2006). Changes in vegetation distribution driven by climate change and related factors will presumably influence soil invertebrate distribution (Wolters, 2001). Would a warming scenario result in fewer species and less resilience to extreme events, or would warming favour some functional groups over epigeic species? These are examples of some of the questions already addressed by several authors (Krab *et al*., 2010). How the vertical distribution of soil invertebrate assemblages will change and how they might affect soil biogeochemistry remains to be seen (Heemsbergen *et al*., 2004). Although still little understood, responses of soil fauna are likely to differ between ecosystems. Swift *et al*. (1979) suggested that cold-limited arctic ecosystems are particularly sensitive to global warming, while nutrient-limited temperate grasslands are susceptible to CO_2 increase and nitrogen depositions.

The role of a diverse assemblage of macro-organisms is crucial to the maintenance of soil structure. This is illustrated, for example, by the results of an experiment performed in the Brazilian Amazon to investigate the effects of an earthworm species, *Pontoscolex corethrurus* (Müller) and a diverse assemblage of other soil organisms (including other earthworms, termites, millipedes, isopods and ants) on soil structure (Case study 26). When soil blocks were removed from pasture and placed into forest, and similar blocks taken from forest and placed into pasture, the structure of the compacted pasture soil was completely restored after one year to levels typical of those in native forest soils (Barros *et al*., 2004). Conversely, the macro-aggregate structure of the forest soil was completely destroyed by the presence of large populations of an invasive earthworm, reaching compaction and porosity levels similar to those of the degraded pasture (Chauvel *et al*., 1999). Therefore, movement of soil could enhance soil functions in some situations although its feasibility would be limited.

Translocation of soil invertebrates

In view of the very positive contribution of soil invertebrates, and how these may be disrupted by climate change, one option that might be considered is the translocation of soil invertebrates on a local or national scale.

On the local scale, the best approach should always be to fully characterize soil invertebrates in a given local area, and identify and use suitable species and functional groups for the processes needed, such as increased soil aggregation. This approach is not in regular practice yet, and no guidelines for management are available.

We are not aware that soil invertebrates are being deliberately moved between countries at present. Given the risks of introducing species that become invasive (e.g. lumbricid worms accidentally introduced to forests in the United States of America), and the many possible contaminants, an appropriate risk-assessment protocol would be needed. **Until we understand soil ecology much better than we do today, such introductions should be avoided.**

4.1.4 Status of current application of genetic technologies

At present, the techniques of genetic modification have not been applied to soil invertebrates, and there is very little scope for this in the foreseeable future.

4.1.5 Gaps: knowledge, collections, characterization

Although some progress has been made in understanding interactions of below-ground processes with climate change, challenges remain (Pendall *et al*., 2008); uncertainties in predicting the interactions of the ecosystem carbon cycle with global warming are to some extent determined by our lack of knowledge of below-ground processes (Davidson and Janssens, 2006). Global climate change may affect soil carbon stocks indirectly through habitat change and hence via changes in the activity of soil invertebrates (Briones *et al*., 2004). There is already sufficient evidence to demonstrate that soil fauna have significant effects on all of the pools and fluxes in the carbon cycle, and soil fauna mineralize more nitrogen than micro-organisms in some habitats (Osler and Sommerkorn, 2007). The role of soil invertebrates in the carbon cycle therefore needs to be understood in order to generate predictive models on how climate change will affect this cycle through its impact on soil invertebrates. New methods are needed in order to make observations across a wide range of spatial and temporal scales, and thereby to improve the reliability of predictions of responses to altered atmospheric CO_2 concentrations, warming temperatures and nutrient deposition.

Multifactorial experiments are needed to investigate the combined effects of warming, eCO_2 and changes in precipitation, on soil (agro-)ecosystems. Few studies have examined the combined effects of changes in climate change-related drivers in the context of soil function and soil invertebrate biodiversity. Johnson *et al.* (2011) emphasized the importance of investigating the effects of climate change-related drivers (such as summer drought) on soil invertebrates, in the context of multi-species plant communities, as interactions can vary between monocultures and multi-species communities (Case study 25).

Appropriate indicator soil species (i.e. those species that by their presence or abundance define a particular condition or characteristic of a particular environment) and functional groups for monitoring responses to climate change need to be identified for particular ecosystems and for different regions. It is important to identify the keystone species and key interactions that must be maintained in order to preserve soil function in the face of climate change.

The lack of knowledge about latitudinal gradients in soil invertebrate distribution makes predictions about adaptation to climate change difficult. So far, biogeographical distributions of soil invertebrates are not well characterized, and there are important knowledge gaps (Decaëns, 2010). At the local scale, habitat constraints (environmental factors) and biotic interactions (competition, predation, etc.) affect the number of species present in a given community as the combination of such factors defines the rules for community assembly. Existing data provide little evidence that climate change driving factors regulate above- and below-ground communities in similar ways (Bardgett *et al*., 2005).

Collections of soil invertebrate genetic resources

There are no such collections at present or foreseen. To be useful such collections will need to be of living invertebrates. The great diversity of soil invertebrates coupled with the lack of knowledge as to which species might be manipulated in agro-ecosystems for the benefit of agriculture or climate change make this impractical. Genetic resources of soil invertebrates must therefore be conserved *in situ*.

Taxonomy and identification

Paradoxically, there is a conspicuous lack of interest from the scientific community in below-ground diversity, and we know very little about its taxonomy, systematics and biogeography (Decaëns *et al*., 2006, 2010). Only a few studies have reported global patterns in soil biodiversity distribution at different spatial and temporal scales (Wardle, 2002; Bardgett *et al*., 2005). To date, such global patterns in many soil animal groups are unknown and complete inventories of soil organisms are not available for certain habitats or regions, although some approximations for soil invertebrate species have been provided (see Decaëns *et al*., 2006, for a review and Decaëns, 2010).

The development and standardization of new molecular-based taxonomic approaches, such as DNA barcoding analysis, are helping to separate and define cryptic species of soil invertebrates in groups such as earthworms (James *et al*., 2010). Deficits in taxonomic knowledge must also be addressed, through actions at different levels that stimulate studies on soil biodiversity and the characterization of the composition of soil communities. Moreover, targeted educational and editorial strategies should be promoted to disseminate knowledge about the importance of soil invertebrates more widely to the general public (Decaëns *et al*., 2008).

Importance of altitudinal gradients

Latitude, altitude and climate change are (with reservations) used as surrogates for each other in a variety of studies. There is a scarcity of data on altitudinal variation in soil invertebrate assemblages. Some researchers have described a continuous decrease in the total number of species against an altitudinal stratum in a given geographical area for several groups, such as termites (Collins, 1980), earthworms (Bouché, 1972) and ants (Cole, 1940). The reduced species richness at high altitudes has been interpreted as the effect of (i) low temperatures, (ii) low levels of available energy which reduces ecosystem carrying capacity, and (iii) small habitat size, compared to lowland areas (Decaëns, 2010).

Invertebrate distribution may show an optimum altitude (i.e. reduced numbers at higher and lower levels). For example, springtail species richness across an altitudinal transect from 950 to 2 150 m in the French Alps (Loranger *et al*., 2001). In the mountains of Sarawak, Malaysia, Diptera richness reached a peak between 1 300 and 1 700 m; and beetles between 500 and 1 200 m (Collins, 1980). In tropical areas, however, a different pattern has been observed: for example, earthworm species richness increased from sea level up to 1 000 m in Puerto Rico (González *et al*., 2007). The northern boundaries of tree distributions are moving polewards and it is assumed that this will provoke corresponding shifts in the range of soil invertebrates. However, further work is needed to explore the potential of soil invertebrate resources to migrate in concert with the current rapid shifts of the tree line. In particular, the rate of movement of soil invertebrates without a motile stage is not known, although it can be assumed that populations of soil invertebrates may be transported to other areas during extreme events like flooding. However, this process has not been quantified. Analogues exist, such as the colonization rates of newly extruded lava from volcanoes surrounded by vegetation, as has been studied on Mount St Helens (Washington, United States of America), or even in highly intensive agricultural systems where the rates of colonization and dispersal can be assessed if natural refuges are adjacent to these areas.

4.1.6 Island versus continental perspective

In general, limited studies suggest that island soil biodiversity is less diverse – and hence more vulnerable – than continental equivalents. Islands provide examples of how soil invertebrate communities assemble, i.e. species assembly rules for community composition and changes under climate change in islands can be identified to serve as examples for continental areas. Furthermore, there is a high degree of endemism in some groups of soil invertebrates (e.g. earthworms) so it is more appropriate to adopt a functional group perspective that can be used in different situations.

4.1.7 Tropical versus temperate comparisons

It has been shown that earthworms maintain the general health (or functioning) of the soil ecosystem by producing biogenic structures which benefit root systems by maintaining soil porosity and preventing compaction. Warmer conditions promote greater abundance of decomposer invertebrates (Seastedt, 2000) and earthworms in tropical areas have a greater role in breaking down recalcitrant components of soil organic matter than do those in cooler climates (Lavelle *et al*., 1995), although responses are species dependent.

Earthworms, and other ecosystem engineers such as termites and ants (especially in the tropics), might help to mitigate some of the effects of climate change by maintaining a well-functioning soil ecosystem that may be able to tolerate some of these effects/changes.

4.1.8 Conclusions

The importance of soil invertebrates in maintaining healthy functional soil ecosystems, and in mitigating some of the effects of climate change both below and above ground, has been highlighted. They have vital roles to play under climate change, e.g. in preserving community structure, incorporating increased leaf litter, enhancing carbon storage, maintaining soil porosity and preventing soil compaction. **More studies are necessary on above-ground – below-ground interactions at**

different successional stages to understand likely responses of soil communities to climate change, even though there appear to be logistical constraints to the empirical approaches that would be needed in order to examine all possible interactions (van der Putten *et al*., 2009).

Our knowledge of the effects of climate change on multitrophic level interactions (i.e. those involving two or more trophic levels in a food web) in the soil is probably more deficient than in any other ecosystem. Given the potential for disruption of such beneficial organisms, whole ecosystem studies on the multiple effects of climate change on below-ground organisms are vitally important, particularly in relation to adaptation mechanisms, changes in cropping regimes and in vulnerable regions, such as the tropics. Taking advantage of the opportunities for combining further empirical studies with modelling approaches could enhance our conceptual understanding and capacity to predict the impact of climate change on soil invertebrates and the processes they mediate. Identifying, and then monitoring, appropriate keystone species and key soil processes/interactions for different geographical regions and soil types is essential.

4.2 BIOLOGICAL CONTROL AGENTS

4.2.1 Possible adaptation by invertebrate genetic resources to the challenges identified

Faced with climatic change and possible extinction, a species must either alter its geographical range to track acceptable conditions or evolve by natural selection to match the new conditions (Coope, 2004). There is abundant evidence of the former, both in sub-fossil records (Coope, 2004; Case study 14) and recent shifts in the distribution of species (e.g. Parmesan *et al*., 1999; Yukawa *et al*., 2007). However, species tied to specific latitudes by photoperiod, or restricted to isolated islands, must adapt through evolution.

The rates of evolutionary change in populations under climate change will depend on levels of heritable variation, genetic interactions among traits, and population processes (Lynch and Lande, 1993). **Populations of many natural BCA species contain much heritable variation in traits that affect responses to climate, other abiotic factors and biotic factors. Where adaptation has been looked for, usually it has been found** (e.g. White *et al*., 1970; Potting *et al*., 1997; Henry *et al*., 2010), although as yet there is a shortage of studies that assess local adaptation to climate change factors. The indications are that adaptation will be based on existing genetic diversity, rather than new mutations. The evidence from glaciation history indicates that there is a limit to the ability to adapt based on existing genetic diversity, after which BCAs must move (Case study 14). This has been most clearly demonstrated for detritivores and predators, but it is clear that specialist herbivores cannot move until their preferred food plants have moved and, equally, specialist BCAs cannot move until their preferred host/prey has moved. Where spread is to contiguous areas, BCAs are likely to track their hosts/prey. However, where barriers intervene, such as in many fragmented agricultural landscapes, there is likely to be a lag between a pest passing a barrier and its natural enemies catching up, due to the effects of distance, different dispersal mechanisms, inadvertent human assistance and chance.

We are not aware of studies that demonstrate that natural enemies are able to track the poleward movement of pests in response to climate change, but the evidence from the introduction of classical BCAs shows that natural enemies can have great dispersive power. The 2-mm-long South American parasitoid *Anagyrus lopezi* (De Santis) (Hymenoptera: Encyrtidae) was imported into Nigeria for control of the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae) and first released in 1981/82 (Case study 3). Within three years it dispersed over 200 000 km^2 in southwestern Nigeria, occupying between 70 percent and 98 percent of all fields (Herren *et al*., 1987). Similarly, Assefa *et al*. (2008) studied the spread of the 4-mm-long *Cotesia flavipes* (Cameron) to Ethiopia from releases in Kenya and Somalia against stem borers of Poaceae crops, and concluded that it may have spread by more than 200 km per year. There are many other examples. Dispersal is a mixture of local movement and unusual long-distance (salutatory) movements, some of which will be inadvertently assisted by human activities. It is therefore likely that **if pests move polewards at the rates predicted (Section 3.3.1), most natural enemies will have little difficulty tracking their**

hosts/prey. Barriers, such as mountains and deserts, can be expected to slow the spread of both pests and natural enemies, as might anthropic fragmentation of habitats, but not necessarily by much, especially if there is substantial human movement by land across the barrier. Sea barriers are likely to be more effective, and so this issue will be accentuated for islands. Soil-dwelling and flightless groups of BCAs may not move as readily.

4.2.2 Capacity for evolutionary adaptation

BCAs may be affected by a number of features of a changing climate, and these effects have potential consequences for the performance of BCAs in agro-ecosystems, particularly in IPM systems (Section 2.2). **As yet, we know relatively little about how BCAs can adapt or be assisted to overcome these challenges.**

Average temperature and seasonality

In response to global warming, the seasonal activity of organisms, including invertebrate pests of agriculture, is changing (Section 3.3.4). Asymmetric shifts in seasonality in biological control food webs, as a result of advancing springs and delayed winters, may result in loss of life-history synchrony between pests and natural enemies. In temperate climates, this decoupling of life histories could result in pest populations escaping from BCA regulation in the spring. In the autumn, it could result in pests achieving additional generations after BCAs have become dormant. However, the relatively few studies that have examined the effects of temperature changes on synchrony and natural enemy performance have not found evidence for such effects (Bezemer *et al*., 1999; Klapwijk *et al*., 2010). Using a mathematical model, Hoover and Newman (2004) predicted that the combination of increased temperature and CO_2 on aphid food webs is likely to have little impact on the parasitoid–prey system compared to current ambient conditions.

Augmentative BCAs are not meant to establish widespread breeding populations. Their presence is a result of deliberate seasonal introductions, and farmers can adjust the timing and location of these introductions. For all three classes of biological control, but especially for classical and augmentative biological control, **there is potential to assist adaptation to changes in seasonality through selection** (e.g. Gilkeson and Hill, 1986) and by transplanting locally adapted strains that have appropriate responses to seasonal cues (Gillespie and Quiring, 1993, 2005).

Classical BCAs, and the generalist and specialist natural BCAs that are important in agro-ecosystems, tend to be widely distributed. Overall, temperature and seasonal responses in populations of widely distributed insect and mite pests and their natural enemies are either locally adapted, i.e. the responses to seasonal cues and the tolerances to extremes have evolved to suit the local conditions (Traoré *et al*., 2006; Frago *et al*., 2010), or are governed by phenotypic plasticity resulting from genetic diversity in local populations (Chen *et al*., 2006; Hodek and Michaud, 2008). Changes in seasonality of a pest species as a result of climate change would need to be rapidly followed by adaptive responses by its associated natural enemy communities. Without such adaptations, outbreaks of pests might occur. As introductions of almost all classical BCAs are derived from a very small sample of individuals from one or a very few localities, **the genetic diversity of classical BCAs may be severely constrained, and it is not known whether they contain the capacity to adapt or respond to changes in the seasonal availability of hosts** (Section 4.2.4). Conversely, the required genetic variation should exist in natural BCA populations (e.g. Henry *et al*., 2010; Case study 27).

Atmospheric CO_2

The flow-on effects of eCO_2 on BCAs seem to be highly idiosyncratic (Section 3.3.5), and it is therefore not possible to reach any conclusions regarding the adaptation, or assisted adaptation, of BCAs to this aspect of climate change.

Rainfall and drought

The biology (mortality and reproduction) of both pests and BCAs can be affected by rainfall and drought, and this is likely to be mediated through effects on natural enemy populations (Section 3.3.6). In general, drought, like other weather extremes, can be expected to disrupt pest–natural enemy interactions, leading to both pest outbreaks (which are noticed) and pest crashes (which are easily overlooked).

There is some scope to adapt BCAs and their use to try and redress the disruptions caused by rainfall and drought. Augmentative releases in covered crops are not likely to be significantly affected, but open field releases are likely to be adversely affected by dry conditions. As humidity is likely to be higher at night, there may be advantages to releasing augmentative BCAs at dusk, rather than in the morning, but this tactic would need evaluation. It is common practice to spray microbial insecticides at dusk, because these are often sensitive to low humidity. The development of augmentative BCAs adapted to hot and dry conditions is an option (Grewal *et al*., 1996; Mukuka *et al*., 2010), also considered below in response to extreme events. Application of entomopathogenic nematodes (EPNs), in which host location and survival would generally be favoured by wet conditions and impaired by drought (Grant and Villani, 2003), could be made with or at the same time as irrigation water, or, as above, applied at dusk. Some types of conservation biological control may enable BCAs to persist where otherwise they would have been largely eliminated; for example, mulching may provide natural enemies with protection against extreme rainfall.

At present, the management options described above are speculative – research and field testing will be needed to explore what tactics can be used cost effectively to help BCAs adapt to rainfall and drought.

Extreme events

Increases in the frequency of extreme weather events (heat waves, unseasonal cold, floods, storms) are likely under most climate change scenarios (Section 3.3). All of these factors have the potential to disrupt biological control as a result of catastrophic impacts on cropping systems. Augmentative biological control is especially vulnerable to disruption of transportation networks by extreme weather events. Although not climate-related, this was demonstrated when the eruption of Eyjafjallajökull in Iceland in 2010 disrupted the supply of augmentative BCAs of greenhouse pests from Europe to North America.

Episodic extreme temperature (heat waves and unseasonal cold) has the potential to disrupt biological control food webs independently of the disruption of cropping systems (Section 3.3.2). Although thermal stress may adversely affect pest population growth in the short term, BCA and pest populations have demonstrated the capacity for rapid evolution in response to such stresses (White *et al*., 1970; Amice *et al*., 2008; Harmon *et al*., 2009). This last point suggests that adaptations to extreme events such as high temperatures may take place in BCA populations, and will help to moderate climate change impacts on biological control systems in sustainable agriculture. For augmentative biological control, it may be necessary to use strains that are more tolerant of extremes of temperature, although this would increase the risk that they become established.

4.2.3 Potential of invertebrate genetic resources to mitigate climate change

It is unlikely that BCAs and biological control will contribute in any meaningful direct way to mitigation of climate change. Certainly, effective biological control leads to more plant growth in cropping systems, but unless that carbon is stored (e.g. in the soil) it would be released at the end of the cropping cycle. Habitat set aside for conservation biological control (grasses and woody shrubs, for example) may have more carbon storage capacity than adjoining croplands. However, Costanza *et al*. (1997) assigned climate regulation values (CO_2 storage) to temperate and tropical forests, and biological control in forests is likely to have a significant CO_2 mitigation effect.

The majority of the climate change footprint in agriculture comes from fertilizer application (Hillier *et al*., 2009). In an analysis of 57 farms in Scotland, the application of all pest control products accounted for less than 3 percent of carbon costs, compared with fertilizer applications which accounted for over 80 percent of the carbon footprint on the same farms (Hillier *et al*., 2009). Thus the scope for reducing carbon footprints by increasing reliance on BCAs and reducing pesticide applications is very limited. Nonetheless, there are other, very good, reasons – related to human health and environmental impacts – for reducing pesticide inputs and increasing reliance on BCAs.

4.2.4 Analysis of present use of invertebrates relevant to food and agriculture

All BCA invertebrate genetic resources are natural, unmodified species, or populations, and are thus already available to be used or developed. There is some potential for selection of strains with desirable characteristics in augmentative BCAs, for example, heat resistance, greater fecundity, acceptance of more species of hosts. A starting point for such a selection process might well be to collect populations of the BCA from different areas, especially those with characteristics that match the target area.

Climate change will lead to pest species changing their ranges to track the movement of the habitats where they are well adapted. Since this spread will initially be without specialized natural enemies, **there will be increased demand for classical BCAs**, particularly in those locations where the newly found pest is separated from other populations of the pest by barriers such as mountain ranges or the sea (Case study 17). Therefore, access to new classical BCAs will be crucial for agriculture, especially in island countries.

Climate change is predicted to cause uncertainty and volatility in food supply and pricing (Foresight, 2011). Reliance on BCAs in sustainable agriculture is knowledge based, and is dependent on farmer confidence in BCA–pest interactions that are delayed in time (most BCA–pest population dynamics are delayed density dependent) and that are not necessarily apparent. If farmers are not completely confident in BCA-based IPM systems, they may respond to the uncertainty and volatility in demand and pricing with increased reliance on broad-spectrum chemical insecticides, which provide immediate and obvious impacts on pest numbers. If such responses occur, they would lead to an erosion of BCA performance, as has occurred in the past. The applications of broad-spectrum products would also adversely affect pollinator and soil invertebrate functions.

An important consideration for classical biological control programmes is that, due to genetic bottlenecks, many introduced populations of natural enemies are likely to possess relatively little genetic variation. With reduced potential for rapid adaptive evolution compared with populations that are more heterogeneous, these populations may not have the genetic diversity required to continue to provide their ecosystem service in the face of climate change (Mackauer, 1976; Fauvergue and Hopper, 2009; Case study 27). If herbivores alter voltinism under climate change (Case study 19), parasitoids or predators will need to evolve or respond by plastic changes to synchronize their development with that of their host (Thomson *et al*., 2010).

There are only a few evolutionary studies in natural enemies that consider synchronization (Phillips *et al*., 2008) although there is evidence of genetic variation in generation time in parasitoids (Samara *et al*., 2008). Whether specialist parasitoids, predators and herbivores show much evolutionary potential remains to be seen, but this could be manipulated or artificially enhanced (Thomson *et al*., 2010). It may be possible, therefore, to mitigate the impacts of climate change on the efficacy of classical BCAs by increasing their genetic variability, and thus their potential for adaptation, through the introduction of additional genetic stock (Case study 28). Therefore, **access to new genetic diversity or genetic resources may be required** in order to widen the existing genetic diversity of the BCA.

The risks of failing to maintain diversity (both species and genetic) of the bacterial endosymbiont community within BCAs in the face of climate change has been identified (Section 3.3.2). There are no opportunities to address this problem in natural biological control systems. For classical and, especially, augmentative biological control systems, the identification and introduction of BCA strains with high-temperature-tolerant endosymbionts might be possible, or even necessary.

For the foreseeable future, the technology to effectively store or maintain BCAs *ex situ* does not exist. There are no long-lived dormant stages like seeds or spores that can be used. The only option is to maintain populations of BCAs in culture, but it is known that genetic diversity is lost when species are taken into culture, and more is lost over time as the culture is maintained over generations (Mackauer, 1976; Roush, 1990; van Lenteren, 2003). Accordingly, **BCAs can only be satisfactorily maintained *in situ*.** The most important reservoirs are agro-ecosystems that favour BCAs (e.g. organic and other pesticide-free systems), and especially in regions where wild or early domesticated crop lines still persist. However, these agro-ecosystems are recent in evolutionary terms and, although pests and BCAs have adapted to them, both pests and BCAs originally evolved in natural ecosystems and spread from there into the new agro-ecosystems. Some will evolve to the extent that they no longer occur in natural ecosystems, although this is more likely for pathogens (e.g. Brunner *et al*., 2009) than for invertebrates, but for most pests and BCAs there should be an original natural ecosystem, which is likely to have different genetic diversity and perhaps different species of BCAs that have not (yet) managed to spread to agro-ecosystems, but still have an impact on the pest in its natural ecosystem. In many cases we do not know where the pests and their natural enemies came from, although, in general, pests of arable crops are likely to come from early succession or temporary habitats, while tree pests are more likely to come from forest ecosystems, and so on. Thus conservation of all types of ecosystems will play a role in conserving the original sources of BCAs, but more studies would be needed to know which ecosystems preserve which BCAs (Case study 29).

4.2.5 Status of current application of genetic technologies

At present, **there are no transgenic BCAs in use.** Traditional selection of BCAs for desirable traits has been attempted for only a very few augmentative agents (Ashburner *et al*., 1998; Hoy, 2000). Selection of predatory mites used in augmentative biological control for resistance to pesticides was conducted in the 1980s (Hoy, 1985), but the selected strains were not used extensively. Considerable genetic diversity is present in BCA populations (e.g. Henry *et al*., 2010), but it remains largely unexploited. In cases where assisted adaptation is required in classical and augmentative BCAs, selection by classical breeding methods is likely to be sufficient (e.g. White *et al.* 1970; Gilkeson and Hill, 1986).

There is scope to transform crops to allow them to be grown or continue to be grown in new climate zones (Sun *et al*., 2009; Messmer and Stamp, 2010). This might cause crops to be present in local climates where BCA communities are unable to regulate pests. Weed communities in maize are predicted to undergo significant regional changes under climate change (McDonald *et al*., 2009). Finally, as noted above, climate change effects on plants may alter the suitability of host plants for the BCA. BCAs rely heavily on plant-based resources in the crop and in the local habitat. These include pollen, nectar and extra-floral nectaries (Van Rijn and Tanigoshi, 1999; Robinson *et al*., 2008), refuges such as leaf domatia (tiny chambers produced by plants that house arthropods) (Agrawal *et al*., 2000; Roda *et al*., 2000), and herbivore-induced plant volatiles (HIPV) that help BCAs to locate hosts (Hare, 2011). Adding these attributes to cropping systems could enhance BCA performance where climate change has otherwise limited their impact on pest populations. This would rely on plant genetic resources, and could be done through creation of conservation habitat (adding new plant species), by conventional breeding for desired attributes, or by genetic transformations.

4.2.6 Gaps: knowledge, collections, characterization

Most of the above is speculative, and huge knowledge gaps exist with respect to the responses of BCAs to climate change. Research conducted to date suggests that responses are specific to particular pest/BCA food webs, and therefore general predictions are difficult to make.

Biological control food webs are likely to contain key interspecies interactions (e.g. competition, trait-mediated interactions) that define pest status, and the success of the BCA programme (e.g.

Gilman *et al*., 2010). Knowing how these key interactions respond to climate change factors would help enormously in predicting the impact on pest populations. Furthermore, a few good case studies may show that it is possible to generalize and make predictions with respect to responses of BCAs to climate change. Gilman *et al*. (2010) suggest that, despite the complexity of communities and food webs, it is possible to make such predictions. Along these lines, Vellend (2010) suggested that the apparent complexity of community ecology (the study of the forces that shape the diversity and abundance of species in communities) could be reduced to four processes: (i) selection of species within communities via differential fitness, (ii) stochastic changes in species abundance, (iii) evolution of new species/traits, and (iv) dispersal in space. Studies of the effects of climate change parameters on the strength and frequency of these processes might lead to predictions of how BCAs will respond to climate change.

In general, **the ability to genetically characterize BCAs needs specific attention**. This work must be linked to competent morphological taxonomy, and to ecological performance indicators. Tools for recognizing climatically adapted strains in surveys, and in laboratory and field studies, are needed.

Island versus continental perspective

As species move in response to climate change, barriers will be a big issue, as pests will always move over barriers first, and usually without their associated BCAs. Sea barriers will be more effective than most, and demand for new BCAs (classical and augmentative) will be greater on islands as a result. In continental situations, natural and classical BCAs will normally spread with the crop and pest as they move with climate into new geographical areas, even when the landscape is broken up into a mosaic of agricultural and non-agricultural habitats.

Tropical versus temperate perspective

All of the evidence in the fossil record of responses of invertebrates to climate change comes from temperate regions. Data are badly needed from tropical regions, because we are assuming there will be similar responses in those regions to temperate regions. Tropical pollen cores have been collected from the tropics, e.g. along the Amazon equator (Colinvaux, 2005), and assessing whether these contain identifiable insect parts would be a useful starting point.

4.3 POLLINATORS

4.3.1 Possible adaptations to ensure future food security

To ensure future food security in the face of climate change, it is essential that pollination services are maintained at levels that allow long-term production of a diversity of crops in all regions, but also meet the expected increase in demand and changes in crop choice by farmers. Possible areas of adaptation are discussed below.

Provision of resources within landscapes to support pollinators

The natural habitats of wild pollinators should be identified and preserved or provided. Once future land uses are forecast, corridors of suitable habitat can be formed or maintained to conserve and ensure connectivity of pollinator food/nesting resources within critical areas of the landscape and at critical times (Case study 30). Through the use of climate-resilient plantings relevant to the region, it should be possible to provide the diversity, abundance and succession of habitats and floral resources necessary for sustaining populations of wild pollinators and managed bees at levels optimal to agriculture. **The presence of natural and semi-natural habitats in agro-ecosystems enhance pollinator richness and diversity as well as pollinator services and crop yield** (e.g. Steffan-Dewenter and Tscharntke, 1999; Morandin and Winston, 2006; Ricketts *et al*., 2008). For example, rape (canola) fields with more uncultivated land within 750 m of field edges had higher bee abundance and seed set. A cost–benefit model estimated that rape yield and profit could be maximized with 30 percent of land uncultivated within 750 m of field edges (Morandin and Winston, 2006).

An advantage of having a range of (non-crop) food resources available in the landscape is that a more diverse vegetation is likely to support a more diverse assemblage of pollinators. This is important as most crops with generalized flowers (i.e. that can be pollinated by a range of species) might produce more reliably when a suite of pollinators is present, including honeybees (Greenleaf and Kremen, 2006; Hoehn *et al*., 2008; Winfree and Kremen, 2009). Pollinator species are likely to differ in their responses to environmental or biotic (e.g. competition) conditions leading to a reduced probability of insufficient pollination. The "insurance" provided by a diverse pollinator assemblage might also facilitate adaptation to future conditions. In this way, **pollination resilience can be built into agro-ecosystems by promoting a diversity of plant food resources that in turn support a range of managed and wild pollinators.**

Effects of altitude

Pollinator communities tend to change with increasing elevation. At higher altitudes the average size of pollinators increases (Malo and Baonza, 2002), but pollinator abundance is lower (Arroyo *et al*., 1982). In addition, flies tend to become the dominant pollinator group, mainly because other groups are restricted to lower areas (Kearns, 1992). In the Rocky Mountains (United States of America), flies replace bees as main pollinators (Kearns 1992), whereas in the Andes of South America, tachinid flies and hummingbirds replace bee flies (Bombyliidae) and bees at higher altitudes (Arroyo *et al*., 1982). In addition, flower size tends to increase (Malo and Baonza, 2002). The lower pollinator abundance results in lower pollinator to flower ratios and lower seed set in plants at higher altitudes (Arroyo *et al*., 1985; Malo and Baonza, 2002). Temperature increases might lead to pollinators moving to higher altitudes and might change pollination levels in plants. The arrival of more pollinator species (including bees) and individuals on mountains might make these areas suitable for cultivation of crops that are highly dependent on pollinators, which at present would suffer pollination limitation.

Selection of climate-adapted managed pollinators

The honeybee is the main managed pollinator around the world (Section 2.3). This reflects the adaptability of the species to many different conditions from arctic to tropical and from rainforests to deserts. In the context of climate change, **local beekeeping practices may have to adopt different honeybee races or hybrids that suit local conditions** (e.g. with traits such as drought resistance and non-absconding). Alternatively, **management of other bee (or pollinator) species could be developed or improved**. For example, some stingless bees (Meliponinae) (Case study 31) and stem-nesting solitary bees, like *Osmia* and *Megachile* spp. (Megachilidae), can be selected for domestication and mass breeding based on their ecological traits and climatic or environmental tolerances (e.g. generalist food and nesting habits, short life cycles). Some bee species are more susceptible to environmental changes and anthropogenic pressure than others. Evidence for susceptibility is the presence of high diploid male frequencies (indication of inbreeding) in euglossine bees (Lopez-Uribe *et al*., 2007) and low genetic diversity of North American bumblebee populations (Cameron *et al*., 2011) which both suggest population declines.

One needs to be aware, however, of the general risk of the use of managed organisms in new environments, namely that they may interfere with the native organisms. This can be through direct competition for resources (e.g. food, nest sites) or indirectly through transmission of pests and diseases to native flora and fauna or from them to the managed organism. A notorious example of this is the transfer of the *Varroa* mite from its host, the Asian honeybee *Apis cerana* (F.) (Hymenoptera: Apidae), to the managed honeybee after its transfer to Southeast Asia. Infection of honeybee hives with *Varroa* mites are now a global concern in beekeeping, mainly because they transmit viruses to the bees, which lowers bee longevity and weakens the colonies. The use of non-native subspecies can also be risky. The bumblebee *Bombus terrestris* L. (Hymenoptera: Apidae), has been mass produced for crop pollination across the world and non-native strains introduced. However, the introduced bumblebees outcompete the local strains of this species in the British Isles. They can now only be used in greenhouses, and some bumblebee breeders have started to produce native British bumblebees for pollination purposes. Given the risks, it is extremely important that transport of any managed organisms is based on established risk assessment procedures to minimize the risks. The oil palm pollinator weevil (Case study 8) provides one example where the protocols of weed biological control were used effectively, but pure pollinators would have to be evaluated differently.

Factors that currently compromise pollination

Crop systems and landscapes differ in the options they offer for managing crop pollination, e.g. use of wild pollinators, managed honeybees, hand pollination or a combination of these (see Chapter II). The recent problems with managed honeybees in parts of the world have raised awareness of the vulnerability of pollination services. Crop pollination at present is probably limited by different factors in different locations (e.g. crop management, lack of pollinator habitat, pesticide application, climate). These factors are likely to intensify with climate change, and mitigation will need to be integrated into farm management systems or landscape-level management. For example, shifting from monocultures to mixed cropping systems and agroforestry plantations might mitigate climate extremes through provision of more suitable microclimates and alternative foraging and nesting resources.

In the case of the recent declines in managed honeybees, it is also not clear whether climate change will improve the conditions for beekeeping (e.g. better adapted tropical strains will move into new areas, as in the case of the Africanized honeybee in the Americas) or increase the risk that new pests and diseases (e.g. the small hive beetle, *Aethina tumida* (Murray); Coleoptera: Nitidulidae) may spread into Europe because of more amenable climatic conditions.

The transfer of pollinators between countries

To consider the opportunities, procedures and risks associated with the movement of pollinators, we recognize that some pollinators naturally move long distances across borders unassisted (Case Study 30), but domesticated species, such as honeybees and some bumblebees, are regularly moved between countries, and if domestication of other social pollinators such as stingless bees (Case Study 31) expands, there may well be scope to move them between countries too. **In general, climate change is expected to increase demand for transborder movement of pollinators.** However, introductions of pollinators to areas where they do not naturally occur have caused some significant problems (Generesch and Aubert, 2010).

International trade in honeybees and their products is governed by relatively new international laws, which provide a framework for protection of the honeybee industry and legitimate certified trade (Brown, 2008). The World Organisation for Animal Health (OIE) is the relevant international organization for developing standards, guidelines and recommendations relating to animal health. For honeybees, the international standard for animal health is the Terrestrial Animal Health Code (OIE, 2010), the aim of which is to assure the sanitary safety of international trade in terrestrial animals and their products. As yet, these **regulations do not cover environmental risks of introducing pollinators, such as displacement of indigenous pollinators, or risks associated with pollinators other than honeybees**. One can consider several categories of pollinators that are, or might be, moved between countries:

- **Honeybees and bumblebees**. Honeybees can be found throughout the world already, but there is likely to be continued and increasing demand for new strains or improved stock, and hence movement of queens, nucleus colonies and colonies between countries. The movement of honeybees between countries has been implicated in the spread of pests and diseases. Several regulations must be met before honeybee queens (and attending workers) can be imported including verifications on the absence of several diseases (for details see Brown, 2008; OIE, 2010). This has not, however, prevented the spread of varroa mites and other pests and pathogens. Similarly, the movement of non-native bumblebee species and subspecies has led to negative impacts on native bee fauna and insect-dependent plant species (Goulson *et al.*, 2002). This has already led to regulations in the United Kingdom prohibiting the entry of foreign strains of the bumblebee *Bombus terrestris* into the country for pollination of greenhouse crops. Clearly, improved guidelines and protocols may be needed, especially in light of anticipated demand for pollinator transportation.

- **Other domesticated bees**. Stingless bees from South America have been used in Japan for pollination of greenhouse strawberries and some trials have been carried out in the Netherlands for greenhouse crops (Slaa *et al*., 2006). These species require tropical conditions and would not survive as colonies in the wild in temperate countries. Even though there is a low probability of stingless-bee pathogens switching host to native bees outside the area of the introduced bees' origin (none of which would be closely related), some regulations may be needed in the future. One reason that no regulation is in place could be that suitable risk assessment protocols are not available, and these would be needed to ensure that risks associated with future introductions are adequately evaluated.
- **Pollinators that may be domesticated in the future**. Domestication of wild pollinators is likely to increase the scope for movement of newly domesticated species between countries. Guidelines and protocols for risk assessment should be developed if the risks associated with such introductions are to be managed.
- **Specialist pollinators**. If crops with specialized pollinators are grown in new areas, introduction of the specialized pollinators might be needed. Highly specialized pollinators associated with a particular crop are uncommon in agriculture (Section 2.3.2), and the oil palm weevil is the only one that has been deliberately introduced to new continents (Case Study 8). In this case, the procedures and protocols of weed biological control were successfully used to assess the risks to plants, and they should be the starting point for the consideration of any future introductions.

4.3.2 Potential of pollinators to mitigate climate change

While pollinators cannot directly mitigate climate change, they can influence vegetation composition through their pollination activities and the seed dispersal resulting from it. It would, therefore, be important to integrate knowledge of pollination and seed dispersal into carbon fixing projects to ensure plantings used to counteract climate change are self-perpetuating. To our knowledge. there have been no studies assessing the long-term benefits of pollinators on vegetation composition and climate moderation.

4.3.3 Impacts on islands versus continents

With climate change, **it is islands, rather than continents, that are likely to experience the greatest challenges in meeting their pollinator requirements.** New crops may appear more economically and climatically sustainable than those traditionally grown. However, it will be necessary to assess whether the existing pollinator diversity and assemblages can provide adequate pollination. Where exotic introductions are considered, careful risk analysis would be required (see above). Some crops may have specific pollinator requirements (cocoa, pawpaw (papaya), passion fruit) and may need more specific habitat or cultivation adaptations to accommodate pollinators. Islands are also vulnerable to loss of diversity in their pollinator resources through extreme climatic events (extinction very likely, colonization very unlikely).

4.3.4 Temperate versus tropical impacts of climate change

Bawa (1990) states that there are four major differences between pollination systems of tropical lowland rainforests (TLRF) and northern temperate zone forests (NTZF). First, in aseasonal TLRF, pollination at the community level occurs throughout the year, whereas flowering in NTZF is mostly confined to late spring and summer. Second, flower longevity is much shorter in TLRF (1–2 days) than in NTZF (up to seven days). One possible explanation is that unpredictable weather conditions in NTZF, and consequently increased uncertainty in pollination success, have resulted in extended flower longevity. Third, the pollen vectors are different, with vertebrates often being important in

TLRF but largely lacking in NTZF (although important in temperate Australia and South Africa). Finally, the proportion of wind-pollinated plants steadily increases as one moves from the equatorial region, reaching 80–100 percent among trees in some of the northern-most latitudes.

Based on these four differences we can expect that:

- Climate change may affect the seasonality (or aseasonality) of flower and pollinator activity patterns. More severe droughts or rainfall might make tropical habitats shift from aseasonal to seasonal, whereas longer seasons in temperate zones might extend the active seasons of pollinators and flowering periods of plants. It is anticipated that tropical regions will experience less temporal decoupling of pollination services than temperate regions.
- Temperate plant species with shorter flower life might benefit more from a warming-induced increase in pollinator activity than temperate species with longer flower life.
- An increase in pollination success of animal-dependent plants might result from the increased pollinator activity in response to higher temperatures.

Tropical zones have a greater range of different pollinators (but not necessarily more species) and with general warming there may be increased spread from these zones into the (wetter) subtropics. In addition, biodiversity hotspots (including many tropical areas) harbour more plant species, which compete more for pollinators, and as a consequence more often suffer from pollen limitation (i.e. suboptimal levels of pollination and seed set). Because plants spread more slowly than pollinators, climate change-driven shifts in distribution may create more competition for floral resources in subtropical areas (i.e. higher pollinator/plant ratios). The outcome for crop pollination may not be so clear: on the one hand more potential pollinator species should result in higher resilience of pollination services (possibly the case for attractive crops), on the other hand less attractive crops might experience more competition with native plants for pollinators (as the reproduction of native plant species increases due to an increase in pollinators) and therefore decreased pollination levels. Similarly, the higher plant and pollinator diversity in Mediterranean habitats compared to higher latitudes may mean that with climate warming many new pollinator species will move into the higher latitudes first and thus increase the diversity of potential pollinators for most plants, including crops, followed by spread of plant species to these areas which might lead to increased competition for pollination services (Vamosi *et al.*, 2006).

Domesticated honeybees are expected to remain effective in tropical zones under the temperatures predicted for the next century, but foraging behaviour will be altered under increased rainfall, resulting in reduced productivity of honey and crops. It is likely that domesticated western honeybee races in warmer climatic conditions will need more intensive disease management than they currently do. One way to adapt to this is to adopt (sub)tropical races in managed beekeeping. This has been done in the American tropics where Africanized honeybees are now routinely used in countries such as Brazil and are more productive than temperate honeybee races there.

4.3.5 Gaps in our knowledge on climate change impacts

There are still many gaps in our knowledge of the possible consequences of climate change for pollinators and crop pollination. To date, there is a no holistic approach that includes pollinator-derived goods and services in assessments of climate change impacts on productive agricultural ecosystems. Declines and shifts in plant pollinators have been observed, but the causes and their interactions are not well known. It is often unclear whether shifts are due to climate change or to other human activities, such as intensification of agriculture, pesticide and fertilizer use, and land clearance and management. **Our understanding of the interactions between the multiple drivers is still in its infancy.**

In addition, there are many unknowns with regard to the role of wild pollinators in crop pollination. What species are important and what is their contribution to crop production in developed and developing countries? What are the rearing and breeding techniques required to shift existing wild bees and other pollinator species to domestication? What will be the effect of eCO_2 on wild compared to domesticated pollinators? Will the effect of climate change on plant phenology differentially affect resource availability and the foraging behaviour of wild and domesticated pollinators? It seems that eCO_2 lowers nutritional value of leaves, but it is not clear how flowering intensity and pollen/nectar availability will change. A more specific knowledge gap is how climate change will affect bee pests and diseases.

4.4 INVERTEBRATES AS A SOURCE OF PRODUCTS AND FOOD

We have recognized that some invertebrates are important food items and that several sectors rely on products from insects. Climate change will surely affect these uses, but the scale of use and current lack of information creates little scope to comment on the potential for adaptation or mitigation.

Products from insects

Honey production is dependent on honeybees, which have already been dealt with under Section 4.3, above. Sericulture is dependent upon the growth of mulberry (*Morus* spp.; Moraceae) to feed the silkworms, and climate change will have implications as to where mulberry will grow well, and hence where sericulture is most practical, but we know of no studies on this. We conclude that research on improving sericulture in general will be valuable in helping the industry adapt to climate change.

Harvesting edible invertebrates

The collection of wild invertebrates as food will depend on availability, and as the distribution of food sources and the invertebrates change in response to climate change, this will define where different species of invertebrate food can be collected. For example, the collection of Saturniidae caterpillars (Case study 12) is linked to miombo woodland in southern Africa; if the extent of the woodland changes, the places where caterpillars can be collected will also be redefined. A better understanding of the role and scale of invertebrate harvesting and consumption should clarify an important ecosystem service of natural habitats, and help preserve these carbon sinks (i.e. reservoirs that accumulate and store some carbon-containing chemical compound for an indefinite period). However, **we see little scope for the deliberate redistribution of wild edible invertebrates at this time.**

Production of invertebrates for food

The domestication and production of invertebrates has the potential to address several factors related to climate change, including more efficient use of resources and thereby reducing the pressure to convert more land to agriculture. Oonincx *et al*. (2011) recently showed that edible insects produce much smaller quantities of greenhouse gases per kilogram of meat than conventional livestock. For example, mealworms produces between ten and a hundred times less greenhouse gas per kilogram than pigs. Furthermore, compared to cattle or pigs, insects produce significantly less ammonia, which can causes acidification and eutrophication of water.

However, **the development of invertebrate production for food is so little advanced, that basic studies would be the critical step in exploring the viability of the concept**, before the implications of climate change can be considered properly. We recommend more research in this area.

CHAPTER V. CONCLUSIONS AND KEY GAPS

In this report, we have found that there are many gaps in our knowledge of invertebrate genetic resources as affected by climate change and how to use them in response to climate change. Specific conclusions regarding the impact of climate change on particular elements of invertebrate genetic resources in agriculture are not possible yet. However, three general conclusions are evident. Firstly, it is likely that **climate change will disrupt the use of invertebrates in agriculture, especially sustainable agriculture, even though the precise nature of the disruptions is not yet known.** Secondly, that, without intervention, these disruptions will result in production losses particularly in sustainable agriculture, even though the scale and extent of the losses is not yet known. Thirdly, that the extent of some of the losses will justify intervention to facilitate adaptations of the invertebrates, even though the methods with which to intervene and policies to facilitate this intervention are not yet in place. Below we identify the priority gaps that need to be addressed in the context of these conclusions.

Scientific knowledge

- Improvement to knowledge and understanding of (i) wild pollinators of major crops, (ii) soil invertebrates, (iii) natural BCAs, and (iv) their contribution to crop production in developed and developing countries. We found that the knowledge of the contribution of these unmanaged invertebrates to sustainable agriculture systems is generally lacking, particularly in developing countries.
- Quantification of the responses of invertebrate species, communities, food webs and different types of interactions to climate change factors. It is only within the last two decades that scientists have begun to study the responses of key species to climate change factors. A plethora of mechanisms has been identified, but a unified understanding of the impact of these on community and food web structure and performance has not yet emerged.
- Further investigation of past climate change in tropical areas, and assessment of how invertebrate species have responded in terms of distribution (based on sub-fossil records). Past climate change events are relatively well documented in the temperate zones (tree rings, glaciers, well-preserved sub-fossils), but parallel data are as yet largely lacking in tropical zones. Understanding the progress of climate change in these zones and its impact on invertebrates, will be essential for the development of strategies to mitigate the impacts of climate change on sustainable agriculture and a large fraction of the human population.
- Taxonomy and genetic characterization of invertebrates of agro-ecosystems, especially critical BCA and soil invertebrate faunal groups. We found that the biodiversity and taxonomic identity of the soil invertebrate fauna are relatively unknown, and a sustained effort is required so that impacts of climate change on this crucial biodiversity can be assessed. Recent studies have revealed that what appear to be generalist BCA parasitoid species are often a complex of previously unrecognized specialist species. As specialists are generally more susceptible than generalists to disruption by perturbations, it is possible that the supply of biological control services may be disrupted by climate change-driven losses of key, specialist, BCA invertebrates.
- More studies on rates of movement of selected key species, especially soil invertebrates without a motile stage, perhaps based on the northern boundaries of the tree line, or colonization of recently erupted volcanoes. We found abundant evidence of changes in ranges of motile species in response to climate change, but no studies on relatively non-motile species. Similarly, there appear to be no studies of the movement of BCAs in response to range changes in their hosts. Knowledge in this area is essential to understanding the need to develop strategies that facilitate adaptation of invertebrates and sustainable agriculture systems to climate change.

Conservation, use and access

- Rearing technologies to shift selected wild bee and other pollinator species to domestication. We found that, for crops that are dependent on specialist pollinators, climate change-induced changes in location of production, or loss of synchrony between pollinators and flowering seasons are likely. Adapting and preserving these production systems will be dependent on the domestication and manipulation of their specialist pollinators.
- Technologies and approaches to ensure the conservation and promotion of generalist natural enemies in agricultural landscapes through improved knowledge of landscape-level movement, and the effects of resources such as spatial and temporal refugia and alternative food sources.
- Identification and conservation of source habitats of pests and associated BCAs. We found that, under climate change, there will probably be a need to access the genetic diversity of classical

BCAs that is present in their source habitats, to facilitate adaptation of BCAs to changing climates.

- Development of mass production methods for some important soil ecosystem engineers so as to facilitate experimental evaluation of their use in soil management practices.
- Further research on the sustainable exploitation and domestication of edible invertebrates. This potentially valuable food resource has been neglected. If it can be developed as a viable alternative to other animal food sources, it could help mitigate climate change.

Facilitating policy environment

- An overarching holistic strategy that integrates invertebrates with the other ecosystem components to better design and manage future agro-ecosystems for food security in the face of climate change.
- Guidelines for facilitating and regulating the movement of invertebrate genetic resources between countries, which build on what is so far available for BCAs and include emergency responses and pest risk assessment protocols. As climate change progresses, new invasive pests are likely. A coordinated development of standard protocols for pest risk assessment, e.g. ISPM2 (IPPC, 2007) would facilitate survey and detection efforts and allow timely responses to new invasions. Similarly, responses to invasive pests will probably involve release of classical BCAs, and it may be appropriate to revisit ISPM3 in the context of emergency responses to new invasive threats.
- Recognition that in implementing the Nagoya Protocol, countries need to take into consideration the need for invertebrate genetic resources to sustain agriculture, food production and world food security when drafting national strategies (e.g. producing guidelines and procedures).
- Further development and implementation of existing national biodiversity programmes. As noted above, the role and importance of invertebrate genetic resources diversity in relation to sustainable agricultural production are not well known, particularly in relation to soil invertebrates and pollinators in general, and in relation to some biological control invertebrates.

Islands versus continental areas

- Policy support for island states, that will probably not be original sources of BCAs (or pests), but will need new BCAs. We found that islands are particularly susceptible to pest invasions and this will increase with climate change. Furthermore these invasions resulting from range shifts are unlikely to be accompanied by existing natural enemies, unlike the situation in continental areas. Hence, there is likely to be a disproportionate increase in demand for BCAs for islands, and it may be appropriate to promote a policy environment that will address this.

Temperate versus tropical

- Attention to the question of how species ranges will change in tropical regions. This area of scientific knowledge has not been widely addressed and there is a relative dearth of studies on the sensitivity of tropical ecosystems to climate change.
- Testing the hypothesis that tropical species may be more sensitive to climate change as a result of narrower biotic ranges and lack of exposure to climatic variation. Addressing this specific scientific knowledge gap would help determine whether there are specific and special concerns with respect to the conservation of useful invertebrate biodiversity in the tropics.

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CASE STUDIES

Case study 1. Rehabilitation of degraded soils by triggering soil invertebrate activities in Africa

In the Sahel, the “zaï” is a traditional soil and water conservation (SWC) technique developed in the semi-arid lands (yearly average rainfall < 600 mm) in northern Burkina Faso (Yatenga Province) where the soils are heavily encrusted. The zaï is usually a hole or basin with a diameter of 20–30 cm and depth of 10–15 cm set at intervals of 1–5 m, with between 12 000 and 15 000 holes per hectare; part of the soil that has been removed is combined with organic matter and put back into the hole. The holes are above all used to rehabilitate the lateritic and sandy-clay soils that the Mossi call “zippelle” (“clearing” or “bare soil”) and are dug during the dry season (November to May). Subsequently, seeds of crops or whole crop plants are placed in the zaï. The incorporation of organic matter increases the nutrient status of the soil. Runoff from the crusted soils will tend to infiltrate into the depressions which consequently become microsites of greater soil water content.

During the dry season the zaïs collect the leaves, twigs and fine sand carried by the wind. In addition, organic mulch is placed in the holes by farmers in order to trigger termite activity; the termites dig underground galleries that facilitate the deep infiltration of rainwater and runoff. Termites improve the structure of crusted soils by reducing soil compaction, increasing soil porosity and improving water infiltration. A study showed that this termite disturbance resulted in a viable management option and improved growth and yield of crops. Yields reached one tonne per hectare where cow manure had been added and termites were present.

Another agricultural technique used in a number of tropical countries in Africa to ameliorate soil conditions for crops is “ecobuage”. This is a traditional complex agricultural system, more evolved than the slash-and-burn technique, that entails incinerating herbaceous vegetation piled up in mounds and buried under a layer of soil taken from the surroundings. The technique supplies the soil with mineral nutrients through slashes, and increases soil pH. In a study conducted in Bouenza (Congo), the use of “maalas” (ecobuage) increased soil invertebrate communities, especially earthworms, which led to improved soil structural stability, creating good conditions for plant root development.

Prepared by Juan J. Jiménez

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Case study 2. Beetle banks for conservation of generalist predatory beetles

Conservation biological control need not be extensive or complicated. The application of “beetle banks” in row crops is a case in point. Generalist predatory beetles in the families Carabidae and Staphylinidae (ground beetles and rove beetles, respectively), are key predators of arthropods in several cropping systems. They are long lived, and highly mobile. Both adults and larvae are predatory. Shelter and alternative food are key habitat components for these beetles. Shelter provides hiding places for the mainly nocturnal beetles, and a refuge and source of alternative food during periods of disruption in crops (such as tilling or pesticide application). Shelter is essential during winter, when beetles must find protected, undisturbed sites. In small fields, beetles are able to invade from unmanaged edges. Field sizes have increased in modern agriculture, and the edges of fields cannot serve as a source of beetles for the large acreages. Moreover, land-use patterns have changed, and unmanaged, grassy edges are not necessarily present.

Beetle banks provide a mechanism for conservation of populations of these important biological control agents (BCAs), and for maintenance of the natural biological control ecosystem service. The banks are narrow strips of mixed grass species, planted within and on the margins of large fields. The grasses consist of native tussock species (grasses that form clumps) together with other grasses and herbs. These strips increase the abundance of predatory beetles within fields, and can result in substantially lower populations of pests on crops. In addition to promoting predatory beetles, the beetle banks serve as conservation habitat for other predators, for example, wolf spiders, *Paradosa* spp. (Araneae: Lycosidae). Beetle banks also serve as habitat for ground-nesting birds, and as a source of prey for raptors and owls. Costs of establishment and maintenance are minimal. Management of invasive weeds in the grass strips is probably the only long-term management issue. Although there is a potential small loss of production by devoting farmland to these strips, long-term reductions of pest control costs would more than offset this loss.

Conclusions: conservation habitat such as beetle banks can restore important natural biological control ecosystem services, and provide other conservation values in the maintenance of biodiversity in farm landscapes.

Prepared by D. Gillespie

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Case study 3. Saving millions of cassava smallholder farmers in Africa

Cassava, yucca or manioc (*Manihot esculenta*; Euphorbiaceae) was introduced from South America into Africa by the Portuguese in the sixteenth century and today is a staple root crop for more than 200 million people in Africa alone. This major source of carbohydrates came under threat from a devastating pest, the cassava mealybug (*Phenacoccus manihoti* Matile-Ferrero; Hemiptera: Pseudococcidae).

The cassava mealybug was first recorded in Congo and Zaire (now the Democratic Republic of the Congo) in the early 1970s. It remains unclear how the mealybug crossed the Atlantic from its home range in South America to Africa, but increasing trade provided enough opportunity for transport even across large distances. Once in Africa, since there were no natural enemies to control it in its new habitat, cassava mealybug quickly spread through the whole cassava growing area, causing cassava production to collapse.

In a combined effort involving IITA (International Institute of Tropical Agriculture), CABI, IAPSC (Inter-African Phytosanitary Council) and other agencies, biological control agents (BCAs) were found in three South American countries (Paraguay, Brazil and Bolivia) following extensive surveys. A parasitoid wasp *Anagyrus lopezi* (De Santis) (= *Epidinocarsis lopezi*) (Hymenoptera: Encyrtidae) was quarantined in the United Kingdom, shipped to Africa, mass reared, and finally, after the local authorities granted permission, released in field trials. The operation was so successful that throughout sub-Saharan Africa cassava mealybug is now under complete control and no longer poses a threat to cassava production.

Besides the successful control of cassava mealybug, this joint effort led to close South–South and international cooperation and to a significant increase in the capacities in biological control and agricultural entomology in sub-Saharan Africa. Many African agricultural entomologists of that generation were educated through this programme. The programme cost, according to Swindale (1997) was about US$27 million, while the benefits are estimated at US$450 million!

The beneficiaries are the millions of cassava growing smallholders who – often unaware of the programme or the parasitoid wasp – enjoy the fruits of this work. Food security has been increased through improved harvests and health through reduced pesticide use, both of which would otherwise come at no cost to the smallholders, who nevertheless receive the full benefits for free.

Prepared by Fabian Haas, *icipe* (in Cock *et al*., 2009)

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Case study 4. Augmentative biological control of greenhouse whitefly on greenhouse crops

Augmentative biological control of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) is a keystone of the IPM (integrated pest management) system in greenhouse tomato production. Damage comes from honeydew exuded by nymphs and adults, which is a substrate for growth of sooty moulds that cover leaves and reduce photosynthesis, and from growth and yield reductions due to the removal of plant sap. In England in the mid 1920s, whitefly nymphs were found to be attacked and killed by the parasitoid *Encarsia formosa* (Gahan) (Hymenoptera: Aphelinidae). Both the greenhouse whitefly and *E. formosa* are probably indigenous to Mexico or Central America. In the 1920s and 1930s, *E. formosa* was produced in vast numbers and shipped around the world where it was released for control of greenhouse whitefly. The development of chemical insecticides in the 1940s resulted in the termination of this programme. Insecticide resistance in whitefly populations around the world prompted researchers and growers to resume biological control for greenhouse whiteflies in the late 1970s.

The majority of *E. formosa* used in biological control are produced by a few large companies, and are shipped nationally or internationally to customers. During shipping, the parasitoid is fragile and is sensitive to exposure to heat and cold and to shipping delays. This is the case for most augmentative biological control products. Delays in delivery can result in growers receiving a dead product and consequently experiencing difficulties establishing or maintaining successful biological control programmes. The product consists of cards with *E. formosa* pupae, which are placed into the crop every week through most of the cropping season. This ensures that parasitoids are present and hunting for hosts at all times. Other parasitoids may also be used, particularly *Eretmocerus* spp. (Hymenoptera: Aphelinidae), which are reportedly better able to cope with the hotter periods of the year. In some regions, predatory bugs, particularly omnivorous Miridae such as *Macrolophus* spp. or *Dicyphus* spp., are also introduced into the crop.

Conclusions: Modern augmentative biological control strategies involve the introduction of constructed food webs. These systems are built around mass-production capacity in a relatively few centres, are dependent on just-in-time delivery strategies, and are sensitive to disruptions in transportation systems.

Prepared by Dave Gillespie

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Case study 5. Generalist augmentative biological control agents can prevent new pests disrupting integrated pest management: South American tomato pinworm

When IPM (integrated pest management) systems rely on natural or augmentative biological control, the introduction or spread of a new pest can disrupt that system, and cause farmers to turn to broad-spectrum insecticides for pest control. The invasion of the South American tomato pinworm, *Tuta absoluta* (Cameron) (Lepidoptera: Gelechiidae), from South America into the Mediterranean basin of Europe and North Africa in about 2006 had the potential to do just that. This pest attacks tomato, some related crop plants, such as aubergine (eggplant) and potato, and some solanaceaous weeds in South America, where it is indigenous. On tomato, it mines in the fruit, causing fruit rots, and rendering fruit unmarketable. The IPM system in protected culture of tomato in the Mediterranean area is largely based on the release of biological control agents (BCAs). Broad-spectrum insecticides are rarely used and it is possible to produce a crop without such intervention. With the introduction of *T. absoluta*, this IPM system was expected to be disrupted.

Although some knowledge of the biology and efficacy of the natural enemies of *T. absoluta* is available in South America, time and much additional research would have been needed to develop the knowledge required to make introductions of these species to Europe. Up until now, access to these potentially useful BCAs has been blocked by unresolved benefit-sharing considerations in South America. European researchers and biological control companies responded with intensive investigations of the impacts of existing augmentative BCAs on *T. absoluta* and identified species that could be used to manage this pest. This will help to buffer the tomato industry against disruption of its augmentative biological control programmes, and in fact, has stimulated the uptake of augmentative biological control due to the high efficacy of one of the agents (K. Bolckmans, Koppert B.V., pers. comm., 2011). In the long term, a classical biological control solution may need to be implemented.

Conclusions: Although invasive pests can be highly disruptive to existing IPM programmes that are based on biological control, application of existing generalist BCAs may resolve this. Timely access to genetic resources used in biological control is essential to the sustainability of IPM programmes.

Prepared by Dave Gillespie

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Case study 6. The potato/tomato psyllid, *Bactericera cockerelli,* disrupts greenhouse integrated pest management

The potato/tomato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Psyllidae) is a pest of tomato and potato in North America. It overwinters in the southern regions of the United States of America, and migrates northward annually, as temperatures warm, occasionally reaching Canada. Saliva injected into the tomato plant during feeding causes a physiological injury known as psyllid yellows. This is characterized by interveinal chlorosis, and is accompanied by a dramatic loss of growth and production. In mid 1996, *B. cockerelli* invaded tomato greenhouses in British Columbia, Canada. It spread rapidly to other greenhouses due to movement of equipment and personnel between sites. Its presence and the associated injury prompted growers to apply broad-spectrum pyrethroid, organophosphate and carbamate insecticides, which generated secondary outbreaks of greenhouse whiteflies (*Trialeurodes vaporariorum* (Westwood); Hemiptera: Aleyrodidae) and two-spotted spider mites (*Tetranychus urticae* Koch; Acari: Tetranychidae), due to the loss of the biological control agents (BCAs) of these pests. At present, *B. cockerelli* continues to be invasive in greenhouses, although it is not present in every year, or in every greenhouse. Although an augmentative BCA was developed and tested in the tomato industry in Canada, the inconsistency in the need for this agent has made it expensive to produce and difficult to obtain. More recently, *B. cockerelli* has invaded New Zealand, where it is causing serious disruptions to the IPM (integrated pest management) programmes on protected tomatoes, and on potato crops.

Prepared by Dave Gillespie

Sources:

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Case study 7. Crop dependence on pollination

About two-thirds of the major food crops used for human consumption across the world depend to some degree on pollination by insects. Klein *et al*. (2007) compiled published information on major crops and categorized them from “insect pollination essential” to “no increase with insects present”. Some of the important crops in each category include:

- **Essential**: watermelons, melons, pumpkins, squashes, marrows (zucchini), kiwifruits, *Annona reticulata* L.(custard apples), pawpaws, passion fruits, Brazil nuts, macadamia, cocoa, vanilla;
- **High dependence on pollination**: cucumbers, buckwheat, carambolas, avocados, durians, plums, peaches, cherries (sweet and sour), apricots, apples, pears, mangoes, blackberries, raspberries, *Solanum quitoense* (naranjilla), blueberries, cranberries, almonds, cashews, turnip rape, kola nuts, *Coriandrum sativum* (coriander), *Cuminum cyminum* (cumin), cardamoms, fennel (seed), nutmegs, allspice;
- **Modest dependence**: okras, aubergines (eggplants), guavas, pomegranates, strawberries, black currants, red currants, chestnuts, mustard (seed), rapeseed, coconuts, soyabeans, cotton (seed), sunflowers, sesame, faba beans (broad beans), *Vitellaria paradoxa* (shea nuts), coffee, caraway;
- **Little dependence**: pigeon peas, tomatoes, *Phaseolus vulgaris* (kidney beans), citrus fruits, rambutans, tamarinds, groundnuts (peanuts), oil palms, flax (seed), *Capsicum* (red pepper), chillies;
- **No increase with insects present**: lentils, peas, grapes, olives, black pepper, *Chenopodium quinoa* (quinoa), chickpeas, wheat, barley, maize and other grain crops.

The insects responsible for crop pollination range from managed honeybees and bumblebees to solitary bees, dung flies, carrion flies, midges, moths and hoverflies. Many crops can be pollinated by managed honeybees as well as a range of wild pollinators. Other crops need specific groups of insects: cocoa is pollinated by ceratopogonid midges, pawpaw by carrion and dung flies, oil palm by a weevil, and figs by fig wasps.

Information on pollination of many crops is still incomplete or even lacking completely. Crops have been moved across the world and in that process will certainly have lost old pollinator species and groups and picked up new ones. Movement of crops and habitat destruction has led to severe problems in crop pollination as well, for example, the need for hand pollination of vanilla in Madagascar (where it is not indigenous) and apple in China (where it is probably indigenous, but there are few native pollinators due to intensive land use).

Prepared by Koos Biesmeijer

Source:

Klein, A.M., Vaissière, B.E., Cane, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. and Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* 274, 303–313.

Case study 8. The million dollar oil palm pollinator weevil

Up until the 1980s it was assumed that oil palms are wind pollinated. However, pollination has never been a problem in West Africa, the original home of the commercial oil palm (*Elaeis guineensis*; Arecaceae), whereas in Malaysia, especially Sabah, assisted pollination was necessary and even then yields were lower than those in Africa.

In 1977 the Unilever Plantations Group started a research programme with the Commonwealth Institute of Biological Control. Dr R.A. Syed investigated the possibility that pollinating agents are involved in Cameroon. He found that both male and female flowers are attended by a complex of weevils (Curculionidae) of the subfamily, Derelominae, a group which is associated with palm flowers. The beetles breed in the flowers of both sexes and had been reported to cause damage.

Careful observations showed that weevils breeding in male flowers are all species now placed in the genus *Elaeidobius*, while those breeding in female flowers are *Prosoestus* spp. *Elaeidobius* spp. are attracted to male flowers only during anthesis when a strong aniseed-like scent is emitted. When the stigmas are receptive, the female flower emits short pulses of a similar but sharper and more penetrating odour which attracts *Elaeidobius* spp. away from the male flowers. On arrival in the female inflorescence, the beetles find no food and soon leave. Oviposition takes place after anthesis so that the larvae develop on tissue which has served its purpose and no longer has any function for the palm and therefore *Elaeidobius* spp. cause no significant damage. Syed went on to demonstrate that during the wet season, very little pollen is carried in the air and that if insects are excluded, pollination does not take place. Examination of *Elaeidobius* spp. showed that they become covered in pollen which is shed when they clamber about the female inflorescence. In all, there are six species of *Elaidobius* in Cameroun. Each species is dominant in a different zone of each male flower spike, and each has slightly different climatic requirements so that the relative abundance of the species changes from the wet coastal zone to the drier interior. Thus, the six species are able to coexist on the same resource.

Elaeidobius kamerunicus was selected for Malaysian conditions and subjected to intensive screening tests using the protocols that had been developed for organisms to be used in biological weed control. The weevil was not attracted to or able to survive for long on the flowers of other palms, except to a limited extent on the South American oil palm (*Elaeis oleijera*). For importation into Malaysia, *Elaeidobius kamerunicus* was bred in captivity on sterilized oil palm flowers, and carried in the pupal stage to Kuala Lumpur in individual glass tubes. En route, the contents were examined in the United Kingdom and repacked to ensure that no contaminants were inadvertently introduced along with the pollinator. These precautions were necessary to eliminate oil palm pathogens and natural enemies of *E. kamerunicus*, which is infested with mites and nematode larvae in Africa. Two releases were made in February 1981 and within a year, the weevil had spread throughout Peninsular Malaysia and was extremely abundant in all plantations. The weevils were taken to Sabah in March 1981, with even more impressive results. In the early 1980s they were also taken to Papua New Guinea, the Solomon Islands, Sumatra and Thailand, leading to successful establishment and enhanced yields. The introduction of *E. kamerunicus* into new isolated plantings of oil palm has become standard practice.

Oil palm fruit set in Malaysia now regularly reaches the levels found in Cameroon, hand pollination has been discontinued, and yields raised by about 20 percent. Calculations indicated that, with the money saved on hand pollination, the introduction of the pollinator was worth some US$115 million per year to the planters. This is the only example of a pollinator other than bees that has been deliberately introduced widely. The protocols to assess the risk of its introduction based on those used for the classical biological control of weeds proved satisfactory.

Prepared by Matthew J.W. Cock

Source:

Greathead, D.J. (1983) The multi-million dollar weevil that pollinates oil palms. *Antenna, Bulletin of the Royal Entomological Society of London* 7, 105–107.

Case study 9. The role of varroa mites in infections of Kashmir bee virus and deformed wing virus in honeybee

Varroa mites (*Varroa destructor* Anderson and Trueman; Acari: Varroidae) have been blamed for the outbreaks of so-called parasitic mite syndrome, a condition with complicated and highly variable symptoms, in the western honeybee *Apis mellifera* L. (Hymenoptera: Apidae). Despite variability, all varroa-infested colonies have an unusual presence of diseased brood, which is often infected with one or more bee viruses. Although it is not clear how mites kill bee colonies, a general presumption is that varroa mites have a significant influence on virus infections of bees with the possibility of mites serving as vectors or activators of the viruses.

The varroa mite is the most serious pest of the honeybee known to date. The ectoparasitic mite *V. destructor* harms both brood and adult bees causing a disease called varroosis or parasitic mite syndrome and including a form of brood damage termed snotty brood. From the beekeeping point of view there are thresholds for economic damage and for irreversible colony damage. At low infestation rates clinical symptoms are not visible, and infestations often remain undetected. Moderate infestation rates reduce the growth of the honeybee population and, therefore, the honey yield. Gradual increase in the parasite population during the autumn leads to greater losses of adult honeybees which, weakened by impact of the mite, may die prematurely or fail to return to the hive because learning has been compromised. The final breakdown of a honeybee colony is associated with typical symptoms of parasitic mite syndrome such as scattered brood, crawling and crippled bees, superseding of queens, etc. Several reports confirm that under temperate conditions untreated colonies may collapse due to varroosis 3–4 years after the initial infestation. It is clear that mite population growth is lower in subtropical and tropical climates.

Varroa destructor is a vector for various honeybee viruses. So far, about 18 different viruses have been isolated from honeybees. For Kashmir bee virus (KBV), sacbrood virus, acute bee paralysis virus (ABPV), Israel acute paralysis virus (IAPV) and deformed wing virus (DWV), it has been proven that they can be vectored by *V. destructor*. In the absence of the mite, these viruses cause covert infections and have been considered a minor problem to honeybee health. Feeding activities of the mite increase levels of these viruses in individual bees by spreading the viral particles. Studies have also indicated that the mites activate viral replication and increase the virulence of the viruses, leading to overt diseases with which the weakened immune system of the bees is unable to cope.

Prepared by Suresh K. Raina

Sources:

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Shimanuki, H. and Knox, D.A. (1997) Bee health and international trade. *Revue Scientifique et Technique Office International des Epizooties* 16, 172–176.

Case study 10. *Cordyceps* harvesting in the Himalayas

Ophiocordyceps sinensis (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones and Spatafora (better known as *Cordyceps sinensis* or by its Tibetan name yartsa gunbu) is one of the most highly prized and expensive natural products used in traditional Oriental medicine. It is used as a remedy for a wide range of conditions, especially to aid in building strength and recovery from illness. Several factors over the past ten years and more have combined to increase demand, including widespread publicity surrounding its use by record-breaking Chinese athletes, health concerns caused by the SARS (severe acute respiratory syndrome) and bird flu outbreaks in Asia, and increasing affluence in China, its principal market.

Yartsa gunbu is collected intensively throughout alpine grasslands of the eastern Himalayas and parts of the Tibetan Plateau. It consists of dried fruiting bodies of the entomopathogenic fungus *O. sinensis* and cuticular remains of its insect host, a subterranean caterpillar, which retains its distinctive shape.

As the only known hosts for *O. sinensis*, members of the ghost moth genus *Thitarodes* (Hepialidae), play a significant role in the ecological system at the heart of harvest and trade of yartsa gunbu. Caterpillars of this genus are subterranean root feeders living polyphagously on alpine forbs and sedges. Caterpillars take 2–6 years to reach maturity depending on the species and environmental conditions. It is assumed that caterpillars of this genus are infected by spores of the *Ophiocordyceps* fungus during early life stages after which they stay dormant for a considerable time. Death occurs in the final caterpillar instar prior to pupation with the host being consumed by the growing mycelium, turning it into a solid “mummy”. An elongate fruiting body emerges after snow melt in spring from behind the head capsule of the former caterpillar and the combined feature is intensively collected at this time of the year.

Every year, from Bhutan alone, millions of these “chinese caterpillars” are exported as part of a worldwide multi-million dollar trade in this commodity. Despite being of such high ecological and economic importance, for large parts of the collecting area, the identities of the host moths have only recently been resolved by the description of new species.

Over the past ten years the financial value of yartsa gunbu has increased dramatically, with collectors paid as much as US$12 500/kg for top-quality material. This is causing significant distortion to local economies, and there is widespread concern that the current rate of collection is unsustainable.

Prepared by Matthew J.W. Cock

Sources:

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Case study 11. Edible soil invertebrate consumption in tropical areas of South America

More than 2 000 species of invertebrates are used as food resource by humans worldwide. The use of soil animals as a protein source in human nutrition is still widely represented in indigenous populations in most regions of the world. Harvesting soil invertebrates is a common practice of local communities in the tropical lowlands of South America. In Amazonia for example, at least 32 ethnic groups consume a significant amount of small terrestrial invertebrates, and the total number of edible invertebrate species used as food in this area exceeds one hundred. These include invertebrates of the following trophic groups: geophagous, detritivorous, saproxylophagous, leaf cutters, predators and generalists.

Small invertebrates can make a significant contribution to the diet. Invertebrate consumption can provide significant amounts of animal proteins, especially during difficult periods of the year (e.g. rainy seasons) during which fish and game is scarce, e.g. 60 percent of animal protein in the diet during the rainy season for Guajivos Amerindians of Venezuela. Among the Tukanoan Indians (Colombia), insects and other small invertebrates provide up to 12 percent of the animal protein in men’s diets and 26 percent in women’s diets during the early months of the rainy season (May and June). Local people know not only the species eaten, but also other species not considered resources, for example, no terrestrial snails are mentioned as edible.

Amerindians value soil invertebrates for their flavour as well as for their nutritional value. Soil invertebrates are consumed as delicious and highly nutritive local snacks in parts of this region. For example, during the onset of the rainy season, native habitants of the Orinoco Llanos in Colombia hunt very enthusiastically for swarming females of *Atta laevigata* (Smith) (Hymenoptera: Formicidae), locally named “culonas”. These ants are consumed like peanuts after toasting their large abdomens which are full of sugars and lipids (T. Decaëns and J.J. Jiménez, pers. obs. and tasting). In the Bolivarian Republic of Venezuela, the Ye’Kuana ethnic group collect and consume at least two different edible earthworm species that are highly prized compared to other food such as fish, game, pork or beef.

Prepared by Juan J. Jiménez and Thibaud Decaëns, Université de Rouen, France

Sources:

Cerda, H., Martinez, R., Briceno, N., Pizzoferrato, L., Manzi, P., Tommaseo Ponzetta, M., Marin, O. and Paoletti, M.G. (2000) Palm worm: (*Rhychophorus palmarum*) traditional food in Amazonas, Venezuela: nutritional composition, small scale production and tourist palatability. *Ecology of Food and Nutrition* 40, 13–32.

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Case study 12. Edible caterpillars of the miombo woodland, southern Africa

Insects are an essential component of the diet of many traditional communities in Africa. Over 50 different species of caterpillars are known to be eaten in Africa but the Saturniidae are most used. In South Africa and Botswana, the mopane worm, *Gonimbrasia belina* (Westwood), larvae of the mopane emperor moth, has become a cash crop. Several different species of caterpillars, some of which have yet to be identified, are of increasing socio-economic importance among local people in the miombo, a woodland ecosystem extending from the southern part of the United Republic of Tanzania to Zimbabwe and from Angola to northern Mozambique. The common edible caterpillars in the miombo are of the Saturniidae genera *Gonimbrasia*, *Gynanisa*, *Imbrasia* and *Cirina*. In this region the caterpillars feed on over 20 species of the miombo trees.

The caterpillars are highly sought after as relish to supplement the traditional cereal-based diet. Nutrient analyses of caterpillars in Zambia and the Democratic Republic of the Congo (DRC) revealed 63–65 g protein per 100 g of dried caterpillars. Kilocalories per 100 g averaged 457, and most species provided an excellent source of iron, with 100 g providing on average 335 percent of the recommended daily requirement. Caterpillars are an important source of nutrients especially during the first part of the rainy season, when the other food sources are in short supply.

Harvesting and marketing of caterpillars is a viable enterprise for rural communities. A study in Malawi showed that caterpillar collection produced twice to several times the gross margin values of maize, beans and groundnuts, and did not directly compete for labour with the existing agricultural enterprises in rural households. Similarly, in northern Zambia incomes from caterpillar harvesting are higher than incomes from the sale of agricultural crops. A person can pick about 20 litres per day, and in seven days picking, can earn the equivalent of a month’s salary for a general worker in Zambia. People travel 200–300 km to pick caterpillars, and traders travel up to 900 km (from Lusaka and the Copper Belt) to buy them in northern Zambia.

Sustainable utilization of edible caterpillars in the miombo is constrained by several factors. Hardly anything is known of the biology, ecology and rearing of these caterpillars, in contrast to the mopane worm in southern Africa, which is industrially processed for the South African market. Another constraint is the depletion and local extinction of the miombo caterpillars, due to over-harvesting and destruction of their natural habitat and host plants by deforestation, forest fires or overgrazing. These are the same forces that lead to the dwindling of the miombo woodlands. Caterpillar collection is itself a primary cause of habitat loss because trees are often cut down for harvesting. Sustainable utilization of the edible caterpillars and conservation of the miombo woodland are therefore interdependent.

In addition, technical constraints in the use of caterpillars as food are their unpredictability, small size and problems associated with processing and storage. Many of these constraints could be overcome by the development of sustainable collecting and rearing methods. Edible caterpillars could be reared in semi-natural or artificial conditions, at farm or community level, and integrated into agroforestry programmes. The first step, however, is to acquire basic knowledge on their identification, distribution and biology/ecology.

Prepared by Marc Kenis, CABI Europe – Switzerland

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Case study 13. Functional shifts in community composition of soil invertebrates under elevated CO_2

Increased CO_2 concentration is predicted to stimulate both primary production and decomposition, resulting in an increase in soil organic matter. Clear evidence exists for the potential impact of climate change-related factors such as eCO_2 (elevated levels of CO_2), temperature change and altered rainfall patterns on community composition of soil invertebrates. Among these, micro-arthropods living in the litter and the topsoil represent an important functional group in nutrient cycling and litter decomposition.

Under increased CO_2 there are important functional changes in the community composition of soil invertebrates. In a FACE (Free-Air Carbon dioxide Enrichment) experiment it was observed that mean micro-arthropod abundance was 33 percent lower in the eCO_2 treatment, but with significant decline only for oribatid mites. Other studies report increases in microbial-feeding, free-living nematodes, enchytraeid worms, and even earthworm biomass. Functional groups can exhibit different responses to soil warming, for example, depletion of epigeic species of ecosystem engineers, and augmentation of fungivorous mites. Collembolan populations have increased in most studies of eCO_2, although some have reported lower collembolan numbers. Both negative and positive single responses of eCO_2 on soil micro-arthropods have been found and can be explained by the inherently high soil CO_2 concentration, so certain species are already adapted to these conditions. The responses of soil invertebrates have been interpreted as responses to increased root-derived carbon and subsequent microbial community changes.

How soil communities will be affected by climate change-related factors acting simultaneously is not known although indirect effects are envisaged as both plant composition and productivity can promote important functional shifts. The structure of soil invertebrate communities is affected and impact is driven by changes in soil moisture content. Several climate change factors acting simultaneously will result in reduced moisture causing changes in soil micro-arthropod communities that can affect the functions that these organisms provide, such as decomposition.

Responses of micro-arthropod communities seem to be specific to particular plant communities and ecosystems. Functional changes within soil invertebrate communities due to climate change are expected to occur although more evidence is required.

Prepared by Juan J. Jiménez

Sources:

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Case study 14. Insect adaption or movement: the evidence from the sub-fossil record in glaciation history

We live in an interglacial period in a 2.6 million year sequence of alternating glacial and interglacial periods (the Quaternary Period). During this period, the world has certainly been warmer than it is now in this interglacial period, but for much of the time it has been colder, and the transitions between the two extremes have been rapid.

Sub-fossil remains in temperate regions are available in dated layers for many insects covering much of this period. Examination of these remains can give us insight into evolution, extinction and movement of insect populations during periods of climate change, helping us to understand how insects and other invertebrates are likely to respond during the anticipated climate change to come.

The sub-fossil record shows little evidence of evolution of new species or mass extinction of species during the Quaternary. The sub-fossil remains can nearly all be matched to existing species, and the fact that species occur in similar associations implies that their physiological and ecological requirements have not changed significantly. There is evidence that species disappeared from the sub-fossil record at the beginning of the Quaternary, but little evidence for significant mass extinction since then. This implies that the species that exist today have mostly existed unchanged since the beginning of the Quaternary, and that they have survived repeated glacial and interglacial periods.

What the sub-fossil evidence does show, however, is that insect species have been geographically highly mobile. Broadly speaking, the species found in temperate regions during glacial periods are now restricted to cold areas of the subarctic and high mountains such as the Himalayas, whereas the species found in temperate regions during warmer periods are those which we now associate with the subtropics. The implication is clear: species do not adapt to changing climate, but they move to areas where they are well adapted to the climate.

The sub-fossil evidence also indicates that insects move fairly rapidly when necessary. The changes between glacial and interglacial periods and back have been rapid and the insect groups studied (detritivores and predators) have kept track with the areas to which they are adapted. There is less evidence as yet for herbivores, which can only spread to climatically suitable areas where suitable food plants already occur, or for flightless insects. For the latter, particularly soil invertebrates, it would be desirable to know more about the sub-fossil record, to better predict what might happen now.

We do not have comparable data for insect species in the tropics, and this is a gap that should be filled if possible. There is evidence from Africa which indicates that rainfall was reduced in glacial periods and much of Africa became savanna, and so species adapted to rainforest became concentrated in refugia where rainfall persisted, or at higher altitude on mountains. It is not clear to what extent species may have moved out of Africa. In contrast, the Amazon Basin remained as rainfall forest during glacial periods, albeit 5–7°C colder, which allowed plant species that are now restricted to higher altitude in the Andes to spread into the Amazon Basin, albeit at low densities. The species that are now present in the Amazon seem to have persisted *in situ* during glacial periods. Studies of sub-fossil insects from these regions are needed. This will be difficult and time consuming because of the shortage of suitable depositions and the huge number of species likely to be involved, but should throw further light on how invertebrates respond to climate change, and help improve predictions for invertebrates of agricultural importance in the tropics.

Prepared by Matthew J.W. Cock

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Case study 15. Climate change-related expansions in the range of the southern green stink bug, a cosmopolitan invader.

The geographical ranges of many invertebrate pests are expected to expand under climate change as a result of temperature-related increases in the suitability of new habitats. The southern green stink bug (SGSB), or green vegetable bug, *Nezara viriduala* (L.) (Hemiptera: Pentatomidae) is a cosmopolitan, highly polyphagous species which attacks many important food and fibre crops including rice, soyabean, maize (corn), tomato and aubergine (eggplant). In warmer climates there may be four generations per year with a life cycle of about 70 days. The SGSB probably originated in Africa, but over the past 250 years it has spread all over the world and now occurs in most tropical and subtropical regions. In some areas, such as Brazil, there are genetically distinct SGSB populations which are adapted to colonize different environments. Some geographical expansion is related to the planting of its preferred hosts (e.g. soyabeans) in new regions, but it is also spreading northwards to new areas in temperate zones as a result of climate change. For example, the discovery of breeding colonies in the United Kingdom – further north than was previously predicted – has been taken as a sign of climate change, although its potential impact needs further study.

The SGSB has been extensively studied in Japan, where its initial increase was related to the cultivation of early planted rice in the 1950s. In central Japan, however, its range has now shifted northwards, by some 85 km since the early 1960s, probably as a result of milder winters. The northern limit appears to be defined by a +5°C isothermal line for mean January temperatures in Japan. Expansion into new areas has a direct economic impact, e.g. it can seriously affect rice production, and continued global warming will probably further increase the winter and spring survival of *N. viridula* in temperate regions where it is currently at the limit of its range. More adults will survive the winter and be available to help establish the species in newly colonized areas, and a 2.0–2.5°C increase in average temperatures could produce another full generation in central Japan.

In the tropics, however, where insects are often living relatively close to their physiological optima, further increases in temperature may have a negative effect on their performance: e.g. a simulated increase in temperatures of 2.5°C had a strongly deleterious effect on SGSB. *Nezara viridula* has symbiotic bacteria in its gut, and climate change can act via these mutualistic organisms – which are eliminated at high temperatures – to indirectly affect the host population; whether heat stress due to global warming will have such an effect on SGSB in tropical regions remains to be seen. In conclusion, SGSB is an invasive alien species which has increased its range in a number of regions as a result of both land-use changes and global warming. Winter temperatures determine the survival and establishment of such above-ground invertebrates and climate change is expected to result in range expansions of many other species, in a similar way to that illustrated here by the SGSB.

Prepared by Raymond J.C. Cannon

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Case study 16. Coffee's most intractable insect pest: the coffee berry borer

The coffee berry borer (CBB; *Hypothenemus hampei* (Ferrari)) is an African scolytid beetle that bores into the ripening coffee bean where it produces about 30 first-generation offspring. Like most insect borers, it has relatively few natural enemies and where such agents have been introduced, they have not been capable of maintaining the pest below an economic threshold. The most common and effective forms of control are chemicals and regular but very laborious hand picking to remove all ripe, over-ripe and fallen berries.

The very highest quality arabica coffee is little troubled by the borer, because it grows at such an altitude that the pest cannot complete more than a generation before harvest. Hence the finest Ethiopian coffees have been little troubled by CBB, but this is now changing; the climate around Jimma in Ethiopia, for instance, was too cold for CBB before about 1984 but now, because of climate change, it may be able to complete one to two generations per year.

In Colombia, it is a common experience that the lower altitude limit of coffee itself is rising and difficulties in controlling the borer have been cited as a factor in farmers' decision to quit growing coffee. In July 2010, the president of Quindío's coffee committee said that the warmest parts of the department had become marginal for coffee – "the temperature has gone up a degree and in the heat, management of the borer is impossible", he said. In Indonesia CBB has been mostly a robusta coffee pest at low altitudes, but over the last ten years it has been found increasingly in the higher arabica coffee growing areas in northern Sumatra and Aceh, where high-quality Mandheling coffee originates.

It is not only temperature that is affecting efforts to control CBB. Climate change is causing more extremes of weather such as prolonged dry and wet spells. Dry hot spells can be especially favourable for CBB as its progeny develop in the virtually sealed fallen berries that remain buried under leaf litter after harvest; there they suffer low mortality and then suddenly emerge en masse after rainfall. Farmers are frequently not aware of this problem, especially if previous wet periods have tended to keep CBB under better control.

In India both the showers that initiate flowering and those that support fruit setting are becoming less reliable. This can lead to smaller multiple flowerings which provide a year-round food source for CBB. Dr J.K. Kimemia, head of Kenya's Coffee Research Foundation confirms this: "You look at a coffee tree and cannot determine the season because it has beans of all ages. That is a problem when it comes to disease management, insect management and the worst problem is in harvesting, the cost is enormous."

Efforts to find new ways to control the borer are currently few. Heavy shade trees in coffee agroforestry systems can reduce temperature, humidity and solar radiation extremes but field studies can find no clear relationship between CBB infestation and shade intensity. With the general prohibition of the most effective chemical control (endosulfan), and the prospect of accelerating climate change, it is increasingly clear that long-term control of CBB needs to be rethought.

Prepared by Peter S. Baker, CABI

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Case study 17. Climate change may increase wind-assisted migration of invertebrates into New Zealand

Wind-borne migration enables insects as diverse as minute flies to large moths to track changing habitats on spatial scales ranging from local to intercontinental (Gatehouse, 1997). This strategy is successful in spite of the randomness of the destinations reached and the losses that occur from failure to locate a suitable habitat. New Zealand’s geographical isolation has been an enormous help in preventing the invasion of unwanted organisms that could attack crops, interfere with efficacy of beneficial organisms and endanger native biodiversity. However, there is compelling evidence that many invertebrates that utilize wind for dispersal frequently cross the 2 000 km of ocean between Australia and New Zealand, ranging from aphids to butterflies (Tomlinson, 1973), e.g. the nymphalid butterfly *Hypolimnas bolina nerina* (F.) is found in considerable numbers some years, but is not established in New Zealand.

In the latitude of New Zealand and Australia, the weather is dominated by eastward moving anticyclones and depressions. As the associated fronts move over Australia, the warm air ahead rises, providing lift to invertebrates which can then be carried across the Tasman Sea on the westerly winds. They are deposited in western parts of New Zealand as the winds weaken. Similarly, hot dry conditions in Australia can generate thermals that can lift insects above the ground to a level of the prevailing westerly winds. Meteorological conditions favouring migration of Australian invertebrates across the Tasman Sea at a transit level of 300–1 000 m were estimated to occur just over 20 times per year based on weather data for the years 1961–70 (Tomlinson, 1973). In most cases, the scarcity of available hosts, mates, habitat and climatic conditions in New Zealand prevents establishment of viable populations.

Climate change projections indicate that south-eastern Australia is likely to become hotter and drier in future and there will be an increase in the strength of the mid-latitude westerly winds. Therefore, the frequency of favourable migration conditions is likely to increase. When combined with the prediction that New Zealand’s climate on average will be around 2°C warmer by 2090 than in 1990, and that the north-western regions may become frost-free, many of the regular Australian migrants may become permanently established.

Prepared by Pip Gerard

Sources:

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Case study 18. The Argentine ant, one of the world's worst invasive aliens.

The Argentine ant (*Linepithema humile* (Mayr): Hymenoptera: Formicidae), is a widespread and highly invasive species. Native to South America, Argentine ants have spread throughout the world (to all continents apart from Antarctica), as a result of least 28 separate introductions, mainly as a result of human commercial activities. However, this species still has the potential to become established in new areas, beyond its present distributional range, as a result of global climate change. The Argentine ant is most likely to occur where the mean daily temperature in midwinter is 7–14°C and maximum daily temperatures during the hottest month average 19–30°C. Therefore, many uninvaded regions are vulnerable to future establishment, including southern China, Taiwan, Zimbabwe, central Madagascar, Morocco, high-elevation Ethiopia, Yemen and many oceanic islands.

Linepithema humile remains a serious threat to native species and ecosystems in many islands, such as New Zealand, where it is concentrated in urban centres but has the potential to establish itself more widely, particularly in urban areas and disturbed habitat. The Argentine ant is an ecologically damaging invasive species that forms "supercolonies" which are a threat to biodiversity as it can displace most other ant species through competition. Argentine ants can also have impacts on other invertebrates via direct predation, competition and egg predation. In addition, *L. humile* can be an agricultural pest, enhancing populations of sap-sucking Hemiptera which damage plants and can vector diseases.

The spread of the Argentine ant has been facilitated by so-called "jump dispersal", typically a human-mediated long-distance mode of dispersal that can disseminate a species widely and result in colonization of new continents. Virtually no country or island is too isolated for potential establishment by this species and climate change could exacerbate the process, with tropical coastal Africa and South-east Asia being particularly vulnerable to invasion. However, global warming may result in a general reduction in the distribution of *L. humile* in tropical areas, with a shift to higher latitudes and altitudes as they become more suitable for invasion and establishment.

Prepared by Raymond J.C. Cannon

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Case study 19. The European corn borer: range shifts and an increased number of generations – climate change in action

The European corn borer (ECB), *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), is a serious pest of maize in Europe and since 1909 in North America. Although highly polyphagous, it is most damaging to maize crops. The caterpillars feed on the leaves at first – causing characteristic leaf "windowing" – but later instars enter the stem and hollow out the internodes causing the stems to break. The larvae can also feed on the cobs and crop losses can be severe. In the northern parts of its range, ECB has only one generation per year (univoltine), but in warmer latitudes there may be two or three generations. *Ostrinia nubilalis* already appears to be expanding northward in Europe and global warming may result in substantial future expansions in the range of this species as well as other maize pests which are currently limited by low winter temperatures. The northern limit is expected to shift northward by more than 100 km with every 1ºC rise in the average temperature. In Hungary, there has been a gradual disappearance of the univoltine type, coincidental with the gradual appearance of a two generational (bivoltine) ecotype, between 1991 and 2004. The ECB may also become bivoltine in the Czech Republic and other more northerly European countries, possibly affecting substantially more arable land and causing increased damage in maize growing areas by 2050.

A 3ºC increase in mean annual temperatures would advance the limit for maize to the extent of including virtually all of the United Kingdom, and this could provide the means for a substantial shift in the distribution of *O. nubilalis*. The area of maize cultivation in the United Kingdom has already increased from about 25 000 to 172 000 ha in the last 30 years. For species such as *O. nubilalis*, which are already distributed over a very wide latitudinal range in Europe, successful colonization of northwardly expanded maize crops will depend on factors such as migration ability and the rate at which the climate changes. Up until the 1930s, ECB was classed as a rare migrant to the British Isles, at or near the northern limit of its range in southern England, but since then it has been progressively extending northwards and is now a regular migrant. Breeding colonies have been established in England for many years, feeding almost exclusively on mugwort (*Artemisia vulgaris*; Asteraceae), but in 2010, for the first time, the pest caused damage to two maize crops in the south-west of England. In conclusion, the ECB is expected to occupy a wider area and exert increased pest pressure as a result of an increase in the number of generations per year, due to the climate change.

Prepared by Raymond J.C. Cannon

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Case study 20. Critical regional host: parasitoid population interaction may be jeopardized by climate change

The introduced lucerne weevil, *Sitona discoideus* Gyllenhal (Coleoptera: Curculionidae), became a severe pest of lucerne (alfalfa) in Australia in the 1960s and in New Zealand in the 1970s. In 1977, the parasitoid *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae) was introduced from Morocco into Australia to control this pest, and from there into New Zealand in 1982. The parasitoids lay eggs inside adult weevils, and female weevils become sterile almost immediately afterwards. The solitary larvae develop within the live hosts and the weevils die when the mature larvae emerge to pupate.

Sitona discoideus has one generation per year. The weevil over-summers (aestivates) as a pre-reproductive adult in a sheltered place away from lucerne, then returns to the lucerne in autumn and commences reproduction which continues until spring. The *M. aethiopoides* larva generally develops only when its host is reproductive. The parasitoid over-summers as a non-developing larva in aestivating *S. discoideus* and then resumes its development once its host has returned to the lucerne. Under these conditions, *M. aethiopoides* has two generations for every host generation. This occurs in its natural range in Europe, and in Australia where it is not an effective biological control agent (BCA). However, in New Zealand, around 3 percent of the non-reproductive *S. discoideus* do not aestivate. They stay in the lucerne crop throughout summer, supporting an additional four parasitoid generations. This allows the parasitoid population to build up to effective levels by autumn, preventing damaging weevil larval populations.

The most likely reason for the atypical behaviour appears to be seasonal differences in climate (perhaps interacting with day length) between New Zealand and other regions such as Australia and Mediterranean Europe.

With climate change predictions indicating that eastern parts of New Zealand will become generally drier, lucerne is expected to become an increasingly important fodder crop. However, examination of climate data suggests that areas of New Zealand where the biological control is currently successful may become increasingly similar to Australian areas where biological control is ineffective. While the mechanistic trigger for atypical parasitoid development in New Zealand has not been confirmed, New Zealand lucerne growers will need to be alert for weevil outbreaks that may signal that the BCAs are becoming ineffective.

This case study exemplifies how a small but critically important population interaction related to climate may determine the regional efficacy of a BCA, and how this could be affected by climate change.

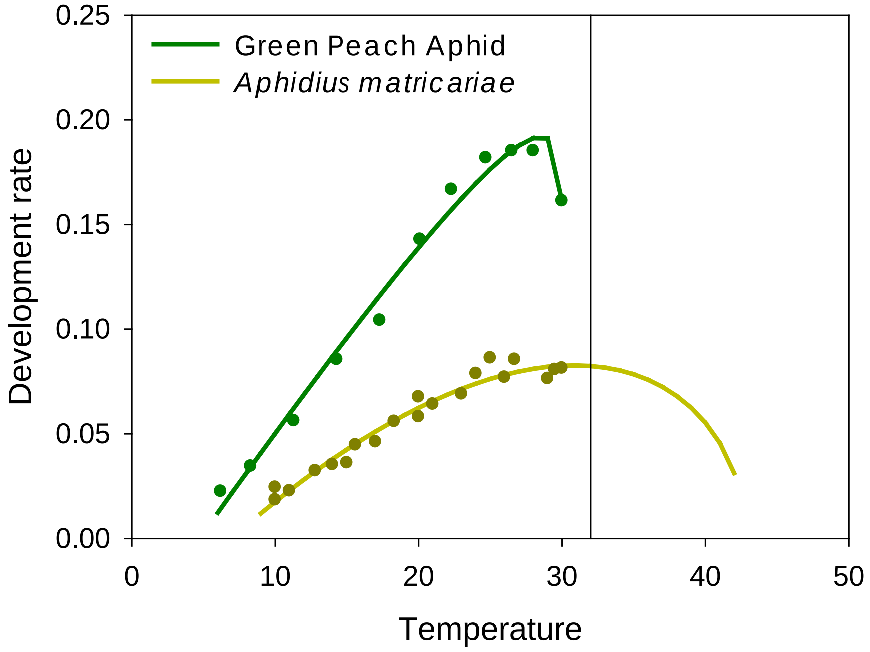
Prepared by John Kean, AgResearch Ltd, New Zealand

Source:

Goldson, S.L. (2006) Climate change in biological control. In: Newton, P.C.D., Carran, R.A., Edwards, G.R. and Niklaus, P.A. (eds) *Agroecosystems in a Changing Climate*. Taylor & Francis, London, UK, pp. 329–332.

Case study 21. Differential responses to temperature by pests and biological control agents may be important in determining the effects of climate change

Differential responses to temperature by species in food webs may be important in determining effects of climate change on the performance of biological control functions. Here, the effects of temperature on development rates are plotted for two species: the green peach aphid, *Myzus persicae* (Sulzer) and one of its hymenopteran parasitoids, *Aphidius matricariae* Haliday (Braconidae). Development rate accelerates differently for each, and each has a different apparent optimum and projected upper development threshold. In invertebrates, most biological processes are dependent to some degree on environmental temperatures, and exhibit similar shapes. The differences in slopes, optima and upper thresholds may be important in determining the responses of BCAs to thermal stress under climate change.



Prepared by: Dave Gillespie

Sources:

Bernal, J. and Gonzalez, D. (1993) Temperature requirements of four parasites of the Russian wheat aphid *Diuraphis noxia*. *Entomologia Experimentalis et Applicata* 69, 173–182.

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Case study 22. Synchronization of a pest population can lead to outbreaks due to disruption of biological control agents: coconut leaf beetle in Fiji

Coconut has long been an important tree both culturally and economically in the islands of the Pacific. Hence it caused considerable concern in the 1920s, when an indigenous leaf-mining hispine beetle, *Promecotheca reichei* Baly, came to prominence as a devastating outbreak pest of coconut in Fiji. A campaign was begun in 1929 which led to the successful biological control programme against the pest, which in the process generated considerable information about the population dynamics of *P. reichei* and its natural enemies, stimulating thinking about the regulation of populations in the tropics.

Studies showed that in normal circumstances, the generations of the beetle overlap so that the various developmental stages occur together, parasitoids are able to breed continuously, and a satisfactory low equilibrium was maintained by the inter-relations of indigenous primary and secondary parasitoids. In the 1920s, however, this equilibrium was upset in certain parts of Fiji by a predatory mite, *Pyemotes ventricosus* (Newport) (Acari: Pyemotidae), which was first recorded there in 1921, though it had probably been introduced long before. This mite attacks the larvae, pupae and freshly emerged adults of *Promecotheca reichei*, multiplies rapidly, and periodically eliminates all the larvae and pupae in a site of infestation. After this, its numbers decline, but rise again with those of the host. As a result, a condition is produced and maintained in which the stages of *P. reichei* do not overlap, and in this condition it was no longer controlled by indigenous parasites and so assumed the status of a pest.

The predatory mite made the beetle a pest, not by elimination of the indigenous natural enemies by direct attack, but by periodic elimination of all developmental stages of *P. reichei* except adults, thus causing and maintaining a condition comparable to that of insects in temperate countries, where development and time of occurrence are controlled by seasonal climatic changes, and successive generations cannot appreciably overlap. The synchronized condition was maintained because *P. reichei* has only a short oviposition period – if the oviposition period were long, the population would rapidly revert to a condition where all developmental stages were present. The generation time of the indigenous parasitoids proved ill adapted for coping with this new condition, as they emerged when no suitable hosts were available, so that as long as the pest remained synchronized they could not breed continuously. The beetle anomalously became a pest in the presence of the very parasitoids that normally controlled it. It was evident that in these very special circumstances, the problem of restoring the insect to a state of economic harmlessness necessitated the discovery of a parasitoid capable of satisfying requirements of an unusually rigid and exacting nature, i.e. one with a life cycle duration that would enable it to breed continuously on a synchronized host population.

Based on this criterion, surveys in Indonesia led to the selection of *Pediobius parvulus* (Ferrière) (Hymenoptera: Eulophidae), as theoretically suitable. Following its introduction, it became established and suppressed the hispine beetle rapidly and effectively.

This work suggested that synchronization of a pest population, whether by another natural enemy, an extreme climate event, or colonization of a new area, leading to the disruption of effective continuously breeding biological control agents (BCAs), may be more common than realized in the tropics. Building on this study 50 years later, Godfray and Hassell (1987) noted that such synchronized populations were quite widespread, and a common factor in these examples is the presence of insect parasitoids as a major mortality factor. They went on to demonstrate, using theoretical population models, that parasitism can be the cause of discrete pest generations, and in particular, that the ratio of the lengths of the host and parasitoid life cycles is of prime importance in determining whether generations tend to be discrete or continuous.

Prepared by: Matthew J.W. Cock

Sources:

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Case study 23: Biological control of corn earworm, *Helicoverpa armigera*, in New Zealand threatened by climate change

Climate change may allow more generations of this pest to develop each season, potentially exacerbating pest threats beyond the ability of current biological control agents (BCAs) to maintain effective suppression.

In New Zealand, the corn earworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), is the key insect pest of processing tomatoes in the main growing region of Hawke's Bay. Two larval braconid parasitoids were successfully introduced into New Zealand: *Cotesia kazak* (Telenga) in 1977, and *Microplitis croceipes* (Cresson) in 1986. These now cause 60–80 percent parasitism and form the basis of an integrated pest management (IPM) programme to control corn earworm in outdoor tomato crops. *Cotesia kazak* is the dominant parasitoid, reared from about 90 percent of parasitized larvae, and usually killing larvae before they cause damage.

Corn earworm normally has three generations a year in the North Island of New Zealand, but in cooler summers and in cooler regions there are only two generations a year. Despite the action of the parasitoids, the third generation, when present, can lead to severe crop losses in sweetcorn, tomatoes and leafy vegetable crops such as cabbage and lettuce. In areas where this third generation is common, the processing industry does not plant late crops of sweetcorn and processing tomatoes.

The projected changes over New Zealand for the A1B (medium emissions) scenario of the IPCC are for annual mean temperatures to increase by about 1°C by 2040, and 2°C by 2090, with the changes most pronounced in the north of the South Island, and most of the North Island. Development parameters were used to calculate the expected number of corn earworm and parasitoid generations per year and showed that the expected climate warming in New Zealand may allow a third generation of the pest to occur in cooler seasons and in cooler regions. This would have a major impact on the pest status of *H. armigera* in these areas, particularly in the South Island. The results suggest that even under a moderate emissions scenario corn earworm is expected to become increasingly problematic, and by 2090 may be affecting late-season crops of tomato and maize as far south as Canterbury. Given that *C. kazak* has not been effective at controlling corn earworm in warmer areas overseas, the future viability of the current IPM systems may be compromised.

Prepared by Graham Walker, The New Zealand Institute for Plant & Food Research Limited

Sources:

Cameron, P.J., Walker, G.P., Herman, T.J.B. and Wallace, AR. (2001) Development of economic thresholds and monitoring systems for *Helicoverpa armigera* (Lepidoptera: Noctuidae) in tomatoes. *Journal of Economic Entomology* 94, 1104–1112.

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Walker, G.P., Herman, T.J.B., Kale, A. and Wallace, A.R. (2010) An adjustable action threshold using larval parasitism of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in IPM for processing tomatoes. *Biological Control* 52, 30–36.

Case study 24. Earthworms enhance plant tolerance to nematode infection through non-trophic effects of ecosystem engineering

Below-ground interactions are complex and so far the mechanisms involved are not well known. Studies on the importance of non-trophic relationships, both above and below ground, are not abundant. As a result, generalizations on the effect of predicted climate change on plant-mediated interactions between earthworms and above-ground multitrophic groups are not possible. Climate change is expected to affect plant production and the incidence of soil pests.

Plant-parasitic nematodes are serious pests that cause crop production losses with high economic damage. Earthworms and vermicompost have been shown to reduce the harmful impact of nematode infestation in banana plantations.

The nematode *Heterodera sacchari* Luc and Merny (Heteroderidae) forms external cysts on rice roots leading to serious damage in upland rice fields in Africa. The effect of an earthworm (*Millsonia anomala* Omodeo; Megascolecidae) on the physiology of nematode-infested plants was demonstrated through selected stress responsive genes coding for lipoxygenase, phospholipase D and cysteine protease. The ability of plants to respond through physiological mechanisms was enhanced by earthworm presence. Decrease in rice growth due to *H. sacchari* was suppressed in the presence of earthworms. Root biomass was not affected by nematodes when earthworms were present and the expression of stress-responsive genes in the leaves was modulated by below-ground activities.

The mechanisms are not known but need to be discovered as climate change may induce important changes in plant production and the incidence of pests in soil.

Prepared by Juan J. Jiménez and Patrick M. Lavelle

Sources:

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Case study 25. Above-ground multitrophic interactions mediated by soil invertebrates and summer drought

Among the expected effects of climate change is the increase of summer drought in some areas that will affect above- and below-ground multi-species community interactions. An extended period of summer drought is predicted in southern Europe. Under drought conditions earthworms can reduce assimilation, transpiration and stomatal conductance of Poaceae species, probably due to reduced soil water storage capacity in the presence of earthworms. In a large-scale study the interactive effects of earthworms (*Aporrectodea caliginosa* (Savigny); Lumbricidae) and summer drought affected multi-species plant communities (*Hordeum vulgare* (Poaceae), *Capsella bursa-pastoris* (Brassicaceae) and *Senecio vulgaris* (Asteraceae)) and how these effects affected number of aphids (*Rhopalosiphum padi* (L.)) and its parasitoid (*Aphidius ervi* Haliday; Hymenoptera: Braconidae).

Summer drought had a very strong negative impact on plant production, especially on *S. vulgaris* shoot and root biomass, but was ameliorated when earthworms were present. This may also indicate that this plant benefits most from any impact of earthworms as it is the plant most severely affected by drought. In general, nitrogen concentration increased in the leaves during drought. Summer drought decreased aphid number by 50 percent, with nearly 10 percent being parasitized. The interaction was moderated by earthworms which caused declines in *R. padi* populations under drought conditions. The interactive effects of earthworms and summer drought affected plant biomass, with an increase of 11 percent when earthworms were present and had the largest impact in monocultures compared to multi-species communities.

This case study shows how plant-mediated effects of summer drought and earthworms on *R. padi* had cascading effects on the parasitoid *A. ervi*. These interactions need to be understood as climate change may induce important changes in the interaction between earthworms and above-ground multitrophic groups. Below-ground interactions can mitigate the effects of climate change-related factors, like increased summer drought.

Prepared by Juan J. Jiménez

Sources:

Blouin, M., Lavelle, P. and Laffray, D. (2007) Drought stress in rice (*Oryza sativa* L.) is enhanced in the presence of the compacting earthworm *Millsonia anomala*. *Environmental and Experimental Botany* 60, 352–359.

Johnson, S.N., Staley, J.T., McLeod, F.A.L. and Hartley, S.E. (2011) Plant-mediated effects of soil invertebrates and summer drought on above-ground multitrophic interactions. *Journal of Ecology* 99, 57–65.

Scheu, S. (2003) Effects of earthworms on plant growth: patterns and perspectives. *Pedobiologia* 47, 846–856.

Case study 26. The invasion and degradation of pastures due to biologically created soil compaction results in negative feedbacks to climate change

In the Brazilian Amazon, 95 percent of the deforested area is converted into pasture, 50 percent of which is considered degraded due to mismanagement, phytosanitary problems, poor soil fertility and soil structural modification (linked to soil macro-invertebrate activity). When the forest is converted to pasture, the use of heavy machinery and, later, cattle trampling lead to severe soil compaction, particularly in the 5–10 cm layer, impeding root development.

The native soil macro-invertebrate communities are radically and drastically depleted, i.e. most of the native taxa disappear (151 vs. 48 morphospecies). An opportunistic invading earthworm (*Pontoscolex corethrurus* (Müller); Glossoscolecidae) benefits from anthropic disturbances and occupies the empty niche left by native earthworms and soil macrofauna, increasing its biomass to more than 450 kg/ha, equivalent to nearly 90 percent of total soil macro-invertebrate biomass. When *P. corethrurus* is present in the forest there is no negative effect on the native species communities, which have similar or higher densities in the presence of *P. corethrus*. The evidence suggests that this invasive species, unlike native species, is able to feed and develop in environments where litter resources are decreased while soils have been enriched in carbon and nutrients by deforestation and burning. It produces more than 100 t/ha of castings, dramatically decreasing soil macroporosity down to a level equivalent to that produced by the action of heavy machinery on soil (2.7 cm^3/100 g). During the rainy season these casts plug up the soil surface, saturating the soil and producing a thick muddy layer, where anaerobic conditions prevail (increasing methane emission and denitrification). In the dry season, desiccation cracks the surface and the inability of roots to extract water from the soil causes the plants to wilt and die, leaving bare patches in the field.

This case study shows how mismanagement linked to high impact of just one soil invertebrate species may bring catastrophic consequences to soil ecosystem functioning by increasing greenhouse gas emissions from soils.

Prepared by Juan J. Jiménez and Patrick M. Lavelle

Sources:

Chauvel, A., Grimaldi, M., Barros, E., Blanchart, E., Desjardins, T., Sarrazin, M. and Lavelle, P. (1999) Pasture damage by an Amazonian earthworm. *Nature* 398, 32–33.

Marichal, R., Feijoo Martinez, A., Praxedes, C., Ruiz, D., Carvajal, A.F., Oszwald, J., Hurtado, M.P., Brown, G.G., Grimaldi, M., Desjardins, T., Sarrazin, M., Decaëns, T., Velasquez, E. and Lavelle, P. (2010) Invasion of *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta) in landscapes of the Amazonian deforestation arc. *Applied Soil Ecology* 46, 443–449.

Case study 27. Genetic bottlenecks may limit the ability of biological control agents to respond to climate change

Genetic bottlenecks occur in populations when a very small number of individuals are introduced to a new region, or survive a strong selection event. When this happens, the genetic diversity in the new population is a fraction of that in the original population, and some traits (i.e. phenotypic expressions of particular alleles) may be lost. This effect can be magnified by the likelihood of inbreeding in very small founding populations. The consequence of such a bottleneck is that, because the population may not contain traits found in the source population, the potential for local adaptation to certain selection pressures may be lost. There is abundant evidence that introduced (classical and augmentative) biological control agents (BCAs) have undergone such bottlenecks. Although bottlenecks have been the likely causes of some failures of BCAs to establish following introductions, there is not a great deal of evidence that bottlenecks have constrained the performance of BCAs following successful establishment. Rapid population increase of classical BCAs following successful introduction would tend to offset and minimize the impacts of population bottlenecks.

An intriguing example of a bottleneck is the increased success of the Argentine ant (*Linepithema humile* (Mayr); Hymenoptera: Formicidae) following introduction to North America. In this case, the bottleneck decreased intra-species aggression and led to increases in density of ants (Tsutsui *et al*., 2000).

New World blue butterflies of the *Polyommatus* group (Lepidoptera: Lycaenidae) demonstrate some of the potential effects of bottlenecks and constrained responses to climate. Vila *et al.* (2011) showed that species in this group crossed the Beringia land bridge in two invasion events approximately ten million years ago, followed by a further three invasion events across the Bering Strait between four and one million years ago. The land surrounding the strait was relatively warm ten million years ago, and has been chilling steadily ever since. The first lineage of *Polyommatus* group blues that made the journey could survive a temperature range that matched the Bering climate of ten million years ago, and is now found in South America in ten genera, mostly in the Andes and the southern part of the continent, although at least three genera have spread into tropical areas. The lineages that came later are more cold hardy, each with a temperature range matching the falling temperatures, and are now found in North America. Thus, climate change events determined the success and eventual distribution of species and genera according to their thermal tolerances.

Therefore, although evidence is lacking for consequences of bottlenecks for adaptation of BCAs to climate change, evidence from past invasions suggests that this is an effect that should be considered. Constrained thermal tolerances might restrict the ability of some species to persist in regions with significantly changed climates. In particular, the ability of badly bottlenecked BCA species to adapt to climate change could be enhanced by inoculative introductions of additional genetic material from the source populations.

Prepared by Dave Gillespie and Matthew J.W. Cock

Sources:

Baker, D.A., Loxdale, H.D. and Edwards, O.R. (2003) Genetic variation and founder effects in the parasitoid wasp, *Diaeretiella rapae* (M'intosh) (Hymenoptera: Braconidae: Aphidiidae), affecting its potential as a biological control agent. *Molecular Ecology* 12, 3303–3311.

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Nei, M., Maruyama, T. and Chakraborty, R. (1975) The bottleneck effect and genetic variability in populations. *Evolution* 29, 1–10.

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Case study 28. Within-species genetic variation enables a biological control agent to adapt to changing conditions

The introduced Argentine stem weevil, *Listronotus bonariensis* (Kuschel) (Coleoptera: Curculionidae), attacks pasture grasses throughout New Zealand. In 1991, an asexually reproducing South American parasitoid wasp, *Microctonus hyperodae* Loan (Hymenoptera: Braconidae), was introduced for its biological control. Two main genotypes were released, one from east of the South American Andes mountains and another from the west. The frequency of each genotype has been measured in *M. hyperodae* populations at 14 New Zealand sites for up to ten years following release and, at most sites in most years, selection has favoured the eastern genotype. However, the frequency of the western genotype increases in warmer seasons.

Information from this study was used to forecast the balance between the *M. hyperodae* genotypes under future climates. The projected changes over New Zealand for the A1B (medium emissions) IPCC scenario are for annual mean temperatures to increase by about 1°C by 2040, and 2°C by 2090, with the changes most pronounced in the north of the South Island, and most of the North Island. Under medium-term (2040) A1B and A2 IPCC scenarios, warming will generally favour the western genotype, but strong A2 long-term (2090) warming will favour the eastern genotype.

These results are preliminary because the models did not consider some important factors such as how climate change could influence the summer emergence date of first generation *L. bonariensis* adults. However, they serve to demonstrate how climate change will inevitably impose new selection pressures on biological control agents (BCAs), and how genetic diversity within BCA populations will be important for them to adapt to those new pressures. The introduction of two *M. hyperodae* genotypes to New Zealand has increased the efficacy of the biological control programme because one compensates for the other as climatic conditions fluctuate, so together they maintain high rates of parasitism of the pest. If the eastern genotype alone had been introduced, then pest suppression would be lower in warm years, and also under the moderate climate change scenario. However, if only the western genotype had been introduced, then suppression would be less in cool years, and probably also under the A2 climate change scenario. Genetic variation within *M. hyperodae* therefore enhances the current biological control of *L. bonariensis*, and increases the resilience of this biological control system to future climatic changes.

This case study exemplifies how within-species genetic variation could assist BCAs to cope with climate change.

Prepared by Craig Phillips, AgResearch Ltd, New Zealand

Sources:

Gerard, P.J., Kean, J.M., Phillips, C.B., Fowler, S.V., Withers, T.M., Walker, G.P. and Charles, J.G. (2010) Possible impacts of climate change on biocontrol systems in New Zealand. Report for MAF Policy Project 0910-11689. AgResearch Ltd, New Zealand, 64 pp. www.maf.govt.nz/environment-natural-resources/climate-change/research-and-funded-projects/research-and-funded-projects-table.aspx

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Case study 29. The search for pests and their biological control agents in natural habitats: sugarcane pests in the Neotropical Region.

In the situation where an indigenous pest adapts to an exotic crop, the pest must have spread from some natural habitat into the agro-ecosystem where the new crop provides an acceptable new food source. In the Neotropical Region, sugarcane is grown as an exotic crop, but its principal pests in Guyana and Trinidad (Trinidad and Tobago) were all indigenous, including the sugarcane froghopper (*Aeneolamia varia* (F.); Hemiptera: Cercopidae), the sugarcane stem borers (*Diatraea* spp.; Lepidoptera: Crambidae) and the larger stem borer (*Telchin licus* (Hübner); Lepidoptera: Castniidae).

The search for natural enemies of these pests included searches for the pests in their natural habitats, where it was anticipated there would be effective natural enemies that could be "forced" onto their hosts in the sugarcane agro-ecosystem, by laboratory rearing using sugarcane and mass releases.

No significant populations of sugarcane froghopper could be located in natural habitats, so it is still not known whether there might be effective natural control agents in one or more natural habitats. *Telchin licus* did not become a significant pest of sugarcane until the beginning of the twentieth century, two centuries after the crop was introduced to the region, probably indicating that it took time to adapt to this new food resource. Surveys showed that normally it is associated with a variety of thick-stemmed monocots, including bananas (*Musa* spp.) and *Heliconia* spp. (Musaceae), *Costus* spp. and *Renealmia bracteosa* (Zingiberaceae) and *Ischnosiphon arouma* (Marantaceae). A parasitic tachinid fly, *Palpozenillia palpalis* (Aldrich), was found to attack *T. licus* in *Heliconia* spp. in north-west Guyana, but a rearing technique was not developed and so releases were inadequate to establish this parasitoid in sugarcane fields.

In the case of *Diatraea* spp., however, there was more success. In the 1930s, entomologist J.G. Myers found populations of *Diatraea* infesting the floating grasses along the edge of the Amazon near Santarem, and these were attacked by another tachinid fly, *Metagonistylum minense* Townsend. Overcoming significant logistic difficulties, Myers brought the "Amazon fly" to Guyana, cultured and released it, leading to effective biological control in Guyana of *Diatraea saccharalis* (F.), the main stem borer of sugarcane at that time.

A priori, one might expect that sugarcane pests and potentially effective natural enemies would originate from a thick-stemmed grass in a natural habitat, but that this habitat would be floating grasses is unexpected. That pests would switch from other monocot families as in the case of *T. licus* is less expected. The conclusion that the natural habitat of a pest and its natural enemies is difficult to predict is clear, so in principle all habitats should be preserved in order to preserve genetic resources potentially directly valuable to agriculture.

Prepared by Matthew J.W. Cock

Sources:

Cock, M.J.W. and Bennett, F.D. (2011) John Golding Myers (1897–1942) an extraordinary exploratory entomologist. *CABI Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* 6(8), 18 pp.

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Case study 30. Corridors for migratory pollinators

For over a decade, biologists have been concerned about apparent declines in pollinators (vertebrates and invertebrates) and the concomitant declines in seed production of flowering plants. This concern over plant–pollinator interactions has contributed to a paradigm shift from protecting individual species to protecting interspecific relationships and landscape-level ecological processes. While an awareness of these relationships and processes is not new to conservation biology, the recent attention given to these topics is. Pollinators that migrate between regions, including several hummingbirds, butterflies and the giant honeybees of South-east Asia pose some unique problems such as the need for provisioning of food sources along the migration route.

Conservation corridors typically conjure up images of continuous linear habitats or greenways that provide for the movements of large predators and other wide-ranging species. In contrast, migratory corridors for winged pollinators might be more aptly described as a mosaic of stepping stones within a larger matrix, with each stone a stopover that migrants use for “refuelling” while following a migratory route that takes advantage of a sequence of plants coming into bloom along the way.

This sequence of flowering plants provides migrants with sugars, lipids and amino acids to fuel their long-distance flights. In seeking out this nectar, pollinators incidentally transfer pollen from one plant to another. By doing so, they facilitate reproduction, genetic mixing and seed set for their floral hosts. When land conversion and fragmentation, toxins, or climatic change weaken one link along the way, the entire chain may be broken. Since the energetic needs of some migratory pollinators are highest when they are migrating, any shortage of fuel en route can have devastating consequences.

It is clear that the anthropogenic stresses faced by migratory pollinators during their annual migrations are substantial and increasing. These migrants are particularly vulnerable during long migrations across arid lands, especially when their stopover sites are affected by land-use changes. In arid and dry subtropical landscapes, farmlands found between protected areas can serve either as oasis-like stopovers for these migrants or as barren, chemical-ridden sites that further stress pollinators during the most energy-intensive phase of their annual cycle.

While migratory pollinators ensure landscape-level linkages among many different plant populations, many non-migratory pollinators visit these same flowers and secondarily benefit from genetic mixing stimulated by the migrants.

The best way to ensure adequate connectivity in regional reserve networks is to better manage intervening private lands in a manner consistent with the needs of migratory wildlife. However, in their current state, many private lands are the weak links in the migratory chain. Restoring the ecological connectivity of these lands will require stronger stewardship collaborations among public agencies and private landowners.

Prepared by Suresh K. Raina

Sources:

Arizona-Sonora Desert Museum (2011) Migratory Pollinators Program. www.desertmuseum.org/pollination/introduction.php (last accessed 9 March 2011)

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Case study 31. Forest habitat conservation in Africa using stingless bees

Honeybees coexist in forest and other ecosystems with many competitors, among them the highly social stingless bees of the genera *Melipona* and *Trigona* (Apidae: Meliponini). Stingless bees originated in Africa and have spread to all tropical and subtropical parts of the world. About 500 species of stingless bees exist worldwide, and they are the only highly social bees besides the honeybees (*Apis*; Apidae: Apinae). These stingless bees are among the principal pollinators of forestry, agricultural, and horticultural plant species, ensuring their survival and contributing to food security for innumerable rural households. Currently in Africa, keeping stingless bees (meliponiculture) is practised on a small to medium scale only in Kenya, Tanzania, Uganda and Angola. Like honeybees, the stingless bees usually live in permanent colonies that consist of the queen, which lays the eggs, drones, and thousands of workers, and they are found in many forms of nests but are commonly located in tree cavities. A few species build underground nests and some build exposed nests surrounded by hard brittle layers hanging over tree branches. These bees show strong hygienic behaviour and remove dead brood to avoid the spread of disease in the colony. Stingless bees use a wide range of materials including resin, sand particles and their excrement in building their nests, which are waterproof and highly resistant to predators. In the nest, stingless bees use propolis (a resinous mixture collected from tree buds, sap flows or other botanical sources, mixed with the bees' wax, which may have antimicrobial properties) to mummify intruders.

Reporting on a project on commercial insects and forest conservation in Kenya, Raina *et al.* (2009) found several species of stingless bees in the Kakamega forests of western Kenya, including *Hypotrigona* and *Meliponula* species (Apidae: Meliponini). These stingless bees depend on tree cavities for nesting and, with deforestation, many nests are being destroyed. Traditionally, the honey is mostly obtained by harvesting from feral colonies, an activity which destroys the colonies. With the project intervention, colonies are being domesticated in hives and farmers trained in colony division. To date, 200 stingless bee hives have been colonized and the population of stingless bees has increased in the forest. The study indicated there was an increase in the number of colonies in the forest, which is beneficial to the rejuvenation of the forest tree species and pollination of certain food crops. Farmers have realized that stingless bees are important for pollination in addition to honey production. The number of colonies domesticated is increasing as the farmers practise colony division.

Prepared by Suresh K. Raina

Sources:

Raina, S.K., Kioko, E.N., Gordon, I. and Nyandiga, C. (compilers) (2009) *Improving Forest Conservation and Community Livelihoods through Income Generation from Commercial Insects in Three Kenyan Forests. icipe* Science Press, Nairobi, Kenya, 87 pp.

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