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Assessing the phytosanitary threats of two non-native crickets under temperature change

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Abstract

Numerous phytosanitary threats challenge global agriculture, ecosystems, and food security. These threats are exacerbated by non-native species and diseases that are projected to intensify in the future due to global warming and anthropogenic habitat alterations. Assessments of the ecological impacts of overlooked phytosanitary threats are urgently needed under shifting environments. In this study, the potential effects of two non-native Orthoptera species (the house cricket *Acheta domesticus* and the two-spotted cricket *Gryllus bimaculatus*) were assessed using functional response analyses. We quantified their potential impacts on agriculturally relevant crops (millet) under increasing temperatures (20 °C, 25 °C, and 30 °C) as individuals and between interspecific pairs. The experiments revealed similar impacts on seeds between both species and across temperatures. Temperature tended to amplify consumption rates and functional responses. The combined interspecific cricket presence generally yielded an additive effect on seeds, with a few instances of synergistic interactions, whereby non-trophic interaction strengths significantly interacted with resource density and temperature. Both species demonstrated remarkable adaptability to varying temperatures, with low mortality accentuating their capacity for impacts under current and future temperatures. This emphasizes the imperative of including both species in phytosanitary assessments. Moreover, population monitoring and the implementation of effective management strategies emerge as pivotal measures for safeguarding agricultural productivity and conserving local ecosystems in the future. The study's findings thus underscore the potential impact of *A. domesticus* and *G. bimaculatus*, particularly in the context of steadily ascending temperatures, to pose a risk to agricultural productivity and food security.

Keywords Orthoptera · Cricket · Invasions · Phytosanitary threat · Pest · Functional response · Non-trophic interaction

Antonín Kouba and Phillip J. Haubrock have equally shared senior authorship.

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Introduction

Phytosanitary threats (e.g. risks posed to plants by pests, diseases, or other harmful organisms) pose significant challenges to agriculture, forestry, and natural ecosystems worldwide, with non-native species and the changing climate being major interconnected contributors (Mainka & Howard 2010; Haubrock et al., 2023). Among the main phytosanitary threats are pests, diseases, and biological invasions (Leal et al. 2010; Lopian 2018; Papyrakis and Tasciotti 2019; Kumar et al. 2021). Especially non-native species have the potential to become phytosanitary threats (Hellmann et al. 2008; Nahrung et al. 2023) and cause extensive damage to native communities and cause shifts in ecosystem functions (Crystal-Ornelas et al. 2021; Kirichenko et al. 2021; Soto et al. 2024). Climate change exacerbates phytosanitary threats because rising temperatures, altered precipitation patterns, and extreme weather events may weaken native community resilience while creating increasingly favorable conditions for the distribution of non-native species, pests, and diseases (Bebber, 2013; Ziska and McConnell 2016; Lopian 2018; Skendžić et al. 2021). Increasing impacts highlight the urgency of understanding and addressing these threats using emerging methods for impact forecasting from biological invasions (Ziska and McConnell 2016; Skendžić et al. 2021).

Orthoptera, which include grasshoppers, crickets, and bush-crickets, are a diverse order of insects that can pose significant phytosanitary threats to agriculture and ecosystems (Ghouri et al., 1961; Kulesa et al. 2023a). Some of them, particularly species like the desert locust *Schistocerca gregaria* (Forskål, 1775), have the ability to form swarms that can devastate crops over vast areas (Kennedy 1951), causing large-scale crop losses potentially resulting in food and economic crises for local communities (Lecoq 2022). The distribution and establishment of Orthoptera species have been influenced by climate change (Saha et al. 2021), as these insects are expanding their ranges and colonizing new locations following temperature increases and shifts in weather patterns (Battisti and Larsson 2015). Especially warmer and humid conditions can accelerate their life cycles, leading to more rapid population growth, increased reproduction rates and feeding activities (Buckley et al., 2014). In turn, rising temperatures, through an accelerated metabolism, development, reproduction and overall activity levels, can further affect their mortality, the exerted impact, as well as a species' functional response to available resources (Kimathi et al. 2020; Saha et al. 2021). Furthermore, anthropogenic changes of natural habitats and land-use can be beneficial for Orthoptera reproduction due to the availability of more suitable habitats (Le Gall et al. 2019; Bauer et al. 2022).

The house cricket *Acheta domesticus* (Linnaeus, 1758) and the two-spotted cricket *Gryllus bimaculatus* (De Geer, 1773), originally native to arid and semi-arid areas of northern Africa or south-western Asia, are two widespread non-native Orthoptera species in Europe (Ghouri 1961; Iba et al. 1995; Tan et al. 2022). Both species can be found in many parts of the world, particularly in anthropogenically altered environments and urban settings, but also in fallow lands and cultivated fields (Lourenço et al. 2022; Lu et al. 2023). Moreover, both species are cultured as pets, feedstock, and used in scientific research (Sorjonen et al. 2019). Although *A. domesticus* tends to occur in urban areas and closely associated agricultural landscapes and *G. bimaculatus* prefers fallow land and cultivated fields, both species occupy similar locations (Ghouri et al. 1961; Iba et al. 1995). The presence of *A. domesticus* in cities can be attributed to accidental introductions through various pathways, including transportation of goods and materials (Lourenço et al. 2022). Due to its adaptability to anthropogenically altered environments and a high reproductive capacity, it can rapidly establish populations in new locations (Weissmann and Rentz 1977; Gardiner 2009). With its opportunistic feeding behavior that encompasses grain, fruits and various plants (Clifford and Woodring 1990; Wilson et al. 2010), it has the potential to become a significant pest for stored crops but also the plants on cultivated fields (Kulesa et al. 2024). The introduction of *G. bimaculatus* and its spread are often associated with human activities, dominated by the trade of agricultural products and travel (Bang and Courchamp 2021). Having a preference for warm habitats, it rapidly adapts to warming climates (Orinda et al. 2017). Similar to *A. domesticus*, *G. bimaculatus* is an opportunistic generalist and can pose a phytosanitary threat to crops (Ventura et al. 2022). *Gryllus bimaculatus* can feed on a wide range of crops and vegetation (Woodring and Lorenz 2007), potentially leading to economic losses for farmers and impacting food production. With ongoing climate change, *G. bimaculatus* could spread poleward and establish new populations in new habitats (Bebber et al. 2013). At the same time, it is possible that with increasing anthropogenic disturbance, habitat alteration, and climate changes, both species could ultimately overlap even more in their non-native distribution.

While the co-occurrence of a non-native and a native species can lead to altered abundances and even displacement of one species (Haubrock et al. 2020a), the co-occurrence of two non-native species can result in non-additive effects that dampen or worsen ecological impacts through differences in trophic interaction strengths or mortality (Jackson 2015; Bissattini et al. 2021; Aksu et al. 2023). Differing food availability in the introduced range, biotic interactions and increasing temperatures can further influence mortality and species impacts (Carey 2001), as non-native species interact in the same ecosystem, competing for limited resources (Haubrock

et al. 2020b). On the other hand, under conditions of high food availability, both non-native species may thrive (Balzani et al. 2020). The extent of the impact will however likely differ for each species based on their adaptations and ability to use available resources. This interaction, despite being mediated by numerous factors such as temperature and habitat structure, could result in even larger impacts on recipient communities or agriculturally relevant plants (Ghoury et al., 1961; Le Gall et al. 2019). Especially the consumption and damage to seeds of agriculturally relevant but also wild plants by highly abundant non-native Orthoptera species could affect seed dispersal and plant reproduction, which can lead to a reduction in food production and supply, as well as ecosystem changes (Samways and Lockwood 1998; Showler et al. 2022; Youngblood et al. 2023).

Despite their adaptability and wide distribution, neither *A. domesticus* nor *G. bimaculatus* have been adequately assessed for their invasiveness, ecological impact, and the potential phytosanitary threat they may embody (Kulesa et al. 2023b). Assessing the functional response of these Orthopterans, that is the feeding behavior of a species to changes in the abundance of resources (i.e. seeds) and changing environmental conditions (Faria et al. 2023), is therefore crucial to approximate their potential impacts on economically relevant plants and other native organisms. In this article, the aim was to use functional response experiments to explore (I) the impact (i.e. consumption rate and functional response) of *A. domesticus* and *G. bimaculatus* on seeds of an agricultural crop (i.e. millet), aiming to evaluate their potential as phytosanitary threats. Furthermore, we infer (II) whether an increase in temperature as expected to occur following common climate change predictions (Lee et al., 2024) affect both species-specific impacts and their potential interactions, and test (III) if the co-occurrence of two non-native orthopterans leads to either a synergistic, additive, or reduced impact due to non-trophic interactions. Finally, (IV) we compared mortality of both species under different temperatures (following climate change scenarios) and assessed whether their interaction affects them. We predicted that (i) the individual impact (i.e. consumption and damage to seeds) of *A. domesticus* and *G. bimaculatus* will not differ but will intensify following an increase in temperature. We further hypothesized that when in co-occurrence, (ii) competitive interactions will lower the combined functional response, due to interspecific antagonisms. Finally, (iii) we predicted that both species would experience higher mortality when in co-occurrence, further exacerbated by increasing temperatures.

Material and methods

Specimen acquisition and housing conditions

Specimens of *A. domesticus* and *G. bimaculatus* used in the experiments were obtained from a specialized local breeder (Rodinná farma Bušanovice, Czech Republic). These commercially bought specimens were housed in a temperature controlled (25 °C) laboratory at the Faculty of Fisheries and Protection of Waters in Vodňany, Czech Republic. Directly upon their arrival, all individuals were transferred into large (58 × 79 × 44 cm) species-specific plastic containers modified to allow ventilation. To provide hiding places for the animals, containers were provided with egg cartons covering two-thirds of the surface area. Specimens were fed daily in excess with fish pellets (TI-2 Tilapia 2.5 mm, Skretting, Norway), following advice of the local supplier, combined with bio-grade apples to reduce a risk of exposure to residual insecticides. The enclosure was cleaned every other day before feeding. To accommodate the nocturnal activity of both species, a light:dark cycle of 3:21 (i.e. light on from 10 am to 1 pm) was set, similarly to the culturing conditions at the local farm.

Acclimatization

The animals were acclimated to the required experimental temperatures of 20, 25 and 30 °C (i.e., ambient 25 °C and 5 °C above or below this ambient acclimation temperature), in the same way as performed by et al. (2024). These temperature treatments were chosen to reflect projected climate change scenarios, where temperatures are expected to increase by approximately 1–4 °C above ambient levels over the coming decades, providing a controlled assessment of potential future conditions (IPCC, 2021). They also reflect conditions during extreme events or potential microclimates on anthropogenic land uses such as farms, which can be greater than mean temperature changes. To do so, at least 200 individuals were moved to three faunaria (EXOTERRA model PT2310, 46 × 30 × 17 cm, HAGEN, Germany) that were placed in three laboratory incubators (Lovibond TC 445 S/445 L, Liebherr, Germany). The acclimatization lasted for ten days. Animals were first kept for a week to capture eventual signs of elevated mortality in the stock, but no relevant mortality was noticed. Then the temperature was changed by 2 °C for two consecutive days and by 1 °C on the third day to gradually reach the final temperature in the first and last tested group. Each incubator, set to 20, 25, or 30 °C, was equipped with two MINIKIN data loggers (Environmental

Measuring Systems, Brno, Czech Republic) placed in different locations to monitor temperature. The recorded temperatures were, on average, slightly lower but accurately reflected the temperature differences between the tested groups (19.3 ± 0.2 , 24.3 ± 0.2 , and 29.3 ± 0.1 °C, respectively). Similarly to the common stock maintenance, the faunaria were equipped with egg cartons, and bio-grade apples were provided in excess. Cleaning was performed daily.

Functional response experiments

As arenas, $114 \times 114 \times 59$ mm sized plastic boxes were used. The cap of an Eppendorf tube was glued to the center of each box and filled with water to offer a water source. Females of acclimatised individuals of *A. domesticus* and *G. bimaculatus* were divided into three groups (i.e., one of each per temperature). For the experiments, 10 replicates were performed for each combination (group 1: *A. domesticus* alone; group 2: *G. bimaculatus* alone; group 3: *A. domesticus* together with *G. bimaculatus*), temperature (20, 25, and 30 °C) and density of seeds (5, 10, 20, and 40; later on referred to as resource density). We chose millet seeds originating from *Panicum miliaceum* which can be purchased commercially; see Supplementary Note S1 and Kulesa et al. 2024). The individuals of *A. domesticus* were, based on a subset of 30 specimens, on average 22.19 ± 1.31 mm body length (with ovipositor: $\sim 34.23 \pm 2.01$ mm). The average size of individuals of *G. bimaculatus* was 23.16 ± 1.56 mm (with ovipositor: 36.24 ± 2.02 mm). Specimens were transferred to individual boxes and starved for 24 h, after which the Eppendorf tube cap was refilled with water and the resource were inserted into the arena. Placement of boxes in the respective incubators followed a randomized block design, with temperature treatments (20, 25, and 30 °C) serving as blocks to control for temperature effects. Cricket species arrangements and prey densities were randomly assigned within each block to ensure balanced comparisons across temperature conditions. After 24 h, individuals were taken out of the box and euthanized by placing them in a fridge to gradually decrease their temperature and then finally frozen. For each temperature and combination, 10 controls were kept in arenas without being fed, to check for background mortality. After each 24 h cycle, potential sources of temperature fluctuations were checked using a data logger that was placed in each incubator. As no fluctuations were recorded, no trial had to be repeated.

In all groups (1–3), the damage to seeds was measured after each trial and completely eaten and partially consumed (i.e., bitten) seeds were distinguished, counted and added together to quantify the number of damaged seeds, assuming that even damaged seeds were not viable anymore. We then tested whether (i) individual functional responses of the two

species differed and (ii) how temperature scenarios affected both species. If an individual had died during either the starvation or feeding stage, their death was noted and the trial was repeated, except for the trials with both species together (Supplementary Note S2). We then (iii) tested whether multiple consumer effects between cricket species led to different functional responses compared to those predicted from individually kept species (i.e., additive, antagonistic or synergistic effect) across temperatures and resource densities. Finally, (iv) we tested whether mortality differed between the cricket species among temperatures when hosted individually or together.

Statistical analyses

Individual effects

A binomial generalized linear model was used to test whether seed consumption differed among the species treatments across temperatures for each of the three types of consumption (i.e., damaged, eaten, and damage + eaten, hereafter total damaged). Here, the proportion of seeds eaten was analyzed as a function of cricket species and interspecific groups (3 levels) and temperature (3 levels), as well as seed density (continuous). The interaction between cricket species and temperature was included to test whether the responses to temperature differed between species. After model fitting, we conducted an analysis of deviance to discern the main effects of species, temperature, and their interaction on seed consumption rates. A Tukey post-hoc comparison was used to adjust for multiple comparisons and further explain significant effects using the `emmeans` R package (Lenth 2023).

To analyze the functional responses and to identify the response type of *A. domesticus* and *G. bimaculatus* to different seed densities and across temperatures, the `fair_test` function of the `frair` R package (Pritchard et al. 2017) was used on the total seeds damaged. For responses that initially did not exhibit evidence of any specific form, we fitted Type II, III, and flexible responses curves using the `frair_fit` function of the `frair` R package (Pritchard et al. 2017). We retained the model that presented the lowest Akaike Information Criterion (AIC) value. All responses exhibited evidence for type II form (i.e., significant negative first-order term) except *A. domesticus* at 25 and 30 °C, but this model nevertheless was the best fit per AIC. As the consumed seeds was not replaced, Rogers' random predator equation was fitted to each subset using the `frair_fit` function (Pritchard et al. 2017):

$$N_e = N_0(1 - \exp(a(N_eh - T))) \quad (1)$$

where N_e refers to the number of seed eaten, N_0 is the initial seed density, a is the attack rate (i.e., the rate at which a consumer finds seeds), h is the handling time (i.e., the time needed to consume a seed) and T is the total experimental period (i.e., 24 h). Then, the shape of the functional response for the six subsets was compared using the 95% confidence intervals. The confidence intervals of each functional response were calculated using the *frair_boot* function of the *frair* R package, with 999 non-parametric bootstraps for a and h parameters per functional response subset (i.e., group and temperature; Pritchard et al. 2017). Significant differences among groups were noted when their confidence intervals diverged, and a lack of significance was inferred when the confidence intervals overlapped (Barrios-O'Neill et al. 2015).

Finally, the functional response ratio (FRR; Cuthbert et al. 2019) was calculated to amalgamate information from the attack rate and handling time parameters, by dividing the attack rate (a) by the handling time (h):

$$FRR = a/h \quad (2)$$

All statistical analyses were conducted in R v.4.3.1 (R Core Team, R Core Team 2021).

Multiple consumer effects

To quantify the interaction between species, we first calculated the interaction strengths (IS), i.e., the magnitude of the observed interactions between consumer and resource that includes both trophic and non-trophic interaction (Sentis and Boukal, 2018) as

$$IS = \text{seeds eaten}/\text{seed density} \quad (3)$$

We then used a two-step process to dissect the observed interaction strength (IS) into its parts: i) the component arising from feeding interactions, i.e., trophic interaction strength (IST), and ii) the component from other forms of interactions, i.e., non-trophic interaction strength (ISNT). Initially, we used a population-dynamic model, by using our functional response parameter estimates, to predict the IST (McCoy et al. 2012). Subsequently, ISNT was determined by calculating the discrepancy between the observed IS and the IST (Sentis et al. 2017; Cuthbert et al. 2021).

Functional response parameters obtained from the experiment with single crickets were applied to predict the feeding rates in scenarios involving multiple crickets, using the population dynamics model at each temperature:

$$\frac{dN}{dt} = -\frac{a_2 N}{1+a_2 h_2 N} P_2 - \frac{a_1 N}{1+a_1 h_1 N} P_1 - \frac{a_0 N}{1+a_0 h_0 N} P_0 \quad (4)$$

where N refers to seed density, P is cricket density (i.e., P_2 : *A. domesticus*; P_1 : *G. bimaculatus*), a is attack rate (i.e.,

a_2 : *A. domesticus*; a_1 : *G. bimaculatus*), and h is handling time (i.e., h_2 : *A. domesticus*; h_1 : *G. bimaculatus*) estimated in the previous experiment. To predict the seeds eaten in the multi-cricket experiment, the initial values of N and P_2 , P_1 , matched the seed and cricket densities of the specific experimental treatment. Additionally, to estimate the variance for each predicted value, we used a sensitivity analysis using the *sensRange* function in the R package *FME* (Soetaert and Petzoldt 2010). We generated 100 sets of randomized parameters using a Latin hypercube sampling algorithm (Soetaert & Petzoldt, 2010). The population dynamic model was applied to each of the 100 parameter sets generated randomly (Sentis et al. 2017; Cuthbert et al. 2021). This yielded the predicted number of seeds in each treatment in the absence of non-trophic interactions (Sentis et al. 2017; Veselý et al. 2019; Soto et al. 2024).

Subsequently, we calculated IST (i.e., trophic interaction strength), as follows:

$$IST = \text{Predicted eaten} / \text{seed density} \quad (5)$$

Lastly, we estimated the non-trophic interaction strength (ISNT) which refers to the magnitude of the interaction between multiple crickets aside from direct consumption and can thus mediate resource risk. Positive values refer to synergistic effects (i.e., combined crickets consume more seeds than predicted), while negative values refer to antagonistic effects (i.e., fewer seeds are eaten than predicted). Then, non-trophic interaction strength was calculated as follows:

$$ISNT = IS - IST \quad (6)$$

To investigate if there are differences in IS and/or ISNT among cricket groups, we fit two non-parametric two-way analysis of variance (Scheirer–Ray–Hare Test) using the *scheirerRayHare* function of *rcompanion* package in R (Mangiafico 2024). We used IS and ISNT as the response variable for each model, respectively, and temperature (3 levels), seed density (continuous), and their interaction as predictors. Subsequently, we performed a post-hoc test to identify which specific group comparisons are driving significant effects, using Bonferroni correction to control for Type I error rate.

Mortality

We analyzed the differences in mortality among the three temperatures for both species, with the species presented singularly and in combination. We counted the number of dead specimens in each group and tested the differences in the probability of mortality of crickets in single-species experiments using generalized linear models (GLMs) with a binomial distribution. The dependent variable in our models was the final status (for each species per replicate), as a binary

response (i.e., survived or dead) and the predictors were the temperature (20, 25, or 30 °C), species (*A. domesticus* or *G. bimaculatus*), and seed density (0, 5, 10, 20, 40), along with an interaction term between temperature and species to assess the differential effects of temperature on mortality between species. In addition, for the replicates with interspecific cricket groups, we employed generalized linear mixed models (GLMMs) to account for the non-independence of

observations, acknowledging that mortality within the same experimental unit could be correlated. The model structure was similar to the single-species GLMs, with species (2 levels), temperature (3 levels), seed density (continuous), and the interactions as fixed effects.

Results

Individual effects

With an increase in temperature, the ratio of damaged seeds generally decreased, whereas the ratio of completely eaten seeds increased in both *A. domesticus* and *G. bimaculatus*, either individually or in combination ($p < 0.01$; Table 1; Table S1). The proportion of seeds bitten, eaten, and their combined total were each significantly affected by the interaction between species and temperature (all $p < 0.01$) (Fig. 1, Table 1; Table S1). This interaction indicates that the comparisons between species treatments differed among temperatures, with for example *A. domesticus* and *G. bimaculatus* statistically similar at 25 °C but differing at warmer temperatures in terms of total consumption (Table S2). Seed density effects on consumption rates were significantly negative by a lower proportion of seeds being eaten as seed density increased (Table 1; Table S1).

The functional response curves of both species, *A. domesticus* (Fig. 2a) and *G. bimaculatus* (Fig. 2b), followed a type II form (Table 2). Increasing temperatures affected the attack rates and handling times of both species (Table 2). Thus, for *A. domesticus* these parameters increased from

Table 1 Analysis of deviance on binomial Generalized Linear Models (GLMs) evaluating the influence of species, temperature, seed density, and the interaction between species and temperature on three types of seed consumption (i.e., total number of damaged or eaten seeds). LR refers to likelihood ratio and Df to degrees of freedom

Total damaged:			
	LR	Df	P-value
Species	354.29	2	< 0.01
Temperature	93.44	2	< 0.01
Seed density	120.80	1	< 0.01
Species:Temperature	22.66	4	< 0.01
Seeds eaten			
Species	371.61	2	< 0.01
Temperature	158.43	2	< 0.01
Seed density	351.32	1	< 0.01
Species:Temperature	20.37	4	< 0.01
Seeds bitten:			
Species	298.72	2	< 0.01
Temperature	36.54	2	< 0.01
Seed density	5.80	1	0.01
Species:Temperature	23.02	4	< 0.01

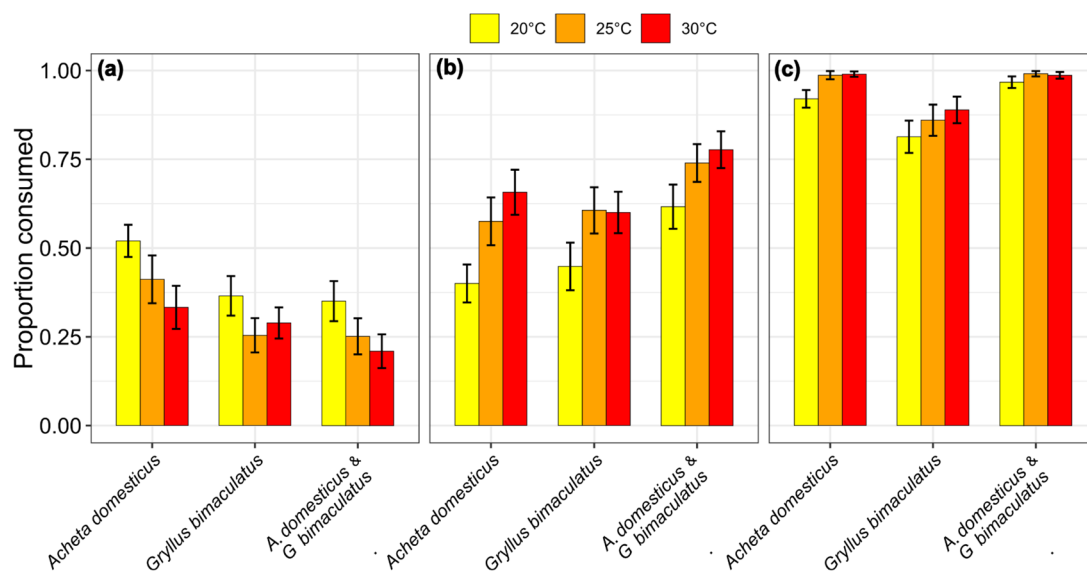


Fig. 1 Comparison of female *Acheta domesticus*, *Gryllus bimaculatus*, and both *A. domesticus* and *G. bimaculatus* combined millet seed damage over a temperature gradient (20, 25 and 30 °C), differentiat-

ing between bitten **a**, completely eaten **b**, and the overall damage to seeds (i.e., bitten and eaten seeds combined; **c**)

Fig. 2 Functional response curves for females of **a** *Acheta domesticus* and **b** *Gryllus bimaculatus* exposed to increasing millet seed density (5, 10, 20, and 40) across a temperature gradient from 20 (yellow), 25 (orange), and 30 °C (red), considering both completely and partially eaten seeds combined. Shaded areas are 95% confidence intervals

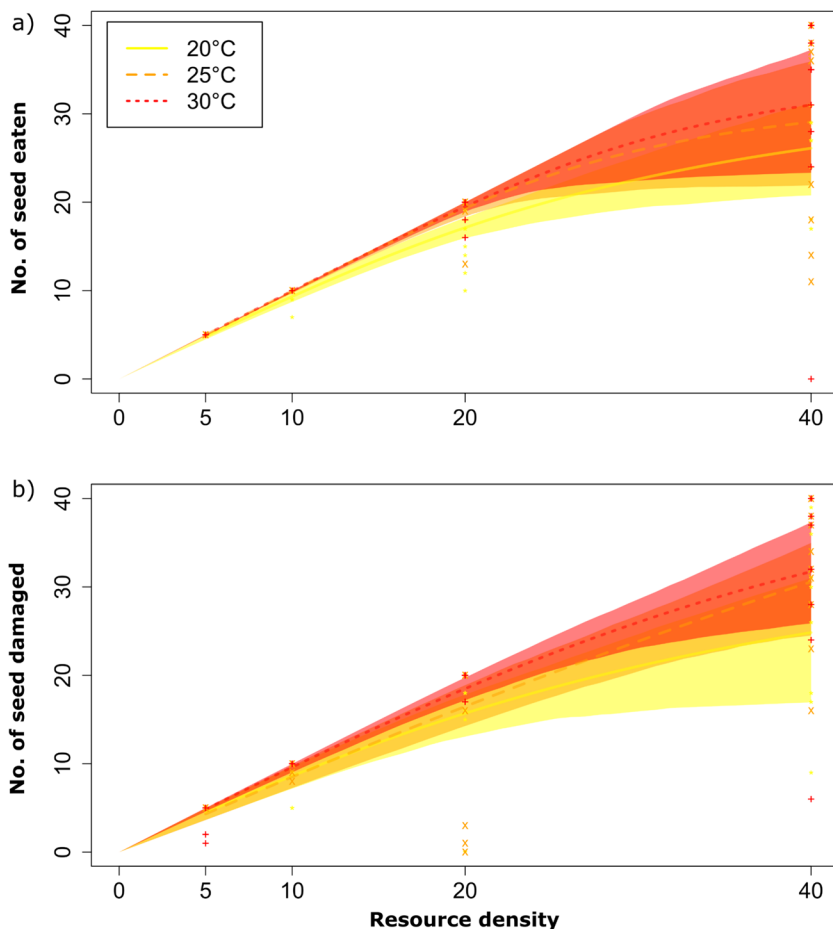


Table 2 Linear coefficients from type II functional responses attack rates and handling times on damaged millet seeds (i.e., completely and partially eaten combined) for female individuals of *Acheta domesticus* and *Gryllus bimaculatus* at three temperatures (20, 25, and 30 °C)

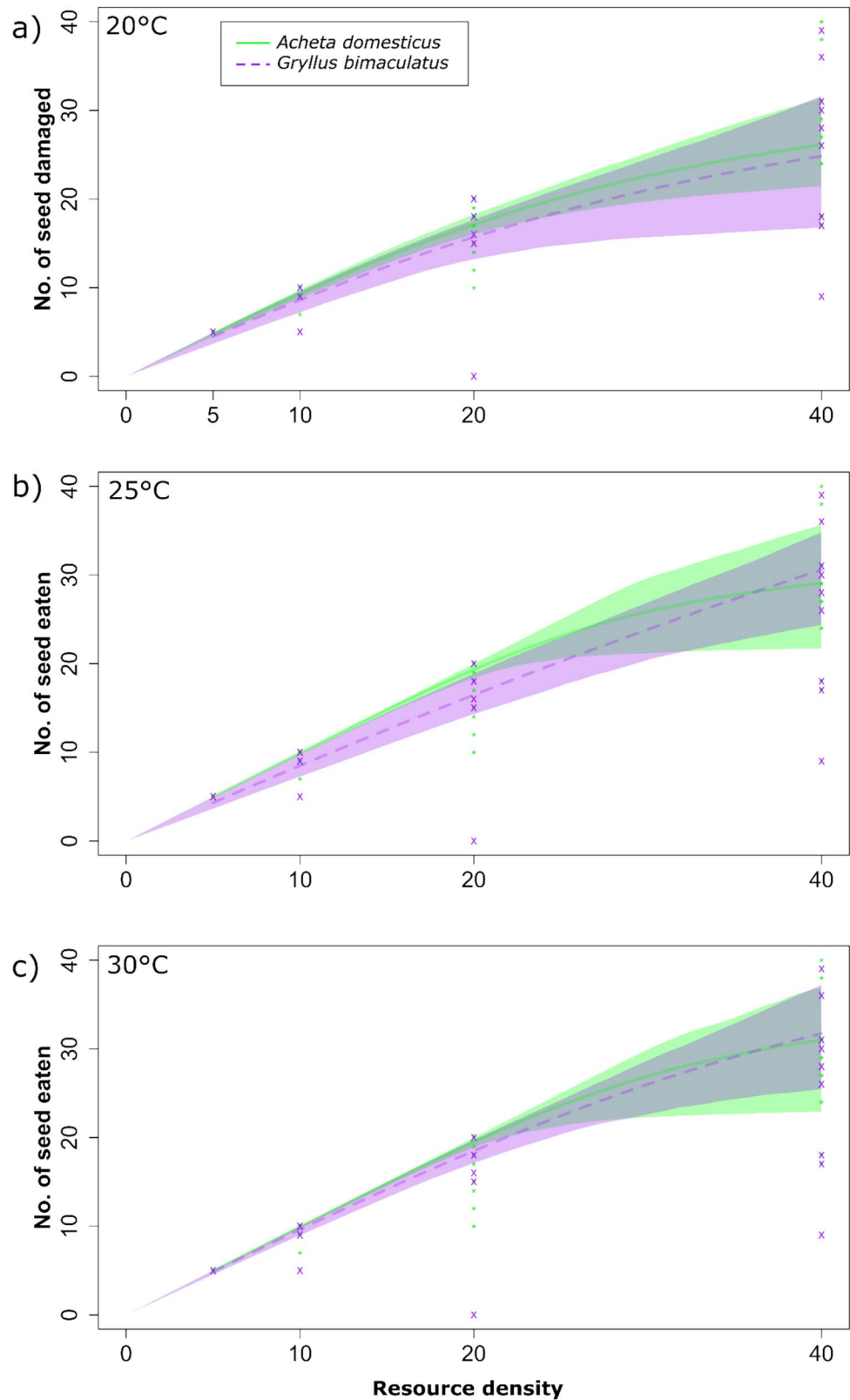
Temperature	Species	Estimate (<i>p</i> value)	Attack rate [a]	Handling time [h]	Functional response ratio [a/h]
20 °C	<i>Acheta domesticus</i>	-0.13 (<0.01)	3.620	0.027	134.07
	<i>Gryllus bimaculatus</i>	No evidence*	2.512	0.024	146.66
25 °C	<i>Acheta domesticus</i>	No evidence*	7.519	0.028	268.21
	<i>Gryllus bimaculatus</i>	-0.03 (<0.01)	2.073	0.009	230
30 °C	<i>Acheta domesticus</i>	-0.01 (0.02)	7.389	0.025	295.2
	<i>Gryllus bimaculatus</i>	-0.06 (<0.01)	3.995	0.019	210.26

*Type II based on the model selection

20 to 25 °C and decreased at 30 °C. The attack rate and handling time of *G. bimaculatus* decreased from 20 to 25 °C and then increased to 30 °C. Furthermore, *A. domesticus* generally reached higher attack rates and longer handling times compared to *G. bimaculatus*. Concomitantly, the functional response ratio (FRR) increased in both species with temperature, but in the case of *G. bimaculatus* it decreased from 25 to 30 °C.

The functional response curves of the two species exhibited general similarity across varying temperatures (Fig. 3). *Acheta domesticus* had a generally higher magnitude functional response at low-intermediate resource densities, which tended to converge at high densities.

Fig. 3 Comparison of functional response curves for females of *Acheta domesticus* and *Gryllus bimaculatus* exposed to different availabilities of millet seeds and temperature levels: **a** 20 °C, **b** 25 °C, and **c** 30 °C. Shaded areas are 95% confidence intervals

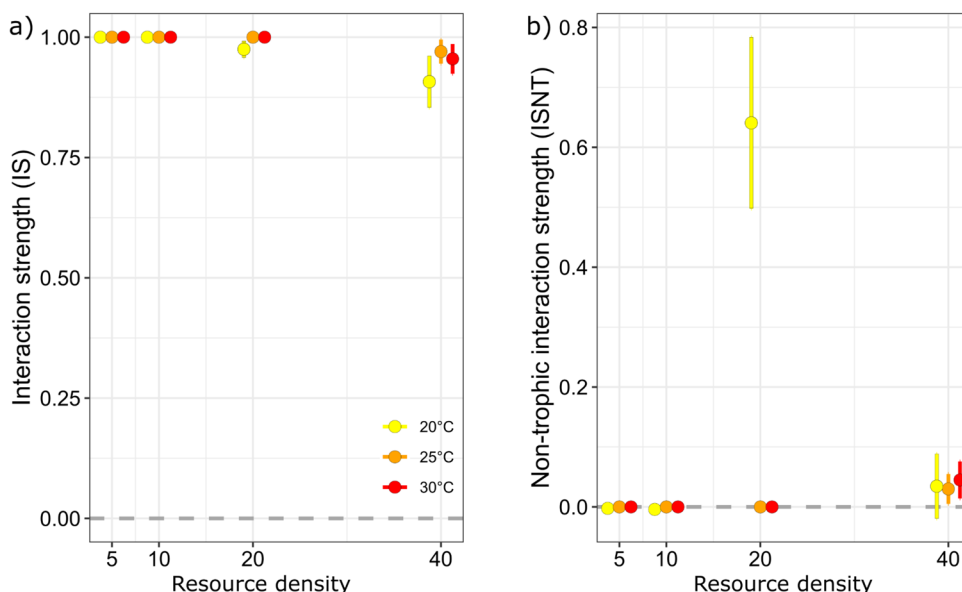


Multiple consumer effects

Interaction strengths (IS) of interspecific cricket pairs were

significantly positively affected by temperature ($H=7.27$, $p=0.02$; Table S3) and significantly negatively affected by seed density ($H=23.21$, $p<0.01$; Table S3) as individual

Fig. 4 Mean interaction strength and standard deviation (\pm SD) **a** and non-trophic interaction strength **b** across different seed densities at three temperature levels (i.e., 20, 25, and 30 °C)

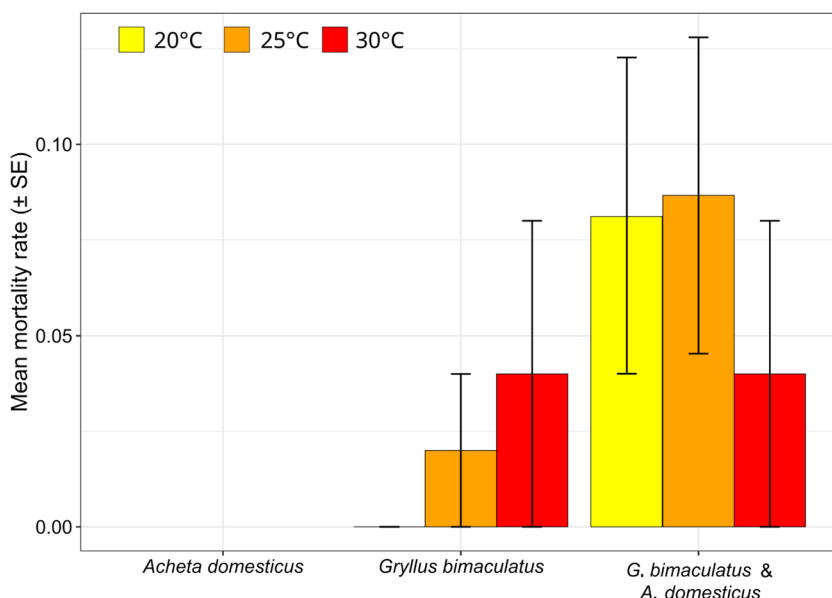


terms, while their interaction was not significant ($H=8.06$, $p=0.21$) (Fig. 4; Table S4). We found no differences among temperatures pairwise (all $p>0.11$) (Table S4). The strength of non-trophic interactions was in turn mediated by a significant interaction between temperature and seed density ($H=12.69$, $p=0.04$; Table S4), with ISNT generally neutral and becoming positive at a resource density of 20 seeds at 20 °C and 40 seeds at all temperatures (Fig. 4; Table S4).

Mortality

Mortality of individual crickets was generally very low, whereby no mortality was observed for *A. domesticus*, while *G. bimaculatus* mortality ranged from 0 (20 °C) to 0.04 (i.e. 4%) (30 °C) on average. When both species were together, the mortality ranged from 0 to 0.08 (i.e. 8%) on average. Mortality did not differ between species in either the singular or interspecific groups ($z=1.38$, $p>0.05$; $z=1.10$, $p>0.05$). The mortality of crickets was not significantly affected by temperature for either species, in both the singular ($z=0.46$, $p>0.05$) and interspecific combinations ($z=0.45$, $p>0.05$; Table S5). There

Fig. 5 Mean mortality (\pm standard error SE) of *Acheta domesticus* and *Gryllus bimaculatus* at varying temperatures for 20 °C (yellow), 25 °C (orange), and 30 °C (red)



was also no significant effect of seed density on singular cricket mortality ($z = 2.79$, $p > 0.05$), but a significant positive effect in the interspecific group ($z = 2.45$, $p < 0.05$; Fig. 5; Table S5). Although the observed differences were minimal, the mortality of *A. domesticus* when kept with *G. bimaculatus* increased from five to seven individuals overall compared to its mortality when kept individually (Supplementary Note S2).

Discussion

The introduction and spread of non-native orthopterans presents a neglected ecological and economic threat (Kulesa et al. 2023a, b). In particular, this group's potential to impact agriculturally relevant crops has not been fully assessed. *Acheta domesticus* and *Gryllus bimaculatus* are two non-native and widely distributed cricket species in Europe that are often found in urban areas (Weissmann and Rentz, 1977; Gardiner 2009). According to our first hypothesis, the individual damage to seeds of both species did not differ significantly. Temperature increases tended to heighten the functional response but did not have a clear effect on mortality. The assessment of the potential impact of two possibly co-occurring non-native Orthoptera species using functional response analysis indicated that both species could present a phytosanitary threat which is exacerbated by rising temperatures and their overlapping invaded range.

Acheta domesticus versus *Gryllus bimaculatus*

The density-dependent feeding tendencies of a consumer play a pivotal role in shaping the interactions with its resources (Faria et al. 2023). Here, higher seed densities correlated with an increase in the ratio of partly consumed seeds and a decrease in the ratio of completely consumed seeds. Therefore, higher temperatures tended to reduce instances of partial consumption due to several ecological reasons (e.g., effects of handling, new group members, new food), but also potentially rising physiological metabolic requirements functioning interactively. Despite slight differences in the observed damage to millet seeds between female individuals of *A. domesticus* and *G. bimaculatus*, they were not found to be significant. The functional responses of both species followed type II curves, with subtle variations, indicating that the predator's consumption rate decreased with increasing seed density (Holling 1959). This means that consumption rates are highest at low resource densities, for then declining asymptotically and approaching a maximum rate as the consumer's efficiency in capturing seed saturates. This is often observed

in consumers that have limitations on their feeding efficiency due to factors such as handling time (Scriber & Slansky 1981; Riechert and Lockley 1984). As seed density increases or temperature accelerates metabolism, the consumer is enabled to capture more seeds up to a certain point, after which they become limited by handling time, which leads to the curve plateauing (Rall et al. 2010; Faria et al. 2023). This finding indicates that the phytosanitary threat presented by non-native orthopterans, at least in the case of *A. domesticus* and *G. bimaculatus*, is not species-specific. This suggests that the numerous non-native orthopterans currently found in Europe (Kulesa et al., 2023b) present a so far unrealized threat.

The extent of the threat posed by non-native orthopterans to agricultural crops will, however, likely also depend on the competitive interactions with native orthopterans and other ecologically and functionally similar species, as well as the efficacy of Integrated Pest Management (IPM) strategies currently in place (Ehler 2006; Koppenhöfer et al., 2013). Existing IPM practices, such as early detection and exclusion, natural predators, or targeted pesticide use, may play a crucial role in mitigating the potential impact of these non-native species, though further assessment of their effectiveness in this specific context is warranted.

The impacts of climate change

Increasing global temperatures will alter the distribution of numerous species in the future, including non-native species that tend to be more physiologically adapted to higher and fluctuating temperatures and thus gain a competitive advantage over native species (Thomas 2010). This temperature increase also influences the metabolic processes, reproductive capabilities, as well as feeding rates of species (Neven 2000). Especially in non-native insects, warmer temperatures in the invaded range may align better with conditions that favor them. As such, temperature increases may result in heightened metabolic activities and thus increased overall activity levels of the invader up to a certain thermal optimum (i.e., a temperature that maximizes the fitness of a given trait such as survivability or consumption rate; Angilletta et al. 2002). This surge in activity can lead to heightened nutritional demands, thereby elevating the rate of consumption (Youngblood et al. 2023). Here, the results indicate that increasing temperatures lead to rising consumption rates and also a higher functional response in both species. This trend was particularly evident for *A. domesticus*, as the consumption rates and correspondingly the functional response continuously increased with rising temperatures, whereas for *G. bimaculatus*, the functional response was generally highest at 25 °C. While this difference may be due to different temperature optima in either species, the overall damage exerted to seeds was similar in both species (Lachenicht et al. 2010).

Generally, the consumption of seed as well as the exerted damage to seeds are a function of a consumer's handling time and attack rate (Haubrock et al. 2020b). Here, *A. domesticus* reached higher attack rates but showed longer handling times. Interestingly, the attack rate and handling time for *A. domesticus* increased from 20 to 25 °C but decreased from 25 to 30 °C, while the opposite pattern was observed for *G. bimaculatus*. The functional response ratio (i.e., the impact) of *A. domesticus* reached its peak at 30 °C and for *G. bimaculatus* at 25 °C, substantiating the relevance of differing temperature *optima*. The decrease in attack rates and handling times from 25 to 30 °C for *A. domesticus* might be attributed to the onset of saturation as the number of seeds increased. Meanwhile, increasing attack rate and handling time from 25 to 30 °C for *G. bimaculatus*, despite the functional response being highest at 25 °C, could reflect differential responses between search efficiency and handling time toward resources with temperature, which have been shown to scale differently with temperature (Rall et al. 2012).

Cumulative impact

The cumulative feeding impact of non-native cricket species can have far-reaching implications for the viability of seeds, the productivity of essential agricultural crops, as well as consequences for food security (Riegler 2018). The interaction of both species yielded an additive impact in terms of damage to millet seeds when considering the overall damaged (i.e., partly and completely consumed) seeds. This effect held across most resource densities and temperatures but became synergistic at intermediate-high resource densities across temperatures. The non-replacement of seeds in our experiment could have constrained the detection of multiple consumer effects at low resource densities. The emergent synergy at high seed densities can thus be attributed to conditions that were not resource-limited and which enabled detection of positive non-trophic interactions experimentally. To prevent complete depletion of resources, future studies should consider elevating or continually replacing the number of seeds, as some trials in the present study resulted in total consumption, potentially limiting the observable impact at lower resource densities. We, however, found a relatively low occurrence of non-trophic interactions overall and a complete absence of antagonisms, whereas past research has found that warming stimulates antagonistic interactions in aquatic invertebrates (Cuthbert et al. 2021). This indicates that these cricket species assessed do not impede each other's feeding interactions when present in interspecific pairs, irrespective of future climate warming and different resource availability. Indeed, our evidence suggests that they can even be facilitative consumers at high resource densities.

Mortality

The intricate interplay between rising temperatures and the co-occurrence of several native and non-native species (Sorte et al. 2013) plays a pivotal role in shaping mortality dynamics within populations (Cuba-Diaz et al. 2023) and invasion dynamics (Soto et al., 2023b; Haubrock et al., 2024). Here, we found a very low mortality in general, which was not significantly mediated by temperature or resource availability. Mortality was, however, slightly elevated in the interspecific cricket group.

Any potential differences in mortality between individual species and interspecific pairs with temperature, albeit not statistically significant here, could be linked to increased stress posed by interspecific interactions under limited space and resource availability. However, ethological studies are needed to fully understand the drivers of mortality under these ecological contexts, such as through mechanisms of stress hormone changes, aggression, or cannibalism. Past research has shown that increases in temperature cause increasing activity levels and stress in several taxa (e.g. Tylanakis et al. 2008). Mortality, despite already being low, could be further affected by the fact that natural habitats are considerably larger than the arenas used in the experiments, increasing the stress due to the inability to avoid each other (Uiterwaal et al. 2019), and thus raising concerns as to whether the observed mortality can be compared to natural conditions. The significant effect of food availability on mortality in interspecific groups which we detected needs to be investigated further for biological meaning, by involving a larger number of replicates and higher seed densities exceeding 40 seeds, paired with behavioral assays.

Phytosanitary threat

The increase in global temperatures may further intensify the negative impacts of non-native orthopterans. While *G. bimaculatus* showed increased feeding behavior at 25 °C and *A. domesticus* at 30 °C, this temperature difference does not imply a substantive contrast in their consumption rates. Both species can tolerate elevated temperatures (Lachenicht et al., 2010). Therefore, the phytosanitary threat that *A. domesticus* and *G. bimaculatus* present is a growing concern due to their association with anthropogenically altered environments (Weissmann and Rentz, 1977; Samways et al. 1996; Żurawlew and Rutkowski 2022). With their ability to further expand their range, these species will hold the potential to significantly impact both biodiversity and economic sectors. However, certain parts of their ranges may already be nearing the upper thermal tolerance threshold, potentially increasing extirpation risks under further warming, especially as feeding rates or other ecological traits could decline beyond thermal *optima*.

Cricket feeding behavior here has been observed to have a negative impact on seeds, where higher seed densities led to an increase in the proportion of damaged seeds. While damage to seeds was observed, further research is needed to confirm if such seeds are rendered unusable or non-viable for growth. This adaptive shift in feeding patterns poses a considerable risk to plant reproduction as well as agricultural productivity. Additionally, both species exhibited an overall comparable capacity to cause seed damage, emphasizing the need for effective management strategies, also regarding the increase in non-native species in general. The co-occurrence of these species has been found to yield an additive if not synergistic effect on the seed damage, suggesting the potential compounded negative outcomes on important crops. Considering these factors, monitoring of population sizes and further spread of these species is essential to limit potential phytosanitary risks and to protect both local ecosystems as well as human livelihoods. One potential direction for future research could be to assess the phytosanitary threat posed by non-native orthopterans under more ecologically relevant conditions, such as natural field settings, rather than in controlled laboratory environments. Such studies would provide insight into how environmental complexities (including more diverse resource communities) influence feeding behavior, interspecific interactions, and crop damage. This approach could enhance our understanding of their threat to agricultural ecosystems.

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Author contributions AKK, PJH, and AK designed the study. AK, PB, MT, and PJH performed the experiments. AK and IS analysed the obtained data. IS, RNC, and AK visualized the results. AK, IS, and PJH wrote the first draft of the manuscript. All authors contributed to the final draft of the manuscript.

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Declarations

Competing Interests The authors have not disclosed any competing interests.

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