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Climate Change Can Generate Enemy-Free Space for Crop-Feeding Herbivores

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ABSTRACT

Crop-feeding herbivores reduce the world's food output by approximately 20% and climate change (CC) is bound to deepen those losses. Endemic or introduced consumer organisms (i.e., biological control agents) naturally regulate herbivore populations and secure a quarter of crop yields, but are exceptionally susceptible to CC-related disturbances. Here, we use niche modeling for 14 globally-important herbivores (or pests) to forecast how richness of the associated biological control agents of each pest—as a proxy of service strength—may alter under a CC-driven range expansion. Results show that 57%–100% of pests are bound to lose parasitoid and predator associates. The cassava mealybug *Phenacoccus manihoti* may experience a 27% decline in parasitoid pressure, whereas cosmopolitan pests of cereal and horticultural crops benefit from 6% to 7% drops in predator pressure. Such 'enemy release' can possibly exacerbate pest-induced yield losses and threaten future harvests. Ant-pest associations change in both directions, implying that pests may either face strengthened or weakened biological control. For pests spreading towards or within food-deficit regions in the equatorial belt, parasitoid declines and increases in ant pressure are most pronounced. By exposing the fragility of biodiversity-based ecological safeguards in farmland, our work calls for urgent, integrative, and nature-friendly solutions to uphold food security under environmental change.

1 | Introduction

Global progress in reducing hunger has reversed. Today, almost 750 million people are undernourished and 2.3 billion people are food insecure (FAO, IFAD, UNICEF, WFP and WHO 2024); estimates that are markedly higher than in 2019. Under- or malnutrition negatively affects human health, workforce productivity, wellbeing and global order (Fanzo et al. 2021; Sachs et al. 2023), reflecting broader inefficiencies and constraints in the global food system (Willett et al. 2019). To uphold or strengthen global food security, it is crucial to sustainably increase productivity in regions with large yield gaps and where population growth and/or dietary shifts are most pronounced, such as Sub-Saharan Africa and South Asia (Foley et al. 2011; Godfray et al. 2010; Van Ittersum et al. 2016). This, however, is challenging, as resource use efficiency and

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overall economic competitiveness of agriculture have been declining. At present, crop yields in multiple key production areas are stagnating or even reducing (Ray et al. 2012; Gerber et al. 2024). Meanwhile, agriculture has become a key driver of climatic warming, biodiversity loss and environmental pollution (Clark et al. 2020; Outhwaite et al. 2022; Richardson et al. 2023). As such, urgent action is needed to ensure that agriculture provides safe, nutritious diets for all within the safe operating space of our planet (Rockström et al. 2020). To achieve this, resolute on-farm action is imperative.

Prior to leaving the farm gate, approx. 40% of food is lost to crop pests, weeds, and diseases (Oerke 2006). Biotic losses are often more pronounced where it matters most that is, in food-deficit regions with fast-growing human populations (Savary et al. 2019), and show no signs of abating. In a warming world, pest-related losses are bound to increase in both magnitude and persistence (Deutsch et al. 2018; Ma et al. 2021). This trend applies to both pests within their native ranges and those that have become invasive in new environments. Invasive invertebrate pests already cause multimillion-dollar losses in global agriculture (Turbelin et al. 2024), and climate change is fueling their spread (Ma et al. 2025). In recent years, several prominent pests from mid-high latitudes have spread into temperate areas (Szyniszewska et al. 2024; Matsukura et al. 2024), which can jeopardize primary productivity in key food staples such as maize and potato (Tito et al. 2018). To tackle the increasing threat of pest-related crop losses, farmers, particularly in low-income countries, resort ever more to chemical pesticides (Shattuck et al. 2023). This trend is notable given that pesticides offer no clear advantage over cost-free, natural forms of pest regulation where effective natural enemies are present (Janssen and van Rijn 2021), yet pose significant hazards for human and environmental health (Huber et al. 2022; Beaumelle et al. 2023; Gandara et al. 2024). Reducing our reliance on pesticides is possible by leveraging biodiversity and agroecological processes (Barnes et al. 2020; Deguine et al. 2023). Such techniques have clear benefits for crop yield, profit and overall farm performance (Wan et al. 2024), whilst simultaneously safeguarding human health, preventing environmental pollution and mitigating biodiversity loss.

Plant, animal and microbial biodiversity forms the foundation of more sustainable forms of pest management by supporting the key ecosystem service of biological control. Under so-called natural biological control, resident predators, parasitoids, or microbiota keep pest populations within bounds, reducing the economic damage that they can inflict (Murdoch 1994). Empirical evidence demonstrates the effectiveness of this process—for instance, naturally occurring predators reduce pest pressure by 73%, thereby raising crop yields by 25% (Boldorini et al. 2024). Generally, more species-rich natural enemy communities provide stronger biological control of endemic pests (Dainese et al. 2019) and enhance biotic resistance against future invaders (Beaury et al. 2020). The interactions between natural enemies and pests can also be harnessed for classical biological control, a strategy in which carefully chosen species are translocated from the pest's native range into its invasive range (Heimpel and Mills 2017), with the aim of restoring ecological balance (Hoddle 2004). This approach has enabled full or partial control of over 220 invasive insect pests globally—several of which pose serious threats to food security (Heimpel and Cock 2018; Wyckhuys et al. 2020). Climate change however may weaken both forms of biological control and thereby threaten long-term food security across diverse farming systems (Skendžić et al. 2021), but concrete evidence of this is scarce.

As most projections focus on one species of pest or natural enemy at a time rather than more complex, bi- or multi-trophic interactions (Zarnetske et al. 2012), they poorly account for climate-induced asymmetries in distribution and the associated spatial and/or phenological mismatches between pests and their antagonists (Thomson et al. 2010; Damien and Tougeron 2019). These mismatches can weaken trophic interactions e.g., predation or parasitism and destabilize biological control outcomes. Even though the few observational studies on this topic remain inconclusive (Wyckhuys et al. 2022), they have uncovered three "first order" impacts of climate change. First, in relatively undisturbed systems such as low-input, perennial crops or natural habitats, natural enemy communities often exhibit high species turnover along climatic gradients which, in turn, sustains richness. Second, given their close dependence on specific hosts or prey, oligophagous parasitoids and predators have limited ability to adapt to changing climates as compared to polyphagous ones (Le Lann et al. 2021). Host-specific natural enemies use more specialized ecological strategies, respond to a smaller repertoire of cues, and are thus more constrained in tracking their hosts' changing life cycles, ontogenetic stages, or range shifts (e.g., Stireman III, Dyer, Janzen, et al. 2005) and/or switch to alternative hosts when their primary hosts become unavailable. Third, as pests are often superior dispersers and colonizers (but see Sivakoff et al. 2012; Evans 2018), they are prone to respond quickly and widely to warming conditions (Thomson et al. 2010; Nyamukondiwa et al. 2022). Under these premises, natural enemy richness and/or the presence of a limited number of plastic or adaptable biological control agents could provide insurance against climate-induced pest outbreaks (Jonsson et al. 2017). Yet, the extent to which insect biodiversity functions as biotic insurance under climate change (Loreau et al. 2021) remains, to date, unquantified.

Here, we employ ecological niche modeling to assess whether and to what extent climate change drives spatial mismatches between target pests and their associated natural enemies, thus potentially weakening on-farm biological control. We focus on a set of 14 historically significant pests of key food or nutrition security crops, which are managed through classical biological control or variably suppressed by resident natural enemies. Using maximum entropy modelling and open-access occurrence data (Phillips et al. 2006), we project both current and future pest distributions under climate change scenarios for the period of 2061–2080. For each pest, we also map the distribution of their introduced biological control agents, and use richness of locally occurring natural enemies that is, predators, parasitoids and ants as a biological control proxy. Finally, we forecast potential spatial mismatches or shifts in natural enemy richness associated with climate-driven range expansion of each target pest. Our findings provide *in silico* support for the biotic insurance hypothesis and offer practical guidance for strengthening landscape-level biological control under climate change.

TABLE 1 | Listing of invasive or cosmopolitan arthropod pests that are under full or partial biological control. A distinction is made between those pests that are suppressed through the action of a few (i.e., 1–3) key natural enemies, oftentimes intentionally or fortuitously introduced non-native species, and those that are partially controlled through a diverse complex of natural enemies, most of which are endemics. For each pest, geographic distribution and the primary host crops are detailed.

Target pest	Taxonomic classification	Natural enemy (guild)	Impacted crop	Geographic range[a]
Group #1: Pests (primarily) suppressed by 1–3 key natural enemies				
Phenacoccus manihoti	Hemiptera: Pseudococcidae	*Anagyrus lopezi*	Cassava	Af, Am, As
Mononychellus tanajoa	Trombidiformes: Tetranychidae	*Typhlodromalus aripo*	Cassava	Af, Am
Phthorimaea operculella	Lepidoptera: Gelechiidae	*Apanteles subandinus*, *Copidosoma koehleri*, *Orgillus lepidus*	Potato	Af, Am, Eu
Paracoccus marginatus	Hemiptera: Pseudococcidae	*Acerophagus papayae*	Multiple	Af, Am, As
Diaphorina citri	Hemiptera: Psyllidae	*Tamarixia radiata*	Citrus	Am, As
Maconellicoccus hirsutus	Hemiptera: Pseudococcidae	*Anagyrus kamali*	Multiple	Am
Bactrocera dorsalis	Diptera: Tephritidae	*Diachasmimorpha longicaudata*, *Fopius arisanus*	Multiple	Af, As
Group #2: Pests suppressed by a speciose natural enemy complex				
Bemisia tabaci	Hemiptera: Aleyrodidae	Parasitoids	Multiple	Af, Am, As, Eu
Spodoptera frugiperda	Lepidoptera: Noctuidae	Parasitoids	Maize	Af, Am, As, Eu
Helicoverpa armigera	Lepidoptera: Noctuidae	Parasitoids	Multiple	Af, Am, As, Eu
Plutella xylostella	Lepidoptera: Plutellidae	Parasitoids	Cabbage	Af, Am, As, Eu
Aphis gossypii	Hemiptera: Aphididae	Parasitoids + predators	Multiple	Af, Am, As, Eu
Sitobion avenae	Hemiptera: Aphididae	Parasitoids + predators	Cereal grains	Af, Am, As, Eu
Nilaparvata lugens	Hemiptera: Delphacidae	Parasitoids + predators	Rice	As

[a] Africa (Af), Americas (Am), Asia-Pacific (As), Europe (Eu).

2 | Materials and Methods

2.1 | Target Pests and Natural Enemies

We identified 14 globally important herbivores (here ‘pests’) which adversely impact food staples such as cereal grains, legumes, and root and tuber crops, and horticultural crops such as fruits and vegetables. We classified these pests into two groups. Group 1 included seven species that were successfully targeted through classical biological control that is, a practice which entails the scientifically-guided introduction of either one or multiple biological control agents from the region of origin of the target pest (Heimpel and Mills 2017). Specifically, suppression of these pests was achieved through the introduction of one (i.e., cassava and papaya mealybug, cassava green mite, pink hibiscus mealybug, citrus psyllid), two (oriental fruit fly) or three (potato tuber moth) species of parasitic wasp (Table 1). These introduced parasitic wasps largely provide stable biological control across diverse agroecological zones and farming contexts. For example, the encyrtid wasp, *Anagyrus lopezi*, provides adequate biological control in over 95% of surveyed sites against the cassava *mealybug Phenacoccus manihoti* (Neuenschwander 2001), whilst the neotropical parasitoid *Acerophagus papayae* attains consistently high performance against the invasive papaya mealybug *Paracoccus marginatus* throughout release sites in the southern United States of America, Caribbean, Pacific, South Asia and eastern Africa (Myrick et al. 2014; Opisa et al. 2024). In most cases, these interventions resulted in 90%–98% reductions in pest populations within one or more years following release.

Group 2, comprising the remaining seven species, are only partially suppressed through natural biological control, with suppression levels linked to local natural enemy richness or diversity (Letourneau et al. 2009; Dainese et al. 2019; Togni et al. 2019). For instance, for the fall armyworm, *Spodoptera frugiperda*, the diamond back month, *Plutella xylostella*, and the sweet potato whitefly, *Bemisia tabaci*, predation from naturally occurring predators consistently poses the largest mortality factor (Varella et al. 2015; Farias et al. 2021; Naranjo et al. 2022). For each of the naturally suppressed pests in the second group, we compiled a list of associated natural enemy species across their global distributional range. This information was sourced from published literature, open-access compendia and species-specific queries on GloBI that is, a searchable, open-access repository of species-interaction data (Poelen et al. 2014; Table S1). GloBI queries were run by manually entering the binomial scientific name of the target pest and extracting all invertebrate natural enemies that featured upon selecting 'ecologically related to', 'has parasite' and 'preyed upon by' under the 'browse' function in GloBI. The relevant relationships were manually selected from the GloBI drop-down menu. In cases where interaction data were inordinately sparse or incomplete, the list was limited to a single guild that is, parasitoids or predators. More so, in several cases, no predator interaction data were available at all. Taxonomy of all associated natural enemy species was revisited using currently accepted nomenclature as specified in the Taxonomy Backbone of GBIF (www.gbif.org) and all duplicate records were removed. This process yielded variably sized natural enemy cohorts per pest: *B. tabaci* (127 species), *S. frugiperda* (234 species), *Helicoverpa armigera* (190 species), *P. xylostella* (83 species), *Aphis gossypii* (152 species), *Sitobion avenae* (111 species), and *Nilaparvata lugens* (103 species). These natural enemies likely acted across ecosystem boundaries that is, not only regulating pest populations in agricultural settings but also in natural or urban environments off-season—which is especially relevant for polyphagous herbivores such as *B. tabaci*, *S. frugiperda* or *H. armigera*.

2.2 | Data Processing and Cleaning

Occurrence records for all 14 pest species and their associated biocontrol agents or natural enemies were collated through a combination of GBIF queries and manual data extraction from both published and unpublished sources. After extracting the raw occurrence data from GBIF using the rgbif package (Chamberlain et al. 2024), records were filtered to remove those with missing coordinates or those with implausible values. Yet, for several pests and their associated natural enemies, information in the GloBl database was incomplete; for those, in-depth literature screening and manual data extraction was required.

For cassava mealybug and its parasitoid *A. lopezi*, we manually extracted occurrence records from Neuenschwander (2001), Wyckhuys et al. (2018) and Pestdisplace (www.pestdisplace.org). The latter platform also yielded occurrence data for the cassava green mite, *Mononychellus tanajoa*, and its predator *Typhlodromalis aripo* across both native and introduced ranges. For *P. marginatus*, we also included its newly published occurrence records in Australia (Yadav et al. 2025), and occurrence data of its parasitoid, *Acerophagus papayae* (Finch et al. 2024). We geo-referenced all manually collected records to obtain standardized coordinates. We filtered all occurrence data for all species, and removed all records with reported spatial uncertainties of greater than 100 km. Finally, all the cleaned datasets were transformed into Simple Features (sf) objects for spatial analysis. and latitude-longitude coordinates (in a WGS84 projection) were converted to Behrmann equal-area projection.

To ensure a consistent spatial resolution across all datasets, we generated a global hexagonal grid with a cell resolution of 20 km (equating to 1039.23 km^2). Occurrence records were then assigned to hexagonal grid cells using the observations2grid() function in the sf package. For the naturally suppressed pests, we only had predator identity records for three species that is, *A. gossypii*, *N. lugens*, and *S. avenae*, therefore we used ant species richness values as an additional proxy of predator-mediated biological control. This was based on previous work showing that ant richness drives predation of some (though not all) herbivores in undisturbed settings (Tiede et al. 2017), and the fact that it has been mapped at high spatial resolutions across temperate and tropical settings. Ant richness data were extracted from Kass et al. (2022) for each hexagonal cell in which the focal pest was either present or predicted to occur based on climate niche modeling (see below). For the explanatory environmental variables, we extracted all 19 bioclimatic predictor variables from WorldClim 2.0 (Fick and Hijmans 2017) at a resolution of 10 arc-minutes.

2.3 | Data Analysis

We used Maximum Entropy Modeling (MaxEnt; Phillips et al. 2006) to model the current distribution of each pest and natural enemy species, separately, through the maxent() function in the "dismo" package (Hijmans et al. 2024). MaxEnt is a machine learning approach that analyzes the environmental characteristics of locations where a species has been recorded and compares them with those of randomly chosen background sites within the study region, where the species' presence is uncertain. Through this comparison, MaxEnt determines which environmental factors are most strongly linked to the species' occurrence, enabling it to estimate the potential suitability for a given species' throughout the area. We did not check for collinearity given that Maxent effectively tackles these issues.

To understand the current potential distribution of the individual pest and natural enemy species, we ran the MaxEnt models with background points automatically generated by the dismo package, the known distributional points of the pests and natural enemies, and current climate data. We only modelled the potential distributions of natural enemy species with more than 30 reliable records. For those with fewer records, only recorded occurrences were used and no modelling was conducted. The above cut-off value was used because Maxent predictions tend to become unreliable below 30–40 valid data points.

Further, for all pest models, we projected the results of these models using two future climate scenarios, a moderate-emission scenario (SSP2-4.5) and a high-emission (business-as-usual) scenario (SSP5-8.5), based on MIROC6 global climate models (Tatebe et al. 2019). Projections were made to a mid-late century period covering 2061–2080. For resident or introduced natural enemies, we assumed that habitat suitability will remain unaffected by climate change, and thus we did not model their potential distribution under these further climate scenarios. Given the lack of sufficient occurrence data for most natural enemies, this decision was made out of necessity and not based on ecological reasoning.

For all models, we restricted the predictions of environmental suitability to a 500 km buffer area around the smallest convex polygon that encloses all reported occurrences of the focal pest. This was to avoid projecting current occurrences onto climatically suitable areas where a given species is not known to occur that is, other continents which the species may possibly invade in the future. We assessed the predictive performance of all models using AUC (Area Under the Curve) scores, and examined response curves to identify the key climatic determinants of pest distributions.

Next, we assessed how the richness of natural enemies associated with each pest species is expected to change as pest distributions expand or contract under future climate scenarios. Even though enemy distributions remained the same in our modeling approach, pest distributions changed and the associated overlapping areas with different enemy richness varied from those under the present scenario. To quantify these changes in parasitoid or predator richness across climatic scenarios, we converted the predicted distribution for each species into a binary presence-absence map. To do this we used a suitability threshold of 0.5 suitability threshold to ensure a robust delineation of suitable habitats. We used the resulting presence-absence prediction maps to compare the spatial overlap between the presence/absence of pest species, and the presence/absence of their biocontrol agents or natural enemies. To do this we calculated, for each pest species, and for each grid cell in which this pest was projected to occur, the number of co-occurring natural enemy species (i.e., parasitoid, predator, or ant pressure). We did this considering both the current potential distribution of the pest, but also the potential distribution of the pest under future climate scenarios. Additionally, for each pest species, we calculated the mean natural enemy richness across its entire distribution area, the total number of pest-occupied grid cells, and the proportions of these occupied grid cells experiencing any natural enemy pressure (i.e., natural enemy count greater than zero). Equally, it is important to emphasize that the above metric of natural enemy pressure does not serve as a valid proxy of parasitism rate or pest mortality due to predation.

To evaluate changes in natural enemy pressure between current and future climate conditions, we calculated Cohen's d effect sizes and the corresponding confidence intervals (CI) for each pest. Seven of our target pest species (in group 1) had less than three associated parasitoids, and thus no meaningful confidence intervals could be calculated. Therefore, in these cases, two-sided t-tests were used to compare current and future parasitoid pressures. All computations were conducted in R version 4.4 (R Core Team 2012), using packages including dplyr (Wickham et al. 2023), exactextractr (Baston 2023), ggplot2 (Wickham 2016), ggpubr (Kassambara 2023), rnaturalearth (Massicotte and South 2023), raster (Hijmans 2025a), and terra (Hijmans 2025b).

3 | Results

3.1 | Pest Distribution

Under the moderate-emission scenario (F1), ten pest species (71%) were projected to experience an increase in distribution while four species (28.6%) were projected to experience a range contraction. Similarly, under the high-emission scenario (F2), a range expansion was projected for 10 pest species, whereas the distributional range of four species was projected to contract. For example, *A. gossypii*, *H. armigera*, *P. manihoti*, *P. marginatus*, and *S. avenae* are all expected to expand their distribution. Specifically, the distribution of *A. gossypii* is projected to broaden by a respective 19.3% and 17.5% under F1 and F2 scenarios, whereas that of *H. armigera* is expected to expand by 7.3% under F2. In contrast, the distribution of *B. tabaci* is projected to contract by 13.5% and 13.7% under the F1 and F2 scenario, respectively, whereas that of *B. dorsalis* is anticipated to shrink by 5.9% under F2. No significant differences were found in the extent of change in occupied area between the two pest groups under either climate change scenario (Kruskal–Wallis $\chi^2 = 0.2$, $p = 0.6547$).

3.2 | Parasitoid Pressure

Across target pests and climate scenarios, the number of parasitoid species ranged from 0 to 28 (mean = 1.67) per grid cell. Under both F1 and F2 scenarios, eight out of 14 species experienced a significant decline in mean parasitoid pressure across their distribution area. The species with the largest change in parasitoid pressure was *P. manihoti, which* experienced significant declines in parasitoid pressure—from an average of 0.78 parasitoid species per cell in the current scenario to 0.57 in the F1 scenario (effect size; Cohen's $d = -0.46$) and 0.58 in the F2 scenario ($d = -0.42$; Figures 1 and 2; Table S2). This was due to future distributions falling outside of the current range of its primary parasitoid *A. lopezi*. Similarly, *P. marginatus* also experienced a moderate decline in parasitoid pressure from 0.31 to 0.27 under the F1 scenario ($d = -0.09$) and 0.25 under the F2 scenario ($d = -0.13$; Figure 2). Further, the parasitoid pressure for *S. avenae* declined from 6.44 to 5.93 and 5.86 parasitoid species per grid cell under the F1 and F2 scenarios, respectively ($d = -0.09, -0.10$, respectively; Table S2). Across both F1 and F2 scenarios, only one species, *S. frugiperda*, was projected to experience an increase in parasitoid pressure (Figure 1; Table S1), with projections showing a 7% increase in parasitoid pressure under both F1 and F2 scenario ($d = 0.07$; Figure 2). Nonetheless, change in parasitoid pressure did not differ between the two pest groups (Kruskal–Wallis $\chi^2 = 0.6898$, $p = 0.4062$ and $\chi^2 = 0.33061$, $p = 0.5653$ for F1 and F2 scenarios, respectively).

Tropical pests, such as *P. manihoti* and *P. marginatus*, were projected to experience reduced parasitoid pressure under both F1 and F2 scenarios, with declines in parasitoid counts being most pronounced around the equatorial belt (Figure 2). Under the F1 scenario, many pests showed a decline in parasitoid pressure, particularly in Sub-Saharan Africa (for cassava and maize pests), South and Southeast Asia (rice and cotton pests), and tropical Latin America (bean and cassava pests). Under F2, pests such as *S. frugiperda*, which are projected to expand poleward,

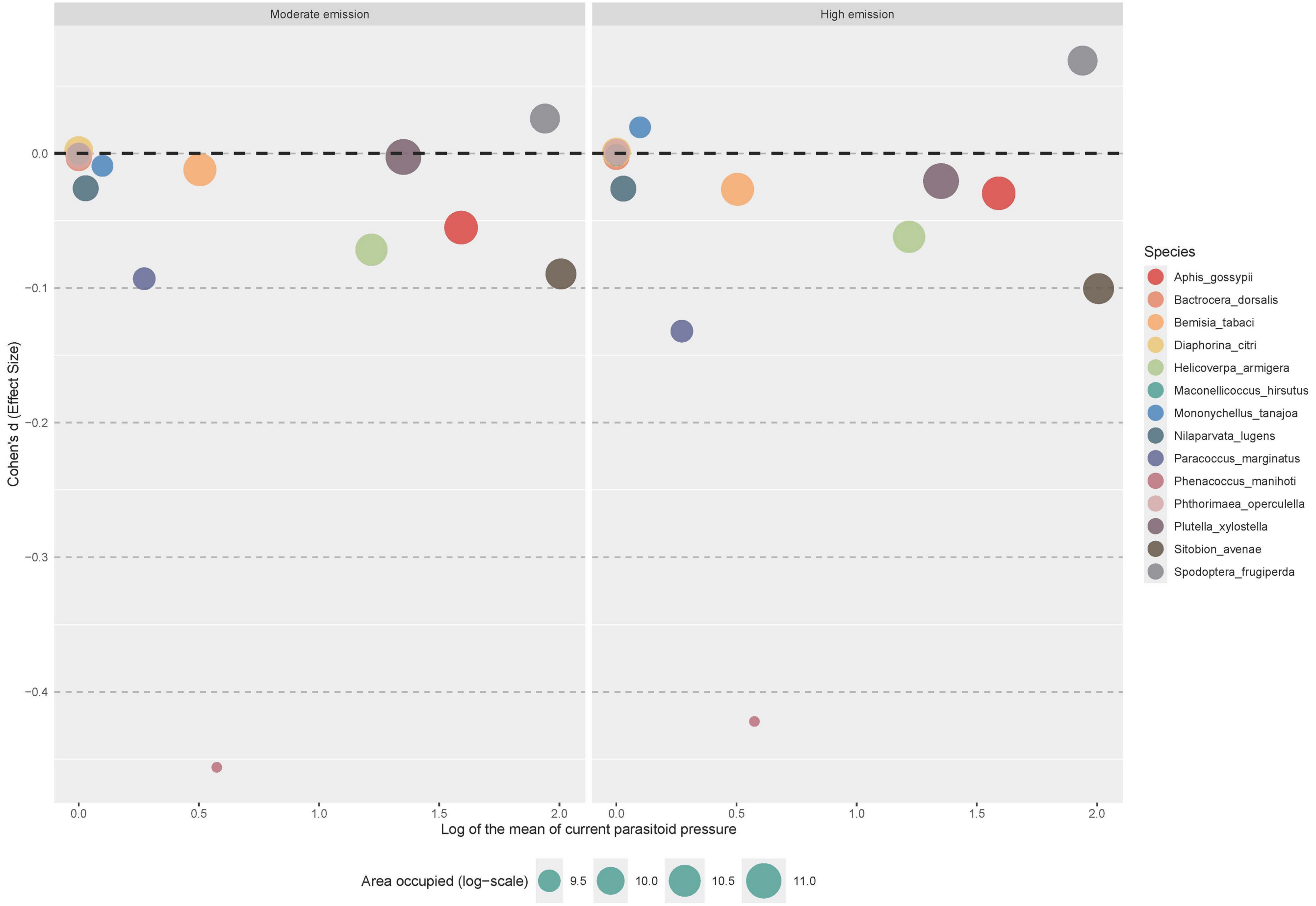

FIGURE 1 | Magnitude and direction of change in parasitoid pressure for 14 agricultural pests subject to climate-driven distributional shifts. Pests are organized per increasing parasitoid pressure under current climatic conditions (*X* axis). Bubble size is reflective of the (absolute) area affected by a given pest under a given scenario. Patterns are plotted for a moderate- and a high-emissions climate change scenario by mid- to late-century (2061–2080). For each pest and climate change scenario, Cohen's *d* effect sizes are shown.

are projected to experience increased parasitoid pressure. While parasitoid pressure under F1 exhibited gradual, regionally consistent changes, F2 projections showed sharp contrasts, with some areas experiencing elevated parasitoid counts adjacent to areas with steep declines. In temperate areas, parasitoid pressure on several pests was anticipated to remain steady or even improve marginally. For example, *S. avenae* was projected to experience stable or slightly elevated parasitoid pressure in northern Europe, although its parasitoid counts declined markedly in North America (Figure 2).

3.3 | Predator and Ant Pressure

Predator data were available for *A. gossypii*, *N. lugens*, and *S. avenae* (mean = 2.35, range = 0–47). All three pest species were projected to experience significant declines in predator pressure under future climate scenarios (Figure 3). For instance, under current climates, *A. gossypii* encounters 9.3 predator species per cell on average. Under future scenarios, predator pressure for this species declines significantly to 8.72 in F1 and 8.75 in F2 with a medium effect size ($d = -0.11$) in both cases (Table S2). Meanwhile, *S. avenae* experiences the highest predator counts under current climates (mean = 17.21 species), but is anticipated to experience a reduction in predator counts to 16.03 in F1 and 16.05 in F2 ($d = -0.09$ in both cases). Similarly, predator pressure on *N. lugens* is projected to decline from 6.35 to 5.95 or 6.05 predator species per cell under F1 or F2, respectively ($d = -0.11$, -0.08, respectively; Figure 3; Table S2).

The ant richness dataset was more extensive globally than the pest-associated predator dataset, with many pests co-occurring with numerous ant species (mean = 62.28, range = 0–554). Under climate change, changes in pest-specific ant pressure were more mixed than those of parasitoids or predators, with roughly half of the pests projected to experience increasing ant pressure and half to be subject to lowered ant pressure (Figure 4). Under the F1 scenario, six out of 14 pests experienced a significant increase in ant pressure, while six underwent a significant decrease. Under F2, this number was five and seven, respectively. The two pest groups showed no differences in the magnitude of ant pressure change in either scenario (Kruskal–Wallis $\chi^2 = 0.49388$, $p = 0.4822$ and $\chi^2 = 0.036735$, $p = 0.848$ for F1 and F2 scenarios, respectively).

Some pests were projected to expand into areas of high ant richness. For example, ant pressure averaged 62.42 in the current

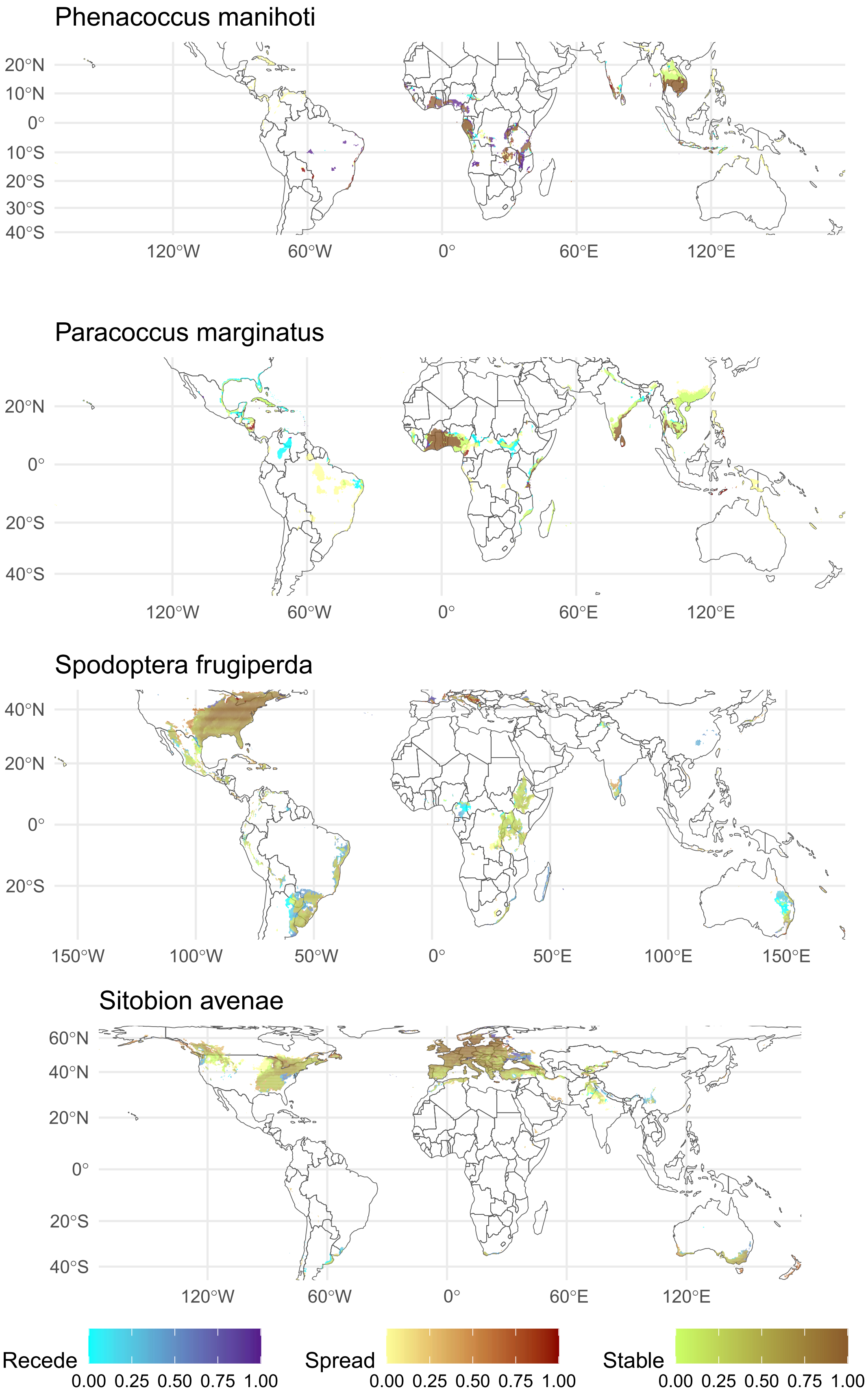

FIGURE 2 | Spatially explicit parasitoid pressure for four agricultural pests with changing distribution under climate change. Patterns are plotted for a moderate- (F1) or high-emission scenario (F2), depicting losses, gains, and stable trends in the distributional range of each pest. Data are shown for *Phenacoccus manihoti* (F1 scenario), *Paracoccus marginatus* (F2), *Spodoptera frugiperda* (F2), and *Sitobion avenae* (F2). Maps are cropped to the actual distribution of each pest species. Different color ranges show pest distributional change, and individual colors indicate z-score standardized parasitoid pressure. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

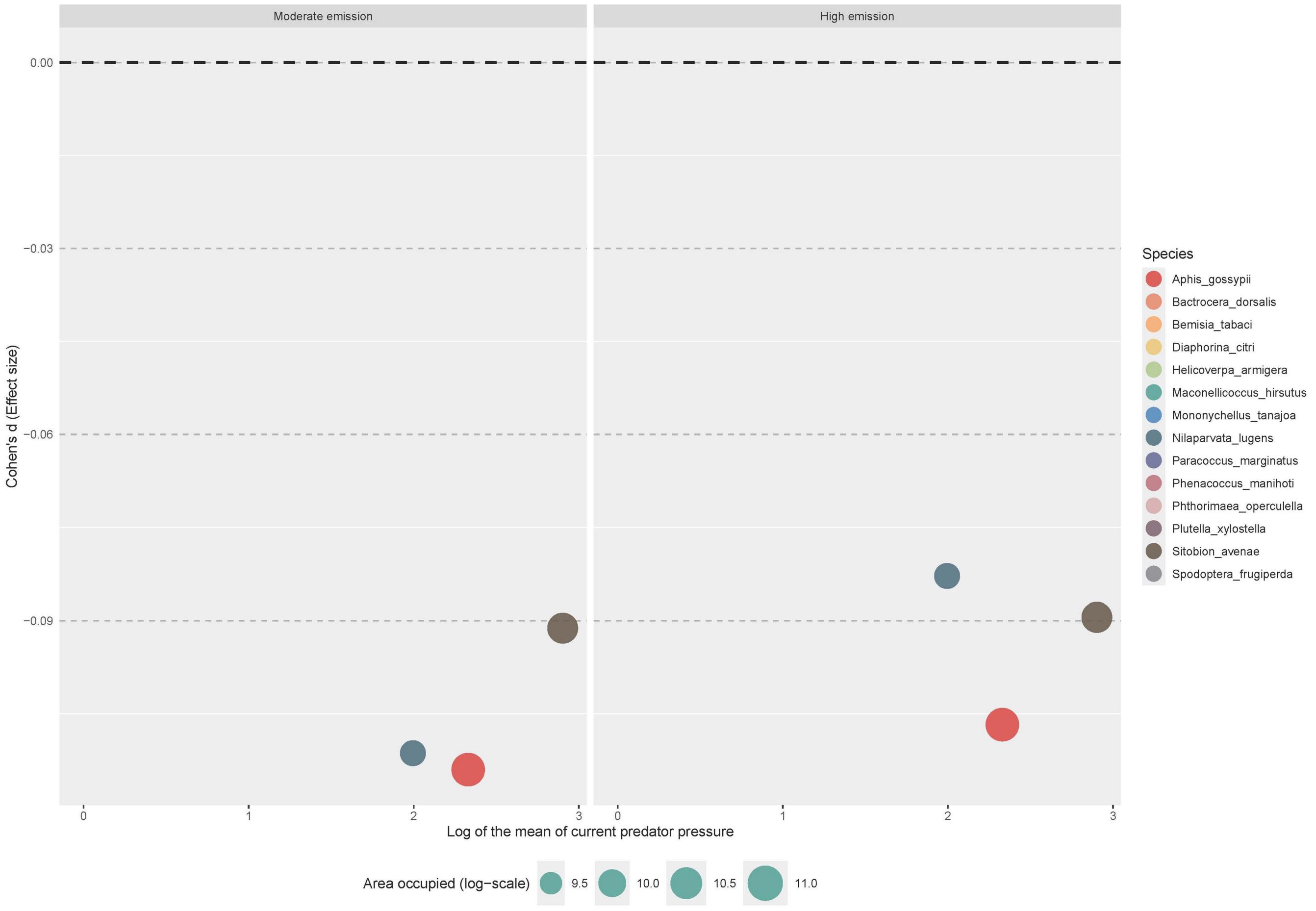

FIGURE 3 | Magnitude and direction of change in predator pressure for three agricultural pests subject to climate-driven distributional shifts. Pests are organized per increasing pressure by their associated invertebrate predators under current climatic conditions (*X* axis). Bubble size is reflective of the (absolute) area affected by a given pest under a given scenario. Patterns are plotted for a moderate- and a high-emissions climate change scenario by mid- to late-century (2061–80). For each pest and climate change scenario, Cohen's *d* effect sizes are shown. The remaining 11 pest species were excluded from the analysis due to lack of sufficient predator occurrence data.

range of *P. marginatus* but this increased under the F1 and F2 scenarios, to 68.84 and 72.43, respectively. The effect sizes were moderately positive ($d = 0.11$, 0.17, respectively; Table S2). Similarly, *P. manihoti* experienced increased ant pressure from 70.8 to 76.3 ($d = 0.12$) under the F2 scenario (Figure 5). In contrast, several pests were projected to experience a reduction in ant pressure in future scenarios. The sweet potato whitefly, *B. tabaci*, was projected to experience the most pronounced decline, with ant pressure declining from 65.6 under the current scenario to 53.3 under the F2 scenario ($d = -0.16$; Figure 5) – freeing space for other key natural enemies to exert greater control. Further, the diamondback moth (*P. xylostella*) was projected to experience a slight decline in ant pressure from 44.72 under current climates to 43.58 under the F2 scenario ($d = -0.04$), and similarly, ant pressure declined for *S. avenae, from* 47.35 to 44.64 under the F2 scenario ($d = -0.11$; Figure 5; Table S2).

Under both climate change scenarios, pests that spread towards the equator were generally subject to stronger ant pressure. This was observed, for example, in *A. gossypii* and *S. avenae*, which were projected to expand from northern and central European temperate zones into tropical areas (Figure 5). Conversely, pests expanding northward were projected to experience limited changes in ant pressure. Those pests expanding within, or into, very hot or arid regions, under both scenarios, experienced reduced ant pressure. This was particularly evident for *P. manihoti*, which was projected to expand into drier savanna regions of West Africa, and for *B. dorsalis* which was projected to expand into the Indian subcontinent, both of which were projected to experience a reduced ant pressure in these areas. Across all pest species, changes in ant pressure tended to be more pronounced under the high- emission (F2) than under the moderate-emission (F1) scenario.

4 | Discussion

Efforts to conserve arthropod biodiversity are constrained by sparse data and lacking awareness of its functional role or broader societal benefits (Eisenhauer et al. 2019; Basset and Lamarre 2019). Aimed at filling this awareness gap, the present study quantitatively assessed the extent to which beneficial arthropods may continue to contribute to natural pest regulation under future climates. Climate niche modeling demonstrated that, for 57%–100% of the globally important pests studied, parasitoid- and predator-mediated biological control is likely to weaken under future climate scenarios, although the associated effect sizes were generally small. In

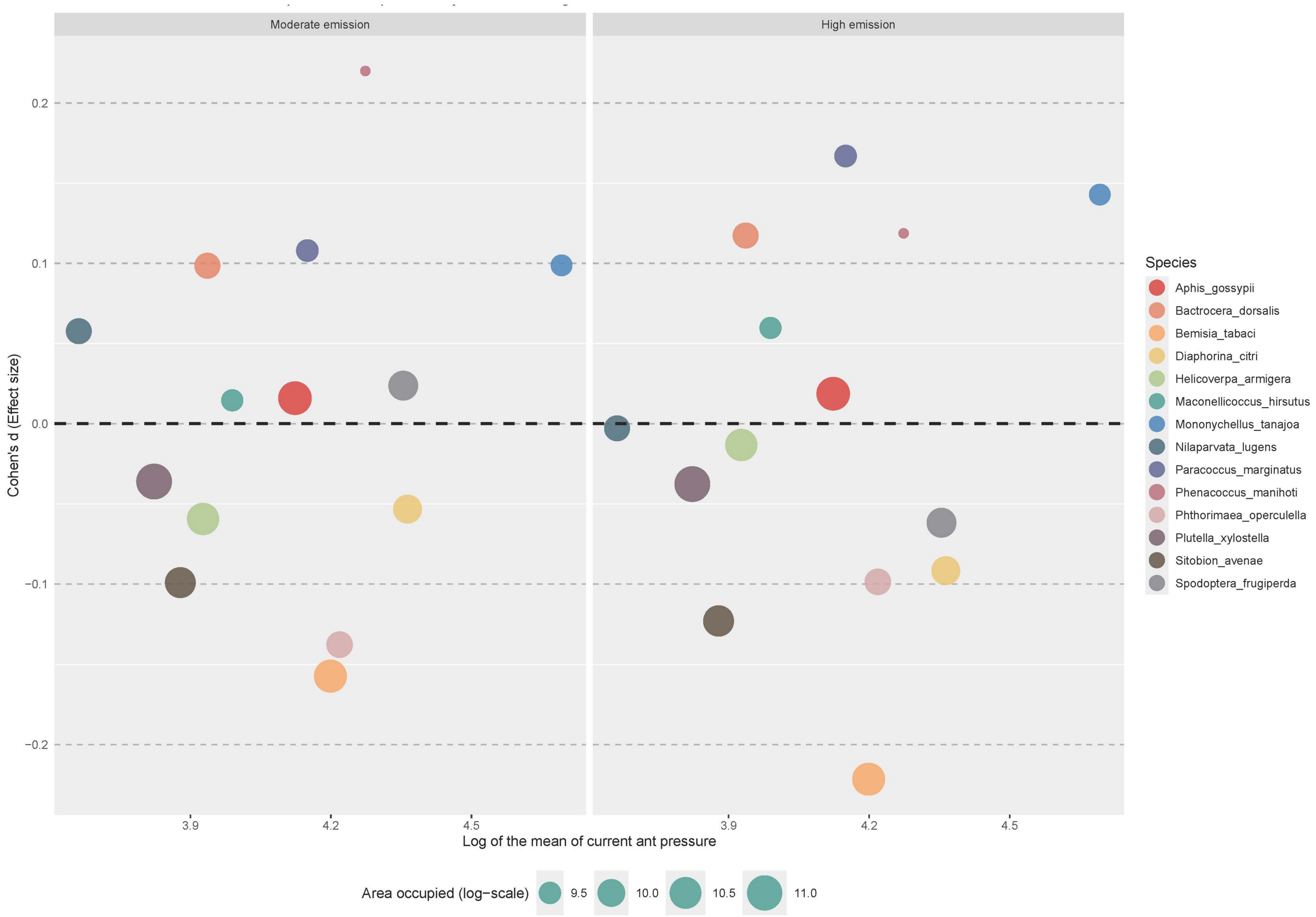

FIGURE 4 | Magnitude and direction of change in ant pressure for 14 agricultural pests subject to climate-driven distributional shifts. Pests are organized per increasing ant pressure under current climatic conditions (*X* axis). Bubble size is reflective of the (absolute) area affected by a given pest under a given scenario. Patterns are plotted for a moderate- and high-emissions climate change scenario by mid- to late-century (2061–80). For each pest and climate change scenario, Cohen's *d* effect sizes are shown.

contrast, projected changes in ant-pest associations were more variable with both positive and negative effects observed. This trend suggests that hemipteran pests may possibly benefit from enhanced ant pressure due to ant tending, whereas lepidopteran pests could be disadvantaged due to elevated predation pressure. Further, we detected no differences in the stability of biological control for pests that are (primarily) kept in check through endemic natural enemies versus those that are being suppressed by introduced ones. These findings illuminate the (potentially) negative impacts of climate change on the natural population regulation of crop pests, calling for amended crop management practices that preserve or fortify biodiversity-mediated ecosystem services.

Our work shows that under future climate scenarios, only 43% of pests are projected to retain their original complements of parasitoids, none retained their full suite of predators, and only 43%–50% maintained equal levels of ant pressure. Most pest species are projected to experience substantial declines in predator or parasitoid pressure that is, a so-called natural enemy 'release'. The effects of a reduction in natural enemy pressure could manifest either directly, through reduced pest mortality due to fewer predators and parasitoids, or indirectly through a progressive simplification or unraveling of food webs. Even though agroecosystems often contain simplified ecological communities, trophic downgrading may further eliminate critical non-consumptive effects, make room for less effective natural enemies, reduce functional redundancy or similarity, and thereby lower the insurance biodiversity provides against environmental or man-made disturbances (Loreau et al. 2021; Eisenhauer et al. 2023). As such, several limiting pests of cassava, maize, beans, or rice could benefit from the marked declines in natural enemy numbers especially near the equator. These patterns apply to both groups of pests covered in our analysis that is, endemic ones under natural biological control and invasive ones that are also impacted by targeted natural enemy releases.

This potential decrease in natural biological control of endemic or cosmopolitan pests will likely be compounded by a continuous 'trophic downgrading' or disproportionate loss of consumer organisms in the world's ecosystems (Estes et al. 2011; Wagner et al. 2021), including in relatively undisturbed habitats (Salcido et al. 2020). Arthropod biodiversity is undergoing a precipitous decline (Wagner et al. 2021; Sullivan and Ozman-Sullivan 2021), with numerous taxa experiencing continuous drops in abundance and species richness, particularly within human-modified environments. For example, recent studies

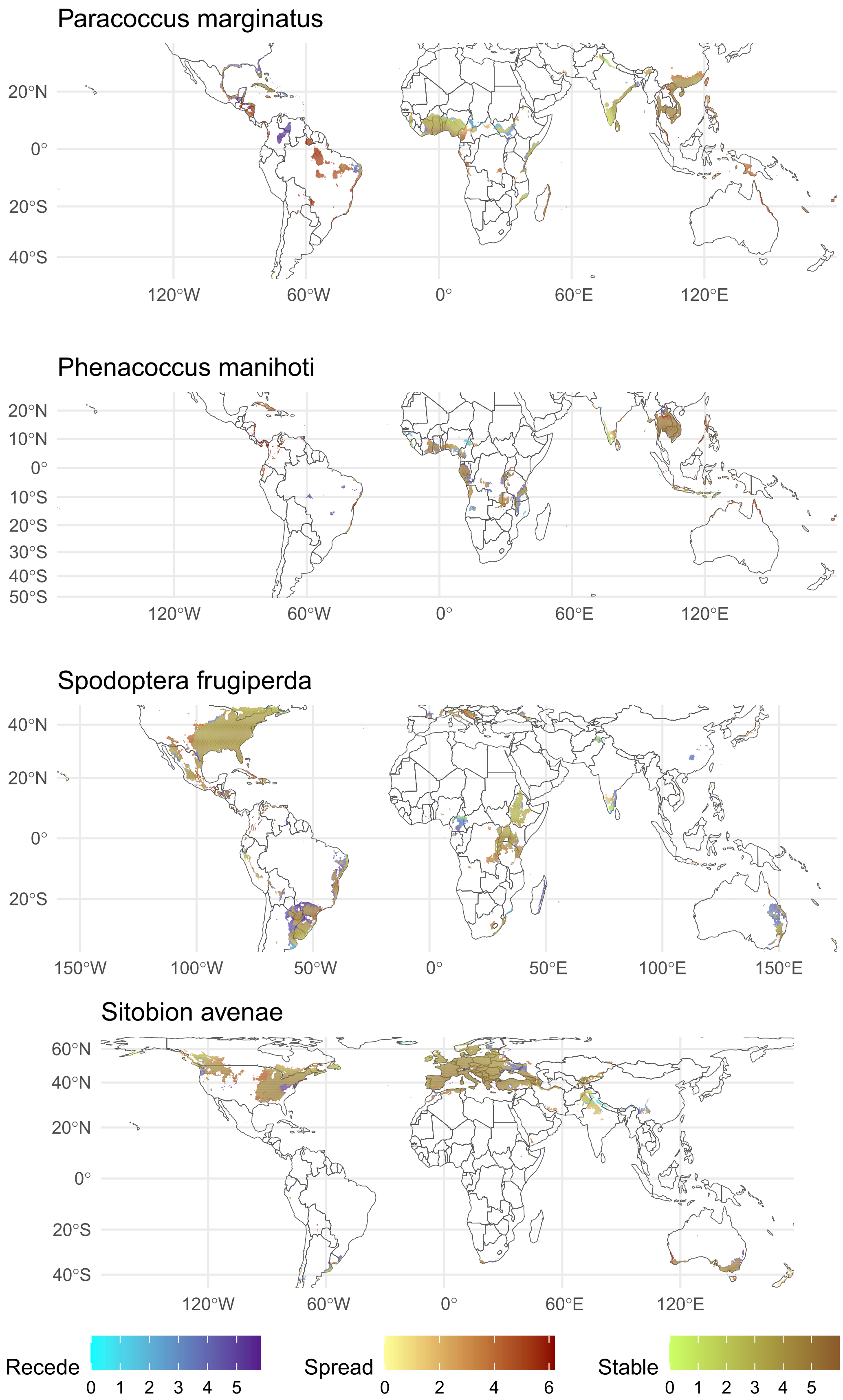

FIGURE 5 | Spatially explicit ant pressure for four agricultural pests with changing distribution under climate change. Patterns are plotted for a moderate- (F1) or high-emission scenario (F2), depicting losses, gains, and stable trends in the distributional range of each pest. Data are shown for *Paracoccus marginatus* (scenario F2), *Phenacoccus manihoti* (F2), *Bemisia tabaci* (F2), and *Sitobion avenae* (F2). Maps are cropped to the actual distribution of each pest species. Different color ranges show pest distributional change, and individual colors indicate z-score standardized ant pressure. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

have documented the disappearance of 75% of parasitoid species from China's maize cropping systems since the 1980s (Hu et al. 2023) and a 0.6% annual decline in airborne natural enemy abundance across seven families over an 18-year period (Zhou et al. 2023). These patterns are mirrored in higher trophic levels, with insectivorous bird populations declining by 13%–28% in Europe over a 25-year span (Bowler et al. 2019). While the ecological consequences of vertebrate loss may be more conspicuous than those of invertebrates (DeLong et al. 2015), the functional contributions of parasitoids and predators in agroecosystems remain significant, particularly given their sheer numerical dominance (but see Díaz-Siefer et al. 2022). The decline of functional biodiversity has been closely linked to agricultural intensification (Outhwaite et al. 2022; Hallmann et al. 2025) and the widespread use of pesticides (Geiger et al. 2010). When combined with climate change, the 'enemy release' phenomenon projected in this study may further escalate pesticide reliance and pest outbreaks (Crossley et al. 2024). It could also drive pesticide resistance development and indirectly reinforce a climate change feedback loop (Yang et al. 2024).

Biodiversity not only provides a 'standing army' against endemic pests that is, those in group 2 (as per Pijnakker et al. 2020) but also offers a functionally diverse 'solutions space' for invasive species mitigation that is, for taxa in group 1. Indeed, a science-driven implementation of classical biological control has historically mitigated numerous threats to food and nutrition security at benefit–cost ratios ranging from 5:1 to over 1000:1 (Naranjo et al. 2015; Heimpel and Cock 2018) and delivered substantial, durable societal benefits (Wyckhuys et al. 2020). This is evident in the patterns documented for pests in group 1, in which successful control can often be attributed to a single natural enemy species (Hawkins et al. 1999). This is exemplified by the durable control of *P. manihoti* by *A. lopezi* across tropical Asia and Africa (Herren and Neuenschwander 1991; Neuenschwander 2001; Wyckhuys et al. 2018) or the 57%–91% yield recovery following releases of *A. papayae* (Opisa et al. 2024). However, introduced parasitoids such as *A. lopezi* and *A. papayae* are mono- or oligophagous, and tightly associated with their host, making them particularly vulnerable to climate-induced disruptions (Le Lann et al. 2021). Climate change could thus potentially lead to spatial mismatches in enemy-pest co-occurrence patterns, generating so-called "enemy-free space" for the pests (Steffan-Dewenter et al. 2024). This is reflected in our analyses. For example, *P. manihoti* is projected to have a 27% decline in its parasitoid pressure, whereas a higher complement of ant associates may provide further protection against the introduced *A. lopezi* (as discussed below). Similarly, *A. gossypii*, *S. avenae* and *N. lugens* are projected to experience 6%–7% reductions in predator pressure. While this suggests a progressive weakening of biological control, it is important to note that the present analysis accounts primarily for species-level patterns, and does not account for inter-species variations which can influence biological control efficacy. For instance, different strains of the eulophid parasitoid *Tamarixia radiata*, adapted to specific agro-climatic conditions, vary widely in effectiveness against the Asian citrus psyllid (Flores and Ciomperlik 2017). This highlights the need for ongoing performance monitoring, incorporation of genetic diversity (Shaw et al. 2025) and timely, adaptive management. The latter involves a careful selection of biological control agents as guided by ecoclimatic niche modeling (Kenis and Seehausen 2025), in which added attention is to be given to genetic variability and phenotypic plasticity of candidates for release.

Our exercise to spotlight the societal importance of agrobiodiversity faces several caveats. First, while species richness is often emphasized, both the identity and abundance of natural enemies also critically influences biological control outcomes (Dainese et al. 2019). Species richness can confer resilience in a food security context (Bullock et al. 2017) through mechanisms such as redundancy, response diversity, and niche complementarity (Naeem 1998; Jonsson et al. 2017). However, as not all species are functionally equivalent, it is not uncommon that a small set of species within a single guild provides most of biological control. For example, a limited number of omnivorous predators such as *Doru* spp. earwigs and the fire ant *Solenopsis geminata*, suppress *S. frugiperda* in its native range (van Huis 1981; Perfecto and Sediles 1992). Disruptions to such key species due to climate change may be buffered by community-level richness effects, although empirical evidence of such processes remains limited. Second, our models do not fully capture species- and context-specific responses. Invertebrate species vary in their thermal sensitivity and response to abiotic conditions. Additionally, climate impacts are expected to be more severe in tropical regions (Outhwaite et al. 2022; Parr and Bishop 2022), where herbivores presently face the strongest predation pressure (Roslin et al. 2017). Further, simplified agricultural settings are particularly prone to climate change induced shifts which favor mobile generalist species (Gámez-Virués et al. 2015) though significant species-level heterogeneity persists (Kishinevsky and Ives 2022). Third, in addition to exerting species-level impacts, climate change is expected to disrupt ecological networks, altering phenological alignment and interaction strength among multiple trophic levels (Damien and Tougeron 2019). Yet, in line with our projections, such climate-induced changes in phenological alignment also threaten parasitoid population persistence, decrease parasitoid pressure, and ultimately favor pest outbreaks (Stireman III, Dyer, Janzen, et al. 2005). The above dynamics are shaped by behavioral adaptations and phenotypic plasticity in response to co-occurring species, plant or habitat structure, and the thermal environment (Schmitz and Barton 2014). Accurate predictions of future biotic interactions thus necessitates a multitrophic approach that accounts for the role of secondary 'support' species and ecological contexts (Yang et al. 2021; Keyes et al. 2021). Fourth, our treatment of ants as predators of all (endemic, invasive) pests may oversimplify their ecological role; for hemipteran pests specifically, ant richness may be a poor measure of biological control success per se. For instance, projected increases in ant associates for *A. gossypii* and *P. marginatus* may hinder the activity of natural enemies (Kaplan and Eubanks 2002), potentially resulting in pest resurgence despite apparent increases in ant-mediated pressure. On the other hand, certain pest species may experience enhanced biological control due to reductions in antagonistic ant activity. For example, the projected 19% decline in ant richness for *B. tabaci* could reduce interference with resident parasitoids and predators, thereby improving biological control outcomes (Anjos et al. 2022). Finally, to refine models and guide interventions, more real-world empirical data are urgently needed, particularly in the Global South (Wilson 2017). Expanding biodiversity monitoring and on-the-ground research will be key to future-proofing biological control under climate change.

Another possible point of contention is the underlying assumption that current stocks of natural enemies will remain static under climate change—which appears increasingly untenable, particularly in disturbed landscapes. Under moderate climate warming scenarios, up to one-third of animal species are projected to become extinct over the next 50 years (Wiens and Zelinka 2024), with species occupying higher trophic levels proving especially vulnerable to climate-driven disruptions (Estes et al. 2011; Zhou et al. 2023). Although natural enemies are expected to respond to elevated temperatures (Thomson et al. 2010; Furlong and Zalucki 2017), these responses may lag behind those of pests, and the resulting ecological dynamics may vary widely across species and contexts. Three other limitations particularly apply to pests in group 1 that is, those that are partially kept in check by resident biota. First, we did not consider whether natural enemies of each given pest actually occur in agroecosystems but rather accepted the number yielded from GloBi queries as a proxy for potential parasitoid or predator pressure. Indeed, published host–parasitoid and insect prey–predator interaction datasets are disproportionately derived from agroecosystems (Stireman III, Dyer, and Matlock 2005; Karp et al. 2018; Miller et al. 2021; Wyckhuys et al. 2021), reflecting a long-standing biological control focus on human-modified environments that has left many (though not all) natural ecosystems comparatively under-sampled in this regard. Moreover, while extensive, these cohorts are likely a vast underrepresentation of the actual numbers of natural enemies that feed upon a given pest across its entire distributional range, especially in the Global South, where biodiversity monitoring is scattered and taxonomic capacity lacking (Eisenhauer et al. 2019; Guerra et al. 2020). Second, building upon the above, our work imperfectly captures the off-farm impacts of natural enemies. While our overall analyses center on crop pests in agroecosystems, natural enemies also regulate the populations of agriculturally important herbivores in natural or urban environments (Wyckhuys, Pozsgai, et al. 2024). This is especially the case for polyphagous crop pests that sustain their off-season populations on non-cultivated plants. As pest survival can be especially low on winter hosts and/or in natural habitats (Naranjo et al. 2022), natural enemies might disproportionately impact pest population dynamics in such settings. Third, our analyses do not account for the contribution of insectivorous birds that is, key natural enemies of several target pests that were included in our study (Díaz-Siefer et al. 2022) and also overlook the impacts of entomopathogenic microorganisms or crop/non-crop plants themselves. As a result, our projections of biological control impacts under climate change are highly conservative.

To ensure that resident natural enemies continue to provide effective biological control under changing climates, biodiversity conservation, and manipulation on- and off-farm will be essential (e.g., Thomson et al. 2010; Wyckhuys, Gu, et al. 2024). Species interactions and associated trophic cascades can be managed to bolster climate resilience (Ripple et al. 2024), which can be achieved through on- and off-farm measures such as crop diversification, flower strips, heterogeneous landscape matrices, or smaller fields (Garibaldi et al. 2021; Tscharntke et al. 2021). Introducing structural or biological complexity into farming systems, for example, through crop diversification (Tamburini et al. 2020), crop varieties conducive to biological control (Stenberg et al. 2015) or ecological infrastructures (Gontijo 2019) can buffer invertebrate communities against climatic stress and, as an added benefit, enhance the multi-trophic control of pests (Barnes et al. 2020). These measures are to be paired with a progressive phasedown of pesticide use (Tscharntke et al. 2016; Harvey et al. 2020; Pandey et al. 2022) and do not necessarily entail trade-offs in yield or profitability (Waddington et al. 2014). Demonstrating and communicating these outcomes to farmers is crucial for wider adoption (Kleijn et al. 2019). Thus, farmers can proactively maintain ecological safeguards that are both cost-free and vital to the resilience of agri-food production systems, ultimately protecting livelihoods and contributing to food security.

5 | Conclusions

This pioneering modeling exercise reveals how beneficial associations between natural enemies and crop pests may be weakened under warming climates. Even under moderate climate change scenarios, 57%–100% of crop pests may lose associated natural enemies while approximately half of pests may benefit from shifts in ant richness. Our projections suggest that several notable crop pests will likely experience climate-induced “enemy release,” particularly in staple crops such as maize, cassava, beans, and rice across equatorial regions. This potentially can deepen crop losses, compromising food security and human wellbeing across the Global South (Burra et al. 2021). Beyond strengthening global efforts to mitigate climate change, there is a clear and urgent need to preserve functional biodiversity within farmland. This can be achieved through both on- and off-farm diversification, reduced field-level disturbance, and a resolute shift away from chemical insecticides. To safeguard future harvests, interdisciplinary and integrative strategies must be employed to reinforce the core ecological functions that underpin sustainable agriculture.

Author Contributions

K.A.G.W. led the idea generation, writing, and editing process. G.P. led the data curation and conducted the formal data analysis. W.Z. ensured funding acquisition. All authors actively contributed to manuscript writing and editing.

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Conflicts of Interest

K.A.G.W. is the chief executive officer of Chrysalis Consulting—a firm which provides tailored support to nature-friendly farming and biological control.

Data Availability Statement

All underlying data and computer code of this study have been made available at https://doi.org/10.5281/zenodo.18609543.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Literature resources or open-access databases that were consulted to compile the lists of biological control agents associated with each target pest. **Table S2:** Changes in natural enemy pressure for 14 globally-important crop pests under varying climate change scenarios.