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Climate change, host plant availability, and irrigation shape future region-specific distributions of the *Sitobion* grain aphid complex

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Abstract

BACKGROUND: Understanding where species occur using species distribution models has become fundamental to ecology. Although much attention has been paid to invasive species, questions about climate change related range shifts of widespread insect pests remain unanswered. Here, we incorporated bioclimatic factors and host plant availability into CLIMEX models to predict distributions under future climate scenarios of major cereal pests of the *Sitobion* grain aphid complex (*Sitobion avenae*, *S. miscanthi*, and *S. akebiae*). Additionally, we incorporated the application of irrigation in our models to explore the relevance of a frequently used management practice that may interact with effects of climate change of the pest distributions.

RESULTS: Our models predicted that the area potentially at high risk of outbreaks of the *Sitobion* grain aphid complex would increase from 41.3% to 53.3% of the global land mass. This expansion was underlined by regional shifts in both directions: expansion of risk areas in North America, Europe, most of Asia, and Oceania, and contraction of risk areas in South America, Africa, and Australia. In addition, we found that host plant availability limited the potential distribution of pests, while the application of irrigation expanded it.

CONCLUSION: Our study provides insights into potential risk areas of insect pests and how climate, host plant availability, and irrigation affect the occurrence of the *Sitobion* grain aphid complex. Our results thereby support agricultural policy makers, farmers, and other stakeholders in their development and application of management practices aimed at maximizing crop yields and minimizing economic losses.

Supporting information may be found in the online version of this article.

Keywords: climate change; CLIMEX; irrigation; species distribution

1 INTRODUCTION

Global climate change, especially changes in temperature and precipitation, is altering dynamics of pests and host plants in agricultural ecosystems.[1] The observed global mean surface temperature for 2006–2015 was 0.87 °C (~1.6 °F) warmer than that of 1850–1900, and it is predicted to continue to increase by 0.2 °C per decade in the foreseeable future.[2] In response to such changes, many species, including insect pests, are predicted to shift their geographic range to higher latitudes and higher elevations.[3–5] Species distribution models are emerging as tools to explicitly forecast species occurrence in space and time. Many studies focus on modeling species of conservation concern or invasive species that have implications for international trade and quarantines. Examples of the latter include forest pests like the coconut hispine beetle (*Brontispa longissimi*)[6] and the fall webworm (*Hyphantria cunea*)[7] and agricultural pests like the

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greenbug (*Schizaphis graminum*)[8] and the Russian wheat aphid (*Diuraphis noxia*).[9,10] To date, less attention has been paid to cosmopolitan crop pests (with a few exceptions, e.g., maize leafhopper (*Dalbulus maidis*)[11] and potato tuber moth (*Phthorimaea operculella*)[12]).

The English grain aphid (*Sitobion avenae*), Indian grain aphid (*Sitobion miscanthi*) and Japanese grain aphid (*Sitobion akebiae*) are major global pests of wheat.[13,14] The three species have very similar morphological and life history characteristics, which leads to frequent misidentification and misreporting in the literature.[15] Additionally, all three species damage wheat by (i) sucking on the developing ear and spikelet, (ii) excreting honeydew that hinders leaf photosynthesis,[16] (iii) and vectoring barley yellow dwarf viruses.[17] Together these actions lead to losses in wheat quantity (i.e., yield losses, up to 9–42% in regions with severe infestations)[17–21] and quality (i.e., reduced protein).[18]

Sitobion avenae is reported to be an ubiquitous and dominant pest of wheat in most of the world, including Europe, North America, South America, and China.[22] *Sitobion miscanthi* is reported in India, Australia, and New Zealand.[23–25] However, since 1999 the dominant wheat aphid in China had been characterized as *S. miscanthi* rather than *S. avenae*.[15] Consequently, both *S. avenae* and *S. miscanthi* are used to identify wheat aphids in China. *S. akebiae*, which is only reported in Japan and Korea, is sometimes treated as a subspecies (*S. avenae akebiae*).[25,26] Results of morphological and genetic analyses failed to show clear differences among species. For example, since morphological characteristics of the species overlapped and average values were very close, the three aphid species could not be distinguished and synonymizing *S. miscanthi* and *S. akebiae* under *S. avenae* was proposed.[26] Divergence at the COI-gene between *S. miscanthi* and *S. avenae* is about 1.5%, which also suggests that these two aphids are not easily distinguished.[27] The need for a thorough revision of Asian *Sitobion* has been noted.[28] As a consequence of their similar characteristics in response to temperature (Supporting Information Fig. S1) and the related taxonomic uncertainty, we treated these three *Sitobion* species as a single complex.

Forecasting changes in distribution of the *Sitobion* grain aphid complex at a global scale is relevant for pest management. Currently, no forecasts of global distribution changes exist for this pest complex; however, a number of factors can impact its potential distribution. Firstly, as ectotherms with small body size and fragile cuticle, these aphids are sensitive to changes in climate factors, especially extreme high temperature,[28] which can affect fitness related performance, including development, reproduction, and survival.[22,28,29] Secondly, biotic interactions, including pest-host interactions, can shape species distribution patterns at regional, continental, and global levels.[30] The presence/absence and condition of host plants can directly affect the occurrence and distribution of pests.[31] Thus, host plant availability should be incorporated into species distribution models of agricultural pests. To do this, previous studies have used host plant relative abundance,[32] productivity,[12] presence or absence.[33] However, these studies did not account for potential climate-change-driven shifts in host plant availability. To address this, an index of host plant availability (θ) has been proposed.[31]

Accounting for management practices targeted at pests or hosts may improve predictions generated by species distribution models, since these practices can mitigate some impacts of climate change.[34] One such practice is irrigation, which is applied to 40% of the global cropland.[35] Water is the most important limiting factor for wheat production throughout large parts of the world,[36–38] and wheat yields with irrigation can be four to five times higher than without.[38] In additional to delivering water, irrigation can, to an extent, reduce temperatures at a microscale. For instance, irrigation can reduce the daytime land surface temperature by 1.6 °C in July in Nebraska, USA.[39] By changing plants and the environment, irrigation directly and indirectly can impact aphids and other pests, including their development time, fecundity, and adult weight.[40–42] Via these same direct and indirect mechanisms, management practices like irrigation can even alter species assemblages.[43] Because these potential effects, incorporating management practices into studies of future species distributions is important.

Species distribution patterns of crop pests in agroecosystems are shaped by biotic factors, environmental variables, and management practices. Predicting changes in distribution patterns of pests is increasingly important in light of climate change, and such predictions will be essential to adapt agricultural production practices in ways that maximize yields and minimize economic losses. Such studies will also yield a better understanding of how interactions between pests and host plants are affected by global climate change and management practices. We used CLIMEX version 4 (Hearne Scientific Software Pty Ltd, Australia) to predict the distribution of the *Sitobion* grain aphid complex under future climate scenarios. We incorporated host plant availability and irrigation in our models to understand their roles in shaping pest distributions. Understanding the potential distribution of aphids in relation to host plant availability and irrigation can help farmers and decision makers optimize pest management practices in the face of climate change.

2 MATERIALS AND METHODS

2.1 CLIMEX model

We used the 'Compare Locations' function in CLIMEX[44,45] to build models for the *Sitobion* grain aphid complex and their host plant *T. aestivum*. CLIMEX produces an ecoclimatic index (EI), which indicates the climate suitability of a location for a particular species. We calculated EI (Eqn (1)) using two indices: (i) the annual growth index (GI_A), and (ii) the stress index (SI). GI_A (Eqn (2)) is based on weekly growth index (GI_W, Eqn (3)), which describes how weekly mean temperature (TI_W) and weekly mean soil moisture (MI_W) impacts population growth. We calculated SI (Eqn (4)) based on cold stress (CS), heat stress (HS), dry stress (DS) and wet stress (WS). All of the above indices are all dimensionless.

$$EI = GI_A \times SI \tag{1}$$

$$GI_A = \left(100\left(\sum_{i=1}^{52} GI_W\right)/52\right) \tag{2}$$

$$GI_W = TI_W \times MI_W \tag{3}$$

$$SI = (1-CS/100)(1-DS/100)(1-HS/100)(1-WS/100) \tag{4}$$

EI ranges from 0 to 100: 0 indicates a location where the climate is completely unsuitable, and 100 indicates a location where the climate is optimal in all respects.[44] We divided the EI values into four categories relating to population growth and stability, following previous studies.[6,31,46] An EI of 0 suggests an inability to

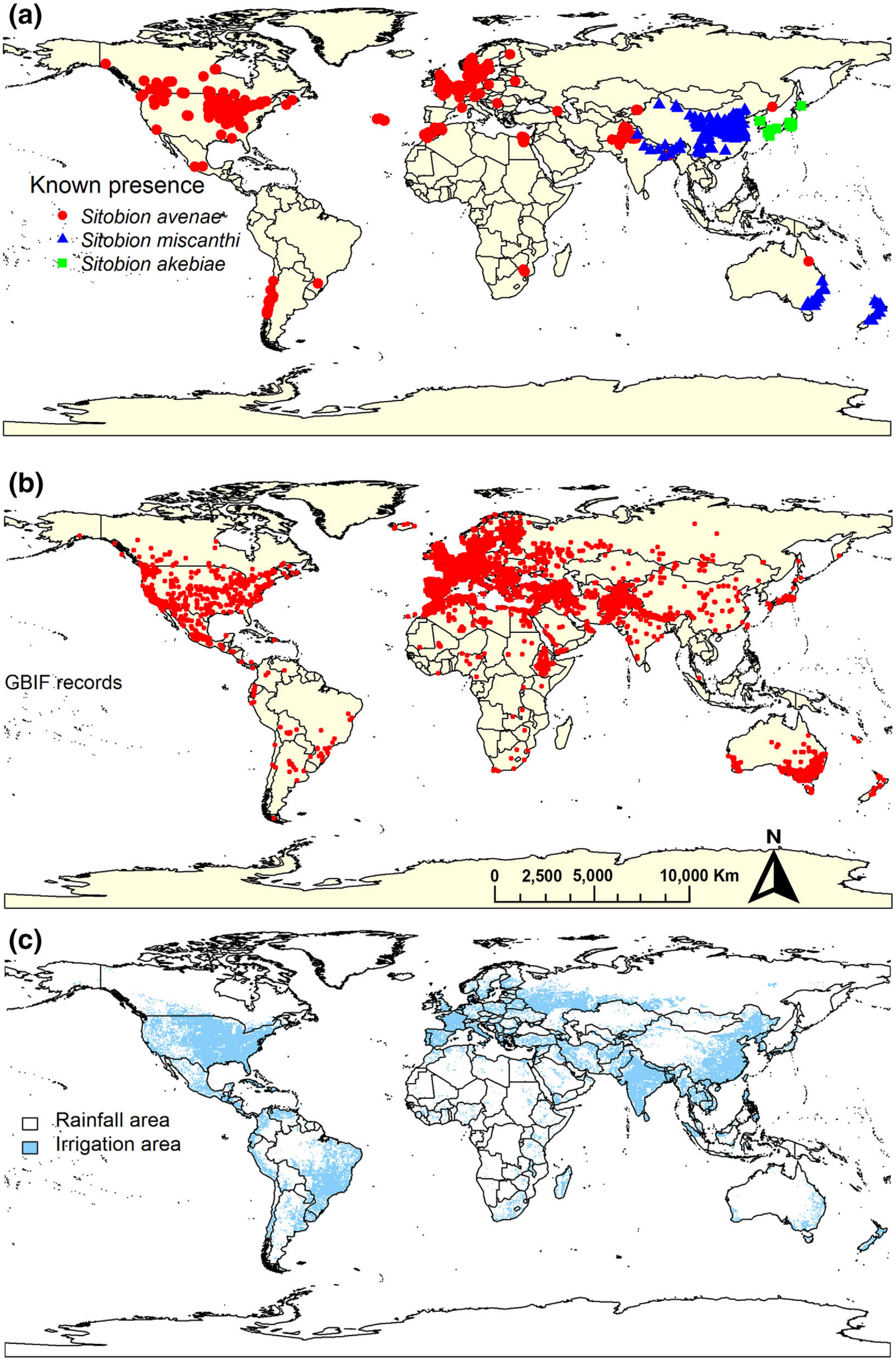

Figure 1. Geographical distribution of the *Sitobion* grain aphid complex and host plant *Triticum aestivum*. (a) Points represent distribution records of the grain aphid complex, *Sitobion avenae* (red) and *Sitobion miscanthi* (blue) and *Sitobion akebiae*. (b) Red dots represent distribution records of host plant *Triticum aestivum* from GBIF that were filtered. (c) Global map of irrigation areas.

support long-term establishment of the species, an EI between 0 and 10 (0 < EI≤10) suggests conditions allowing marginal population growth, an EI between 10 and 20 (10 < EI≤20) suggests conditions are favorable for population growth, and an EI > 20 suggests conditions are very favorable and able to support a large population.

2.2 Data collection

2.2.1 *Current global distribution of the Sitobion grain aphid complex and* T. aestivum

Distribution records of *S. avenae* (Fig. 1(a)) were compiled from two online databases (i) Global Biodiversity Information Facility (GBIF, www.gbif.org) and (ii) Early Detection and Distribution Mapping System (EDDMaps, www.eddmaps.org) and from published studies.[24,47–52] Distribution records of *S. miscanthi* and *S. akebiae* (Fig. 1(a)) were compiled from GBIF and published studies that include locations for *S. miscanthi*[24,25,28,53–62] and *S. akebiae*.[63–70] Distribution records of the host plant, *T. aestivum* (Fig. 1(b)) were obtained from GBIF only. Latitudes and longitudes for locations in published studies that did not report these values were obtained from mapLocation (see https://github.com/sjfkai/mapLocation). Pest and host database records with no geographic coordinates were excluded. The pest and host occurrence datasets were limited to the period 1950 to 2021 because long-term historical records do not reflect current climatic conditions. After removing duplicate records and obvious errors (e.g., points in polar regions or oceans), our dataset included 714 records of the *Sitobion* grain aphid complex from 85 countries and 21 563 records of *T. aestivum* from 110 countries.

2.2.2 *Climate data*

High-resolution (0.5 × 0.5°) climate data for the period 1951–2020 were obtained from the Climate Research Unit (CRU, University of East Anglia) gridded time-series (TS) dataset (version 4.05; available at https://data.ceda.ac.uk/badc/cru/data/cru_ts/cru_ts_4.05/data). Five types of meteorological data were extracted: monthly average maximum air temperature, monthly average minimum air temperature, average monthly rainfall (mm), average relative humidity at 9 a.m., and average relative humidity at 3 p.m. These data were used to build models under the natural rainfall scenario (see below). For future estimates, values for the same five meteorological indices were generated from the Coupled Model Inter-comparison Project Phase 6 (CMIP6) under two scenarios, SSP1-2.6 (SSP126) and SSP5-8.5 (SSP585). These two scenarios represent a low-emissions scenario and a high-emissions scenario, respectively. By 2100, the SSP126 scenario shows a mean warming of 2 °C (relative to 1880–1900), while the new SSP585 scenario shows 5 °C of warming. We used 23 Global Climate Models (GCMs) available in the WorldClim database (www.worldclim.org; see Supporting Information, Table S1) to obtain a multi-model ensemble mean climate dataset for the two target time periods, mid-century (2041–2060) and the end of century (2081–2100).

2.2.3 *Irrigation data*

We used two irrigation scenarios: (i) no artificial irrigation (i.e., natural rainfall only) and (ii) top-up irrigation of up to 2.5 mm day^{-1} throughout the year.[71] The top-up scenario, modelled in CLIMEX, would first judge the amount of rainfall. If a given week at any location had more than 17.5 mm of rainfall, no irrigation was added; however, if there was less than 17.5 mm, CLIMEX would make up the deficit by adding irrigation up to the 17.5 mm weekly threshold. The composite potential distribution model was built based on an updated version of global irrigation areas (Fig. 1(c)) reported by Sieber et al.[72] If a location was irrigated, the EI accounting for irrigation was used; otherwise, the EI accounting only for natural rainfall was used.

2.3 Fitting CLIMEX parameters

2.3.1 *Sitobion grain aphid complex model*

The temperate template in CLIMEX (Table 1) was selected as the initial base to develop the model for the *Sitobion* grain aphid complex, since these globally widespread aphids prefer temperate climates. Parameter values took into account intensive previous studies on the biology of aphids named *S. avenae* or *S. miscanthi* and their known global distributions. Since performance data under different temperatures for aphids named *S. akebiae* were not available, we did not incorporate information for this species. The lower development temperature ranges from 2.3 to 4 °C for *S. avenae and S. miscanthi*,[73,74] so the limiting low temperature (DV0) was set at 4 °C. The optimal temperature range was set between 15 and 23 °C since *S. avenae* and *S. miscanthi* are commonly reared in the lab at 13 ± 1 °C (for sexual clones) or 20 ± 2 °C (for asexual clones).[75–77] The limiting high temperature (DV3) was set at 32 °C, since at this daily maximum temperature the intrinsic rate of increase (r_m) and fitness of *S. miscanthi* started to decline.[28] The limiting low soil moisture (SM0) was set to 0.01 (all soil moisture parameters are dimensionless) to satisfy the known distribution of the *Sitobion* grain aphid complex in Middle Eastern countries, such as Afghanistan, Iran, and Saudi Arabia. This value was chosen to better fit the current aphid presence to ensure that regions with lower soil moisture are included in the model and to correspond to values used in similar studies on insects.[7,8] The lower (SM1) and upper soil moisture (SM2) for optimal development were set to 0.15 and 1.0 to better match current distribution of the *Sitobion* grain aphid complex. The upper soil moisture for development (SM3) was set at 1.4, which allowed for persistence in known distribution regions in South America. The number of degree-days required by *S. avenae* to develop from nymph to adult was about 142 above 3 °C.[75] Accordingly, we set 140°days to agree with known distribution data.

Mated sexual females of *S. avenae* can produce diapausing eggs to tolerate cold periods.[77] Indicators of winter diapause (DPSW) was set to 0, referring to winter diapause. Short days and low temperature conditions can induce sexual morphs.[77,78] Normally, eggs can be obtained in the laboratory with photoperiod $<$ 14 h and temperature $\leq$ 15 °C.[78,79] Therefore, the day length of diapause induction (DPD0) was set to 12 h, and the diapause induction temperature (DPT0) was set at 15 °C. The diapause termination temperature (DPT1) was set at 5 °C, based on laboratory studies.[77] The minimum number of days required to complete diapause development (DPD) was set to 40 days.[77,80] The cold stress temperature threshold (TTCS) was set at −20 °C in accordance with the supercooling point (the temperature when the insect's body fluids begin to freeze, which can reflect cold tolerance) of *S. avenae*.[75] The cold stress temperature rate (THCS, −0.00015 week^{-1}), degree-day cold-stress threshold (DTCS, 25 °C days above DV0) and its accumulation rate (DHCS, −0.00001 week^{-1}) were set to match the current distribution of the *Sitobion* grain aphid complex. The heat stress temperature threshold (TTHS) was set at 32 °C, the same value as the limiting high temperature (DV3). Similarly, the dry stress threshold (SMDS) value was set to be the same as the limiting low soil moisture (SM0 = 0.01), and the wet stress threshold (SMWS) was set to be the same as the limiting high soil moisture (SM3 = 1.4). The rate of heat (0.0001 week^{-1}), dry (−0.001 week^{-1}) and wet stress (0.0002 week^{-1}) were set to match the current distribution of the *Sitobion* grain aphid complex.

Table 1. CLIMEX parameter values for the *Sitobion* grain aphid complex and host plant *T. aestivum*

Parameters	Descriptions	T. aestivum **Shabani F and Kotey (2015)**[81]	T. aestivum Current model	Temperate template	S. avenae Current model
Temperature					
DV0	Lower temperature threshold (°C)	4	4	8	4
DV1	Lower optimum temperature (°C)	14	14	18	15
DV2	Upper optimum temperature (°C)	25	25	24	23
DV3	Upper temperature threshold (°C)	32	**35**	28	32
Moisture					
SM0	Lower soil moisture threshold		**0.016**	0.25	0.01
SM1	Lower optimal soil moisture		**0.15**	0.8	0.15
SM2	Upper optimal soil moisture		**1**	1.5	1
SM3	Upper soil moisture threshold		**1.35**	2.5	1.4
Cold stress					
TTCS	Cold stress temperature threshold (°C)	−10	−25	0	−20
THCS	Cold stress temperature rate (week^{-1})	−0.001	−0.0005	0	−0.0002
DTCS	Degree-day cold-stress threshold		20		25
DHCS	Degree-day cold-stress accumulation rate		−0.00001		−0.00001
Heat stress					
TTHS	Heat stress temperature threshold (°C)	39	39	30	32
THHS	Heat stress temperature rate (week^{-1})	0.005	0.0015	0.005	0.0001
DTHS	Degree-day heat-stress threshold				-
DHHS	Degree-day heat stress threshold				-
Dry stress					
SMDS	Dry stress threshold		**0.01**	0.2	0.01
HDS	Dry stress rate (week^{-1})		**−0.00007**	−0.005	−0.001
Wet stress					
SMWS	Wet stress threshold	3	**1.35**	2.5	1.4
HWS	Wet stress rate (week^{-1})	0	**0.019**	0.002	0.001
Threshold heat					
PDD	Effective accumulated temperature (degree-days)		**500**	600	140
Diapause					
DPD0	Diapause induction day length (h)	-	-	-	12
DPT0	Diapause induction temp. (°C)	-	-	-	14
DPT1	Diapause termination temp (°C)	-	-	-	5
DPD	Diapause development days (days)	-	-	-	40
DPSW	Diapause in winter (0) or summer (1)	-	-	-	0
Irrigation scenario		-	2.5 mm day^{-1} as top-up irrigation	-	2.5 mm day^{-1} as top-up irrigation

2.3.2 Triticum aestivum *model*

Published parameter values for *T. aestivum* were used initially to build our *T. aestivum* model.[81] These values were adjusted iteratively based on physiological data from other studies to better match the current global distribution of *T. aestivum*. The parameters that provided the best fit for the distribution of *T. aestivum* at a global scale were used for further modeling (summarized in Table 1; bold indicates the adjusted values).

The upper temperature threshold (DV3) was set at 35 °C, above which enzymes in *T. aestivum* cease to function.[38] In naturally dry areas, water availability is a key determinant of *T. aestivum*. In our *T. aestivum* model, we set the lower soil moisture threshold (SM0) to 0.01 and lower optimal soil moisture (SM1) to 0.15. With these values, the model can satisfy the dry conditions with low soil moisture such as in Xinjiang province, China and the western USA. *T. aestivum* is especially sensitive to drought stress between the flowering and ripening stages.[82] In order to reflect this, the upper optimal soil moisture value (SM2) was set to 1 and upper threshold value (SM3) was set at 1.35. Under these settings, a simulation showed a good match with the current distribution of *T. aestivum*. Furthermore, the minimum number of growing degree-days needed by *T. aestivum* to complete one generation was set at 500° days to fit the current distribution of *T. aestivum* in high latitude countries of the northern hemisphere, such as Canada.

The cold stress temperature threshold (TTCS) for *T. aestivum* was set at −25 °C, and the accumulation rate was set at −0.0005 week^{-1}. In order to meet the current location in North

America for *T. aestivum*, we set the value of degree-day cold-stress threshold (DTCS) at 20 °C days above DV0 and the accumulation rate (DHCS) at -0.0001 week^{-1}. The heat stress temperature threshold (TTHS) and heat stress temperature rate were maintained at 39 °C and 0.005 week^{-1}, respectively.[77] The soil moisture dry stress threshold (SMDS) was set equal to SM0 (0.016), and the dry stress rate was adjusted to -0.0007 week^{-1} based on *T. aestivum* occurrences in some dry regions of Australia and India. The wet stress threshold (SMWS) was set at 1.4 to match the SM3, and the wet stress rate (HWS) was set at 0.019 week^{-1} to better fit the current distribution of *T. aestivum*.

2.4 Evaluation of host plant availability

The within-year dynamics of aphids are largely determined by seasonal changes in host plant quality: aphid populations tend to increase when host plants thrive.[14] Accordingly, we calculated the host plant availability (θ) based on the methods of Berzitis et al.[31] Original EI values for *T. aestivum* (EI_T) were re-scaled to θ (range 0–1, Eqn (5)). The parameter q stands for the slope of the curve, and h has the same value of EI_T when θ equals 0.5. For our analysis, an approximately sigmoidal curve was simulated with $q = 6$, and $h = 14$, as shown in the Supporting Information, Fig. S2. Then, θ was multiplied by the EI for the *Sitobion* grain aphid complex (EI_a) to obtain a measure of climatic suitability (EI_a'). Thus EI_a' incorporates the climate and host plant availability.[6,31]

$$\theta = \frac{\left(\frac{EI_T}{h}\right)^q}{1 + \left(\frac{EI_T}{h}\right)^q} \tag{5}$$

After projecting the global distribution of wheat based on current climatic conditions alone (EI_T; Supporting Information, Fig. S3), we generated a more refined distribution of the *Sitobion* grain aphid complex based on host plant availability combined with current climate conditions and future climate scenarios (EI_a'). We also mapped the differences between current climate conditions and future climate scenarios with and without host plant availability (EI_a and EI_a'). Finally, we calculated differences of area percentage between EI_a and EI_a' under current climate conditions and future climate scenarios.

2.5 Model validation and analytical results

An independent test dataset, namely the distribution records of the *Sitobion* grain aphid complex from Europe (Fig. 1(a)), was used to validate the bioclimatic envelop models;[8,83–85] the other records were used in parameter fitting. All analyses and visualizations of CLIMEX outputs were performed in R version 4.0 (R Core Team, 2020), including the packages 'raster',[86] 'phylin',[87] 'spatstat',[88] 'Hmisc',[89] 'maptools',[90] 'dplyr',[91] 'colorspace',[92] and 'wesanderson'.[93]

3 RESULTS

3.1 Region-specific distribution of the *Sitobion* grain aphid complex under current and future climate conditions

We predicted the global distribution of the *Sitobion* grain aphid complex under current climate conditions (EI_a, Fig. 2(a)). The model fit the current distribution of the *Sitobion* grain aphid complex well. All but two of the observed records (records from northern Canada) were located within the predicted distribution range, suggesting that parameters we used in our CLIMEX model were appropriate. The results indicated that the grain aphid complex could survive on all continents except for Antarctica. We compared the EI_a values under the SSP585 scenario with those under the current climate conditions and mapped the difference to show changes by 2100 (Fig. 2(b)). In general, the climate suitability (EI_a) in low and middle latitude regions, including the southeastern USA, South America, Africa, and Australia, is predicted to decline. Distributions are predicted to shift northward into the northeast parts of Asia and northern parts of Canada. Percentages of the potential distribution area for the grain aphid complex per continent suggest the potential distribution area for the *Sitobion* grain aphid complex is different in the context of climate change (Fig. 2(c)).

Globally, the potential distribution area for the *Sitobion* grain aphid complex is predicted to increase from 41.3% to 53.3% of the total global land mass (excluding Antarctica) under SSP585 scenario. In Europe, although the total suitable area is predicted to increase, the very favorable area is predicted to shrink. The impact of climate change on climatic suitability for the *Sitobion* grain aphid complex is predicted to also vary in North America. The potential distribution of the *Sitobion* grain aphid complex is predicted to expand in northwestern Canada and the western USA, while it is predicted to shrink in the eastern and central USA (Fig. 2(b)). In Oceania, the potential distribution and the proportion of very favorable region is predicted to decline, but the marginal and favorable region are predicted to increase slightly. In Asia, the potential distribution of the *Sitobion* grain aphid complex is predicted to extend northward, and expand overall. Northern India is predicted to be no longer suitable for the survival of the grain aphid complex. In Africa and South America, suitable area is predicted to greatly decrease overall.

3.2 Impacts of host plant availability of the distribution of the *Sitobion* grain aphid complex

Incorporating *T. aestivum* availability changed the predicted distribution of the *Sitobion* grain aphid complex under current climate conditions (Fig. 3(a), (b)). The presence of the host plant promoted survival and restricted the potential distribution of the *Sitobion* grain aphid complex to some degree. Under the future scenarios (both SSP126 and SSP585 scenarios), the values of EI_a' were less than the values of EI_a, (see Supporting Information, Fig. S4). Unsuitable and marginal areas are predicted to increase globally, while favorable and very favorable areas are predicted to decrease globally (Fig. 3(c)). In addition, the availability of *T. aestivum* had different impacts in different regions. Host availability had the greatest impacts in Asia under the current climate conditions, but the greatest impacts in North America were seen under future climate conditions. The impacts of host availability in Africa and Oceania under both current and future climate conditions were smaller (Fig. 3(c)).

3.3 Impacts of irrigation on the distribution of the *Sitobion* grain aphid complex

We calculated the potential distribution of the *Sitobion* grain aphid complex when irrigation was added to natural rainfall (EI_i, Fig. 4(a)). We also mapped the distribution change between natural rainfall and natural rainfall plus irrigation under current time period (Fig. 4(b)). Irrigation was shown to be an important driver of the potential distribution of the *Sitobion* grain aphid complex (increased EI) in many arid or semiarid locations; however, irrigation reduced EI values for the *Sitobion* grain aphid complex in some wet regions (Fig. 4(b)). In most places and under the current

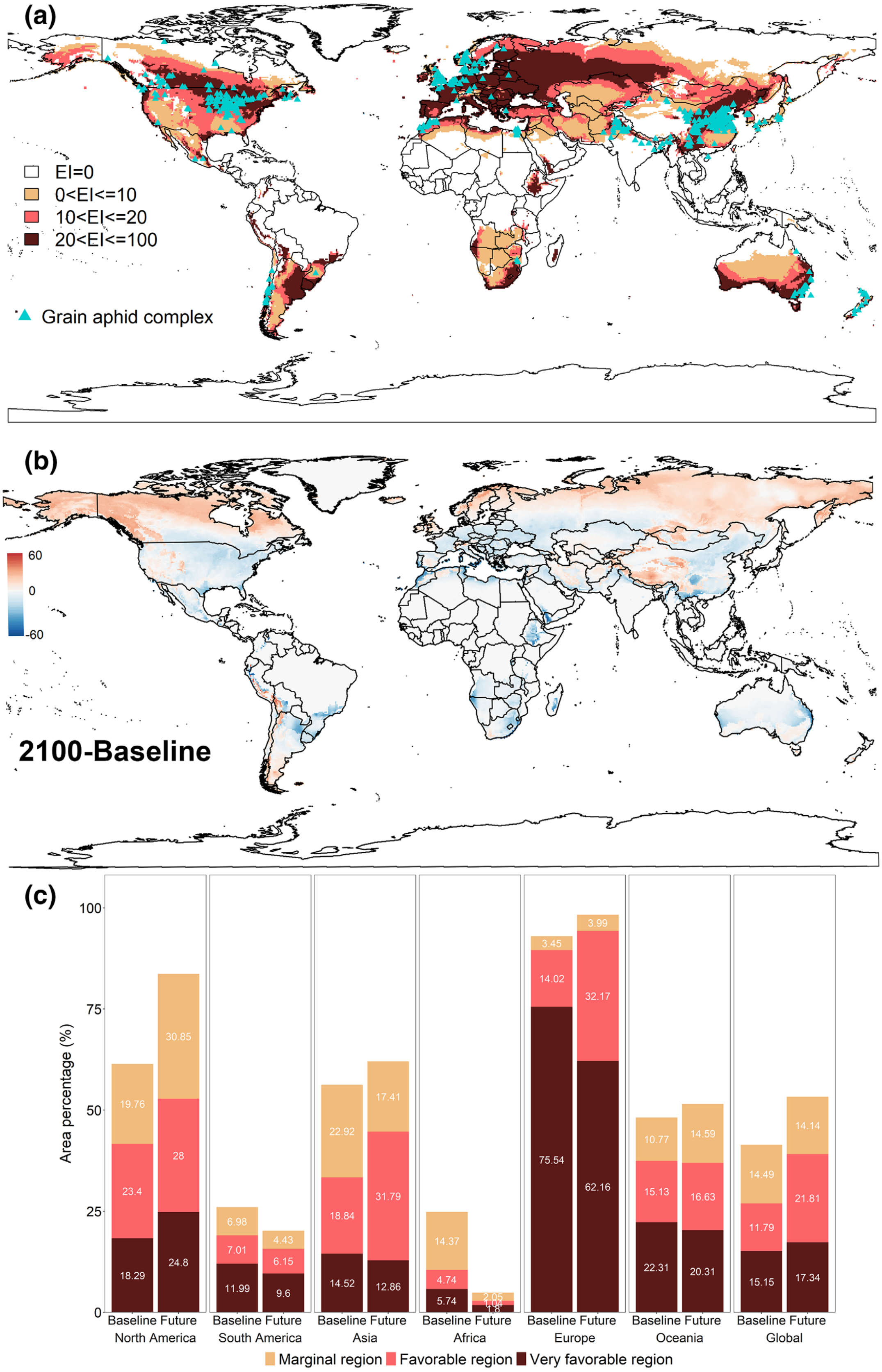

Figure 2. (a) Projected global distribution of the *Sitobion* grain aphid complex under the historical climate. White indicates unsuitable areas (eco-climatic index EI = 0); light orange indicates marginal suitable areas (0 < EI≤10); pink indicates favorable areas (10 < EI ≤ 20); dark red indicates very favorable areas (EI > 20). (b) Differences in the EI values for the *Sitobion* grain aphid complex under historical (1951–2020) and future (2081–2100) climate conditions (SSP585). Red indicates an increase; blue indicates a decrease, and the depth of color indicates the degree of change in EI values. (c) The percentage area of the potential distribution of the *Sitobion* grain aphid complex for historical (1951–2020) and future (2081–2100) climate conditions (SSP585) (marginal 0 < EI ≤ 10, light orange bars; favorable 10 < EI ≤ 20, pink bars; or very favorable EI > 20, dark red bars).

climate scenarios, irrigation is predicted to reduce unsuitable and marginal areas and increase very favorable areas for the *Sitobion* grain aphid complex (Fig. 4(c)). Under future climatic conditions (SSP585 scenario), comparing among areas, Europe is predicted to experience the greatest impacts of irrigation (Fig. 4(c)). Irrigation will strongly reduce the percentage of very favorable area (compared to a slight positive effect with the current climate) and will increase the percentage of marginal and favorable areas (compared to no effect or slight negative effect with the current climate; Fig. 4(c)). In addition, in 2100 for both SSP126 and SSP585, the natural rainfall plus irrigation scenario resulted in increased suitable area for the *Sitobion* grain aphid complex compared with the climate-only scenario (see supporting information, Fig. S4).

3.4 Climatic suitability accounting for host plant availability and irrigation

We calculated the potential global distribution of the *Sitobion* grain aphid complex under different climate scenarios and at different time points while accounting for host plant availability and irrigation (Supporting Information, Fig. S5). With host plant availability and irrigation in our models (Supporting Information, Fig. S5(b)), the sum of marginal, favorable, and very favorable areas (i.e., $EI > 0$) was smaller than the sum of these areas in the climate-only model at both time points under both scenarios (Supporting Information, Fig. S5(a)). An expansion in the distribution of the *Sitobion* grain aphid complex was predicted for future climate conditions (under both SSP126 and SSP585), regardless of host plant availability and irrigation. Under SSP126, the sum of marginal, favorable, and very favorable areas is predicted to increase from the baseline to mid-century (2041–2060) and the end-century (2081–2100). However, under SSP585, the sum of marginal, favorable, and very favorable areas is predicted to increase from the baseline to mid-century and then decline (Supporting Information, Fig. S5(a), (b)).

4 DISCUSSION

The impacts of climate change on agricultural pest distributions are well documented.[5,94–96] In general, ranges tend to shift towards higher latitudes and higher elevations. While ranges can undergo a net expansion, climate-change-driven range contractions can also occur, especially in warmer areas. Thus, pest populations can decline and go locally extinct in some places, while thriving in others.[97] Our results show region-specific patterns for a crop pest under climate change: the *Sitobion* grain aphid complex is predicted to contract in high temperature regions and expand in moderate temperature regions. These results are in line with a previous study in another species of cereal aphid, *S. graminum*.[8] In that study, suitable areas are shown to expand to higher latitudes in the northern hemisphere but to contract in the southern hemisphere.[8] Temperature is the main abiotic factor affecting the distribution of the *Sitobion* grain aphid complex and many other insects.[98] The mechanism by which temperature shapes the distribution of a species involves not only high (daytime) temperature, but also low (nighttime) temperature, which is often ignored. Yet, under climate change, diel warming is asymmetric: rates of increase in minimum temperatures is faster than in maximum temperatures.[99,100] The *Sitobion* grain aphid complex seems to be very sensitive to temperature, and its tolerance to extreme high temperatures is weaker than that of other coexisting aphids, such as *Rhopalosiphum padi*.[22] In the context of future climate change, relatively cooler areas will become suitable for aphids to thrive due to better overwintering survival, while relatively warmer areas, such as in South America, Africa, and Australia, will become too hot for aphids to grow and reproduce. Aphids in these warm areas may be unable to recover from daytime heat injury due to nighttime warming.[101] Populations already have declined or even gone extinct regionally due to the combined effects of increased maximum and minimum daily temperatures, which negatively impact the fecundity, the intrinsic rate of increase (r_m), and ultimately the population dynamics of the *Sitobion* grain aphid complex.[22,101] Overall, our analyses suggest that projected increases in maximum and minimum temperatures will lead to an expansion of the distribution of the *Sitobion* grain aphid complex in temperate regions that exceeds the contractions in subtropical regions. Careful monitoring of the presence and abundance of the *Sitobion* grain aphid complex (and likely other crop pests) in temperate regions in the future will be essential.

Role of host plant availability: Compared with climate factors, biotic factors and species interactions are often thought to play a minor (or even negligible) role in driving species distributions at macroecological scales.[102] However, many critical reviews and studies present evidence to the contrary.[30,103,104] Our results indicated that host plant *T. aestivum* availability impacted the distribution of the *Sitobion* grain aphid complex. For all modeled time periods, the percentage area of the potential distribution decreased by about 2% when host plant availability was incorporated. Thereby, our work highlights the need to incorporate biotic factors, such as host plant availability, when making macroecological predictions about crop pest distributions. Incorporating the predicted potential host plant distribution also helped to improve the accuracy of model predictions. For instance, incorporating host plant availability can represent a more realistic field situation. Host plants provide habitats and food for pests; thus, the presence of host plants, but also host plant traits (e.g., age, condition, etc.), can impact pest population sizes and distributions.[105,106] Other examples of pests with distributions limited by host plant availability include the aphid *R. padi*[33] and the termite *Constrictotermes cyphergaster*.[107]

When predicting distributions of the *Sitobion* grain aphid complex, we only accounted for the cultivation of *T. aestivum*; other less common Gramineae crops, which can also be hosts of the *Sitobion* grain aphid complex, were not taken into account.[14,74,108,109] This point may explain the observed spatial variation in the importance of *T. aestivum* availability for the grain aphid complex, since the relative abundances of the other hosts of the *Sitobion* grain aphid complex also vary spatially.[110] In addition, distributions of different wheat cultivars may also influence pest distributions. For example, transgenic wheat cultivars can reduce the *Sitobion* grain aphid complex fecundity[111] or resist infestation.[112] However, we did not take into account wheat cultivar identity, because at global and continental scales these data are limited.

Role of irrigation, a common management practice: Irrigation is a common agricultural management practice that can have strong impacts on agroecosystems.[113,114] Irrigation has bottom-up effects on pests by altering host plant growth[115] and plant water stress status. Consequently, aphid host choice and feeding behavior can be affected, since aphids prefer well-watered wheat over highly-stressed wheat.[116] Indeed, the *Sitobion* grain aphid complex seems to be sensitive to supplemental irrigation, and even a moderate amount of irrigation increased climatic

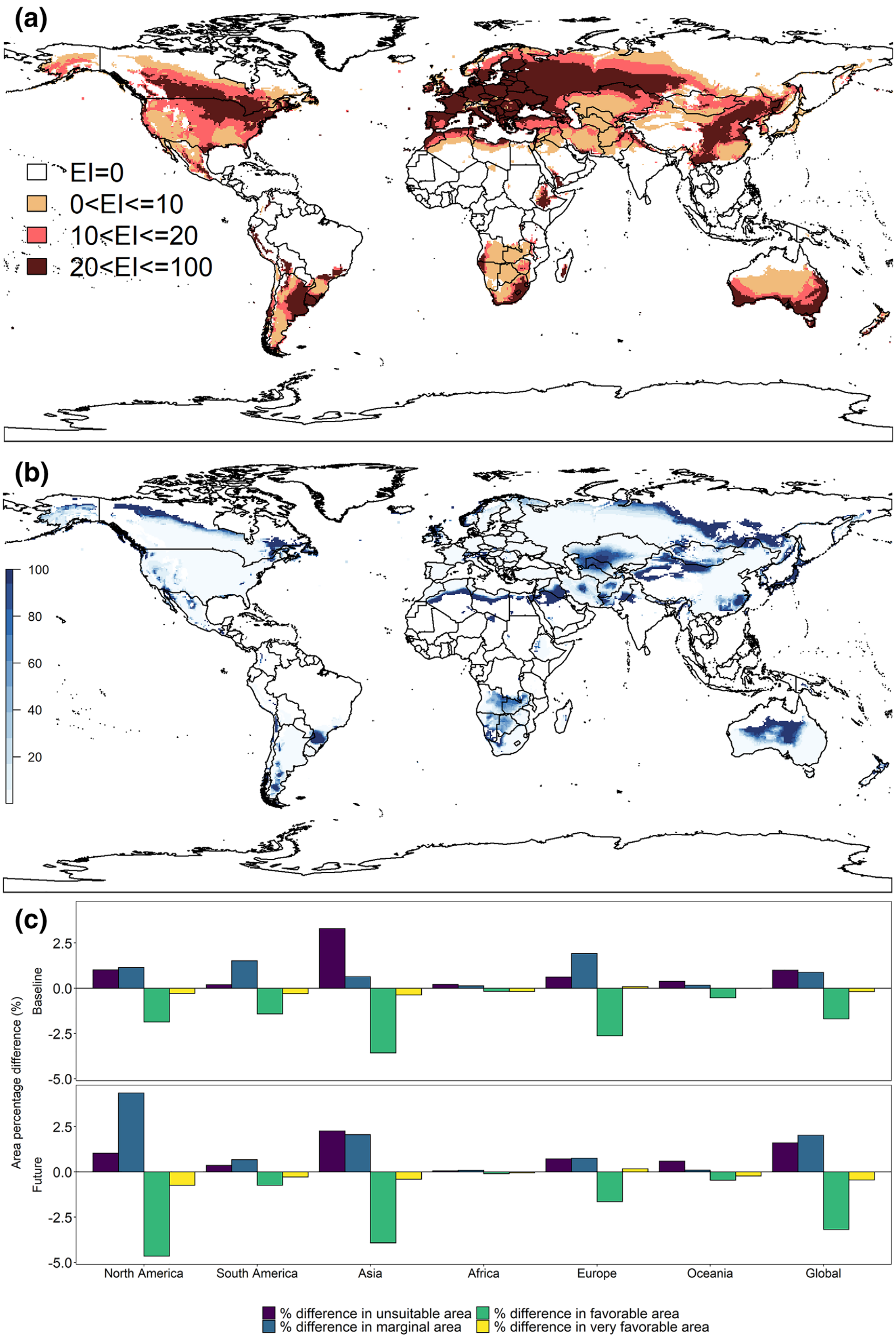

Figure 3. (a) Projected global distribution of the *Sitobion* grain aphid complex when host plant availability was incorporated. White indicates unsuitable areas (eco-climatic index EI = 0); light orange indicates marginal suitable areas ($0 < \mathrm{EI} \le 10$); pink red indicates favorable areas ($10 < \mathrm{EI} \le 20$); dark red indicates very favorable areas (EI > 20). (b) Difference (%) between eco-climatic index without host plant availability ($\mathrm{EI_a}$) and with host plant availability ($\mathrm{EI_a}'$) ($= (1-(\mathrm{EI_a}'/\mathrm{EI_a})) \times 100\%$). Darker blue indicates greater differences between $\mathrm{EI_a}$ and $\mathrm{EI_a}'$. (c) The difference in percentage area between the predictions based solely on climate ($\mathrm{EI_a}$) and climate + host plant availability ($\mathrm{EI_a}'$) under natural rainfall conditions for historical and future (2081–2100) time periods (SSP585) (unsuitable EI = 0, purple bars; marginal $0 < \mathrm{EI} \le 10$, blue bars; favorable $10 < \mathrm{EI} \le 20$; green bars; or very favorable EI > 20; yellow bars).

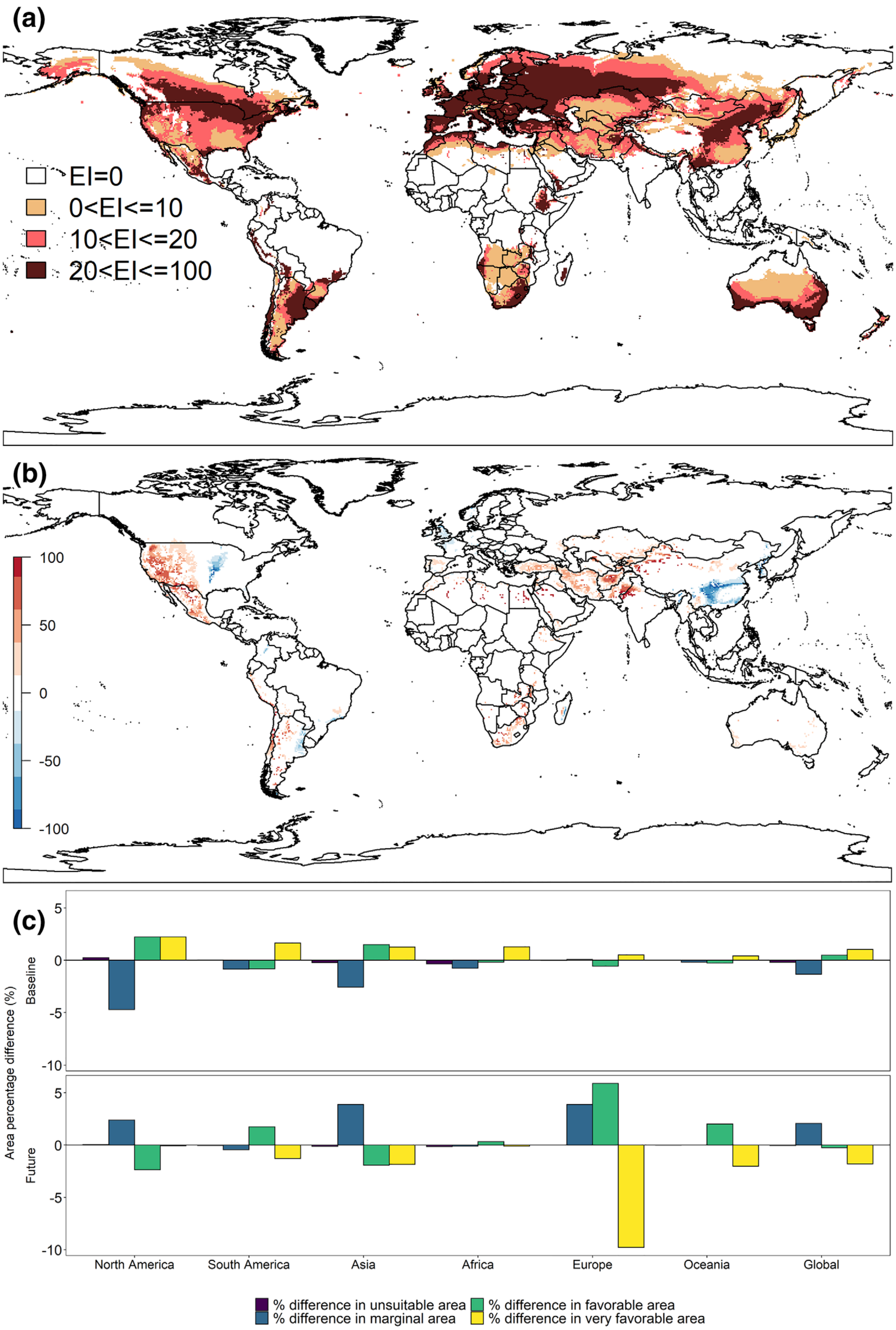

Figure 4. (a) Projected global distribution of the *Sitobion* grain aphid complex when irrigation was incorporated. White indicates unsuitable areas (eco-climatic index EI = 0); light orange indicates marginal suitable areas (0 < EI ≤ 10); pink red indicates favorable areas (10 < EI ≤ 20); dark red indicates very favorable areas (EI > 20) (b) Percent change between eco-climatic index with only natural precipitation (EI_a) and with natural precipitation + irrigation (EI_i) (= $(1-(EI_i/EI_a)) \times 100\%$). Red indicates an increase; blue indicates a decrease, and the depth of color indicates the degree of change in EI values. (c) The difference in percentage area between the predictions based solely on natural climate (EI_a) and natural climate + irrigation (EI_i) for historical and future (2081–2100) time periods (SSP585) (unsuitable EI = 0, purple bars; marginal 0 < EI ≤ 10, blue bars; favorable 10 < EI ≤ 20; green bars; or very favorable EI > 20; yellow bars).

suitability (EI) for this pest. The direct effects of irrigation on pests are twofold: increased relative humidity and decreased temperature. The *Sitobion* grain aphid complex is not very sensitive to relative humidity: it can survive from about 30% to 90%. With other aphids, such as *Aphis spiraecola*, relative humidity is a more important limitation on population growth.[117] Even though the *Sitobion* grain aphid complex can withstand humid environments, irrigation could limit their survival by promoting entomopathogens that can infect aphids.[117] Additionally, recent studies indicate that the temperature-moderating effects of irrigation can alter near surface temperatures by reducing daily maximum temperatures and increasing daily minimum temperatures due to increased evapotranspiration.[34,118] These effects may increase the suitability of wheat for aphids in arid and semi-arid areas. The growth and production of *T. aestivum* is water-intensive, with irrigation playing a pivotal role in arid and semi-arid regions.[119] Irrigation-related increases in host plants can benefit pests. With climate change, the global need for irrigation is predicted to increase by 5–8% until the 2070s.[120] Thus, the direct and indirect effects of irrigation on pests will likely grow in parallel and should be studied further.

Limitations to the study: CLIMEX models depend on species-specific parameters, which are generally set according to mean values (e.g., mean optimal temperature) from lab experiments. However, variation around a mean can be ecologically important. Acute temperature fluctuations, including daily temperature extremes, intra-day changes, and inter-day patterns of extremely hot *versus* normal days can all impact pest demography, including development rate, fecundity, and longevity.[29,121,122] Thus, the use of static parameters, as in our study, may not fully represent the distribution limits of aphids. Dynamics and distributions of aphids are also influenced by fertilization and other farming methods. However, we lacked the necessary data to consider these factors. In addition, for the irrigation scenarios in the present study, we were unable to distinguish among sub-scenarios, such as well-watered, drought, or waterlogged, since data for drainage, soil texture, and the synchronization between precipitation and demands of plants are largely unavailable. Modelling these sub-scenarios would provide additional important information to the model output, but this is unfortunately not feasible at this moment. Future studies focusing on drought and its effects on phloem-feeding insects will likely be particularly valuable, since drought frequency and intensity are expected to increase in the face of climate change.[123] Additionally, the current parameters we used are subject to change via evolution and other processes. With its short generation time (approximately 10 days), the grain aphids may be able to rapidly adapt to climate change.[124] New species distribution modeling frameworks, such as *AdaptR*, can take into account evolutionary adaptation. The use of such tools should be prioritized in future studies aimed at predicting distributions of fast-evolving crop pests and pathogens, especially when modeling decades-long windows of climate change.[125,126] In the current study, however, we lacked the necessary genetic data. Agricultural management practices can also change over time. Because we were unable to obtain localized monthly irrigation data for each region, the irrigation scenario we applied was not very detailed. The areas that rely on irrigation (as well as the amount of irrigation applied) will likely shift in the future depending on prevailing policies and practices. Adjustments to irrigation or any management practice can directly impact on the distribution of crops, pests, and other species. Although we demonstrated an effect of one management practice at a global scale, analyses of other practices and at other scales are also expected to reveal influences of distributions of the *Sitobion* grain aphid complex and other crop pests via direct and indirect mechanisms.

Implications for management: Most studies that assess the impact of climate change on the distribution of pests ignore changes in host plant availability and agricultural management practices such as irrigation. Our analyses demonstrate that accounting for these factors, in combination with the more commonly considered climatic factors, affects predictions about global and regional range shifts of important cereal pest species. Our results can inform pest control strategies and help those in high-risk areas reduce climate-change driven insect damage. For example, farmers may need to modify management practices (e.g., the amount of irrigation applied) to strike a balance between competing climate-change related risks (e.g., reduced crop condition due to heat or drought *vs.* the promotion of pests by the addition of water). A model like ours could be used as a decision support system in which different settings of the 'management layer' (here irrigation) predict different distributions of the (pest) species of interest. Future models, and the farmers they can inform and support, would likely benefit from taking into consideration other agricultural management practices, such as crop rotation, tillage, and fertilization. Creating such models will, of course, require detailed data at the spatial scale of interest, and these data can be limiting, particularly at a global scale.

5 CONCLUSIONS

Our study is the first to illustrate the interactive impacts of climate change, agricultural practices (i.e., irrigation), and host plant availability on pest-crop interactions at a global scale. Our results highlight that predictions of changing distributions of insect pests cannot ignore changes in host plant availability. Climate change is predicted to result in shifts in the pest distributions that are regionally specific. In the case of the *Sitobion* grain aphid complex, distribution in warm regions are predicted to contract, while those in cooler temperate regions are predicted to expand. Overall, the global distribution of the *Sitobion* grain aphid complex is predicted to shrink. These distribution changes are expected to impact farming practices and related policies. By identifying future high-risk areas, monitoring and prophylactic measures can be put into place with the aim of ensuring food security. Similarly, by identifying areas where risk will decline, pesticide application may be able to be reduced to the benefit of the environment and farmers' finances.

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CONFLICT OF INTEREST DECLARATION

Bing-Xin Wang, Anouschka R. Hof, Kevin D. Matson, Frank van Langevelde, and Chun-Sen Ma declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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