

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

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116 **ABSTRACT**

117 Terrestrial invertebrate species play a dominant role in the trophic dynamics of agricultural
118 ecosystems. Subtle changes in the composition of communities and species interactions at
119 different trophic levels, and role of ecosystem engineers can dramatically modify the impacts
120 of invertebrates on plant productivity in agricultural systems.

121 The impact of climate change on relevant invertebrates in agricultural systems, and their
122 potential to adapt or move is discussed. All terrestrial systems (including forestry and
123 pasture) are considered, although the main focus is on crop production systems. Our treatise
124 centres on whole organisms (as opposed to genetic information from invertebrates) that play
125 key roles in agricultural systems. We start with an overview of current thinking on how
126 climate change may affect invertebrates. Then, recognizing the great invertebrate biodiversity
127 associated with agro-ecosystems, the review focuses on three key groups – soil invertebrates,
128 biological control agents and pollinators.

129 A variety of research gaps became apparent during the course of our review. Specific
130 conclusions regarding the impact of climate change on particular elements of invertebrate
131 genetic resources in agriculture are not possible yet. Existing evidence suggests three general
132 assumptions can be made. First, it is likely that climate change will disrupt to varying degrees
133 the role and use of invertebrates in agriculture, especially sustainable agriculture, even though
134 the precise nature of the disruptions is not yet known. Second, without intervention, these
135 disruptions will result in production losses particularly in sustainable agriculture, even though
136 the scale and extent of the losses is not yet known. Third, the extent of some of the losses will
137 justify intervention to facilitate adaptations of the invertebrates, even though the methods
138 with which to intervene and policies to facilitate this intervention are not yet in place.

139 **Key words:** ecology, interactions, soil, biological control, pollinators, Arthropoda, Insecta,
140 Annelida, Nematoda, pests, crops, plant health

141 **INTRODUCTION**

142 Invertebrate species are an essential component in agricultural systems (see review by Cock
143 *et al.* 2012 and sources therein), as they have a major influence on plant health and
144 productivity and therefore play a key role in food security. The vast majority of the
145 invertebrate species in agro-ecosystems belong to the phyla Arthropoda (especially the class
146 Insecta) above ground, and Annelida and Nematoda below ground (Lavelle and Spain, 2001).
147 From an ecological perspective, these animals play important roles in food webs as primary
148 consumers (herbivores); higher-order consumers (predators, parasitoids, and
149 hyperparasitoids); mutualists (facultative and obligate pollinators); parasites of plants,
150 invertebrates and vertebrates; and saprophytes (mediators of decomposition, and energy and
151 nutrient flows into and out of agricultural ecosystems). The different roles that invertebrate
152 species play in an agricultural ecosystem are responsible for a complex web of direct and
153 indirect interactions. For instance, soil invertebrates include the functional group of
154 ecosystem engineers (Jones *et al.*, 1994) that are powerful drivers of soil physical functions
155 (water dynamics, aeration, protection from erosion hazards) due to changes in soil structure.
156 They play an important role in carbon cycling, as they control the carbon sequestration
157 process and influence greenhouse gas emissions. The production of biogenic structures by
158 this group can make carbon inaccessible within aggregates for some time and so slow down
159 the use of carbon by soil organisms.

160 *The expected impact of climate change on agricultural production systems and invertebrates*
161 *relevant to food and agriculture*

162 As areas become more favourable for growing a particular crop, they also become more
163 favourable for a suite of associated crop pests. Pest management practices will therefore need
164 to adapt to such changes. As regions further from the equator become warmer, past
165 experience in pest management from regions closer to the equator may provide guidance.

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

177 Despite many uncertainties and unknowns, there is a growing consensus that climate change
178 could lead to an overall increase in the abundance and diversity of invertebrate pests – and
179 pest pressure – as habitats become more favourable for their establishment and development,
180 new niches appear, stabilizing interactions are decoupled, and invasive species arrive as a
181 result of range expansions (e.g. Cannon, 1998; Patterson *et al.*, 1999; Rosenzweig *et al.*,
182 2001; Fuhrer, 2003; Luedeling *et al.*, 2011). This is not to deny that some impacts of climate
183 change may be beneficial, but the detrimental effects referred to above suggest that, at the
184 very least, “pest and pathogen attacks are likely to be more unpredictable and the amplitude
185 larger” (Gregory *et al.*, 2009).

186 *Potential of invertebrates in agriculture to adapt to and mitigate the impact of climate*
187 *change*

188 Biotic responses to climate change include adaptation *in situ*, range shifts to more tolerable
189 climes or, failing these, extinction (Davis *et al.*, 2005), and as suggested by these authors,
190 organisms will have to ‘adapt, move or die’.

191 Adaptation involves activities that enable ecosystems – and the people that rely on them – to
192 adjust to climate change, for example, by buffering the effects of extreme weather events or
193 decreasing the vulnerability of agro-ecosystems to their impacts (Burgiel and Muir, 2010).
194 Observational data over the last 50 years has shown that adaptation to climate change is
195 species-dependent (Root *et al.*, 2003). The lack of studies makes it risky/inappropriate to
196 generalize on the possible adaptation of invertebrates to the challenges identified.
197 Nevertheless, when expansion of species range takes place, selection will tend to favour
198 individuals with higher propensity for dispersal (Travis and Dytham, 2002), and dispersal
199 ability determines the potential to escape adverse direct and indirect consequences of
200 temperature changes (Watkinson and Gill, 2002) by colonizing new habitats as they become
201 available.

202 As we shall discuss, most invertebrates are expected to change their geographical distribution
203 in response to climate change so as to remain in habitats to which they are well adapted. Sub-
204 fossil evidence from the Quaternary Ice Ages suggests that in times of rapid climate change,
205 insects track acceptable conditions rather than evolving *in situ* (Coope, 2004; Case study 2)
206 and there is evidence that this may be accompanied by genetic increases in dispersal capacity
207 at range boundaries (Hill *et al.*, 2011). Even so, we recognize that the current landscape is
208 very different from any that existed during the Quaternary Period, being divided by barriers
209 created by human activities. However, these barriers are likely to affect species in natural
210 ecosystems rather more than those associated with agro-ecosystems, and the movement of the
211 latter is likely to be facilitated rather than hindered by human-induced landscape changes.
212 Hence, many of the challenges associated with the management of invertebrate genetic
213 resources in agriculture in the context of climate change will relate to climate-driven or
214 human-assisted movement of invertebrate species.

215 Some *in situ* adaptation is expected, especially where movement is not an option (e.g. low,
216 isolated islands) and species have a short generation time and a high rate of reproduction. The
217 ability of a species to adapt rapidly to environmental changes is termed phenotypic plasticity.
218 If, however, conditions exceed the plastic limits of a species, evolutionary change may be
219 necessary in order to prevent extinction. The concept of evolutionary rescue to arrest
220 population decline and allow population recovery before extinction ensues (Gonzalez *et al.*,
221 2012) may be particularly relevant to populations, especially island populations, challenged
222 by climate change. In their review, Donnelly *et al.* (2012) found many reports of direct
223 observations of phenotypic plasticity in species but less conclusive evidence of genetic
224 adaptation.

225 The variability in predictions can be explained by ecological and evolutionary processes that
226 significantly alter the ranges of species. Range movement of species is not exclusively
227 determined by evolutionary responses, based primarily on existing genetic diversity within
228 species. Phenotypic plasticity constitutes a critical survival mechanism for adaptation
229 (Thomas *et al.*, 2001), given that genetic variation already exists within species. Moreover,
230 evolutionary and plastic responses to climate change are not mutually exclusive.

231 Where self-organization and mutualism predominate, as in soils, there is a possibility that
232 systems will adapt more rapidly to the effects of climate change as invertebrates may not be
233 so reliant on their own ability to change. For example, earthworms and termites depend on
234 soil microbiota for their digestion, and as the short generation time of microbiota is likely to
235 enable them to adapt relatively rapidly to new conditions associated with climate change, the
236 invertebrates may profit. Thus, the ability to predict adaptation of organisms to climate
237 change is hampered as many studies focused on individual species overlooking the fact that
238 species interact with other species, and are part of complex interaction networks (Harrington
239 *et al.*, 1999; Walther, 2007). As Berg *et al.* (2010) stated, to study species persistence under
240 global climate change, it is critical to consider the ecology and evolution of multispecies
241 interactions.

242 *Scope and structure of review*

243 The scope of this review is restricted to terrestrial agriculture, and excludes marine and
244 aquatic production systems. Although many invertebrates are important food items in their
245 own right, and several sectors (e.g. honey and silk) rely on products produced by
246 invertebrates, we will not consider these aspects in our review. All terrestrial agricultural

247 systems are considered, including forestry and pasture, but the main focus is on crop
248 production systems. We recognize that in addition to their role in crop production including
249 weed biological control, biological control agents (BCAs) play a role in the protection of
250 stored crops, but the latter role is not treated as a separate topic. The review focuses on whole
251 organisms (as opposed to genes or other genetic information from vertebrates), which play
252 key roles in agricultural systems. First we provide an overview of current thinking on how
253 climate change may affect invertebrates. Then, recognizing the great invertebrate biodiversity
254 associated with agro-ecosystems, the review focuses on three key groups – soil invertebrates,
255 biological control agents and pollinators. Between them, these three groups cover the most
256 important ecosystem services that invertebrates provide to agriculture (Cock *et al.*, 2012), and
257 hence they may be used, manipulated or moved to benefit agriculture. A variety of research
258 gaps became apparent during the course of our review, and these are highlighted in the final
259 section.

260 **EFFECTS OF CLIMATE CHANGE ON INVERTEBRATES RELEVANT TO** 261 **AGRICULTURE**

262 In this section we review the potential direct and indirect impacts of climate on invertebrates
263 relevant to food and agriculture.

264 **Climate change predictions**

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

269 The projections of future changes in climate included:

- 270 • Over the next two decades, a warming of 0.2–0.4°C per decade.
- 271 • Warming and sea-level rise to continue for centuries even if greenhouse-gas
272 concentrations are stabilized.
- 273 • A 1.8°C rise above 1980–1999 levels in global average surface air temperatures by the
274 end of the twenty-first century for a low emission scenario (IPCC B1).
- 275 • A 4.0°C rise above 1980–1999 levels in global average surface air temperatures by the
276 end of the twenty-first century for a high emission fossil-fuel intensive scenario (IPCC
277 A1FI).
- 278 • Warming expected to be greatest over land and at most high northern latitudes.
- 279 • By the end of the twenty-first century, rainfall very likely to have increased in high
280 latitudes and East Africa and decreased in most subtropical regions (Central America,
281 the Mediterranean basin and the subtropical regions of Africa, Australia and Central
282 Asia); increases in tropical precipitation projected during rainy seasons, and over the
283 tropical Pacific in particular.
- 284 • Increase in extreme weather events (droughts, heat waves, heavy precipitation, and
285 intense tropical cyclones).

286 It has been suggested that future climates may consist of novel temperature and precipitation
287 regimes, which have no current climatic equivalent, resulting in new species associations, so-

288 called, ‘no-analog’ communities (Williams *et al.*, 2007), although such climate
289 reconfigurations may well have occurred in past glaciation cycles.

290 Elevated levels of CO₂ (eCO₂), the most important anthropogenic greenhouse gas, have
291 positive effects on plant growth and yield. Levels have increased from a pre-industrial level
292 of about 280 ppm CO₂ to 379 ppm in 2005. On its present trajectory, atmospheric CO₂ will
293 pass 550 ppm by 2050. However, the benefits to plant growth and yield will be restricted by
294 many limiting factors. The major projected impacts of climate change on agriculture (and the
295 IPCC assessment of probability of occurrence) include:

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

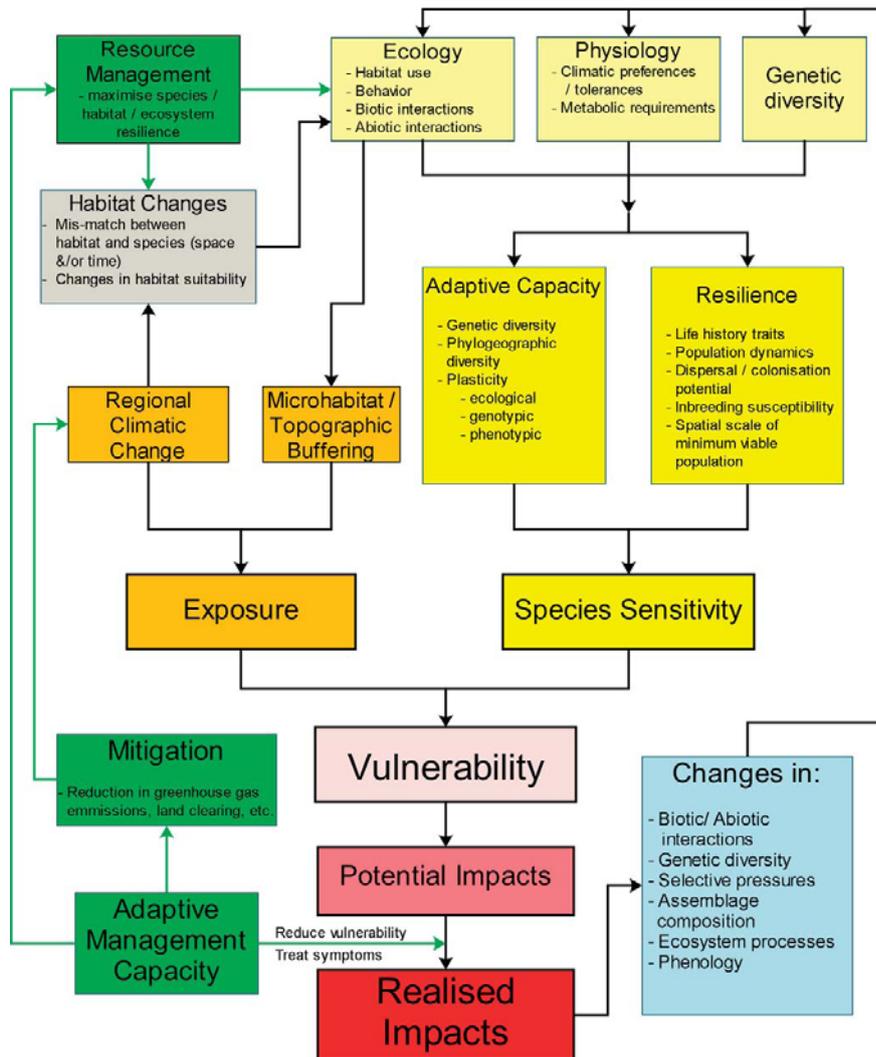
307 Agriculture has historically shown high levels of adaptability to climate variations, and trade
308 has the capacity to reduce regional and global impacts. The dependence of developing
309 countries on food imports is likely to increase as even slight warming reduces yield in
310 seasonally dry and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

312 Management options to optimize yield and/or economic returns listed by Easterling *et al.*
313 (2007) include:

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

319 **Impact of climate change on invertebrates**

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



322

323 **Figure 1.** A general framework showing factors influencing the vulnerability of species to
 324 climate change. Much more detail could be added for most boxes, for example under
 325 “Ecology”, food web interactions and more than 80 types of indirect effects could be
 326 mentioned. Source Williams *et al.* (2008).

327 Single and combined effects are expected, and their responses will be context dependent.
 328 Most studies have dealt with only single factors such as eCO₂, warming or changes in
 329 precipitation. There is a paucity of data on the combined effects of such climate change-
 330 related factors (Kardol *et al.*, 2011; Case study 1) and more realistic multifactorial
 331 experiments are needed to investigate potential non-linear interactions between individual
 332 factors (Mikkelsen *et al.*, 2007).

333 Invertebrates have limited ability to regulate their body temperature and are directly under the
 334 control of temperature for development, reproduction and activity. Whilst some groups such
 335 as soil invertebrates (Staley and Johnson, 2008) and animal ectoparasites (Estrada-Pena,
 336 2008) may be buffered by the niches they occupy, the interaction between a species’ thermal
 337 sensitivities and the abiotic factors determined by climate largely explains its observed
 338 distribution and abundance, although biotic interactions can also potentially influence the
 339 macro-distribution of species (Araújo and Luoto, 2007). Within this distribution, climate

340 change will have further indirect effects on invertebrates through its effects on host
341 availability and the other resources plant communities provide (Kardol *et al.*, 2010).

342 Invertebrates exhibit very wide variations in sensitivity to temperature, depending on their
343 environment, and have therefore developed a range of survival strategies (Bale & Hayward,
344 2010). Berg *et al.* (2010) analysed 50 years of published literature and found pronounced and
345 consistent differences between trophic groups. They concluded that changes in species
346 distribution and abundance will be determined more by the impact of temperature on species
347 interactions, than by the thermal tolerance of individual species. Vulnerability to global
348 warming appears to increase with trophic rank: herbivores respond more strongly to
349 temperature than plants, and warming leads to a disproportionate loss of top predators (Voigt
350 *et al.*, 2003; Schweiger *et al.*, 2008; Thomson *et al.*, 2010). Species at the higher trophic level
351 (parasitoids and predators) depend on the capacity of the lower trophic levels to adapt to
352 changes (Petchey *et al.*, 1999). In other words, climate change effects may be amplified by
353 trophic responses transmitted through natural enemies (Gao *et al.*, 2008) or competitors
354 (Stacey and Fellows, 2002). Natural enemies with very narrow and specific host ranges – a
355 highly desirable attribute for classical biological control programmes – may be more sensitive
356 to climate change than generalist herbivores and predators because they are of necessity
357 precisely synchronized with the development of their hosts (Hance *et al.*, 2007).

358 **Geographical range shifts**

359 With climate change, the crops produced in most regions are expected to change over time as
360 growers select and develop species and varieties that optimize yield and/or economic returns
361 under the prevailing conditions – in other words, adapting agriculture to the climates of the
362 future (Howden *et al.*, 2007).

363 Recent research suggests that there have been very abrupt changes of climate in our planet's
364 recent glacial history (Steffensen *et al.*, 2008) implying that both the current and projected
365 speed of climate change are not without precedent (Hof *et al.*, 2011). Sub-fossil evidence
366 from the Quaternary Ice Ages suggests that in times of rapid climate change, insects track
367 acceptable conditions rather than evolving *in situ* (Coope, 2004; Case study 2) and there is
368 evidence that this may be accompanied by evolutionary increases in dispersal capacity (Hill
369 *et al.*, 2011).

370 Aided by accidental transfer through human activities, the majority of invertebrate pollinators
371 and pests and their natural enemies can be expected to move with their host plants as crop
372 and forage distributions change. The planet has already warmed by about 0.75°C in the
373 twentieth century (Easterling, 2007) and there is compelling evidence for a general poleward
374 shift in the breeding distributions of a large number of invertebrates (e.g. Hickling *et al.*,
375 2006; Musolin and Fujisaki, 2006). Range boundaries are shifting latitudinally (i.e. towards
376 the poles) at an average rate of about 6 km per decade (Parmesan and Yohe, 2003), and
377 altitudinally – assuming a lapse rate of 6.5°C per 1 000 m and 3.5°C rise for the next century
378 – at a rate of at least 50 m per decade (Whittaker and Tribe, 1996; Menéndez, 2007; Colwell
379 *et al.*, 2008); rates that most mobile pest and pollinator species are capable of tracking
380 providing there are no major ecological or physical barriers (Case study 3). As range
381 boundaries shift, existing species composition will shift based on temperature sensitivities.
382 For example, the cold-adapted bumblebee *Bombus bellicosus* Smith (Hymenoptera: Apidae)
383 has become extinct in the former northern portion of its distribution range in Brazil whereas

384 two co-occurring species with wider tolerances have become more abundant (Martins and
385 Melo, 2010).

386 The extent to which invertebrates will be able to track climate change will probably vary
387 enormously, depending on their dispersal abilities and the existence of green bridges (Travis,
388 2003) as well as the responses of their host plants (Pelini *et al.*, 2011). Some species will be
389 tied to specific latitudes because of direct or indirect photoperiod requirements (Saikkonen *et al.*
390 2012). Just as Coope (2004) observed that any thermally sensitive species that were tied to
391 a specific latitude were unlikely to survive the onslaught of the first glacial cooling, so will
392 such species be vulnerable to climate change unless they can shift to higher altitudes or adapt
393 *in situ* (Davis *et al.*, 2005). Those on oceanic islands have similarly limited options. In
394 general, habitat specialists, especially those with poor dispersal ability, will be least able to
395 keep pace with climate change (Travis, 2003). Many soil invertebrates have low dispersal
396 rates, and the time taken for beneficial species to shift to new areas will also be influenced by
397 the availability of supplementary resources (e.g. nectar and pollen, and winter or summer
398 diapause sites). Also, for some species, infrequent extreme weather events may be more
399 important in determining distributions and species persistence than long-term gradual
400 changes in climate (Gutschick and Bassirirad, 2003). The evidence from the geological past
401 also suggests that species are unlikely to respond as intact communities (Russell and Grimm,
402 1990; Lawton, 1998; Colinvaux, 2005). Therefore current communities, especially those
403 specialist invertebrate assemblages associated with exotic crop species, are unlikely to remain
404 intact under climate change and there could be some positive (absence of pest) or negative
405 (absence of beneficial invertebrates) effects on yield as well as possible destabilization of
406 agro-ecosystems.

407 Responses of invertebrates to climate change may be inhibited or hampered by human
408 activities, through habitat loss and fragmentation, land-use changes and reduction of genetic
409 diversity (Thomas *et al.*, 2004) or buffered by conservation (Arribas *et al.*, 2012) and
410 ecological engineering (Mitsch, 2012) practices. How a landscape is managed over time will
411 affect the composition, abundance and status of the invertebrate species present. For example,
412 butterfly species diversity decreased during the rapid industrialization of Europe, at the end of
413 the nineteenth century, and when intensive large-scale farming developed from the middle of
414 the twentieth century (e.g. Laussmann *et al.*, 2010). The grain industry in Australia has also
415 seen major shifts in the status and abundance of different invertebrate pests, over a 30-year
416 period (early 1980s to 2006–07), as a consequence of several drivers, including climate
417 change and intensified farming (Hoffmann *et al.*, 2008). Similarly, long-term studies in
418 western Poland, have documented a progressive increase in the abundance of heat-loving
419 (thermophilic) insects, typically associated with grasslands, probably linked to both climate
420 change (especially droughts) and an increasing proportion of cereals in crop rotations (Karg
421 and Balazy, 2009). It is sometimes difficult to separate out the effects of changes in land use
422 from changes in climate, as they are often linked. Responses to climate may be unpredictable,
423 and existing interdependencies between species may only become apparent when they
424 become uncoupled as a result of asynchronous responses to climate change (Parmesan, 2007).
425 Groffman and Jones (2000) concluded that there have been too few ecosystem-scale
426 experiments on the role of invertebrates; more experiments are needed which reflect the
427 complexities of real agro-ecosystems (Hulme, 2005).

428 **Increased risk of outbreaks**

429 Increases in the frequency of extreme weather events (such as droughts, heat waves,
430 unseasonal cold and frosts, floods and storms) are likely under most climate change
431 scenarios. Such extreme weather events are followed frequently by pest population
432 explosions. These may be indirectly mediated by factors such as improved food quality and
433 quantity due to seasonal rainfall (Branson, 2008; Case study 4) and physical damage such as
434 gaps left when trees are blown down (Bouget and Duelli, 2004). Effects may also be
435 mediated through impact on natural enemies (Stireman *et al.*, 2005). Sequential extremes
436 (e.g. prolonged drought followed by intense precipitation) can decouple long-evolved
437 relationships between species that are essential for controlling pests (Rosenzweig *et al.*,
438 2001). Holt and Colven (1997) highlighted the importance of predation in the prevention of
439 outbreaks of the grasshopper *Oedaleus senegalensis* in the Sahel, an arid zone of Africa and
440 that the risk of outbreaks is highest when this natural regulatory mechanism breaks down
441 with increased frequency and severity of drought. BCAs that rely on their hosts remaining
442 alive throughout their development are particularly vulnerable.

443 Although much of the evidence associating insect outbreaks and drought is circumstantial, or
444 simply correlative – consisting largely of observations that outbreaks of insects such as bark
445 beetles and leaf feeders are typically preceded by unusually warm, dry weather – there is a
446 consistent, positive correlation between insect outbreaks and dry, nutrient-poor sites (Mattson
447 and Haack, 1987). The impact of drought on pests is also likely to be mediated via natural
448 enemies. In New Zealand pastures, grass grub *Costelytra zealandica* (White) (Coleoptera:
449 Scarabaeidae) outbreaks often occur two to four years after severe summer droughts because
450 of the suppression of protozoal and bacterial pathogens in the soil (Popay, 1992). Droughts
451 may induce outbreaks of pests such as spider mites, by reducing the efficacy of natural
452 enemies (English-Loeb, 1990), in part due to the effects of extreme leaf temperatures on the
453 performance of predatory mites (Stavriniades *et al.*, 2010). Some parasitic wasps may be
454 eliminated altogether, as a result of drought-induced elimination of the nectar plants they
455 depend upon. Equally, if droughts reduce pests to a very low level, then associated
456 specialized biological control agents will in turn be reduced, due to host rarity, resulting in a
457 pest outbreak until the population of BCAs recovers.

458 Temperature extremes can also affect the maintenance of diversity (both species and genetic)
459 of the invertebrate bacterial endosymbiont community. These endosymbionts mediate many
460 processes, for example defence against parasitoids and pathogens, tolerance of heat and cold
461 stress, host range, and production of essential amino acids (Werren, 1997; Douglas, 1998;
462 Enigl and Shausberger, 2007).

463 Exposure to temperature extremes induces lethal and sublethal damage in parasitoids, which
464 generally decreases their longevity, fecundity and mobility, along with decreased host-
465 location ability (Hance *et al.*, 2007; Roux *et al.*, 2010). In addition, extreme temperatures
466 increase the efficacy of the host's immune system in resisting and killing parasitoids (Hance
467 *et al.*, 2007), with multiple observations that high temperatures can enhance the survival of
468 parasitized hosts (Thomas and Blanford, 2003).

469 In many parasitoid Hymenoptera, the endosymbiont bacterium *Wolbachia* is a sex ratio
470 distorter, and is responsible for female-biased or even fully thelytokous (female-only) strains
471 and species (Werren *et al.*, 2008; Engelstädter and Hurst, 2009). *Wolbachia* species are
472 present in mature eggs, but not mature sperm, so only infected females pass the infection on
473 to their offspring. *Wolbachia* maximize their spread by significantly altering the reproductive
474 capabilities of its hosts, with four different phenotypes: feminization (infected males develop

475 female characteristics), parthenogenesis (infected females develop embryos without
476 fertilization by males), male killing (eliminates infected males to the advantage of surviving
477 infected female siblings), and sperm–egg incompatibility (or cytoplasmic incompatibility, the
478 inability of *Wolbachia*-infected males to successfully reproduce with uninfected females or
479 females infected with another *Wolbachia* strain). These insect–endosymbiont associations
480 may be impaired, or even eliminated, by exposure to high temperatures (Pintureau *et al.*,
481 1999; Pintureau and Bolland, 2001; Thomas and Blanford; 2003, Guay *et al.*, 2009). Where
482 its presence generates female-biased reproduction in parasitoids, the elimination of
483 *Wolbachia* by heat stress may disrupt the population dynamics of the BCA and cause
484 outbreaks of the pest host (Zhou and Zhang, 2009).

485 **New pest and plant species**

486 The intensification of weather systems, and/or absence of frosts in geographically isolated
487 temperate regions and islands, will increase their vulnerability to colonization via wind
488 dispersal. For instance, New Zealand has been exposed to airborne invertebrates from
489 Australia for millions of years, but most species have not become established (Phillips *et al.*,
490 2006; Case study 5). With increasing temperatures, however, there will be increased use of
491 subtropical plants in production systems and invasive subtropical weed species are likely to
492 become more prevalent. These plants may thrive in the absence of their co-evolved
493 herbivores. Some alien weeds, originally introduced for floral displays may, however, be of
494 benefit to native pollinators. It is inevitable therefore, that establishment events will increase
495 in frequency, as climate change has the potential to affect the introduction, spread and
496 establishment of invasive alien species (Weltzin *et al.*, 2003; Case study 6). Without specific
497 natural enemies, some of these species will become pests and may be more responsive to
498 eCO₂ than native species (Song *et al.*, 2009), with implications for control measures.

499 **Changes in invertebrate development, survival and behaviour**

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

503 Species with long life cycles, especially if controlled by photoperiod, may show little change,
504 whereas species characterized by high growth potential, multivoltinism (Case study 7) and
505 absence of diapause may expand. Under climate change, multivoltine species may be able to
506 produce additional generations, relative to current conditions in a given locale, with a
507 potentially greater impact on their host plants (Tobin *et al.*, 2008). Species that are frost
508 sensitive will benefit from warm winters through increased survival and may increase in pest
509 status. Expansions in the ranges of many pests are already evident as a result of reduced
510 winter mortality (e.g. Yukawa *et al.*, 2007). In contrast, species normally in diapause in
511 winter may decrease in pest status by being disadvantaged as a result of high energy losses,
512 development of pathogens and greater availability to predators (Lastuvka, 2009). Climate
513 change may favour the parasitoid: increased winter temperatures may promote parasitism in
514 regulating populations of the European pine sawfly, *Neodiprion sertifer* (Geoffroy)
515 (Hymenoptera: Diprionidae), due to the lower mortality of parasitized eggs in the winter
516 (Veteli *et al.*, 2005). Similarly, increased summer temperatures can favour increased
517 parasitoid and predator activities (Virtanen and Neuvonen, 1999). In contrast, the solitary
518 bees *Osmia lignaria* Say (Hymenoptera: Megachilidae) will be negatively affected by
519 extended summers under climate change, as few can survive short winter conditions (Bosch

520 *et al.*, 2010). In many cases, the extrinsic factors controlling diapause are complex, often
521 involving interactions between day length, temperature, and other factors such as moisture,
522 nutrition, crowding and maternal effects. The effects of climate change on the abundance and
523 status of a pest species will vary with region, ecosystem and the fitness of the individuals in
524 the population.

525 There is consensus that climate change will have a profound effect on soil-organism
526 performance and the functions they provide (Klironomos *et al.*, 1996; Schröter *et al.*, 2004;
527 Kardol *et al.*, 2010).

528 Elevated CO₂ can change the abundance and species composition of soil organisms (Jones *et al.*
529 *et al.*, 1998). Yeates *et al.* (1997) reported significant responses in the soil fauna to eCO₂ (750
530 parts per million by volume): eight out of ten nematode taxa (mainly omnivore and predator
531 species) reacted positively to increased CO₂ levels, while the bacteria-feeding *Rhabditis* spp.
532 showed a marked decrease. Loranger *et al.* (2004) found that collembolan abundance
533 decreased greatly under eCO₂ and O₃ (another greenhouse gas) in a Free-Air Carbon Dioxide
534 Enrichment (FACE) experiment in northern Wisconsin. Temperature is a key factor
535 regulating many biogeochemical processes such as soil respiration (the emission of CO₂ due
536 to producers or consumers), litter decomposition, nitrogen mineralization (the biological
537 transformation of organically combined nitrogen to ammonium nitrogen during organic
538 matter degradation) and denitrification (the microbially facilitated process of nitrate reduction
539 that may ultimately produce molecular nitrogen, N₂) (Norby *et al.*, 2007).

540 Not all soil fauna will respond in the same way (Roy *et al.*, 2004), with flow-on effects on the
541 abundance and community composition of soil invertebrates. For some, the ability to migrate
542 down the soil profile to cooler and moister levels will remain an important survival strategy.
543 Laboratory experiments have shown that a 3.3°C warming had a positive effect on abundance
544 of saprophagous macro-arthropods (i.e. those feeding on dead organisms) such as millipedes,
545 possibly as a result of increased microbial development in the leaf litter and/or increased food
546 utilization (David and Gillon, 2009). Sohlenius and Boström (1999) moved soil cores from
547 cooler to warmer sites in Sweden and found that total nematode populations and the ratio of
548 fungus- to bacteria-feeding nematodes increased. Similarly, Diptera larvae densities fell and
549 enchytraeid worm densities increased when soil cores were transplanted from high-elevation
550 sites to a lower area with an associated mean annual temperature increase of 2.5°C and drier
551 conditions (Briones *et al.*, 2009). Harte *et al.* (1996) showed that experimental heating of
552 field plots in a subalpine meadow in Colorado reduced biomass of soil mesofauna and
553 macrofauna in dry zones but enhanced biomass in moist zones. Soil invertebrate responses to
554 warming are crucial in controlling carbon fluxes in peat soils (Carrera *et al.*, 2009) and have
555 the potential to speed up the decomposition of organic matter with important implications for
556 the global carbon cycle. Expected increases in temperature will also favour humivorous
557 (humus-feeding) termites and endogeic earthworm species that feed in the soil (Lavelle *et al.*,
558 1997).

559 Warmer temperatures are likely to alter invertebrate behaviour. For instance, “sit and wait”
560 spiders will move to cooler niches in the habitat while active hunting species cover larger
561 territories (Barton and Schmitz, 2009). Such behavioural changes by predators may have
562 flow-on effects. In a field food web, increased temperature intensified the behavioural shift
563 by grasshoppers to feed preferentially on herbs rather than grasses in the presence of hunting
564 spiders (Barton *et al.*, 2009). To ensure generalist natural enemies continue to contribute to
565 effective pest management in future agroecosystems, increased effort is needed now to better

566 understand their requirements and how to support them, including landscape-level movement,
567 refugia in time and space, alternative food sources and other aspects of conservation
568 biological control.

569 Temperature has a direct effect on the pathogenicity of fungi that attack invertebrates, such as
570 *Beauveria bassiana* and *Metarhizium anisopliae*, which can either be very virulent, causing
571 extensive and rapid mortality in days, or virtually benign, with the same hosts surviving for
572 weeks or even months (Thomas and Blanford, 2003).

573 Atmospheric CO₂ levels could have direct effects on invertebrates, but there are few
574 examples (Case study 1). Elevated CO₂ has been reported to affect negatively the avoidance
575 behaviour of invertebrates, such as alarm signalling by aphids in response to a predator
576 (Mondor *et al.*, 2004). While some pests, such as mosquitoes and some plant pests, use CO₂
577 directly in host location (Johnson *et al.*, 2006; Guerenstein and Hildebrand, 2008), there is no
578 evidence for similar behaviours among predators and parasitoid BCAs to date. However, this
579 is likely to occur in at least some species, and host and prey location, and attack and
580 predation rates, might be compromised in future eCO₂ atmospheres. For some plant pests and
581 weed BCAs, response cells saturate under high CO₂ (400 ppm or higher, depending on
582 species) (Guerenstein and Hildebrand, 2008). *Cactoblastis cactorum* (Berg) (Lepidoptera:
583 Pyralidae), an important BCA of prickly pear cactus (*Opuntia* spp.) in some parts of the
584 world, is an example of a BCA in which host location could be impaired by eCO₂ (Stange,
585 1997).

586 Interactions between the effects of different elements of climate change will almost certainly
587 be important, and likely to confound some of the expectations based on a single factor. Soil
588 temperature covaries with soil moisture, and global climate change is likely to involve shifts
589 in rainfall patterns, while elevated temperature would lead to increased evaporation and plant
590 transpiration and affect the frequency of wetting–drying cycles. Therefore, generalizations
591 about the effects of climate change on soil micro-arthropods – and perhaps on all soil
592 invertebrates – must be made with caution. For example, contrary to their expectations,
593 Kardol *et al.* (2011) found no significant direct effect of warming and eCO₂ on abundance of
594 soil mites; instead, abundance and richness were positively related to soil moisture content
595 (Case study 1). They observed that climate change treatments altered the community
596 structure of soil micro-arthropods, although the combination of climate-related factors only
597 explained about 33% of total variation. Other experimental studies have shown that increased
598 temperature would be unlikely to provoke important changes in micro-arthropod populations,
599 although significant increases were observed in an experiment on bacteria- and fungus-
600 feeding nematodes (Ruess *et al.*, 1999).

601 Contrasting outcomes have been observed in model aphid biological control systems. The
602 abundance of peach potato aphid *Myzus persicae* (Sulzer) was enhanced by both eCO₂ and a
603 temperature increase of 2°C, whereas parasitism rates by its parasitoid, *Aphidius matricariae*
604 Haliday (Hymenoptera: Braconidae), only trended upwards in elevated temperature (Bezemer
605 *et al.*, 1998). In contrast, both predator and parasitoid increased attack rate against the grain
606 aphid *Sitobion avenae* (Fabricius) in eCO₂ and as a consequence substantially suppressed
607 aphid abundance (Chen *et al.*, 2007). Population dynamics theory predicts that the extent to
608 which a predator population suppresses its prey population is determined by the ratio of the
609 predator's generation time to that of its prey (Godfray *et al.*, 1994). When the generation time
610 ratio (GTR) is low, a predator population can increase rapidly compared to its prey, and
611 greater suppression is possible. Conversely, a high GTR leads to poor control. Climate

612 change may influence the GTR of biological control systems if the minimum temperature
613 required for development differs between a BCA and its host, or one of the species is in
614 diapause when the other is active.

615 **Phenology and synchrony**

616 Hance *et al.* (2007) stated ‘a key factor determining how climate change may affect the range
617 and abundance of insect populations is the extent to which individual species react
618 independently of the community of which they are a component.’ Aspects of plant life cycle
619 events controlled by temperature, such as the timing and duration of seed germination, bud
620 burst and flowering, are likely to change with warmer temperatures, subject to photoperiod
621 and water availability. So warmer temperatures should encourage many temperate plant
622 species to flower earlier, and this has already been documented in many crop plants and
623 natural ecosystems (Craufurd and Wheeler, 2009 and references therein). Cues in subtropical
624 and tropical areas may differ: delayed seasonal flowering has been observed in Florida (Von
625 Holle *et al.*, 2010). The extent to which an invertebrate is affected by these changes, whether
626 it is a herbivore, predator or parasitoid, will depend on how well its life cycle events are
627 synchronized with its host to ensure optimum survival. Rapid changes in the degree of
628 synchrony between species “seems inevitable” (Singer and Parmesan, 2010) and even small
629 changes between host and parasitoid may change the efficacy of a BCA system locally (Case
630 study 8). An example of an increasing mismatch is provided by egg hatching of the winter
631 moth (*Operophtera brumata* (Linnaeus); Lepidoptera: Geometridae) compared to bud burst
632 of its oak tree host (*Quercus robur*; Fagaceae) (van Asch and Visser, 2007). The poor
633 synchrony is due to an increase in spring temperatures (in particular a decrease in the number
634 of frost days and an increase in temperatures above a baseline of 3.9°C) without a
635 corresponding decrease in the incidence of freezing spells in the winter (Visser and
636 Holleman, 2001). The former provides the temperature cues for the moth, the latter for the
637 tree (Harrington *et al.*, 1999). Conversely, Bean *et al.* (2012) showed that a population of a
638 chrysomelid beetle, *Diorhabda carinulata* (Desbrochers) released in USA for biological
639 control of salt cedar (*Tamarix* spp. Tamaricaceae) that was initially not well synchronized
640 with its target hosts following introduction, over about seven years evolved a range of critical
641 day lengths for diapause induction that permits range expansion and better synchrony with
642 *Tamarix* spp. throughout the range. Thus, classical BCAs, even though they are specialized
643 and often obtained from a limited gene pool, may well possess the capacity to adapt to range
644 shifts.

645 Episodic extreme temperature (heat waves and unseasonal cold) has the potential to disrupt
646 biological control food webs independently of the disruption of cropping systems. Almost all
647 invertebrates are poikilothermic, or cold-blooded, and the rates of biological processes are
648 determined by ambient temperature, between an upper and lower threshold, beyond which the
649 processes do not occur (Case study 9). Differential responses to extreme temperatures by
650 BCAs, target pests and plants, have the potential to change biological control food webs, but
651 there is, at present, insufficient evidence to determine the extent to which this might occur.
652 The growth of pea aphid (*Acyrtosiphon pisum* (Harris)) populations is impaired under heat
653 stress and the degree of impairment is different for two different species of ladybird beetle
654 predators (Harmon *et al.*, 2009).

655 This synchronization between species need not be perfect. In a stable biological control
656 system, the level of regulation is such that sufficient hosts and natural enemies survive to the
657 next growing season to allow similar ongoing regulation in the next. In populations where

658 host and natural enemy have multiple discrete generations a year, imperfect synchronization,
659 allowing some hosts to escape, can stabilize an otherwise unstable interaction (Godfray *et al.*,
660 1994).

661 Where pests and their natural enemies occur in overlapping generations, an extreme weather
662 event may eliminate only vulnerable pest stages, leaving a synchronized population derived
663 from the life cycle stage that was not adversely affected. This can lead to breakdown of
664 natural control, as many parasitoids will emerge and find no hosts of a suitable stage of
665 development available, and so die out and not be available to control the pest when the
666 suitable life stage is available again (Case study 10).

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

- 668 • Increased temperature may cause one species to come out of diapause earlier than
669 another. Should the species in a biological control system have contrasting factors
670 regulating diapause, then a large mismatch, control failure and local extinction are
671 possible.
- 672 • Increased variability between years. Modelling of a simple host–parasitoid system
673 showed that an abnormally warm spring once in 25 years did not affect long-term
674 stability, but the system failed when it occurred more frequently than once in 20 years
675 (Godfray *et al.*, 1994).
- 676 • Increased number of generations per year. If either the host or the natural enemy has an
677 additional generation in a season that is not similarly reflected by the other, then the
678 stability of the biological control system may be at risk (Case study 11).
- 679 • Loss of synchrony between plant and natural enemy; e.g. if the adult activity of seed-
680 feeding weed BCAs is not synchronized with flowering and seed formation, control
681 will fail.
- 682 • Floral or pollen resources may not be present at the right time; e.g. most Diptera natural
683 enemies require pollen in order to produce eggs.

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

687 In response to global warming, the seasonal activity of organisms, including invertebrate
688 pests of agriculture, is changing (as discussed above). Asymmetric shifts in seasonality in
689 biological control food webs, as a result of advancing springs and delayed winters, may result
690 in loss of life-history synchrony between pests and natural enemies. In temperate climates,
691 this decoupling of life histories could result in pest populations escaping from BCA
692 regulation in the spring. In the autumn, it could result in pests achieving additional
693 generations after BCAs have become dormant. However, the relatively few studies that have
694 examined the effects of temperature changes on synchrony and natural enemy performance
695 have not found evidence for such effects (Bezemer *et al.*, 1999; Klapwijk *et al.*, 2010). Using
696 a mathematical model, Hoover and Newman (2004) predicted that the combination of
697 increased temperature and CO₂ on aphid food webs is likely to have little impact on the
698 parasitoid–prey system compared to current ambient conditions.

699 **Plant-mediated effects**

700 Increases in CO₂, changes in water availability and increases in temperature will alter plant
701 chemistry, phenology, growth and distribution, and these changes in the physiology, form and
702 biomass of plants, will in turn alter the nutrients available to plant and sap feeders, and those
703 that prey on them. Increases in the concentration of chemicals that act as defences against
704 insects (such as soluble phenolics and condensed tannins) under eCO₂ can have significant
705 consequences for herbivores (Peñuelas and Estiarte, 1998), including weed BCAs. The
706 complexities of the response of the plant are paralleled by the diversity of the responses of
707 insects (Pritchard *et al.* 2007).

708 Much of the increased plant biomass produced in response to eCO₂ is invested below ground
709 in the root systems (Curtis and Wang, 1998; Lukac *et al.*, 2003). Stiling *et al.* (2010) found
710 that under eCO₂, herbivore guilds increased in abundance, but the effect was not passed on to
711 decomposers such as collembolans, beetles and cockroaches. Increased abundance and
712 performance of herbivores under eCO₂ is most like to occur when nitrogen is not limited, e.g.
713 in the case of clover root weevil, *Sitona lepidus* Gyllenhal (Coleoptera: Curculionidae),
714 feeding on underground root nodules (Johnson and McNicol, 2010).

715 The effects of eCO₂ on BCAs are also likely to be mediated through flow-on effects of CO₂
716 on plants (Coviella and Trumble, 1999). Plants grown under eCO₂ exhibit increased growth,
717 but also increased carbon/nitrogen ratios, and hence lower nutritional quality for protein-
718 limited herbivores (DeLucia *et al.*, 2008). Thus, in general, eCO₂ is associated with increased
719 damage through compensatory insect herbivory in response to decreased nutritional value of
720 plants. Production of phenolic compounds associated with herbivore defence increases under
721 eCO₂ (Bidart-Bouzat and Imeh-Nathaniel, 2008). The net result is either reduced fitness (e.g.
722 size, reproduction) or longer development times in pests (Ode, 2006). The former will tend to
723 decrease performance of natural enemies, as BCA fitness is correlated with host/prey fitness,
724 or may affect natural enemies through the direct effects (toxicity) of secondary plant
725 compounds (organic compounds in plants that are not directly involved in normal growth,
726 development, or reproduction, but often linked to defences against herbivores) (Ode, 2006).
727 Increased development times will tend to increase the impact of natural enemies, especially
728 those that attack feeding stages, as these stages would remain vulnerable longer under eCO₂.
729 Because prey could be smaller under eCO₂, predators may find them easier to handle, and
730 may have a greater impact on prey populations as a result (Coll and Hughes, 2008). Other
731 species may have better survival. For instance, under eCO₂, cotton aphid (*Aphis gossypii*
732 Glover) survival significantly increased but ladybird larval development took significantly
733 longer, increasing the likelihood that these aphids might become more serious pests in the
734 future (Gao *et al.*, 2008).

735 Plants that are under attack by pests produce a wide array of compounds (herbivore-induced
736 plant volatiles or HIPV) that assist generalist and specialist BCAs in finding the prey (De
737 Moraes *et al.*, 1998; Hare, 2011). The production of these compounds is influenced to a great
738 extent by environment (Hare, 2011 and references therein), and it is possible that factors
739 associated with climate change will affect quantity and quality of HIPV. Pinto *et al.* (2007)
740 found that increased O₃ reduced HIPV production in some plants, but not all, but changes in
741 HIPV production did not affect predator-prey associations in their experiments. Volatile
742 emissions from plants generally increase under increased temperatures, but the effects of
743 eCO₂ seem to be variable (Bidart-Bouzat and Imeh-Nathaniel, 2008 and references therein).

744 It is not possible to generalize about the effects that drought stress in plants has on
745 invertebrates, but droughts can have major effects on ecosystems and can change and disrupt

746 plant-mediated competitive interactions between invertebrates feeding on different parts
747 (sites) of the plant. Species within the same guild can vary in response (Staley *et al.*, 2006)
748 and existing plant-mediated interactions between above- and below-ground herbivores can be
749 changed (Staley *et al.*, 2007).

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

759 **Biogeographical differences – temperate, subtropical and tropical zone vulnerabilities**

760 An increase in the capacity to support increased overall plant diversity is expected in most
761 temperate regions, while a strong decline in most tropical and subtropical regions is projected
762 (Sommer *et al.*, 2010), although this is at variance with predictions in South America based
763 on the Quaternary pollen record (Colinvaux, 2005). Hence, land managers in temperate
764 regions should have more options in terms of crops and how to manage ecosystem services
765 supporting pollinators and other beneficial invertebrates compared to those in most tropical
766 and subtropical regions. However, just as temperate regions are most vulnerable to invasion
767 by cosmopolitan weeds (Woodward and Kelly, 2008), so will they be most vulnerable to
768 invasive invertebrates (Case study 3).

769 Under climate change, the tropical monsoon belt is widening (Seidel *et al.*, 2008). For
770 example, Australian monsoon rainforests have expanded within the savannah matrix
771 (Bowman *et al.*, 2010). However, not all species will alter their distribution. Coffee (*Coffea*
772 *arabica* and *C. canephora*, Rubiaceae) is a tropical crop predicted to be severely affected by
773 climate change. It is not expected that it can be moved latitudinally because both species are
774 highly susceptible to changes in photoperiod, while rising temperatures are increasing the
775 number of generations of coffee berry borer beetle, *Hypothenemus hampei* (Ferrari), the
776 principal pest (Jaramillo *et al.*, 2009).

777 Tropical plant–herbivore interactions are considered to be more susceptible to the
778 perturbations of climate change than those in temperate zones. This has been attributed to
779 tighter ecological and evolutionary linkages in the tropics (Coley, 1998), although a recent
780 analysis suggests that food-webs may be more generalised in the tropics (Schleuning *et al.*,
781 2012). Tropical plants are better defended and, unlike in temperate forests where most
782 herbivory (about 75%) occurs on mature leaves, in the tropics most is on young leaves (>
783 70%), an ephemeral resource (Coley, 1998).

784 **SOIL INVERTEBRATES IN THE FACE OF CLIMATE CHANGE**

785 Soil invertebrates are a very important component of agricultural biodiversity (Cock *et al.*,
786 2012), and largely determine the structure and the basic functions of natural ecosystems. Key
787 taxonomic groups of soil invertebrates include Nematoda, Oribatida, Collembola, Diptera,
788 Hymenoptera, Isoptera, Myriapoda, Isopoda, Arachnida, Coleoptera, Mollusca and

789 Oligochaeta. They are an integral part of agricultural ecosystems and are relevant actors in
790 maintaining soil health, ecosystem functions and production at the root of the bottom-up
791 processes governing agricultural productivity. The presence of a range of species and
792 organisms capable of supporting critical soil processes and services is essential for the
793 maintenance of healthy productive soils in the face of changing environmental conditions.
794 The decline of these soil communities and the fact that their beneficial functions in
795 agricultural ecosystems have been overlooked have certainly contributed to increased rates of
796 land degradation, nutrient depletion, pest incidence, fertility decline, water scarcity, all
797 affecting crop productivity and yield reductions. The loss of species with unique roles can
798 have drastic ecological effects and lead to long-term deterioration of soil fertility and
799 agricultural productive capacity. The introduction of a keystone species may have detrimental
800 or beneficial effects depending on the context. The interaction between soil invertebrates and
801 soil micro-organisms is critical; the activities of soil invertebrates regulate microbial activity
802 in soils, and micro-organisms enter into intimate relationships with soil invertebrates to help
803 them degrade highly complex compounds such as cellulose and other resources.

804 **Possible adaptation by soil invertebrates to the challenges identified**

805 Generalizations about the effect of extreme events on soil invertebrates and decomposers are
806 difficult, as these have seldom been addressed in investigations. We can infer that soil
807 invertebrate populations would probably recover from perturbation quickly, due to their
808 inherent resilience, although indirect effects – occurring via changes in the productivity and
809 functional composition of above-ground vegetation – would alter associated soil organism
810 dynamics and processes in the longer term, due to changes in sources of detritus (fragments
811 of organic material) and resources entering the decomposer subsystem (Wolters *et al.*, 2000;
812 Wardle, 2002). In other words, above- and below-ground communities and processes are
813 intrinsically linked (Wardle *et al.*, 2004; van der Putten *et al.*, 2009; Kardol and Wardle,
814 2010). Below-ground species are less exposed to the full climate variability than above-
815 ground species, as they experience microclimates that are buffered by the soil environment
816 (Bale *et al.*, 2002). Generally, how climate change factors will affect soil invertebrate biotic
817 and abiotic interactions remains a research area to be explored. We need more research to
818 increase our knowledge of the evolutionary responses of soil invertebrates to selection
819 pressures due to climate change.

820 Soil microfauna (< 0.1 mm) can tolerate drying events through cryptobiosis (reducing
821 metabolism to imperceptible levels) (Freckman, 1978); micro-arthropods show adaptive
822 strategies that enable them to tolerate or avoid desiccation; and larger soil macrofauna
823 (especially soft bodied taxa > 2mm) exhibit effective strategies to conserve moisture under
824 dry conditions (Jiménez *et al.*, 2000). Although eCO₂, one of the climate change factors, may
825 affect soil ecosystem engineers (such as earthworms, see below) through direct fertilization
826 effects on plant growth, notably an increase in carbon/nitrogen ratios, land-use intensification
827 is of more immediate concern as changes in the functional-group balance within such
828 engineers' communities has been demonstrated (Lavelle *et al.*, 1997).

829 In the case of soil beneficial invertebrates such as earthworms, their maintenance in agro-
830 ecosystems under perturbation such as climate change seems to be determined by (i) their
831 motile potential, (ii) their adaptive strategies, which together determine their population
832 growth rate, and (iii) the functionally similar characteristics of the introduced land use with
833 respect to the original ecosystem (Jiménez and Thomas, 2001). The survival of some soil
834 invertebrates – such as nematodes – is firmly dependent on the maintenance of moisture films

835 around soil aggregates. Micro-arthropods are, however, more resilient to desiccation and not
836 so dependent on soil moisture (Wardle, 2002). A full understanding of how biotic and abiotic
837 factors determine soil invertebrate distribution across different spatial and temporal scales is
838 essential (Jiménez *et al.*, 2012) if we wish to predict the response of such communities to
839 climate change, as well as the impact it will have on the delivery of ecosystem services.

840 Based on Berg *et al.*'s (2010) review of dispersal of trophic-based functional groups for
841 above- and belowground organisms, dispersal and thermal sensitivity of key life-history traits
842 are two important factors enabling species to adapt to climate change in order to obtain a
843 better understanding of the impacts of global warming on species dispersal. Building on this
844 review, H. Eijsacker (pers. comm.) argues that soil invertebrates react at 1% of the speed of
845 plant communities, so they will not be able to keep up with changes in response to shifting
846 climate gradients.

847 Adaptive responses by soil invertebrates to the effects of climate change depend on their
848 limited dispersal abilities. In terms of vertical redistributions within soil horizons, only those
849 invertebrates that are able to move vertically within the soil would be able to counteract the
850 negative effects of climate change, such as increased soil temperature and desiccation. Such
851 shifts in soil invertebrate species distributions might have a substantial effect on the
852 decomposition process because their functional role depends on the species' vertical position
853 within soils. Krab *et al.* (2010) found that springtail (collembolan) species differed in their
854 responses to changes in climate or substrate quality, identifying two types of groups: i.e.
855 'movers' and 'stayers'. They also suggested that interspecific faunal trait variation might
856 provide a useful tool to predict animal responses to climatic changes. Larger soil
857 invertebrates, such as earthworms, show different adaptive strategies and show different
858 vertical stratification in the face of seasonal changes in tropical areas (Jiménez and Decaëns,
859 2000). However, the temperature changes required to cause significant shifts in major groups
860 of decomposer biota are probably likely to be much greater than those predicted to result
861 from global warming, particularly in the deeper, temperature-buffered, layers of soil.

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

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

876 It is necessary, therefore, to ensure that whatever the effects of climate change may be (and
877 these will vary according to crop and region) soil invertebrates must be preserved and
878 maintained in order to carry out their important role in maintaining the vitality of soils and
879 assuring the continued delivery of important ecosystem services. The loss of keystone species

880 from the system can result in dramatic changes and impaired provision of ecosystem services
881 by soil invertebrates. Evans *et al.* (2011) provided evidence that ants and termites play an
882 important role as soil engineers by increasing crop productivity in drier conditions. The
883 removal of just one species of earthworm from the soil led to higher soil compaction, lower
884 plant biomass, lower soil carbon content and higher weed biomass compared to areas where
885 this species was present (Decaëns *et al.*, 1999a).

886 **Potential of soil invertebrates in mitigating climate change**

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

890 *Earthworms ameliorate the effects of climate change*

891 The effects of climate change on the interactions between soil invertebrates, plants and
892 above-ground invertebrates are not fully understood. Better models need to be developed to
893 provide guidance to the empirical studies that are required to enhance our capacity to predict
894 the effect of climate change on soil ecosystems (van der Putten *et al.*, 2009), and hence how
895 soil ecosystems will respond, potentially mitigating the effects of climate change. The fact
896 that there have been only a limited number of studies on the responses of soil invertebrates to
897 interactive effects of climate change-related factors, such as warming, eCO₂ and precipitation
898 patterns, makes generalizations difficult, but it is foreseen that the responses will be context
899 dependent (Case study 1). However, it is known that earthworms have the potential to
900 mitigate climate change in a number of ways. For example, Johnson *et al.* (2011) found that
901 earthworms reduced the negative effects of summer drought on a plant (*Capsella bursa-*
902 *pastoris*) and exacerbated the effects of drought (i.e. a decline in numbers) on above-ground
903 aphids (*Rhopalosiphum padi* (Linnaeus)). A similar mitigating effect was found by Blouin *et*
904 *al.* (2005), who showed that remarkably – and for reasons that are not fully understood – the
905 presence of earthworms helped to mitigate the negative effects of plant-parasitic nematodes
906 on rice plants (Case study 12). Although the earthworms had no direct effect on the
907 nematodes, their presence in the soil somehow reduced nematode feeding damage. So, in
908 both cases, the presence of earthworms reduced the harmful effects of the plant pests (above
909 and below ground), although the actual mechanisms are not totally clear; in other words, they
910 have the potential to reduce the loss of biomass (= yield) under these climate change factors
911 (Case study 13).

912 *Ecosystem engineers help preserve soil vitality*

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

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

931 **Analysis of present role and potential use of soil invertebrates relevant to food and** 932 **agriculture**

933 Increased litter production as a result of the fertilization effect of eCO₂ can increase the
934 resources available for detritivores – potentially resulting in increased abundance of
935 detritivores (Hall *et al.*, 2006) and generalist predators (Settle *et al.*, 1996). Epigeic and
936 anecic earthworms – and some micro-arthropods – have a vital role in incorporating leaf litter
937 and others forms of plant debris into the soil. In light of the potential increases in plant
938 biomass under climate change, this role will become even more important.

939 Global change factors such as land use and climate change and atmospheric inputs, whether
940 acting individually or in combination, may lead to non-linear changes in above- and below-
941 ground relationships, with effects that vary geographically throughout the world (Heal, 1997).
942 Complex and non-linear responses are expected in the interactions between soil invertebrates,
943 plants and ecological processes. Different groups of soil fauna (e.g. isopods, mites,
944 collembolans, centipedes, snails, slugs, etc.) obtain carbon directly from plants' roots
945 (Uvarov *et al.*, 2011) as well as from leaf litter. This might help maintain the community food
946 web, as increased plant biomass production should result in more resources available to soil
947 decomposer communities, although leading to higher CO₂ emissions from soils.
948 Decomposition is driven not only by temperature-induced changes in substrate quality, and/or
949 physico-chemical conditions, but through the interaction of different levels of soil disturbance
950 with animal assemblages mediating ecosystem processes. Increased decomposition rates of
951 organic substrates due to global warming are expected to result in larger net soil CO₂
952 emission and less carbon storage in the soil (Jenkinson *et al.*, 1991; Seastedt, 2000).
953 However, a global analysis demonstrated that decomposition rates in forest soils were not
954 temperature dependent, meaning that global warming may not necessarily accelerate soil
955 carbon losses. Will higher temperatures move decomposition to deeper layers by activating
956 soil microorganisms? In a more recent study, Fontaine *et al.* (2007) demonstrated that the
957 stability of old soil carbon in the subsoil is maintained unless fresh residues are incorporated
958 in deep soil layers. Any change in land use and agricultural practice (e.g. ploughing) that
959 increases the distribution of fresh carbon along the soil profile could, however, stimulate the
960 loss of ancient buried carbon (Fontaine *et al.*, 2007).

961 Although some progress has been made in understanding interactions of below-ground
962 processes with climate change, challenges remain (Pendall *et al.*, 2008); uncertainties in
963 predicting the interactions of the ecosystem carbon cycle with global warming are to some
964 extent determined by our lack of knowledge of below-ground processes (Davidson and
965 Janssens, 2006). Global climate change may affect soil carbon stocks indirectly through
966 habitat change and hence via changes in the activity of soil invertebrates (Briones *et al.*,
967 2004). There is already sufficient evidence to demonstrate that soil fauna have significant
968 effects on all of the pools and fluxes in the carbon cycle, and soil fauna mineralize more
969 nitrogen than micro-organisms in some habitats (Osler and Sommerkorn, 2007). The role of

970 soil invertebrates in the carbon cycle therefore needs to be understood in order to generate
971 predictive models on how climate change will affect this cycle through its impact on soil
972 invertebrates. New methods are needed in order to make observations across a wide range of
973 spatial and temporal scales, and thereby to improve the reliability of predictions of responses
974 to altered atmospheric CO₂ concentrations, warming temperatures and nutrient deposition.

975 Moreover, in response to climate change-related factors, soil invertebrate assemblages may
976 change and hence soil processes will also change. Soil invertebrate communities and
977 decomposition rates are responsive to warming (Aerts, 2006). Changes in vegetation
978 distribution driven by climate change and related factors will presumably influence soil
979 invertebrate distribution (Wolters, 2001). Would a warming scenario result in fewer species
980 and less resilience to extreme events, or would warming favour some functional groups over
981 epigeic species? These are examples of some of the questions already addressed by several
982 authors (Krab *et al.*, 2010). How the vertical distribution of soil invertebrate assemblages will
983 change and how they might affect soil biogeochemistry remains to be seen (Heemsbergen *et*
984 *al.*, 2004). Although still little understood, responses of soil fauna are likely to differ between
985 ecosystems. Swift *et al.* (1979) suggested that cold-limited arctic ecosystems are particularly
986 sensitive to global warming, while nutrient-limited temperate grasslands are susceptible to
987 CO₂ increase and nitrogen depositions.

988 The role of a diverse assemblage of macro-organisms is crucial to the maintenance of soil
989 structure. This is illustrated, for example, by the results of an experiment performed in the
990 Brazilian Amazon to investigate the effects of an earthworm species, *Pontoscolex*
991 *corethrurus* (Müller) and a diverse assemblage of other soil organisms (including other
992 earthworms, termites, millipedes, isopods and ants) on soil structure (Case study 14). When
993 soil blocks were removed from pasture and placed into forest, and similar blocks taken from
994 forest and placed into pasture, the structure of the compacted pasture soil was completely
995 restored after one year to levels typical of those in native forest soils (Barros *et al.*, 2004).
996 Conversely, the macro-aggregate structure of the forest soil was completely destroyed by the
997 presence of large populations of an invasive earthworm, reaching compaction and porosity
998 levels similar to those of the degraded pasture (Chauvel *et al.*, 1999). Therefore, movement of
999 soil could enhance soil functions in some situations although its feasibility would be limited.

1000 *Translocation of soil invertebrates*

1001 In view of the very positive contribution of soil invertebrates, and how these may be
1002 disrupted by climate change, one option that might be considered is the translocation of soil
1003 invertebrates on a local or national scale.

1004 On the local scale, the best approach should always be to fully characterize soil invertebrates
1005 in a given local area, and identify and use suitable species and functional groups for the
1006 processes needed, such as increased soil aggregation. Moreover, some species have a very
1007 narrow distribution, with a high degree of endemism, and in the case of those organisms with
1008 mutualistic relationships such as earthworms and termites this could prevent their successful
1009 introduction. A new focus would be needed by having quite similar species that perform the
1010 function for which they are sought. This approach is not in regular practice yet, and no
1011 guidelines for management are available, so using this approach as a response to climate
1012 change is not yet possible.

1013 We are not aware that soil invertebrates are being deliberately moved between countries at
1014 present, nor should they be. Given the risks of introducing species that become invasive (e.g.
1015 lumbricid worms accidentally introduced to forests in the United States of America), and the
1016 many possible contaminants, an appropriate risk-assessment protocol would need to be
1017 developed. The great diversity of soil invertebrates coupled with the lack of knowledge as to
1018 which species might be manipulated in agro-ecosystems for the benefit of agriculture or
1019 climate change make this impractical. Until we understand soil ecology much better than we
1020 do today, such introductions should be avoided.

1021 **Knowledge gaps restricting our ability to assess soil invertebrate responses to CC**

1022 Studies have shown that some agricultural practices, such as annual crops, adversely affect
1023 survival of soil invertebrates (Lavelle and Pashanasi, 1989; Decaëns and Jiménez, 2002;
1024 Swift *et al.*, 1996). Appropriate indicator soil species (i.e. those species that by their presence
1025 or abundance define a particular condition or characteristic of a particular environment) and
1026 functional groups for monitoring responses to climate change need to be identified for
1027 particular ecosystems and for different regions. Important European initiatives are underway
1028 in countries including France, The Netherlands, and UK for a range of soil organisms. It is
1029 important to identify the keystone species and key interactions that must be maintained in
1030 order to preserve soil function in the face of climate change.

1031 Our ability to assess the response of soil invertebrates to climate change is restricted as few
1032 studies have examined the combined effects of changes in climate change-related drivers in
1033 the context of soil function and soil invertebrate biodiversity. Multifactorial experiments have
1034 been started, but more are needed to investigate the combined effects of warming, eCO₂ and
1035 changes in precipitation, on soil (agro-)ecosystems. Johnson *et al.* (2011) emphasized the
1036 importance of investigating the effects of climate change-related drivers (such as summer
1037 drought) on soil invertebrates, in the context of multi-species plant communities, as
1038 interactions can vary between monocultures and multi-species communities (Case study 13).
1039 Further studies are anticipated.

1040 One limitation is that our lack of knowledge about latitudinal gradients in soil invertebrate
1041 distribution makes predictions about adaptation to climate change difficult. So far,
1042 biogeographical distributions of soil invertebrates are not well characterized, and there are
1043 important knowledge gaps (Decaëns, 2010). At the local scale, habitat constraints
1044 (environmental factors) and biotic interactions (competition, predation, etc.) affect the
1045 number of species present in a given community as the combination of such factors defines
1046 the rules for community assembly. Existing data provide little evidence that climate change
1047 driving factors regulate above- and below-ground communities in similar ways (Bardgett *et al.*,
1048 2005).

1049 *Taxonomy and identification of soil invertebrates*

1050 Paradoxically, there is a conspicuous lack of interest from the scientific community in below-
1051 ground diversity, compared to more charismatic organisms, and we know very little about its
1052 taxonomy, systematics and biogeography (Decaëns *et al.*, 2006, 2010). Only a few studies
1053 have reported global patterns in soil biodiversity distribution at different spatial and temporal
1054 scales (Wardle, 2002; Bardgett *et al.*, 2005). To date, such global patterns in many soil
1055 animal groups are unknown and complete inventories of soil organisms are not available for

1056 certain habitats or regions, although some approximations for soil invertebrate species have
1057 been provided (see Decaëns *et al.*, 2006, for a review and Decaëns, 2010).

1058 The development and standardization of new molecular-based taxonomic approaches, such as
1059 DNA barcoding analysis, are helping to separate and define cryptic species of soil
1060 invertebrates in groups such as earthworms (James *et al.*, 2010) and Collembola (Porco *et al.*,
1061 2012). Deficits in taxonomic knowledge must also be addressed, through actions at different
1062 levels that stimulate studies on soil biodiversity and the characterization of the composition
1063 of soil communities. Broad surveys of soil communities covering several taxonomic groups
1064 at the same time are being carried out. Subsequently, it is expected that in the years to come
1065 an unknown number of new species will be named, and after that more time will be needed to
1066 describe their function in soils and how they will respond to climate change related factors.
1067 Unless inventories of soil organisms (their functions and interactions) can be developed,
1068 many changes anticipated under climate change cannot be detected at this level, only where
1069 ecosystem services are disrupted which may be due to changes in soil invertebrate activities.

1070 *Importance of altitudinal gradients*

1071 Latitude, altitude and climate change are (with reservations) used as surrogates for each other
1072 in a variety of studies. There is a scarcity of data on altitudinal variation in soil invertebrate
1073 assemblages. Some researchers have described a continuous decrease in the total number of
1074 species against an altitudinal stratum in a given geographical area for several groups, such as
1075 termites (Collins, 1980), earthworms (Bouché, 1972) and ants (Cole, 1940). The reduced
1076 species richness at high altitudes has been interpreted as the effect of (i) low temperatures, (ii)
1077 low levels of available energy which reduces ecosystem carrying capacity, and (iii) small
1078 habitat size, compared to lowland areas (Decaëns, 2010).

1079 Invertebrate distribution may show an optimum altitude (i.e. reduced numbers at higher and
1080 lower levels). For example, springtail species richness across an altitudinal transect from 950
1081 to 2 150 m in the French Alps (Loranger *et al.*, 2001). In the mountains of Sarawak,
1082 Malaysia, Diptera richness reached a peak between 1 300 and 1 700 m; and beetles between
1083 500 and 1 200 m (Collins, 1980). In tropical areas, however, a different pattern has been
1084 observed: for example, earthworm species richness increased from sea level up to 1 000 m in
1085 Puerto Rico (González *et al.*, 2007). The northern boundaries of tree distributions are moving
1086 polewards and it is assumed that this will provoke corresponding shifts in the range of soil
1087 invertebrates. However, further work is needed to explore the potential of soil invertebrate
1088 resources to migrate in concert with the current rapid shifts of the tree line. In particular, the
1089 rate of movement of soil invertebrates without a motile stage is not known, although it can be
1090 assumed that populations of soil invertebrates may be transported to other areas during
1091 extreme events like flooding. However, this process has not been quantified. Analogues exist,
1092 such as the colonization rates of newly extruded lava from volcanoes surrounded by
1093 vegetation, as has been studied on Mount St Helens (Washington, United States of America)
1094 or even in highly intensive agricultural systems where the rates of colonization and dispersal
1095 can be assessed if natural refuges are adjacent to these areas.

1096 **Conclusions**

1097 The importance of soil invertebrates in maintaining healthy functional soil ecosystems, and in
1098 mitigating some of the effects of climate change both below and above ground, has been
1099 highlighted. They have vital roles to play under climate change, e.g. in preserving community

1100 structure, incorporating increased leaf litter, enhancing carbon storage, maintaining soil
1101 porosity and preventing soil compaction. More studies are necessary on above-ground –
1102 below-ground interactions at different successional stages to understand likely responses of
1103 soil communities to climate change, even though there appear to be logistical constraints to
1104 the empirical approaches that would be needed in order to examine all possible interactions
1105 (van der Putten *et al.*, 2009; Kardol and Wardle, 2010).

1106 Our knowledge of the effects of climate change on multitrophic level interactions (i.e. those
1107 involving two or more trophic levels in a food web) in the soil is probably more deficient
1108 than in any other ecosystem. Given the potential for disruption of such beneficial organisms,
1109 whole ecosystem studies on the multiple effects of climate change on below-ground
1110 organisms are vitally important, particularly in relation to adaptation mechanisms, changes in
1111 cropping regimes and in vulnerable regions, such as the tropics. Taking advantage of the
1112 opportunities for combining further empirical studies with modelling approaches could
1113 enhance our conceptual understanding and capacity to predict the impact of climate change
1114 on soil invertebrates and the processes they mediate. Identifying, and then monitoring,
1115 appropriate keystone species and key soil processes/interactions for different geographical
1116 regions and soil types is essential.

1117 **INVERTEBRATE BIOLOGICAL CONTROL AGENTS IN THE FACE OF** 1118 **CLIMATE CHANGE**

1119 Biological control is the use of natural enemies to regulate pest populations. Natural enemies
1120 of pests are biological control agents (BCAs) and provide an ecosystem service (Costanza *et*
1121 *al.*, 1997; MEA, 2005). Natural biological control encompasses both implicit reliance on this
1122 ecosystem service, and manipulation of the service through conservation biological control
1123 methods. Integrated pest management (IPM) is ‘a strategy of pest containment which seeks to
1124 maximise natural control forces such as predators and parasites [i.e. parasitoids] and to utilise
1125 other tactics only as needed and with a minimum of environmental disturbance’ (Glass in
1126 Davis and McMurtry, 1979). Thus, biological control, particularly natural biological control,
1127 underlies all IPM programmes.

1128 Classical biological control is the introduction of an exotic BCA of an exotic pest or weed
1129 into a new ecoregion (or a new country in the same ecoregion) with the purpose of regulating
1130 the pest’s numbers. Also known as introduction or importation biological control, it requires
1131 the selection, introduction and establishment of one, or a very small number of, BCA(s) that
1132 is/are likely to regulate the pest, while not causing any adverse impacts on other species in
1133 the new habitat. Classical BCAs, once established, become part of the natural biological
1134 control ecosystem service. Van Lenteren (2007) estimates that classical biological control is
1135 applied on 350 million hectares worldwide.

1136 Augmentative biological control differs considerably from the preceding two strategies. The
1137 BCA is introduced, usually directly onto the crop to be protected, once or several times in a
1138 cropping cycle. The purpose is to induce sufficient mortality in the target pest population to
1139 ensure that economic injury thresholds (levels at which damage costs more than the cost of
1140 control) are not exceeded during the current cropping season. The BCAs are generally
1141 purchased from suppliers, or produced by a growers’ cooperative, and are mass reared on
1142 natural or factitious hosts or prey. Van Lenteren (2007) estimates that augmentative BCAs
1143 are applied on 16 million hectares annually.

1144 Because classical biological control and augmentative biological control using exotic BCAs
1145 involve the deliberate introduction of alien species, these processes are carefully regulated
1146 according to national legislation, which varies from country to country, usually within the
1147 framework of *International Standards for Phytosanitary Measures No. 3. Guidelines for the*
1148 *Export, Shipment, Import and Release of Biological Control Agents and Other Beneficial*
1149 *Organisms* (ISPM3) (IPPC, 2005).

1150 Given that the losses caused by pre- and post-harvest pests can be very substantial, and are
1151 likely to increase as a consequence of climate change, the potential benefits of using
1152 invertebrates as BCAs are vast, but as yet only partially tapped (Cock *et al.* 2012).

1153 **Geographical range shifts**

1154 The evidence from glaciation history indicates that there is a limit to the ability of species to
1155 adapt based on existing genetic diversity, after which BCAs must move. Amongst
1156 invertebrates, this has been most clearly demonstrated for insect detritivores and predators
1157 (Coope, 2004, Case study 2). It is clear that specialist herbivores cannot move until their
1158 preferred food plants have moved and, equally, specialist BCAs cannot move until their
1159 preferred host/prey has moved. Where spread is to contiguous areas, BCAs are likely to track
1160 their hosts/prey. However, where barriers intervene, such as in many fragmented agricultural
1161 landscapes, there is likely to be a lag between a pest passing a barrier and its natural enemies
1162 catching up, due to the effects of distance, different dispersal mechanisms, inadvertent human
1163 assistance and chance.

1164 We are not aware of studies that demonstrate that natural enemies are able to track the
1165 poleward movement of pests in response to climate change, but the evidence from the
1166 introduction of classical BCAs shows that many natural enemies have great dispersive
1167 powers. For example, a 2-mm-long South American parasitoid *Anagyrus lopezi* (De Santis)
1168 (Hymenoptera: Encyrtidae) was imported into Nigeria for control of the cassava mealybug,
1169 *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae) and first released in
1170 1981/82 (Neuenschwander, 2003). Within three years, this very small insect dispersed over
1171 200 000 km² in southwestern Nigeria, occupying between 70% and 98% of all fields (Herren
1172 *et al.*, 1987). Similarly, Assefa *et al.* (2008) studied the spread of the 4-mm-long *Cotesia*
1173 *flavipes* (Cameron) to Ethiopia from releases in Kenya and Somalia against stem borers of
1174 Poaceae crops, and concluded that it may have spread by more than 200 km per year. There
1175 are many other examples for natural enemies that can fly, but little information for flightless
1176 species of natural enemies, which have usually been spread by human intervention. For
1177 example, when the flightless encyrtid parasitoid, *Neodusmetia sangwani* (Subba Rao), was
1178 introduced into Texas for the control of Rhodesgrass mealybug, *Antonina graminis*
1179 (Maskell), once local releases showed that it was an effective BCA, it was redistributed by
1180 dropping parasitized mealybugs on grass stems from an aircraft (Dean *et al.*, 1979).

1181 Dispersal of both pests and natural enemies is a mixture of local movement and unusual long-
1182 distance (saltatory) movements, some of which will be inadvertently or deliberately assisted
1183 by human activities. It is therefore likely that if pests move polewards at the rates predicted
1184 under climate warming scenarios, most natural enemies that can fly will have little difficulty
1185 tracking their hosts/prey, but flightless species may well lag behind. Barriers, such as
1186 mountains and deserts, can be expected to slow the spread of both pests and natural enemies,
1187 as might anthropic fragmentation of habitats, but not necessarily by much, especially if there

1188 is substantial human movement by land across the barrier. Sea barriers are likely to be more
1189 effective, and so this issue will be accentuated for islands, particularly oceanic islands.

1190 **Evolutionary adaptation**

1191 The rates of evolutionary change in populations under climate change, including BCAs, will
1192 depend on levels of heritable variation, genetic interactions among traits, and population
1193 processes (Lynch and Lande, 1993). Populations of many natural BCA species contain much
1194 heritable variation in traits that affect responses to climate, and other abiotic and biotic
1195 factors. Where adaptation has been looked for, usually it has been found (e.g. White *et al.*,
1196 1970; Potting *et al.*, 1997; Henry *et al.*, 2010), although as yet there is a shortage of studies
1197 that assess local adaptation to climate change factors. Many species predate the Quaternary,
1198 and many of the remainder evolved during this period, and so have already survived repeated
1199 global warming and cooling during the Quaternary. Hence, the indications are that adaptation
1200 to climate change will be based on existing genetic diversity, some of which may be released
1201 by epigenetic mechanisms (Rando & Verstrepen 2007), rather than new mutations.

1202 **Ability of BCAs to respond to elements of climate change**

1203 BCAs may be affected by a number of features of a changing climate, and these effects have
1204 potential consequences for the performance of BCAs in agro-ecosystems, particularly in
1205 integrated pest management (IPM) systems. As yet, we know relatively little about how
1206 BCAs can adapt or be assisted to overcome these challenges, although this is an area of active
1207 research (Roderick *et al.*, 2012).

1208 *Average temperature and seasonality*

1209 For all three classes of biological control, but especially for classical and augmentative
1210 biological control, there is potential to assist adaptation to changes in seasonality through
1211 selection (e.g. Gilkeson and Hill, 1986) and by transplanting locally adapted strains that have
1212 appropriate responses to seasonal cues (Gillespie and Quiring, 1993, 2005). Augmentative
1213 BCAs are not meant to establish widespread breeding populations. Their presence is a result
1214 of deliberate seasonal introductions, and farmers can adjust the timing and location of these
1215 introductions.

1216 The effects of scale mean that widespread effective BCAs will have more impact than
1217 localized natural enemies. Similarly, introduced classical BCAs that cannot disperse through
1218 most of the range of the target will be less effective. Hence, we suggest that BCAs that are
1219 important in agricultural systems are usually relatively widespread species, although we are
1220 not aware of any analysis to test this. BCAs that are more widespread are likely to be more
1221 genetically diverse and more resilient to the effects of climate change. Overall, temperature
1222 and seasonal responses in populations of widely distributed insect and mite pests and their
1223 natural enemies are either locally adapted, i.e. the responses to seasonal cues and the
1224 tolerances to extremes have evolved to suit the local conditions (Traoré *et al.*, 2006; Frago *et al.*
1225 *et al.*, 2010), or are governed by phenotypic plasticity resulting from genetic diversity in local
1226 populations (Chen *et al.*, 2006; Hodek and Michaud, 2008). Changes in seasonality of a pest
1227 species as a result of climate change would need to be rapidly followed by adaptive responses
1228 by its associated natural enemy communities. Without such adaptations, outbreaks of pests
1229 can be expected. As introductions of almost all classical BCAs are derived from a very small
1230 sample of individuals from one or a very few localities, the genetic diversity of classical

1231 BCAs may be severely constrained, and it is not known whether they contain the capacity to
1232 adapt or respond to changes in the seasonal availability of hosts. Conversely, the required
1233 genetic variation should exist in natural BCA populations (e.g. Henry *et al.*, 2010; Case study
1234 15).

1235 *Atmospheric CO₂*

1236 The flow-on effects of eCO₂ on arthropods including BCAs seem to be highly idiosyncratic
1237 (Coviella and Trumble, 1999), and we consider that it is not possible to reach any conclusions
1238 regarding the adaptation, or assisted adaptation, of BCAs to this aspect of climate change at
1239 this time.

1240 *Rainfall and drought*

1241 The development, mortality and reproduction of both pests and BCAs can be affected by
1242 rainfall and drought, and this is likely to affect their abundance both directly and through
1243 their interactions. In general, drought, like other weather extremes, can be expected to disrupt
1244 pest–natural enemy interactions, leading to both pest outbreaks (which are noticed) and pest
1245 crashes (which are easily overlooked).

1246 There is some scope to adapt BCAs and their use to redress the disruptions caused by rainfall
1247 and drought. Augmentative releases in covered crops are not likely to be significantly
1248 affected, but open field releases are likely to be adversely affected by dry conditions. It is
1249 common practice to spray microbial insecticides at dusk, because these are often sensitive to
1250 low humidity. Similar tactics of dusk releases for some augmentative BCAs may be
1251 advantageous and need evaluation. The development of augmentative BCAs adapted to hot
1252 and dry conditions is an option (Grewal *et al.*, 1996; Mukuka *et al.*, 2010), also considered
1253 below in response to extreme events. Application of entomopathogenic nematodes (EPNs), in
1254 which host location and survival would generally be favoured by wet conditions and impaired
1255 by drought (Grant and Villani, 2003), could be made with or at the same time as irrigation
1256 water, or, as above, applied at dusk. Some conservation biological control strategies may
1257 enable BCAs to persist where otherwise they would have been largely eliminated; for
1258 example, mulching may provide natural enemies with protection against extreme dryness or
1259 extreme rainfall.

1260 At present, the management options described above are untested as responses to climate
1261 change – research and field testing will be needed to explore what tactics can be used cost
1262 effectively to help BCAs adapt to reduced rainfall and drought.

1263 *Extreme events*

1264 Episodic extreme temperature (heat waves and unseasonal cold) has the potential to disrupt
1265 biological control food webs independently of the disruption of cropping systems. Although
1266 thermal stress may adversely affect pest population growth in the short term, BCA and pest
1267 populations have demonstrated the capacity for rapid adaptation to such stresses (White *et al.*,
1268 1970; Amice *et al.*, 2008; Harmon *et al.*, 2009). This last point suggests that adaptations to
1269 extreme events such as high temperatures may take place in BCA populations, and will help
1270 to moderate climate change impacts on biological control systems in sustainable agriculture.

1271 For augmentative biological control, it may be necessary to use strains or species that are
1272 more tolerant of extremes of temperature, although this would increase the risk that they
1273 become established. In simple, augmentative biological control communities, extreme heat
1274 stress affects the costs of defence against parasitoids and causes shifts in parasitoid
1275 community structure (Bannerman *et al.*, 2011; Gillespie *et al.*, 2012). Augmentative
1276 biological control is especially vulnerable to disruption of transportation networks by extreme
1277 weather events. Although not climate-related, this was demonstrated when the eruption of
1278 Eyjafjallajökull in Iceland in 2010 disrupted the supply of augmentative BCAs of greenhouse
1279 pests from Europe to North America.

1280 **Biological control agents to mitigate climate change**

1281 It is unlikely that BCAs and biological control will contribute in any meaningful direct way
1282 to mitigation of climate change. Certainly, effective biological control leads to more plant
1283 growth in cropping systems, but unless that carbon is stored (e.g. in the soil) it would be
1284 released at the end of the cropping cycle. Habitat set aside for conservation biological control
1285 (grasses and woody shrubs, for example) may have more carbon storage capacity than
1286 adjoining croplands. However, Costanza *et al.* (1997) assigned climate regulation values
1287 (CO₂ storage) to temperate and tropical forests, and biological control in forests is likely to
1288 have a significant CO₂ mitigation effect.

1289 The majority of the climate change footprint in agriculture comes from fertilizer application
1290 (Hillier *et al.*, 2009). In an analysis of 57 farms in Scotland, the application of all pest control
1291 products accounted for less than 3% of carbon costs, compared with fertilizer applications
1292 which accounted for over 80% of the carbon footprint on the same farms (Hillier *et al.*,
1293 2009). Thus the scope for reducing carbon footprints by increasing reliance on BCAs and
1294 reducing pesticide applications is very limited. However, the burning of agricultural crop
1295 residues is a significant source of greenhouse gases and while more environmentally
1296 sustainable practices have been adopted in some regions, the withdrawal of some commonly
1297 used pesticides may prolong the widespread use of burning for weed and pest control. In
1298 addition, soil and post-harvest fumigants such as sulfuryl fluoride and methyl bromide are
1299 potent greenhouse gases. Therefore, there are very good, reasons, including human health and
1300 environmental impacts, for reducing reliance on pesticide inputs and increasing reliance on
1301 BCAs.

1302 **Implications of climate change for future use of biological control agents in agriculture**

1303 All BCA invertebrate genetic resources are natural, unmodified species, or populations, and
1304 are thus already available to be used or developed. There is some potential for selection of
1305 strains with desirable characteristics in augmentative BCAs, for example, heat resistance,
1306 greater fecundity, and acceptance of more species of hosts. A starting point for such a
1307 selection process might well be to collect populations of the BCA from different areas,
1308 especially those with characteristics that match the target area.

1309 Climate change will lead to pest species changing their ranges to track the movement of the
1310 habitats where they are well adapted. Since this spread will initially be without specialized
1311 natural enemies, there may be increased demand for classical BCAs, particularly in those
1312 locations where the newly found pest is separated from other populations of the pest by
1313 barriers such as mountain ranges or the sea (Case study 5). Therefore, access to new classical
1314 BCAs will be crucial for agriculture, especially in island countries.

1315 Climate change is predicted to cause uncertainty and volatility in food supply and pricing
1316 (Foresight, 2011). Reliance on BCAs in sustainable agriculture is knowledge based, and is
1317 dependent on farmer confidence in BCA–pest interactions that are delayed in time (most
1318 BCA–pest population dynamics are delayed density dependent) and that are not necessarily
1319 apparent. If farmers are not completely confident in BCA-based IPM systems, they may
1320 respond to the uncertainty and volatility in demand and pricing with increased reliance on
1321 broad-spectrum chemical insecticides, which provide immediate and obvious impacts on pest
1322 numbers. If such responses occur, they would lead to an erosion of BCA performance, as has
1323 occurred in the past. The applications of broad-spectrum products would also adversely affect
1324 pollinator and soil invertebrate functions.

1325 An important consideration for classical biological control programmes is that, due to genetic
1326 bottlenecks, many introduced populations of natural enemies are likely to possess relatively
1327 little genetic variation. With reduced potential for rapid adaptive evolution compared with
1328 populations that are more heterogeneous, these populations may not have the genetic
1329 diversity required to continue to provide their ecosystem service in the face of climate change
1330 (Mackauer, 1976; Fauvergue and Hopper, 2009; Case study 15). If herbivores alter voltinism
1331 under climate change (Case study 7), parasitoids or predators will need to evolve or respond
1332 by plastic changes to synchronize their development with that of their host (Thomson *et al.*,
1333 2010).

1334 There are only a few evolutionary studies on natural enemies that consider synchronization
1335 (Phillips *et al.*, 2008) although there is evidence of genetic variation in generation time in
1336 parasitoids (Samara *et al.*, 2008). Whether specialist parasitoids, predators and herbivores
1337 show much evolutionary potential remains to be seen, but this could be manipulated or
1338 artificially enhanced (Thomson *et al.*, 2010). It may be possible, therefore, to mitigate the
1339 impacts of climate change on the efficacy of classical BCAs by increasing their genetic
1340 variability, and thus their potential for adaptation, through the introduction of additional
1341 genetic stock (Case study 16). Therefore, access to new genetic diversity or genetic resources
1342 may be required to widen the existing genetic diversity of the BCA.

1343 The risks of failing to maintain diversity (both species and genetic) of the bacterial
1344 endosymbiont community within BCAs in the face of climate change have been identified.
1345 There are no opportunities to address this problem in natural biological control systems. For
1346 classical and, especially, augmentative biological control systems, the identification and
1347 introduction of BCA strains with high-temperature-tolerant endosymbionts might be possible,
1348 or even necessary.

1349 For the foreseeable future, the technology to effectively store or maintain BCAs *ex situ* does
1350 not exist. There are no long-lived dormant stages like seeds or spores that can be used. The
1351 only option is to maintain populations of BCAs in culture, but it is known that genetic
1352 diversity is lost when species are taken into culture, and more is lost over time as the culture
1353 is maintained over generations (Mackauer, 1976; Roush, 1990; van Lenteren, 2003).
1354 Accordingly, BCAs can only be satisfactorily maintained *in situ*. The most important
1355 reservoirs are agro-ecosystems that favour BCAs (e.g. organic and other pesticide-free
1356 systems), especially in regions where wild or early-domesticated crop lines still persist.
1357 However, these agro-ecosystems are recent in evolutionary terms and, although some species
1358 will have evolved to the extent that they no longer occur in natural ecosystems (this is more
1359 likely for pathogens (e.g. Brunner *et al.*, 2009) than for invertebrates) for most pests and
1360 BCAs there should be an original natural ecosystem. This is likely to have different genetic

1361 diversity and perhaps different species of BCAs that have not (yet) managed to spread to
1362 agro-ecosystems, but still have an impact on the pest in its natural ecosystem. In many cases
1363 where the pests and their natural enemies came from is unknown, although we may surmise
1364 pests of arable crops are likely to come from early succession or temporary habitats, while
1365 tree pests are more likely to come from forest ecosystems. Thus conservation of all types of
1366 ecosystems will play a role in conserving the original sources of BCAs, but more studies
1367 would be needed to know which ecosystems preserve which BCAs (Myers 1932, Case study
1368 17).

1369 **Status of current application of genetic technologies**

1370 At present, there are no transgenic BCAs in use. Traditional selection of BCAs for desirable
1371 traits has been attempted for only a very few augmentative agents (Ashburner *et al.*, 1998;
1372 Hoy, 2000). Selection of predatory mites used in augmentative biological control for
1373 resistance to pesticides was conducted in the 1980s (Hoy, 1985), but the selected strains were
1374 not used extensively. Considerable genetic diversity is present in BCA populations (e.g.
1375 Henry *et al.*, 2010), but it remains largely unexploited. In cases where assisted adaptation is
1376 required in classical and augmentative BCAs, selection by classical breeding methods is
1377 likely to be sufficient (e.g. White *et al.* 1970; Gilkeson and Hill, 1986).

1378 There is scope to use genetic engineering to transform crops to allow them to continue to be
1379 grown in areas where climate changes or be grown in new climate zones (Sun *et al.*, 2009;
1380 Messmer and Stamp, 2010). This might lead to crops being grown in local climates where
1381 BCA communities are unable to regulate pests. As noted above, climate change effects on
1382 plants may alter the suitability of host plants for the BCA. BCAs rely heavily on plant-based
1383 resources in the crop and in the local habitat. These include pollen, nectar and extra-floral
1384 nectaries (Van Rijn and Tanigoshi, 1999; Robinson *et al.*, 2008), refuges such as leaf domatia
1385 (tiny chambers produced by plants that house arthropods) (Agrawal *et al.*, 2000; Roda *et al.*,
1386 2000), and herbivore-induced plant volatiles (HIPV) that help BCAs to locate hosts (Hare,
1387 2011). Adding these attributes to cropping systems could enhance BCA performance where
1388 climate change has otherwise limited their impact on pest populations. This could be done
1389 through creation of conservation habitat (adding new plant species), by conventional breeding
1390 for desired attributes, or by genetic transformations.

1391 **Biological control agents: Gaps regarding knowledge, collections and characterization**

1392 Huge knowledge gaps exist with respect to the responses of BCAs to climate change, and
1393 many of the suggestions above will need research and validation before they can be used.

1394 Predictions of future scenarios cannot ignore the potential of invertebrates to adapt rapidly to
1395 changing climate based on existing genetic diversity, although more studies are needed to
1396 assess the scope and speed of such potential adaptation. However, research conducted to date
1397 suggests that responses are specific to particular pest/BCA food webs, and therefore general
1398 predictions are difficult to make.

1399 Biological control food webs are likely to contain key interspecies interactions (e.g.
1400 competition, trait-mediated interactions) that define pest status, and the success of the BCA
1401 programme (e.g. Gilman *et al.*, 2010). Knowing how these key interactions respond to
1402 climate change factors would help enormously in predicting the impact on pest populations.
1403 Furthermore, good case studies may show that it is possible to generalize and make

1404 predictions with respect to responses of BCAs to climate change. Gilman *et al.* (2010)
1405 suggest that, despite the complexity of communities and food webs, it is possible to make
1406 such predictions. Along these lines, Vellend (2010) suggested that the apparent complexity of
1407 community ecology (the study of the forces that shape the diversity and abundance of species
1408 in communities) could be reduced to four processes: (i) selection of species within
1409 communities via differential fitness, (ii) stochastic changes in species abundance, (iii)
1410 evolution of new species/traits, and (iv) dispersal in space. Studies of the effects of climate
1411 change parameters on the strength and frequency of these processes might lead to predictions
1412 of how BCAs will respond to climate change.

1413 Because many BCAs have wide intraspecific variation in host range and climatic tolerances,
1414 the ability to genetically characterize BCAs needs specific attention. This work must be
1415 linked to competent morphological taxonomy, and to ecological performance indicators.
1416 Tools for recognizing climatically adapted strains in surveys, and in laboratory and field
1417 studies, are needed.

1418 **INVERTEBRATE POLLINATORS IN THE FACE OF CLIMATE CHANGE**

1419 Species are inseparably interdependent and interact with each other. An abiotic factor, such
1420 as climate change, has the potential to put out of phase the biological phenomenon of
1421 interdependence of species, with potentially catastrophic effects on species relationships (and
1422 food security and natural ecosystems). Phenologies can evolve, but the role of evolution in
1423 the response of mutualisms to climate change is poorly understood. Abundant alternative
1424 mutualist partners with broad temporal distributions can make a mutualism more robust to
1425 climate change, while abundant alternative partners with narrow temporal distributions can
1426 make a mutualism less robust. Community composition and the rate of climate change affect
1427 the persistence of mutualisms and are mediated by two-species Allee thresholds.
1428 Understanding these thresholds will help researchers to identify those mutualisms at highest
1429 risk owing to climate change (Gilman *et al.*, 2012).

1430 Pollination services by animals, especially insects, are among the most widespread and
1431 important processes that structure ecological communities in both natural and agricultural
1432 landscapes (Cock *et al.*, 2012). An estimated 78% of the world's flowering plants – including
1433 a range of economically important species – depend on insects for pollination (Ollerton *et al.*,
1434 2011). Crop pollination used to be (and often still is) provided by wild pollinators spilling
1435 over from natural and semi-natural habitats close to crop fields (Garibaldi *et al.*, 2011). This
1436 service has generally been free and therefore has received little attention in agricultural
1437 management (but see Garibaldi *et al.*, 2013). If wild pollinators are lacking or additional
1438 pollination is required, as is the case in many intensive agricultural production systems,
1439 farmers in some developed countries can buy or rent managed honeybees or sometimes other
1440 species (e.g. bumblebees, alfalfa leafcutter bees, mason bees). Both options – i.e. use of wild
1441 species and managed bees – have recently come under pressure, a development that is
1442 sometimes referred to as the “pollination crisis” – where the decline in pollinators is enough
1443 to threaten the human food supply. Concern has been raised over a looming potential
1444 pollination crisis as currently, insect pollination is endangered by a number of environmental
1445 and anthropogenic factors, and although data on the impacts of climate change on crop
1446 pollination are still limited, climate change may be a further threat to pollination services
1447 (Hegland *et al.*, 2009; Kjøhl *et al.*, 2011).

1448 **Possible adaptations to ensure future food security**

1449 To ensure future food security in the face of climate change, it is essential that pollination
1450 services are maintained at levels that, not only allow long-term production of a diversity of
1451 crops in all regions, but also meet the expected increase in demand and changes in crop
1452 choice of farmers. Possible areas of adaptation are discussed below.

1453 *Provision of resources within landscapes to support pollinators*

1454 The natural habitats of wild pollinators should be identified and preserved or provided. Once
1455 future land uses are forecast, corridors of suitable habitat can be formed or maintained to
1456 conserve and ensure connectivity of pollinator food/nesting resources within critical areas of
1457 the landscape and at critical times (Case study 18). Through the use of climate-resilient
1458 plantings relevant to the region, it should be possible to provide the diversity, abundance and
1459 succession of habitats and floral resources necessary for sustaining populations of wild
1460 pollinators and managed bees at levels optimal to agriculture.

1461 *Effects of altitude*

1462 As discussed above, the effects of elevation are often used as an alternative for assessing the
1463 potential effects of climate change, particularly changes in temperature. Pollinator
1464 communities tend to change with increasing elevation (and decreasing temperature). At
1465 higher altitudes the average size of pollinators increases (Malo and Baonza, 2002), but
1466 pollinator abundance is lower (Arroyo *et al.*, 1982). In addition, flies tend to become the
1467 dominant pollinator group, mainly because other groups are restricted to lower areas (Kearns,
1468 1992). In the Rocky Mountains (United States of America), flies replace bees as the main
1469 pollinators (Kearns 1992), while in the Andes of South America, tachinid flies and
1470 hummingbirds replace bee flies (Bombyliidae) and bees at higher altitudes (Arroyo *et al.*,
1471 1982). In addition, flower size tends to increase (Malo and Baonza, 2002). The lower
1472 pollinator abundance results in lower pollinator to flower ratios and lower seed set in plants at
1473 higher altitudes (Arroyo *et al.*, 1985; Malo and Baonza, 2002). Temperature increases might
1474 lead to pollinators moving to higher altitudes and might change pollination levels in plants.
1475 The arrival of more pollinator species (including bees) and individuals on mountains might
1476 make these areas suitable for cultivation of crops that are highly dependent on pollinators,
1477 which at present would suffer pollination limitation. Alternatively, change in pollinator
1478 communities might lead to a breakdown of pollination services at higher altitudes. Even
1479 though this might be the case for wild plants, there do not seem to be important crops that
1480 would suffer from pollination loss.

1481 *Selection of climate-adapted managed pollinators*

1482 The honeybee is the main managed pollinator around the world. This reflects the adaptability
1483 of the species to many different conditions from arctic to tropical and from rainforests to
1484 deserts. In the context of climate change, local beekeeping practices may have to adopt
1485 different honeybee races or hybrids that suit local conditions (e.g. with traits such as drought
1486 resistance and non-absconding). Alternatively, management of other bee (or pollinator)
1487 species could be developed or improved. For example, some stingless bees (Meliponinae)
1488 (Case study 19) and stem-nesting solitary bees, like *Osmia* and *Megachile* spp.
1489 (*Megachilidae*), can be selected for domestication and mass breeding based on their
1490 ecological traits and climatic or environmental tolerances (e.g. generalist food and nesting
1491 habits, short life cycles). Some bee species are more susceptible to environmental changes
1492 and anthropogenic pressure than others. Evidence for susceptibility is the presence of high

1493 diploid male frequencies (indication of inbreeding) in euglossine bees (Lopez-Urbe *et al.*,
1494 2007) and low genetic diversity of North American bumblebee populations (Cameron *et al.*,
1495 2011) which both suggest population declines.

1496 However, it is necessary to be aware of the risks associated with the use of managed
1497 organisms in new environments, namely that they may interfere with or be affected by native
1498 organisms. This can be through direct competition for resources (e.g. food, nest sites) or
1499 indirectly through transmission of pests and diseases to native flora and fauna or from them
1500 to the managed organism. A notorious example of this is the transfer of the *Varroa* mite from
1501 its host, the Asian honeybee *Apis cerana* (Fabricius) (Hymenoptera: Apidae), to the managed
1502 western honeybee, *Apis mellifera* L., after its introduction to Southeast Asia. Infection of
1503 honeybee hives with *Varroa* mites is now a global concern in beekeeping, mainly because
1504 they transmit viruses to the bees, which lowers bee longevity and weakens the colonies. The
1505 use of non-native subspecies can also be risky. The bumblebee, *Bombus terrestris* L.
1506 (Hymenoptera: Apidae) has been mass-produced for crop pollination across the world.
1507 However, the introduced bumblebees outcompete the local strains of this species in the
1508 British Isles. They can now only be used in greenhouses, and some bumblebee breeders have
1509 started to produce native British bumblebees for pollination purposes. Similar trends are
1510 occurring elsewhere. To minimize these risks, it is extremely important that transport of any
1511 managed organisms is based on established risk assessment procedures. The oil palm
1512 pollinator weevil (Case study 20) provides one example where the protocols of weed
1513 biological control were used effectively to evaluate the risk of damage to plants by the larvae
1514 of the weevils, but traditional pollinators would have to be evaluated following a different
1515 protocol.

1516 *Factors that currently compromise pollination*

1517 Crop systems and landscapes differ in the options they offer for managing crop pollination,
1518 e.g. use of wild pollinators, managed honeybees and other managed pollinators, hand
1519 pollination or a combination of these. The recent problems with managed honeybees in parts
1520 of the world have raised awareness of the vulnerability of pollination services. Crop
1521 pollination at present is probably limited by different factors in different locations (e.g. crop
1522 management, lack of pollinator habitat, pesticide application, and unsuitable climate). These
1523 factors are likely to intensify with climate change, and mitigation will need to be integrated
1524 into farm or landscape-level management. For example, shifting from monocultures to mixed
1525 cropping systems and agroforestry plantations might mitigate climate extremes through
1526 provision of more suitable microclimates and alternative foraging and nesting resources.

1527 In the case of the recent declines in managed honeybees, it is also not clear whether climate
1528 change will improve the conditions for beekeeping (e.g. better adapted tropical strains will
1529 move into new areas, as in the case of the Africanized honeybee in the Americas) or increase
1530 the risk that new pests and diseases (e.g. the small hive beetle, *Aethina tumida* (Murray);
1531 Coleoptera: Nitidulidae) may spread into Europe because of more amenable climatic
1532 conditions.

1533 *The transfer of pollinators between countries*

1534 To consider the opportunities, procedures and risks associated with the movement of
1535 pollinators, we recognize that some pollinators naturally move long distances across borders
1536 unassisted (Case study 18), but domesticated species, such as honeybees and some

1537 bumblebees, are regularly moved between countries, and if domestication of other social
1538 pollinators such as stingless bees (Case study 19) expands, there may well be scope to move
1539 them between countries too. In general, climate change is expected to increase demand for
1540 transborder movement of pollinators. However, introductions of pollinators to areas where
1541 they do not naturally occur have caused some significant problems (Generesch and Aubert,
1542 2010).

1543 One can consider several categories of pollinators that are, or might be, moved between
1544 countries:

- 1545 • **Honeybees and bumblebees.** There is likely to be continued and increasing demand
1546 for new strains or improved stock in response to climate change, and hence movement
1547 of queens, nucleus colonies and colonies between countries. The movement of both
1548 groups between countries has been implicated in the spread of pests and diseases.
1549 Several regulations must be met before honeybee queens (and attending workers) can
1550 be imported including verification of the absence of several diseases (for details see
1551 Brown, 2008; OIE, 2010). As yet, these regulations do not cover bumblebees,
1552 environmental risks of introducing pollinators, such as displacement of indigenous
1553 pollinators, or risks associated with pollinators other than honeybees.
- 1554 • **Stingless bees** from South America have been used in Japan for pollination of
1555 greenhouse strawberries and some trials have been carried out in the Netherlands for
1556 greenhouse crops (Slaa *et al.*, 2007). These species require tropical conditions and
1557 would not survive as colonies in the wild in temperate countries. Even though there is a
1558 low probability of stingless-bee pathogens switching host to native bees outside the
1559 area of the introduced bees' origin (none of which would be closely related), some
1560 regulations may be needed in the future.
- 1561 • **Other domesticated pollinators.** Domestication of wild pollinators is likely to increase
1562 the scope for movement of newly domesticated species between countries. Highly
1563 specialized pollinators associated with a particular crop are uncommon in agriculture,
1564 and the oil palm weevil is the only one that has been deliberately introduced to new
1565 continents (Case study 20). However, introduction of specialized pollinators might be
1566 needed in some cases. Guidelines and protocols for risk assessment should be
1567 developed if the risks associated with such introductions are to be managed. Protocols
1568 of weed biological control could be a starting point for the consideration of any future
1569 introductions of specialist pollinators.

1570 **Potential of pollinators to mitigate climate change**

1571 While pollinators cannot directly mitigate climate change, they can influence vegetation
1572 composition through their pollination activities and the seed dispersal resulting from it. It
1573 would, therefore, be important to integrate knowledge of pollination and seed dispersal into
1574 carbon fixing projects to ensure plantings used to counteract climate change are self-
1575 perpetuating. To our knowledge, there have been no studies assessing the long-term benefits
1576 of pollinators on vegetation composition and climate moderation.

1577 **Gaps in our knowledge on climate change impacts on pollinators**

1578 There are still many gaps in our knowledge of the possible consequences of climate change
1579 for pollinators and crop pollination. To date, there is a no holistic approach that includes

1580 pollinator-derived goods and services in assessments of climate change impacts on
1581 productive agricultural ecosystems. Declines and shifts in plant pollinators have been
1582 observed, but the causes and their interactions are not well known. It is often unclear whether
1583 shifts are due to climate change or to other human activities, such as intensification of
1584 agriculture, pesticide and fertilizer use, and land clearance and management. In addition,
1585 there are many unknowns with regard to the role of wild pollinators in crop pollination. A
1586 more specific knowledge gap is how climate change will affect bee pests and diseases.

1587 **DISCUSSION**

1588 The three key groups of invertebrates have been treated separately in the preceding review
1589 and discussion, and there are clearly good reasons for this approach. The soil invertebrate
1590 group is taxonomically and functionally diverse. Organisms range from microscopic
1591 multicellular animals such as nematodes and rotifers, through to large earthworms and
1592 arthropods. The functions of organisms in these communities include development and
1593 maintenance of soil structure, decomposition of organic detritus, and population regulation
1594 through predation and parasitism. Generally speaking, there is very little intentional
1595 management of these organisms, and only few attempts have been made to manage selected
1596 groups, for example earthworms in tropical areas, using in-soil or off-soil techniques
1597 (Senapati *et al.*, 1999). Overall the taxonomic diversity is poorly known, although important
1598 efforts are underway to combine morphological and molecular approaches.

1599 Invertebrate biological control organisms are dominated by arthropods, and functionally, the
1600 group is relatively uniform. The arthropod predators and parasitoids of arthropod pests of
1601 plants, and the arthropod herbivores of weeds regulate populations of pests and weeds
1602 respectively. There is considerable management of biological control organisms, but
1603 unmanaged impacts of biological control organisms on pests are nonetheless, of much greater
1604 global importance in agriculture.

1605 Invertebrate pollinators are the least diverse of the three groups, both from a taxonomic and
1606 functional perspective. This group consists primarily of insects, and almost all share
1607 mutualistic and highly co-evolved relationships with flowering plants whereby pollen is
1608 transferred from anthers to stigma by the insects in exchange for nectar and pollen rewards
1609 from the flower. Although some cropping systems rely heavily on wild pollination, the
1610 majority of horticultural crops are pollinated by a single, highly-managed species, the
1611 honeybee. Yet, evidence is accumulating that a diverse pollinator community generally
1612 provides better, more stable, pollination services than any single species alone.

1613 These differences in taxonomic and functional breadth, and in degree of management in the
1614 three groups, create some important considerations for impacts of global climate change on
1615 these groups, and for approaches to management of those impacts.

1616 Overall, most of the soil invertebrate communities are highly endemic, with some exceptions
1617 such as European earthworms and soil-dwelling beetles. The communities are determined not
1618 just by geographic region but also by their interactions with the underlying geomorphic
1619 substrate, the overlying plant community, and the prevailing climate (heat, rainfall). Although
1620 often well protected from short-term climate change in the soil, most organisms are slow-
1621 moving and may be greatly affected by geographic shifts in climate. Because of their
1622 importance in sustainable agriculture production and their potential role in carbon
1623 sequestration through production of biogenic structures that retain C and slow down

1624 decomposition, some degree of management of these communities will be required in the
1625 context of adaptation to climate change in agriculture.

1626 The biological control arthropods tend to be somewhat less restricted in distribution. The
1627 important natural enemies of pests and weeds are mostly as widely distributed as the crop
1628 system and pests that they attack. Most are highly mobile, and many have been shown to
1629 move rapidly with their pest or weed resource. In general, these species will mostly track
1630 geographic shifts in climate. The functions of biological control communities is very much
1631 dependent on temperature, and prolonged, more frequent and more severe episodes of
1632 extreme heat may change the impact of these organisms on their target populations. Again,
1633 management of biological control communities may be required in the context of adaptation
1634 to climate change, but these requirements are likely to emerge only as climate change
1635 progresses, and loss of biological control functions is observed in agricultural crops.

1636 The pollination function in crops relies heavily on honeybees, and this species has been
1637 moved around the world. In other words, to a large extent endemism is not a great factor in
1638 pollination functions, and strains of honeybees exist that are adapted to specific climate
1639 conditions. For honeybee-managed pollination systems, it is likely that only a modest degree
1640 of adaptation will be required, such as the importation of new strains and the movement of
1641 bee producers to new centres of crop production. A much greater threat exists for agricultural
1642 crops that rely on wild pollinators, which may be more widespread than previously thought
1643 (see Garibaldi *et al.* 2013). Although most crops have generalist pollination systems, some
1644 may need specialist wild pollinators. Such pollinators may have restricted ranges, which
1645 make mismatches as a result of climate change highly likely. In these cases, intervention and
1646 management are likely to be required in the context of adaptation to climate change.

1647 Although climate change is a global phenomenon, not all areas of the globe will be affected
1648 in the same way or to the same degree. Moreover, agricultural production and the underlying
1649 invertebrate biodiversity associated with agriculture are not evenly distributed across the
1650 globe. Geographic and social barriers exist that restrict the potential for cropping systems and
1651 the underlying invertebrate biodiversity to track geographic shifts in suitable climate. These
1652 differences and barriers are likely to affect the three groups of invertebrates in different ways,
1653 and this is discussed further below.

1654 **Island versus continental perspective**

1655 In general, biodiversity is reduced on islands compared to continental equivalents. Moreover,
1656 oceanic islands characteristically have a great number of endemic species adapted to local
1657 niches. Most crops grown on islands, especially oceanic islands are not indigenous. The
1658 reduced diversity of indigenous invertebrates compared to similar continental areas, means
1659 there will be relatively few invertebrate species able to spread into crop agroecosystems, i.e.
1660 there will be fewer indigenous pests, but correspondingly a shortage of beneficial species to
1661 provide the services discussed here and in Cock *et al.* (2012). With the accidental assistance
1662 of man, alien phytophagous pests make their way to islands more efficiently than do their
1663 natural enemies, or plant pollinators, especially the social species. In the past soil organisms
1664 have been moved rather freely with planting material of indigenous crops and ornamentals,
1665 but normally this is now prevented with standard phytosanitary procedures.

1666 As climates and crops change, pests of agricultural crops always move past barriers first and
1667 usually without their associated BCAs. Sea barriers will be more effective than most other

1668 barriers as constraints to movement of invertebrates including BCAs, and demand for new
1669 BCAs (classical and augmentative) will be greater on islands as a result. In continental
1670 situations, natural and classical BCAs will normally spread with the crop and pest as they
1671 move with changing climate into new geographical areas, even when the landscape is broken
1672 up into a mosaic of agricultural and non-agricultural habitats.

1673 With climate change, it is islands, rather than continents, that are likely to experience the
1674 greatest challenges in meeting their pollinator requirements. New crops may appear more
1675 economically and climatically sustainable than those traditionally grown. Where those crops
1676 rely on wild pollinators, it will be necessary to assess whether the existing pollinator diversity
1677 and assemblages can provide adequate pollination. Where exotic introductions are
1678 considered, careful risk analysis would be required. Some crops may have specific pollinator
1679 requirements (cocoa, pawpaw (papaya), and passion fruit) and may need more specific
1680 habitat or cultivation adaptations to accommodate pollinators. Islands are also vulnerable to
1681 loss of diversity in their pollinator resources through extreme climatic events (extinction very
1682 likely, colonization very unlikely). If new crops rely primarily on managed (honeybee)
1683 pollinator services, it may be necessary to determine if the honeybee industry on the island is
1684 adequate to provide the necessary services. If other exotic bees are to be introduced (e.g.,
1685 bumblebees) some form of risk assessment should be made for the impacts of these exotics,
1686 particularly on the endemic pollinator species.

1687 **Tropical versus temperate comparisons**

1688 There is a developing country / developed country divide that aligns with tropical / temperate
1689 – generally developing countries have more subsistence farmers, more of the population
1690 directly involved in agriculture, less food security, more fragile ecosystems and highly-
1691 degraded soils, greater dependence on natural biological control, and hence are likely to be
1692 severely affected by a reduction in the role of beneficial invertebrate functional groups
1693 caused by climate change. Development assistance is needed for research to address the
1694 knowledge gaps identified below.

1695 All of the evidence in the fossil record of responses of invertebrates to climate change comes
1696 from temperate regions (Case study 2). Data are badly needed from tropical regions, because
1697 we are assuming there will be similar responses in those regions to temperate regions.
1698 Tropical pollen cores have been collected, e.g. along the Amazon equator (Colinvaux, 2005),
1699 and assessing whether these contain identifiable insect parts would be a useful starting point.

1700 There are differences between the invertebrate soil fauna and their functioning in tropical and
1701 temperate regions, for example, warmer conditions promote greater abundance of
1702 decomposer invertebrates (Seastedt, 2000) and earthworms in tropical areas have a greater
1703 role in breaking down recalcitrant components of soil organic matter than do those in cooler
1704 climates (Lavelle *et al.*, 1995). However, differences are species dependent, and our depth of
1705 knowledge may make it premature to look for differences that will be important in the face of
1706 climate change.

1707 Essentially, tropical production systems are bimodal in their approach to pest management
1708 and their use of biological control. On the one hand, subsistence farmers rely heavily on
1709 natural and unmanaged biological control. On the other, the relatively few, larger scale
1710 production systems in tropical zones often rely heavily on the use of chemical pesticides.
1711 With a few exceptions, in neither system have the support and inputs been developed to

1712 enable growers to rely on integrated systems that incorporate the deliberate augmentation and
1713 management of BCAs that is a feature of many production systems in temperate agriculture.

1714 It is not particularly likely that the interference of climate change with natural biological
1715 control is going to be of primary concern for subsistence farmers. It is much more likely that
1716 climate change effects that increase drought, and flooding and interfere directly with food
1717 production will be of primary concern. Nonetheless, particularly for the staple crops that are
1718 widespread and central to subsistence farming in the tropics (rice, maize, cassava, yams,
1719 sweet potato, Andean potato, taro, etc.) some consideration should be given to the effects of
1720 changing climate on BCAs. To our knowledge, this need has not been adequately addressed
1721 as yet, and development aid-funded research is needed to address this knowledge gap.

1722 In general, the contrasts between tropical and temperate zone pollination have received more
1723 attention than is the case for soil and BCA invertebrates. Bawa (1990) states that there are
1724 four major differences between pollination systems of tropical lowland rainforests and
1725 northern temperate zone forests: (1) in aseasonal tropical forests pollination occurs
1726 throughout the year, whereas in temperate forests flowering is mostly confined to late spring
1727 and summer; (2) flower longevity is much shorter in tropical forests (1–2 days) than in
1728 temperate forest (up to seven days, perhaps in response to unpredictable weather conditions
1729 unsuitable for pollinators); (3) vertebrates are often important pollinators in tropical forests,
1730 but not usually significant in temperate forests (apart from temperate Australia and South
1731 Africa); and (4) the proportion of wind-pollinated plants steadily increases as one moves
1732 from the equatorial region, reaching 80–100% among trees in some of the northern-most
1733 latitudes. Based on these differences we might anticipate that: tropical regions will
1734 experience less temporal decoupling of pollination services than temperate regions, temperate
1735 plant species with shorter flower life might benefit more from a warming-induced increase in
1736 pollinator activity than temperate species with longer flower life, and there may be an
1737 increase in pollination success of animal-dependent plants in the tropics due to increased
1738 pollinator activity in response to higher temperatures.

1739 Domesticated honeybees are expected to remain effective in tropical zones under the
1740 temperatures predicted for the next century, but foraging behaviour will be altered under
1741 increased rainfall, resulting in reduced productivity of honey and crops (Delgado *et al.*,
1742 2012). It is likely that domesticated western honeybee races in warmer climatic conditions
1743 will need more intensive disease management than they currently do. One way to adapt to
1744 this is to adopt (sub)tropical races in managed beekeeping. This has been done in the
1745 American tropics where Africanized honeybees are now routinely used in countries such as
1746 Brazil and are more productive than temperate honeybee races there (Kaplan, 2004).

1747 **Potential to manage invertebrates so as to mitigate climate change**

1748 For the foreseeable future, there seems to be very little or no practical scope to manage
1749 invertebrates in order to mitigate climate change. There may be some modest potential for
1750 management of soil invertebrates to contribute to increasing carbon sequestration in soils, but
1751 much research and assessment will be needed first. Pollinators and pests can influence
1752 vegetation composition; accordingly, integrating knowledge of pollination and pest dynamics
1753 (and the role of BCAs) into carbon fixing projects will ensure that plantings used to
1754 counteract climate change are sustainable and self-perpetuating, but as yet there is little
1755 detailed practical guidance available.

1756 **Status of current application of genetic technologies**

1757 There are no transgenic biological control agents, pollinators or soil invertebrates in use at
1758 this time. The genetic diversity found in these populations is largely unexploited in this
1759 regard. Deliberate enhancement of BCAs, pollinators or selected soil invertebrates is an
1760 option that may be practical in the future as knowledge, capability and experience increase.

1761 In a changed climate, if crops are grown in the new climate zones, the impact of BCAs'
1762 performance on some pest populations might be limited. Adding suitable attributes to crops
1763 could enhance the performance of BCAs, and so access to crop and related plant genetic
1764 resources will be needed. Similarly changes could be considered in relation to the other key
1765 groups, such as enhanced nectar composition for pollinators, and root zone changes to
1766 prevent or cope with the loss of invertebrates due to climate change.

1767 **Overlaps and interactions between key invertebrate groups**

1768 There are significant overlaps and interactions between the three key groups on which this
1769 review has focused. Of these, interactions and overlaps between soil invertebrates and
1770 biological control agents are probably the most important (Cock *et al.*, 2012). However,
1771 given the complexity of these mechanisms, especially those involving above ground and
1772 below ground elements mediated through plants, there is little specific that can be said about
1773 the potential effects of climate change on them, although there will undoubtedly be important
1774 effects.

1775 **CONCLUSIONS AND KEY GAPS**

1776 In this review, we have found that there are many gaps in our knowledge of invertebrate
1777 genetic resources as affected by climate change and how to use them in response to climate
1778 change. Specific conclusions regarding the impact of climate change on particular elements
1779 of invertebrate genetic resources in agriculture are not possible yet. However, three general
1780 conclusions are evident. Firstly, it is likely that climate change will disrupt the use of
1781 invertebrates in agriculture, especially sustainable agriculture, even though the precise nature
1782 of the disruptions is not yet known. Secondly, that, without intervention, these disruptions
1783 will result in production losses particularly in sustainable agriculture, even though the scale
1784 and extent of the losses is not yet known. Thirdly, that the extent of some of the losses will
1785 justify intervention to facilitate adaptations of the invertebrates, even though the methods
1786 with which to intervene and policies to facilitate this intervention are not yet in place.

1787 We have identified the following priority gaps in knowledge that need to be addressed in the
1788 context of these conclusions.

1789 *Scientific knowledge*

- 1790 • Improvement to knowledge and understanding of (i) soil invertebrates, (ii) natural
1791 BCAs, (iii) wild pollinators of major crops, and (iv) their contribution to crop
1792 production in developed and developing countries. We found that the knowledge of the
1793 contribution of these unmanaged invertebrates to sustainable agriculture systems is
1794 generally lacking, particularly in developing countries, so any changes due to climate
1795 change would be difficult to assess.

- 1796 • Quantification of the responses of invertebrate species, communities, food webs and
1797 different types of interactions to climate change factors. It is only within the last two
1798 decades that scientists have begun to study the responses of key species to climate
1799 change factors. A plethora of mechanisms has been identified, but a unified
1800 understanding of the impact of these on community and food web structure and
1801 performance has not yet emerged.
- 1802 • Further investigation of past climate change in tropical areas, and assessment of how
1803 invertebrate species have responded in terms of distribution (based on sub-fossil
1804 records). Past climate change events are relatively well documented in the temperate
1805 zones (tree rings, glaciers, well-preserved sub-fossils), but parallel data are as yet
1806 largely lacking in tropical zones. Understanding the progress of climate change in these
1807 zones, and its impact on invertebrates, will be essential for the development of
1808 strategies to mitigate the impacts of climate change on sustainable agriculture and a
1809 large fraction of the human population.
- 1810 • Taxonomy and genetic characterization of invertebrates of agro-ecosystems. We found
1811 that the biodiversity and taxonomic identity of the soil invertebrate fauna are relatively
1812 unknown, and a sustained effort is required so that impacts of climate change on this
1813 crucial biodiversity can be assessed. Recent studies have revealed that what appear to
1814 be generalist BCA parasitoid species are often a complex of previously unrecognized
1815 specialist species. As specialists are generally more susceptible than generalists to
1816 disruption by perturbations, it is possible that the supply of biological control and
1817 pollination services may be disrupted by climate change-driven losses of key
1818 invertebrates.
- 1819 • More studies on rates of movement of selected key species, especially soil invertebrates
1820 without a motile stage, perhaps based on the northern boundaries of the tree line, or
1821 colonization of recently erupted volcanoes. We found abundant evidence of changes in
1822 ranges of motile species in response to climate change, but no studies on relatively non-
1823 motile species. Similarly, there appear to be no studies of the movement of BCAs in
1824 response to range changes in their hosts. Knowledge in this area is essential to
1825 understanding the need to develop strategies that facilitate adaptation of invertebrates
1826 and sustainable agriculture systems to climate change.

1827 *Conservation, use and access*

- 1828 • Rearing technologies to shift selected wild bee and other pollinator species to
1829 domestication. We found that for crops that are dependent on specialist pollinators,
1830 climate change-induced changes in location of production, or loss of synchrony
1831 between pollinators and flowering seasons are likely. Adapting and preserving these
1832 production systems for use in response to changing climate will be dependent on the
1833 domestication and manipulation of their specialist pollinators.
- 1834 • Technologies and approaches to ensure the conservation and promotion of generalist
1835 natural enemies in agricultural landscapes through improved knowledge of landscape-
1836 level movement, and the effects of resources such as spatial and temporal refugia and
1837 alternative food sources. This will add robustness to agricultural systems strengthening
1838 their adaptability in response to climate change.
- 1839 • Identification and conservation of source habitats of pests and associated BCAs. We
1840 found that, under climate change, there will probably be a need to access the genetic

- 1841 diversity of classical BCAs that is present in their source habitats, to facilitate
1842 adaptation of BCAs to changing climates.
- 1843 • Development of mass production methods for some important soil ecosystem engineers
1844 so as to facilitate experimental evaluation of their use in soil management practices
1845 both for immediate use and in response to climate change.

1846 *Facilitating policy environment*

- 1847 • An overarching holistic strategy that integrates invertebrates with the other ecosystem
1848 components to better design and manage future agro-ecosystems for food security in
1849 the face of climate change.
- 1850 • Guidelines for facilitating and regulating the movement of invertebrate genetic
1851 resources between countries, which build on what is so far available for BCAs and
1852 include emergency responses and pest risk assessment protocols. As climate change
1853 progresses, new invasive pests are likely. A coordinated development of standard
1854 protocols for pest risk assessment, e.g. International Standards for Phytosanitary
1855 Measures (ISPM) 2 (IPPC, 2007) would facilitate survey and detection efforts and
1856 allow timely responses to new invasions. Similarly, responses to invasive pests will
1857 probably involve release of classical BCAs, and it may be appropriate to revisit ISPM3
1858 in the context of emergency responses to new invasive threats.
- 1859 • Recognition that in implementing the Nagoya Protocol, when drafting national
1860 strategies (e.g. producing guidelines and procedures), countries need to take into
1861 consideration the need for invertebrate genetic resources to sustain agriculture, food
1862 production and world food security in the face of climate change.
- 1863 • Further development and implementation of existing national biodiversity programmes.
1864 As noted above, the role and importance of invertebrate genetic resources diversity in
1865 relation to sustainable agricultural production are not well known, particularly in
1866 relation to soil invertebrates and pollinators in general, and in relation to some
1867 biological control invertebrates. This knowledge will help evaluate options for response
1868 to changing conditions in the face of climate change.

1869 *Islands versus continental areas*

- 1870 • Policy support for island states, that will probably not be original sources of BCAs (or
1871 pests), but will need new BCAs. We found that islands are particularly susceptible to
1872 pest invasions and this will increase with climate change. Furthermore these invasions
1873 resulting from range shifts are unlikely to be accompanied by existing natural enemies,
1874 unlike the situation in continental areas. Hence, there is likely to be a disproportionate
1875 increase in demand for BCAs for islands, and it may be appropriate to promote a policy
1876 environment that will address this.

1877 *Tropical versus temperate*

- 1878 • Attention to the question of how species ranges will change in tropical regions in
1879 response to climate change, particularly in temperature and rainfall. This area of
1880 scientific knowledge has not been widely addressed and there is a relative dearth of
1881 studies on the sensitivity of tropical ecosystems to climate changes. Will pantropical
1882 species expand their distribution?

- 1883 • Testing the hypothesis that tropical species may be more sensitive to climate change as
1884 a result of narrower biotic ranges and lack of exposure to climatic variation. Addressing
1885 this specific scientific knowledge gap would help determine whether there are specific
1886 and special concerns with respect to the conservation of useful invertebrate biodiversity
1887 in the tropics.

1888 ACKNOWLEDGEMENTS

1889 This review is based in part on a report that the authors prepared for the Commission on
1890 Genetic Resources for Agriculture (CGRFA), at the Food and Agriculture Organization of the
1891 United Nations (FAO), Rome, on climate change and invertebrate genetic resources for food
1892 and agriculture (Cock *et al.* 2011). We thank Kim-Anh Tempelman and colleagues at the
1893 CGRFA for their interest, support and encouragement in preparing that report.

1894 We also thank Peter S. Baker (CABI), John Kean (AgResearch Ltd, New Zealand), Graham
1895 Walker (The New Zealand Institute for Plant & Food Research Limited), and Craig Phillips
1896 (AgResearch Ltd, New Zealand), who contributed Case Studies as indicated; Joop van
1897 Lenteren (Wageningen University, The Netherlands), Peter Baker and several anonymous
1898 scientists of the CGRFA and FAO who reviewed parts of a draft of the report from which this
1899 review was derived; and Rebecca J Murphy (United Kingdom) and Dafydd Pilling (FAO) for
1900 editorial inputs to that report.

1901 REFERENCES

- 1902 Aerts, R. (2006) The freezer defrosting: global warming and litter decomposition rates in cold
1903 biomes. *Journal of Ecology* 94, 713–724.
- 1904 Agrawal, A.A., Karban, R. and Colfer, R.G. (2000) How leaf domatia and induced plant
1905 resistance affect herbivores, natural enemies and plant performance. *Oikos* 89, 70–80.
- 1906 Amice, G., Vernon, P., Outreman, Y., Van Alphen, J. and Van Baaren, J. (2008) Variability
1907 in responses to thermal stress in parasitoids. *Ecological Entomology* 33, 701–708.
- 1908 Araújo, M.B. and Luoto, M. (2007) The importance of biotic interactions for modelling
1909 species distributions under climate change. *Global Ecology and Biogeography* 16, 743–
1910 753.
- 1911 Arribas, P., Abellan, P., Velasco, J., Bilton, D.T., Millan, A. and Sanchez-Fernandez, D.
1912 (2012) Evaluating drivers of vulnerability to climate change: a guide for insect
1913 conservation strategies. *Global Change Biology* 18, 2135–2146.
- 1914 Arroyo, M.T., Primack, R. and Armesto, J.J. (1982) Community studies in pollination
1915 ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and
1916 altitudinal variation. *American Journal of Botany* 69, 82–97.
- 1917 Arroyo, M.T.K., Armesto, J.J. and Primack, R.B. (1985) Community studies in pollination
1918 ecology in the high temperate Andes of central Chile II. Effect of temperature on visitation
1919 rates and pollination possibilities. *Plant Systematics and Evolution* 149, 187–203.
- 1920 Ashburner, M., Hoy, M.A. and Peloquin, J.J. (1998) Prospects for the genetic transformation
1921 of arthropods. *Insect Molecular Biology* 7, 201–213.
- 1922 Assefa, Y., Mitchell, A., Conlong, D.E. and Muirhead, K.A. (2008) Establishment of *Cotesia*
1923 *flavipes* (Hymenoptera: Braconidae) in sugarcane fields of Ethiopia and origin of founding
1924 population. *Journal of Economic Entomology* 101, 686–691.
- 1925 Bale, J.S. and Hayward, S.A.L. (2010) Insect overwintering in a changing climate. *Journal of*
1926 *Experimental Biology* 213, 980–994.
- 1927 Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K.,
1928 Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G. Harrington, R., Hartley, S.,

- 1929 Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. and Whittaker, J.B.
 1930 (2002) Herbivory in global climate change research: direct effects of rising temperature on
 1931 insect herbivores. *Global Change Biology* 8, 1–16.
- 1932 Bannerman, J.A., Gillespie, D.R. and Roitberg, B.D. (2011) The impacts of extreme and
 1933 fluctuating temperatures on trait-mediated indirect aphid-parasitoid interactions.
 1934 *Ecological Entomology* 36, 490–498.
- 1935 Bardgett, R.D., Yeates, G.W. and Anderson, J.M. (2005) Patterns and determinants of soil
 1936 biological diversity. In: Bardgett, R.D., Usher, M.B. and Hopkins, D.W. (eds) *Biological
 1937 Diversity and Function in Soils*. Cambridge University Press, Cambridge, UK, pp. 100–
 1938 118.
- 1939 Barros, E., Grimaldi, M., Sarrazin, M., Chauvel, M., Mitja, D., Desjardins, T. and Lavelle, P.
 1940 (2004) Soil physical degradation and changes in macrofaunal communities in Central
 1941 Amazon. *Applied Soil Ecology* 26, 157–168.
- 1942 Barton, B.T. and Schmitz, O.J. (2009) Experimental warming transforms multiple predator
 1943 effects in a grassland food web. *Ecology Letters* 12, 1317–1325.
- 1944 Barton, B.T., Beckerman, A.P. and Schmitz, O.J. (2009) Climate warming strengthens
 1945 indirect interactions in an old-field food web. *Ecology* 90, 2346–2351.
- 1946 Bawa, K.S. (1990) Plant-pollinator interactions in tropical rain forests. *Annual Review of
 1947 Ecology and Systematics* 21, 399–422.
- 1948 Bean, D.W., Dalin, P. and Dudley, T.L. (2012) Evolution of critical day length for diapause
 1949 induction enables range expansion of *Diorhabda carinulata*, a biological control agent
 1950 against tamarisk (*Tamarix* spp.). *Evolutionary Applications* 5, 511–523.
- 1951 Berg, M.P., Kiers, E.T., Driessen, G., van der Heijden, M., Kooi, B.W., Kuenen, F., Liefting,
 1952 M., Verhoef, H.A. and Ellers, J. (2010) Adapt or disperse: understanding species
 1953 persistence in a changing world. *Global Change Biology* 16, 587–598.
- 1954 Bezemer, T.M., Jones, T.H. and Knight, K.J. (1998) Long-term effects of elevated CO₂ and
 1955 temperature on populations of the peach potato aphid *Myzus persicae* and its parasitoid
 1956 *Aphidius matricariae*. *Oecologia* 116, 128–135.
- 1957 Bezemer, T.M., Knight, K.J., Newington, J.E. and Jones, T.H. (1999) How general are aphid
 1958 responses to elevated atmospheric CO₂? *Annals of the Entomological Society of America*
 1959 92, 724–730.
- 1960 Bidart-Bouzat, M.G. and Imeh-Nathaniel, A. (2008) Global change effects on plant chemical
 1961 defenses against insect herbivores. *Journal of Integrative Plant Biology* 50, 1339–1354.
- 1962 Blouin, M., Zuily-Fodil, Y., Pham-Thi, A.T., Laffray, D., Reversat, G., Pando, A., Tondoh, J.
 1963 and Lavelle, P. (2005) Belowground organism activities affect plant aboveground
 1964 phenotype, inducing plant tolerance to parasites. *Ecology Letters* 8, 202–208.
- 1965 Bosch, J., Sgolastra, F., William P. and Kemp, W.P. (2010) Timing of eclosion affects
 1966 diapause development, fat body consumption and longevity in *Osmia lignaria*, a
 1967 univoltine, adult-wintering solitary bee. *Journal of Insect Physiology* 56, 1949–1957.
- 1968 Bouché, M.B. (1972) *Lombriciens de France, Ecologie et Systématique*. Institut national de
 1969 la Recherche agronomique, Paris, France, 671 pp.
- 1970 Bouget, C. and Duelli, P. (2004) The effects of windthrow on forest insect communities: a
 1971 literature review. *Biological Conservation* 118, 281–299.
- 1972 Bowman, D.M.J.S., Murphy, B.P. and Banfai, D.S. (2010) Has global environmental change
 1973 caused monsoon rainforests to expand in the Australian monsoon tropics? (Special issue:
 1974 Landscape ecology as an integrated science for sustainability in a changing world.)
 1975 *Landscape Ecology* 25, 1247–1260.

- 1976 Branson, D.H. (2008) Influence of a large late summer precipitation event on food limitation
1977 and grasshopper population dynamics in a northern Great Plains grassland. *Environmental*
1978 *Entomology* 37, 686–695.
- 1979 Briones, M.J.I., Ostle, N.J., McNamara, N.P. and Poskitt, J. (2009) Functional shifts of
1980 grassland soil communities in response to soil warming. *Soil Biology & Biochemistry* 41,
1981 315–322.
- 1982 Briones, M.J.I., Poskitt, J. and Ostle, N. (2004) Influence of warming and enchytraeid
1983 activities on soil CO₂ and CH₄ fluxes. *Soil Biology & Biochemistry* 36, 1851–1859.
- 1984 Brown, M. (2008) Overview of the regulatory framework for apiculture. In: Aubert M., Ball,
1985 B., Fries, I., Moritz, R., Milani, N. and Bernardinelli, I. (eds) *Virology and the Honeybee*.
1986 Project Report EUR 21937. Office for Official Publications of the European Communities,
1987 Luxembourg, pp. 371–420.
- 1988 Brunner, P.C., Keller, N. and McDonald, B.A. (2009) Wheat domestication accelerated
1989 evolution and triggered positive selection in the beta-xylosidase enzyme of
1990 *Mycosphaerella graminicola*. *PLoS ONE* 4(11), e7884, 8 pp.
- 1991 Burgiel, S.W. and Muir, A.A. (2010) *Invasive Species, Climate Change and Ecosystem-*
1992 *Based Adaptation: Addressing Multiple Drivers of Global Change*. Global Invasive
1993 Species Programme (GISP), Washington, DC, and Nairobi, Kenya, 55 pp.
- 1994 Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.P., Cordes, N., Solter, L.F. and Griswold,
1995 T.L. (2011) Patterns of widespread decline in North American bumble bees. *Proceedings*
1996 *of the National Academy of Sciences USA* 108, 662–667.
- 1997 Cannon, R.J.C. (1998) The implications of predicted climate change for insect pests in the
1998 UK, with emphasis on non-indigenous species. *Global Change Biology* 4, 785–796.
- 1999 Carrera, N., Barreal, M.E., Gallego, P.P. and Briones, M.J.I. (2009) Soil invertebrates control
2000 peatland C fluxes in response to warming. *Functional Ecology* 23, 637–648.
- 2001 Chauvel, A., Grimaldi, M., Barros, E., Blanchart, E., Desjardins, T., Sarrazin, M. and
2002 Lavelle, P. (1999) Pasture damage by an Amazonian earthworm. *Nature* 398, 32–33.
- 2003 Chen, F.J., Wu, G., Parajulee, M.N. and Ge, F. (2007) Impact of elevated CO₂ on the third
2004 trophic level: a predator *Harmonia axyridis* and a parasitoid *Aphidius picipes*. *Biocontrol*
2005 *Science and Technology* 17, 313–324.
- 2006 Chen, Y.H., Opp, S.B., Berlocher, S.H. and Roderick, G.K. (2006) Are bottlenecks associated
2007 with colonization? Genetic diversity and diapause variation of native and introduced
2008 *Rhagoletis completa* populations. *Oecologia* 149, 656–667.
- 2009 Cock, M.J.W., Biesmeijer, J.C., Cannon, R.J.C., Gerard, P.J., Gillespie, D., Jiménez, J.J.,
2010 Lavelle, P.M. and Raina, S.K. (2011) Climate change and invertebrate genetic resources
2011 for food and agriculture: state of knowledge, risks and opportunities. Commission on
2012 Genetic Resources for Food and Agriculture, Background Study Paper No. 54. FAO,
2013 Rome, 105pp. <http://www.fao.org/docrep/meeting/022/mb390e.pdf>
- 2014 Cock, M.J.W., Biesmeijer, J.C., Cannon, R.J.C., Gerard, P.J., Gillespie, D., Jiménez, J.J.,
2015 Lavelle, P.M. and Raina, S.K. (2012) The positive contribution of invertebrates to
2016 sustainable agriculture and food security. *CAB Reviews: Perspectives in Agriculture,*
2017 *Veterinary Science, Nutrition and Natural Resources* 0(0), 00 pp.
- 2018 Cole, A.C. Jr (1940) A guide to the ants of the Great Smoky Mountains National Park,
2019 Tennessee. *American Midland Naturalist* 24, 1–88.
- 2020 Coley, P.D. (1998) Possible effects of climate change on plant/herbivore interactions in moist
2021 tropical forests. *Climatic Change* 39, 455–472.
- 2022 Colinvaux, P. (2005) The Pleistocene vector of neotropical diversity. In: Bermingham, E.,
2023 Dick, C.W. and Moritz, C. (eds) *Tropical Rainforests: Past, Present and Future*.
2024 University of Chicago Press, Chicago, Illinois, pp. 78–106.

- 2025 Coll, M. and Hughes, L. (2008) Effects of elevated CO₂ on an insect omnivore: a test for
 2026 nutritional effects mediated by host plants and prey. *Agriculture, Ecosystems &*
 2027 *Environment* 123, 271–279.
- 2028 Collins, N.M. (1980) The distribution of soil macrofauna on the West Ridge of Gunung
 2029 (Mount) Mulu, Sarawak. *Oecologia* 44, 263–275.
- 2030 Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C. and Longino, J.T. (2008) Global
 2031 warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*
 2032 322, 258–261.
- 2033 Coope, G.R. (2004) Several million years of stability among insect species because of, or in
 2034 spite of, Ice Age climatic instability? *Philosophical Transactions of the Royal Society B:*
 2035 *Biological Sciences* 359, 209–214.
- 2036 Costanza, R., d’Arge, R., de Groot, R., Farberk, S., Grasso, M., Hannon, B., Limburg, K.,
 2037 Naeem, S., O’Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. and van den Belt, M. (1997)
 2038 The value of the world’s ecosystem services and natural capital. *Nature* 387, 253–260.
- 2039 Coviella, C. and Trumble, J. (1999) Effects of elevated atmospheric carbon dioxide on
 2040 insect–plant interactions. *Conservation Biology* 13, 700–712.
- 2041 Craufurd, P.Q. and Wheeler, T.R. (2009) Climate change and the flowering time of annual
 2042 crops. *Journal of Experimental Botany* 60, 2529–2539.
- 2043 Curtis, P.S. and Wang, X. (1998) A meta-analysis of elevated CO₂ effects on woody plant
 2044 mass, form and physiology. *Oecologia* 113, 299–313.
- 2045 David, J.-F. and Gillon, D. (2009) Combined effects of elevated temperatures and reduced
 2046 leaf litter quality on the life-history parameters of a saprophagous macroarthropod. *Global*
 2047 *Change Biology* 15, 156–165.
- 2048 Davidson, E.A. and Janssens, I.A. (2006) Temperature sensitivity of soil carbon
 2049 decomposition and feedbacks to climate change. *Nature* 440, 165–173.
- 2050 Davis, D.W. and McMurtry, J.A. (1979) Introduction. In: Davis, D.W., Hoyt, S.C.,
 2051 McMurtry, J.A. and AliNiazee, M.T. (eds) *Biological Control and Insect Pest*
 2052 *Management*. University of California, Division of Agricultural Sciences, Publication
 2053 4096. University of California Press, Oakland, California, pp. i–ii.
- 2054 Davis, M.B., Shaw, R.G. and Etterson, J.R. (2005) Evolutionary responses to changing
 2055 climate. *Ecology* 86, 1704–1714.
- 2056 De Moraes, C.M., Lewis, W.J., Pare, P.W., Alborn, H.T. and Tumlinson, J.H. (1998)
 2057 Herbivore-infested plants selectively attract parasitoids. *Nature* 393, 570–573.
- 2058 Dean, H.A., Schuster, M.F., Boling, J.C. and Riherd, P.T. (1979) Complete biological control
 2059 of *Antonina graminis* in Texas with *Neodusmetia sangwani* (a classic example). *Bulletin of*
 2060 *the Entomological Society of America* 25, 262–267.
- 2061 Decaëns, T. (2010) Macroecological patterns in soil communities. *Global Ecology and*
 2062 *Biogeography* 19, 287–302.
- 2063 Decaëns, T. and Jiménez, J.J. (2002) Earthworm communities under an agricultural
 2064 intensification gradient in Colombia. *Plant and Soil* 240, 133–143.
- 2065 Decaëns, T., Jiménez, J.J. and Lavelle, P. (1999b) Effect of exclusion of the anecic
 2066 earthworm *Martiodrilus carimaguensis* Jiménez and Moreno on soil properties and plant
 2067 growth in grasslands of the eastern plains of Colombia. *Pedobiologia* 43, 835–841.
- 2068 Decaëns, T., Jiménez, J.J., Gioia, C., Measey, G.J. and Lavelle, P. (2006) The values of soil
 2069 animals for conservation biology. *European Journal of Soil Biology* 42, S23–S38.
- 2070 Decaëns, T., Rangel, A.F., Asakawa, N. and Thomas, R.J. (1999a) Carbon and nitrogen
 2071 dynamics in ageing earthworm casts in grasslands of the eastern plains of Colombia.
 2072 *Biology and Fertility of Soils* 30, 20–28.

- 2073 Delgado D.L., Pérez M. E., Galindo-Cardona A., Giray T., and Restrepo, C. (2012)
 2074 Forecasting the influence of climate change on agroecosystem services: potential impacts
 2075 on honey yields in a small-island developing state. *Psyche* 2012, Article ID 951215, 10 pp.
 2076 doi:10.1155/2012/951215
- 2077 DeLucia, E.H., Casteel, C.L., Nability, P.D. and O'Neill, B.F. (2008) Insects take a bigger bite
 2078 out of plants in a warmer, higher carbon dioxide world. *Proceedings of the National*
 2079 *Academy of Sciences USA* 105, 1781–1782.
- 2080 Donnelly, A., Caffarra, A., Kelleher, C.T., O'Neill, B.F., Diskin, E., Pletsers, A., Proctor, H.,
 2081 Stirnemann, R., O'Halloran, J., Penuelas, J., Hodkinson, T.R. and Sparks, T.H. (2012)
 2082 Surviving in a warmer world: environmental and genetic responses. *Climate Research* 53,
 2083 245–262.
- 2084 Douglas, A.E. (1998) Nutritional interactions in insect-microbial symbioses: aphids and their
 2085 symbiotic bacteria *Buchnera*. *Annual Review of Entomology* 43, 17–37.
- 2086 Easterling, W.E., Aggarwal, P.K., Batima, P., Brander, K.M., Erda, L., Howden, S.M.,
 2087 Kirilenko, A., Morton, J., Soussana, J.-F., Schmidhuber, J. and Tubiello, F.N. (2007)
 2088 Food, fibre and forest products. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der
 2089 Linden, P.J. and Hanson, C.E. (eds) *Climate Change 2007: Impacts, Adaptation and*
 2090 *Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the*
 2091 *Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge,
 2092 UK, pp. 273–313.
- 2093 Engelstädter, J. and Hurst, G.D.D. (2009) The ecology and evolution of microbes that
 2094 manipulate host reproduction. *Annual Review of Ecology, Evolution, and Systematics* 40,
 2095 127–149.
- 2096 English-Loeb, G.M. (1990) Plant drought stress and outbreaks of spider mites: a field test.
 2097 *Ecology* 71, 1401–1411.
- 2098 Enigl, M. and Schausberger, P. (2007) Incidence of the endosymbionts *Wolbachia*,
 2099 *Cardinium* and *Spiroplasma* in phytoseiid mites and associated prey. *Experimental and*
 2100 *Applied Acarology* 42, 75–85.
- 2101 Estrada-Pena, A. (2008) Climate, niche, ticks, and models: what they are and how should we
 2102 interpret them. *Parasitology Research (Suppl. 1)* 103, S87–S95.
- 2103 Evans, T.A., Dawes, T.Z., Ward, P.R. and Lo, N. (2011) Ants and termites increase crop
 2104 yield in a dry climate. *Nature Communications* 2, 262. doi:10.1038/ncomms125.
- 2105 Fauvergue, X. and Hopper, K.R. (2009) French wasps in the New World: experimental
 2106 biological control introductions reveal a demographic Allee effect. *Population Ecology* 51,
 2107 385–397.
- 2108 Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B. and Rumpel, C. (2007) Stability of
 2109 organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* 450, 277–
 2110 281.
- 2111 Foresight. The Future of Food and Farming (2011) Final Project Report. The Government
 2112 Office for Science, London, UK, 40 pp.
 2113 [www.bis.gov.uk/assets/bispartners/foresight/docs/food-and-farming/11-546-future-of-](http://www.bis.gov.uk/assets/bispartners/foresight/docs/food-and-farming/11-546-future-of-food-and-farming-report.pdf)
 2114 [food-and-farming-report.pdf](http://www.bis.gov.uk/assets/bispartners/foresight/docs/food-and-farming/11-546-future-of-food-and-farming-report.pdf)
- 2115 Frago, E., Guara, M., Pujade-Villar, J. and Selfa, J. (2010) Winter feeding leads to a shifted
 2116 phenology in the browntail moth *Euproctis chrysorrhoea* on the evergreen strawberry tree
 2117 *Arbutus unedo*. *Agricultural and Forest Entomology* 12, 381–388.
- 2118 Freckman, D.W. (1978) Ecology of anhydrobiotic nematodes. In: Crowe, J.H. and Clegly, J.S.
 2119 (eds) *Dried Biological Systems*. Academic Press, New York, pp. 345–357.
- 2120 Fuhrer, J. (2003) Agroecosystem responses to combinations of elevated CO₂, ozone, and
 2121 global climate change. *Agriculture, Ecosystems & Environment* 97, 1–20.

- 2122 Gao, F., Zhu, S.-R., Sun, Y.-C., Du, L., Parajulee, M., Kang, L. and Ge, F. (2008) Interactive
 2123 effects of elevated CO₂ and cotton cultivar on tri-trophic interaction of *Gossypium*
 2124 *hirsutum*, *Aphis gossypii* [sic], and *Propylaea japonica*. *Environmental Entomology* 37,
 2125 29–37.
- 2126 Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R.,
 2127 Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S.,
 2128 Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A.,
 2129 Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R. and
 2130 Klein, A.M. (2011) Stability of pollination services decreases with isolation from natural
 2131 areas despite honey bee visits. *Ecology Letters* 14, 1062–1072.
- 2132 Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham,
 2133 S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F.,
 2134 Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J.,
 2135 Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy,
 2136 C.M., Krewenka, K., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli,
 2137 T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H.,
 2138 Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tschardt, T.,
 2139 Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M. (2013)
 2140 Wild pollinators enhance fruit set of crops regardless of honey-bee abundance. *Science*
 2141 doi:10.1126/science.1230200 Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*
 2142 405, 220–227.
- 2143 Gilkeson, L.A. and Hill, S.B. (1986) Genetic selection for and evaluation of nondiapause
 2144 lines of predatory midge, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae).
 2145 *Canadian Entomologist* 118, 869–879.
- 2146 Gillespie, D.R. and Quiring, D.M.J. (1993) Extending seasonal limits on biological control.
 2147 *IOBC/WPRS Bulletin* 16, 43–45.
- 2148 Gillespie, D.R. and Quiring, D.M.J. (2005) Diapause induction under greenhouse conditions
 2149 in two populations of *Dicyphus hesperus* (Hemiptera: Miridae). *Biocontrol Science and*
 2150 *Technology* 15, 571–583.
- 2151 Gillespie, D.R., Nasreen, A., Moffat, C.E., Clarke, P. and Roitberg, B.D. (2012) Effects of
 2152 simulated heat waves on an experimental community of pepper plants, green peach aphids
 2153 and two parasitoid species. *Oikos* 121, 149–159.
- 2154 Gilman R.T., Fabina N.S., Abbott K.C. and Rafferty N.E. (2012) Evolution of plant–
 2155 pollinator mutualisms in response to climate change. *Evolutionary Applications* 5(1), 2–
 2156 16.
- 2157 Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. and Holt, R.D. (2010) A
 2158 framework for community interactions under climate change. *Trends in Ecology &*
 2159 *Evolution* 25, 325–331.
- 2160 Godfray, H.C.J., Hassell, M.P. and Holt, R.D. (1994) The population dynamic consequences
 2161 of phenological asynchrony between parasitoids and their hosts. *Journal of Animal*
 2162 *Ecology* 63, 1–10.
- 2163 González, G., García, E., Cruz, V., Borges, S., Zalamea, M. and Rivera, M.M. (2007)
 2164 Earthworm communities along an elevation gradient in northeastern Puerto Rico.
 2165 *European Journal of Soil Biology* 43, S24–S32.
- 2166 Gonzalez, A., Ronce, O., Ferriere, R. and Hochberg, M.E. (2012) Evolutionary rescue: an
 2167 emerging focus at the intersection between ecology and evolution. *Philosophical*
 2168 *Transactions of the Royal Society B: Biological Sciences* 368(1610),
 2169 doi:org/10.1098/rstb.2012.0404.

- 2170 Grant, J.A. and Villani, M.G. (2003) Soil moisture effects on entomopathogenic nematodes.
 2171 *Environmental Entomology* 32, 80–87.
- 2172 Gregory, P.J., Johnson, S.N., Newton A.C. and Ingram, J.S.I. (2009) Integrating pests and
 2173 pathogens into the climate change/food security debate. *Journal of Experimental Botany*
 2174 60, 2827–2838.
- 2175 Grewal, P.S., Gaugler, R. and Wang, Y. (1996) Enhanced cold tolerance of the
 2176 entomopathogenic nematode *Steinernema feltiae* through genetic selection. *Annals of*
 2177 *Applied Biology* 129, 335–341.
- 2178 Groffman, P.M. and Jones, C.G. (2000) Soil processes and global change: will invertebrates
 2179 make a difference? In: Coleman, D.C. and Hendrix, P.F. (eds) *Invertebrates as*
 2180 *Webmasters in Ecosystems*. CABI, Wallingford, UK, pp. 313–326.
- 2181 Guay, J.F., Boudreault, S., Michaud, D. and Cloutier, C. (2009) Impact of environmental
 2182 stress on aphid clonal resistance to parasitoids: role of *Hamiltonella defensa* bacterial
 2183 symbiosis in association with a new facultative symbiont of the pea aphid. *Journal of*
 2184 *Insect Physiology* 55, 919–926.
- 2185 Guerenstein, P.G. and Hildebrand, J.G. (2008) Roles and effects of environmental carbon
 2186 dioxide in insect life. *Annual Review of Entomology* 53, 161–178.
- 2187 Gutschick, V.P. and Bassirirad, H. (2003) Extreme events as shaping physiology, ecology,
 2188 and evolution of plants: toward a unified definition and evaluation of their consequences.
 2189 *New Phytologist* 160, 21–42.
- 2190 Hall, M.C., Stiling, P., Moon, D.C., Drake, B.G. and Hunter, M.D. (2006) Elevated CO₂
 2191 increases the long-term decomposition rate of *Quercus myrtifolia* leaf litter. *Global*
 2192 *Change Biology* 12, 568–577.
- 2193 Hance, T., Van Baaren, J., Vernon, P. and Boivin, G. (2007) Impact of extreme temperatures
 2194 on parasitoids in a climate change perspective. *Annual Review of Entomology* 52, 107–
 2195 126.
- 2196 Hare, J.D. (2011) Ecological role of volatiles produced by plants in response to damage by
 2197 herbivorous insects. *Annual Review of Entomology* 56, 161–180.
- 2198 Harmon, J.P., Moran, N.A. and Ives, A.R. (2009) Species response to environmental change:
 2199 impacts of food web interactions and evolution. *Science* 323, 1347–1350.
- 2200 Harrington, R., Woiwod, I. and Sparks, T. (1999) Climate change and trophic interactions.
 2201 *Trends in Ecology & Evolution* 14, 146–150.
- 2202 Harte, J., Rawa, A. and Price, V. (1996) Effects of manipulated soil microclimate on
 2203 mesofaunal biomass and diversity. *Soil Biology & Biochemistry* 28, 313–322.
- 2204 Heal, O.W. (1997) Effects of global change on diversity–function relationships in soil. In:
 2205 Wolters, V. (ed) *Functional Implications of Biodiversity in Soil: Proceedings of a*
 2206 *Workshop: 14–20 September 1996, Schloss Rauischholzhausen*. Ecosystems Research
 2207 Report 24. Office for Official Publications of the Europe Communities, Luxembourg, pp.
 2208 27–37.
- 2209 Heemsbergen, D.A., Berg, M.P., Loreau, M., van Hal, J.R., Faber, J.H. and Verhoef, H.A.
 2210 (2004) Biodiversity effects on soil processes explained by interspecific functional
 2211 dissimilarity. *Science* 306, 1019–1020.
- 2212 Hegland, S.J., Nielsen, A., Lázaro, A., Bjercknes, A.-L. and Totland, Ø. (2009) How does
 2213 climate warming affect plant-pollinator interactions? *Ecology Letters* 12, 184–195.
- 2214 Henry, L.M., May, N., Acheampong, S., Gillespie, D.R. and Roitberg, B.D. (2010) Host-
 2215 adapted parasitoids in biological control: does source matter? *Ecological Applications* 20,
 2216 242–250.
- 2217 Herren, H.R., Neuenschwander, P., Hennessey, R.D. and Hammond, W.N.O. (1987)
 2218 Introduction and dispersal of *Epidinocarsis lopezi* (Hym., Encyrtidae), an exotic parasitoid

- 2219 of the cassava mealybug, *Phenacoccus manihoti* (Hom., Pseudococcidae), in Africa.
 2220 *Agriculture, Ecosystems & Environment* 19, 131–144.
- 2221 Hickling, R., Roy, D.B., Hill, J.K., Fox, R. and Thomas, C.D. (2006) The distributions of a
 2222 wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12,
 2223 450–455.
- 2224 Hill, J.K., Griffiths, H.M. and Thomas, C.D. (2011) Climate change and evolutionary
 2225 adaptations at species' range margins. *Annual Review of Entomology* 56, 143–159.
- 2226 Hillier, J., Hawes, C., Squire, G., Hilton, A., Wale, S. and Smith, P. (2009) The carbon
 2227 footprints of food crop production. *International Journal of Agricultural Sustainability* 7,
 2228 107–118.
- 2229 Hodek, I. and Michaud, J.P. (2008) Why is *Coccinella septempunctata* so successful? (A
 2230 point-of-view). *European Journal of Entomology* 105, 1–12.
- 2231 Hof, C., Levinsky, I., Araújo, M.B. and Rahbek, C. (2011) Rethinking species' ability to cope
 2232 with rapid climate change. *Global Change Biology* 17, 2987–2990.
- 2233 Hoffmann, A.A., Weeks, A.R., Nash, M.A., Mangano, G.P. and Umina, P.A. (2008) The
 2234 changing status of invertebrate pests and the future of pest management in the Australian
 2235 grains industry. *Australian Journal of Experimental Agriculture* 48, 1481–1493.
- 2236 Holt, J. and Colvin, J. (1997) A differential equation model of the interaction between
 2237 themigration of the Senegalese grasshopper, *Oedaleus senegalensis*, its predators, and a
 2238 seasonal habitat. *Ecological Modelling* 101, 185–193.
- 2239 Hoover, J.K. and Newman, J.A. (2004) Tritrophic interactions in the context of climate
 2240 change: a model of grasses, cereal aphids and their parasitoids. *Global Change Biology* 10,
 2241 1197–1208.
- 2242 Howden, S.M., Soussana, J.-F., Tubiello, F.N., Chhetri, N., Dunlop, M. and Meinke, H.
 2243 (2007) Adapting agriculture to climate change. *Proceedings of the National Academy of*
 2244 *Sciences USA* 104, 1961–1969.
- 2245 Hoy, M.A. (1985) Recent advances in genetics and genetic improvement of the Phytoseiidae.
 2246 *Annual Review of Entomology* 30, 345–370.
- 2247 Hoy, M.A. (2000) Transgenic arthropods for pest management programs: risks and realities.
 2248 *Experimental and Applied Acarology* 24, 463–495.
- 2249 Hulme, P.E. (2005) Adapting to climate change: is there scope for ecological management in
 2250 the face of a global threat? *Journal of Applied Ecology* 42, 784–794.
- 2251 IPPC (2005) Guidelines for the Export, Shipment, Import and Release of Biological Control
 2252 Agents and Other Beneficial Organisms. International Standards for Phytosanitary
 2253 Measures No. 3. FAO, Rome, Italy, 32 pp.
 2254 https://www.ippc.int/file_uploaded/1146657660135_ISPM3.pdf
- 2255 IPCC (2007a) Summary for Policymakers. In: Solomon, S., Qin, D., Manning, M., Chen, Z.,
 2256 Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L. (eds) *Climate Change 2007: the*
 2257 *Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report*
 2258 *of the Intergovernmental Panel on Climate Change*. Cambridge University Press,
 2259 Cambridge, UK and New York, pp. 2–18.
- 2260 IPCC (2007b) Summary for Policymakers. In: Parry, M.L., Canziani, O.F., Palutikof, J.P.,
 2261 van der Linden, P.J. and Hanson, C.E. (eds) *Climate Change 2007: Impacts, adaptation*
 2262 *and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of*
 2263 *the Intergovernmental Panel on Climate Change*. Cambridge University Press,
 2264 Cambridge, UK and New York, pp. 7–22.
- 2265 IPPC (2007) *Framework for Pest Risk Analysis*. International Standards for Phytosanitary
 2266 Measures No. 2. FAO, Rome, Italy, 15 pp.
 2267 https://www.ippc.int/file_uploaded/1179929048771_ISPM02_2007_E.pdf

- 2268 James, S.W., Porco, D., Decaëns, T., Richard, B., Rougerie, R. and Erséus, C. (2010) DNA
2269 barcoding reveals cryptic diversity in *Lumbricus terrestris* L., 1758 (Clitellata):
2270 resurrection of *L. herculeus* (Savigny, 1826). *PLoS ONE* 5(12), e15629, 8 pp.
- 2271 Jaramillo, J., Chabi-Olaye, A., Kamonjo, C., Jaramillo, A., Vega, F.E., Poehling, H.M. and
2272 Borgemeister, C. (2009) Thermal tolerance of the coffee berry borer *Hypothenemus*
2273 *hampei*: predictions of climate change impact on a tropical insect pest. *PLoS ONE* 4(8),
2274 e6487, 11 pp.
- 2275 Jenkinson, D.S., Adams, D.E. and Wild, A. (1991) Model estimates of CO₂ emissions from
2276 soil in response to global warming. *Nature* 351, 304–306.
- 2277 Jiménez, J.J. and Decaëns, T. (2000) Vertical distribution of earthworms in grassland soils of
2278 the Colombian Llanos. *Biology and Fertility of Soils* 32, 463–473.
- 2279 Jiménez, J.J., Brown, G.G., Decaëns, T., Feijoo, A. and Lavelle, P. (2000) Differences in the
2280 timing of diapause and patterns of aestivation in tropical earthworms. *Pedobiologia* 44,
2281 677–694.
- 2282 Jiménez, J.J., Decaëns, T. and Rossi, J.-P. (2012) Soil environmental heterogeneity allows
2283 spatial co-occurrence of competitor earthworm species in a gallery forest of the
2284 Colombian ‘Llanos’. *Oikos* 121, 915–926.
- 2285 Johnson, S.N. and McNicol, J.W. (2010) Elevated CO₂ and aboveground–belowground
2286 herbivory by the clover root weevil. *Oecologia* 162, 209–216.
- 2287 Johnson, S.N., Staley, J.T., McLeod, F.A.L. and Hartley, S.E. (2011) Plant-mediated effects
2288 of soil invertebrates and summer drought on above-ground multitrophic interactions.
2289 *Journal of Ecology* 99, 57–65.
- 2290 Johnson, S.N., Zhang, X.X., Crawford, J.W., Gregory, P.J., Hix, N.J., Jarvis, S.C., Murray,
2291 P.J. and Young, I.M. (2006) Effects of carbon dioxide on the searching behaviour of the
2292 root-feeding clover weevil *Sitona lepidus* (Coleoptera: Curculionidae). *Bulletin of*
2293 *Entomological Research* 96, 361–366.
- 2294 Jones, T.H., Thompson, L.J., Lawton, J.H., Bezemer, T.M., Bardgett, R.D., Blackburn, T.M.,
2295 Bruce, K.D., Cannon, P.F., Hall, G.S., Hartley, S.E., Howson, G., Jones, C.G.,
2296 Kampichler, C., Kandeler, E. and Ritchie D.A. (1998) Impacts of rising atmospheric
2297 carbon dioxide on model terrestrial ecosystems. *Science* 280, 441–443.
- 2298 Kaplan, J.K. (2004) What's buzzing with Africanized honey bees? *Agricultural Research*
2299 *Magazine (USDA)* 52(3), 4–8.
- 2300 Kardol, P. and Wardle, D.A. (2010) How understanding aboveground-belowground linkages
2301 can assist restoration ecology. *Trends in Ecology and Evolution* 25, 670–679.
- 2302 Kardol, P., Cregger, M.A., Company, C.E. and Classen, A.T. (2010) Soil ecosystem
2303 functioning under climate change: plant species and community effects. *Ecology* 91, 767–
2304 781.
- 2305 Kardol, P., Reynolds, W.N., Norby, R.J. and Classen, A.T. (2011) Climate change effects on
2306 soil microarthropod abundance and community. *Applied Soil Ecology* 47, 37–44.
- 2307 Karg, J. and Bałazy, S. (2009) Wpływ struktury krajobrazu na występowanie agrofagów i ich
2308 antagonistów w uprawach rolniczych. [Effect of landscape structure on the occurrence of
2309 agrophagous pests and their antagonists.] *Progress in Plant Protection* 49, 1015–1034.
- 2310 Kauffman, W.C. and Kennedy, G.G. (1989) Inhibition of *Campoletis sonorensis* parasitism
2311 of *Heliothis zea* and of parasitoid development by 2-tridecanone-mediated insect
2312 resistance of wild tomato. *Journal of Chemical Ecology* 15, 1919–1930.
- 2313 Kearns, C.A. (1992) Anthophilous fly distribution across an elevation gradient. *American*
2314 *Midland Naturalist* 127, 172–182.

- 2315 Kjøhl, M., Nielsen, A. and Stenseth, N.C. (2011) Potential Effects of Climate Change on
 2316 Crop Pollination. *Pollination Services for Sustainable Agriculture: Extension of*
 2317 *Knowledge Base*. FAO, Rome, vii + 38pp.
- 2318 Klapwijk, M.J., Gröbler, B.C., Ward, K., Wheeler, D. and Lewis, O.T. (2010) Influence of
 2319 experimental warming and shading on host–parasitoid synchrony. *Global Change Biology*
 2320 16, 102–112.
- 2321 Klironomos, J.N., Rillig, M.C. and Allen, M.F. (1996) Below-ground microbial and
 2322 microfaunal responses to *Artemisia tridentata* grown in elevated atmospheric CO₂.
 2323 *Functional Ecology* 10, 527–534.
- 2324 Krab, E.J., Oorsprong, H., Berg, M.P. and Cornelissen, J.H.C. (2010) Turning northern
 2325 peatlands upside down: disentangling microclimate and substrate quality effects on
 2326 vertical distribution of Collembola. *Functional Ecology* 24, 1362–1369.
- 2327 Lastuvka, Z. (2009) Climate change and its possible influence on the occurrence and
 2328 importance of insect pests. (Special issue: Climate change and plant pathogens, pests and
 2329 weeds.) *Plant Protection Science* 45, S53–S62.
- 2330 Lausmann, T., Radtke, A., Wiemert, T. and Dahl, A. (2010) 150 Jahre
 2331 Schmetterlingsbeobachtung in Wuppertal – Auswirkungen von Klima- und
 2332 Landschaftsveränderungen (Lepidoptera). [150 years of butterfly monitoring in Wuppertal
 2333 – effects of climate and landscape change (Lepidoptera).] *Entomologische Zeitschrift,*
 2334 *Stuttgart* 120, 269–277.
- 2335 Lavelle, P. and Pashanasi, B. (1989) Soil macrofauna and land management in Peruvian
 2336 Amazonia (Yurimaguas, Loreto). *Pedobiologia* 33, 283–409.
- 2337 Lavelle, P. and Spain, A.V. (2001) *Soil Ecology*. Springer, Dordrecht, Netherlands, 684 pp.
- 2338 Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O.W. and
 2339 Dhillon, S. (1997) Soil function in a changing world: the role of invertebrate ecosystems
 2340 engineers. *European Journal of Soil Biology* 33, 159–193.
- 2341 Lavelle, P., Lattaud, C., Trigo, D. and Barois, I. (1995) Mutualism and biodiversity in soils.
 2342 *Plant and Soil* 170, 23–33.
- 2343 Lawton, J.H. (1998) Small earthquakes in Chile and climate change. *Oikos* 82, 209–211.
- 2344 Lopez-Uribe, M.M., Almanza, M.T. and Ordonez M. (2007) Diploid male frequencies in
 2345 Colombian populations of euglossine bees. *Biotropica* 39, 660–662.
- 2346 Loranger, G., Bandyopadhyaya, I., Razaka, B. and Ponge, J.F. (2001) Does soil acidity
 2347 explain altitudinal sequences in collembolan communities? *Soil Biology & Biochemistry*
 2348 33, 381–393.
- 2349 Loranger, G.I., Pregitzer, K.S. and King, J.S. (2004) Elevated CO₂ and O_{3t} concentrations
 2350 differentially affect selected groups of the fauna in temperate forest soils. *Soil Biology &*
 2351 *Biochemistry* 36, 1521–1524.
- 2352 Luedeling, E., Steinmann, K.P., Zhang, M., Brown, P.H., Grant, J. and Girvetz, E.H. (2011)
 2353 Climate change effects on walnut pests in California. *Global Change Biology* 17, 228–
 2354 238.
- 2355 Lukac, M., Calfapietra, C. and Godbold, D.L. (2003) Production, turnover and mycorrhizal
 2356 colonization of root systems of three *Populus* species grown under elevated CO₂
 2357 (POPFACE). *Global Change Biology* 9, 838–848.
- 2358 Lynch, M. and Lande, R. (1993) Evolution and extinction in response to environmental
 2359 change. In: Kareiva, P., Kingsolver, J. and Huey, R. (eds) *Biotic Interactions and Global*
 2360 *Change*. Sinauer Assocs., Inc., Sunderland, Massachusetts, pp. 234–250.
- 2361 Mackauer, M. (1976) Genetic problems in the production of biological control agents. *Annual*
 2362 *Review of Entomology* 21, 369–385.

- 2363 Malo, J.E. and Baonza J. (2002) Are there predictable clines in plant–pollinator interactions
 2364 along altitudinal gradients? The example of *Cytisus scoparius* (L.) Link in the Sierra de
 2365 Guadarrama (central Spain). *Diversity and Distributions* 8, 365–371.
- 2366 Marinissen, J.C.Y. and van den Bosch, F. (1992) Colonization of new habitats by
 2367 earthworms. *Oecologia* 91, 371–376.
- 2368 Martins, A.C. and Melo, G.A.R. (2010) Has the bumblebee *Bombus bellicosus* gone extinct
 2369 in the northern portion of its distribution range in Brazil? *Journal of Insect Conservation*
 2370 14, 207–210.
- 2371 Mattson, W.J. and Haack, R.A. (1987) The role of drought in outbreaks of plant-eating
 2372 insects. *BioScience* 37, 110–118.
- 2373 MEA (Millennium Ecosystem Assessment) (2005) *Ecosystems and Human Well-Being:
 2374 Current State and Trends*. Island Press, Washington, DC, 917 pp.
 2375 www.maweb.org/en/Condition.aspx.
- 2376 Menéndez, R. (2007) How are insects responding to global warming? *Tijdschrift voor
 2377 Entomologie* 15, 355–365.
- 2378 Messmer, R. and Stamp, P. (2010) Trends in drought research. *Kasetsart Journal – Natural
 2379 Science* 44, 507–516.
- 2380 Micha, S.G., Kistenmacher, S., Molck, G. and Wyss, U. (2000) Tritrophic interactions
 2381 between cereals, aphids and parasitoids: discrimination of different plant-host complexes
 2382 by *Aphidius rhopalosiphi* (Hymenoptera: Aphidiidae). *European Journal of Entomology*
 2383 97, 539–543.
- 2384 Mikkelsen, T.N., Beier, C., Jonasson, S., Holmstrup, M., Schmidt, I.K., Ambus, P., Pilegaard,
 2385 K., Michelsen, A., Albert, K., Andresen, L.C., Arndal, M.F., Bruun, N., Christensen, S.,
 2386 Danbæk, S., Gundersen, P., Jørgensen, P., Linden, L.G., Kongstad, J., Maraldo, K.,
 2387 Priomé, A., Riis-Nielsen, T., Ro-Poulsen, H., Stevnbak, K., Selsted, M.B., Sørensen, P.,
 2388 Larsen, K.S., Carter, M.S., Ibrom, A., Martinussen, T., Miglietta, F. and Sverdrup, H.
 2389 (2007) Experimental design of multifactor climate change experiments with elevated CO₂,
 2390 warming and drought: the CLIMAITE project. *Functional Ecology* 22, 185–195.
- 2391 Mitsch, W.J. (2012) What is ecological engineering? (Special Issue: Ecological engineering -
 2392 its development, application and challenges.). *Ecological Engineering* 45, 5–12.
- 2393 Mondor, E.B., Tremblay, M.N. and Lindroth, R.L. (2004) Transgenerational phenotypic
 2394 plasticity under future atmospheric conditions. *Ecology Letters* 7, 941–946.
- 2395 Mukuka, J., Strauch, O. and Ehlers, R.U. (2010) Variability in desiccation tolerance among
 2396 different strains of the entomopathogenic nematode *Heterorhabditis bacteriophora*.
 2397 *Nematology* 12, 711–720.
- 2398 Musolin, D.L. and Fujisaki, K. (2006) Changes in ranges: trends in distribution of true bugs
 2399 (Heteroptera) under conditions of the current climate warming. *Russian Entomological
 2400 Journal* 15, 175–179.
- 2401 Myers, J.G. (1932) The original habitat and hosts of three major sugar-cane pests of tropical
 2402 America. (*Diatraea*, *Castnia* and *Tomaspis*). *Bulletin of Entomological Research* 23, 257–
 2403 71, pl. XIII.
- 2404 Norby, R.J., Rustad, L.E., Dukes, J.S., Ojima, D.S., Parton, W.J., Del Grosso, S.J.,
 2405 McMurtrie, R.E. and Pepper, D.P. (2007) Ecosystem responses to warming and interacting
 2406 global change factors. In: Canadell, J.G., Pataki, D.E. and Pitelka, L.F. (eds) *Terrestrial
 2407 Ecosystems in a Changing World*. Springer-Verlag, Berlin, Germany, pp. 45–58.
- 2408 Ode, P.J. (2006) Plant chemistry and natural enemy fitness: effects on herbivore and natural
 2409 enemy interactions. *Annual Review of Entomology* 51, 163–185.

- 2410 OIE (Office International des Épizooties) (2010) *Terrestrial Animal Health Code*, 19th edn.
 2411 World Organisation for Animal Health, Rome, Italy. (Online)
 2412 www.oie.int/eng/normes/mcode/en_sommaire.htm
- 2413 Ollerton, J., Winfree, R. and Tarrant, S. (2011) How many flowering plants are pollinated by
 2414 animals? *Oikos* 120, 321–326.
- 2415 Osler, G.H.R. and Sommerkorn, M. (2007) Toward a complete soil C and N cycle:
 2416 incorporating the soil fauna. *Ecology* 88, 1611–1621.
- 2417 Parmesan, C. (2007) Influences of species, latitudes and methodologies on estimates of
 2418 phenological response to global warming. *Global Change Biology* 13, 1860–1872.
- 2419 Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts
 2420 across natural systems. *Nature* 421, 39–42.
- 2421 Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley,
 2422 B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. and Warren, M.
 2423 (1999) Poleward shifts in geographical ranges of butterfly species associated with regional
 2424 warming. *Nature* 399, 579–583.
- 2425 Patterson, D.T., Westbrook, J.K., Joyce, R.J.V., Lingren, P.D. and Rogasik, J. (1999) Weeds,
 2426 insects, and diseases. *Climatic Change* 43, 711–727.
- 2427 Pelini, S.L. Keppel, J.A. Kelley, A.E. and Hellmann J.J. (2010) Adaptation to host plants may
 2428 prevent rapid insect responses to climate change. *Global Change Biology* 16, 2923–2929.
- 2429 Pendall, E., Rustad, L. and Schimel, J. (2008) Towards a predictive understanding of
 2430 belowground process responses to climate change: have we moved any closer? *Functional*
 2431 *Ecology* 22, 937–940.
- 2432 Peñuelas, J. and Estiarte, M. (1998) Can elevated CO₂ affect secondary metabolism and
 2433 ecosystem function? *Trends in Ecology & Evolution* 13, 20–24.
- 2434 Peñuelas, J., Rutishauser, T. and Filella, I. (2009) Phenology feedbacks on climate change.
 2435 *Science* 324, 887–888.
- 2436 Petchey, O.L., McPhearson, P.T., Casey, T.M. and Morin, P.J. (1999) Environmental
 2437 warming alters food-web structure and ecosystem function. *Nature* 402, 69–72.
- 2438 Phillips, C., Townsend, H. and Vink, C. (2006) Blown in the wind or border slippage? What
 2439 natural dispersal of exotic species to New Zealand has to do with biosecurity. *Biosecurity*
 2440 69, 14–15.
- 2441 Phillips, C.B., Vink, C.J., Blanchet, A. and Hoelmer, K.A. (2008) Hosts are more important
 2442 than destinations: what genetic variation in *Microctonus aethiopoides* (Hymenoptera:
 2443 Braconidae) means for foreign exploration for natural enemies. *Molecular Phylogenetics*
 2444 *& Evolution* 49, 467–476.
- 2445 Pinto, D.M., Blande, J.D., Nykänen, R., Dong, W.X., Nerg, A.M. and Holopainen, J.K.
 2446 (2007) Ozone degrades common herbivore-induced plant volatiles: does this affect
 2447 herbivore prey location by predators and parasitoids? *Journal of Chemical Ecology* 33,
 2448 683–694.
- 2449 Pintureau, B. and Bolland, P. (2001) A *Trichogramma* species showing a better adaptation to
 2450 high temperature than its symbionts. *Biocontrol Science and Technology* 11, 13–20.
- 2451 Pintureau, B., Chapelle, L. and Delobel, B. (1999) Effects of repeated thermic and antibiotic
 2452 treatments on a *Trichogramma* (Hym., Trichogrammatidae) symbiont. *Journal of Applied*
 2453 *Entomology* 123, 473–483.
- 2454 Popay, A.J. (1992) Population regulation of *Costelytra zealandica* by pathogens in the North
 2455 Island of New Zealand. In: Jackson, T.A. and Glare, T.R. (eds) *Use of Pathogens in*
 2456 *Scarab Pest Management*. Intercept, Andover, UK, pp. 141–151.
- 2457 Porco, D., Decaëns, T., Deharveng, L., James, S.W., Skarżyński, D., Erséus, C., Butt, K.R.,
 2458 Richard, B. and Hebert, P.D.N. (2012) Biological invasions in soil: DNA barcoding as a

2459 monitoring tool in a multiple taxa survey targeting European earthworms and springtails in
2460 North America. *Biological Invasions*. doi:10.1007/s10530-012-0338-2.

2461 Potting, R.P.J., Vet, L.E.M. and Overholt, W.A. (1997) Geographic variation in host selection
2462 behaviour and reproductive success in the stemborer parasitoid *Cotesia flavipes*
2463 (Hymenoptera: Braconidae). *Bulletin of Entomological Research* 87, 515–524.

2464 Pritchard, J., Griffiths, B. and Hunt, E.J. (2007) Can the plant-mediated impacts on aphids of
2465 elevated CO₂ and drought be predicted? *Global Change Biology* 13, 1616–1629.

2466 Rando, O.J. and Verstrepen, K.J. (2007) Timescales of genetic and epigenetic inheritance.
2467 *Cell* 128, 655–668.

2468 Robinson, K.A., Jonsson, M., Wratten, S.D., Wade, M.R. and Buckley, H.L. (2008)
2469 Implications of floral resources for predation by an omnivorous lacewing. *Basic and*
2470 *Applied Ecology* 9, 172–181.

2471 Roda, A., Nyrop, J., Dicke, M. and English-Loeb, G. (2000) Trichomes and spider-mite
2472 webbing protect predatory mite eggs from intraguild predation. *Oecologia* 125, 428–435.

2473 Roderick, G.K., Hufbauer, R. and Navajas, M. (eds) (2012) Special issue: Evolution and
2474 biological control. *Evolutionary Applications* 5(5), 419–536.

2475 Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. and Pounds, J.A. (2003)
2476 Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60.

2477 Rosenzweig, C., Iglesias, A., Yang, X.B., Epstein, P.R. and Chivian, E. (2001) Climate
2478 change and extreme weather events; implications for food production, plant diseases, and
2479 pests. *Global Change & Human Health* 2, 90–104.

2480 Roush, R.T. (1990) Genetic variation in natural enemies: critical issues for colonization in
2481 biological control. In: Mackauer, M., Ehler, L.E. and Roland, J. (eds) *Critical Issues in*
2482 *Biological Control*. Intercept, Andover, UK, pp. 263–288.

2483 Roux, O., Le Lann, C., van Alphen, J.J.M. and van Baaren, J. (2010) How does heat shock
2484 affect the life history traits of adults and progeny of the aphid parasitoid *Aphidius avenae*
2485 (Hymenoptera: Aphidiidae)? *Bulletin of Entomological Research* 100, 1–7.

2486 Roy, B., Gusewell, A.S. and Harte, J. (2004) Response of plant pathogens and herbivores to a
2487 warming experiment. *Ecology* 85, 2570–2581.

2488 Ruess, L., Michelsen, A., Schmidt, I.K. and Jonasson, S. (1999) Simulated climate change
2489 affecting microorganisms, nematode density and biodiversity in subarctic soils. *Plant and*
2490 *Soil* 212, 63–73.

2491 Russell, W.G. and Grimm, E.C. (1990) Effects of global climate change on the patterns of
2492 terrestrial biological communities. *Trends in Ecology & Evolution* 5, 289–292.

2493 Saikkonen, K., Taulavuori, K., Hyvönen, T., Gundel, P.E., Hamilton, C.E., Vänninen, I.,
2494 Nissinen, A. and Helander, M. (2012) Climate change-driven species' range shifts filtered
2495 by photoperiodism. *Nature Climate Change* 2(4), 239–242.

2496 Samara, R.Y., Monje, J.C. and Zebitz, C.P.W. (2008) Comparison of different European
2497 strains of *Trichogramma aurosom* (Hymenoptera: Trichogrammatidae) using fertility life
2498 tables. *Biocontrol Science and Technology* 18, 75–86.

2499 Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M.,
2500 Andersson, G.K.S., Bazarian, S., Böhning-Gaese, K., Bommarco, R., Dalsgaard, B.,
2501 Dehling, D.M., Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C.N.,
2502 Kreft, H., Morris, R.J., Sandel, B., Sutherland, W.J., Svenning, J.-C., Tscharrntke, T.,
2503 Watts, S., Weiner, C.N., Werner, M., Williams, N.M., Winqvist, C., Dormann, C.F. and
2504 Blüthgen, N. (2012) Specialization of mutualistic interaction networks decreases toward
2505 tropical latitudes. *Current Biology* 22(20), 1925–1931.

- 2506 Schröter, D., Brussaard, L., De Geyn, G., Poveda, K., Brown, V.K., Berg, M.P., Wardle,
 2507 D.A., Moore, J. and Wall, D.H. (2004) Trophic interactions in a changing world: modeling
 2508 aboveground–belowground interactions. *Basic and Applied Ecology* 5, 515–528.
- 2509 Schweiger, O., Settele, J., Kudrna, O., Klotz, S. and Kühn, I. (2008) Climate change can
 2510 cause spatial mismatch of trophically interacting species. *Ecology* 89, 3472–3479.
- 2511 Seastedt, T.R. (2000) Soil fauna and controls of carbon dynamics: comparisons of rangelands
 2512 and forests across latitudinal gradients. In: Hendrix, P.F. and Coleman, D.C. (eds)
 2513 *Invertebrates as Webmasters in Ecosystems*. CAB International, Wallingford, UK, pp.
 2514 293–312.
- 2515 Seidel, D.J., Fu, Q.A., Randel, W.J. and Reichler, T.J. (2008) Widening of the tropical belt in
 2516 a changing climate. *Nature Geoscience* 1, 21–24.
- 2517 Senapati, B.K., Lavelle, P., Giri, S., Pashanasi, B., Alegre, J., Decaëns, T., Jiménez, J.J.,
 2518 Albrecht, A. Blanchart, E., Mahieux, M., Rousseaux, L., Thomas, R., Panigrahi, P.K. and
 2519 Venkatachalam, M. (1999) In-soil earthworm technologies for tropical agroecosystems.
 2520 In: Lavelle, P., Brussaard, L. and Hendrix, P.F. (eds) *Earthworm Management in Tropical*
 2521 *Agroecosystems*. CABI, Wallingford, UK, pp. 199–237.
- 2522 Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L., Hindayana, D., Lestari,
 2523 A.S., Pajarningsih and Sartanto (1996) Managing tropical rice pests through conservation
 2524 of generalist natural enemies and alternative prey. *Ecology* 77, 1975–1988.
- 2525 Singer, M.C. and Parmesan, C. (2010) Phenological asynchrony between herbivorous insects
 2526 and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical*
 2527 *Transactions of the Royal Society B: Biological Sciences* 365, 3161–3176.
- 2528 Slaa, E.J., Sanchez-Chaves, L.A., Malagodi-Braga, K.S. and Hofstede, F.E. (2007) Stingless
 2529 bees in applied pollination: practice and perspectives. *Apidologie* 37 (2006), 293–315.
- 2530 Sohlenius, B. and Boström, S. (1999) Effects of climate change on soil factors and metazoan
 2531 microfauna (nematodes, tardigrades and rotifers) in a Swedish tundra soil – a soil
 2532 transplantation experiment. *Applied Soil Ecology* 12, 113–128.
- 2533 Sommer, J.H., Kreft, H., Kier, G., Jetz, W., Mutke, J. and Barthlott, W. (2010) Projected
 2534 impacts of climate change on regional capacities for global plant species richness.
 2535 *Proceedings of the Royal Society B: Biological Sciences* 277, 2271–2280.
- 2536 Song, L., Wu, J., Li, C., Li, F., Peng, S. and Chen, B. (2009) Different responses of invasive
 2537 and native species to elevated CO₂ concentration. *Acta Oecologia* 35, 128–135.
- 2538 Stacey, D.A. and Fellowes, M.D.E. (2002) Influence of elevated CO₂ on interspecific
 2539 interactions at higher trophic levels. *Global Change Biology* 6, 668–678.
- 2540 Staley, J.T. and Johnson, S.N. (2008) Climate change impacts on root herbivores. In:
 2541 Johnson, S.N. and Murray, P.J. (eds) *Root Feeders: an Ecosystem Approach*. CABI,
 2542 Wallingford, UK, pp. 192–213.
- 2543 Staley, J.T., Mortimer, S.R., Masters, G.J., Morecroft, M.D., Brown, V.K. and Taylor, M.E.
 2544 (2006) Drought stress differentially affects leaf-mining species, *Ecological Entomology*
 2545 31, 460–469.
- 2546 Staley, J.T., Mortimer, S.R., Morecroft, M.D., Brown, V.K. and Masters, G.J. (2007)
 2547 Summer drought alters plant-mediated competition between foliar- and root-feeding
 2548 insects. *Global Change Biology* 13, 866–877.
- 2549 Stange, G. (1997) Effects of changes in atmospheric carbon dioxide on the location of hosts
 2550 by the moth, *Cactoblastis cactorum*. *Oecologia* 110, 539–545.
- 2551 Stavrinides, M.C., Daane, K.M., Lampinen, B.D. and Mills, N.J. (2010) Plant water stress,
 2552 leaf temperature, and spider mite (Acari: Tetranychidae) outbreaks in California
 2553 vineyards. *Environmental Entomology* 39, 1232–1241.

- 2554 Steffensen, J.P., Andersen, K.K., Bigler, M., Clausen, H.B., Dahl-Jensen, D., Fischer, H.,
 2555 Goto-Azuma, K., Hansson, M., Johnsen, S.J., Jouzel, J., Masson-Delmotte, V., Popp, T.,
 2556 Rasmussen, S.O., Rothlisberger, R., Ruth, U., Stauffer, B., Siggaard-Andersen, M.-L.,
 2557 Sveinbjörnsdóttir, A.E., Svensson, A. and White, J.W.C. (2008) High-resolution
 2558 Greenland ice core data show abrupt climate change happens in few years. *Science*
 2559 321(5889), 680–684.
- 2560 Stiling, P., Forkner, R. and Drake, B. (2010) Long-term exposure to elevated CO₂ in a Florida
 2561 scrub-oak forest increases herbivore densities but has no effect on other arthropod guilds.
 2562 *Insect Conservation and Diversity* 3, 152–156.
- 2563 Stireman, J.O. III, Dyer, L.A., Janzen, D.H., Singer, M.S., Lill, J.T., Marquis, J.T., Ricklefs,
 2564 R.E., Gentry, G.L., Hallwachs, W., Coley, P.D., Barone, J.A., Greeney, H.F., Connahs, H.,
 2565 Barbosa, P., Morais, H.C. and Diniz, I. R. (2005) Climatic unpredictability and parasitism
 2566 of caterpillars: Implications of global warming. *Proceedings of the National Academy of*
 2567 *Sciences USA* 102, 17384–17387.
- 2568 Sun, J., Yang, L., Wang, Y. and Ort, D. R. (2009) FACE-ing the global change: opportunities
 2569 for improvement in photosynthetic radiation use efficiency and crop yield. *Plant Science*
 2570 177, 511–522.
- 2571 Swift, M.J., Heal, O.W. and Anderson, J.M. (1979) *Decomposition in Terrestrial Ecosystems*.
 2572 Blackwell Scientific, Oxford, UK, 372 pp.
- 2573 Swift, M.J., Vandermeer, J., Ramakrishnan, P.S., Anderson, J.M., Ong, C. K. and Hawkins,
 2574 B.A. (1996) Biodiversity and agroecosystem function. In: Mooney, H.A., Cushman, J.H.,
 2575 Medina, E., Sala, O.E. and Schulze, E.D. (eds) *Functional Roles of Biodiversity: A Global*
 2576 *Perspective*. SCOPE, John Wiley & Sons Ltd. pp 261–298.
- 2577 Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. and
 2578 Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins.
 2579 *Nature* 411, 577–581.
- 2580 Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C.,
 2581 Erasmus, B.F.N., Siqueira, M.F.D., Grainger, A. and Hannah, L. (2004) Extinction risk
 2582 from climate change. *Nature* 427, 145–148.
- 2583 Thomas, M.B. and Blanford, S. (2003) Thermal biology in insect-parasite interactions,
 2584 *Trends in Ecology & Evolution* 18, 344–350.
- 2585 Thomson, L.J., Macfadyen, S. and Hoffmann, A.A. (2010) Predicting the effects of climate
 2586 change on natural enemies of agricultural pests. *Biological Control* 52, 296–306.
- 2587 Tobin, P.C., Nagarkatti, S., Loeb, G. and Saunders M.C. (2008) Historical and projected
 2588 interactions between climate change and insect voltinism in a multivoltine species. *Global*
 2589 *Change Biology* 14, 951–957.
- 2590 Traoré, L., Pilon, J.G., Fournier, F. and Boivin, G. (2006) Adaptation of the developmental
 2591 process of *Anaphes victus* (Hymenoptera: Mymaridae) to local climatic conditions across
 2592 North America. *Annals of the Entomological Society of America* 99, 1121–1126.
- 2593 Travis, J.M.J. (2003) Climate change and habitat destruction: a deadly anthropogenic
 2594 cocktail. *Proceedings of the Royal Society B: Biological Sciences* 270, 467–473.
- 2595 Travis, J.M.J. and Dytham, C. (2002) Dispersal evolution during invasions. *Evolutionary*
 2596 *Ecology Research* 4, 1119–1129.
- 2597 Uvarov, A.V., Tiunov, A.V. and Scheu, S. (2011) Effects of seasonal and diurnal temperature
 2598 fluctuations on population dynamics of two epigeic earthworm species in forest soil. *Soil*
 2599 *Biology & Biochemistry* 43, 559–570.
- 2600 van Asch, M. and Visser, M.E. (2007) Phenology of forest caterpillars and their host trees:
 2601 the importance of synchrony. *Annual Review of Entomology* 52, 37–55.

- 2602 van der Putten, W.H., Bardgett, R.D., de Ruiter, P.C., Hol, W.H.G., Meyer, K.M., Bezemer,
2603 T.M., Bradford, M.A., Christensen, S., Eppinga, M.B., Fukami, T., Hemerik, L.,
2604 Molofsky, J., Schädler, M., Scherber, C., Strauss, S.Y., Vos, M. and Wardle, D.A. (2009)
2605 Empirical and theoretical challenges in aboveground–belowground ecology. *Oecologia*
2606 161, 1–14.
- 2607 van Lenteren, J.C. (ed.) (2003) Quality Control and Production of Biological Control Agents:
2608 Theory and Testing Procedures. CABI, Wallingford, UK, 327 pp.
- 2609 Van Rijn, P.C.J. and Tanigoshi, L.K. (1999) The contribution of extrafloral nectar to survival
2610 and reproduction of the predatory mite *Iphiseius degenerans* on *Ricinus communis*.
2611 *Experimental and Applied Acarology* 23, 281–296.
- 2612 Vellend, M. (2010) Conceptual synthesis in community ecology. *Quarterly Review of*
2613 *Biology* 85, 183–206.
- 2614 Veteli, T.O., Lahtinen, A., Repo, T., Niemelä, P. and Varama, M. (2005) Geographic
2615 variation in winter freezing susceptibility in the eggs of the European pine sawfly
2616 (*Neodiprion sertifer*). *Agricultural and Forest Entomology* 7, 115–120.
- 2617 Virtanen, T. and Neuvonen, S. (1999) Performance of moth larvae on birch in relation to
2618 altitude, climate, host quality and parasitoids. *Oecologia* 120, 92–101.
- 2619 Visser, M.E. and Holleman, J.M. (2001) Warmer springs disrupt the synchrony of oak and
2620 winter moth phenology. *Proceedings of the Royal Society B: Biological Sciences* 268,
2621 289–294.
- 2622 Voigt, W., Perner, J., Davis, A.J., Eggers, T., Schumacher, J., Bahrmann, R., Fabian, B.,
2623 Heinrich, W., Köhler, G., Lichter, D., Marstaller, R. and Sander, F.W. (2003) Trophic
2624 levels are differentially sensitive to climate. *Ecology* 84, 2444–2453.
- 2625 Von Holle, B., Wei, Y. and Nickerson, D. (2010) Climatic variability leads to later seasonal
2626 flowering of Floridian plants. *PLoS ONE* 5(7), e11500, 9 pp.
- 2627 Walther, G.R. (2007) Tackling ecological complexity in climate impact research. *Science*
2628 315, 606–607.
- 2629 Wardle, D.A. (2002) *Communities and Ecosystems - Linking the Aboveground and*
2630 *Belowground Components*. Princeton University Press, Princeton, New Jersey, 400 pp.
- 2631 Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Van der Putten, W.H. and Wall,
2632 D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science*
2633 304, 1629–1633.
- 2634 Watkinson, A.R. and Gill, J.A. (2002) Climate change and dispersal. In: Bullock, J.M.,
2635 Kenward, R.E. and Hails, R.S. (eds) *Dispersal Ecology*. Blackwell Science Publishing,
2636 Oxford, pp. 45–56.
- 2637 Weltzin, J.F., Belote, R.T. and Sanders N.J. (2003) Biological invaders in a greenhouse
2638 world: will elevated CO₂ fuel plant invasions? *Frontiers in Ecology and the Environment*
2639 1, 146–153.
- 2640 Werren, J.H. (1997) Biology of *Wolbachia*. *Annual Review of Entomology* 42, 587–609.
- 2641 Werren, J.H., Baldo, L. and Clark, M.E. (2008) *Wolbachia*: master manipulators of
2642 invertebrate biology. *Nature Reviews Microbiology* 6(10), 741–751.
- 2643 White, E.B., DeBach, P. and Garber, M.J. (1970) Artificial selection for genetic adaptation to
2644 temperature extremes in *Aphytis lingnanensis* Compère (Hymenoptera: Aphelinidae).
2645 *Hilgardia* 40, 161–192.
- 2646 Whittaker, J.B. and Tribe, N.P. (1996) An altitudinal transect as an indicator of responses of a
2647 spittlebug (Auchenorrhyncha: Cercopidae) to climate change. *European Journal of*
2648 *Entomology* 93, 319–324.

- 2649 Williams, J.W., Jackson, S.T., and Kutzbach, J.E. (2007) Projected distributions of novel and
 2650 disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences USA*
 2651 104, 5738–5742.
- 2652 Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A. and Langham, G. (2008) Towards an
 2653 integrated framework for assessing the vulnerability of species to climate change. *PLoS*
 2654 *Biology*, 6, e325, 6 pp.
- 2655 Wolters, V. (2001) Biodiversity of soil animals and its function. *European Journal of Soil*
 2656 *Biology* 37, 221–227.
- 2657 Wolters, V., Silver, W.L., Bignell, D.E., Coleman, D.C., Lavelle, P., van der Putten, W.H., de
 2658 Ruyter, P., Rusek, J., Wall, D.H., Wardle, D.A., Brussaard, L., Dangerfield, J.M., Brown,
 2659 V.K., Giller, K.E., Hooper, D.U., Sala, O., Tiedje, J.M. and Van Veen, J.A. (2000) Effects
 2660 of global changes on above- and belowground biodiversity in terrestrial ecosystems:
 2661 implications for ecosystem functioning. *BioScience* 50, 1089–1098.
- 2662 Woodward, F.I. and Kelly, C.K. (2008) Responses of global plant diversity capacity to
 2663 changes in carbon dioxide concentration and climate. *Ecology Letters* 11, 1229–1237.
- 2664 Yeates, G.W., Tate, K.R. and Newton, P.C.D. (1997) Response of the fauna of a grassland
 2665 soil to doubling of atmospheric carbon dioxide concentration. *Biology and Fertility of*
 2666 *Soils* 25, 307–315.
- 2667 Yukawa, J., Kiritani, K., Gyoutoku, N., Uechi, N., Yamaguchi, D., Kamitani, S. (2007)
 2668 Distribution range shift of two allied species, *Nezara viridula* and *N. antennata*
 2669 (Hemiptera: Pentatomidae), in Japan, possibly due to global warming. *Applied*
 2670 *Entomology and Zoology* 42, 205–215.
- 2671 Zhou S.-X., Li Y. and Zhang F. (2009) Influences of high temperature shock on the
 2672 reproduction and development of the *Wolbachia*-induced parthenogenetic parasitoid wasp,
 2673 *Encarsia formosa* (Gahan). *Shengtai Xuebao/Acta Ecologica Sinica* 29, 4732–4737.
 2674

2675 **CASE STUDIES**

2676 *Case study 1. Functional shifts in community composition of soil invertebrates under elevated*
2677 *CO₂*

2678 Increased CO₂ concentration is predicted to stimulate both primary production and
2679 decomposition, resulting in an increase in soil organic matter. Clear evidence exists for the
2680 potential impact of climate change-related factors such as eCO₂ (elevated levels of CO₂),
2681 temperature change and altered rainfall patterns on community composition of soil
2682 invertebrates. Among these, micro-arthropods living in the litter and the topsoil represent an
2683 important functional group in nutrient cycling and litter decomposition.

2684 Under increased CO₂ there are important functional changes in the community composition
2685 of soil invertebrates. In a FACE (Free-Air Carbon dioxide Enrichment) experiment it was
2686 observed that mean micro-arthropod abundance was 33% lower in the eCO₂ treatment, but
2687 with significant decline only for oribatid mites. Other studies report increases in microbial-
2688 feeding, free-living nematodes, enchytraeid worms, and even earthworm biomass. Functional
2689 groups can exhibit different responses to soil warming, for example, depletion of epigeic
2690 species of ecosystem engineers, and augmentation of fungivorous mites. Collembolan
2691 populations have increased in most studies of eCO₂, although some have reported lower
2692 collembolan numbers. Both negative and positive single responses of eCO₂ on soil micro-
2693 arthropods have been found and can be explained by the inherently high soil CO₂
2694 concentration, so certain species are already adapted to these conditions. The responses of
2695 soil invertebrates have been interpreted as responses to increased root-derived carbon and
2696 subsequent microbial community changes.

2697 How soil communities will be affected by climate change-related factors acting
2698 simultaneously is not known although indirect effects are envisaged as both plant
2699 composition and productivity can promote important functional shifts. The structure of soil
2700 invertebrate communities is affected and impact is driven by changes in soil moisture content.
2701 Several climate change factors acting simultaneously will result in reduced moisture causing
2702 changes in soil micro-arthropod communities that can affect the functions that these
2703 organisms provide, such as decomposition.

2704 Responses of micro-arthropod communities seem to be specific to particular plant
2705 communities and ecosystems. Functional changes within soil invertebrate communities due to
2706 climate change are expected to occur although more evidence is required.

2707 Prepared by Juan J. Jiménez

2708 Sources:

2709 Briones, M.J.I., Ostle, N., McNamara, N.P. and Poskitt, J. (2009) Functional shifts of
2710 grassland soil communities in response to soil warming. *Soil Biology and Biochemistry* 41,
2711 315–322.

2712 Hansen, R.A., Williams, R.S., Degenhardt, D.C. and Lincoln, D.E. (2001) Non-litter effects
2713 of elevated CO₂ on forest floor microarthropod abundances. *Plant and Soil* 236, 139–144.

2714 Kardol, P., Reynolds, W.N., Norby, R.J. and Classen, A.T. (2011) Climate change effects on
2715 soil microarthropod abundance and community. *Applied Soil Ecology* 47, 37–44.

- 2716 Klironomos, J.N., Rillig, M.C. and Allen, M.F. (1996) Below-ground microbial and
2717 microfauna response to *Artemisia tridentata* grown under elevated atmospheric CO₂.
2718 *Functional Ecology* 10, 527–734.
- 2719 Schröter, D., Brussaard, L., De Geyn, G., Poveda, K., Brown, V.K., Berg, M.P., Wardle,
2720 D.A., Moore, J. and Wall, D.H. (2004) Trophic interactions in a changing world: modeling
2721 above- and belowground interactions. *Basic and Applied Ecology* 5, 515–528.
2722

2723 *Case study 2. Insect adaption or movement: the evidence from the sub-fossil record in*
2724 *glaciation history*

2725 We live in an interglacial period in a 2.6 million year sequence of alternating glacial and
2726 interglacial periods (the Quaternary Period). During this period, the world has certainly been
2727 warmer than it is now in this interglacial period, but for much of the time it has been colder,
2728 and the transitions between the two extremes have been rapid.

2729 Sub-fossil remains in temperate regions are available in dated layers for many insects
2730 covering much of this period. Examination of these remains can give us insight into
2731 evolution, extinction and movement of insect populations during periods of climate change,
2732 helping us to understand how insects and other invertebrates are likely to respond during the
2733 anticipated climate change to come.

2734 The sub-fossil record shows little evidence of evolution of new species or mass extinction of
2735 species during the Quaternary. The sub-fossil remains can nearly all be matched to existing
2736 species, and the fact that species occur in similar associations implies that their physiological
2737 and ecological requirements have not changed significantly. There is evidence that species
2738 disappeared from the sub-fossil record at the beginning of the Quaternary, but little evidence
2739 for significant mass extinction since then. This implies that the species that exist today have
2740 mostly existed unchanged since the beginning of the Quaternary, and that they have survived
2741 repeated glacial and interglacial periods.

2742 What the sub-fossil evidence does show, however, is that insect species have been
2743 geographically highly mobile. Broadly speaking, the species found in temperate regions
2744 during glacial periods are now restricted to cold areas of the subarctic and high mountains
2745 such as the Himalayas, whereas the species found in temperate regions during warmer
2746 periods are those which we now associate with the subtropics. The implication is clear:
2747 species do not adapt to changing climate, but they move to areas where they are well adapted
2748 to the climate.

2749 The sub-fossil evidence also indicates that insects move fairly rapidly when necessary. The
2750 changes between glacial and interglacial periods and back have been rapid and the insect
2751 groups studied (detritivores and predators) have kept track with the areas to which they are
2752 adapted. There is less evidence as yet for herbivores, which can only spread to climatically
2753 suitable areas where suitable food plants already occur, or for flightless insects. For the latter,
2754 particularly soil invertebrates, it would be desirable to know more about the sub-fossil record,
2755 to better predict what might happen now.

2756 We do not have comparable data for insect species in the tropics, and this is a gap that should
2757 be filled if possible. There is evidence from Africa indicating that rainfall was reduced in
2758 glacial periods and much of Africa became savannah, and so species adapted to rainforest
2759 became concentrated in refugia where rainfall persisted, or at higher altitude on mountains. It
2760 is not clear to what extent species may have moved out of Africa. In contrast, the Amazon
2761 Basin remained as rainfall forest during glacial periods, albeit 5–7°C colder, which allowed
2762 plant species that are now restricted to higher altitude in the Andes to spread into the Amazon
2763 Basin, albeit at low densities. The species that are now present in the Amazon seem to have
2764 persisted *in situ* during glacial periods. Studies of sub-fossil insects from these regions are
2765 needed. This will be difficult and time consuming because of the shortage of suitable

2766 depositions and the huge number of species likely to be involved, but should throw further
2767 light on how invertebrates respond to climate change, and help improve predictions for
2768 invertebrates of agricultural importance in the tropics.

2769 Prepared by Matthew J.W. Cock

2770 Sources:

2771 Colinvaux, P. (2005) The Pleistocene vector of Neotropical diversity. In: Bermingham, E.,
2772 Dick, C.W. and Moritz, C. (eds) *Tropical Rainforests: Past, Present and Future*.

2773 University of Chicago Press, Chicago, Illinois, pp. 78–106.

2774 Coope, G.R. (2004) Several million years of stability among insect species because of, or in
2775 spite of, Ice Age climatic instability? *Philosophical Transactions of the Royal Society B:*
2776 *Biological Sciences* 359, 209–214.

2777 Kingdom, J. (1990) *Island Africa: the Evolution of Africa's Rare Animals and Plants*.

2778 Collins, London, UK, 287 pp.

2779 Case study 3. Climate change-related expansions in the range of the southern green stink
2780 bug, a cosmopolitan invader.

2781 The geographical ranges of many invertebrate pests are expected to expand under climate
2782 change as a result of temperature-related increases in the suitability of new habitats. The
2783 southern green stink bug (SGSB), or green vegetable bug, *Nezara viridula* (Linnaeus)
2784 (Hemiptera: Pentatomidae) is a cosmopolitan, highly polyphagous species, which attacks
2785 many important food and fibre crops including rice, soya bean, maize (corn), tomato and
2786 aubergine (eggplant). In warmer climates there may be four generations per year with a life
2787 cycle of about 70 days. The SGSB probably originated in Africa, but over the past 250 years
2788 it has spread all over the world and now occurs in most tropical and subtropical regions. In
2789 some areas, such as Brazil, there are genetically distinct SGSB populations adapted to
2790 colonize different environments. Some geographical expansion is related to the planting of its
2791 preferred hosts (e.g. soya beans) in new regions, but it is also spreading northwards to new
2792 areas in temperate zones as a result of climate change. For example, the discovery of
2793 breeding colonies in the United Kingdom – further north than was previously predicted – has
2794 been taken as a sign of climate change, although its potential impact needs further study.

2795 The SGSB has been extensively studied in Japan, where its initial increase was related to the
2796 cultivation of early-planted rice in the 1950s. In central Japan, however, its range has now
2797 shifted northwards, by some 85 km since the early 1960s, probably as a result of milder
2798 winters. The northern limit appears to be defined by a +5°C isothermal line for mean January
2799 temperatures in Japan. Expansion into new areas has a direct economic impact, e.g. it can
2800 seriously affect rice production, and continued global warming will probably further increase
2801 the winter and spring survival of *N. viridula* in temperate regions where it is currently at the
2802 limit of its range. More adults will survive the winter and be available to help establish the
2803 species in newly colonized areas, and a 2.0–2.5°C increase in average temperatures could
2804 produce another full generation in central Japan.

2805 In the tropics, however, where insects are often living relatively close to their physiological
2806 optima, further increases in temperature may have a negative effect on their performance: e.g.
2807 a simulated increase in temperatures of 2.5°C had a strongly deleterious effect on SGSB.
2808 *Nezara viridula* has symbiotic bacteria in its gut, and climate change can act via these
2809 mutualistic organisms – which are eliminated at high temperatures – to indirectly affect the
2810 host population; whether heat stress due to global warming will have such an effect on SGSB
2811 in tropical regions remains to be seen. In conclusion, SGSB is an invasive alien species that
2812 has increased its range in a number of regions as a result of both land-use changes and global
2813 warming. Winter temperatures determine the survival and establishment of such above-
2814 ground invertebrates and climate change is expected to result in range expansions of many
2815 other species, in a similar way to that illustrated here by the SGSB.

2816 Prepared by Raymond J.C. Cannon

2817 Sources:

2818 Kiritani, K. (2011) Impacts of global warming on *Nezara viridula* and its native congeneric
2819 species. *Journal of Asia-Pacific Entomology* on-line.

2820 Musolin, D.L., Tougou, D. and Fujisaki, K. (2010) Too hot to handle? Phenological and life-
2821 history responses to simulated climate change of the southern green stink bug *Nezara*
2822 *viridula* (Heteroptera: Pentatomidae). *Global Change Biology* 16, 73–78.

- 2823 Salisbury, A., Barclay, M.V.L., Reid, S. and Halstead, A. (2009) The current status of the
2824 southern green shield bug, *Nezara viridula* (Hemiptera; Pentatomidae), an introduced pest
2825 species recently established in south-east England. *British Journal of Entomology and*
2826 *Natural History* 22, 189–194.
- 2827 Takeda, K., Musolin, D.L. and Fujisaki, K. (2010) Dissecting insect responses to climate
2828 warming: overwintering and post-diapause performance in southern stink bug, *Nezara*
2829 *viridula*, under simulated climate-change conditions. *Physiological Entomology* 35, 343–
2830 353.
- 2831 Todd, J.W. (1989) Ecology and behavior of *Nezara viridula*. *Annual Review of Entomology*
2832 34, 273–292.
- 2833 Vivan, L.M. and Panizzi, A.R. (2006) Geographical distribution of genetically determined
2834 types of *Nezara viridula* (L.) (Heteroptera: Pentatomidae) in Brazil. *Neotropical*
2835 *Entomology* 35, 175–181.
- 2836 Yukawa, J., Kiritani, K., Gyoutoku, N., Uechi, N., Yamaguchi, D. and Kamitani, S. (2007)
2837 Distribution range shift of two allied species, *Nezara viridula* and *N. antennata*
2838 (Hemiptera: Pentatomidae), in Japan, possibly due to global warming. *Applied*
2839 *Entomology & Zoology* 42, 205–215.

2840 *Case study 4. Coffee's most intractable insect pest: the coffee berry borer*

2841 The coffee berry borer (CBB; *Hypothenemus hampei* (Ferrari)) is an African scolytid beetle
2842 that bores into the ripening coffee bean where it produces about 30 first-generation offspring.
2843 Like most insect borers, it has relatively few natural enemies and where such agents have
2844 been introduced, they have not been capable of maintaining the pest below an economic
2845 threshold. The most common and effective forms of control are chemicals and regular but
2846 very laborious hand picking to remove all ripe, over-ripe and fallen berries.

2847 The very highest quality arabica coffee is little troubled by the borer, because it grows at such
2848 an altitude that the pest cannot complete more than a generation before harvest. Hence the
2849 finest Ethiopian coffees have been little troubled by CBB, but this is now changing; the
2850 climate around Jimma in Ethiopia, for instance, was too cold for CBB before about 1984 but
2851 now, because of increased temperatures, it may be able to complete one to two generations
2852 per year.

2853 In Colombia, it is a common experience that the lower altitude limit of coffee itself is rising
2854 and difficulties in controlling the borer have been cited as a factor in farmers' decision to quit
2855 growing coffee. In July 2010, the president of Quindío's coffee committee said that the
2856 warmest parts of the department had become marginal for coffee – “the temperature has gone
2857 up a degree and in the heat, management of the borer is impossible”, he said. In Indonesia
2858 CBB has been mostly a robusta coffee pest at low altitudes, but over the last ten years it has
2859 been found increasingly in the higher arabica coffee growing areas in northern Sumatra and
2860 Aceh, where high-quality Mandheling coffee originates.

2861 It is not only temperature that is affecting efforts to control CBB. Climate change is causing
2862 more extremes of weather such as prolonged dry and wet spells. Dry hot spells can be
2863 especially favourable for CBB as its progeny develop in the virtually sealed fallen berries that
2864 remain buried under leaf litter after harvest; there they suffer low mortality and then suddenly
2865 emerge en masse after rainfall. Farmers are frequently not aware of this problem, especially if
2866 previous wet periods have tended to keep CBB under better control.

2867 In India both the showers that initiate flowering and those that support fruit setting are
2868 becoming less reliable. This can lead to smaller multiple flowerings, providing a year-round
2869 food source for CBB. Dr J.K. Kimemia, head of Kenya's Coffee Research Foundation
2870 confirms this: “You look at a coffee tree and cannot determine the season because it has
2871 beans of all ages. That is a problem when it comes to disease management, insect
2872 management and the worst problem is in harvesting, the cost is enormous.”

2873 Efforts to find new ways to control the borer are currently few. Heavy shade trees in coffee
2874 agroforestry systems can reduce temperature, humidity and solar radiation extremes but field
2875 studies can find no clear relationship between CBB infestation and shade intensity. With the
2876 general prohibition of the most effective chemical control (endosulfan), and the prospect of
2877 accelerating climate change, it is increasingly clear that long-term control of CBB needs to be
2878 rethought.

2879 Prepared by Peter S. Baker, CABI

2880 Sources:

- 2881 Lin, B.B. (2007) Agroforestry management as an adaptive strategy against potential
2882 microclimate extremes in coffee agriculture. *Agricultural and Forest Meteorology* 144,
2883 85–94.
- 2884 Jaramillo, J., Chabi-Olaye, A., Kamonjo, C., Jaramillo, A., Vega, F.E., Poehling, H.M. and
2885 Borgemeister, C. (2009) Thermal tolerance of the coffee berry borer *Hypothenemus*
2886 *hampei*: predictions of climate change impact on a tropical insect pest. *PLoS ONE* 4,
2887 e6487, 11 pp.
- 2888 Jayarama (2010) Weather change in coffee plantation areas in India. *Indian Coffee* 74(1), 17–
2889 19.
- 2890 Mawardi, S. and Wiryadiputra, S. (2009) Recent status of coffee berry borer in Indonesia.
2891 International Coffee Organization Seminar on Coffee Berry Borer, 17 March 2009.
- 2892 Ruiz-Cárdenas, R. and Baker, P. (2010) Life table of *Hypothenemus hampei* (Ferrari) in
2893 relation to coffee berry phenology under Colombian field conditions. *Scientia Agricola*
2894 (*Piracicaba, Brazil*) 67, 658–668.
- 2895 Soto-Pinto, L., Perfecto, I. and Caballero-Nieto, J. (2002) Shade over coffee: its effects on
2896 berry borer, leaf rust and spontaneous herbs in Chiapas, Mexico. *Agroforestry Systems* 55,
2897 37–45.

2898 *Case study 5. Climate change may increase wind-assisted migration of invertebrates into*
2899 *New Zealand*

2900 Wind-borne migration enables insects as diverse as minute flies to large moths to track
2901 changing habitats on spatial scales ranging from local to intercontinental (Gatehouse, 1997).
2902 This strategy is successful in spite of the randomness of the destinations reached and the
2903 losses that occur from failure to locate a suitable habitat. New Zealand's geographical
2904 isolation has been an enormous help in preventing the invasion of unwanted organisms that
2905 could attack crops, interfere with efficacy of beneficial organisms and endanger native
2906 biodiversity. However, there is compelling evidence that many invertebrates that utilize wind
2907 for dispersal frequently cross the 2 000 km of ocean between Australia and New Zealand,
2908 ranging from aphids to butterflies (Tomlinson, 1973), e.g. the nymphalid butterfly
2909 *Hypolimnas bolina nerina* (Fabricius) is found in considerable numbers some years, but is not
2910 established in New Zealand.

2911 In the latitudes of New Zealand and Australia, the weather is dominated by eastward moving
2912 anticyclones and depressions. As the associated fronts move over Australia, the warm air
2913 ahead rises, providing lift to invertebrates which can then be carried across the Tasman Sea
2914 on the westerly winds. They are deposited in western parts of New Zealand as the winds
2915 weaken. Similarly, hot dry conditions in Australia can generate thermals that can lift insects
2916 above the ground to a level of the prevailing westerly winds. Meteorological conditions
2917 favouring migration of Australian invertebrates across the Tasman Sea at a transit level of
2918 300–1 000 m were estimated to occur just over 20 times per year based on weather data for
2919 the years 1961–70 (Tomlinson, 1973). In most cases, the scarcity of available hosts, mates,
2920 habitat and climatic conditions in New Zealand prevents establishment of viable populations.

2921 Climate change projections indicate that south-eastern Australia is likely to become hotter
2922 and drier in future and there will be an increase in the strength of the mid-latitude westerly
2923 winds. Therefore, the frequency of favourable migration conditions is likely to increase.
2924 When combined with the prediction that New Zealand's climate on average will be around
2925 2°C warmer by 2090 than in 1990, and that the north-western regions may become frost-free,
2926 many of the regular Australian migrants may become permanently established.

2927 Prepared by Pip Gerard

2928 Sources:

2929 Gatehouse, A.G. (1997) Behavior and ecological genetics of wind-borne migration by
2930 insects. *Annual Review of Entomology* 42, 475–502.

2931 Tomlinson, A.I. (1973) Meteorological aspects of trans-Tasman insect dispersal. *New*
2932 *Zealand Entomologist* 5, 253–268.

2933

2934 Case study 6. *The Argentine ant, one of the world's worst invasive aliens.*

2935 The Argentine ant (*Linepithema humile* (Mayr): Hymenoptera: Formicidae) is a widespread
2936 and highly invasive species. Native to South America, Argentine ants have spread throughout
2937 the world (to all continents apart from Antarctica), as a result of least 28 separate
2938 introductions, mainly as a result of human commercial activities. However, this species still
2939 has the potential to become established in new areas, beyond its present distributional range,
2940 as a result of global climate change. The Argentine ant is most likely to occur where the mean
2941 daily temperature in midwinter is 7–14°C and maximum daily temperatures during the hottest
2942 month average 19–30°C. Therefore, many uninvaded regions are vulnerable to future
2943 establishment, including southern China, Taiwan, Zimbabwe, central Madagascar, Morocco,
2944 high-elevation Ethiopia, Yemen and many oceanic islands.

2945 *Linepithema humile* remains a serious threat to native species and ecosystems in many
2946 islands, such as New Zealand, where it is concentrated in urban centres but has the potential
2947 to establish itself more widely, particularly in urban areas and disturbed habitat. The
2948 Argentine ant is an ecologically damaging invasive species that forms “supercolonies” which
2949 are a threat to biodiversity as it can displace most other ant species through competition.
2950 Argentine ants can also have impacts on other invertebrates via direct predation, competition
2951 and egg predation. In addition, *L. humile* can be an agricultural pest, enhancing populations
2952 of sap-sucking Hemiptera that damage plants and can vector diseases.

2953 The spread of the Argentine ant has been facilitated by so-called “jump dispersal”, typically a
2954 human-mediated long-distance mode of dispersal that can disseminate a species widely and
2955 result in colonization of new continents. Virtually no country or island is too isolated for
2956 potential establishment by this species and climate change could exacerbate the process, with
2957 tropical coastal Africa and South-east Asia being particularly vulnerable to invasion.
2958 However, global warming may result in a general reduction in the distribution of *L. humile* in
2959 tropical areas, with a shift to higher latitudes and altitudes as they become more suitable for
2960 invasion and establishment.

2961 Prepared by Raymond J.C. Cannon

2962 Sources:

2963 Hartley, S., Harris, R. and Lester, P.J. (2006) Quantifying uncertainty in the potential
2964 distribution of an invasive species: climate and the Argentine ant. *Ecology Letters* 9,
2965 1068–1079.

2966 Roura-Pascual, N., Suarez, A.V., Gómez, C., Pons, P., Touyama, Y., Wild, A.L. and
2967 Peterson, A.T. (2004) Geographical potential of Argentine ants (*Linepithema humile*
2968 Mayr) in the face of global climate change. *Proceedings of the Royal Society B: Biological*
2969 *Sciences* 271, 2527–2534.

2970 Roura-Pascual, N., Hui, C., Ikeda, T., Leday, G., Richardson, D.M., Carpintero, S.,
2971 Espadaler, X., Gómez, C., Guénard, B., Hartley, S., Krushelnycky, P., Lester, P.J.,
2972 McGeoch, M.A., Menke, S.B., Pedersen, J.S., Pitt, J.P., Reyes, J., Sanders, N.J., Suarez,
2973 A.V., Touyama, Y., Ward, D., Ward, P.S. and Worner, S.P. (2011) Relative roles of
2974 climatic suitability and anthropogenic influence in determining the pattern of spread in a
2975 global invader. *Proceedings of the National Academy of Sciences USA* 108, 220–225.

- 2976 Suarez, A.V., Holway, D.A. and Case, T.J. (2001). Patterns of spread in biological invasions
2977 dominated by long-distance jump dispersal: insights from Argentine ants. *Proceedings of*
2978 *the National Academy of Sciences USA* 98, 1095–1100.
- 2979 Ward, D.F. and Harris, R.J. (2005) Invasibility of native habitats by Argentine ants,
2980 *Linepithema humile*, in New Zealand. *New Zealand Journal of Ecology* 29, 215–219.
- 2981 Wetterer, J.K., Wild, A.L., Suarez, A.V., Roura-Pascual, N. and Espadaler, X. (2009)
2982 Worldwide spread of the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae).
2983 *Myrmecological News* 12, 187–194.
- 2984

2985 *Case study 7. The European corn borer: range shifts and an increased number of generations*
2986 *– climate change in action*

2987 The European corn borer (ECB), *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), is a
2988 serious pest of maize in Europe and since 1909 in North America. Although highly
2989 polyphagous, it is most damaging to maize crops. The caterpillars feed on the leaves at first –
2990 causing characteristic leaf “windowing” – but later instars enter the stem and hollow out the
2991 internodes causing the stems to break. The larvae can also feed on the cobs and crop losses
2992 can be severe. In the northern parts of its range, ECB has only one generation per year
2993 (univoltine), but in warmer latitudes there may be two or three generations. *Ostrinia nubilalis*
2994 already appears to be expanding northward in Europe and global warming may result in
2995 substantial future expansions in the range of this species as well as other maize pests that are
2996 currently limited by low winter temperatures. The northern limit is expected to shift
2997 northward by more than 100 km with every 1°C rise in the average temperature. In Hungary,
2998 there has been a gradual disappearance of the univoltine type, coincidental with the gradual
2999 appearance of a two generational (bivoltine) ecotype, between 1991 and 2004. The ECB may
3000 also become bivoltine in the Czech Republic and other more northerly European countries,
3001 possibly affecting substantially more arable land and causing increased damage in maize
3002 growing areas by 2050.

3003 A 3°C increase in mean annual temperatures would advance the limit for maize to the extent
3004 of including virtually all of the United Kingdom, and this could provide the means for a
3005 substantial shift in the distribution of *O. nubilalis*. The area of maize cultivation in the United
3006 Kingdom has already increased from about 25 000 to 172 000 ha in the last 30 years. For
3007 species such as *O. nubilalis*, which are already distributed over a very wide latitudinal range
3008 in Europe, successful colonization of northwardly expanded maize crops will depend on
3009 factors such as migration ability and the rate at which the climate changes. Up until the
3010 1930s, ECB was classed as a rare migrant to the British Isles, at or near the northern limit of
3011 its range in southern England, but since then it has been progressively extending northwards
3012 and is now a regular migrant. Breeding colonies have been established in England for many
3013 years, feeding almost exclusively on mugwort (*Artemisia vulgaris*; Asteraceae), but in 2010,
3014 for the first time, the pest caused damage to two maize crops in the south-west of England. In
3015 conclusion, the ECB is expected to occupy a wider area and exert increased pest pressure as a
3016 result of an increase in the number of generations per year, due to the climate change.

3017 Prepared by Raymond J.C. Cannon

3018 Sources:

3019 Gathmann, A. and Rothmeier, I. (2005) Dispersal of the European corn borer (*Ostrinia*
3020 *nubilalis* Hbn.) in southern Rhineland – results of the infestation assessment 2002 and
3021 2003. *Journal of Plant Diseases and Protection* 112, 200–203.

3022 Keszthelyi, S., Puskás, J. and Nowinszky, L. (2008) Changing of flight phenology and
3023 ecotype expansion of the European corn borer (*Ostrinia nubilalis* Hbn.) in Hungary.
3024 *Cereal Research Communications* 36, 647–657.

3025 Kocmánková, E., Trnka, M., Juroch, J., Dubrovský, M., Semerádová, D., Možný, M. and
3026 Žalud, Z. (2009) Impact of climate change on the occurrence and activity of harmful
3027 organisms. *Plant Protection Science* 45 (Special Issue), S48–S52.

3028 Korycinska, A. and Ostojá-Starzewski, J. (2010). A new threat to maize crops in the UK?
3029 Fera Plant Clinic News, August–September 2010, unpaginated.

3030 [www.fera.defra.gov.uk/plants/publications/documents/plantClinicNews/augSept10Issue.p](http://www.fera.defra.gov.uk/plants/publications/documents/plantClinicNews/augSept10Issue.pdf)
3031 [df](http://www.fera.defra.gov.uk/plants/publications/documents/plantClinicNews/augSept10Issue.pdf)
3032 Trnka, M., Muska, F., Semeradova, D., Dubrovsky, M., Kocmankova, E. and Zalud, Z.
3033 (2007) European corn borer life stage model: Regional estimates of pest development and
3034 spatial distribution under present and future climate. *Ecological Modelling* 207, 61–84.

3035 *Case study 8. Critical regional host: parasitoid population interaction may be jeopardized by*
3036 *climate change*

3037 The introduced lucerne weevil, *Sitona discoideus* Gyllenhal (Coleoptera: Curculionidae),
3038 became a severe pest of lucerne (alfalfa) in Australia in the 1960s and in New Zealand in the
3039 1970s. In 1977, the parasitoid *Microctonus aethiopoidea* Loan (Hymenoptera: Braconidae)
3040 was introduced from Morocco into Australia to control this pest, and from Australia into New
3041 Zealand in 1982. The parasitoids lay eggs inside adult weevils, and female weevils become
3042 sterile almost immediately afterwards. The solitary larvae develop within the live hosts and
3043 the weevils die when the mature larvae emerge to pupate.

3044 *Sitona discoideus* has one generation per year. The weevil over-summer (aestivates) as a
3045 pre-reproductive adult in a sheltered place away from lucerne, then returns to the lucerne in
3046 autumn and commences reproduction, which continues until spring. The *M. aethiopoidea*
3047 larva generally develops only when its host is reproductive. The parasitoid over-summer as a
3048 non-developing larva in aestivating *S. discoideus* and then resumes its development once its
3049 host has returned to the lucerne. Under these conditions, *M. aethiopoidea* has two generations
3050 for every host generation. This occurs in its natural range in Europe, and in Australia where it
3051 is not an effective biological control agent (BCA). However, in New Zealand, around 3% of
3052 the non-reproductive *S. discoideus* do not aestivate. They stay in the lucerne crop throughout
3053 summer, supporting an additional four parasitoid generations. This allows the parasitoid
3054 population to build up to effective levels by autumn, preventing damaging weevil larval
3055 populations.

3056 The most likely reason for the atypical behaviour appears to be seasonal differences in
3057 climate (perhaps interacting with day length) between New Zealand and other regions such as
3058 Australia and Mediterranean Europe.

3059 With climate change predictions indicating that eastern parts of New Zealand will become
3060 generally drier, lucerne is expected to become an increasingly important fodder crop.
3061 However, examination of climate data suggests that areas of New Zealand where the
3062 biological control is currently successful may become increasingly similar to Australian areas
3063 where biological control is ineffective. While the mechanistic trigger for atypical parasitoid
3064 development in New Zealand has not been confirmed, New Zealand lucerne growers will
3065 need to be alert for weevil outbreaks that may signal that the BCAs are becoming ineffective.

3066 This case study exemplifies how a small but critically important population interaction
3067 related to climate may determine the regional efficacy of a BCA, and how this could be
3068 affected by climate change.

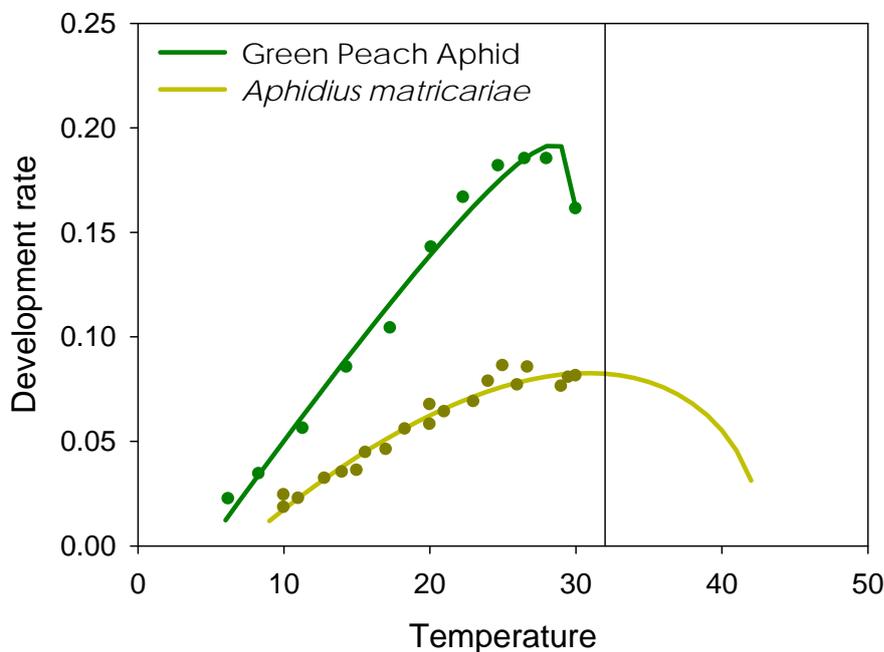
3069 Prepared by John Kean, AgResearch Ltd, New Zealand

3070 Source:

3071 Goldson, S.L. (2006) Climate change in biological control. In: Newton, P.C.D., Carran, R.A.,
3072 Edwards, G.R. and Niklaus, P.A. (eds) *Agroecosystems in a Changing Climate*. Taylor &
3073 Francis, London, UK, pp. 329–332.

3074 Case study 9. Differential responses to temperature by pests and biological control agents
3075 may be important in determining the effects of climate change

3076 Differential responses to temperature by species in food webs may be important in
3077 determining effects of climate change on the performance of biological control functions.
3078 Here, the effects of temperature on development rates are plotted for two species: the green
3079 peach aphid, *Myzus persicae* (Sulzer) and one of its hymenopteran parasitoids, *Aphidius*
3080 *matricariae* Haliday (Braconidae). Development rate accelerates differently for each, and
3081 each has a different apparent optimum and projected upper development threshold. In
3082 invertebrates, most biological processes are dependent to some degree on environmental
3083 temperatures, and exhibit similar shapes. The differences in slopes, optima and upper
3084 thresholds may be important in determining the responses of BCAs to thermal stress under
3085 climate change.



3086

3087

3088 Prepared by: Dave Gillespie

3089 Sources:

3090 Bernal, J. and Gonzalez, D. (1993) Temperature requirements of four parasites of the Russian
3091 wheat aphid *Diuraphis noxia*. *Entomologia Experimentalis et Applicata* 69, 173–182.

3092 Davis, J.A., Radcliffe, E.B. and Ragsdale, D.W. (2006) Effects of high and fluctuating
3093 temperatures on *Myzus persicae* (Hemiptera: Aphididae). *Environmental Entomology* 35,
3094 1461–1468.

3095

3096 *Case study 10. Synchronization of a pest population can lead to outbreaks due to disruption*
3097 *of biological control agents: coconut leaf beetle in Fiji*

3098 Coconut has long been an important tree both culturally and economically in the islands of
3099 the Pacific. Hence it caused considerable concern in the 1920s, when an indigenous leaf-
3100 mining hispine beetle, *Promecotheca reichei* Baly, came to prominence as a devastating
3101 outbreak pest of coconut in Fiji. A campaign was begun in 1929 which led to the successful
3102 biological control programme against the pest, which in the process generated considerable
3103 information about the population dynamics of *P. reichei* and its natural enemies, stimulating
3104 thinking about the regulation of populations in the tropics.

3105 Studies showed that in normal circumstances, the generations of the beetle overlap so that the
3106 various developmental stages occur together, parasitoids are able to breed continuously, and a
3107 satisfactory low equilibrium was maintained by the inter-relations of indigenous primary and
3108 secondary parasitoids. In the 1920s, however, this equilibrium was upset in certain parts of
3109 Fiji by a predatory mite, *Pyemotes ventricosus* (Newport) (Acari: Pyemotidae), which was
3110 first recorded there in 1921, though it had probably been introduced long before. This mite
3111 attacks the larvae, pupae and freshly emerged adults of *Promecotheca reichei*, multiplies
3112 rapidly, and periodically eliminates all the larvae and pupae in a site of infestation. After this,
3113 its numbers decline, but rise again with those of the host. As a result, a condition is produced
3114 and maintained in which the stages of *P. reichei* do not overlap, and in this condition it was
3115 no longer controlled by indigenous parasites and so assumed the status of a pest.

3116 The predatory mite made the beetle a pest, not by elimination of the indigenous natural
3117 enemies by direct attack, but by periodic elimination of all developmental stages of *P. reichei*
3118 except adults, thus causing and maintaining a condition comparable to that of insects in
3119 temperate countries, where development and time of occurrence are controlled by seasonal
3120 climatic changes, and successive generations cannot appreciably overlap. The synchronized
3121 condition was maintained because *P. reichei* has only a short oviposition period – if the
3122 oviposition period were long, the population would rapidly revert to a condition where all
3123 developmental stages were present. The generation time of the indigenous parasitoids proved
3124 ill adapted for coping with this new condition, as they emerged when no suitable hosts were
3125 available, so that as long as the pest remained synchronized they could not breed
3126 continuously. The beetle anomalously became a pest in the presence of the very parasitoids
3127 that normally controlled it. It was evident that in these very special circumstances, the
3128 problem of restoring the insect to a state of economic harmlessness necessitated the discovery
3129 of a parasitoid capable of satisfying requirements of an unusually rigid and exacting nature,
3130 i.e. one with a life cycle duration that would enable it to breed continuously on a
3131 synchronized host population.

3132 Based on this criterion, surveys in Indonesia led to the selection of *Pediobius parvulus*
3133 (Ferrière) (Hymenoptera: Eulophidae), as theoretically suitable. Following its introduction, it
3134 became established and suppressed the hispine beetle rapidly and effectively.

3135 This work suggested that synchronization of a pest population, whether by another natural
3136 enemy, an extreme climate event, or colonization of a new area, leading to the disruption of
3137 effective continuously breeding biological control agents (BCAs), may be more common than
3138 realized in the tropics. Building on this study 50 years later, Godfray and Hassell (1987)
3139 noted that such synchronized populations were quite widespread, and a common factor in

3140 these examples is the presence of insect parasitoids as a major mortality factor. They went on
3141 to demonstrate, using theoretical population models, that parasitism can be the cause of
3142 discrete pest generations, and in particular, that the ratio of the lengths of the host and
3143 parasitoid life cycles is of prime importance in determining whether generations tend to be
3144 discrete or continuous.

3145 Prepared by: Matthew J.W. Cock

3146 Sources:

3147 Godfray, H.C.J. and Hassell, M.P. (1987) Natural enemies can cause discrete generations in
3148 tropical insects. *Nature* 327, 144–147.

3149 Taylor, T.H.C. (1937) The Biological Control of an Insect in Fiji. An Account of the Coconut
3150 Leaf-mining Beetle and its Parasite Complex. The Imperial Institute of Entomology,
3151 London, UK, 239 pp.

3152 *Case study 11: Biological control of corn earworm, *Helicoverpa armigera*, in New Zealand*
3153 *threatened by climate change*

3154 Climate change may allow more generations of this pest to develop each season, potentially
3155 exacerbating pest threats beyond the ability of current biological control agents (BCAs) to
3156 maintain effective suppression.

3157 In New Zealand, the corn earworm, *Helicoverpa armigera* (Hübner) (Lepidoptera:
3158 Noctuidae), is the key insect pest of processing tomatoes in the main growing region of
3159 Hawke’s Bay. Two larval braconid parasitoids were successfully introduced into New
3160 Zealand: *Cotesia kazak* (Telenga) in 1977 and *Microplitis croceipes* (Cresson) in 1986. These
3161 now cause 60–80% parasitism and form the basis of an integrated pest management (IPM)
3162 programme to control corn earworm in outdoor tomato crops. *Cotesia kazak* is the dominant
3163 parasitoid, reared from about 90% of parasitized larvae, and usually killing larvae before they
3164 cause damage.

3165 Corn earworm normally has three generations a year in the North Island of New Zealand, but
3166 in cooler summers and in cooler regions there are only two generations a year. Despite the
3167 action of the parasitoids, the third generation, when present, can lead to severe crop losses in
3168 sweet corn, tomatoes and leafy vegetable crops such as cabbage and lettuce. In areas where
3169 this third generation is common, the processing industry does not plant late crops of sweet
3170 corn and processing tomatoes.

3171 The projected changes over New Zealand for the A1B (medium emissions) scenario of the
3172 IPCC are for annual mean temperatures to increase by about 1°C by 2040, and 2°C by 2090,
3173 with the changes most pronounced in the north of the South Island, and most of the North
3174 Island. Development parameters were used to calculate the expected number of corn earworm
3175 and parasitoid generations per year and showed that the expected climate warming in New
3176 Zealand may allow a third generation of the pest to occur in cooler seasons and in cooler
3177 regions. This would have a major impact on the pest status of *H. armigera* in these areas,
3178 particularly in the South Island. The results suggest that even under a moderate emissions
3179 scenario, corn earworm is expected to become increasingly problematic, and by 2090 may be
3180 affecting late-season crops of tomato and maize as far south as Canterbury. Given that *C.*
3181 *kazak* has not been effective at controlling corn earworm in warmer areas overseas, the future
3182 viability of the current IPM systems may be compromised.

3183 Prepared by Graham Walker, The New Zealand Institute for Plant & Food Research Limited

3184 Sources:

3185 Cameron, P.J., Walker, G.P., Herman, T.J.B. and Wallace, A.R. (2001) Development of
3186 economic thresholds and monitoring systems for *Helicoverpa armigera* (Lepidoptera:
3187 Noctuidae) in tomatoes. *Journal of Economic Entomology* 94, 1104–1112.

3188 Gerard, P.J.; Kean, J.M.; Phillips, C.B.; Fowler, S.V.; Withers, T.M.; Walker, G.P.; Charles,
3189 J.G. (2010) Possible impacts of climate change on biocontrol systems in New Zealand.
3190 AgResearch Ltd Report for MAF Policy, 64 pp.

3191 Walker, G.P., Herman, T.J.B., Kale, A. and Wallace, A.R. (2010) An adjustable action
3192 threshold using larval parasitism of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in
3193 IPM for processing tomatoes. *Biological Control* 52, 30–36.

3194 *Case study 12. Earthworms enhance plant tolerance to nematode infection through non-*
3195 *trophic effects of ecosystem engineering*

3196 Below-ground interactions are complex and so far the mechanisms involved are not well
3197 known. Studies on the importance of non-trophic relationships, both above and below
3198 ground, are not abundant. As a result, generalizations on the effect of predicted climate
3199 change on plant-mediated interactions between earthworms and above-ground multitrophic
3200 groups are not possible. Climate change is expected to affect plant production and the
3201 incidence of soil pests.

3202 Plant-parasitic nematodes are serious pests that cause crop production losses with high
3203 economic damage. Earthworms and vermicompost have been shown to reduce the harmful
3204 impact of nematode infestation in banana plantations.

3205 The nematode *Heterodera sacchari* Luc and Merny (Heteroderidae) forms external cysts on
3206 rice roots leading to serious damage in upland rice fields in Africa. The effect of an
3207 earthworm (*Millsonia anomala* Omodeo; Megascolecidae) on the physiology of nematode-
3208 infested plants was demonstrated through selected stress responsive genes coding for
3209 lipoygenase, phospholipase D and cysteine protease. The ability of plants to respond
3210 through physiological mechanisms was enhanced by earthworm presence. Decrease in rice
3211 growth due to *H. sacchari* was suppressed in the presence of earthworms. Root biomass was
3212 not affected by nematodes when earthworms were present and the expression of stress-
3213 responsive genes in the leaves was modulated by below-ground activities.

3214 The mechanisms are not known but need to be discovered as climate change may induce
3215 important changes in plant production and the incidence of pests in soil.

3216 Prepared by Juan J. Jiménez and Patrick M. Lavelle

3217 Sources:

3218 Blouin, M., Zuily-Fodil, Y., Pham-Thi, A.T., Laffray, D., Reversat, G., Pando, A., Tondoh, J.
3219 and Lavelle, P. (2005) Belowground organism activities affect plant aboveground
3220 phenotype, inducing plant tolerance to parasites. *Ecology Letters* 8, 202–208.

3221 Brown, G.G., Pashanasi, B., Villenave, C., Patron, J.C., Senapati, B.K., Giri, S., Barois, I.,
3222 Lavelle, P., Blanchart, E., Blakemore, R.J., Spatin, A.V. and Boyer, J. (1999). Effects of
3223 earthworms on plant production in the tropics. In: Lavelle, P., Brussaard, L. and Hendrix,
3224 P. (eds) *The Management of Earthworms in Tropical Agroecosystems*. CAB International,
3225 Wallingford, UK, pp. 87–148.

3226

3227 *Case study 13. Above-ground multitrophic interactions mediated by soil invertebrates and*
3228 *summer drought*

3229 Among the expected effects of climate change is the increase of summer drought in some
3230 areas that will affect above- and below-ground multi-species community interactions. An
3231 extended period of summer drought is predicted in southern Europe. Under drought
3232 conditions earthworms can reduce assimilation, transpiration and stomatal conductance of
3233 Poaceae species, probably due to reduced soil water storage capacity in the presence of
3234 earthworms. In a large-scale study the interactive effects of earthworms (*Aporrectodea*
3235 *caliginosa* (Savigny); Lumbricidae) and summer drought affected multi-species plant
3236 communities (*Hordeum vulgare* (Poaceae), *Capsella bursa-pastoris* (Brassicaceae) and
3237 *Senecio vulgaris* (Asteraceae)) and how these effects affected number of aphids
3238 (*Rhopalosiphum padi* (Linnaeus)) and its parasitoid (*Aphidius ervi* Haliday; Hymenoptera:
3239 Braconidae).

3240 Summer drought had a very strong negative impact on plant production, especially on *S.*
3241 *vulgaris* shoot and root biomass, but was ameliorated when earthworms were present. This
3242 may also indicate that this plant benefits most from any impact of earthworms, as it is the
3243 plant most severely affected by drought. In general, nitrogen concentration increased in the
3244 leaves during drought. Summer drought decreased aphid number by 50%, with nearly 10%
3245 being parasitized. Although the mechanism is not clearly understood, and more studies are
3246 needed, the interaction was moderated by earthworms, which caused declines in *R. padi*
3247 populations under drought conditions. The interactive effects of earthworms and summer
3248 drought affected plant biomass, with an increase of 11% when earthworms were present and
3249 had the largest impact in monocultures compared to multi-species communities.

3250 This case study shows how plant-mediated effects of summer drought and earthworms on *R.*
3251 *padi* had cascading effects on the parasitoid *A. ervi*. These interactions need to be understood
3252 as climate change may induce important changes in the interaction between earthworms and
3253 above-ground multitrophic groups. Below-ground interactions can mitigate the effects of
3254 climate change-related factors, like increased summer drought.

3255 Prepared by Juan J. Jiménez

3256 Sources:

3257 Blouin, M., Lavelle, P. and Laffray, D. (2007) Drought stress in rice (*Oryza sativa* L.) is
3258 enhanced in the presence of the compacting earthworm *Millsonia anomala*. *Environmental*
3259 *and Experimental Botany* 60, 352–359.

3260 Johnson, S.N., Staley, J.T., McLeod, F.A.L. and Hartley, S.E. (2011) Plant-mediated effects
3261 of soil invertebrates and summer drought on above-ground multitrophic interactions.
3262 *Journal of Ecology* 99, 57–65.

3263 Scheu, S. (2003) Effects of earthworms on plant growth: patterns and perspectives.
3264 *Pedobiologia* 47, 846–856.

3265 *Case study 14. The invasion and degradation of pastures due to biologically created soil*
3266 *compaction results in negative feedbacks to climate change*

3267 In the Brazilian Amazon, 95% of the deforested area is converted into pasture, 50% of which
3268 is considered degraded due to mismanagement, phytosanitary problems, poor soil fertility and
3269 soil structural modification (linked to soil macro-invertebrate activity). When the forest is
3270 converted to pasture, the use of heavy machinery and, later, cattle trampling lead to severe
3271 soil compaction, particularly in the 5–10 cm layer, impeding root development.

3272 The native soil macro-invertebrate communities are radically and drastically depleted, i.e.
3273 most of the native taxa disappear (151 vs. 48 morphospecies). An opportunistic invading
3274 earthworm (*Pontoscolex corethrurus* (Müller); Glossoscolecidae) benefits from anthropic
3275 disturbances and occupies the empty niche left by native earthworms and soil macrofauna,
3276 increasing its biomass to more than 450 kg/ha, equivalent to nearly 90% of total soil macro-
3277 invertebrate biomass. When *P. corethrurus* is present in the forest there is no negative effect
3278 on the native species communities, which have similar or higher densities in the presence of
3279 *P. corethrurus*. The evidence suggests that this invasive species, unlike native species, is able
3280 to feed and develop in environments where litter resources are decreased while soils have
3281 been enriched in carbon and nutrients by deforestation and burning. It produces more than
3282 100 t/ha of castings, dramatically decreasing soil macroporosity down to a level equivalent to
3283 that produced by the action of heavy machinery on soil (2.7 cm³/100 g). During the rainy
3284 season these casts plug up the soil surface, saturating the soil and producing a thick muddy
3285 layer, where anaerobic conditions prevail (increasing methane emission and denitrification).
3286 In the dry season, desiccation cracks the surface and the inability of roots to extract water
3287 from the soil causes the plants to wilt and die, leaving bare patches in the field.

3288 This case study shows how mismanagement linked to high impact of just one soil
3289 invertebrate species may bring catastrophic consequences to soil ecosystem functioning by
3290 increasing greenhouse gas emissions from soils.

3291 Prepared by Juan J. Jiménez and Patrick M. Lavelle

3292 Sources:

3293 Chauvel, A., Grimaldi, M., Barros, E., Blanchart, E., Desjardins, T., Sarrazin, M. and
3294 Lavelle, P. (1999) Pasture damage by an Amazonian earthworm. *Nature* 398, 32–33.

3295 Marichal, R., Feijoo Martinez, A., Praxedes, C., Ruiz, D., Carvajal, A.F., Oszwald, J.,
3296 Hurtado, M.P., Brown, G.G., Grimaldi, M., Desjardins, T., Sarrazin, M., Decaëns, T.,
3297 Velasquez, E. and Lavelle, P. (2010) Invasion of *Pontoscolex corethrurus*
3298 (*Glossoscolecidae*, *Oligochaeta*) in landscapes of the Amazonian deforestation arc.
3299 *Applied Soil Ecology* 46, 443–449.

3300

3301 *Case study 15. Genetic bottlenecks may limit the ability of biological control agents to*
3302 *respond to climate change*

3303 Genetic bottlenecks occur in populations when a very small number of individuals are
3304 introduced to a new region, or survive a strong selection event. When this happens, the
3305 genetic diversity in the new population is a fraction of that in the original population, and
3306 some traits (i.e. phenotypic expressions of particular alleles) may be lost. This effect can be
3307 magnified by the likelihood of inbreeding in very small founding populations. The
3308 consequence of such a bottleneck is that, because the population may not contain traits found
3309 in the source population, the potential for local adaptation to certain selection pressures may
3310 be lost. There is abundant evidence that introduced (classical and augmentative) biological
3311 control agents (BCAs) have undergone such bottlenecks. Although bottlenecks have been the
3312 likely causes of some failures of BCAs to establish following introductions, there is not a
3313 great deal of evidence that bottlenecks have constrained the performance of BCAs following
3314 successful establishment. Rapid population increase of classical BCAs following successful
3315 introduction would tend to offset and minimize the impacts of population bottlenecks.

3316 An intriguing example of a bottleneck is the increased success of the Argentine ant
3317 (*Linepithema humile* (Mayr); Hymenoptera: Formicidae) following introduction to North
3318 America. In this case, the bottleneck decreased intra-species aggression and led to increases
3319 in density of ants (Tsutsui *et al.*, 2000).

3320 New World blue butterflies of the *Polyommatus* group (Lepidoptera: Lycaenidae)
3321 demonstrate some of the potential effects of bottlenecks and constrained responses to climate.
3322 Vila *et al.* (2011) showed that species in this group crossed the Beringia land bridge in two
3323 invasion events approximately ten million years ago, followed by a further three invasion
3324 events across the Bering Strait between four and one million years ago. The land surrounding
3325 the strait was relatively warm ten million years ago, and has been chilling steadily ever since.
3326 The first lineage of *Polyommatus* group blues that made the journey could survive a
3327 temperature range that matched the Bering climate of ten million years ago, and is now found
3328 in South America in ten genera, mostly in the Andes and the southern part of the continent,
3329 although at least three genera have spread into tropical areas. The lineages that came later are
3330 more cold hardy, each with a temperature range matching the falling temperatures, and are
3331 now found in North America. Thus, climate change events determined the success and
3332 eventual distribution of species and genera according to their thermal tolerances.

3333 Therefore, although evidence is lacking for consequences of bottlenecks for adaptation of
3334 BCAs to climate change, evidence from past invasions suggests that this is an effect that
3335 should be considered. Constrained thermal tolerances might restrict the ability of some
3336 species to persist in regions with significantly changed climates. In particular, the ability of
3337 badly bottlenecked BCA species to adapt to climate change could be enhanced by inoculative
3338 introductions of additional genetic material from the source populations.

3339 Prepared by Dave Gillespie and Matthew J.W. Cock

3340 Sources:

3341 Baker, D.A., Loxdale, H.D. and Edwards, O.R. (2003) Genetic variation and founder effects
3342 in the parasitoid wasp, *Diaeretiella rapae* (M'intosh) (Hymenoptera: Braconidae:

3343 Aphidiidae), affecting its potential as a biological control agent. *Molecular Ecology* 12,
3344 3303–3311.

3345 Fauvergue, X. and Hopper, K.R. (2009) French wasps in the New World: experimental
3346 biological control introductions reveal a demographic Allee effect. *Population Ecology* 51,
3347 385–397.

3348 Hufbauer, R.A., Bogdanowicz, S.M. and Harrison, R.G. (2004) The population genetics of a
3349 biological control introduction: mitochondrial DNA and microsatellite variation in native
3350 and introduced populations of *Aphidus ervi*, a parasitoid wasp. *Molecular Ecology* 13,
3351 337–348.

3352 Nei, M., Maruyama, T. and Chakraborty, R. (1975) The bottleneck effect and genetic
3353 variability in populations. *Evolution* 29, 1–10.

3354 Tsutsui, N.D., Suarez, A.V., Holway, D.A. and Case, T.J. (2000) Reduced genetic variation
3355 and the success of an invasive species. *Proceedings of the National Academy of Sciences*
3356 *USA* 97, 5948–5953.

3357 Vila, R., Bell, C.D., Macniven, R., Goldman-Huertas, B., Ree, R.H., Marshall, C.R., Bálint,
3358 Z., Johnson, K., Benyamini, D. and Pierce, N.E. (2011) Phylogeny and palaeoecology of
3359 *Polyommatus* blue butterflies show Beringia was a climate-regulated gateway to the New
3360 World. *Proceedings of the Royal Society B: Biological Sciences*. (Online)

3361 *Case study 16. Within-species genetic variation enables a biological control agent to adapt to*
3362 *changing conditions*

3363 The introduced Argentine stem weevil, *Listronotus bonariensis* (Kuschel) (Coleoptera:
3364 Curculionidae), attacks pasture grasses throughout New Zealand. In 1991, an asexually
3365 reproducing South American parasitoid wasp, *Microctonus hyperodae* Loan (Hymenoptera:
3366 Braconidae), was introduced for its biological control. Two main genotypes were released,
3367 one from east of the South American Andes mountains and another from the west. The
3368 frequency of each genotype has been measured in *M. hyperodae* populations at 14 New
3369 Zealand sites for up to ten years following release and, at most sites in most years, selection
3370 has favoured the eastern genotype. However, the frequency of the western genotype increases
3371 in warmer seasons.

3372 Information from this study was used to forecast the balance between the *M. hyperodae*
3373 genotypes under future climates. The projected changes over New Zealand for the A1B
3374 (medium emissions) IPCC scenario are for annual mean temperatures to increase by about
3375 1°C by 2040, and 2°C by 2090, with the changes most pronounced in the north of the South
3376 Island, and most of the North Island. Under medium-term (2040) A1B and A2 IPCC
3377 scenarios, warming will generally favour the western genotype, but strong A2 long-term
3378 (2090) warming will favour the eastern genotype.

3379 These results are preliminary because the models did not consider some important factors
3380 such as how climate change could influence the summer emergence date of first generation *L.*
3381 *bonariensis* adults. However, they serve to demonstrate how climate change will inevitably
3382 impose new selection pressures on biological control agents (BCAs), and how genetic
3383 diversity within BCA populations will be important for them to adapt to those new pressures.
3384 The introduction of two *M. hyperodae* genotypes to New Zealand has increased the efficacy
3385 of the biological control programme because one compensates for the other as climatic
3386 conditions fluctuate, so together they maintain high rates of parasitism of the pest. If the
3387 eastern genotype alone had been introduced, then pest suppression would be lower in warm
3388 years, and also under the moderate climate change scenario. However, if only the western
3389 genotype had been introduced, then suppression would be less in cool years, and probably
3390 also under the A2 climate change scenario. Genetic variation within *M. hyperodae* therefore
3391 enhances the current biological control of *L. bonariensis*, and increases the resilience of this
3392 biological control system to future climatic changes.

3393 This case study exemplifies how within-species genetic variation could assist BCAs to cope
3394 with climate change.

3395 Prepared by Craig Phillips, AgResearch Ltd, New Zealand

3396 Sources:

3397 Gerard, P.J., Kean, J.M., Phillips, C.B., Fowler, S.V., Withers, T.M., Walker, G.P. and
3398 Charles, J.G. (2010) Possible impacts of climate change on biocontrol systems in New
3399 Zealand. Report for MAF Policy Project 0910-11689. AgResearch Ltd, New Zealand, 64
3400 pp. [www.maf.govt.nz/environment-natural-resources/climate-change/research-and-](http://www.maf.govt.nz/environment-natural-resources/climate-change/research-and-funded-projects/research-and-funded-projects-table.aspx)
3401 [funded-projects/research-and-funded-projects-table.aspx](http://www.maf.govt.nz/environment-natural-resources/climate-change/research-and-funded-projects/research-and-funded-projects-table.aspx)

3402 Phillips, C.B., Baird, D.B., Iline, I.I., McNeill, M.R., Proffitt, J.R., Goldson, S.L. and Kean,
3403 J.M. (2008) East meets West: adaptive evolution of an insect introduced for biological
3404 control. *Journal of Applied Ecology* 45, 948–956.

3405 *Case study 17. The search for pests and their biological control agents in natural habitats:*
3406 *sugarcane pests in the Neotropical Region.*

3407 In the situation where an indigenous pest adapts to an exotic crop, the pest must have spread
3408 from some natural habitat into the agro-ecosystem where the new crop provides an acceptable
3409 new food source. In the Neotropical Region, sugarcane is grown as an exotic crop, but its
3410 principal pests in Guyana and Trinidad (Trinidad and Tobago) were all indigenous, including
3411 the sugarcane froghopper (*Aeneolamia varia* (Fabricius); Hemiptera: Cercopidae), the
3412 sugarcane stem borers (*Diatraea* spp.; Lepidoptera: Crambidae) and the larger stem borer
3413 (*Telchin licus* (Hübner); Lepidoptera: Castniidae).

3414 The search for natural enemies of these pests included searches for the pests in their natural
3415 habitats, where it was anticipated there would be effective natural enemies that could be
3416 “forced” onto their hosts in the sugarcane agro-ecosystem, by laboratory rearing using
3417 sugarcane and mass releases.

3418 No significant populations of sugarcane froghopper could be located in natural habitats, so it
3419 is still not known whether there might be effective natural control agents in one or more
3420 natural habitats. *Telchin licus* did not become a significant pest of sugarcane until the
3421 beginning of the twentieth century, two centuries after the crop was introduced to the region,
3422 probably indicating that it took time to adapt to this new food resource. Surveys showed that
3423 normally it is associated with a variety of thick-stemmed monocots, including bananas (*Musa*
3424 spp.) and *Heliconia* spp. (Musaceae), *Costus* spp. and *Renealmia bracteosa* (Zingiberaceae)
3425 and *Ischnosiphon arouma* (Marantaceae). A parasitic tachinid fly, *Palpozenillia palpalis*
3426 (Aldrich), was found to attack *T. licus* in *Heliconia* spp. in north-west Guyana, but a rearing
3427 technique was not developed and so releases were inadequate to establish this parasitoid in
3428 sugarcane fields.

3429 In the case of *Diatraea* spp., however, there was more success. In the 1930s, entomologist
3430 J.G. Myers found populations of *Diatraea* infesting the floating grasses along the edge of the
3431 Amazon near Santarem, and these were attacked by another tachinid fly, *Metagonistylum*
3432 *minense* Townsend. Overcoming significant logistic difficulties, Myers brought the “Amazon
3433 fly” to Guyana, cultured and released it, leading to effective biological control in Guyana of
3434 *Diatraea saccharalis* (Fabricius), the main stem borer of sugarcane at that time.

3435 *A priori*, one might expect that sugarcane pests and potentially effective natural enemies
3436 would originate from a thick-stemmed grass in a natural habitat, but that this habitat would be
3437 floating grasses is unexpected. That pests would switch from other monocotyledon families
3438 as in the case of *T. licus* is less expected. The conclusion that the natural habitat of a pest and
3439 its natural enemies is difficult to predict is clear, so in principle all habitats should be
3440 preserved in order to preserve genetic resources potentially directly valuable to agriculture.

3441 Prepared by Matthew J.W. Cock

3442 Sources:

3443 Cock, M.J.W. and Bennett, F.D. (2011) John Golding Myers (1897–1942) an extraordinary
3444 exploratory entomologist. *CABI Reviews: Perspectives in Agriculture, Veterinary Science,*
3445 *Nutrition and Natural Resources* 6(8), 18 pp.

- 3446 González, J.M. and Cock, M.J.W. (2004) A synopsis of the Castniidae (Lepidoptera) of
3447 Trinidad and Tobago. *Zootaxa* 762, 1–19.
- 3448 Myers, J.G. (1934) The discovery and introduction of the Amazon fly. A new parasite for
3449 cane-borers (*Diatraea* spp.). *Tropical Agriculture* 11, 191–195.

3450 *Case study 18. Corridors for migratory pollinators during climate change scenario*
3451 Climate change will have impacts on all major ecological communities. As far as
3452 terrestrial biodiversity is concerned, the range of potential impacts includes, for
3453 disturbance regimes, protected areas without usable connecting migration corridors.

3454 For over a decade, biologists have been concerned about apparent declines in pollinators
3455 (vertebrates and invertebrates) and the concomitant declines in seed production of flowering
3456 plants. This concern over plant–pollinator interactions has contributed to a paradigm shift
3457 from protecting individual species to protecting interspecific relationships and landscape-
3458 level ecological processes. While an awareness of these relationships and processes is not
3459 new to conservation biology, the recent attention given to these topics is. Pollinators that
3460 migrate between regions, including several hummingbirds, butterflies and the giant
3461 honeybees of South-east Asia pose some unique problems such as the need for provisioning
3462 of food sources along the migration route.

3463 Conservation corridors typically conjure up images of continuous linear habitats or
3464 greenways that provide for the movements of large predators and other wide-ranging species.
3465 In contrast, migratory corridors for winged pollinators might be more aptly described as a
3466 mosaic of stepping stones within a larger matrix, with each stone a stopover that migrants use
3467 for “refuelling” while following a migratory route that takes advantage of a sequence of
3468 plants coming into bloom along the way.

3469 This sequence of flowering plants provides migrants with sugars, lipids and amino acids to
3470 fuel their long-distance flights. In seeking out this nectar, pollinators incidentally transfer
3471 pollen from one plant to another. By doing so, they facilitate reproduction, genetic mixing
3472 and seed set for their floral hosts. When land conversion and fragmentation, toxins, or
3473 climatic change weaken one link along the way, the entire chain may be broken. Since the
3474 energetic needs of some migratory pollinators are highest when they are migrating, any
3475 shortage of fuel en route can have devastating consequences.

3476 It is clear that the anthropogenic stresses faced by migratory pollinators during their annual
3477 migrations are substantial and increasing. These migrants are particularly vulnerable during
3478 long migrations across arid lands, especially when their stopover sites are affected by land-
3479 use changes. In arid and dry subtropical landscapes, farmlands found between protected areas
3480 can serve either as oasis-like stopovers for these migrants or as barren, chemical-ridden sites
3481 that further stress pollinators during the most energy-intensive phase of their annual cycle.

3482 While migratory pollinators ensure landscape-level linkages among many different plant
3483 populations, many non-migratory pollinators visit these same flowers and secondarily benefit
3484 from genetic mixing stimulated by the migrants.

3485 The best way to ensure adequate connectivity in regional reserve networks is to better
3486 manage intervening private lands in a manner consistent with the needs of migratory wildlife.
3487 However, in their current state, many private lands are the weak links in the migratory chain.
3488 Restoring the ecological connectivity of these lands will require stronger stewardship
3489 collaborations among public agencies and private landowners.

3490 Prepared by Suresh K. Raina

- 3491 Sources:
3492 Arizona-Sonora Desert Museum (2011) Migratory Pollinators Program.
3493 www.desertmuseum.org/pollination/introduction.php (last accessed 9 March 2011)
3494 Collette, A. (ed.) (2007) Climate Change and World Heritage. UNESCO World Heritage
3495 Centre, Paris, 51 pp.
3496 Nabhan, G.P. (2001) Nectar trails of migratory pollinators restoring corridors on private
3497 lands. *Conservation in Practice* 2, 20–26.

3498 *Case study 19. Forest habitat conservation in Africa using stingless bees.*

3499 In social insects, foraging activity and hence pollination, are influenced by climatic
3500 conditions. In light of climate change, such as global warming, it has become increasingly
3501 important to obtain baseline data on the relationship between climate and the foraging action
3502 of keystone species such as stingless bees, one of the most important pollinators in the
3503 African forest ecosystem. The influence of weather on the flight activity of Meliponini bees
3504 has been studied, and seasonal variations have been found in flight activity, as well as
3505 correlations between flight activity and weather variables, especially temperature and
3506 luminosity.

3507 Honeybees coexist in forest and other ecosystems with many competitors, among them the
3508 highly social stingless bees of the genera *Melipona* and *Trigona* (Apidae: Meliponini).
3509 Stingless bees originated in Africa and have spread to all tropical and subtropical parts of the
3510 world. About 500 species of stingless bees exist worldwide, and they are the only highly
3511 social bees besides the honeybees (*Apis*; Apidae: Apinae). These stingless bees are among the
3512 principal pollinators of forestry, agricultural, and horticultural plant species, ensuring their
3513 survival and contributing to food security for innumerable rural households. Currently in
3514 Africa, keeping stingless bees (meliponiculture) is practised on a small to medium scale only
3515 in Kenya, Tanzania, Uganda and Angola, for example in semi-arid hilltop forest areas found
3516 in Mwingi in Kenya, and fragile forest ecosystems like Kakamega forest, the only remnant in
3517 Kenya of the unique Guineo–Congolian forest ecosystem.

3518 Reporting on a project on commercial insects and forest conservation in Kenya, Raina *et al.*
3519 (2009) found several species of stingless bees in the Kakamega forests of western Kenya,
3520 including *Hypotrigona* and *Meliponula* species (Apidae: Meliponini). These stingless bees
3521 depend on tree cavities for nesting and, and with deforestation, many nests are being
3522 destroyed. Traditionally, the honey is mostly obtained by harvesting from feral colonies, an
3523 activity which destroys the colonies. With the project intervention, colonies are being
3524 domesticated in hives and farmers trained in colony division. To date, 200 stingless beehives
3525 have been colonized and the population of stingless bees has increased in the forest. The
3526 study indicated there was an increase in the number of colonies in the forest, which is
3527 beneficial to the rejuvenation of the forest tree species and pollination of certain food crops.
3528 Farmers have realized that stingless bees are important for pollination in addition to honey
3529 production. The number of colonies domesticated is increasing as the farmers practise colony
3530 division.

3531 Prepared by Suresh K. Raina

3532 Sources:

3533 Hilario, S. D.: Imperatriz-Fonseca, V. L.: Kleinert, A. D. M. P. 2000. Flight activity and
3534 colony strength in the stingless bee *Melipona bicolor bicolor* (Apidae: Meliponinae).
3535 *Revista Brasileiro de Biologia* 60, 299–306.

3536 Michener C. D. (2000) *The Bees of the World*. Johns Hopkins University Press, Baltimore
3537 and London, UK. 913 pp.

3538 Raina, S.K., Kioko, E.N., Gordon, I. and Nyandiga, C. (compilers) (2009) *Improving Forest
3539 Conservation and Community Livelihoods through Income Generation from Commercial
3540 Insects in Three Kenyan Forests*. icipe Science Press, Nairobi, Kenya, 87 pp.

3541 Raina, S.K., Kioko, E., Zethner, O. and Wren, S. (2011) Forest habitat conservation in Africa
3542 using commercially important insects. *Annual Review of Entomology* 56, 465–485.

- 3543 Roubik D. W. (1989) *Ecology and Natural History of Tropical Bees*. Cambridge University
3544 Press, Cambridge. 514 pp.
3545 Whittaker, J. B. (2001) Insects and plants in a changing atmosphere. *Journal of Ecology* 89,
3546 507–518.

3547 Case study 20. The million dollar oil palm pollinator weevil

3548 Up until the 1980s it was assumed that oil palms are wind pollinated. However, pollination
3549 has never been a problem in West Africa, the original home of the commercial oil palm
3550 (*Elaeis guineensis*; Arecaceae) whereas in Malaysia, especially Sabah, assisted pollination
3551 was necessary and even then yields were lower than those in Africa.

3552 In 1977 the Unilever Plantations Group started a research programme with the
3553 Commonwealth Institute of Biological Control. Dr R.A. Syed investigated the possibility that
3554 pollinating agents are involved in Cameroon. He found that both male and female flowers are
3555 attended by a complex of weevils (Curculionidae) of the subfamily, Derelominae, a group
3556 that is associated with palm flowers. The beetles breed in the flowers of both sexes, and had
3557 been reported to cause damage.

3558 Careful observations showed that weevils breeding in male flowers are all species now placed
3559 in the genus *Elaeidobius*, while those breeding in female flowers are *Prosoestus* spp.
3560 *Elaeidobius* spp. are attracted to male flowers only during anthesis when a strong aniseed-like
3561 scent is emitted. When the stigmas are receptive, the female flower emits short pulses of a
3562 similar but sharper and more penetrating odour that attracts *Elaeidobius* spp. away from the
3563 male flowers. On arrival in the female inflorescence, the beetles find no food and soon leave.
3564 Oviposition takes place after anthesis so that the larvae develop on tissue, which has served
3565 its purpose and no longer has any function for the palm and therefore *Elaeidobius* spp. cause
3566 no significant damage. Syed went on to demonstrate that during the wet season, very little
3567 pollen is carried in the air and that if insects are excluded, pollination does not take place.
3568 Examination of *Elaeidobius* spp. showed that they become covered in pollen, which is shed
3569 when they clamber about the female inflorescence. In all, there are six species of *Elaeidobius*
3570 in Cameroun. Each species is dominant in a different zone of each male flower spike, and
3571 each has slightly different climatic requirements so that the relative abundance of the species
3572 changes from the wet coastal zone to the drier interior. Thus, the six species are able to
3573 coexist on the same resource.

3574 *Elaeidobius kamerunicus* was selected for Malaysian conditions and subjected to intensive
3575 screening tests using the protocols that had been developed for organisms to be used in
3576 biological weed control. The weevil was not attracted to or able to survive for long on the
3577 flowers of other palms, except to a limited extent on the South American oil palm (*Elaeis
3578 oleijera*). For importation into Malaysia, *Elaeidobius kamerunicus* was bred in captivity on
3579 sterilized oil palm flowers, and carried in the pupal stage to Kuala Lumpur in individual glass
3580 tubes. En route, the contents were examined in the United Kingdom and repacked to ensure
3581 that no contaminants were inadvertently introduced along with the pollinator. These
3582 precautions were necessary to eliminate oil palm pathogens and natural enemies of *E.
3583 kamerunicus*, which is infested with mites and nematode larvae in Africa. Two releases were
3584 made in February 1981, and within a year the weevil had spread throughout Peninsular
3585 Malaysia and was extremely abundant in all plantations. The weevils were taken to Sabah in
3586 March 1981, with even more impressive results. In the early 1980s they were also taken to
3587 Papua New Guinea, the Solomon Islands, Sumatra and Thailand, leading to successful
3588 establishment and enhanced yields. The introduction of *E. kamerunicus* into new isolated
3589 plantings of oil palm has become standard practice.

3590 Oil palm fruit set in Malaysia now regularly reaches the levels found in Cameroon, hand
3591 pollination has been discontinued, and yields raised by about 20%. Calculations indicated

3592 that, with the money saved on hand pollination, the introduction of the pollinator was worth
3593 some US\$115 million per year to the planters. This is the only example of a pollinator other
3594 than bees that has been deliberately introduced widely. The protocols to assess the risk of its
3595 introduction based on those used for the classical biological control of weeds proved
3596 satisfactory.

3597 Prepared by Matthew J.W. Cock

3598 Source:

3599 Greathead, D.J. (1983) The multi-million dollar weevil that pollinates oil palms. *Antenna*,
3600 *Bulletin of the Royal Entomological Society of London* 7, 105–107.