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Biological control agents in the Anthropocene: current risks and future options

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Global climate change is often expected to disrupt biological control. Predicting the effects of climate change on biological control, and identifying natural enemies that will thrive in future climate scenarios, is thus essential to ensure agricultural sustainability. To promote biological control under climate change, land managers should prioritise the conservation of natural enemy diversity to ensure some effective natural enemies are always present despite often-unpredictable climate scenarios. In addition, ecophysiological and habitat domain models should be combined to predict climate change-induced shifts in predation by diverse predator communities. Finally, insights from land managers during extreme weather events, such as droughts and heat waves, may be invaluable in the effort to identify key biological control agents for future scenarios.

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Introduction

Agricultural pest control is a major challenge for ensuring global food security [1,2•]. Biological control is one pest management tactic that reduces yield loss [3•] and pesticide use while promoting agricultural sustainability and human health [4•]. Small-scale farms in developing countries are particularly reliant on biological control due to limited access to alternative tactics. However, climate models predict a higher frequency of extreme weather conditions, which may disrupt the effectiveness of the biological control agents currently providing the greatest impact on pest abundance [5,6•,7].

Given the predicted increases in pest outbreaks, and the potential breakdown of current biological control agents under global climate change [7,8], novel approaches are needed to improve biological control. One option to mitigate increases in future pest damage is to use augmentative releases of natural enemies to maintain high densities of biological control agents even in suboptimal conditions [9]. However, this will often be expensive or logistically infeasible [10]. Land managers may therefore need to proactively identify biological control agents better adapted to the novel environmental conditions to optimise control for pests under future climate scenarios. There are generally trade-offs whereby species performing well in one set of environmental conditions perform poorer in another [11], and thus we would expect that biological control agents suited for future climate scenarios differ from those relied upon today. As environmental niches likely vary from species to species within a given predator community, the key may be to identify and conserve populations of predators with environmental niches best suited for future climatic scenarios. For example, as droughts are often expected to increase in future climate scenarios [12], it may be important to identify drought-resistant soil-borne insect pathogens. However, systematically testing environmental responses by a suite of available biological control agents is likely to be expensive and time consuming. Here, we identify four anticipated difficulties associated with maintaining effective biological control in a changing environment. In turn, for each anticipated difficulty we present potential mitigation strategies to ensure a viable future of biological control.

Problem 1: Pest distribution shifts

As the global climate changes, environmental conditions formerly unsuitable for pest establishment may become suitable, leading to pest range shifts [1] and increased frequency of invasions [13•]. For example, the melon pest and virus vector, *Thrips palmi*, is predicted to expand its range in the United Kingdom and Korea due to global climate change as more areas of these countries become inhabitable [14,15]. Such range expansions may inhibit biological control if pests expand more rapidly than their natural enemies [16], and if new natural enemies are unable to attack the pest in the expanded range [17,18]. The ability of biological control agents to expand their ranges naturally may be limited. For example, after recording the continuous range expansions of eight invasive herbivorous gall wasps in Britain, Schonrogge *et al.* [19] found that none of the pest's native enemies from continental Europe had also expanded their range. Although there is potential for native enemies to follow pest range expansion or for native predators to adapt to the new food resource, it is likely that pest distribution shifts will result in more occurrences of pest outbreaks under the current conditions of biological control [13•].

Mitigation strategy 1: Controlling pests with generalist predators

The introduction of biological control agents specialising on an invasive pest (i.e., classical biological control) is an obvious option for controlling invasive pests. However, given the expected increases in invasion rates with climate change [20], it may be difficult to identify, test, and import classical biological control agents fast enough to keep up with invasion pressure. Instead, it is predicted that invasion of novel hosts will pressure local natural enemies to reassemble and adapt to feeding upon the invasive pests [19]. Therefore, we should investigate the potential of biological control agents already present in the novel environment to prey upon pests in newly expanded ranges, as these predators will already exhibit adaptations for the surrounding climate (Figure 1a). When conducting surveys for potential biological control agents of invasive pests, we should direct our attentions to natural enemies that generalise in both prey preferences and environmental conditions. Even when introducing new species, it may be advantageous to release species more generalised in their host range and environmental preferences. For example, in an effort to control the invasive *Drosophila suzukii*, Daane *et al.* [21•] determined several potential biocontrol agents, and out of their suggested agents, *Asobara japonica*, a generalist parasitoid wasp appears to be the most promising due to its high parasitism rates and large geographic range. This large distribution may be attributed to its generalist nature and make it useful as a future biocontrol agent throughout the United States and Europe [21•]. When determining which potential agents to assess, focusing on generalists like this wasp may speed along the discovery of agents well suited to the novel environments of their host or prey.

Problem 2: Conditions become unsuitable for primary biological control agents

Global climate change is often expected to lead to new pest outbreaks as changing environmental conditions allow insect pests to move from endemic to epidemic densities, either through increased pest growth rates or decreased predation rates [5]. Higher temperatures, for example, often promote pest outbreaks [5] that occur earlier in crop growing seasons [22•]. Furthermore, the relationship between predation rates and temperature is generally unimodal, with an optimal temperature that maximises attack rates [23] (Figure 1b). Increasing temperatures beyond this optimum will decrease predation rates [24,25•]. Similarly, increases in the severity and abundance of droughts may reduce control by soil-borne insect pathogens, particularly if the pathogens lose their effectiveness in drier soil [26,27].

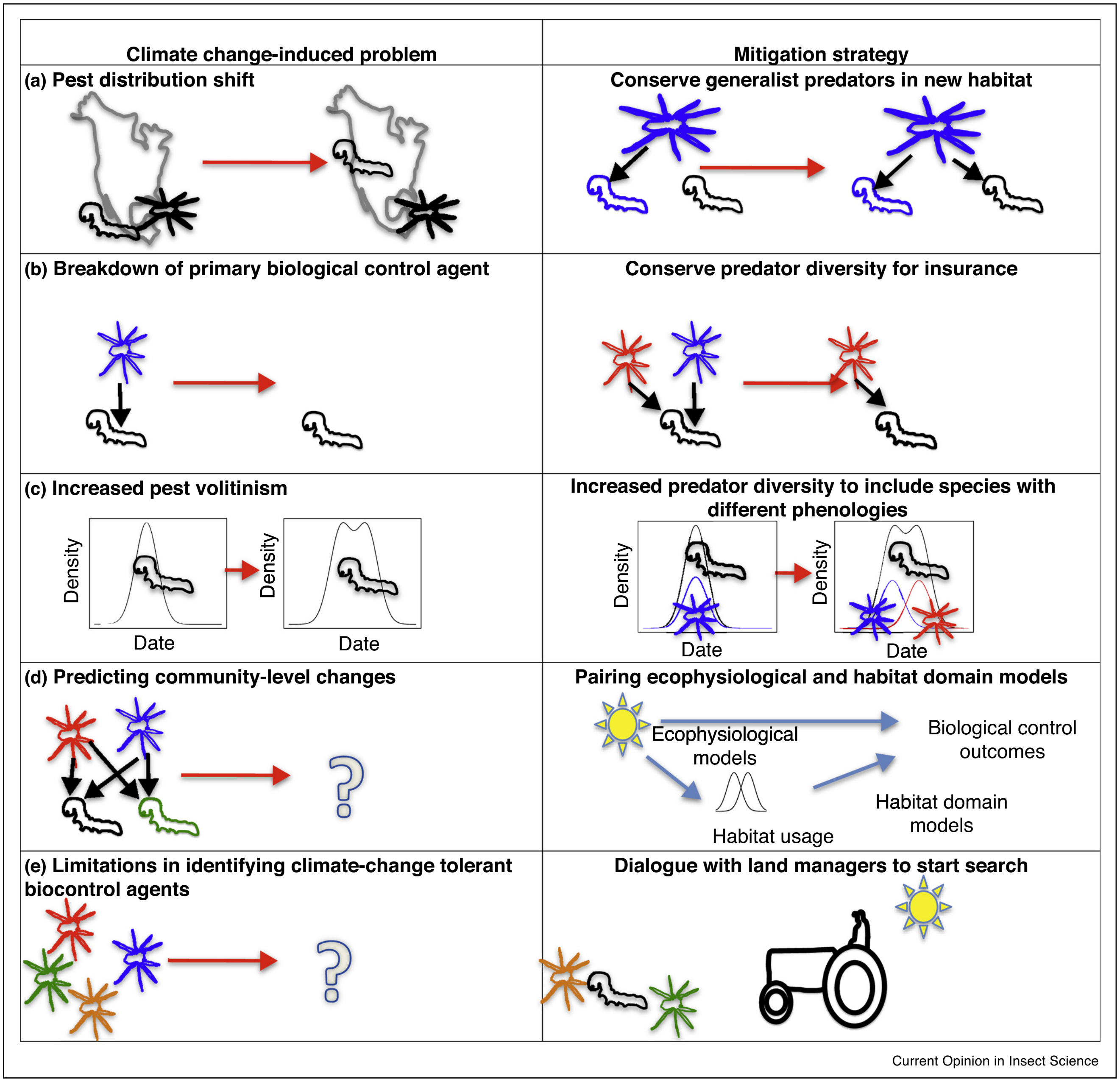
Global climate change may also affect insect phenology as insects adapt to changing environments [28]. Temperature is a key component to determining generational time of insects [29], and generations per year [28]. For example, since 1980 in Central Europe, 44 different moth species have been observed to have an extra generation per year due to warming climates [28]. This might contribute to pest outbreaks by increasing pest abundance, creating longer windows of pest damage, and if predator phenology does not change accordingly, this could disrupt synchrony with natural enemies [7,17,28] (Figure 1c).

Mitigation strategy 2: Conservation of natural predator diversity

One obvious strategy to combat climate change-induced breakdown in biological control is to focus on conserving genetic diversity, such that predator populations are able to adapt to new environments [30•]. The potential for this evolutionary change is apparent in the differences in environmental suitability in predator populations inhabiting different geographical regions. For example, Barton [31] found that while increased temperatures can disrupt top-down control of grasshoppers by spider communities from higher latitudes, the temperature effect was reduced when spiders were collected from latitudes where increased temperatures commonly occur, suggesting they had adapted to the conditions. Thus, if given enough time, genetic diversity, and gene flow, natural enemies may adapt to changing environments alongside their pestiferous prey.

When predator populations cannot adapt to climate change fast enough, we may observe local extinctions of biological control agents, and loss of pest regulation [7]. However, biological control agents generally vary in their responses to climatic changes [24,32•], suggesting that diverse communities of biological control agents may include some species that are able to persist in future climate scenarios. For example, in a field experiment, heat shocks led to dramatic declines in aphid densities, which was followed by a decline in *Harmonia axyridis* ladybeetle predators [24]. However, another ladybeetle (*Coccinella septempunctata*) was slower to respond to the heat shocks, presumably because it was better adapted to higher temperatures. When the aphid pests evolved resistance to the heat shocks, *C. septempunctata* was able to control the pest population. Conservation of natural predator diversity in agricultural systems can act as a reservoir for future biological control agents (Figure 1b), and species diversity can act as a buffer to lessen the impacts

Figure 1



Problems with biological control arising from climate change (left column), and associated strategies to mitigate these problems (right column). **(a)** Pest geographical distributions are often expected to shift towards the poles through range shifts and exotic introductions, often without their associated natural enemies. However, conserving generalist predators in the newly inhabited environment may reduce the impact of the pests in the new environment. **(b)** Climate change may lead to environmental conditions unsuitable for control by primary biological control agents, leading to pest outbreaks. Thus, it may be important to promote biological control agent diversity to increase the chance of one or more beneficial species persisting. **(c)** Climate change is often predicted to allow longer pest growing seasons, increasing the number of generations per year, and potentially allowing pests to persist during seasonal periods not suitable to the primary biological control agent. Thus, conserving predator diversity, including predators with different phenologies can help provide biological control throughout the year. **(d)** Ecophysiological models can be used to predict climate-associated changes in metabolic rates and microhabitat use, and habitat domain models can be used to relate those to interspecific interactions within a community of biological control agents and pests. **(e)** Experiments to systematically identify effective biological control agents suitable for future climatic scenarios may be logistically infeasible. Therefore, it is important to maintain dialogue with land managers to identify natural enemy species that are abundant during extreme climatic events such as droughts and heat waves.

of environmental fluctuations in agroecosystems [33]. Thus, in the absence of in depth knowledge of each species' response to environmental change, one can encourage general diversity of predator species. Increasing predator diversity can increase predation simply by increasing the chance of conserving the best predator [34•,35]. Because natural enemies often differ in their phenology, increasing the natural enemy diversity can lead to longer temporal windows of pest suppression. This may reduce problems associated with disruption of pest-biological control synchrony, brought on by climatic changes inducing longer growing windows for pests (Figure 1c).

Problem 3: Biological control breakdown depends on complex species interactions

Changing environments can indirectly alter biological control by altering interactions within natural enemy communities [32•,36]. For example, Barton and Schmitz [36] found that increased temperatures increased niche overlap between two spider species, increasing intraguild predation and weakening biological control of their grasshopper prey. Similarly, in mild conditions, two predacious mites (*Euseius stipulatus* and *E. scutalis*) attacking persea mites (*Oligonychus perseae*) coexist on Mediterranean avocado farms [32•]. However, *E. scutalis* competitively excludes *E. stipulatus* under hotter and drier conditions [32•], potentially weakening biological control. Environmentally mediated changes in prey communities can also alter biological control. For example, Barton and Ives [37] showed that drought conditions reduced densities of pea aphids (*Acyrthosiphon pisum*), which reduced predator recruitment and released spotted alfalfa aphids (*Therioaphis maculata*) from predation. However, it is not logistically possible to experimentally recreate each type of environmental change for all affected species to predict biological control effectiveness in future scenarios. Thus, what is needed is a mechanistic understanding of how environmental conditions alter community interactions [38].

Mitigation strategy 3: Pairing ecophysiological models with habitat domain concepts

Mechanistic ecophysiological models can help predict climate-induced changes in growth and predation rates associated with differences in metabolism [39], and changes in habitat use associated with changes in microclimatic conditions [40]. This approach uses models describing environmental conditions within microclimates inhabited by a particular species, and describing processes such as to thermodynamics to predict metabolic rates, and growth parameters in those microclimates [40]. This physiological approach can be effective for predicting the direct effects of climate change on individual species [41], but has limitations for predicting more complex community interactions. However, empirical synthesis suggests that habitat domain concepts have been highly effective at predicting community interactions [35,42], and may be complementary to ecophysiological models. In this approach, the spatial patterns of habitat use are used to predict species interactions within the community and ultimately predation rates by the entire predator guild. Northfield *et al.* [43•] used trait-based Lotka–Volterra predation models to evaluate the effects of habitat use by predators and prey on multiple predator effects on prey consumption, based on habitat domain concepts. These models provide a basis for using basic biological characteristics such as maximum growth and/or predation rates and spatial habitat use for each species to develop quantitative estimates of biological control by the diverse community. Ecophysiological and microhabitat models could be embedded into this framework to create testable hypotheses for how climate change will alter natural pest control by diverse communities of biological control agents.

Problem 4: Knowledge limitations

Climate change is expected to alter environmental conditions in many ways (e.g., changes in temperature, rainfall, and CO_2) simultaneously, with potentially non-additive effects on biological control agents and their prey [44]. This non-additive nature of environmental changes, coupled with the already difficult task of experimentally evaluating each environmental change on each predator can make it arduous to identify potential biological control agents for future climate scenarios [45•]. Thus, what is needed is constant observation of pests and their natural enemies across typical and extreme environmental conditions. However, researchers are generally limited in time availability, making it difficult to observe such fluctuations in community change without help from outside the scientific community.

Mitigation strategy 4: Insights from land managers

Land manager expertise can be used to prioritise research needs and fill gaps in current scientific understanding [46]. Identifying a fleet of biological control agents for future climate scenarios may rely upon the aid of land managers that observe which natural enemies are currently present in crop systems and to identify species that should be studied for these predictive success traits. Insights about biological control can then be used in collaboration with growers to put these findings into practice [46,47•,48]. Collaborations between land managers and scientists also create networks that support conservation practices, a reinforcement that has previously been documented as crucial for sustainable agriculture [49].

Conclusion

Climate change may often increase pest outbreaks through direct effects on pest metabolism and range shifts, and through indirect effects mediated by a weakening of biological control. However, by focusing on the currently most effective biological control agents, we may be looking in the wrong place. A combined approach of conserving generalist predators as a front line of defence against invasive species, encouraging diversity of natural predators, pairing ecophysiological with spatially-explicit predator-prey models, and working with local land managers to identify biological control agents suitable for future climate scenarios may provide the path forward to sustainable pest management in the Anthropocene.

Conflicts of interest

The others declare no conflicts of interest

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