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The implications of climate change for positive contributions of invertebrates to world agriculture

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Abstract

Terrestrial invertebrate species play a dominant role in the trophic dynamics of agricultural ecosystems. Subtle changes in the composition of communities and species interactions at different trophic levels, and role of ecosystem engineers can dramatically modify the effects of invertebrates on plant productivity in agricultural systems. The effect of climate change on relevant invertebrates in agricultural systems, and their potential to adapt or move is discussed. All terrestrial systems (including forestry and pasture) are considered, although the main focus is on crop production systems. Our treatise centres on whole organisms (as opposed to genetic information from invertebrates) that play key roles in agricultural systems. We start with an overview of current thinking on how climate change may affect invertebrates. Then, recognizing the great invertebrate biodiversity associated with agro-ecosystems, the review focuses on three key groups – soil invertebrates, biological control agents and pollinators. A variety of research gaps became apparent during the course of our review. Specific conclusions regarding the impact of climate change on particular elements of invertebrate genetic resources in agriculture are not possible yet. Existing evidence suggests that three general assumptions can be made. First, it is probable that climate change will disrupt to varying degrees the role and use of invertebrates in agriculture, especially sustainable agriculture, even though the precise nature of the disruptions is not yet known. Second, 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. Third, 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.

Keywords: Ecology, Interactions, Soil, Biological control, Pollinators, Arthropoda, Insecta, Annelida, Nematoda, Pests, Crops, Plant health

Introduction

Invertebrate species are an essential component in agricultural systems (see review by Cock *et al.* [1] and sources therein), as they have a major influence on plant health and productivity and therefore play a key role in food security. The vast majority of invertebrate species in agro-ecosystems belong to the phyla Arthropoda (especially the class Insecta) above ground, and Annelida and Nematoda below ground [2]. From an ecological perspective, these animals play important roles in food webs as primary consumers (herbivores); higher-order consumers (predators, parasitoids and 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). The different roles that invertebrate species play in an agricultural ecosystem are responsible for a complex web of direct and indirect interactions. For instance, soil invertebrates include the functional group of ecosystem engineers [3] that are powerful drivers of soil physical functions (water dynamics, aeration and protection from erosion hazards) owing to changes in soil structure. They play an important role in carbon cycling, as they control the carbon sequestration process and influence greenhouse gas emissions. The production of biogenic structures by this group can make carbon inaccessible within aggregates for some time and so slow down the use of carbon by soil organisms.

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, past experience in pest management from regions closer to the equator may provide guidance.

Land-use changes, whether as responses to climate change or socio-economic factors, are expected to have a greater effect on the occurrence of invertebrate pests than 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, pest species, and changes in vegetation cover can modify the climate via alterations in the surface reflectivity (albedo) and the roughness of the land [4]. 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. [5–9]). This is not to deny that some effects 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' [10].

Potential of invertebrates in agriculture to adapt to and mitigate the effect of climate change

Biotic responses to climate change include adaptation *in situ*, range shifts to more tolerable climes or, failing these, extinction [11], and as suggested by these authors, organisms will have to 'adapt, move or die'.

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 [12]. Observational data over the last 50 years have shown that adaptation to climate change is species-dependent [13]. The lack of studies makes it risky/inappropriate to generalize on the possible adaptation of invertebrates to the challenges identified. Nevertheless, when expansion of species range takes place, selection will tend to favour individuals with higher propensity for dispersal [14], and dispersal ability determines the potential to escape adverse direct and indirect consequences of temperature changes [15] by colonizing new habitats as they become available.

As we shall discuss, most invertebrates are expected to change their geographical distribution in response to climate change so as to remain in habitats to which they are well adapted. 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* ([16]; Case study 2) and there is evidence that this may be accompanied by genetic increases in dispersal capacity at range boundaries [17]. 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. 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.

Some *in situ* adaptation is expected, especially where movement is not an option (e.g. low, isolated islands) and species have a short generation time and a high rate of reproduction. The ability of a species to adapt rapidly to environmental changes is termed phenotypic plasticity. If, however, conditions exceed the plastic limits of a species, evolutionary change may be necessary in order to prevent extinction. The concept of evolutionary rescue to arrest population decline and allow population recovery before extinction ensues [18] may be particularly relevant to populations, especially island populations, challenged by climate change. In their review, Donnelly *et al.* [19] found many reports of direct observations of phenotypic plasticity in species but less conclusive evidence of genetic adaptation.

The variability in predictions can be explained by ecological and evolutionary processes that significantly alter the ranges of species. Range movement of species is not exclusively determined by evolutionary responses, based primarily on existing genetic diversity within species. Phenotypic plasticity constitutes a critical survival mechanism for adaptation [20], given that genetic variation already exists within species. Moreover, evolutionary and plastic responses to climate change are not mutually exclusive.

Where self-organization and mutualism predominate, 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 microbiota for their digestion, and as the short generation time of microbiota is likely to enable them to adapt relatively rapidly to new conditions associated with climate change, the invertebrates may profit. Thus, the ability to predict adaptation of organisms to climate change is hampered as many studies focused on individual species overlooking the fact that species interact with other species, and are part of complex interaction networks [21, 22]. As Berg *et al.* [23] stated, to study species persistence under global climate change, it is critical to consider the ecology and evolution of multispecies interactions.

Scope and structure of review

The scope of this review is restricted to terrestrial agriculture, and excludes marine and aquatic production systems. Although many invertebrates are important food items in their own right, and several sectors (e.g. honey and silk) rely on products produced by invertebrates, we will not consider these aspects in our review. 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 including weed biological control, biological control agents (BCAs) play a role in the protection of stored crops, but the latter role is not treated as a separate topic. The review focuses on whole organisms (as opposed to genes or other genetic information from vertebrates), which play key roles in agricultural systems. First, we provide an overview of current thinking on how climate change may affect invertebrates. Then, recognizing the great invertebrate biodiversity associated with agro-ecosystems, the review focuses on three key groups – soil invertebrates, BCAs and pollinators. Between them, these three groups cover the most important ecosystem services that invertebrates provide to agriculture [1], and hence they may be used, manipulated or moved to benefit agriculture. A variety of research gaps became apparent during the course of our review, and these are highlighted in the final section.

Effects of Climate Change on Invertebrates Relevant to Agriculture

In this section, we review the potential direct and indirect effects of climate on invertebrates relevant to food and agriculture.

Climate change predictions

In 2007, the IPCC completed the Fourth Assessment Report of current scientific understanding of climate change [24], which included scenarios projecting future climatic changes and their probable effects on natural and managed systems, the vulnerability of these systems and their capacity to adapt [25].

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 A1FI).
- 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 and intense tropical cyclones).

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, so-called, ‘no-analogue’ communities [26], although such climate reconfigurations may well have occurred in past glaciation cycles.

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 effects of climate change on agriculture (and the IPCC assessment of probability of occurrence) include:

- Increased crop and pasture yields in colder environments and decreased yields in warmer and seasonally dry environments (99%).
- Increased insect outbreaks (99%).
- Reduction in yields in warmer regions due to heat stress (>90%).
- Increased heavy precipitation events, causing damage to crops, soil erosion and difficulty in land cultivation (>90%).
- Increased area affected by drought, leading to land degradation, lower yields/crop damage and failure, and more livestock deaths (>66%).
- Storm intensity increased, leading to damaged crops and uprooting of trees (>66%).
- Increased incidence of extreme high seas, causing salinization of irrigation water and freshwater systems (>66%).

Agriculture has historically shown high levels of adaptability to climate variations, and trade has the capacity to reduce regional and global effects. 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.* [27] include:

- altering timing, location, variety or species of crop planted to match prevailing conditions and markets in a better manner;
- 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.

Effect of climate change on invertebrates

Even in simplified agricultural ecosystems, the sheer number of potential interactions makes predicting the effect of climate change on invertebrates daunting (Figure 1).

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 precipitation. There is a paucity of data on the combined effects of such climate change-related factors ([29]; Case study 1) and more realistic multifactorial experiments are needed to investigate potential non-linear interactions between individual factors [30].

Invertebrates have limited ability to regulate their body temperature and are directly under the control of temperature for development, reproduction and activity. Although some groups such as soil invertebrates [31] and animal ectoparasites [32] 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, although biotic interactions can also potentially influence macro-distribution of species [33]. Within this distribution, climate change will have further indirect effect on invertebrates through its effects on host availability and the other resources plant communities provide [34].

Invertebrates exhibit very wide variations in sensitivity to temperature, depending on their environment, and have therefore developed a range of survival strategies [35]. Berg *et al.* [23] analysed 50 years of published literature and found pronounced and consistent differences between trophic groups. They concluded that changes in species distribution and abundance will be determined more by the impact of temperature on species interactions, than by the thermal tolerance of individual species. Vulnerability to global warming appears to increase with trophic rank: herbivores respond more strongly to temperature than plants, and warming leads to a disproportionate loss of top predators [36–38]. Species at the higher trophic level (parasitoids and predators) depend on the capacity of the lower trophic levels to adapt to changes [39]. In other words, climate change effects may be amplified by trophic responses transmitted through natural enemies [40] or competitors [41]. 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 [42].

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 – in

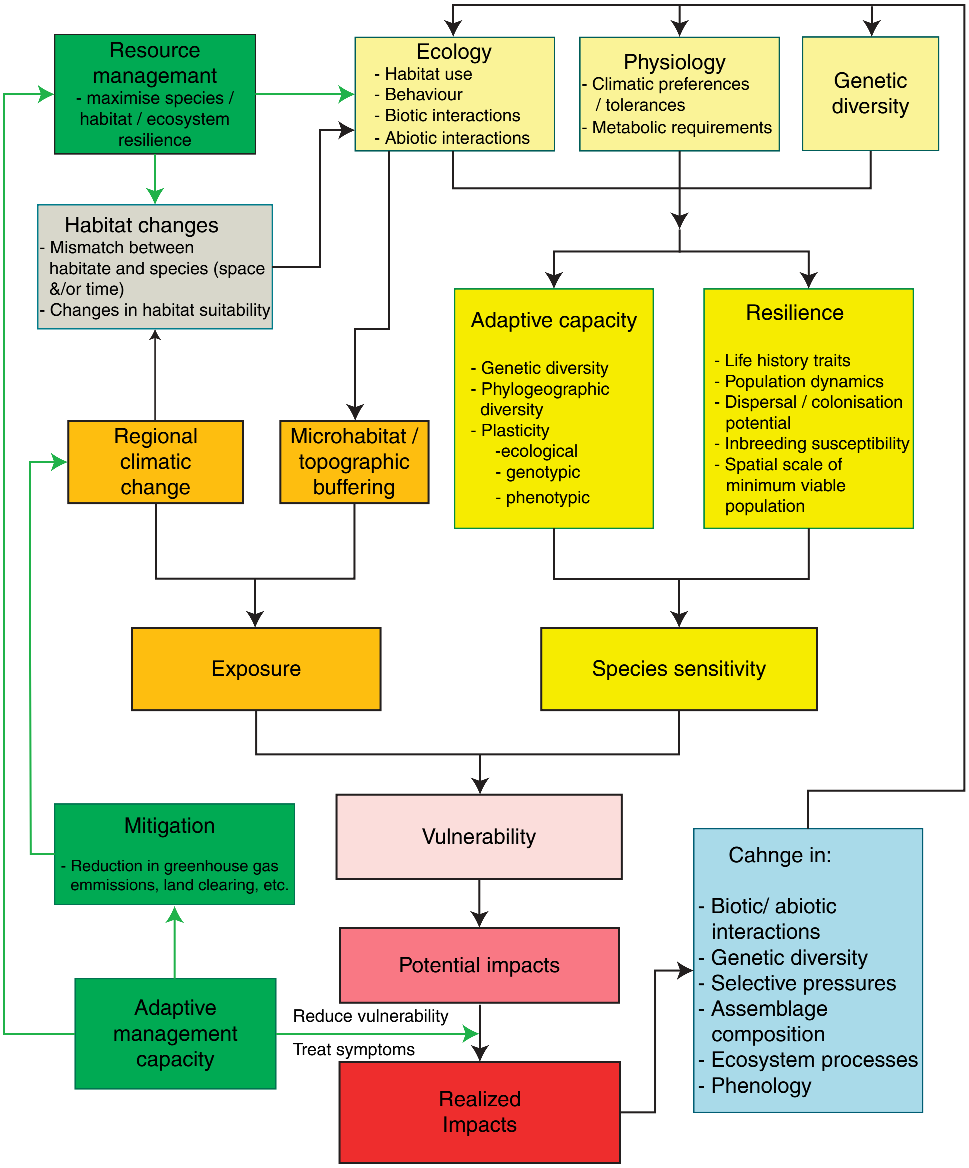


Figure 1. A general framework showing factors influencing the vulnerability of species to climate change. Much more detail could be added for most boxes, for example under 'Ecology', food web interactions and more than 80 types of indirect effects could be mentioned. Source Williams *et al*. [28].

other words, adapting agriculture to the climates of the future [43].

Recent research suggests that there have been very abrupt changes of climate in our planet's recent glacial history [44] implying that both the current and projected speed of climate change are not without precedent [45]. 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* ([16]; Case study 2) and there is evidence that this may be accompanied by evolutionary increases in dispersal capacity [17].

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 0.75°C in the twentieth century [46] and there is compelling evidence for a general poleward shift in the breeding distributions of a large number of invertebrates (e.g. [47–49]). Range boundaries are shifting latitudinally (i.e. towards the poles) at an average rate of about 6 km per decade [50], and altitudinally – assuming a lapse rate of 6.5°C per 1000 m and 3.5°C rise for the next century – at a rate of at least 50 m per decade [51–53]; rates that most mobile pest and pollinator species are capable of tracking providing there are no major ecological or physical barriers (Case study 3). 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 [54].

The extent to which invertebrates will be able to track climate change will probably vary enormously, depending on their dispersal abilities and the existence of green bridges [55] as well as the responses of their host plants [56]. Some species will be tied to specific latitudes because of direct or indirect photoperiod requirements [57]. Just as Coope [16] 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* [11]. 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 [55]. Many soil invertebrates have low dispersal rates, and the time taken for beneficial species to shift to new areas will also be influenced by the availability of supplementary resources (e.g. nectar and pollen, and winter or summer diapause sites). Also, for some species, infrequent extreme weather events may be more important in determining distributions and species persistence than long-term gradual changes in climate [58]. The evidence from the geological past also suggests that species are unlikely to respond as intact communities [59–61]. Therefore current communities, especially those specialist invertebrate assemblages associated with exotic crop species, are unlikely to remain intact under climate change and there could be some positive (absence of pest) or negative (absence of beneficial invertebrates) effects on yield as well as possible destabilization of agro-ecosystems.

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 [62] or buffered by conservation [63] and ecological engineering [64] practices. How a landscape is managed over time will affect the composition, abundance and status of the invertebrate species present. For example, butterfly species diversity decreased during the rapid industrialization of Europe, at the end of the nineteenth century, and when intensive large-scale farming developed from the middle of the twentieth century (e.g. [65]). The grain industry in Australia has also seen major shifts in the status and abundance of different invertebrate pests, over a 30-year period (from early 1980s to 2006–2007), as a consequence of several drivers, including climate change and intensified farming [66]. Similarly, long-term studies in western Poland, have documented a progressive increase in the abundance of heat-loving (thermophilic) insects, typically associated with grasslands, probably linked to both climate change (especially droughts) and an increasing proportion of cereals in crop rotations [67]. It is sometimes difficult to separate out the effects of changes in land use from changes in climate, as they are often linked. Responses to climate 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 [68]. Groffman and Jones [69] concluded that there have been too few ecosystem-scale experiments on the role of invertebrates; more experiments are needed which reflect the complexities of real agro-ecosystems [70].

Increased risk of outbreaks

Increases in the frequency of extreme weather events (such as droughts, heat waves, unseasonal cold and frosts, floods and storms) are probable under most climate change scenarios. Such extreme weather events are followed frequently by pest population explosions. These may be indirectly mediated by factors such as improved food quality and quantity owing to seasonal rainfall ([71]; Case study 4) and physical damage such as gaps left when trees are blown down [72]. The effects may also be mediated through impact on natural enemies [73]. Sequential extremes (e.g. prolonged drought followed by intense precipitation) can decouple long-evolved relationships between species that are essential for controlling pests [7]. Holt and Colvin [74] highlighted the importance of predation in the prevention of outbreaks of the grasshopper *Oedaleus senegalensis* in the Sahel, an arid zone of Africa and that the risk of outbreaks is highest when this natural regulatory mechanism breaks down with increased frequency and severity of drought. BCAs that rely on their hosts remaining alive throughout their development are particularly vulnerable.

Although much of the evidence associating insect outbreaks and drought is circumstantial or simply correlative – consisting largely of observations that outbreaks of insects such as bark beetles and leaf feeders are typically preceded by unusually warm, dry weather – there is a consistent, positive correlation between insect outbreaks and dry, nutrient-poor sites [75]. The impact of drought on pests is also likely to be mediated via natural enemies. In New Zealand pastures, grass grub *Costelytra zealandica* (White) (Coleoptera: Scarabaeidae) outbreaks often occur 2–4 years after severe summer droughts because of the suppression of protozoal and bacterial pathogens in the soil [76]. Droughts may induce outbreaks of pests such as spider mites, by reducing the efficacy of natural enemies [77], in part because of the effects of extreme leaf temperatures on the performance of predatory mites [78]. Some parasitic wasps may be eliminated altogether, as a result of drought-induced elimination of the nectar plants they depend upon. Equally, if droughts reduce pests to a very low level, then associated specialized BCAs will in turn be reduced, due to host rarity, resulting in a pest outbreak until the population of BCAs recovers.

Temperature extremes can also affect the maintenance of diversity (both species and genetic) of the invertebrate bacterial endosymbiont community. These endosymbionts mediate many processes, for example, defence against parasitoids and pathogens, tolerance of heat and cold stress, host range and production of essential amino acids [79–81].

Exposure to temperature extremes induces lethal and sublethal damage in parasitoids, which generally decreases their longevity, fecundity and mobility, along with decreased host-location ability [42, 82]. In addition, extreme temperatures increase the efficacy of the host's immune system in resisting and killing parasitoids [42], with multiple observations that high temperatures can enhance the survival of parasitized hosts [83].

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 [84, 85]. *Wolbachia* species are present in mature eggs, but not mature sperm; so only infected females pass the infection on to their offspring. *Wolbachia* maximize their spread by significantly altering the reproductive capabilities of its hosts, with four different phenotypes: feminization (infected males develop female characteristics), parthenogenesis (infected females develop embryos without fertilization by males), male killing (eliminates infected males to the advantage of surviving infected female siblings) and sperm–egg incompatibility (or cytoplasmic incompatibility, the inability of *Wolbachia*-infected males to successfully reproduce with uninfected females or females infected with another *Wolbachia* strain). These insect–endosymbiont associations may be impaired, or even eliminated, by exposure to high temperatures [83, 86–88]. 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 [89].

New pest and plant species

The intensification of weather systems, and/or absence of frosts in geographically isolated temperate regions and islands, will increase their vulnerability to colonization via wind dispersal. For instance, New Zealand has been exposed to airborne invertebrates from Australia for millions of years, but most species have not become established ([90]; Case study 5). With increasing temperatures, however, there will be increased use of subtropical plants in production systems and invasive subtropical weed species may probably become more prevalent. These plants may thrive in the absence of their co-evolved herbivores. Some alien weeds, originally introduced for floral displays may, however, be of benefit to native pollinators. It is inevitable therefore, that establishment events will increase in frequency, because climate change has the potential to affect the introduction, spread and establishment of invasive alien species ([91]; Case study 6). Without specific natural enemies, some of these species will become pests and may be more responsive to eCO_2 than native species [92], with implications for control measures.

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 [93], and there is already overwhelming evidence of this for some herbivores and their host plants (e.g. [13]).

Species with long life cycles, especially if controlled by photoperiod, may show little change, whereas species characterized by high growth potential, multivoltinism (Case study 7) 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 [94]. 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. [95]). 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 [96]. 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 [97]. Similarly, increased summer temperatures can favour increased parasitoid and predator activities [98]. In contrast, 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 [99]. 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 [34, 100, 101].

Elevated CO_2 can change the abundance and species composition of soil organisms [102]. Yeates *et al.* [103] 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, whereas the bacteria-feeding *Rhabditis* spp. showed a marked decrease. Loranger *et al.* [104] found that collembolan abundance decreased greatly under eCO_2 and O_3 (another greenhouse gas) 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 associated with 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) [105].

Not all soil fauna will respond in the same way [106], 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 [107]. Sohlenius and Boström [108] moved soil cores from cooler to warmer sites in Sweden and found that total nematode populations and the ratio of fungus- 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 2.5°C and drier conditions [109]. Harte *et al.* [110] 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 [111] 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 [112].

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 [113]. 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 [114]. To ensure generalist natural enemies continue to contribute to effective pest management in future agro-ecosystems, increased effort is needed now to better understand their requirements and how to support them, including landscape-level movement, refugia in time and space, alternative food sources and other aspects of conservation biological control.

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 [83].

Atmospheric CO_2 levels could have direct effects on invertebrates, but there are very few examples (Case study 1). 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 [115]. While some pests, such as mosquitoes and some plant pests, use CO_2 directly in host location [116, 117], 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) [117]. *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 [118].

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.* [29] 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 1). 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% 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 [119].

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 [120]. In contrast, both predator and parasitoid increased attack rate against the grain aphid *Sitobion avenae* (Fabricius) in eCO_2 and as a consequence substantially suppressed aphid abundance [121]. 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 [122]. When the generation time ratio (GTR) is low, a predator population can increase rapidly compared with 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.

Phenology and synchrony

Hance *et al.* [42] stated '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 ([123] and references therein). Cues in subtropical and tropical areas may differ: delayed seasonal flowering has been observed in Florida [124]. 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' [125] and even small changes between host and parasitoid may change the efficacy of a BCA system locally (Case study 8). An example of an increasing mismatch is provided by egg hatching of the winter moth (*Operophtera brumata* (Linnaeus); Lepidoptera: Geometridae) compared with bud burst of its oak tree host (*Quercus robur*; Fagaceae) [126]. 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 [127]. The former provides the temperature cues for the moth, the latter for the tree [21]. Conversely, Bean *et al.* [128] showed that a population of a chrysomelid beetle, *Diorhabda carinulata* (Desbrochers) released in USA for biological control of salt cedar (*Tamarix* spp. Tamaricaceae) that was initially not well synchronized with its target hosts following introduction, over about seven years evolved a range of critical day lengths for diapause induction that permits range expansion and better synchrony with *Tamarix* spp. throughout the range. Thus, classical BCAs, even though they are specialized and often obtained from a limited gene pool, may well possess the capacity to adapt to range shifts.

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, beyond which the processes do not occur (Case study 9). 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 impairment is different for two different species of ladybird beetle predators [129].

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 [122].

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 10).

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 a large mismatch, control failure and local extinction are possible.

- 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 once in 20 years [122].
- 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 11).
- 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 [130].

In response to global warming, the seasonal activity of organisms, including invertebrate pests of agriculture, is changing (as discussed above). 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 [131, 132]. Using a mathematical model, Hoover and Newman [133] 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 with current ambient conditions.

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 nutrients available to plant and sap feeders, 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 [134], including weed BCAs. The complexities of the response of the plant are paralleled by the diversity of the responses of insects [135].

Much of the increased plant biomass produced in response to eCO_2 is invested below ground in the root systems [136, 137]. Stiling *et al.* [138] 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 [139].

The effects of eCO_2 on BCAs are also likely to be mediated through flow-on effects of CO_2 on plants [140]. Plants grown under eCO_2 not only exhibit increased growth, but also increased carbon/nitrogen ratios, and hence lower nutritional quality for protein-limited herbivores [141]. 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 [142]. The net result is either reduced fitness (e.g. size, reproduction) or longer development times in pests [143]. 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) [143]. 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. Since 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 [144]. 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 might become more serious pests in the future [40].

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 [145, 146]. The production of these compounds is influenced to a great extent by environment ([146] and references therein), and it is possible that factors associated with climate change will affect quantity and quality of HIPV. Pinto *et al.* [147] 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 ([142] 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 [148] and existing plant-mediated interactions between above- and below-ground herbivores can be changed [149].

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 [75] and there can be flow-on effects to parasitoids [150]. Weed BCAs and parasitoids often depend on volatile organic compounds to locate hosts [151]. 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 ([42] and references therein).

Biogeographical differences – temperate, subtropical and tropical zone vulnerabilities

An increase in the capacity to support increased overall plant diversity is expected in most temperate regions, while a strong decline in most tropical and subtropical regions is projected [152], although this is at variance with predictions in South America based on the Quaternary pollen record [61]. Hence, land managers in temperate regions should have more options in terms of crops and how to manage ecosystem services supporting pollinators and other beneficial invertebrates compared with those in most tropical and subtropical regions. However, just as temperate regions are most vulnerable to invasion by cosmopolitan weeds [153], so will they be most vulnerable to invasive invertebrates (Case study 3).

Under climate change, the tropical monsoon belt is widening [154]. For example, Australian monsoon rainforests have expanded within the savannah matrix [155]. However, not all species will alter their distribution. Coffee (*Coffea arabica* and *Coffea canephora*, Rubiaceae) is a tropical crop predicted to be severely affected by climate change. It is not expected that it can be moved latitudinally because both species are highly susceptible to changes in photoperiod, while rising temperatures are increasing the number of generations of coffee berry borer beetle, *Hypothenemus hampei* (Ferrari), the principal pest [156].

Tropical plant–herbivore interactions are considered to be more susceptible to the perturbations of climate change than those in temperate zones. This has been attributed to tighter ecological and evolutionary linkages in the tropics [157], although a recent analysis suggests that food-webs may be more generalized in the tropics [158]. Tropical plants are better defended and, unlike in temperate forests where most herbivory (about 75%) occurs on mature leaves, in the tropics most is on young leaves (>70%), an ephemeral resource [157].

Soil Invertebrates in the Face of Climate Change

Soil invertebrates are a very important component of agricultural biodiversity [1], and largely determine the structure and the basic functions of natural ecosystems. Key taxonomic groups of soil invertebrates include Nematoda, Oribatida, Collembola, Diptera, Hymenoptera, Isoptera, Myriapoda, Isopoda, Arachnida, Coleoptera, Mollusca and Oligochaeta. They are an integral part of agricultural ecosystems and are relevant actors in maintaining soil health, ecosystem functions and production at the root of the bottom-up processes governing agricultural productivity. The presence of a range of species and organisms capable of supporting critical soil processes and services 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, pest incidence, fertility decline, water scarcity, all affecting crop productivity and yield reductions. The loss of species with unique roles can have drastic ecological effects and lead to 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 and other resources.

Possible adaptation by soil invertebrates to the challenges identified

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 from perturbation quickly, owing to their inherent resilience, although indirect effects – occurring via changes in the productivity and functional composition of aboveground vegetation – would alter associated soil organism dynamics and processes in the longer term, owing to changes in sources of detritus (fragments of organic material) and resources entering the decomposer subsystem [159, 160]. In other words, above- and belowground communities and processes are intrinsically linked [161–163]. Below-ground species are less exposed to the full climate variability than above-ground species, as they experience microclimates that are buffered by the soil environment [93]. Generally, how climate change factors will affect soil invertebrate biotic and abiotic interactions remains a research area to be explored. We need more research to increase our knowledge of the evolutionary responses of soil invertebrates to selection pressures owing to climate change.

Soil microfauna (<0.1 mm) can tolerate drying events through cryptobiosis (reducing metabolism to imperceptible levels) [164]; micro-arthropods show adaptive strategies that enable them to tolerate or avoid desiccation; and larger soil macrofauna (especially soft bodied taxa >2 mm) exhibit effective strategies to conserve moisture under dry conditions [165]. Although eCO_2, one of the climate change factors, 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 [112].

In the case of soil beneficial invertebrates such as earthworms, their maintenance in agro-ecosystems under perturbation such as climate change seems to be determined by (i) their motile potential; (ii) their adaptive strategies, which together determine their population growth rate; and (iii) the functionally similar characteristics of the introduced land use with respect to the original ecosystem [166]. 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 [160]. A full understanding of how biotic and abiotic factors determine soil invertebrate distribution across different spatial and temporal scales is essential [167] 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.

Based on Berg *et al.*'s [23] review of dispersal of trophic-based functional groups for above- and below-ground organisms, dispersal and thermal sensitivity of key life-history traits are two important factors enabling species to adapt to climate change in order to obtain a better understanding of the impacts of global warming on species dispersal. Building on this review, H. Eijsacker (personal communication) argues that soil invertebrates react at 1% of the speed of plant communities, so they will not be able to keep up with changes in response to shifting climate gradients.

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.* [168] 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 might 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 [169]. However, the temperature changes required to cause significant shifts in major groups of decomposer biota are 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, whereas 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/year [170], but this is specific to ecological category, with anecic (surface-feeding) earthworms having more rapid dispersal rates than endogeic (soil dwelling) 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 [171] 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 [172]. 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. Evans *et al.* [173] provided evidence that ants and termites play an important role as soil engineers by increasing crop productivity in drier conditions. 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 with areas where this species was present [174].

Potential of soil invertebrates 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 [162], and hence how soil ecosystems will respond, potentially mitigating the effects of climate change. 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 1). However, it is known that earthworms have the potential to mitigate climate change in a number of ways. For example, Johnson *et al.* [175] found that earthworms reduced the negative 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* (Linnaeus)). A similar mitigating effect was found by Blouin *et al.* [176], 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 12). 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), although the actual mechanisms are not totally clear; in other words, they have the potential to reduce the loss of biomass (=yield) under these climate change factors (Case study 13).

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 [112].

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 owing to the enormous quantities of soil egested as casts. These have been estimated to be as high as 8.6 tonnes of carbon/ha/year in a tropical grassland [177]. This carbon pool represents 30% 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).

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 [178] and generalist predators [179]. Epigeic and anecic earthworms – and some microarthropods – 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 [180]. Complex and non-linear responses are expected in the interactions between soil invertebrates, plants and ecological processes. Different groups of soil fauna (e.g. isopods, mites, collembolans, centipedes, snails, slugs, etc.) obtain carbon directly from plants' roots [181] as well as from leaf litter. This might help maintain the community food web, as increased plant biomass production should 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 owing to global warming are expected to result in larger net soil CO_2 emission and less carbon storage in the soil [182, 183]. 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 by activating soil micro-organisms? In a more recent study, Fontaine *et al.* [184] 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 [184].

Although some progress has been made in understanding interactions of below-ground processes with climate change, challenges remain [185]; 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 [186]. Global climate change may affect soil carbon stocks indirectly through habitat change and hence via changes in the activity of soil invertebrates [187]. 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 [188]. 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.

Moreover, in response to climate change-related factors, soil invertebrate assemblages may change and hence soil processes will also change. Soil invertebrate communities and decomposition rates are responsive to warming [189]. Changes in vegetation distribution driven by climate change and related factors will presumably influence soil invertebrate distribution [190]. 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 [168]. How the vertical distribution of soil invertebrate assemblages will change and how they might affect soil biogeochemistry remains to be seen [191]. Although still little understood, responses of soil fauna are likely to differ between ecosystems. Swift *et al.* [192] 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 14). 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 1 year to levels typical of those in native forest soils [193]. Conversely, the macroaggregate 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 [194]. 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. Moreover, some species have a very narrow distribution, with a high degree of endemism, and in the case of those organisms with mutualistic relationships such as earthworms and termites this could prevent their successful introduction. A new focus would be needed by having quite similar species that perform the function for which they are sought. This approach is not in regular practice yet, and no guidelines for management are available, so using this approach as a response to climate change is not yet possible.

We are not aware that soil invertebrates are being deliberately moved between countries at present, nor should they be. Given the risks of introducing species that become invasive (e.g. lumbricid worms accidentally introduced to forests in USA), and the many possible contaminants, an appropriate risk-assessment protocol would need to be developed. 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. Until we understand soil ecology much better than we do today, such introductions should be avoided.

Knowledge gaps restricting our ability to assess soil invertebrate responses to climate change

Studies have shown that some agricultural practices, such as annual crops, adversely affect survival of soil invertebrates [195–197]. 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. Important European initiatives are underway in countries including France, The Netherlands and UK for a range of soil organisms. 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.

Our ability to assess the response of soil invertebrates to climate change is restricted as few studies have examined the combined effects of changes in climate-change-related drivers in the context of soil function and soil invertebrate biodiversity. Multifactorial experiments have been started, but more are needed to investigate the combined effects of warming, eCO_2 and changes in precipitation, on soil (agro-)ecosystems. Johnson *et al.* [175] 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 13). Further studies are anticipated.

One limitation is that our 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 [171]. 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 [198].

Taxonomy and identification of soil invertebrates

Paradoxically, there is a conspicuous lack of interest from the scientific community in below-ground diversity, compared with more charismatic organisms, and we know very little about its taxonomy, systematics and biogeography [171, 199]. Only a few studies have reported global patterns in soil biodiversity distribution at different spatial and temporal scales [160, 198]. 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 [199], for a review and [171]).

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 [200] and Collembola [201]. 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. Broad surveys of soil communities covering several taxonomic groups at the same time are being carried out. Subsequently, it is expected that in the years to come an unknown number of new species will be named, and after that more time will be needed to describe their function in soils and how they will respond to climate-change-related factors. Unless inventories of soil organisms (their functions and interactions) can be developed, many changes anticipated under climate change cannot be detected at this level, only where ecosystem services are disrupted, which may be due to changes in soil invertebrate activities.

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 [202], earthworms [203] and ants [204]. The reduced species richness at higher 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 with lowland areas [171].

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 2150 m in the French Alps [205]. In the mountains of Sarawak, Malaysia, Diptera richness reached a peak between 1300 and 1700 m; and beetles between 500 and 1200 m [202]. In tropical areas, however, a different pattern has been observed: for example, earthworm species richness increased from sea level up to 1000 m in Puerto Rico [206]. 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, USA) 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.

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 probable 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 [162, 163].

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.

Invertebrate BCAs in the Face of Climate Change

Biological control is the use of natural enemies to regulate pest populations. Natural enemies of pests are BCAs and provide an ecosystem service [207, 208]. Natural biological control encompasses both implicit reliance on this ecosystem service, and manipulation of the service through conservation biological control methods. Integrated pest management (IPM) is ‘a strategy of pest containment which seeks to maximize 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 [209]). Thus, biological control, particularly natural biological control, underlies all IPM programmes.

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. 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 [210] estimates that classical biological control is applied on 350 million ha 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. The purpose is to induce sufficient mortality in the target pest population 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 [210] estimates that augmentative BCAs are applied on 16 million ha annually.

Since 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, usually within the framework of *International Standards for Phytosanitary Measures No. 3. Guidelines for the Export, Shipment, Import and Release of* BCAs *and Other Beneficial Organisms* (ISPM3) [211].

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 [1].

Geographical range shifts

The evidence from glaciation history indicates that there is a limit to the ability of species to adapt based on existing genetic diversity, after which BCAs must move. Amongst invertebrates, this has been most clearly demonstrated for insect detritivores and predators ([16], Case study 2). 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, owing 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 many natural enemies have great dispersive powers. For example, a 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 [212]. Within 3 years, this very small insect dispersed over 200 000 km^2 in southwestern Nigeria, occupying between

70 and 98% of all fields [213]. Similarly, Assefa *et al.* [214] 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/year. There are many other examples for natural enemies that can fly, but little information for flightless species of natural enemies, which have usually been spread by human intervention. For example, when the flightless encyrtid parasitoid, *Neodusmetia sangwani* (Subba Rao), was introduced into Texas for the control of Rhodesgrass mealybug, *Antonina graminis* (Maskell), once local releases showed that it was an effective BCA, it was redistributed by dropping parasitized mealybugs on grass stems from an aircraft [215].

Dispersal of both pests and natural enemies is a mixture of local movement and unusual long-distance (saltatory) movements, some of which will be inadvertently or deliberately assisted by human activities. It is therefore probably that if pests move polewards at the rates predicted under climate warming scenarios, most natural enemies that can fly will have little difficulty tracking their hosts/prey, but flightless species may well lag behind. 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, particularly oceanic islands.

Evolutionary adaptation

The rates of evolutionary change in populations under climate change, including BCAs, will depend on levels of heritable variation, genetic interactions among traits and population processes [216]. Populations of many natural BCA species contain much heritable variation in traits that affect responses to climate, and other abiotic and biotic factors. Where adaptation has been looked for, usually it has been found (e.g. [217–219]), although as yet there is a shortage of studies that assess local adaptation to climate change factors. Many species predate the Quaternary, and many of the remainder evolved during this period, and so have already survived repeated global warming and cooling during the Quaternary. Hence, the indications are that adaptation to climate change will be based on existing genetic diversity, some of which may be released by epigenetic mechanisms [220], rather than new mutations.

Ability of BCAs to respond to elements of climate change

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. As yet, we know relatively little about how BCAs can adapt or be assisted to overcome these challenges, although this is an area of active research [221].

Average temperature and seasonality

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. [222]) and by transplanting locally adapted strains that have appropriate responses to seasonal cues [223, 224]. 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.

The effects of scale mean that widespread effective BCAs will have more impact than localized natural enemies. Similarly, introduced classical BCAs that cannot disperse through most of the range of the target will be less effective. Hence, we suggest that BCAs that are important in agricultural systems are usually relatively widespread species, although we are not aware of any analysis to test this. BCAs that are more widespread are likely to be more genetically diverse and more resilient to the effects of climate change. 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 [225, 226], or are governed by phenotypic plasticity resulting from genetic diversity in local populations [227, 228]. 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 can be expected. 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. Conversely, the required genetic variation should exist in natural BCA populations (e.g. [219]; Case study 15).

Atmospheric CO_2

The flow-on effects of eCO_2 on arthropods including BCAs seem to be highly idiosyncratic [140], and we consider that it is not possible to reach any conclusions regarding the adaptation, or assisted adaptation, of BCAs to this aspect of climate change at this time.

Rainfall and drought

The development, mortality and reproduction of both pests and BCAs can be affected by rainfall and drought, and this is likely to affect their abundance both directly and through their interactions. 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 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. It is common practice to spray microbial insecticides at dusk, because these are often sensitive to low humidity. Similar tactics of dusk releases for some augmentative BCAs may be advantageous and need evaluation. The development of augmentative BCAs adapted to hot and dry conditions is an option [229, 230], 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 [231], could be made with or at the same time as irrigation water, or, as above, applied at dusk. Some conservation biological control strategies may enable BCAs to persist where otherwise they would have been largely eliminated; for example, mulching may provide natural enemies with protection against extreme dryness or extreme rainfall.

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

Extreme events

Episodic extreme temperature (heat waves and unseasonal cold) has the potential to disrupt biological control food webs independently of the disruption of cropping systems. Although thermal stress may adversely affect pest population growth in the short term, BCA and pest populations have demonstrated the capacity for rapid adaptation to such stresses [129, 217, 232]. 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 or species that are more tolerant of extremes of temperature, although this would increase the risk that they become established. In simple, augmentative biological control communities, extreme heat stress affects the costs of defence against parasitoids and causes shifts in parasitoid community structure [233, 234]. 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.

BCAs 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.* [207] 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 [235]. In an analysis of 57 farms in Scotland, the application of all pest control products accounted for less than 3% of carbon costs, compared with fertilizer applications which accounted for over 80% of the carbon footprint on the same farms [235]. Thus, the scope for reducing carbon footprints by increasing reliance on BCAs and reducing pesticide applications is very limited. However, the burning of agricultural crop residues is a significant source of greenhouse gases and while more environmentally sustainable practices have been adopted in some regions, the withdrawal of some commonly used pesticides may prolong the widespread use of burning for weed and pest control. In addition, soil and post-harvest fumigants such as sulfuryl fluoride and methyl bromide are potent greenhouse gases. Therefore, there are very good, reasons, including human health and environmental impacts, for reducing reliance on pesticide inputs and increasing reliance on BCAs.

Implications of climate change for future use of BCAs in 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 and 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 may 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 5). 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 [236]. 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 ([237, 238]; Case study 15). If herbivores alter voltinism under climate change (Case study 7), parasitoids or predators will need to evolve or respond by plastic changes to synchronize their development with that of their host [38].

There are only a few evolutionary studies on natural enemies that consider synchronization [239] although there is evidence of genetic variation in generation time in parasitoids [240]. Whether specialist parasitoids, predators and herbivores show much evolutionary potential remains to be seen, but this could be manipulated or artificially enhanced [38]. 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 16). Therefore, access to new genetic diversity or genetic resources may be required 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 have been identified. 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 [237, 241, 242]. 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), especially in regions where wild or early domesticated crop lines still persist. However, these agro-ecosystems are recent in evolutionary terms and, although some species will have evolved to the extent that they no longer occur in natural ecosystems (this is more probably for pathogens (e.g. [243]) than for invertebrates) for most pests and BCAs there should be an original natural ecosystem. This 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 where the pests and their natural enemies came from is unknown, although we may surmise 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. 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 ([244], Case study 17).

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 [245, 246]. Selection of predatory mites used in augmentative biological control for resistance to pesticides was conducted in the 1980s [247], but the selected strains were not used extensively. Considerable genetic diversity is present in BCA populations (e.g. [219]), 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. [217, 222]).

There is scope to use genetic engineering to transform crops to allow them to continue to be grown in areas where climate changes or be grown in new climate zones [248, 249]. This might lead to crops being grown in local climates where BCA communities are unable to regulate pests. 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 [250, 251], refuges such as leaf domatia (tiny chambers produced by plants that house arthropods) [252, 253], and HIPV that help BCAs to locate hosts [146].

Adding these attributes to cropping systems could enhance BCA performance where climate change has otherwise limited their impact on pest populations. This could be done through creation of conservation habitat (adding new plant species), by conventional breeding for desired attributes or by genetic transformations.

BCAs: gaps regarding knowledge, collections and characterization

Huge knowledge gaps exist with respect to the responses of BCAs to climate change, and many of the suggestions above will need research and validation before they can be used.

Predictions of future scenarios cannot ignore the potential of invertebrates to adapt rapidly to changing climate based on existing genetic diversity, although more studies are needed to assess the scope and speed of such potential adaptation. However, 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. [254]). Knowing how these key interactions respond to climate change factors would help enormously in predicting the impact on pest populations. Furthermore, 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.* [254] suggest that, despite the complexity of communities and food webs, it is possible to make such predictions. Along these lines, Vellend [255] 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.

Since many BCAs have wide intraspecific variation in host range and climatic tolerances, 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.

Invertebrate Pollinators in the Face of Climate Change

Species are inseparably interdependent and interact with each other. An abiotic factor, such as climate change, has the potential to put out of phase the biological phenomenon of interdependence of species, with potentially catastrophic effects on species relationships (and food security and natural ecosystems). Phenologies can evolve, but the role of evolution in the response of mutualisms to climate change is poorly understood. Abundant alternative mutualist partners with broad temporal distributions can make a mutualism more robust to climate change, while abundant alternative partners with narrow temporal distributions can make a mutualism less robust. Community composition and the rate of climate change affect the persistence of mutualisms and are mediated by two-species Allee thresholds. Understanding these thresholds will help researchers to identify those mutualisms at highest risk owing to climate change [256].

Pollination services by animals, especially insects, are among the most widespread and important processes that structure ecological communities in both natural and agricultural landscapes [1]. An estimated 78% of the world's flowering plants – including a range of economically important species – depend on insects for pollination [257]. 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 [258]. This service has generally been free and therefore has received little attention in agricultural management (but see [259]). 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, mason 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' – where the decline in pollinators is enough to threaten the human food supply. Concern has been raised over a looming potential pollination crisis as currently, insect pollination is endangered by a number of environmental and anthropogenic factors, and although data on the impacts of climate change on crop pollination are still limited, climate change may be a further threat to pollination services [130, 260].

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, not only 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 of 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 18). 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.

Effects of altitude

As discussed above, the effects of elevation are often used as an alternative for assessing the potential effects of climate change, particularly changes in temperature. Pollinator communities tend to change with increasing elevation (and decreasing temperature). At higher altitudes the average size of pollinators increases [261], but pollinator abundance is lower [262]. In addition, flies tend to become the dominant pollinator group, mainly because other groups are restricted to lower areas [263]. In the Rocky Mountains (USA), flies replace bees as the main pollinators [263], whereas in the Andes of South America, tachinid flies and hummingbirds replace bee flies (Bombyliidae) and bees at higher altitudes [262]. In addition, flower size tends to increase [261]. The lower pollinator abundance results in lower pollinator to flower ratios and lower seed set in plants at higher altitudes [261, 264]. 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. Alternatively, change in pollinator communities might lead to a breakdown of pollination services at higher altitudes. Even though this might be the case for wild plants, there do not seem to be important crops that would suffer from pollination loss.

Selection of climate-adapted managed pollinators

The honeybee is the main managed pollinator around the world. 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 19) and stem-nesting solitary bees, such as *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 [265] and low genetic diversity of North American bumblebee populations [266], which both suggest population declines.

However, it is necessary to be aware of the risks associated with the use of managed organisms in new environments, namely that they may interfere with or be affected by 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* (Fabricius) (Hymenoptera: Apidae), to the managed western honeybee, *Apis mellifera* L., after its introduction to Southeast Asia. Infection of honeybee hives with *Varroa* mites is 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. 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. Similar trends are occurring elsewhere. To minimize these risks, it is extremely important that transport of any managed organisms is based on established risk assessment procedures. The oil palm pollinator weevil (Case study 20) provides one example where the protocols of weed biological control were used effectively to evaluate the risk of damage to plants by the larvae of the weevils, but traditional pollinators would have to be evaluated following a different protocol.

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 and other managed pollinators, hand pollination or a combination of these. 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 and unsuitable climate). These factors are likely to intensify with climate change, and mitigation will need to be integrated into farm 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 18), 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 19) 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 [267].

One can consider several categories of pollinators that are, or might be, moved between countries:

- *Honeybees and bumblebees.* There is likely to be continued and increasing demand for new strains or improved stock in response to climate change, and hence movement of queens, nucleus colonies and colonies between countries. The movement of both groups 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 verification of the absence of several diseases (for details see [268, 269]). As yet, these regulations do not cover bumblebees, environmental risks of introducing pollinators, such as displacement of indigenous pollinators, or risks associated with pollinators other than honeybees.
- *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 [270]. 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.
- *Other domesticated pollinators.* Domestication of wild pollinators is likely to increase the scope for movement of newly domesticated species between countries. Highly specialized pollinators associated with a particular crop are uncommon in agriculture, and the oil palm weevil is the only one that has been deliberately introduced to new continents (Case study 20). However, introduction of specialized pollinators might be needed in some cases. Guidelines and protocols for risk assessment should be developed if the risks associated with such introductions are to be managed. Protocols of weed biological control could be a starting point for the consideration of any future introductions of specialist pollinators.

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.

Gaps in our knowledge on climate change impacts on pollinators

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. In addition, there are many unknowns with regard to the role of wild pollinators in crop pollination. A more specific knowledge gap is how climate change will affect bee pests and diseases.

Discussion

The three key groups of invertebrates have been treated separately in the preceding review and discussion, and there are clearly good reasons for this approach. The soil invertebrate group is taxonomically and functionally diverse. Organisms range from microscopic multicellular animals such as nematodes and rotifers, through to large earthworms and arthropods. The functions of organisms in these communities include development and maintenance of soil structure, decomposition of organic detritus, and population regulation through predation and parasitism. Generally speaking, there is very little intentional management of these organisms, and only very few attempts have been made to manage selected groups, for example earthworms in tropical areas, using in-soil or off-soil techniques [271]. Overall the taxonomic diversity is poorly known, although important efforts are underway to combine morphological and molecular approaches.

Invertebrate biological control organisms are dominated by arthropods, and functionally, the group is relatively uniform. The arthropod predators and parasitoids of arthropod pests of plants, and the arthropod herbivores of weeds regulate populations of pests and weeds, respectively. There is considerable management of biological control organisms, but unmanaged impacts of biological control organisms on pests are nonetheless, of much greater global importance in agriculture.

Invertebrate pollinators are the least diverse of the three groups, both from a taxonomic and functional perspective. This group consists primarily of insects, and almost all share mutualistic and highly co-evolved relationships with flowering plants whereby pollen is transferred from anthers to stigma by the insects in exchange for nectar and pollen rewards from the flower. Although some cropping systems rely heavily on wild pollination, the majority of horticultural crops are pollinated by a single, highly managed species, the honeybee. However, evidence is accumulating that a diverse pollinator community generally provides better, more stable, pollination services than any single species alone.

These differences in taxonomic and functional breadth, and in degree of management in the three groups, create some important considerations for impacts of global climate change on these groups, and for approaches to management of those impacts.

Overall, most of the soil invertebrate communities are highly endemic, with some exceptions such as European earthworms and soil-dwelling beetles. The communities are determined not just by geographic region but also by their interactions with the underlying geomorphic substrate, the overlying plant community, and the prevailing climate (heat, rainfall). Although often well protected from short-term climate change in the soil, most organisms are slow-moving and may be greatly affected by geographic shifts in climate. Owing to their importance in sustainable agriculture production and their potential role in carbon sequestration through production of biogenic structures that retain C and slow down decomposition, some degree of management of these communities will be required in the context of adaptation to climate change in agriculture.

The biological control arthropods tend to be somewhat less restricted in distribution. The important natural enemies of pests and weeds are mostly as widely distributed as the crop system and pests that they attack. Most are highly mobile, and many have been shown to move rapidly with their pest or weed resource. In general, these species will mostly track geographic shifts in climate. The functions of biological control communities is very much dependent on temperature, and prolonged, more frequent and more severe episodes of extreme heat may change the impact of these organisms on their target populations. Again, management of biological control communities may be required in the context of adaptation to climate change, but these requirements are likely to emerge only as climate change progresses, and loss of biological control functions is observed in agricultural crops.

The pollination function in crops relies heavily on honeybees, and this species has been moved around the world. In other words, to a large extent endemism is not a great factor in pollination functions, and strains of honeybees exist that are adapted to specific climate conditions. For honeybee-managed pollination systems, it is probably that only a modest degree of adaptation will be required, such as the importation of new strains and the movement of bee producers to new centres of crop production. A much greater threat exists for agricultural crops that rely on wild pollinators, which may be more widespread than previously thought (see [259]). Although most crops have generalist pollination systems, some may need specialist wild pollinators. Such pollinators may have restricted ranges, which make mismatches as a result of climate change highly likely. In these cases, intervention and management are likely to be required in the context of adaptation to climate change.

Although climate change is a global phenomenon, not all areas of the globe will be affected in the same way or to the same degree. Moreover, agricultural production and the underlying invertebrate biodiversity associated with agriculture are not evenly distributed across the globe. Geographic and social barriers exist that restrict the potential for cropping systems and the underlying invertebrate biodiversity to track geographic shifts in suitable climate. These differences and barriers are likely to affect the three groups of invertebrates in different ways, and this is discussed further below.

Island versus continental perspective

In general, biodiversity is reduced on islands compared with continental equivalents. Moreover, oceanic islands characteristically have a great number of endemic species adapted to local niches. Most crops grown on islands, especially oceanic islands are not indigenous. The reduced diversity of indigenous invertebrates compared with similar continental areas, means there will be relatively few invertebrate species able to spread into crop agroecosystems, i.e. there will be fewer indigenous pests, but correspondingly a shortage of beneficial species to provide the services discussed here and in Cock *et al.* [1]. With the accidental assistance of man, alien phytophagous pests make their way to islands more efficiently that do their natural enemies, or plant pollinators, especially the social species. In the past, soil organisms have been moved rather freely with planting material of indigenous crops and ornamentals, but normally this is now prevented with standard phytosanitary procedures.

As climates and crops change, pests of agricultural crops always move past barriers first and usually without their associated BCAs. Sea barriers will be more effective than most other barriers as constraints to movement of invertebrates including BCAs, 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 changing climate into new geographical areas, even when the landscape is broken up into a mosaic of agricultural and non-agricultural habitats.

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. Where those crops rely on wild pollinators, 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. Some crops may have specific pollinator requirements (cocoa, pawpaw (papaya) and 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). If new crops rely primarily on managed (honeybee) pollinator services, it may be necessary to determine if the honeybee industry on the island is adequate to provide the necessary services. If other exotic bees are to be introduced (e.g., bumblebees) some form of risk assessment should be made for the impacts of these exotics, particularly on the endemic pollinator species.

Tropical versus temperate comparisons

There is a developing country/developed country divide that aligns with tropical/temperate – generally, developing countries have more subsistence farmers, more of the population directly involved in agriculture, less food security, more fragile ecosystems and highly degraded soils, greater dependence on natural biological control, and hence are likely to be severely affected by a reduction in the role of beneficial invertebrate functional groups caused by climate change. Development assistance is needed for research to address the knowledge gaps identified below.

All of the evidence in the fossil record of responses of invertebrates to climate change comes from temperate regions (Case study 2). 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, e.g. along the Amazon equator [61], and assessing whether these contain identifiable insect parts would be a useful starting point.

There are differences between the invertebrate soil fauna and their functioning in tropical and temperate regions, for example, warmer conditions promote greater abundance of decomposer invertebrates [183] and earthworms in tropical areas have a greater role in breaking down recalcitrant components of soil organic matter than do those in cooler climates [272]. However, differences are species-dependent, and our depth of knowledge may make it premature to look for differences that will be important in the face of climate change.

Essentially, tropical production systems are bimodal in their approach to pest management and their use of biological control. On the one hand, subsistence farmers rely heavily on natural and unmanaged biological control. On the other hand, the relatively few, larger-scale production systems in tropical zones often rely heavily on the use of chemical pesticides. With a few exceptions, in neither system have the support and inputs been developed to enable growers to rely on integrated systems that incorporate the deliberate augmentation and management of BCAs that is a feature of many productions systems in temperate agriculture.

It is not particularly likely that the interference of climate change with natural biological control is going to be of primary concern for subsistence farmers. It is much more probably that climate change effects that increase drought, and flooding and interfere directly with food production will be of primary concern. Nonetheless, particularly for the staple crops that are widespread and central to subsistence farming in the tropics (rice, maize, cassava, yams, sweet potato, Andean potato, taro, etc.) some consideration should be given to the effects of changing climate on BCAs. To our knowledge, this need has not been adequately addressed as yet, and development aid-funded research is needed to address this knowledge gap.

In general, the contrasts between tropical and temperate zone pollination have received more attention than is the case for soil and BCA invertebrates. Bawa [273] states that there are four major differences between pollination systems of tropical lowland rainforests and northern temperate zone forests: (1) in aseasonal tropical forests pollination occurs throughout the year, whereas in temperate forests flowering is mostly confined to late spring and summer; (2) flower longevity is much shorter in tropical forests (1–2 days) than in temperate forest (up to seven days, perhaps in response to unpredictable weather conditions unsuitable for pollinators); (3) vertebrates are often important pollinators in tropical forests, but not usually significant in temperate forests (apart from temperate Australia and South Africa); and (4) the proportion of wind-pollinated plants steadily increases as one moves from the equatorial region, reaching 80–100% among trees in some of the northern-most latitudes. Based on these differences we might anticipate that: (a) tropical regions will experience less temporal decoupling of pollination services than temperate regions; (b) 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; and (c) there may be an increase in pollination success of animal-dependent plants in the tropics owing to increased pollinator activity in response to higher temperatures.

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 [274]. It is probably 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 [275].

Potential to manage invertebrates so as to mitigate climate change

For the foreseeable future, there seems to be very little or no practical scope to manage invertebrates in order to mitigate climate change. There may be some modest potential for management of soil invertebrates to contribute to increasing carbon sequestration in soils, but much research and assessment will be needed first. Pollinators and pests can influence vegetation composition; accordingly, integrating knowledge of pollination and pest dynamics (and the role of BCAs) into carbon fixing projects will ensure that plantings used to counteract climate change are sustainable and self-perpetuating, but as yet there is little detailed practical guidance available.

Status of current application of genetic technologies

There are no transgenic BCAs, pollinators or soils invertebrates in use at this time. The genetic diversity found in these populations is largely unexploited in this regard. Deliberate enhancement of BCAs, pollinators or selected soil invertebrates is an option that may be practical in the future as knowledge, capability and experience increase.

In a changed climate, if crops are grown in the new climate zones, the impact of BCAs' performance on some pest populations might be limited. Adding suitable attributes to crops could enhance the performance of BCAs, and so access to crop and related plant genetic resources will be needed. Similarly changes could be considered in relation to the other key groups, such as enhanced nectar composition for pollinators, and root zone changes to prevent or cope with the loss of invertebrates owing to climate change.

Overlaps and interactions between key invertebrate groups

There are significant overlaps and interactions between the three key groups on which this review has focused. Of these, interactions and overlaps between soil invertebrates and BCAs are probably the most important [1]. However, given the complexity of these mechanisms, especially those involving above ground and below ground elements mediated through plants, there is little specific that can be said about the potential effects of climate change on them, although there will undoubtedly be important effects.

Conclusions and Key Gaps

In this review, 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. First, 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. Second, 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. Third, 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.

We have identified the following priority gaps in knowledge that need to be addressed in the context of these conclusions.

Scientific knowledge

- Improvement to knowledge and understanding of (i) soil invertebrates, (ii) natural BCAs, (iii) wild pollinators of major crops, 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, so any changes because of climate change would be difficult to assess.
- 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. 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 and pollination services may be disrupted by climate change-driven losses of key 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 for use in response to changing climate 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. This will add robustness to agricultural systems strengthening their adaptability in response to climate change.
- 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 both for immediate use and in response to 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. ISPM 2 [276] 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, when drafting national strategies (e.g. producing guidelines and procedures), countries need to take into consideration the need for invertebrate genetic resources to sustain agriculture, food production and world food security in the face of climate change.
- 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. This knowledge will help evaluate options for response to changing conditions in the face of climate change.

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.

Tropical versus temperate

- Attention to the question of how species ranges will change in tropical regions in response to climate change, particularly in temperature and rainfall. 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 changes. Will pantropical species expand their distribution?
- 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.

Case Studies

Case study 1. 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 elevated levels of CO_2 (eCO_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 experiment it was observed that mean micro-arthropod abundance was 33% 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 because ofo climate change are expected to occur although more evidence is required.

Prepared by Juan J. Jiménez

Sources:

Briones MJI, Ostle N, McNamara NP, Poskitt J. Functional shifts of grassland soil communities in response to soil warming. Soil Biology and Biochemistry 2009; 41:315–22.

Hansen RA, Williams RS, Degenhardt DC, Lincoln DE. Non-litter effects of elevated CO_2 on forest floor micro-arthropod abundances. Plant and Soil 2001;236:139–44.

Kardol P, Reynolds WN, Norby RJ, ClassenAT. Climate change effects on soil micro-arthropod abundance and community. Applied Soil Ecology 2011;47:37–44.

Klironomos JN, Rillig MC, Allen MF. Below-ground microbial and microfauna response to *Artemisia tridentata* grown under elevated atmospheric CO_2. Functional Ecology 1996;10:527–34.

Schröter D, Brussaard L, De Geyn G, Poveda K, Brown VK, Berg MP, Wardle DA, Moore J, Wall DH. Trophic interactions in a changing world: modeling above- and below ground interactions. Basic and Applied Ecology 2004;5:515–28.

Case study 2. 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 indicating that rainfall was reduced in glacial periods and much of Africa became savannah, 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

Sources:

Colinvaux P. The Pleistocene vector of Neotropical diversity. In: Bermingham E, Dick CW, Moritz C, editors. Tropical Rainforests: Past, Present and Future. University of Chicago Press, Chicago, Illinois; 2005. p. 78–106.

Coope GR. Several million years of stability among insect species because of, or in spite of, Ice Age climatic instability? Philosophical Transactions of the Royal Society B: Biological Sciences 2004;359:209–14.

Kingdom J. Island Africa: the Evolution of Africa's Rare Animals and Plants. Collins, London, UK; 1990. 287 pp.

Case study 3. 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 viridula* (Linnaeus) (Hemiptera: Pentatomidae) is a cosmopolitan, highly polyphagous species, which attacks many important food and fibre crops including rice, soya bean, 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 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 UK – 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. *N. viridula* has symbiotic bacteria in its gut, and climate change can act via these mutualistic organisms – which are eliminated at higher temperatures – to indirectly affect the host population; whether heat stress because of global warming will have such an effect on SGSB in tropical regions remains to be seen. In conclusion, SGSB is an invasive alien species that 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

Sources:

Kiritani K. Impacts of global warming on *Nezara viridula* and its native congeneric species. Journal of Asia-Pacific Entomology 2011; on-line.

Musolin DL, Tougou D, Fujisaki K. Too hot to handle? Phenological and life-history responses to simulated climate change of the southern green stink bug *Nezara viridula* (Heteroptera: Pentatomidae). Global Change Biology 2010;16:73–8.

Salisbury A, Barclay MVL, Reid S, Halstead A. The current status of the southern green shield bug, *Nezara viridula* (Hemiptera; Pentatomidae), an introduced pest species recently established in south-east England. British Journal of Entomology and Natural History 2009;22: 189–94.

Takeda K, Musolin DL, Fujisaki K. Dissecting insect responses to climate warming: overwintering and post-diapause performance in southern stink bug, *Nezara viridula*, under simulated climate-change conditions. Physiological Entomology 2010;35:343–53.

Todd JW. Ecology and behavior of *Nezara viridula*. Annual Review of Entomology 1989;34:273–92.

Vivan LM, Panizzi AR. Geographical distribution of genetically determined types of *Nezara viridula* (L.) (Heteroptera: Pentatomidae) in Brazil. Neotropical Entomology 2006;35:175–81.

Yukawa J, Kiritani K, Gyoutoku N, Uechi N, Yamaguchi D, Kamitani S. Distribution range shift of two allied species, *Nezara viridula* and *N. antennata* (Hemiptera: Pentatomidae), in Japan, possibly due to global warming. Applied Entomology and Zoology 2007;42:205–15.

Case study 4. Coffee's most intractable insect pest: the coffee berry borer

The coffee berry borer (CBB; *H. 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 increased temperatures, 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, providing a year-round food source for CBB. 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

Sources:

Lin BB. Agroforestry management as an adaptive strategy against potential microclimate extremes in coffee agriculture. Agricultural and Forest Meteorology 2007; 144:85–94.

Jaramillo J, Chabi-Olaye A, Kamonjo C, Jaramillo A, Vega FE, Poehling HM, Borgemeister C. Thermal tolerance of the coffee berry borer *Hypothenemus hampei*: predictions of climate change impact on a tropical insect pest. PLoS ONE 2009;4:e6487, 11 pp.

Jayarama. Weather change in coffee plantation areas in India. Indian Coffee 2010;74(1):17–9.

Mawardi S, Wiryadiputra S. Recent status of coffee berry borer in Indonesia. International Coffee Organization Seminar on Coffee Berry Borer, 17 March 2009.

Ruiz-Cárdenas R, Baker P. Life table of *Hypothenemus hampei* (Ferrari) in relation to coffee berry phenology under Colombian field conditions. Scientia Agricola (Piracicaba, Brazil) 2010;67:658–68.

Soto-Pinto L, Perfecto I, Caballero-Nieto J. Shade over coffee: its effects on berry borer, leaf rust and spontaneous herbs in Chiapas, Mexico. Agroforestry Systems 2002;55:37–45.

Case study 5. 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 2000 km of ocean between Australia and New Zealand, ranging from aphids to butterflies (Tomlinson, 1973), e.g. the nymphalid butterfly *Hypolimnas bolina nerina* (Fabricius) is found in considerable numbers some years, but is not established in New Zealand.

In the latitudes 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 300–1000 m were estimated to occur just over 20 times per year based on weather data for the years 1961–1970 (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:

Gatehouse AG. Behavior and ecological genetics of wind-borne migration by insects. Annual Review of Entomology 1997;42:475–502.

Tomlinson AI. Meteorological aspects of trans-Tasman insect dispersal. New Zealand Entomologist 1973;5: 253–68.

Case study 6. 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.

L. 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 that 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

Sources:

Hartley S, Harris R, Lester PJ. Quantifying uncertainty in the potential distribution of an invasive species: climate and the Argentine ant. Ecology Letters 2006;9:1068–79.

Roura-Pascual N, Suarez AV, Gómez C, Pons P, Touyama Y, Wild AL, Peterson AT. Geographical potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. Proceedings of the Royal Society B: Biological Sciences 2004;271:2527–34.

Roura-Pascual N, Hui C, Ikeda T, Leday G, Richardson DM, Carpintero S, *et al.* Relative roles of climatic suitability and anthropogenic influence in determining the pattern of spread in a global invader. Proceedings of the National Academy of Sciences USA 2011;108:220–5.

Suarez AV, Holway DA, Case TJ. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proceedings of the National Academy of Sciences USA 2001;98:1095–100.

Ward DF, Harris RJ. Invasibility of native habitats by Argentine ants, *Linepithema humile,* in New Zealand. New Zealand Journal of Ecology 2005;29:215–9.

Wetterer JK, Wild AL, Suarez AV, Roura-Pascual N, Espadaler X. Worldwide spread of the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). Myrmecological News 2009;12:187–94.

Case study 7. 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. *O. 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 that are currently limited by low winter temperatures. The northern limit is expected to shift northward by more than 100 km with every 1°C 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 3°C increase in mean annual temperatures would advance the limit for maize to the extent of including virtually all of the UK, and this could provide the means for a substantial shift in the distribution of *O. nubilalis*. The area of maize cultivation in the UK has already increased from about 25 000–172 000 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, owing to the climate change.

Prepared by Raymond J.C. Cannon

Sources:

Gathmann A, Rothmeier I. Dispersal of the European corn borer (*Ostrinia nubilalis* Hbn.) in southern Rhineland – results of the infestation assessment 2002 and 2003. Journal of Plant Diseases and Protection 2005;112:200–3.

Keszthelyi S, Puskás J, Nowinszky L. Changing of flight phenology and ecotype expansion of the European corn borer (*Ostrinia nubilalis* Hbn.) in Hungary. Cereal Research Communications 2008;36:647–57.

Kocmánková E, Trnka M, Juroch J, Dubrovský M, Semerádová D, Možný M, Žalud Z. Impact of climate change on the occurrence and activity of harmful organisms. Plant Protection Science 2009;45(Special Issue):S48–52.

Korycinska A, Ostojá-Starzewski J. A new threat to maize crops in the UK? Fera Plant Clinic News, August–September 2010, unpaginated; 2010. Available from: URL: www.fera.defra.gov.uk/plants/publications/documents/plantClinicNews/augSept10Issue.pdf

Trnka M, Muska F, Semeradova D, Dubrovsky M, Kocmankova E, Zalud Z. European corn borer life stage model: Regional estimates of pest development and spatial distribution under present and future climate. Ecological Modelling 2007;207:61–84.

Case study 8. 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 Australia 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.

S. 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 BCA. However, in New Zealand, around 3% 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.

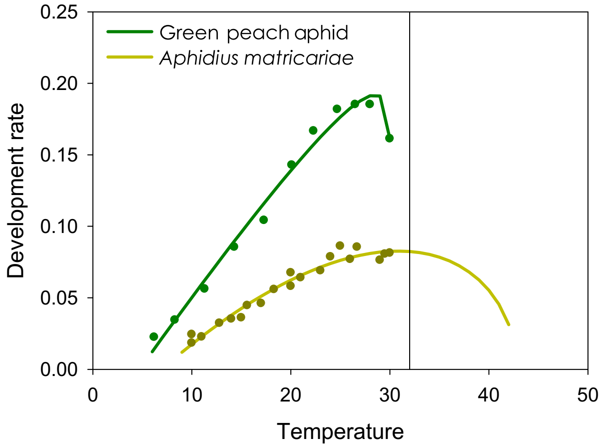
This case study exemplifies how a small but critically important population interaction related to climate may determine the regional efficacy of a BCA, and how this could be affected by climate change.

Prepared by John Kean, AgResearch Ltd, New Zealand
Source:

Goldson SL. Climate change in biological control. In: Newton PCD, Carran RA, Edwards GR, Niklaus PA, editors. Agroecosystems in a Changing Climate. Taylor & Francis, London, UK; 2006. p. 329–32.

Case study 9. Differential responses to temperature by pests and BCAs 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, Gonzalez D. Temperature requirements of four parasites of the Russian wheat aphid *Diuraphis noxia*. Entomologia Experimentalis et Applicata 1993;69:173–82.

Davis JA, Radcliffe EB, Ragsdale DW. The effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera: Aphididae). Environmental Entomology 2006; 35:1461–8.

Case study 10. Synchronization of a pest population can lead to outbreaks due to disruption of BCAs: 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 *P. 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 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:

Godfray HCJ, Hassell MP. Natural enemies can cause discrete generations in tropical insects. Nature 1987;327: 144–7.

Taylor THC. The Biological Control of an Insect in Fiji. An Account of the Coconut Leaf-mining Beetle and its Parasite Complex. The Imperial Institute of Entomology, London, UK; 1937. 239 pp.

Case study 11: 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 BCAs to maintain effective suppression.

In New Zealand, the corn earworm, *H. 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% parasitism and form the basis of an integrated pest management (IPM) programme to control corn earworm in outdoor tomato crops. *C. kazak* is the dominant parasitoid, reared from about

90% 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 sweet corn, 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 sweet corn 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 PJ, Walker GP, Herman TJB, Wallace AR. Development of economic thresholds and monitoring systems for *Helicoverpa armigera* (Lepidoptera: Noctuidae) in tomatoes. Journal of Economic Entomology 2001; 94:1104–12.

Gerard PJ, Kean JM, Phillips CB, Fowler SV, Withers TM, Walker GP, *et al.* Possible impacts of climate change on biocontrol systems in New Zealand. AgResearch Ltd Report for MAF Policy, 2010; 64 pp.

Walker GP, Herman TJB, Kale A, Wallace AR. An adjustable action threshold using larval parasitism of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in IPM for processing tomatoes. Biological Control 2010;52:30–6.

Case study 12. 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:

Blouin M, Zuily-Fodil Y, Pham-Thi AT, Laffray D, Reversat G, Pando A, *et al.* Belowground organism activities affect plant aboveground phenotype, inducing plant tolerance to parasites. Ecology Letters 2005;8: 202–8.

Brown GG, Pashanasi B, Villenave C, Patron JC, Senapati BK, Giri S, *et al.* Effects of earthworms on plant production in the tropics. In: Lavelle P, Brussaard L, Hendrix P, editors. The Management of Earthworms in Tropical Agroecosystems. CAB International, Wallingford, UK; 1999. p. 87–148.

Case study 13. 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* (Linnaeus)) 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%, with nearly 10% being parasitized. Although the mechanism is not clearly understood, and more studies are needed, 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% when earthworms were present and had the largest impact in monocultures compared with 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, such as increased summer drought.

Prepared by Juan J. Jiménez

Sources:

Blouin M, Lavelle P, Laffray D. Drought stress in rice (*Oryza sativa* L.) is enhanced in the presence of the compacting earthworm *Millsonia anomala*. Environmental and Experimental Botany 2007;60:352–9.

Johnson SN, Staley JT, McLeod FAL, Hartley SE. Plant-mediated effects of soil invertebrates and summer drought on above-ground multitrophic interactions. Journal of Ecology 2011;99:57–65.

Scheu S. Effects of earthworms on plant growth: patterns and perspectives. Pedobiologia 2003;47:846–56.

Case study 14. The invasion and degradation of pastures due to biologically created soil compaction results in negative feedbacks to climate change

In the Brazilian Amazon, 95% of the deforested area is converted into pasture, 50% 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 versus 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% 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. corethrurus*. 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 tonnes/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, *et al.* Pasture damage by an Amazonian earthworm. Nature 1999;398:32–3.

Marichal R, Feijoo Martinez A, Praxedes C, Ruiz D, Carvajal AF, Oszwald J, *et al.* Invasion of *P. corethrurus* (Glossoscolecidae, Oligochaeta) in landscapes of the Amazonian deforestation arc. Applied Soil Ecology 2010;46:443–9.

Case study 15. Genetic bottlenecks may limit the ability of BCAs 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) 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 DA, Loxdale HD, Edwards OR. 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 2003;12:3303–11.

Fauvergue X, Hopper KR. French wasps in the New World: experimental biological control introductions reveal a demographic Allee effect. Population Ecology 2009; 51:385–97.

Hufbauer RA, Bogdanowicz SM, Harrison RG. The population genetics of a biological control introduction: mitochondrial DNA and microsatellie variation in native and introduced populations of *Aphidus ervi,* a parasitoid wasp. Molecular Ecology 2004;13:337–48.

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

Tsutsui ND, Suarez AV, Holway DA, Case TJ. Reduced genetic variation and the success of an invasive species. Proceedings of the National Academy of Sciences USA 2000;97:5948–53.

Vila R, Bell CD, Macniven R, Goldman-Huertas B, Ree RH, Marshall CR, *et al.* Phylogeny and palaeoecology of *Polyommatus* blue butterflies show Beringia was a climate-regulated gateway to the New World. Proceedings of the Royal Society B: Biological Sciences 2011; (Online).

Case study 16. Within-species genetic variation enables BCA 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 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 PJ, Kean JM, Phillips CB, Fowler SV, Withers TM, Walker GP, *et al.* Possible impacts of climate change on biocontrol systems in New Zealand. Report for MAF Policy Project 0910-11689. AgResearch Ltd, New Zealand; 2010. 64 pp. Available from: URL: www.maf.govt.nz/environment-natural-resources/climate-change/research-and-funded-projects/research-and-funded-projects-table.aspx

Phillips CB, Baird DB, Iline II, McNeill MR, Proffitt JR, Goldson SL, *et al.* East meets West: adaptive evolution of an insect introduced for biological control. Journal of Applied Ecology 2008;45:948–56.

Case study 17. The search for pests and their BCAs 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* (Fabricius); 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. *T. 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* (Fabricius), 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. Those pests would switch from other monocotyledon 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 MJW, Bennett FD. John Golding Myers (1897–1942) an extraordinary exploratory entomologist. CABI Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources 2011;6(8):18 pp.

González JM, Cock MJW. A synopsis of the Castniidae (Lepidoptera) of Trinidad and Tobago. Zootaxa 2004; 762:1–19.

Myers JG. The discovery and introduction of the Amazon fly. A new parasite for cane-borers (*Diatraea* spp.). Tropical Agriculture 1934;11:191–5.

Case study 18. Corridors for migratory pollinators during climate change scenario

Climate change will have impacts on all major ecological communities. As far as terrestrial biodiversity is concerned, the range of potential impacts includes, for disturbance regimes, protected areas without usable connecting migration corridors.

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. Available from: URL: www.desertmuseum.org/pollination/introduction.php (last accessed 9 March 2011).

Collette A. (ed.). Climate Change and World Heritage. UNESCO World Heritage Centre, Paris; 2007. 51 pp.

Nabhan GP. Nectar trails of migratory pollinators restoring corridors on private lands. Conservation in Practice 2001;2:20–6.

Case study 19. Forest habitat conservation in Africa using stingless bees

In social insects, foraging activity and hence pollination, are influenced by climatic conditions. In light of climate change, such as global warming, it has become increasingly important to obtain baseline data on the relationship between climate and the foraging action of keystone species such as stingless bees, one of the most important pollinators in the African forest ecosytem. The influence of weather on the flight activity of Meliponini bees has been studied, and seasonal variations have been found in flight activity, as well as correlations between flight activity and weather variables, especially temperature and luminosity.

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, for example in semi-arid hilltop forest areas found in Mwingi in Kenya, and fragile forest ecosystems such as Kakamega forest, the only remnant in Kenya of the unique Guineo–Congolian *forest ecosystem*.

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, 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 beehives 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:

Hilario SD, Imperatriz-Fonseca VL, Kleinert ADMP. Flight activity and colony strength in the stingless bee *Melipona bicolor bicolor* (Apidae: Meliponinae). Revista Brasileiro de Biologia 2000;60:299–306.

Michener CD. The Bees of the World. Johns Hopkins University Press, Baltimore and London, UK; 2000; 913 pp.

Raina SK, Kioko EN, Gordon I, Nyandiga C. (compilers). Improving Forest Conservation and Community Livelihoods through Income Generation from Commercial Insects in Three Kenyan Forests. ICIPE Science Press, Nairobi, Kenya, 2009; 87 pp.

Raina SK, Kioko E, Zethner O, Wren S. Forest habitat conservation in Africa using commercially important insects. Annual Review of Entomology 2011;56:465–85.

Roubik DW. Ecology and Natural History of Tropical Bees. Cambridge University Press, Cambridge; 1989. 514 pp.

Whittaker JB. Insects and plants in a changing atmosphere. Journal of Ecology 2001;89:507–18.

Case study 20. 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 that 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 that 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 *Elaeidobius* 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, *E. 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 UK 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%. 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 DJ. The multi-million dollar weevil that pollinates oil palms. Antenna, Bulletin of the Royal Entomological Society of London 1983;7:105–7.

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References

1. Cock MJW, Biesmeijer JC, Cannon RJC, Gerard PJ, Gillespie D, Jiménez JJ, *et al.* The positive contribution of invertebrates to sustainable agriculture and food security. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources 2012;7(43): 27 pp.
2. Lavelle P, Spain AV. Soil Ecology. Springer, Dordecht, Netherlands; 2001. p. 684.
3. Jones CG, Lawton JH, Shachak M. Organisms as ecosystem engineers. Oikos 1994;69:373–86.
4. Peñuelas J, Rutishauser T, Filella I. Phenology feedbacks on climate change. Science 2009;324:887–8.
5. Cannon RJC. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. Global Change Biology 1998;4:785–96.
6. Patterson DT, Westbrook JK, Joyce RJV, Lingren PD, Rogasik J. Weeds, insects, and diseases. Climatic Change 1999;43:711–27.
7. Rosenzweig C, Iglesias A, Yang XB, Epstein PR, Chivian E. Climate change and extreme weather events; implications for food production, plant diseases, and pests. Global Change and Human Health 2001;2:90–104.
8. Fuhrer J. Agroecosystem responses to combinations of elevated CO_2, ozone, and global climate change. Agriculture, Ecosystems and Environment 2003;97:1–20.
9. Luedeling E, Steinmann KP, Zhang M, Brown PH, Grant J, Girvetz EH. Climate change effects on walnut pests in California. Global Change Biology 2011;17:228–38.
10. Gregory PJ, Johnson SN, Newton AC, Ingram JSI. Integrating pests and pathogens into the climate change/food security debate. Journal of Experimental Botany 2009;60:2827–38.
11. Davis MB, Shaw RG, Etterson JR. Evolutionary responses to changing climate. Ecology 2005;86:1704–14.
12. Burgiel SW, Muir AA. Invasive Species, Climate Change and Ecosystem-Based Adaptation: Addressing Multiple Drivers of Global Change. Global Invasive Species Programme (GISP), Washington, DC, and Nairobi, Kenya, 2010. p. 55.
13. Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. Fingerprints of global warming on wild animals and plants. Nature 2003;421:57–60.
14. Travis JMJ, Dytham C. Dispersal evolution during invasions. Evolutionary Ecology Research 2002;4:1119–29.
15. Watkinson AR, Gill JA. Climate change and dispersal. In: Bullock JM, Kenward RE, Hails RS, editors. Dispersal Ecology. Blackwell Science Publishing, Oxford, 2002. p. 45–56.
16. Coope GR. Several million years of stability among insect species because of, or in spite of, Ice Age climatic instability? Philosophical Transactions of the Royal Society B: Biological Sciences 2004;359:209–14.
17. Hill JK, Griffiths HM, Thomas CD. Climate change and evolutionary adaptations at species' range margins. Annual Review of Entomology 2011;56:143–59.
18. Gonzalez A, Ronce O, Ferriere R, Hochberg ME. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. Philosophical Transactions of the Royal Society B: Biological Sciences 2012;368(1610): 8 pp.
19. Donnelly A, Caffarra A, Kelleher CT, O'Neill BF, Diskin E, Pletsers A, *et al.* Surviving in a warmer world: environmental and genetic responses. Climate Research 2012;53:245–62.
20. Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, *et al.* Ecological and evolutionary processes at expanding range margins. Nature 2001;411:577–81.
21. Harrington R, Woiwod I, Sparks T. Climate change and trophic interactions. Trends in Ecology and Evolution 1999;14:146–50.
22. Walther GR. Tackling ecological complexity in climate impact research. Science 2007;315:606–7.
23. Berg MP, Kiers ET, Driessen G, van der Heijden M, Kooi BW, Kuenen F, *et al.* Adapt or disperse: understanding species persistence in a changing world. Global Change Biology 2010;16:587–98.
24. IPCC. Summary for Policymakers. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, editors. Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, 2007. p. 2–18.
25. IPCC. Summary for Policymakers. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Climate Change 2007: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, 2007. p. 7–22.

26. Williams JW, Jackson ST, Kutzbach JE. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences USA 2007;104:5738–42.

27. Easterling WE, Aggarwal PK, Batima P, Brander KM, Erda L, Howden SM, *et al.* Food, fibre and forest products. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE, editors. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK; 2007. p. 273–313.

28. Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G. Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biology 2008;6:e325, 6 pp.

29. Kardol P, Reynolds WN, Norby RJ, Classen AT. Climate change effects on soil microarthropod abundance and community. Applied Soil Ecology 2011;47:37–44.

30. Mikkelsen TN, Beier C, Jonasson S, Holmstrup M, Schmidt IK, Ambus P, *et al.* Experimental design of multifactor climate change experiments with elevated CO_2, warming and drought: the CLIMAITE project. Functional Ecology 2007;22:185–95.

31. Staley JT, Johnson SN. Climate change impacts on root herbivores. In: Johnson SN, Murray PJ, editors. Root Feeders: an Ecosystem Approach. CABI, Wallingford, UK, 2008. p. 192–213.

32. Estrada-Pena A. Climate, niche, ticks, and models: what they are and how should we interpret them. Parasitology Research 2008;103(Suppl. 1):S87–95.

33. Araújo MB, Luoto M. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 2007;16:743–53.

34. Kardol P, Cregger MA, Campany CE, Classen AT. Soil ecosystem functioning under climate change: plant species and community effects. Ecology 2010;91:767–81.

35. Bale JS, Hayward SAL. Insect overwintering in a changing climate. Journal of Experimental Biology 2010;213:980–94.

36. Voigt W, Perner J, Davis AJ, Eggers T, Schumacher J, Bahrmann R, *et al.* Trophic levels are differentially sensitive to climate. Ecology 2003;84:2444–53.

37. Schweiger O, Settele J, Kudrna O, Klotz S, Kühn I. Climate change can cause spatial mismatch of trophically interacting species. Ecology 2008;89:3472–9.

38. Thomson LJ, Macfadyen S, Hoffmann AA. Predicting the effects of climate change on natural enemies of agricultural pests. Biological Control 2010;52:296–306.

39. Petchey OL, McPhearson PT, Casey TM, Morin PJ. Environmental warming alters food-web structure and ecosystem function. Nature 1999;402:69–72.

40. Gao F, Zhu S-R, Sun Y-C, Du L, Parajulee M, Kang L, Ge F. Interactive effects of elevated CO_2 and cotton cultivar on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossyppii* [sic], and *Propylaea japonica*. Environmental Entomology 2008;37:29–37.

41. Stacey DA, Fellowes MDE. Influence of elevated CO_2 on interspecific interactions at higher trophic levels. Global Change Biology 2002;6:668–78.

42. Hance T, Van Baaren J, Vernon P, Boivin G. Impact of extreme temperatures on parasitoids in a climate change perspective. Annual Review of Entomology 2007;52:107–26.

43. Howden SM, Soussana J-F, Tubiello FN, Chhetri N, Dunlop M, Meinke H. Adapting agriculture to climate change. Proceedings of the National Academy of Sciences USA 2007;104:1961–9.

44. Steffensen JP, Andersen KK, Bigler M, Clausen HB, Dahl-Jensen D, Fischer H, *et al.* High-resolution Greenland ice core data show abrupt climate change happens in few years. Science 2008;321(5889):680–4.

45. Hof C, Levinsky I, Araújo MB, Rahbek C. Rethinking species' ability to cope with rapid climate change. Global Change Biology 2011;17:2987–90.

46. Easterling WE, Aggarwal PK, Batima P, Brander KM, Erda L, Howden SM, *et al.* Food, fibre and forest products. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE, editors. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK; 2007. p. 273–313.

47. Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 1999;399:579–83.

48. Hickling R, Roy DB, Hill JK, Fox R, Thomas CD. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 2006;12:450–5.

49. Musolin DL, Fujisaki K. Changes in ranges: trends in distribution of true bugs (Heteroptera) under conditions of the current climate warming. Russian Entomological Journal 2006;15:175–9.

50. Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. Nature 2003;421:39–42.

51. Whittaker JB, Tribe NP. An altitudinal transect as an indicator of responses of a spittlebug (Auchenorrhyncha: Cercopidae) to climate change. European Journal of Entomology 1996;93:319–24.

52. Menéndez R. How are insects responding to global warming? Tijdschrift voor Entomologie 2007;15:355–65.

53. Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 2008;322:258–61.

54. Martins AC, Melo GAR. Has the bumblebee *Bombus bellicosus* gone extinct in the northern portion of its distribution range in Brazil? Journal of Insect Conservation 2010;14:207–10.

55. Travis JMJ. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society B: Biological Sciences 2003;270:467–73.

56. Pelini SL Keppel JA, Kelley AE, Hellmann JJ. Adaptation to host plants may prevent rapid insect responses to climate change. Global Change Biology 2010;16:2923–9.

57. Saikkonen K, Taulavuori K, Hyvönen T, Gundel PE, Hamilton CE, Vänninen I, *et al.* Climate change-driven species' range

shifts filtered by photoperiodism. Nature Climate Change 2012;2(4):239–42.

58. Gutschick VP, Bassirirad H. Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. New Phytologist 2003;160:21–42.
59. Russell WG, Grimm EC. Effects of global climate change on the patterns of terrestrial biological communities. Trends in Ecology and Evolution 1990;5:289–92.
60. Lawton JH. Small earthquakes in Chile and climate change. Oikos 1998;82:209–11.
61. Colinvaux P. The Pleistocene vector of neotropical diversity. In: Bermingham E, Dick CW, Moritz C, editors. *Tropical Rainforests: Past, Present and Future*. University of Chicago Press, Chicago, Illinois, 2005. p. 78–106.
62. Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, *et al.* Extinction risk from climate change. Nature 2004;427:145–8.
63. Arribas P, Abellan P, Velasco J, Bilton DT, Millan A, Sanchez-Fernandez D. Evaluating drivers of vulnerability to climate change: a guide for insect conservation strategies. Global Change Biology 2012;18:2135–46.
64. Mitsch WJ. What is ecological engineering? (Special Issue: Ecological engineering – its development, application and challenges.). Ecological Engineering 2012;45:5–12.
65. Laussmann T, Radtke A, Wiemert T, Dahl A. 150 Jahre Schmetterlingsbeobachtung in Wuppertal – Auswirkungen von Klima- und Landschaftsveränderungen (Lepidoptera). [150 years of butterfly monitoring in Wuppertal – effects of climate and landscape change (Lepidoptera)]. Entomologische Zeitschrift, Stuttgart 2010;120:269–77.
66. Hoffmann AA, Weeks AR, Nash MA, Mangano GP, Umina PA. The changing status of invertebrate pests and the future of pest management in the Australian grains industry. Australian Journal of Experimental Agriculture 2008;48:1481–93.
67. Karg J, Bałazy S. Wpływ struktury krajobrazu na wystepowanie agrofagów i ich antagonistów w uprawach rolniczych. [Effect of landscape structure on the occurrence of agrophagous pests and their antagonists.] Progress in Plant Protection 2009;49:1015–34.
68. Parmesan C. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology 2007;13:1860–72.
69. Groffman PM, Jones CG. Soil processes and global change: will invertebrates make a difference? In: Coleman DC, Hendrix PF, editors. Invertebrates as Webmasters in Ecosystems. CABI, Wallingford, UK, 2000. p. 313–26.
70. Hulme PE. Adapting to climate change: is there scope for ecological management in the face of a global threat? Journal of Applied Ecology 2005;42:784–94.
71. Branson DH. Influence of a large late summer precipitation event on food limitation and grasshopper population dynamics in a northern Great Plains grassland. Environmental Entomology 2008;37:686–95.
72. Bouget C, Duelli P. The effects of windthrow on forest insect communities: a literature review. Biological Conservation 2004;118:281–99.
73. Stireman JO III, Dyer LA, Janzen DH, Singer MS, Lill JT, Marquis JT, *et al.* Climatic unpredictability and parasitism of caterpillars: implications of global warming. Proceedings of the National Academy of Sciences USA 2005;102:17384–87.
74. Holt J, Colvin J. A differential equation model of the interaction between the migration of the Senegalese grasshopper, *Oedaleus senegalensis*, its predators, and a seasonal habitat. Ecological Modelling 1997;101:185–93.
75. Mattson WJ, Haack RA. The role of drought in outbreaks of plant-eating insects. BioScience 1987;37:110–8.
76. Popay AJ. Population regulation of *Costelytra zealandica* by pathogens in the North Island of New Zealand. In: Jackson TA, Glare TR (eds) *Use of Pathogens in Scarab Pest Management*. Intercept, Andover, UK, 1992. p. 141–51.
77. English-Loeb GM. Plant drought stress and outbreaks of spider mites: a field test. Ecology 1990;71:1401–11.
78. Stavrinides MC, Daane KM, Lampinen BD, Mills NJ. Plant water stress, leaf temperature, and spider mite (Acari: Tetranychidae) outbreaks in California vineyards. Environmental Entomology 2010;39:1232–41.
79. Werren JH. Biology of *Wolbachia*. Annual Review of Entomology 1997;42:587–609.
80. Douglas AE. Nutritional interactions in insect-microbial symbioses: aphids and their symbiotic bacteria *Buchnera*. Annual Review of Entomology 1998;43:17–37.
81. Enigl M, Schausberger P. Incidence of the endosymbionts *Wolbachia*, *Cardinium* and *Spiroplasma* in phytoseiid mites and associated prey. Experimental and Applied Acarology 2007;42:75–85.
82. Roux O, Le Lann C, van Alphen JJM, van Baaren J. How does heat shock affect the life history traits of adults and progeny of the aphid parasitoid *Aphidius avenae* (Hymenoptera: Aphidiidae)? Bulletin of Entomological Research 2010;100:1–7.
83. Thomas MB, Blanford S. Thermal biology in insect-parasite interactions. Trends in Ecology and Evolution 2003;18: 344–50.
84. Werren JH, Baldo L, Clark ME. *Wolbachia*: master manipulators of invertebrate biology. Nature Reviews Microbiology 2008;6(10):741–51.
85. Engelstädter J, Hurst GDD. The ecology and evolution of microbes that manipulate host reproduction. Annual Review of Ecology, Evolution, and Systematics 2009;40:127–49.
86. Pintureau B, Chapelle L, Delobel B. Effects of repeated thermic and antibiotic treatments on a *Trichogramma* (Hym., Trichogrammatidae) symbiont. Journal of Applied Entomology 1999;123:473–83.
87. Pintureau B, Bolland P. A *Trichogramma* species showing a better adaptation to high temperature than its symbionts. Biocontrol Science and Technology 2001;11:13–20.
88. Guay JF, Boudreault S, Michaud D, Cloutier C. Impact of environmental stress on aphid clonal resistance to parasitoids: role of *Hamiltonella defensa* bacterial symbiosis in association with a new facultative symbiont of the pea aphid. Journal of Insect Physiology 2009;55:919–26.
89. Zhou S-X, Li Y, Zhang F. Influences of high temperature shock on the reproduction and development of the *Wolbachia*-induced parthenogenetic parasitoid wasp, *Encarsia formosa* (Gahan). Shengtai Xuebao/Acta Ecologica Sinica 2009;29:4732–7.

90. Phillips C, Townsend H, Vink C. Blown in the wind or border slippage? What natural dispersal of exotic species to New Zealand has to do with biosecurity. Biosecurity 2006;69:14–5.
91. Weltzin JF, Belote RT, Sanders NJ. Biological invaders in a greenhouse world: will elevated CO_2 fuel plant invasions? Frontiers in Ecology and the Environment 2003;1:146–53.
92. Song L, Wu J, Li C, Li F, Peng S, Chen B. Different responses of invasive and native species to elevated CO_2 concentration. Acta Oecologia 2009;35:128–35.
93. Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, *et al.* Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 2002;8:1–16.
94. Tobin PC, Nagarkatti S, Loeb G, Saunders MC. Historical and projected interactions between climate change and insect voltinism in a multivoltine species. Global Change Biology 2008;14:951–7.
95. Yukawa J, Kiritani K, Gyoutoku N, Uechi N, Yamaguchi D, Kamitani S. Distribution range shift of two allied species, *Nezara viridula* and *N. antennata* (Hemiptera: Pentatomidae), in Japan, possibly due to global warming. Applied Entomology and Zoology 2007;42:205–15.
96. Lastuvka Z. Climate change and its possible influence on the occurrence and importance of insect pests. (Special issue: climate change and plant pathogens, pests and weeds). Plant Protection Science 2009;45: S53–62.
97. Veteli TO, Lahtinen A, Repo T, Niemelä P, Varama M. Geographic variation in winter freezing susceptibility in the eggs of the European pine sawfly (*Neodiprion sertifer*). Agricultural and Forest Entomology 2005;7:115–20.
98. Virtanen T, Neuvonen S. Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids. Oecologia 1999;120:92–101.
99. Bosch J, Sgolastra F, William P, Kemp WP. Timing of eclosion affects diapause development, fat body consumption and longevity in *Osmia lignaria*, a univoltine, adult-wintering solitary bee. Journal of Insect Physiology 2010;56:1949–57.
100. Klironomos JN, Rillig MC, Allen MF. Below-ground microbial and microfaunal responses to *Artemisia tridentata* grown in elevated atmospheric CO_2. Functional Ecology 1996;10: 527–34.
101. Schröter D, Brussaard L, De Geyn G, Poveda K, Brown VK, Berg MP, *et al.* Trophic interactions in a changing world: modeling aboveground–belowground interactions. Basic and Applied Ecology 2004;5:515–28.
102. Jones TH, Thompson LJ, Lawton JH, Bezemer TM, Bardgett RD, Blackburn TM, *et al.* Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. Science 1998;280:441–3.
103. Yeates GW, Tate KR, Newton PCD. Response of the fauna of a grassland soil to doubling of atmospheric carbon dioxide concentration. Biology and Fertility of Soils 1997;25:307–15.
104. Loranger GI, Pregitzer KS, King JS. Elevated CO_2 and O_{3t} concentrations differentially affect selected groups of the fauna in temperate forest soils. Soil Biology and Biochemistry 2004;36:1521–4.
105. Norby RJ, Rustad LE, Dukes JS, Ojima DS, Parton WJ, Del Grosso SJ, *et al.* Ecosystem responses to warming and interacting global change factors. In: Canadell JG, Pataki DE, Pitelka LF, editors. Terrestrial Ecosystems in a Changing World. Springer-Verlag, Berlin, Germany; 2007. p. 45–58.
106. Roy B, Gusewell AS, Harte J. Response of plant pathogens and herbivores to a warming experiment. Ecology 2004;85:2570–81.
107. David J-F, Gillon D. Combined effects of elevated temperatures and reduced leaf litter quality on the life-history parameters of a saprophagous macroarthropod. Global Change Biology 2009;15:156–65.
108. Sohlenius B, Boström S. Effects of climate change on soil factors and metazoan microfauna (nematodes, tardigrades and rotifers) in a Swedish tundra soil – a soil transplantation experiment. Applied Soil Ecology 1999;12:113–28.
109. Briones MJI, Ostle NJ, McNamara NP, Poskitt J. Functional shifts of grassland soil communities in response to soil warming. Soil Biology and Biochemistry 2009;41:315–22.
110. Harte J, Rawa A, Price V. Effects of manipulated soil microclimate on mesofaunal biomass and diversity. Soil Biology and Biochemistry 1996;28:313–22.
111. Carrera N, Barreal ME, Gallego PP, Briones MJI. Soil invertebrates control peatland C fluxes in response to warming. Functional Ecology 2009;23:637–48.
112. Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, *et al.* Soil function in a changing world: the role of invertebrate ecosystems engineers. European Journal of Soil Biology 1997;33:159–93.
113. Barton BT, Schmitz OJ. Experimental warming transforms multiple predator effects in a grassland food web. Ecology Letters 2009;12:1317–25.
114. Barton BT, Beckerman AP, Schmitz OJ. Climate warming strengthens indirect interactions in an old-field food web. Ecology 2009;90:2346–51.
115. Mondor EB, Tremblay MN, Lindroth RL. Transgenerational phenotypic plasticity under future atmospheric conditions. Ecology Letters 2004;7:941–6.
116. Johnson SN, Zhang XX, Crawford JW, Gregory PJ, Hix NJ, Jarvis SC, *et al.* Effects of carbon dioxide on the searching behaviour of the root-feeding clover weevil *Sitona lepidus* (Coleoptera: Curculionidae). Bulletin of Entomological Research 2006;96:361–6.
117. Guerenstein PG, Hildebrand JG. Roles and effects of environmental carbon dioxide in insect life. Annual Review of Entomology 2008;53:161–78.
118. Stange G. Effects of changes in atmospheric carbon dioxide on the location of hosts by the moth, *Cactoblastis cactorum*. Oecologia 1997;110:539–45.
119. Ruess L, Michelsen A, Schmidt IK, Jonasson S. Simulated climate change affecting microorganisms, nematode density and biodiversity in subarctic soils. Plant and Soil 1999;212:63–73.
120. Bezemer TM, Jones TH, Knight KJ. Long-term effects of elevated CO_2 and temperature on populations of the peach potato aphid *Myzus persicae* and its parasitoid *Aphidius matricariae*. Oecologia 1998;116:128–35.
121. Chen FJ, Wu G, Parajulee MN, Ge F. Impact of elevated CO_2 on the third trophic level: a predator *Harmonia axyridis* and a

parasitoid *Aphidius picipes*. Biocontrol Science and Technology 2007;17:313–24.

122. Godfray HCJ, Hassell MP, Holt RD. The population dynamic consequences of phenological asynchrony between parasitoids and their hosts. Journal of Animal Ecology 1994;63:1–10.

123. Craufurd PQ, Wheeler TR. Climate change and the flowering time of annual crops. Journal of Experimental Botany 2009;60:2529–39.

124. Von Holle B, Wei Y, Nickerson D. Climatic variability leads to later seasonal flowering of Floridian plants. PLoS ONE 2010;5(7):e11500, 9 pp.

125. Singer MC, Parmesan C. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? Philosophical Transactions of the Royal Society B: Biological Sciences 2010;365:3161–76.

126. van Asch M, Visser ME. Phenology of forest caterpillars and their host trees: the importance of synchrony. Annual Review of Entomology 2007;52:37–55.

127. Visser ME, Holleman JM. Warmer springs disrupt the synchrony of oak and winter moth phenology. Proceedings of the Royal Society B: Biological Sciences 2001;268:289–94.

128. Bean DW, Dalin P, Dudley TL. Evolution of critical day length for diapause induction enables range expansion of *Diorhabda carinulata*, a biological control agent against tamarisk (*Tamarix* spp.). Evolutionary Applications 2012;5:511–23.

129. Harmon JP, Moran NA, Ives AR. Species response to environmental change: impacts of food web interactions and evolution. Science 2009;323:1347–50.

130. Hegland SJ, Nielsen A, Lázaro A, Bjerknes A-L, Totland Ø. How does climate warming affect plant-pollinator interactions? Ecology Letters 2009;12:184–95.

131. Bezemer TM, Knight KJ, Newington JE, Jones TH. How general are aphid responses to elevated atmospheric CO_2? Annals of the Entomological Society of America 1999;92:724–30.

132. Klapwijk MJ, Gröbler BC, Ward K, Wheeler D, Lewis OT. Influence of experimental warming and shading on host–parasitoid synchrony. Global Change Biology 2010;16:102–12.

133. Hoover JK, Newman JA. Tritrophic interactions in the context of climate change: a model of grasses, cereal aphids and their parasitoids. Global Change Biology 2004;10:1197–208.

134. Peñuelas J, Estiarte M. Can elevated CO_2 affect secondary metabolism and ecosystem function? Trends in Ecology and Evolution 1998;13:20–4.

135. Pritchard J, Griffiths B, Hunt EJ. Can the plant-mediated impacts on aphids of elevated CO_2 and drought be predicted? Global Change Biology 2007;13:1616–29.

136. Curtis PS, Wang X. A meta-analysis of elevated CO_2 effects on woody plant mass, form and physiology. Oecologia 1998;113:299–313.

137. Lukac M, Calfapietra C, Godbold DL. Production, turnover and mycorrizal colonization of root systems of three *Populus* species grown under elevated CO_2 (POPFACE). Global Change Biology 2003;9:838–48.

138. Stiling P, Forkner R, Drake B. Long-term exposure to elevated CO_2 in a Florida scrub-oak forest increases herbivore densities but has no effect on other arthropod guilds. Insect Conservation and Diversity 2010;3:152–6.

139. Johnson SN, McNicol JW. Elevated CO_2 and aboveground–belowground herbivory by the clover root weevil. Oecologia 2010;162:209–16.

140. Coviella C, Trumble J. Effects of elevated atmospheric carbon dioxide on insect–plant interactions. Conservation Biology 1999;13:700–12.

141. DeLucia EH, Casteel CL, Nabity PD, O'Neill BF. Insects take a bigger bite out of plants in a warmer, higher carbon dioxide world. Proceedings of the National Academy of Sciences USA 2008;105:1781–2.

142. Bidart-Bouzat MG, Imeh-Nathaniel A. Global change effects on plant chemical defenses against insect herbivores. Journal of Integrative Plant Biology 2008;50:1339–54.

143. Ode PJ. Plant chemistry and natural enemy fitness: effects on herbivore and natural enemy interactions. Annual Review of Entomology 2006;51:163–85.

144. Coll M, Hughes L. Effects of elevated CO_2 on an insect omnivore: a test for nutritional effects mediated by host plants and prey. Agriculture, Ecosystems and Environment 2008;123:271–9.

145. De Moraes CM, Lewis WJ, Pare PW, Alborn HT, Tumlinson JH. Herbivore-infested plants selectively attract parasitoids. Nature 1998;393:570–3.

146. Hare JD. Ecological role of volatiles produced by plants in response to damage by herbivorous insects. Annual Review of Entomology 2011;56:161–80.

147. Pinto DM, Blande JD, Nykänen R, Dong WX, Nerg AM, Holopainen JK. Ozone degrades common herbivore-induced plant volatiles: does this affect herbivore prey location by predators and parasitoids? Journal of Chemical Ecology 2007;33:683–94.

148. Staley JT, Mortimer SR, Masters GJ, Morecroft MD, Brown VK, Taylor ME. Drought stress differentially affects leaf-mining species. Ecological Entomology 2006;31:460–9.

149. Staley JT, Mortimer SR, Morecroft MD, Brown VK, Masters GJ. Summer drought alters plant-mediated competition between foliar- and root-feeding insects. Global Change Biology 2007;13:866–77.

150. Kauffman WC, Kennedy GG. Inhibition of *Campoletis sonorensis* parasitism of *Heliothis zea* and of parasitoid development by 2-tridecanone-mediated insect resistance of wild tomato. Journal of Chemical Ecology 1989;15:1919–30.

151. Micha SG, Kistenmacher S, Molck G, Wyss U. Tritrophic interactions between cereals, aphids and parasitoids: discrimination of different plant-host complexes by *Aphidius rhopalosiphi* (Hymenoptera: Aphidiidae). European Journal of Entomology 2000;97:539–43.

152. Sommer JH, Kreft H, Kier G, Jetz W, Mutke J, Barthlott W. Projected impacts of climate change on regional capacities for global plant species richness. Proceedings of the Royal Society B: Biological Sciences 2010;277:2271–80.

153. Woodward FI, Kelly CK. Responses of global plant diversity capacity to changes in carbon dioxide concentration and climate. Ecology Letters 2008;11:1229–37.

154. Seidel DJ, Fu QA, Randel WJ, Reichler TJ. Widening of the tropical belt in a changing climate. Nature Geoscience 2008;1:21–4.

155. Bowman DMJS, Murphy BP, Banfai DS. Has global environmental change caused monsoon rainforests to expand in the Australian monsoon tropics? (Special issue: Landscape ecology as an integrated science for sustainability in a changing world.). Landscape Ecology 2010;25:1247–60.

156. Jaramillo J, Chabi-Olaye A, Kamonjo C, Jaramillo A, Vega FE, Poehling HM, *et al.* Thermal tolerance of the coffee berry borer *Hypothenemus hampei*: predictions of climate change impact on a tropical insect pest. PLoS ONE 2009;4(8):e6487, 11 pp.

157. Coley PD. Possible effects of climate change on plant/herbivore interactions in moist tropical forests. Climatic Change 1998;39:455–72.

158. Schleuning M, Fründ J, Klein, A-M, Abrahamczyk S, Alarcón R, Albrecht M, *et al.* Specialization of mutualistic interaction networks decreases toward tropical latitudes. Current Biology 2012;22(20):1925–31.

159. Wolters V, Silver WL, Bignell DE, Coleman DC, Lavelle P, van der Putten WH, *et al.* Effects of global changes on above- and belowground biodiversity in terrestrial ecosystems: implications for ecosystem functioning. BioScience 2000;50:1089–98.

160. Wardle DA. Communities and Ecosystems – Linking the Aboveground and Belowground Components. Princeton University Press, Princeton, New Jersey; 2002. p. 400.

161. Wardle DA, Bardgett RD, Klironomos JN, Setälä H, Van der Putten WH, Wall DH. Ecological linkages between aboveground and belowground biota. Science 2004;304:1629–33.

162. van der Putten WH, Bardgett RD, de Ruiter PC, Hol WHG, Meyer KM, Bezemer TM, *et al.* Empirical and theoretical challenges in aboveground–belowground ecology. Oecologia 2009;161:1–14.

163. Kardol P, Wardle DA. How understanding aboveground-belowground linkages can assist restoration ecology. Trends in Ecology and Evolution 2010;25:670–9.

164. Freckman DW. Ecology of anhydrobiotic nematodes. In: Crowe JH, Clegy JS, editors. Dried Biological Systems. Academic Press, New York, 1978. p. 345–57.

165. Jiménez JJ, Brown GG, Decaëns T, Feijoo A, Lavelle P. Differences in the timing of diapause and patterns of aestivation in tropical earthworms. Pedobiologia 2000;44:677–94.

166. Jiménez JJ, Thomas RJ. (eds) Soil Macroinvertebrate Communities in the Neotropical Savannas of Colombia. CIAT Publication No. 324. Centro Internacional de Agricultura Tropical, Cali, Colombia; 2001. 389 pp.

167. Jiménez JJ, Decaëns T, Rossi J-P. Soil environmental heterogeneity allows spatial co-occurrence of competitor earthworm species in a gallery forest of the Colombian 'Llanos'. Oikos 2012;121:915–26.

168. Krab EJ, Oorsprong H, Berg MP, Cornelissen JHC. Turning northern peatlands upside down: disentangling microclimate and substrate quality effects on vertical distribution of Collembola. Functional Ecology 2010;24:1362–9.

169. Jiménez JJ, Decaëns T. Vertical distribution of earthworms in grassland soils of the Colombian Llanos. Biology and Fertility of Soils 2000;32:463–73.

170. Marinissen JCY, van den Bosch F. Colonization of new habitats by earthworms. Oecologia 1992;91:371–6.

171. Decaëns T. Macroecological patterns in soil communities. Global Ecology and Biogeography 2010;19:287–302.

172. Gaston KJ. Global patterns in biodiversity. Nature 2000;405:220–7.

173. Evans TA, Dawes TZ, Ward PR, Lo N. Ants and termites increase crop yield in a dry climate. Nature Communications 2011;2:262. doi:10.1038/ncomms125.

174. Decaëns T, Rangel AF, Asakawa N, Thomas RJ. Carbon and nitrogen dynamics in ageing earthworm casts in grasslands of the eastern plains of Colombia. Biology and Fertility of Soils 1999;30:20–8.

175. Johnson SN, Staley JT, McLeod FAL, Hartley SE. Plant-mediated effects of soil invertebrates and summer drought on above-ground multitrophic interactions. Journal of Ecology 2011;99:57–65.

176. Blouin M, Zuily-Fodil Y, Pham-Thi AT, Laffray D, Reversat G, Pando A, *et al.* Belowground organism activities affect plant aboveground phenotype, inducing plant tolerance to parasites. Ecology Letters 2005;8:202–8.

177. Decaëns T, Jiménez JJ, Lavelle P. Effect of exclusion of the anecic earthworm *Martiodrilus carimaguensis* Jiménez and Moreno on soil properties and plant growth in grasslands of the eastern plains of Colombia. Pedobiologia 1999; 43:835–41.

178. Hall MC, Stiling P, Moon DC, Drake BG, Hunter MD. Elevated CO_2 increases the long-term decomposition rate of *Quercus myrtifolia* leaf litter. Global Change Biology 2006;12:568–77.

179. Settle WH, Ariawan H, Astuti ET, Cahyana W, Hakim AL, Hindayana D, *et al.* Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology 1996;77:1975–88.

180. Heal OW. Effects of global change on diversity–function relationships in soil. In: Wolters V, editors, *Functional Implications of Biodiversity in Soil: Proceedings of a Workshop*: *14–20 September 1996, Schloss Rauischholzhausen*. Ecosystems Research Report 24. Office for Official Publications of the Europe Communities, Luxembourg, 1997. p. 27–37.

181. Uvarov AV, Tiunov AV, Scheu S. Effects of seasonal and diurnal temperature fluctuations on population dynamics of two epigeic earthworm species in forest soil. Soil Biology and Biochemistry 2011;43:559–70.

182. Jenkinson DS, Adams DE, Wild A. Model estimates of CO_2 emissions from soil in response to global warming. Nature 1991;351:304–6.

183. Seastedt TR. Soil fauna and controls of carbon dynamics: comparisons of rangelands and forests across latitudinal gradients. In: Hendrix PF, Coleman DC, editors. Invertebrates as Webmasters in Ecosystems. CAB International, Wallingford, UK, 2000. p. 293–312.

184. Fontaine S, Barot S, Barré P, Bdioui N, Mary B, Rumpel C. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 2007;450:277–81.

185. Pendall E, Rustad L, Schimel J. Towards a predictive understanding of belowground process responses to climate change: have we moved any closer? Functional Ecology 2008;22:937–40.

186. Davidson EA, Janssens IA. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 2006;440:165–73.

187. Briones MJI, Poskitt J, Ostle N. Influence of warming and enchytraeid activities on soil CO_2 and CH_4 fluxes. Soil Biology and Biochemistry 2004;36:1851–9.

188. Osler GHR, Sommerkorn M. Toward a complete soil C and N cycle: incorporating the soil fauna. Ecology 2007;88: 1611–21.

189. Aerts R. The freezer defrosting: global warming and litter decomposition rates in cold biomes. Journal of Ecology 2006;94:713–24.

190. Wolters V. Biodiversity of soil animals and its function. European Journal of Soil Biology 2001;37:221–7.

191. Heemsbergen DA, Berg MP, Loreau M, van Hal JR, Faber JH, Verhoef HA. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science 2004;306:1019–20.

192. Swift MJ, Heal OW, Anderson JM. Decomposition in Terrestrial Ecosystems. Blackwell Scientific, Oxford, UK; 1979. p. 372.

193. Barros E, Grimaldi M, Sarrazin M, Chauvel M, Mitja D, Desjardins T, Lavelle P. Soil physical degradation and changes in macrofaunal communities in Central Amazon. Applied Soil Ecology 2004;26:157–68.

194. Chauvel A, Grimaldi M, Barros E, Blanchart E, Desjardins T, Sarrazin M, *et al.* Pasture damage by an Amazonian earthworm. Nature 1999;398:32–3.

195. Lavelle P, Pashanasi B. Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). Pedobiologia 1989;33:283–409.

196. Decaëns T, Jiménez JJ. Earthworm communities under an agricultural intensification gradient in Colombia. Plant and Soil 2002;240:133–43.

197. Swift MJ, Vandermeer J, Ramakrishnan PS, Anderson JM, Ong CK, Hawkins BA. Biodiversity and agroecosystem function. In: Mooney HA, Cushman JH, Medina E, Sala OE, Schulze ED, editors. Functional Roles of Biodiversity: A Global Perspective. SCOPE, John Wiley & Sons Ltd, Chichester, West Sussex, UK; 1996. p. 261–98.

198. Bardgett RD, Yeates GW, Anderson JM. Patterns and determinants of soil biological diversity. In: Bardgett RD, Usher MB, Hopkins DW, editors. Biological Diversity and Function in Soils. Cambridge University Press, Cambridge, UK, 2005. p. 100–18.

199. Decaëns T, Jiménez JJ, Gioia C, Measey GJ, Lavelle P. The values of soil animals for conservation biology. European Journal of Soil Biology 2006;42:S23–38.

200. James SW, Porco D, Decaëns T, Richard B, Rougerie R, Erséus C. DNA barcoding reveals cryptic diversity in *Lumbricus terrestris* L., 1758 (Clitellata): resurrection of *L. herculeus* (Savigny, 1826). PLoS ONE 2010;5(12): e15629, 8 pp.

201. Porco D, Decaëns T, Deharveng L, James SW, Skarzyński D, Erséus C, *et al.* Biological invasions in soil: DNA barcoding as a monitoring tool in a multiple taxa survey targeting European earthworms and springtails in North America. Biological Invasions 2013;15:899–910.

202. Collins NM. The distribution of soil macrofauna on the West Ridge of Gunung (Mount) Mulu, Sarawak. Oecologia 1980;44:263–75.

203. Bouché MB. Lombriciens de France, Ecologie et Systématique. Institut national de la Recherche agronomique, Paris, France, 1972. p. 671.

204. Cole AC Jr. A guide to the ants of the Great Smoky Mountains National Park, Tennessee. American Midland Naturalist 1940;24:1–88.

205. Loranger G, Bandyopadhyaya I, Razaka B, Ponge JF. Does soil acidity explain altitudinal sequences in collembolan communities? Soil Biology and Biochemistry 2001;33: 381–93.

206. González G, García E, Cruz V, Borges S, Zalamea M, Rivera MM. Earthworm communities along an elevation gradient in northeastern Puerto Rico. European Journal of Soil Biology 2007;43:S24–32.

207. Costanza R, d'Arge R, de Groot R, Farberk S, Grasso M, Hannon B, *et al.* The value of the world's ecosystem services and natural capital. Nature 1997;387:253–60.

208. MEA (Millennium Ecosystem Assessment). Ecosystems and Human Well-Being: Current State and Trends. Island Press, Washington, DC; 2005. p. 917. Available from: URL: www.maweb.org/en/Condition.aspx.

209. Davis DW, McMurtry JA. Introduction. In: Davis DW, Hoyt SC, McMurtry JA, AliNiazee MT, editors. Biological Control and Insect Pest Management. University of California, Division of Agricultural Sciences, Publication 4096. University of California Press, Oakland, California, 1979. p. i–ii.

210. van Lenteren JC. Internet Book of Biological Control. International Organization for Biological Control, Wageningen, The Netherlands; 2007. Available from: URL: www.IOBC-Global.org.

211. IPPC. Guidelines for the Export, Shipment, Import and Release of Biological Control Agents and Other Beneficial Organisms. International Standards for Phytosanitary Measures No. 3. FAO, Rome, Italy, 2005. 32 pp. Available from: URL: www.ippc.int/file_uploaded/1146657660135_ISPM3.pdf

212. Neuenschwander P. Biological control of cassava and mango mealybugs in Africa. In: Neuenschwander P, Borgemeister C, Langewald J, editors. Biological Control in IPM Systems in Africa. CABI Publishing, Wallingford, UK; 2003. p. 45–59.

213. Herren HR, Neuenschwander P, Hennessey RD, Hammond WNO. Introduction and dispersal of *Epidinocarsis lopezi* (Hym., Encyrtidae), an exotic parasitoid of the cassava mealybug, *Phenacoccus manihoti* (Hom., Pseudococcidae), in Africa. Agriculture, Ecosystems and Environment 1987;19:131–44.

214. Assefa Y, Mitchell A, Conlong DE, Muirhead KA. Establishment of *Cotesia flavipes* (Hymenoptera: Braconidae) in sugarcane fields of Ethiopia and origin of founding population. Journal of Economic Entomology 2008;101:686–91.

215. Dean HA, Schuster MF, Boling JC, Riherd PT. Complete biological control of *Antonina graminis* in Texas with *Neodusmetia sangwani* (a classic example). Bulletin of the Entomological Society of America 1979;25:262–7.

216. Lynch M, Lande R. Evolution and extinction in response to environmental change. In: Kareiva P, Kingsolver J, Huey R,

editors. Biotic Interactions and Global Change. Sinauer Assocs., Inc., Sunderland, Massachusetts, 1993. p. 234–50.

217. White EB, DeBach P, Garber MJ. Artificial selection for genetic adaptation to temperature extremes in *Aphytis lingnanensis* Compère (Hymenoptera: Aphelinidae). Hilgardia 1970;40:161–92.
218. Potting RPJ, Vet LEM, Overholt WA. Geographic variation in host selection behaviour and reproductive success in the stemborer parasitoid *Cotesia flavipes* (Hymenoptera: Braconidae). Bulletin of Entomological Research 1997;87:515–24.
219. Henry LM, May N, Acheampong S, Gillespie DR, Roitberg BD. Host-adapted parasitoids in biological control: does source matter? Ecological Applications 2010;20: 242–50.
220. Rando OJ, Verstrepen KJ. Timescales of genetic and epigenetic inheritance. Cell 2007;128:655–68.
221. Roderick GK, Hufbauer R, Navajas M. Special issue: evolution and biological control. Evolutionary Applications 2012;5(5):419–536.
222. Gilkeson LA, Hill SB. Genetic selection for and evaluation of nondiapause lines of predatory midge, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae). Canadian Entomologist 1986;118:869–79.
223. Gillespie DR, Quiring DMJ. Extending seasonal limits on biological control. IOBC/WPRS Bulletin 1993;16:43–5.
224. Gillespie DR, Quiring DMJ. Diapause induction under greenhouse conditions in two populations of *Dicyphus hesperus* (Hemiptera: Miridae). Biocontrol Science and Technology 2005;15:571–83.
225. Traoré, L, Pilon JG, Fournier F, Boivin G. Adaptation of the developmental process of *Anaphes victus* (Hymenoptera: Mymaridae) to local climatic conditions across North America. Annals of the Entomological Society of America 2006;99:1121–6.
226. Frago E, Guara M, Pujade-Villar J, Selfa J. Winter feeding leads to a shifted phenology in the browntail moth *Euproctis chrysorrhoea* on the evergreen strawberry tree *Arbutus unedo*. Agricultural and Forest Entomology 2010;12:381–8.
227. Chen YH, Opp SB, Berlocher SH, Roderick GK. Are bottlenecks associated with colonization? Genetic diversity and diapause variation of native and introduced *Rhagoletis completa* populations. Oecologia 2006;149:656–67.
228. Hodek I, Michaud JP. Why is *Coccinella septempunctata* so successful? (A point-of-view). European Journal of Entomology 2008;105:1–12.
229. Grewal PS, Gaugler R, Wang Y. Enhanced cold tolerance of the entomopathogenic nematode *Steinernema feltiae* through genetic selection. Annals of Applied Biology 1996;129:335–41.
230. Mukuka J, Strauch O, Ehlers RU. Variability in desiccation tolerance among different strains of the entomopathogenic nematode *Heterorhabditis bacteriophora*. Nematology 2010;12:711–20.
231. Grant JA, Villani MG. Soil moisture effects on entomopathogenic nematodes. Environmental Entomology 2003;32:80–7.
232. Amice G, Vernon P, Outreman Y, Van Alphen J, Van Baaren J. Variability in responses to thermal stress in parasitoids. Ecological Entomology 2008;33:701–8.
233. Bannerman JA, Gillespie DR, Roitberg BD. The impacts of extreme and fluctuating temperatures on trait-mediated indirect aphid-parasitoid interactions. Ecological Entomology 2011;36:490–8.
234. Gillespie DR, Nasreen A, Moffat CE, Clarke P, Roitberg BD. Effects of simulated heat waves on an experimental community of pepper plants, green peach aphids and two parasitoid species. Oikos 2012;121:149–59.
235. Hillier J, Hawes C, Squire G, Hilton A, Wale S, Smith P. The carbon footprints of food crop production. International Journal of Agricultural Sustainability 2009;7:107–18.
236. Foresight. The Future of Food and Farming (2011) Final Project Report. The Government Office for Science, London, UK, 40 pp. Available from: URL: www.bis.gov.uk/assets/bispartners/foresight/docs/food-and-farming/11-546-future-of-food-and-farming-report.pdf
237. Mackauer M. Genetic problems in the production of biological control agents. Annual Review of Entomology 1976;21:369–85.
238. Fauvergue X, Hopper KR. French wasps in the New World: experimental biological control introductions reveal a demographic Allee effect. Population Ecology 2009;51: 385–97.
239. Phillips CB, Vink CJ, Blanchet A, Hoelmer KA. Hosts are more important than destinations: what genetic variation in *Microctonus aethiopoides* (Hymenoptera: Braconidae) means for foreign exploration for natural enemies. Molecular Phylogenetics and Evolution 2008;49:467–76.
240. Samara RY, Monje JC, Zebitz CPW. Comparison of different European strains of *Trichogramma aurosum* (Hymenoptera: Trichogrammatidae) using fertility life tables. Biocontrol Science and Technology 2008;18:75–86.
241. Roush RT. Genetic variation in natural enemies: critical issues for colonization in biological control. In: Mackauer M, Ehler LE, Roland J, editors. Critical Issues in Biological Control. Intercept, Andover, UK, 1990. p. 263–88.
242. van Lenteren JC (ed.) Quality Control and Production of Biological Control Agents: Theory and Testing Procedures. CABI, Wallingford, UK, 2003. p. 327.
243. Brunner PC, Keller N, McDonald BA. Wheat domestication accelerated evolution and triggered positive selection in the beta-xylosidase enzyme of *Mycosphaerella graminicola*. PLoS ONE 2009;4(11):e7884, 8.
244. Myers JG. The original habitat and hosts of three major sugar-cane pests of tropical America. (*Diatraea*, *Castnia* and *Tomaspis*). Bulletin of Entomological Research 1932;23: 257–71, p. XIII.
245. Ashburner M, Hoy MA, Peloquin JJ. Prospects for the genetic transformation of arthropods. Insect Molecular Biology 1998;7:201–13.
246. Hoy MA. Transgenic arthropods for pest management programs: risks and realities. Experimental and Applied Acarology 2000;24:463–95.
247. Hoy MA. Recent advances in genetics and genetic improvement of the Phytoseiidae. Annual Review of Entomology 1985;30:345–70.
248. Sun J, Yang L, Wang Y, Ort DR. FACE-ing the global change: opportunities for improvement in photosynthetic radiation use efficiency and crop yield. Plant Science 2009;177:511–22.

249. Messmer R, Stamp P. Trends in drought research. Kasetsart Journal – Natural Science 2010;44:507–16.

250. Van Rijn PCJ, Tanigoshi LK. The contribution of extrafloral nectar to survival and reproduction of the predatory mite *Iphiseius degenerans* on *Ricinus communis*. Experimental and Applied Acarology 1999;23:281–96.

251. Robinson KA, Jonsson M, Wratten SD, Wade MR, Buckley HL. Implications of floral resources for predation by an omnivorous lacewing. Basic and Applied Ecology 2008;9:172–81.

252. Agrawal AA, Karban R, Colfer RG. How leaf domatia and induced plant resistance affect herbivores, natural enemies and plant performance. Oikos 2000;89:70–80.

253. Roda A, Nyrop J, Dicke M, English-Loeb G. Trichomes and spider-mite webbing protect predatory mite eggs from intraguild predation. Oecologia 2000;125:428–35.

254. Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD. A framework for community interactions under climate change. Trends in Ecology and Evolution 2010;25:325–31.

255. Vellend M. Conceptual synthesis in community ecology. Quarterly Review of Biology 2010;85:183–206.

256. Gilman RT, Fabina NS, Abbott KC, Rafferty NE. Evolution of plant–pollinator mutualisms in response to climate change. Evolutionary Applications 2012;5(1):2–16.

257. Ollerton J, Winfree R, Tarrant S. How many flowering plants are pollinated by animals? Oikos 2011;120:321–6.

258. Garibaldi LA, Steffan-Dewenter I, Kremen C, Morales JM, Bommarco R, Cunningham SA, *et al.* Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology Letters 2011;14:1062–72.

259. Garibaldi LA, Steffan-Dewenter, I, Winfree, R, Aizen MA, Bommarco R, Cunningham SA, *et al.* Wild pollinators enhance fruit set of crops regardless of honey-bee abundance. Science 2013;339(6127):1608–11.

260. Kjøhl M, Nielsen A, Stenseth NC. Potential Effects of Climate Change on Crop Pollination. Pollination Services for Sustainable Agriculture: Extension of Knowledge Base. FAO, Rome; 2011. vii + 38 p.

261. Malo JE, Baonza J. Are there predictable clines in plant–pollinator interactions along altitudinal gradients? The example of *Cytisus scoparius* (L.) Link in the Sierra de Guadarrama (central Spain). Diversity and Distributions 2002;8:365–71.

262. Arroyo MT, Primack R, Armesto JJ. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. American Journal of Botany 1982;69:82–97.

263. Kearns CA. Anthophilous fly distribution across an elevation gradient. American Midland Naturalist 1992;127:172–82.

264. Arroyo MTK, Armesto JJ, Primack RB. Community studies in pollination ecology in the high temperate Andes of central Chile II. Effect of temperature on visitation rates and pollination possibilities. Plant Systematics and Evolution 1985;149:187–203.

265. Lopez-Uribe MM, Almanza MT, Ordonez M. Diploid male frequencies in Colombian populations of euglossine bees. Biotropica 2007;39:660–2.

266. Cameron SA, Lozier JD, Strange JP, Koch JP, Cordes N, Solter LF, Griswold TL. Patterns of widespread decline in North American bumble bees. Proceedings of the National Academy of Sciences USA 2011;108:662–7.

267. Genersch E, Aubert M. Emerging and re-emerging viruses of the honey bee (*Apis mellifera* L.). Veterinary Research 2010;41(6), 54. doi: 10.1051/vetres/2010027

268. Brown M. Overview of the regulatory framework for apiculture. In: Aubert M, Ball B, Fries I, Moritz R, Milani N, Bernardinelli I, editors. Virology and the Honeybee. Project Report EUR 21937. Office for Official Publications of the European Communities, Luxembourg, 2008. p. 371–420.

269. OIE (Office International des Épizooties). *Terrestrial Animal Health Code*, 19th edn. World Organisation for Animal Health, Rome, Italy; 2010. Available from: URL: www.oie.int/eng/normes/mcode/en_sommaire.htm

270. Slaa EJ, Sanchez-Chaves LA, Malagodi-Braga KS, Hofstede FE. Stingless bees in applied pollination: practice and perspectives. Apidologie 2007;37(2006):293–315.

271. Senapati BK, Lavelle P, Giri S, Pashanasi B, Alegre J, Decaëns T, *et al.* In-soil earthworm technologies for tropical agroecosystems. In: Lavelle P, Brussaard L, Hendrix PF, editors. Earthworm Management in Tropical Agroecosystems. CABI, Wallingford, UK, 1999. p. 199–237.

272. Lavelle P, Lattaud C, Trigo D, Barois I. Mutualism and biodiversity in soils. Plant and Soil 1995;170:23–33.

273. Bawa KS. Plant-pollinator interactions in tropical rain forests. Annual Review of Ecology and Systematics 1990;21: 399–422.

274. Delgado DL, Pérez ME, Galindo-Cardona A, Giray T, Restrepo C. Forecasting the influence of climate change on agroecosystem services: potential impacts on honey yields in a small-island developing state. Psyche 2012, Article ID 951215, 10 pp. doi:10.1155/2012/951215

275. Kaplan JK. What's buzzing with Africanized honey bees? Agricultural Research Magazine (USDA) 2004;52(3):4–8.

276. IPPC. *Framework for Pest Risk Analysis*. International Standards for Phytosanitary Measures No. 2. FAO, Rome, Italy, 2007. p. 15. Available from: URL: www.ippc.int/file_uploaded/1179929048771_ISPM02_2007_E.pdf

277. Cock MJW, Biesmeijer JC, Cannon RJC, Gerard PJ, Gillespie D, Jiménez JJ, *et al.* Climate change and invertebrate genetic resources for food and agriculture: state of knowledge, risks and opportunities. Commission on Genetic Resources for Food and Agriculture, Background Study Paper No. 54. FAO, Rome, 2011; p. 105. Available from: URL: www.fao.org/docrep/meeting/022/mb390e.pdf