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Abhishek Bansal
M.Sc. Entomology, Sardar
Vallabhbhai Patel University of
Agriculture and Technology,
Modipuram, Meerut, Uttar
Pradesh

Dr. Anuj Bansal
SMS, Plant Protection, KVK
Rampur, Sardar Vallabhbhai Patel
University of Agriculture and
Technology, Meerut, Uttar
Pradesh, India

Corresponding Author:
Dr. Anuj Bansal
SMS, Plant Protection, KVK
Rampur, Sardar Vallabhbhai Patel
University of Agriculture and
Technology, Meerut, Uttar
Pradesh, India

A review on conservation biological control under climate change and the limits of habitat-based resilience

Abhishek Bansal and Anuj Bansal

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Abstract

Conservation biological control rests on the premise that resident natural enemy communities can be sustained and strengthened through deliberate manipulation of farmland habitat, thereby reducing dependence on synthetic inputs. Rising temperatures, altered precipitation regimes and elevated atmospheric carbon dioxide are now reshaping the physiological, phenological and behavioural foundations on which this premise depends. Predator and parasitoid guilds differ markedly in thermal tolerance, voltinism and dispersal capacity, and these differences are beginning to translate into asymmetric responses across trophic levels that habitat management alone may not fully offset. Evidence from temperate and tropical agroecosystems shows that landscape complexity can buffer some climatic perturbations, yet its stabilising effect appears contingent on the identity of the pest-enemy pair, the intensity of the climatic anomaly and the spatial grain at which habitat resources are distributed. Divergent findings across studies point to unresolved questions about whether warming primarily disrupts synchrony, physiological performance or the availability of alternative resources such as floral nectar and overwintering refugia. This synthesis draws together physiological, phenological and landscape-scale evidence to identify where conservation biological control is likely to remain robust under climatic change and where its foundational assumptions require revision. Particular attention is given to methodological inconsistencies that limit cross-study comparison and to the design features that future field experiments would need to incorporate for more reliable, climate-adjusted pest management guidance.

Keywords: Natural enemies, climate warming, habitat management, trophic asynchrony, landscape complexity, parasitoid-host interactions

Introduction

Conservation biological control occupies a distinctive position among pest management strategies because it does not introduce new organisms into an agroecosystem but instead seeks to retain, augment and redirect the natural enemies already present within it (Landis, Wratten and Gurr, 2000) ^[13]. Its conceptual foundation rests on decades of evidence that predators and parasitoids respond positively to increased floral resources, structurally diverse field margins and reduced disturbance, and that these responses translate, at least under favourable conditions, into measurable suppression of herbivore populations (Gurr, Wratten, Landis and You, 2017) ^[10]. The approach has attracted sustained interest precisely because it promises pest regulation without the recurring costs and resistance risks associated with insecticide-based control, and because it aligns with broader agroecological goals of reducing external inputs while maintaining farmland biodiversity (Bianchi, Booij and Tscharntke, 2006) ^[4].

What has received comparatively less attention until the past fifteen years is the extent to which the ecological relationships underpinning conservation biological control are themselves sensitive to a changing climate. Predators and parasitoids are ectothermic, and their development, foraging activity, fecundity and survival are governed proximately by temperature in ways that differ systematically from the herbivores they attack (Hance, van Baaren, Vernon and Boivin, 2007) ^[11]. Where a pest and its natural enemy share similar thermal optima, warming may leave their interaction broadly intact; where their optima diverge, even modest temperature increases can decouple the timing of attack from the timing of vulnerability, eroding top-down control despite unchanged habitat provision (Furlong and Zalucki, 2017) ^[9]. Because most conservation biological control research has been conducted under the implicit assumption

of a stable climatic baseline, the field now faces the task of re-evaluating whether habitat-based interventions remain sufficient, or whether they must be recalibrated against a background of shifting thermal regimes, altered rainfall patterns and elevated carbon dioxide concentrations that reshape host plant chemistry. Three lines of evidence bear on this question. The first concerns the direct physiological consequences of temperature change for natural enemies relative to their hosts or prey, which determine whether trophic interaction strength is likely to strengthen, weaken or remain neutral under warming (Barton, 2011) ^[2]. The second concerns phenological synchrony, since even physiologically tolerant natural enemies can fail to suppress pests if seasonal timing shifts asymmetrically across trophic levels (Stireman *et al.*, 2005) ^[17]. The third concerns whether landscape-scale habitat complexity, long promoted as the principal lever of conservation biological control, can compensate for climatic disruption or whether its stabilising influence itself depends on climatic stability (Chaplin-Kramer, O'Rourke, Blitzer and Kremen, 2011) ^[5]. These three strands are examined in turn below, followed by a critical assessment of where the evidence base remains thin and where methodological inconsistency across studies limits confident generalisation.

The stakes attached to this re-evaluation extend beyond academic interest. Conservation biological control is promoted in national and regional agricultural policy, in certification schemes for sustainably produced commodities and in extension advice delivered to farmers as a lower-cost, lower-risk alternative to calendar-based insecticide application (Bianchi, Booij and Tscharntke, 2006) ^[4]. Advice built on pre-climate-change evidence risks overstating the reliability of habitat-based pest suppression precisely in the regions and cropping systems where farmers can least afford a control failure, a concern that sharpens rather than diminishes the need for a critical, rather than promotional, synthesis of the available evidence.

Climate Driven Asynchrony Between Natural Enemies and Pest Phenology

Synchrony between a natural enemy and its host or prey is not a fixed property of the relationship but an emergent outcome of two independently responding developmental clocks. Insect phenology is driven overwhelmingly by accumulated thermal units, and because different species convert degree-days into developmental milestones at different rates, warming rarely advances the phenology of interacting species by equal amounts (Altermatt, 2010) ^[1]. Stireman *et al.*, (2005) ^[17] demonstrated across a broad sample of caterpillar-parasitoid associations in North America that unusually warm years were associated with reduced parasitism rates, and argued that climatic variability itself, rather than mean warming alone, was eroding the reliability of parasitoid attack. This finding is important because it reframes the climate change problem confronting conservation biological control away from a simple shift in means and toward an increase in the variance of climatic conditions that natural enemies must track.

Subsequent work has offered a more nuanced picture. Jeffs and Lewis (2013) ^[12], reviewing experimental manipulations of temperature in host-parasitoid systems, found that warming effects on synchrony were highly taxon-specific and often contingent on whether the parasitoid overwinters in a more or less cold-hardy life stage than its host. Where parasitoids diapause in a stage with narrower thermal tolerance than the host insect, warming tends to advance host emergence disproportionately, producing a phenological gap during which the vulnerable host stage passes before the parasitoid becomes

active. Where the reverse is true, some parasitoid populations have been shown to track host phenology closely even under considerable warming, preserving control efficacy. This taxon dependence complicates any attempt to generalise about whether climate change will systematically favour pests over their natural enemies, and it argues against treating conservation biological control recommendations as climate-neutral prescriptions applicable across all pest-enemy pairs.

Voltinism adds a further layer of complexity that is often collapsed too quickly into a single narrative of more generations producing more pest pressure. Altermatt (2010) ^[1] documented that a majority of European butterfly and moth species examined had already increased their number of annual generations in response to recent warming, and comparable shifts have been inferred for several agricultural pest lepidopterans. An additional generation benefits a pest only if its natural enemies fail to track the same shift; several parasitoid guilds, particularly generalist and polyphagous species with broader host ranges, appear capable of exploiting additional host generations rather than falling behind them (Furlong and Zalucki, 2017) ^[9]. The asymmetry, where it exists, tends to be concentrated in specialist parasitoids with narrow phenological windows, precisely the guild that classical and augmentative biological control has historically relied upon most heavily and that conservation biological control seeks to support through resource provisioning. Habitat management measures such as flowering strips extend adult parasitoid longevity and fecundity, but they do not, by themselves, correct a mismatch that originates in diapause termination cues rather than in adult resource availability, a distinction not always made explicit in the applied literature.

The practical consequence of this taxon-dependent asymmetry is that blanket statements about climate change either favouring or disfavoring biological control obscure more than they reveal. A pest-enemy pair in which both partners share a similar thermal development threshold may show negligible change in synchrony under a two or three degree warming scenario, while a superficially similar pair with divergent thresholds may show pronounced decoupling under the same scenario. Very few conservation biological control programmes currently incorporate thermal threshold data for both the target pest and its principal natural enemies into their design, despite such data being obtainable through standard degree-day rearing studies, and this omission represents one of the more tractable gaps that applied entomology could close in the near term without requiring new theoretical development.

Thermal Physiology and Trophic Interaction Strength Under Warming

Beyond timing, the intrinsic performance of natural enemies under elevated temperature determines whether an encounter between predator and prey, once it occurs, still results in effective suppression. Predators and parasitoids generally show optimal performance curves that are narrower and more skewed than those of their generalist herbivorous hosts, a pattern attributed to their position at a higher trophic level and, in the case of parasitoids, their comparatively smaller body size (Furlong and Zalucki, 2017) ^[9]. Romo and Tylianakis (2013) ^[16] manipulated temperature and moisture in a factorial design and found that elevated temperature combined with drought reduced parasitism rates substantially more than either stressor applied alone, indicating that single-factor warming experiments, still the norm in the literature, likely underestimate the combined effect of realistic multi-stressor climate scenarios on biological

control.

Barton (2011) ^[2] offered evidence running counter to a purely pessimistic reading of thermal sensitivity. Working with a grassland food web involving grasshoppers and their spider predators, Barton found that predator populations from warmer sites had locally adapted thermal tolerances that preserved top-down control even as regional temperatures rose, suggesting that standing genetic variation within natural enemy populations may buffer some of the physiological mismatch documented in shorter-term laboratory studies. This result has since been cited as a caution against extrapolating single-population physiological data to predict landscape-level or regional outcomes, since populations with a longer history of exposure to warmer conditions may already carry adaptive capacity that populations sampled from cooler regions lack.

A further complication concerns the indirect, plant-mediated pathway through which elevated carbon dioxide and temperature influence natural enemy performance. Herbivores feeding on plants grown under elevated carbon dioxide frequently show altered developmental rates and nutritional quality, and these changes propagate upward to affect the parasitoids and predators that attack them (Coviella and Trumble, 1999; Bezemer and Jones, 1998) ^[7, 3]. Zvereva and Kozlov (2006) ^[19], in a meta-analysis combining elevated carbon dioxide and temperature treatments, found that the two factors interacted rather than acting additively, and that herbivore performance responses under combined treatments were frequently opposite in sign to those predicted from single-factor experiments. Because most conservation biological control research addresses habitat manipulation at the third trophic level without reference to bottom-up chemical change at the first, the interactive effects documented by Zvereva and Kozlov remain almost entirely unincorporated into applied recommendations, a conceptual gap rather than merely a data gap.

The practical implication of locally adapted thermal tolerance, as reported by Barton (2011) ^[2], is that natural enemy populations cannot be treated as thermally interchangeable across a species range when predicting climate change impacts on biological control. A predator population sourced from, or historically exposed to, a warmer regional climate may retain functional predation rates at temperatures that would substantially depress a cooler-adapted population of the same nominal species. This carries direct relevance for augmentative release programmes that source natural enemies from commercial suppliers without regard to the climatic provenance of the reared stock, and it suggests that conservation biological control strategies relying on resident, locally adapted populations may in some circumstances retain an advantage over augmentation with non-local stock, an advantage rarely framed explicitly in comparative terms within the applied literature.

Landscape Complexity and Habitat Management as Buffers Against Climatic Instability

Landscape complexity has long been treated as the principal lever available to conservation biological control practitioners, on the reasoning that a heterogeneous matrix of semi-natural habitat supplies natural enemies with the floral resources, alternative prey and overwintering sites that intensively managed monocultures withhold (Bianchi, Booij and Tscharntke, 2006) ^[4]. Chaplin-Kramer, O'Rourke, Blitzer and

Kremen (2011) ^[5], synthesising data across dozens of landscapes in a formal meta-analysis, confirmed that natural enemy abundance generally increased with landscape complexity while pest abundance showed a weaker and more variable response, a discrepancy that has fuelled debate about whether habitat provisioning reliably translates into pest suppression or merely into higher predator counts that fail to constrain herbivore populations proportionally.

Whether this stabilising landscape effect persists under climatic stress is a separate and less settled question. Rand and Tscharntke (2007) ^[15] had already shown, in a pre-climate-change framing, that generalist natural enemies respond differently to habitat loss than specialists, with generalists often able to persist in simplified landscapes by exploiting alternative resources. Extending this logic to climatic rather than compositional disturbance, several authors have argued that landscape complexity should confer resilience against climatic anomalies by providing natural enemies with a diversity of microhabitats across which to buffer unfavourable conditions, effectively spreading risk in space the way life-history diversification spreads risk in time (Tscharntke, Klein, Kruess, Steffan-Dewenter and Thies, 2005) ^[18]. Empirical tests of this proposition specifically under warming or drought remain scarce relative to tests of landscape effects under stable climatic baselines, and the available evidence is mixed rather than confirmatory.

Facey *et al.*, (2014) ^[8] examined woodland arthropod communities under long-term atmospheric change and found that declines were concentrated in specific trophic groups rather than distributed evenly, with parasitic groups showing disproportionate sensitivity relative to predatory groups occupying superficially similar niches. This selective vulnerability suggests that the protective value of landscape complexity may itself be trophic-group specific, favouring predators that can shift diet breadth in response to changing prey availability while offering less compensation to parasitoids whose fitness depends on a narrower set of host developmental windows. If this pattern generalises, then conservation biological control strategies built around generic habitat enhancement risk overestimating the resilience of parasitoid-dependent control while adequately protecting predator-dependent control, a distinction rarely made explicit in habitat management guidelines aimed at practitioners rather than researchers.

A further consideration concerns the mismatch in spatial scale between the grain at which habitat interventions are typically implemented and the grain at which climatic anomalies operate. Field margins and beetle banks act at the scale of tens to hundreds of metres, whereas a heatwave or an anomalously dry season affects an entire region more or less uniformly, offering natural enemies little opportunity to escape unfavourable conditions by moving between habitat patches within the intervention area itself (Tscharntke, Klein, Kruess, Steffan-Dewenter and Thies, 2005) ^[18]. Landscape complexity may therefore buffer chronic, spatially patchy stressors such as habitat fragmentation considerably more effectively than it buffers acute, spatially synchronous stressors such as a regional heatwave, a distinction with implications for how habitat management is prioritised as an adaptation strategy relative to complementary approaches such as breeding or selecting locally adapted natural enemy stock.

Table 1: Comparative thermal and climatic sensitivity of natural enemy guilds relevant to conservation biological control, synthesised across physiological and field studies

Natural enemy guild	Reported thermal	Proposed mechanism	References
Specialist koinobiont parasitoids (Hymenoptera)	Narrow thermal tolerance; disrupted synchrony under warming	Diapause timing mismatch with host emergence	Jefferies and Lewis (2013) ^[12]
Generalist idiobiont parasitoids (Hymenoptera)	Broader host range buffers phenological mismatch	Ability to exploit alternative host stages	Furlong and Zalucki (2017) ^[9]
Predatory Coccinellidae	Moderate tolerance; consumption decline above optimal range	Reduced prey capture rate at high temperature	Furlong and Zalucki (2017) ^[9]
Predatory Araneae	Local thermal adaptation in warm-origin populations	Standing genetic variation in thermal tolerance	Barton (2011) ^[2]
Predatory Heteroptera (Anthracoridae, Miridae)	Data limited; inferred moderate sensitivity	Field-realistic fluctuating regimes rarely tested	Hance <i>et al.</i> , (2007) ^[11]
Tachinid parasitoids (Diptera)	Reduced parasitism recorded in unusually warm years	Climatic variability, not mean warming alone	Stireman <i>et al.</i> , (2005) ^[17]
Aphidiine parasitoids (Hymenoptera)	Sensitive to combined CO ₂ and temperature interactions	Host nutritional quality altered under elevated CO ₂	Newman (2004) ^[14]
Coccinellid predators of aphids	Population dynamics lag host response under elevated CO ₂	Bottom-up nutritional cascade	Coviella and Trumble (1999) ^[7]
Chrysopidae (lacewings)	Limited direct climate data; intermediate sensitivity inferred	Broad diet breadth assumed to confer buffering	Bianchi <i>et al.</i> , (2006) ^[4]
Braconid parasitoids of Lepidoptera	Reduced parasitism under combined warming and drought	Multi-stressor interaction effect	Romo and Tylianakis (2013) ^[16]
Ichneumonid parasitoids	Taxon-specific synchrony outcomes	Overwintering stage thermal tolerance mismatch	Jefferies and Lewis (2013) ^[12]
Generalist Carabidae	Relatively resilient; landscape effect maintained	Broad diet and mobility across habitat patches	Rand and Tscharntke (2007) ^[15]

Conflicting Evidence and Methodological Gaps in Climate and Conservation Biological Control Research

Reconciling the physiological, phenological and landscape-scale literatures reviewed above is complicated by inconsistencies in experimental design that make direct comparison across studies difficult. A substantial proportion of the physiological evidence derives from short-duration laboratory assays exposing insects to constant temperatures, a design that captures acute thermal tolerance but poorly represents the fluctuating diurnal and seasonal temperature regimes that field populations actually experience (Hance, van Baaren, Vernon and Boivin, 2007) ^[11]. Constant-temperature assays tend to systematically overestimate upper thermal limits relative to fluctuating-temperature regimes, because brief exposure to near-lethal temperatures during a natural diurnal cycle is buffered by cooler intervening periods in a way that constant exposure protocols cannot replicate, and this discrepancy alone may explain part of the disagreement between laboratory-derived predictions of natural enemy decline and field observations of relatively stable parasitism rates in some systems.

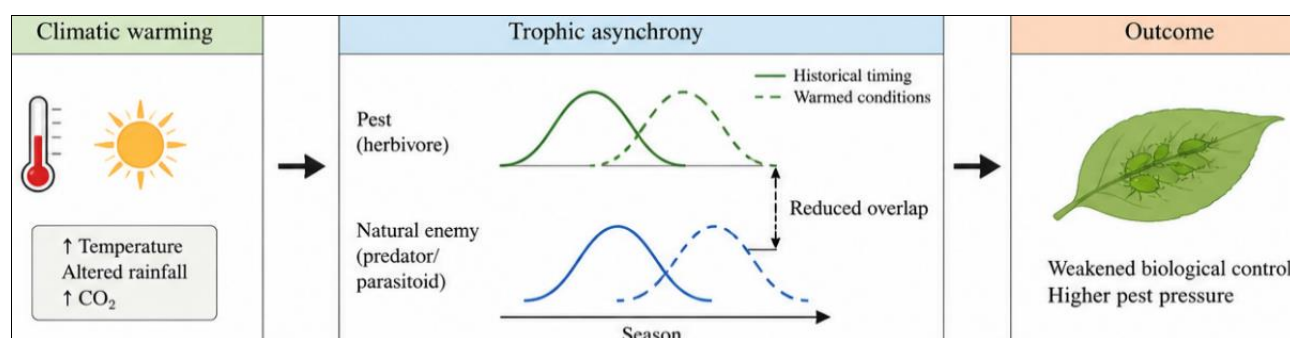
A second source of inconsistency concerns the near total separation, within the published literature, between studies of elevated carbon dioxide effects on plant-herbivore-enemy interactions and studies of temperature effects on the same food webs, despite both being simultaneous features of anthropogenic climate change. Very few experiments have manipulated temperature and carbon dioxide factorially alongside third-trophic-level responses, and where such designs exist they tend to be restricted to a narrow set of model systems, most commonly aphids and their parasitoids under controlled glasshouse conditions (Newman, 2004) ^[14]. Generalising from aphid-parasitoid systems, which are unusual in their short generation times and high fecundity, to the lepidopteran and coleopteran pest complexes that dominate field crop production in many regions introduces an additional layer of uncertainty that the literature rarely acknowledges explicitly.

A third gap concerns geographic and taxonomic bias. The overwhelming majority of climate and biological control research to date has been conducted in temperate agricultural systems in Europe, North America and Australasia, with comparatively little attention to tropical and subtropical cropping systems where natural enemy communities, pest complexes and baseline thermal regimes differ substantially (Cornelissen, 2011) ^[6]. Because tropical ectotherms are frequently reported to live closer to their upper thermal limits than temperate ectotherms, and therefore to have less thermal buffering capacity against further warming, extrapolating temperate-derived conclusions about the relative resilience of conservation biological control to tropical systems is questionable, yet it is precisely in many tropical smallholder systems that conservation biological control is promoted most actively as a low-input alternative to insecticide reliance. Closing this geographic gap, alongside adopting fluctuating-temperature and multi-factorial experimental designs, would substantially strengthen the evidence base on which climate-adjusted habitat management recommendations could be built.

A fourth, more structural gap concerns publication bias toward positive or dramatic findings. Studies reporting collapse of biological control under climatic stress are arguably more publishable, and more citable, than studies reporting no detectable change, which risks skewing the synthesised literature toward pessimistic conclusions even where the underlying body of unpublished or underreported null results might paint a more balanced picture. Meta-analytic techniques such as those applied by Chaplin-Kramer, O'Rourke, Blitzer and Kremen (2011) ^[5] partially mitigate this risk by aggregating effect sizes across studies regardless of individual statistical significance, but such techniques have been applied far more often to landscape complexity effects than to climate manipulation effects specifically, leaving the latter body of evidence more vulnerable to selective reporting than the former.

Table 2: Common conservation biological control interventions and their reported resilience to climatic stress, synthesised across the landscape and habitat management literature

Habitat management intervention	Primary mechanism	Reported outcome under climatic stress	References
Flowering field margins	Nectar and pollen provision for adult parasitoids	Extends longevity and fecundity; does not correct diapause-driven mismatch	Gurr <i>et al.</i> , (2017) ^[10]
Beetle banks	Overwintering refugia for carabid predators	Maintains abundance in mild winters; extreme-winter response untested	Landis <i>et al.</i> , (2000) ^[13]
Hedgerows and woody margins	Microclimate buffering and alternative prey	Buffers local temperature extremes; benefit concentrated in predatory guilds	Facey <i>et al.</i> , (2014) ^[8]
Reduced tillage	Conserves soil-dwelling predator populations	Indirect climate benefit via soil moisture; direct interaction untested	Bianchi <i>et al.</i> , (2006) ^[4]
Intercropping and companion planting	Increases resource and structural heterogeneity	Pest suppression response weaker and more variable than enemy abundance response	Chaplin-Kramer <i>et al.</i> , (2011) ^[5]
Cover cropping	Maintains alternative prey and hosts between seasons	Little direct climate-manipulation evidence available	Gap identified in this review
Semi-natural habitat proximity	Source-sink recolonisation of natural enemies	Generalist predators buffered; specialist parasitoids show selective decline	Facey <i>et al.</i> , (2014) ^[8]
Trap cropping	Spatial concentration of pest-enemy interaction	Climate interaction not examined in reviewed literature	Gap identified in this review
Reduced insecticide use in conservation zones	Preserves standing natural enemy populations	Indirect resilience benefit; magnitude depends on background climatic stress	Bianchi <i>et al.</i> , (2006) ^[4]
Diversified crop rotation	Maintains landscape-scale habitat turnover	Long-term resilience data scarce under climate manipulation	Gap identified in this review

**Fig 1:** Climatic warming can induce trophic asynchrony between pests and their natural enemies, reducing the effectiveness of biological control

Implications for Applied Conservation Biological Control Under a Variable Climate

Translating the physiological, phenological and landscape evidence reviewed above into applied guidance requires distinguishing between interventions that address resource limitation and interventions that address timing mismatch, since the two failure modes call for different remedies. Where suppression fails because natural enemies lack sufficient nectar, alternative prey or overwintering habitat, conventional conservation biological control measures such as flowering margins and beetle banks remain directly applicable and there is little reason from the climate literature to expect their effectiveness to diminish, provided the plant species selected for these interventions themselves remain phenologically and physiologically suited to the shifting local climate (Gurr, Wratten, Landis and You, 2017) ^[10]. Where suppression fails because a natural enemy developmental timing has decoupled from its host, habitat provisioning cannot correct the underlying mismatch, and adaptation instead requires either breeding or selecting natural enemy strains with altered diapause cueing, or supplementing resident populations through timed augmentative release calibrated to the pest climate-shifted phenology rather than to a historical calendar date.

This distinction carries particular relevance for smallholder and resource-constrained farming systems in South Asia and elsewhere, where conservation biological control is frequently promoted as the primary, and sometimes the only, pest

management strategy available within integrated pest management extension programmes. Where such programmes have been designed around temperate research findings without local validation, there is a risk that habitat management advice is applied uniformly across pest-enemy pairs with very different underlying failure modes, some of which habitat management can address and some of which it cannot. Regionally specific monitoring of natural enemy phenology relative to pest phenology, rather than reliance on generic habitat prescriptions transferred from temperate literature, would allow extension advice to differentiate cases where habitat enhancement alone is likely to remain sufficient from cases where it should be paired with complementary tactics.

A related implication concerns the choice of indicator species used to evaluate conservation biological control performance in monitoring programmes. Because generalist predators appear more resilient to climatic disruption than specialist parasitoids across much of the reviewed evidence, monitoring programmes that rely primarily on predator abundance as a proxy for overall biological control health risk masking a decline in parasitoid-mediated suppression occurring in parallel. Incorporating parasitism rate data specifically, rather than natural enemy abundance data alone, into routine monitoring would provide an earlier and more sensitive warning of climate-driven erosion in control efficacy, allowing intervention before pest outbreaks become apparent through crop damage alone.

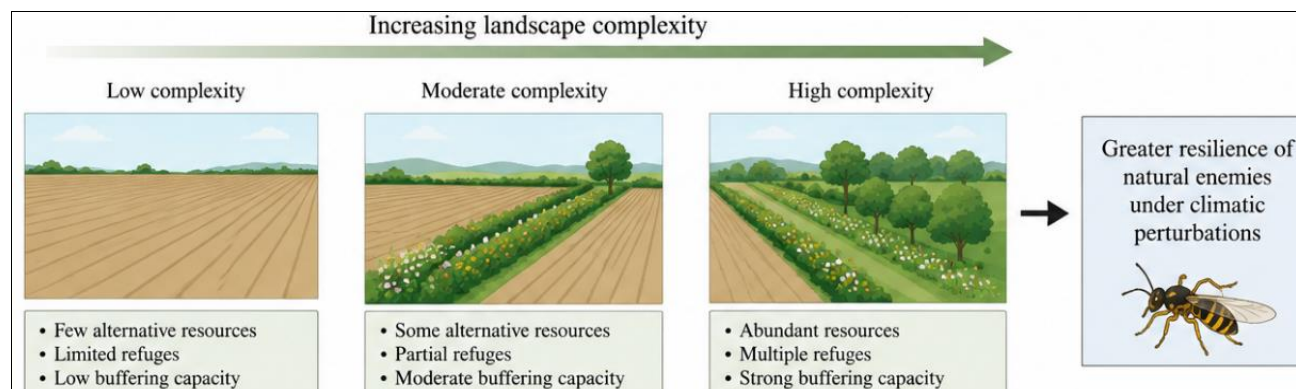


Fig 2: Landscape complexity enhances resource availability and refugia, increasing the resilience of natural enemy communities to climate perturbations

Conclusion

Conservation biological control was conceived and largely validated under an implicit assumption of climatic stability that no longer holds. The evidence assembled here does not support a uniformly pessimistic or uniformly reassuring conclusion; instead it points toward a guild-dependent and pair-specific outcome in which generalist predators with broad diet breadth and dispersal capacity retain much of their regulatory function under warming, while specialist parasitoids tied to narrow phenological windows and particular diapause cues are disproportionately exposed to climatic disruption. Habitat management interventions remain valuable, but their protective effect appears strongest where the underlying mismatch originates in resource scarcity and weakest where it originates in decoupled developmental timing, a distinction that current habitat management guidelines rarely draw. Future research would benefit from field-realistic fluctuating temperature regimes rather than constant-temperature assays, from factorial designs that combine temperature, moisture and carbon dioxide manipulation rather than isolating single stressors, and from a deliberate expansion of study systems beyond the temperate aphid-parasitoid model that currently dominates the literature. Extending empirical attention to tropical and subtropical smallholder systems, where conservation biological control is often promoted as a primary pest management strategy and where baseline thermal margins are already narrower, would close one of the more consequential gaps identified in this synthesis. Practitioners advising on habitat-based pest management should treat climatic context as a variable that modifies expected outcomes rather than as background noise, and should calibrate recommendations to the specific pest-enemy pair and guild composition of the system in question rather than applying uniform habitat prescriptions across climatically divergent regions.

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