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1 Complex responses of global insect pests to climate change

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22 Abstract

Phytophagous insect pests strongly affect the productivity and profitability of agriculture 23 24 and forestry. Despite the well-known sensitivity of insects to abiotic effects such as temperature, their potential responses to ongoing climate change remain unclear. Here 25 we compile and review documented climate change responses of 31 of the globally 26 27 most severe insect pests of agriculture and forestry, focussing on species for which long-term, high-quality data are available. Most of the selected species show at least 28 29 one response affecting their severity as pests, including changes in geographic range, 30 population dynamics, life-history traits, and/or trophic interactions. The agricultural pests show strikingly more diverse and generally weaker responses to climate change than 31 the forestry pests. However, the agricultural pests seem to increase more in detrimental 32 ecological impact than do the forestry pests. Unexpectedly, 59% of the species show 33 responses of reduced potential impacts as pests under ongoing climate change. This 34 35 reduction in impact is further supported by a thermal sensitivity analysis showing little benefit of climate warming in relation to the optimal developmental temperatures for the 36 majority of these pests under both current climate and future projections. The 37 38 documented variation in responses indicates that efforts to mitigate undesirable climate change effects must target individual species, taking into account the complex 39 40 ecological and evolutionary mechanisms underlying their responses. 41

Keywords: climate adaptation, abiotic stress, integrated pest management, agricultural
 pest, forestry pest

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45 Significance statement

Here we show that 31 global insect pests in agriculture and forestry have responded to 46 climate change in ways that both increase and decrease their socioeconomic and/or 47 ecological impact. Most pests have responded in more than one major biological trait 48 and furthermore the type and/or direction of responses differ regionally. The agricultural 49 50 pests show more diverse and generally weaker responses to climate change than the forestry pests. Together these data show the same large variability in responses also 51 documented in non-pest insects, and highlight that efforts to mitigate change effects 52 53 must target individual species, taking into account the complex both ecological and evolutionary mechanisms underlying their responses. 54

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Climate change and insect pest impact. Insect pests have major detrimental impacts 56 on agricultural and forestry production¹ that are likely to increase with anticipated rise in 57 demands for food², bioenergy feedstocks and other agricultural products. For example, 58 animal pests (mainly insects) cause estimated losses of ca. 18% of total global annual 59 crop production³. Many forest pests, such as the gypsy moth (Lymantria dispar) and 60 61 mountain pine beetle (*Dendroctonus ponderosae*), also have severe ecological impacts: displacing native species, causing widespread defoliation and tree mortality, disrupting 62 ecosystem functions and diminishing biodiversity^{4,5}. Further, managing insect pests is 63 64 financially costly. For example, estimated global costs of managing only one pest species, the diamondback moth (*Plutella xylostella*), are 4-5 billion USD annually⁶. 65 66 Moreover, many agricultural and forest insect pests are also invasive species that

contribute to negative ecological consequences and the costs of managing or mitigating
such invasions are estimated to exceed 76.9 billion USD annually globally⁷.

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The substantial global challenges posed by phytophagous insect pests can be 70 exacerbated by ongoing and projected large-scale climatic changes⁸ which could 71 promote increases in pest populations and resulting economic losses⁹⁻¹¹. Alternatively, 72 pests can be constrained by their environmental niche requirements, physiological 73 tolerances, and phenological or life-history responses to climate, leading to local 74 population declines or extinctions as climates change^{12,13}. Clearly, detailed knowledge 75 of insect pests' current and likely responses to ongoing climate change is essential to 76 counter changing risks. Widespread ecological damage through range expansions and 77 increasing frequencies of outbreaks are increasingly reported¹³⁻¹⁶, but there is a severe 78 deficiency in comprehensive information on insect pests' responses¹⁷⁻¹⁹. 79

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Climate change and insect pest biology. Efforts to predict climate change impacts on 81 insect pests are typically based on empirical studies of insect responses to geographical 82 and temporal variation in climate^{20,21}, mechanistic studies of insect responses to varying 83 abiotic conditions (often in controlled laboratory environments)²², climate modelling 84 studies^{23,24}, or some combination of these approaches¹⁸. A common assumption in 85 86 studies of pests' responses is that climate-limiting factors are constant across their geographic ranges. Thus studies typically ignore intraspecific variation, a well-known 87 source of variability in climate responses^{9,21}. Also, pest ranges generally span multiple 88 89 environments, often including various types of managed landscapes²⁵, forming complex

dynamic matrices of pest-ecosystem interactions¹⁹. Furthermore, analyses tend to
consider a single response (e.g. range expansion), rather than the wide range of pests'
potential responses to climate change¹⁹, which can be divided into at least four main
categories that are non-mutually exclusive: changes in geographic range, life-history
traits, population dynamics, and trophic interactions (Fig 1). Changes in range and
particularly population dynamics are likely to be directly linked to economic damage.

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To assess current empirically-based knowledge within these four categories of 97 response to climate change, we reviewed primary literature on 31 globally detrimental 98 insect pest species. Species were selected to cover both agricultural and forestry pests, 99 representing various feeding guilds (Supplement 1, Fig S1), being present in various 100 101 biomes and having large geographic ranges (Fig. 1). Furthermore, we only selected species that have been well studied over a long period. While this approach perhaps 102 leads to biases in terms of geographical range and taxonomy, we feel that it is 103 compensated by having high-quality comprehensive datasets available for the species. 104 This is also critical for allowing an integrated assessment of all the four major response 105 106 categories outlined above in each species and would not be possible otherwise. As 107 there is a need for more information on biological mechanisms relating to past and present climate change responses in several key biological traits for single organisms¹⁷, 108 109 we here provide an update on a number of such mechanisms (range expansion, lifehistory, population dynamics and trophic interactions) for the selected species in hopes 110 111 that the data can be used for further predictive modelling. This information is presented 112 in the form of species-specific descriptions and data tables in Supplement 2. We also

identify critical knowledge gaps, and highlight aspects that require further research toanticipate, mitigate and manage climate-driven changes in pest impacts.

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Insect pest responses to contemporary climate change are complex. Of the 31 116 insect pest species selected for the study, 29 (94%) reportedly show some response 117 118 attributable to contemporary climate change (Table S1), and 28 (90%) present more than one response (Fig. 2a). Of the 29 showing some response 26 (90%), 18 (62%), 16 119 (55%) and 4 (14%) respectively show changes in: geographic range, population 120 121 dynamics, life-history (traits related to phenology and voltinism), and trophic interactions (Fig. 2b). While at least one reported response of almost all of these species is likely to 122 increase pest severity (e.g. range expansion or increases in population density), 59% 123 124 (17/29) of them also show responses likely to reduce pest severity (e.g. range contraction or decreased physiological performance), and often this reduction occurs 125 simultaneously with other responses likely to increase severity (Fig. 2c). The most 126 common severity-reducing responses are reduction in pest population density (13/29), 127 followed by range contraction (6/29) (Fig. 2c). 128

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Responses of 59% (17/29) of the pest species with reported sensitivity to contemporary climate change have also varied between different parts of their ranges. For example, the range of the Colorado potato beetle (*Leptinotarsa decemlineata*) has expanded northwards in recent decades, and its population density has increased in core European areas (Table S1). The range of the winter moth (*Operophtera brumata*) has also expanded, towards higher latitudes and more continental areas at the northern

European edge of its range, and its trophic interactions have changed in the boreal-136 tundra ecotone, where outbreaks have spread from the main host Betula pubescens to 137 138 an alternative host (*B. nana*) above the tree-line (Table S1). Several species also show both severity-increasing and severity-reducing responses in different parts of their 139 ranges. Notably, thermal tracking has been observed in some species (4/17), e.g. 140 141 spruce budworm (*Choristoneura fumiferana*; Table S1), as their geographic range has expanded towards higher latitudes while it has retracted, or their abundance has 142 declined, at lower latitudes. Similarly, northward range expansion of the hemlock woolly 143 144 adelgid (Adelges tsugae) has been observed in the USA, while the economic damage it causes is decreasing in the southern part of its range due to poor heat tolerance of 145 young nymphs during summer (Table S1). 146

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Disparate responses of pests of agriculture and forestry. The main response 148 149 patterns of pests of agricultural (mainly annual) and forestry (perennial) crops are similar, but there are some striking differences. Contrary to expectations based on 150 differences in feeding or host ecology, and evolutionary constraints, pests of agricultural 151 152 crops show more severity-reducing responses than pests of forest trees. To assess the potential impact of agricultural and forest pest responses to climate change, we 153 154 categorized the species according to their historic and current socio-economic and 155 ecological impacts, and effects of contemporary climate change on those impacts. Overall socio-economic and ecological impacts have reportedly increased across the 156 geographic ranges of species that have responded to climate change^{11,19}. More 157 158 importantly, while all the considered forestry pests already have large ecological impact,

85% (17/20) of the agricultural pests currently have relatively low ecological impact 159 beyond the cropping systems they infest. However, climate change might be inducing 160 increases in the relatively low impact of some agricultural pests. For instance, the green 161 stink bug (Nezara viridula) and maize stem borer (Chilo partellus) displace native bugs 162 and borers, respectively, as their ranges expand (Table S1). Further, the range of the 163 western corn rootworm (Diabrotica virgifera virgifera) in Europe has expanded, and it 164 can cause large ecological damage by spreading maize chlorotic mottle virus to several 165 natural hosts (Table S1). A potential explanation is that reductions in phenological 166 167 constraints associated with climate warming (mediated for instance by increases in host growth season, or shorter and milder winters²⁶), can increase interactions between 168 pests in annual agricultural habitats and surrounding ecosystems^{27,28}, thereby 169 170 increasing ecological impacts. Indeed even small phenological mismatches might have large knock on effects for ecosystem function and predator prey interactions^{13,28}. 171

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In addition to the fact that latitudinal differences in pest distributions might modulate 173 climate change effects, several other mechanisms could be involved in the divergence 174 175 of responses in annual and perennial systems. Unlike forestry pests, agricultural pests are generally associated with fragmented habitats²⁹ and may therefore have higher local 176 extinction risks due to Allee effects when climate changes¹². Further, while climate 177 178 change can disrupt biological control by natural enemies in either annual or perennial systems³⁰, the biological control agents frequently introduced in annual systems may 179 180 have lower genetic diversity than native agents, and hence lower adaptive capacity to 181 respond to environmental changes³¹. Direct effects of climate change on the

performance and phenology of pests have been detected in both annual and perennial 182 systems. Since pests often persist through part of the season in a resting or dormant 183 stage, especially at high latitudes and/or altitudes²⁶, climate change can contribute to 184 phenological mismatches between hosts and emergence of key life-stages^{13,21,27}, as 185 seen in O. brumata (Table S1). However, pests in annual and perennial systems might 186 differ in general susceptibility to phenological mismatching, inter alia the former might 187 be more sensitive to phenological host limitation; especially relative to bark beetles and 188 root feeders. 189

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Past, present and future temperature stress on the major insect pests. It has been 191 argued that pests may suffer negative consequences of ongoing climate change owing 192 to reduced thermal suitability and increasing frequency of high temperature extremes 193 leading to population reductions³². For further exploration of this in our focal species, we 194 assess the proximity of optimum development temperature (Topt) of the 31 pest insects 195 compared to their ambient habitat air temperatures (T_{amb}) (Fig. 3). Relating ambient 196 temperature during the growing season in past, present and future climates to T_{opt} 197 198 shows large variability in how pests are expected to benefit from climate change owing to regional complexity. In general, warming climates are expected to be beneficial for 199 200 growth and development, and indeed, in all but two cases T_{amb} closely approached T_{opt} 201 when comparing past, current, near future and future climates (Fig. 3B). This conclusion was also supported by a phylogenetically-informed regression analysis (Table S4). 202 203 Further, this analysis suggested that pests at higher latitudes have greater disparity 204 between T_{amb} and T_{opt}, indicating greater capacity to benefit from climate warming,

unlike more low latitude pests that are already close to T_{opt} . Low latitude species also potentially risk increasing frequency and intensity of heat stress as climate warms³³, a notion receiving support in a recent analysis of the upper thermal tolerance of 15 dipteran pests³².

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However, examination of patterns in more species, as well as on other thermal traits, 210 especially upper thermal limits or feeding (damage) rates, would be required to validate 211 this hypothesis. Agricultural pests accounted for only 4% of the ca. 380 species 212 included in the database of upper thermal limits compiled by Hoffmann et al.³⁴, 213 highlighting a potential information gap in the current literature. While the pests in the 214 current data represent a wide geographic distribution (Fig. 1A), the studies on T_{opt} used 215 216 here mostly reflect populations sampled in the northern hemisphere (Fig. 3C). This is a general problem found in other large-scale analyses of climate change responses, such 217 as phenology²⁸ and insect metabolic or development rate-temperature databases³⁵ 218 showing a need for further studies covering underrepresented locations. Finally, as air 219 temperatures are reported in the global temperature database, there is risk of 220 underestimation of microclimate variability³³ and thus the extent of potential buffering 221 owing to three-dimensional habitat complexity of operative temperatures^{33,36}. 222

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Evolutionary responses of insect pests to climate change. Insect pests may evolve
 rapidly in response to contemporary climate change^{15,37-41}. Thus, apparently sound
 projections of insect pest responses to climate change¹¹ may be compromised if
 evolutionary responses are not considered⁴². Indeed, rapid evolutionary effects have

influenced - or could influence further - projections for several of the 31 species 228 considered here (Supplement 2). For example, disruption of phenological synchrony 229 between *O. brumata* and oak in temperate Europe due to increasing temperatures³⁰ has 230 been apparently restored by a hereditary change in egg hatching dates⁴³. Also, range 231 expansions of some of the forestry pests induced by climate change have resulted in 232 233 colonization of areas with novel host tree species that have little innate resistance due to lack of co-evolution with the pests⁵. In contrast, the similarity of crops grown across 234 large areas might promote co-evolution between agricultural pests and their hosts⁴⁴. 235 236 Links between biological invasions or range expansion events, climate change and evolutionary processes have received recent attention^{9,16,20,41}, but there is still pressing 237 need for further research in this field. The effects of management practices and 238 evolution have generally been considered too much in isolation, especially in climate-239 change contexts^{17,31}. 240

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Conclusions. The 31 widely-distributed pest insects that seriously affect agricultural or 242 forestry systems studied here show multiple and varying responses to climate change. 243 244 By providing an up-to-date database that reviews biological responses to climate change in the selected pests (Supplement 2) we offer standardized information that can 245 be further explored by other researchers. Although the present analyses cannot be 246 247 considered absolute, complete, and without taxonomic, geographic and study intensity biases¹⁰, we nevertheless detected several overarching patterns that allow us to draw 248 249 some general conclusions.

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1. The data suggest that determining the net severity change of pests to climate 251 change is complex since most species considered here have shown multiple 252 responses that vary spatially²³. The present study also provides evidence for mixed 253 directionality of responses as well as potential explanations thereof based on major 254 mechanisms. This set of complex but predictable outcomes and regional 255 256 heterogeneity of responses is challenging for management but cannot be ignored as it is the emerging consensus in this and other studies^{11,18}. 257 2. The current study urges caution in performing large-scale analyses only with single 258 259 traits, since single pests often show mixed directionality of effects of climate change in different traits. Lacking the interactions among different traits in each pest species 260 may easily lead to incomplete conclusions. To correct this we recommend more in-261 262 depth studies of biological mechanisms in a few representative species. For example, a recent meta-analysis shows that models integrating biological 263 mechanisms from multiple traits significantly improve predictions of climate change 264 impacts on global biodiversity¹⁷. 265 3. Mounting evidence suggests that pests and their hosts are responding not only 266 through ecological, but also evolutionary processes to climate change^{16,40,41}. Thus, 267 evolutionary approaches might be under-exploited in pest management strategies³¹. 268 Including evolutionary and ecological information when formulating integrated 269 270 management strategies may facilitate robust intervention and control (as recently demonstrated in disease vector control programs⁴⁵). Furthermore, it would be useful 271 to pinpoint species with high evolvability in traits relevant to climate change¹⁶, or that 272

show trade-offs between traits linked to basal climatic stress resistance and
 plasticity^{41,46}.

4. Combining data from large-scale experiments (e.g. mesocosm) and computational 275 models may improve estimates of climate change effects^{18,41,47}. Experiments should 276 be designed to assess variance components with indicated importance in climate 277 modelling studies, to identify the factors related to climate change that most strongly 278 influence pest population growth and performance, such as for example the 279 increased feeding efficacy of the Japanese beetle (Popillia japonica) on carbon 280 dioxide-enriched soybean⁴⁸. Indications that the response to climate change differ 281 among trophic levels, translating into shifts in the relative importance of bottom-up 282 and top-down population processes⁴⁹ needs to be studied further as even relatively 283 284 small changes could result in large effects when multiple interactions are affected simultaneously⁵⁰. Standardized experiments enable high-throughput investigation of 285 pests (for recent example see⁵¹) and facilitate the development of watchlists or 286 prioritization tools (such as The UK Plant Health Risk Register⁵²) of key species that 287 require further study. However, as the current data suggest large regional variability 288 289 in pest responses to climate change, national or regional databases, while excellent locally, might offer poor insight into invasions into other regions unless coordinated 290 or standardized efforts are attained, especially across political boundaries. 291 292 5. As T_{amb} is generally increasing towards T_{opt} for growth and development in these species, there is an expectation of increasing pest severity under future climate 293

negligible for many of the studied pests (Fig. 3C). Indeed, since low-latitude species

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scenarios⁵³. However, the relative benefit of increasing ambient temperatures is

296		already showed T_{amb} close to T_{opt} , as climates warm T_{amb} for these species may
297		surpass T_{opt} , thus decreasing pest severity, under future climates ^{32,33} .
298	6.	Finally, and importantly, the patterns of regional variability and complexity described
299		here are likely to apply to non-pest insects as well as non-insect species in addition
300		to the 31 insect pest species assessed here. The extent of generality of responses
301		across various taxa will be important to assess in future studies ^{13,19,41,47} .

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Methods. Thirty-one of the socioeconomically and ecologically most detrimental insect 303 pests globally were selected that collectively: infest both agricultural and forestry crops, 304 represent diverse feeding guilds, originate from both tropical and temperate 305 environments, have large geographic ranges (preferably covering several continents). 306 and have been well studied and monitored over recent decades (Fig. 1A & 1B). A lack 307 308 of rigorous long-term monitoring, with consistent sampling effort, is probably the biggest 309 limitation hindering efforts to characterize biological systems' responses to climate change robustly. Because of their large economic impact, insect pests represent a 310 311 group of organisms with relatively good data compared to other groups; data are collected frequently but not consistently and data quality tend to be positively correlated 312 to density and range expansion of the species. Thus, pests are good models for such 313 314 efforts because abundant information about their distributions, impacts and interactions is routinely collected. However, since we selected species with large ranges, our results 315 can be biased towards responses of species with broad thermal niches, thus the 316 317 indicated general effects of climate change are likely conservative. Further, since habitats strongly affect insect ecology, we assume that species in disparate habitats will 318 319 have different potential responses to climate change, so we chose species prevalent in

a wide spectrum of lightly-managed to heavily-managed habitats. Then, using Web of 320 Science searches (Thomson Reuters), we selected three types of studies. First, studies 321 that compared climate trends and empirically determined trends in relevant aspects of 322 the chosen pests, e.g. range, abundance or damage (economic and/or ecological). 323 Second, studies that tracked population-dependent differences in relevant traits (e.g. 324 325 voltinism) of the pests across time. Third, studies that modelled attributes of the pests, including a substantial historical data component. The responses recorded in these 326 studies were classified into four major types (Fig. 1D), and as either increasing or 327 328 decreasing pest severity. We used a modified version of a semi-quantitative generic impact score system to assess impact and severity⁵⁴. The data sources include studies 329 published in scientific journals, pest management databases (e.g. EPPO and CABI) and 330 records from national environment/pest management institutions. We also contacted 331 several experts for assessments of data quality. A non-parametric rank order correlation 332 333 analysis of explanatory and response variables was used to identify significant patterns among pest responses, ecological factors, and habitats (Table S3). Thermal suitability 334 in different climate periods was investigated using phylogenetically corrected 335 336 generalized linear least square models of thermal performance traits coupled with climate data within sampled areas (Supplement 1). 337

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- 347

348 Author contributions

- All authors jointly designed the study and collected species data. SN performed the rank
- 350 correlation analysis, PL, JST, MB performed the optimum temperature analysis. All
- authors contributed to preparation of the supplements. PL, MB, AB, SDE, JST and CB
- 352 prepared the first draft of the paper, and all authors edited the final version. The authors
- 353 declare no conflicts of interest.
- 354
- 355 **Supplement 1:** Extended materials and methods
- 356 **Supplement 2:** Species descriptions with associated references
- 357 **Supplement 3:** Data used in analysis
- 358

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493 Figure legends

Fig. 1. The distribution of 31 insect pests according to (A) the number of species in the 494 495 study occurring in each continent (with % of all those included) according to CABI. Note 496 that many species occur on multiple continents. Flanking each continent are pie charts showing the distribution of social ecological impacts and ecological impacts caused by 497 these species. (B) Schematic representation of four major categories of responses to 498 climate change: range changes, life-history traits, population dynamics and trophic 499 interactions (see Supplement 1). (C) A phylogenetic tree (compiled from the Tree-of-life 500 project) of the 31 species considered in this analysis. 501

502

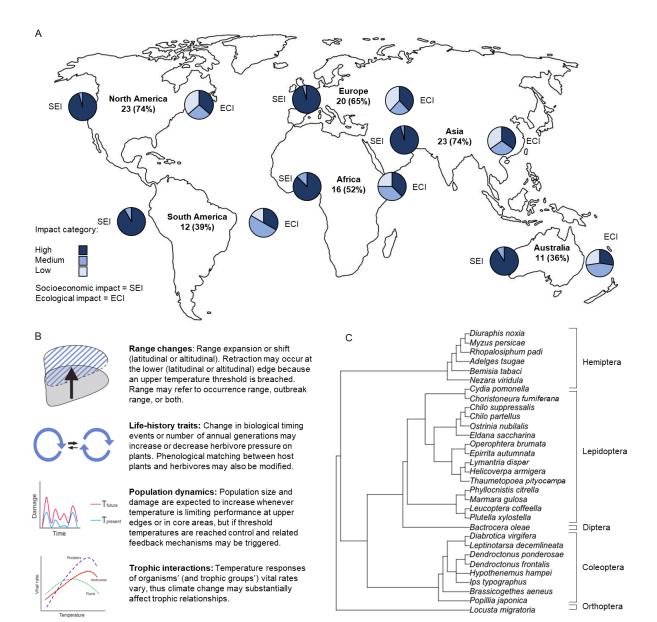
503 Fig. 2. Responses to climate change of 31 insect pests with high socioeconomic and/or ecological impact. (A) Shows the number of species responding in 0 to 4 traits to 504 505 ongoing climate change. Dark and light blue columns in (B-E) show percentages of species displaying severity-increasing responses (e.g. increased range) and severity-506 507 decreasing responses (e.g. decreased economic damage due to smaller population size) to climate change. Single species may show multiple responses and (B-E) only 508 509 display data for the 29 species that showed some response attributable to climate change (see Supplement 1). Observe that in (B-E) some species showed neither a 510 511 positive or negative response in some traits, so total percentages in these cases are 512 less than 100%.

513

Fig. 3. Summary figure of thermal sensitivity analysis of 31 insect pests. As input we 514 use published optimum temperatures of the species (T_{opt}, the temperature at which 515 performance is maximised, U_{max}) and mean ambient temperature (T_{amb}) during the 516 growing season. This includes the whole year below 45°S/N, and the summer months 517 above 45°S/N. (A) Schematic thermal performance curve including the two metrics 518 519 extracted. (B) Here T_{amb} / T_{opt} is plotted against latitude for the four periods investigated (historical: 1960-1969 [blue triangles and dotted line], present: 2006-2015 [fine dashed 520 line], near future: 2056-2065 [coarse dashed line] and future: 2070-2079 [red circles and 521 solid line]). Stars denote significant correlations in a phylogenetically corrected 522

- 523 generalized linear least square model: * = P<0.05, ** = P<0.005 (Supplement 1). (C)
- 524 Shows how many degrees T_{amb} differs from T_{opt} in past (left half of circle) and future
- 525 (right half of the circle) climates. Circles have been placed in the approximate location
- ⁵²⁶ where individual studies sampled the respective pests. Darker colors reflect ambient
- 527 temperatures near the optimum temperature and therefore climates likely beneficial for
- 528 pests.

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530

531 Figure 1

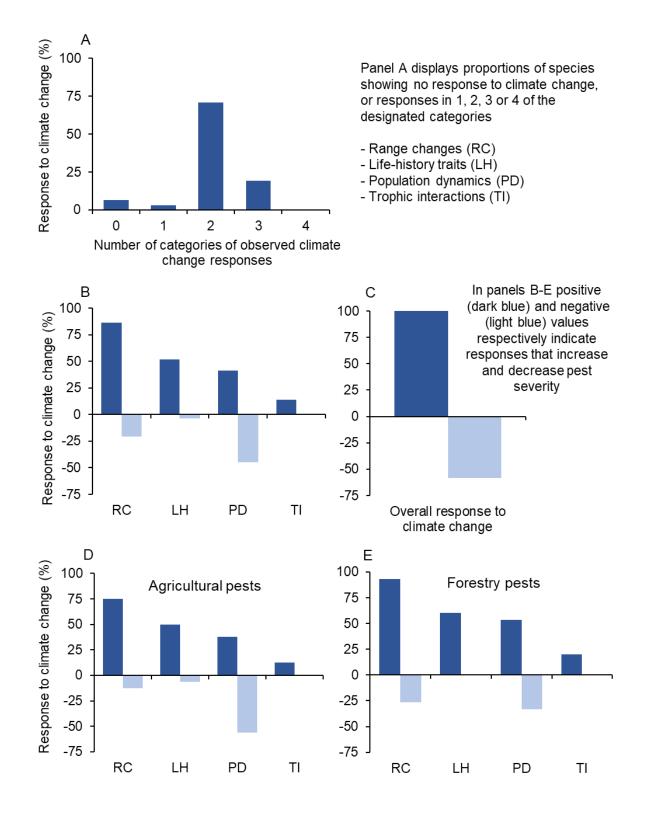
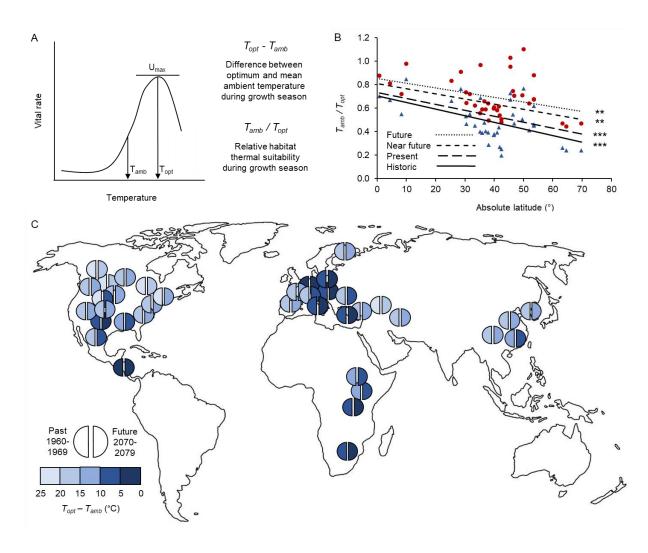


Figure 2

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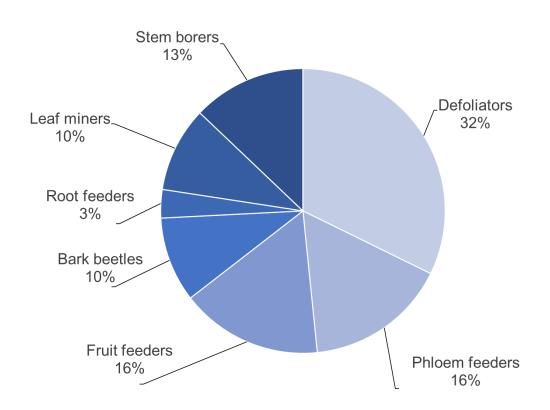
537 Figure 3

bioRxiv preprint doi: https://doi.org/10.1101/425488; this version posted September 24, 2018. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission. 1 Supplement 1 2 3 Complex responses of global insect pests to climate change 4 Philipp Lehmann^{1,2,4*}, Tea Ammunét^{3†}, Madeleine Barton^{4†}, Andrea Battisti^{5†}, 5 6 Sanford D. Eigenbrode^{6†}, Jane Uhd Jepsen^{7†}, Gregor Kalinkat^{8†}, Seppo Neuvonen^{9†}, Pekka Niemelä^{10†}, Bjørn Økland^{11†}, John S. Terblanche^{4†}, Christer Björkman³ 7 8 ¹Department of Zoology, Stockholm University, Sweden. ²Centre of Excellence in 9 Biological Interactions Research, Department of Biological and Environmental 10 Science, University of Jyväskylä, Finland. ³Department of Ecology, Swedish 11 University of Agricultural Sciences, Sweden. ⁴Centre for Invasion Biology, 12 Department of Conservation Ecology and Entomology, Stellenbosch University, 13 14 South Africa. ⁵Department of Agronomy, Food, Natural Resources, Animals and the Environment, University of Padova, Italy. ⁶Department of Entomology, Plant 15 Pathology and Nematology, University of Idaho, United States of America. 16 ⁷Department of Arctic Ecology, Norwegian Institute for Nature Research, Norway. 17 ⁸Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater 18 19 Ecology and Inland Fisheries, Germany. ⁹Natural Resources Institute Finland, Finland. ¹⁰Biodiversity Unit, University of Turku, Finland. ¹¹Norwegian Institute of 20 Bioeconomy Research, Norway. 21 22 *Corresponding author: Philipp Lehmann, philipp.lehmann@zoologi.su.se 23

24 [†]Contributing authors listed alphabetically

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- 25 Materials and methods Definitions and classifications used in the report
- 26 Data were acquired from scientific articles, governmental reports or pest record
- 27 databases (e.g. EPPO, CABI). Relevant articles were primarily obtained from
- searches of Web of Science (https://apps.webofknowledge.com/). Although not a
- 29 formal meta-analysis (due to the methods of selecting sources), our assessment is
- 30 based on published material on the selected species that are methodologically
- 31 sound and address recent and historic climate change-related responses of these
- 32 species.
- 33
- 34 Feeding guilds/Functional groups (Figure S1)
- Defoliators (external feeders)
- Phloem feeders (external feeders)
- Fruit feeders (internal feeders)
- Stem borers (internal feeders)
- Bark beetles (internal feeders)
- Leaf miners (internal feeders)
- Root feeders (internal feeders)
- 42



43

44 **Figure S1** The distribution of the selected 31 insect pests according to feeding guild.

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45 Annual or Perennial host(s):

- 46 Annual
- Annual and Perennial host(s)
- 48 Perennial
- 49

50 Latitude	
-------------	--

- 51 Tundra (highest latitude)
- 52 Boreal (high latitude)
- Temperate (low latitude)
- Tropical (lowest latitude)
- 55

56 Categories of responses to climate change

- 57 Changes in:
- Range changes: expansion/retraction or shift in either latitudinal or altitudinal
 range. Warming may increase performance at range edges if temperature has
 previously limited performance. Retraction may occur if a high temperature
 threshold is breached. Range may refer to occurrence range, outbreak range or
 both.
- Life-history traits. A change in generation time or number of generations per year
 may increase or decrease herbivore pressure on plants. Phenological matching
 between host plants and herbivores may also be modified (but such responses
 are classified here as "Trophic interactions", see below).
- Population dynamics. Damage to host plants, for various possible reasons, e.g.
 more frequent pest outbreaks, more intense defoliation). Expected to increase
 whenever temperature is limiting performance at upper edges or in core areas.
 Threshold levels may be reached, triggering control and related feedback
 mechanisms.
- Trophic interactions (e.g. host shift or a decrease in efficacy of natural predators
 following warming). Temperature responses of organisms' (and trophic groups')
 vital rates vary, thus climate change may substantially affect trophic relationships.
 We include changes in trophic interactions that have arisen due to direct impacts
 of climate change on the insects' phenology.
- 77

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78 Direction

- 79 This refers to the tendency of observed responses to increase, reduce or have
- 80 neutral effects on pests' severity.
- 81

82 Geographical variation in responses

Responses of pests to climate change may vary in different parts of their ranges in
terms of degree, type and direction (i.e. the responses may increase or decrease
pests' severity) due to: genetic or plastic population-dependent differences, spatial
climatic variability across the range, and varying permutations of these and other
factors.

88

89 **Definitions of Socioeconomic impact**

1) Small impact: Negative impact, at most minor (if quantified). Such species are

91 more nuisances than pests.

92

2) Medium impact: Significant reduction in performance of host (e.g. decreased

94 fecundity, stunted growth), significant economic losses due to direct (e.g. sales) or

⁹⁵ indirect (e.g. ecosystem services, tourism) effects. Pest controllable without active

96 management, or with reasonably small, often local, effort.

97

3) Large impact: Very significant reduction in performance of host (e.g. leading to
death or destruction of usable product), significant economic losses due to direct or
indirect effects. Pest not controllable without active, often nationwide, management,
or simply not controllable.

102

103 **Definitions of Ecological impact**

1) Small impact: Primarily restricted to cultivated host. None or few interactions withnative species.

106

107 2) Medium impact: Primarily restricted to cultivated host. Some negative interactions

with native species (e.g. competition for food or resources, spread of pathogens).

- 3) Large impact: Host is part of natural ecosystem (even though potentially
- 111 cultivated) or pest can use natural species as hosts and thus spread to the natural

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environment. Many negative interactions with native species (e.g. competition for food or resources, spread of pathogens). Some pests may extensively kill hosts that are key species in the ecosystem.

115

116 Direction of change in impact category

Decrease: Published records show decreasing severity of pest damage, due to
 reductions in population densities, feeding efficacy, outbreak frequency, range, or
 other reasons attributable to climate change (i.e. declines in pest species fitness that
 have occurred in the absence of increased management actions). Reductions in
 management costs also indicate reductions in impact, but only indirectly so they are
 not used as criteria here.

123

2) Stable: No compelling evidence of climate-change related responses has been 124 detected in considered studies. This could be due to several factors, but three main 125 explanations have been proposed. (1) The phenology, abundance or distribution of 126 the focal species may not be strongly influenced by climatic factors. (2) The focal 127 species may be responding at rates (or in ways) that are undetectable using the 128 129 applied methodology. (3) The phenology, abundance or distribution of the species may be influenced by climatic factors, but responses to current climate change may 130 not yet be detectable due (for instance) to anthropogenic dispersal barriers (habitat 131 fragmentation) or lags in responses¹. 132

133

3) Increase: Records show increasing severity of pest damage, in either or both
socioeconomic or ecological terms. Increases in damage may occur for any of the
reasons outlined above, including (for instance) expansion of range or outbreak
range to new cultivated areas, spread to novel hosts, spread of pathogens to novel
hosts, and/or increases in number of annual generations.

139

140 Critical assessment of species' responses to climate change (Table S1)

Due to large variation in the amount of data available for the considered species prediction-strength is strongly biased towards the most intensively studied pests. We classify the strength of response-predictions as either strong or weak. Predictions for focal species are regarded as strong if empirically observed biological or ecological changes can be correlated with climatic changes, and reinforced if corroborated by

bioRxiv preprint doi: https://doi.org/10.1101/425488; this version posted September 24, 2018. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission. modelling or laboratory studies. In a few cases predictions based on extensive 146 species-specific modelling with extensive historic data components are also deemed 147 strong. In contrast, predictions are regarded as weak if reported responses are 148 based purely on modelling, modelling and laboratory studies, and/or some 149 observations that may be correlated with climactic change, but there are strongly 150 confounding effects of other biological or ecological factors (e.g. invasion dynamics). 151 Predictions for responses of 23 (74%) and eight (23%) of the 31 species considered 152 here were regarded as strong and weak, respectively. Two pests (Marmara gulosa 153 154 and *Phyllocnistis citrella*) were removed from the main analysis (Table S1) since no pertinent information was found. 155

156

The assessments for each species can be found in Supplementary File 2, while 157 relevant studies showing or suggesting responses are cited in Table S1. As has 158 been suggested in several recent studies²⁻⁴ holistic integrated analyses are to be 159 preferred over single-trait analyses when assessing climate change responses, and 160 this is what we attempted to achieve with our approach. Thus while the present study 161 is neither a formal meta-analysis nor exhaustive, it synthesizes current knowledge of 162 163 integrated climatic responses of 31 pests with the aim to illustrate general patterns, problems and challenges, in a precautionary manner. 164

165

166 Rank order correlation (Table S2)

Associations between explanatory and response variables regarding effects of 167 climate change on the 31 selected serious insect pests were explored by Kendall 168 rank order correlation analysis. The results are presented in Table S3, and the 169 following list explains abbreviations and the range of these variables, which are listed 170 in the beginning of this supplementary document and used in the table. NRT = 171 Number of response categories (1 - 3), PA = Perennial or annual host (1 [perennial]) 172 - 3 [annual]), IE = Internal or external feeder (1 [external] - 2 [internal]), BRANK = 173 Mean habitat biome ranked from tundra to tropical (1 [tundra] - 4 [tropical]), AF = 174 Agricultural or Forestry pest (1 [agricultural] – 2 [forestry]), SEI = Socioeconomic 175 impact (2 [low] – 3 [high]), SEId = Change in Socioeconomic impact (1 [decrease] – 176 3 [increase]), ECI = Ecological impact (1 [low] - 3 [high]), ECId = Change in 177 ecological impact (1 [decrease] - 3 [increase]), GD = Difference between 178 geographical areas of range (1 [no] - 2 [yes]). 179

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180

The results of the correlation analysis were briefly as follows. For some traits, such 181 as NRT, there was very little variation among pests (Fig. 2a), and thus no significant 182 correlations with other variables. There were some expected correlations between 183 explanatory variables such as: a positive correlation between PA and AF, indicating 184 that most pests on forestry hosts are pests on perennial plants; a negative 185 correlation between IE and Brank, indicating that internally feeding pests become 186 less common as latitude increases, and finally; a negative correlation between Brank 187 188 and AF, indicating that pests in agricultural habitats are generally found at lower latitudes than pests in forestry habitats (Table S2). 189

190

There were several strong correlations between explanatory and response variables, 191 and interestingly most of these concerned the ecological impact, rather than 192 193 socioeconomic impact, of the pests. This is likely due to selection bias, since pests of high socioeconomic impact were chosen, thus there was little baseline variation in 194 195 that variable. However, there was a positive correlation between IE and SEI, indicating that external feeders among the selected pests generally have higher 196 197 socioeconomic impact than the internal feeders. ECI was found to be significantly positively correlated with PA, IE, Brank and AF. These findings indicate, briefly, that 198 pests' ecological impact increases with latitude, and externally feeding forest pests 199 have stronger ecological impacts than internally feeding agricultural pests. 200

201

The most interesting finding, in the context of this study, was that several of both the 202 explanatory and response variables were significantly correlated with ECId, inter alia 203 as Brank was negatively correlated with ECId, indicating that changes in ecological 204 205 impact increase as latitude increases. There was also a positive correlation between AF and SEId, suggesting that the severity of agricultural pests is increasing more 206 than forestry pests' severity (possibly because most serious forestry pests already 207 have major ecological impact). Furthermore, there was a positive correlation 208 209 between ECId and SEId, suggesting that pests that are becoming more socioeconomically destructive are also becoming more ecologically damaging. 210 Finally, there was a positive correlation between ECI and ECId, suggesting that 211 pests with the strongest current ecological impacts are more likely to become 212 increasingly damaging than pests with low current ecological impact. 213

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214

Optimal temperature in the past, the present and the future (Table S3 and S4)

A meta-analysis on optimal temperatures of the 31 insect pest species was 216 conducted to quantify potential climate change stress. We extracted optimal 217 temperatures for development (T_{opt}) for the species from the primary literature, giving 218 priority to studies investigating temperature dependence of the whole life-cycle, as 219 well as using populations from the core of the range. Latitude and longitude 220 coordinates were either copied straight from the article, or extracted from global 221 222 maps based on the sampling location reported in the original article. The data is shown in Table S3. 223

224

Ambient temperatures at each location in our species database (Table 3) were 225 extracted from a Global Circulation Model that forms part of the Coupled Model 226 Intercomparison Project phase 5^{5,6}, which we sourced directly from the Earth System 227 Grid database (http://pcmdi9.llnl.gov/). More specifically we considered predictions of 228 average monthly near surface temperature (ambient temperature hereafter, T_{amb}) 229 from the HadGEM2-CC model⁷. For the present and future conditions, we 230 considered models with a radiative forcing of 8.5Wm⁻² (Representative 231 Concentration Pathway 8.5), the most extreme climate warming scenario included in 232 the IPCC Fourth Assessment report⁸, and that which is most representative of 233 current trajectories⁹. Here, we aimed to capture "present" ambient temperatures 234 (2006-2015), "near-future" ambient temperatures (2056-2065) and "future" ambient 235 temperatures (2070-2079). The "past" temperatures were extracted from the 236 237 historical experiment of the same model. Across each of these four decades, we calculated an overall average mean temperature from the 12 monthly averages for 238 each year. As species at high latitudes in the northern hemisphere undergo a period 239 of dormancy during winter (and hence are buffered from winter temperatures), for 240 locations above 45° latitude (15 of 38 locations, Table 3), we considered only 241 temperatures during the summer months from May to September inclusive. Data 242 were extracted from raw files, and subsequently cleaned using functions in the 243 "raster" package for R¹⁰. The full R-code workflow can be found at GitHub: XXX 244 245

- 246 The overall T_{amb} for each of the four decades were compared against the species
- 247 T_{opt} at each location in two ways. First by visually comparing the differential between
- ²⁴⁸ T_{opt} and T_{amb} (Fig. 3) and then with a phylogenetically corrected generalized linear
- least square model (pgls) investigating the relationship between thermal suitability
- 250 (expressed as T_{opt} / T_{amb}) and absolute latitude. Data were extracted from the
- literature (Table S3) and the models run using primarily the "pgls" function in the
- ²⁵² "caper" package for R¹¹. Overall model results are shown in Table S4 and the full R-
- code workflow can be found at GitHub: XXX

Table S1 The 31 major pest species' responses to ongoing climate change in four major categories (range change, life-history

traits, population dynamics and trophic interactions), showing whether they are likely to increase or reduce the pests' severity.

Trait		Range	change	l ife-hist	tory traits	Population dynamics		Trophic i	interaction	
Change in severity		Increase	Decrease	Increase	Decrease	Increase	Decrease	Increase	Decrease	
Name	Order: Family	Increase	Declease	Increase	Declease	Increase	Declease	Increase	Declease	
Choristoneura fumiferana	Lepidoptera: Tortricidae	12-14	15	-	-	12				
Lymantria dispar	Lepidoptera: Erebidae	16-18	15	-	-	15	- 15	-	-	
Operophtera brumata	Lepidoptera: Geometridae	19-21	-	-	-	22	-	23,24	-	
Epirrita autumnata	Lepidoptera: Geometridae	19,20			-	-	25,26	20,21	-	
	Lepidoptera: Thaumetopoeidae	27-30	-	-	-			- 31		
Thaumetopoea pityocampa		32-37	-	- 34,37,38	- 34	-	-	01	-	
Leptinotarsa decemlineata	Coleoptera: Chrysomelidae	32 31	- 39,40	34,57,50		-	- 39,40	-	-	
Locusta migratoria	Orthoptera: Acrididae	- 41-43		-	-	-	,	-	-	
Meligethes aeneus	Coleoptera: Nitidulidae	41-43	-	- 46	-	-	-	-	-	
Plutella xylostella	Lepidoptera: Plutellidae	-	-		-	-	-	-	-	
Rhopalosiphum padi	Hemiptera: Aphididae	47-49	-	49,50	-	49	49	-	-	
Diuraphis noxia	Hemiptera: Aphididae	51	-	-	-	51	51,52	-	-	
Adelges tsugae	Hemiptera: Adelgidae	53-56	-	54	-	55-56	53		-	
Bemisia tabaci	Hemiptera: Aleyrodidae	57,58	-	-	-	58	59	-	-	
Nezara viridula	Hemiptera: Pentatomidae	60	-	61	-	-	61	-	-	
Chilo suppressalis	Lepidoptera: Crambidae	62	-	62,63	-	-	62	-	-	
Ostrinia nubilalis	Lepidoptera: Crambidae	-	-	64-66	-	67,68	-	-	-	
Helicoverpa armigera	Lepidoptera: Noctuidae	68-70	-	-	-	69,71-73	74	-	-	
Dendroctonus ponderosae	Coleoptera: Curculionidae	75,76	-	76	-	75	-	-	-	
Dendroctonus frontalis	Coleoptera: Curculionidae	77-81	-	77,79	-	-	-	-	-	
lps typographus	Coleoptera: Curculionidae	82,83	-	82-87	-	84,86,87	-	-	-	
Bactrocera oleae	Diptera: Tephritidae	88,89	88	-	-	89,90	89	-	-	
Cydia pomonella	Lepidoptera: Tortricidae	91	92,93	91,94,95	-	-	-	-	-	
Hypothenemus hampei	Coleoptera: Curculionidae	96,97	-	96-98	-	-	-	-	-	
Diabrotica virgifera	Coleoptera: Chrysomelidae	99-101	-	-	-	-	-	-	-	
Popillia japonica	Coleoptera: Scarabaeidae	-	-	-	-	102-107	108	106	-	
Eldana saccharina	Lepidoptera: Pyralidae	109,110	-	-	-	-	111,112	-	-	
Leucoptera coffeella	Lepidoptera: Lyonetiidae	113,114	-	113	-	-	-	-	-	
Marmara gulosa	Lepidoptera: Gracillariidae	-	-	-	-	-	-	-	-	
Phyllocnistis citrella	Lepidoptera: Gracillariidae	-	-	-	-	-	-	-	-	
Chilo partellus	Lepidoptera: Crambidae	115,116	117	117	-	-	-	-	-	
Myzus persicae	Hemiptera: Aphididae	-	-	118	-	118	-	119	-	
	ar studios, while sumbars refer to indi			· · · · ·	L				1	

256

Empty cells indicate lack of data or studies, while numbers refer to individual studies showing (empirical studies) or suggesting (modelling and laboratory studies) a response.

Table S2 Kendall rank order correlations of background traits and responses to ongoing climate change investigated in the 31

serious insect pests.

	NRT ¹	PA ²	IE ³	Brank ⁴	AF ⁵	SEI ⁶	SEId ⁷	ECI ⁸	ECId ⁹	GD ¹⁰
Ν	29	29	29	29	29	29	29	29	29	29
NRT	1									
PA	0.251	1								
IE	-0.248	-0.099	1							
Brank	-0.043	-0.194	-0.310	1						
AF	0.236	0.699	0.155	<u>-0.461</u>	1					
SEI	-0.109	0.103	0.377	-0.143	-0.017	1				
SEId	-0.023	0.097	-0.138	-0.190	0.167	0.084	1			
ECI	0.199	0.349	0.376	-0.349	0.647	0.123	0.085	1		
ECId	-0.009	0.132	0.126	-0.344	0.447	-0.084	0.597	0.463	1	
GD	0.068	0.116	-0.276	-0.122	0.064	-0.032	0.318	0.154	0.316	1

259 The following list explains abbreviations used (listed in the beginning of this supplement): ¹Number of response types, ²Perennial or annual host, ³External or internal feeder,

⁴Mean habitat biome ranked from tundra to tropical, ⁵Agricultural or Forestry pest, ⁶Socioeconomic impact, ⁷Change in Socioeconomic impact, ⁸Ecological impact, ⁹Change in 261

ecological impact, ¹⁰Difference between geographical areas of range. Significant two-tailed correlation coefficient values where p<0.05 (>0.312), and p<0.01 (>0.430) are indicated in bold, and both bold and underlined, respectively.

Table S3 Input data for optimal temperature analysis.

Scientific name	Topt	Lifestage	Latitude	Longitude	Position in range	Invasion status	Reference	Avg temp	Avg Temp	Avg temp	Avg temp
					in lange	Status		1960- 1969	2006- 2016	2050- 2059	2070- 2079
Choristoneura fumiferana	28.7	Egg to pupa	63,22	-123,48	CR	Native	120	7,5	9,4	12,0	13,5
Choristoneura fumiferana	28.6	Egg to pupa	53,50	-113,53	CR	Native	120	12,9	14,3	17,5	19,4
Choristoneura fumiferana	29.2	Egg to pupa	64,67	-124,92	CR	Native	120	7,1	8,8	11,4	13,0
Choristoneura fumiferana	29.1	Egg to pupa	51,95	-114,25	CR	Native	120	12,0	13,5	16,8	18,6
Choristoneura fumiferana	30.9	Egg to pupa	53,52	-113,26	CR	Native	120	14,3	15,7	19,1	20,9
Choristoneura fumiferana	33.0	Egg to pupa	49,65	-110,03	CR	Native	120	16,7	17,9	21,7	23,5
Lymantria dispar	28,0	Egg to pupa	39,83	-74,87	CR	Native	121	10,4	12,3	15,1	16,7
Operophtera brumata	22,0	Larva	69,64	19,01	CR	Native	122	16,9	19,0	21,7	24,3
Epirrita autumnata	25,0	Larva	50,09	7,32	CR	Native	123	6,1	7,8	10,5	11,7
Thaumetopoea pityocampa	25,0	Larva	69,64	19,01	CR	Native	124	18,2	19,6	23,9	25,8
Leptinotarsa decemlineata	28,0	Egg to pupa	69,73	27,01	UN, HA	Invasive	125	7,0	9,1	12,3	14,1
Locusta migratoria	30,0	Nymph	45,50	11,15	CR	Native	126	13,6	14,1	17,4	18,7
Meligethes aeneus	24,0	Egg to pupa	42,41	-71,38	CR	Native	127	14,9	16,9	19,1	21,1
Plutella xylostella	28,8	Whole life cycle	33,46	120,01	CR	Native	128	11,2	13,0	15,3	16,9
Rhopalosiphum padi	28,5	Whole life cycle	53,53	10,01	CR	Native	129,130	12,5	13,5	16,6	17,5
Diuraphis noxia	20,0	Whole life cycle	35,84	50,96	CR	Invasive	131,132	13,7	15,7	17,6	19,3

Adelges	Х	Х	Х	Х	Х	Х	Х	Х		Х	Х
tsugae											
Bemisia	31,0	Whole life	35,16	128,14	CR	Native	133,134	12,4	13,3	16,3	17,3
tabaci		cycle									
Nezara	27,0	Nymph	37,99	-84,66	CR	Native	135	10,6	12,5	15,5	17,3
viridula											
Chilo	31,0	Egg to pupa	30,53	114,33	CR	Native	136	14,5	15,3	18,4	20,0
suppressalis											
Ostrinia	34,0	Larva	46,40	0,05	CR	Native	137	18,6	20,5	22,8	25,4
nubilalis					-						
Helicoverpa	27,5	Whole life	40,97	23,59	CR	Native	138	10,8	12,2	15,3	16,0
armigera		cycle					400				
Dendroctonus	24,0	Whole life	41,83	-111,60	CR	Native	139	6,5	8,4	11,1	13,0
ponderosae		cycle					140		10.0		
Dendroctonus	31,1	Whole life	31,59	-94,80	CR	Native	140	17,1	18,6	21,0	22,5
frontalis	00.4	cycle	40.00	0.00	0.0	Nec	141,142	44.0	45.0	40.0	01.1
lps	30,4	Whole life	46,86	9,66	CR	Native	141,142	14,2	15,6	19,2	21,4
typographus	07.0	cycle	45 50	44.45		les recipre	143,144	10.0	10.0	22.0	25.0
Bactrocera oleae	27,0	Egg to pupa	45,50	11,15	CR	Invasive	143,144	18,2	19,6	23,9	25,8
Cydia	30,7	Larva	38,10	46,48	CR	Native	145	8,9	10,9	13,6	15,2
pomonella	30,7	Laiva	50,10	40,40	OK	Native		0,9	10,9	13,0	15,2
Hypothenemus	26,7	Whole life	-0,76	34,72	CR	Native	96	18,7	19,8	22,1	23,4
hampei	20,1	cycle	0,70	04,72	ÖN	Native		10,7	10,0	<i>22</i> , 1	20,4
Diabrotica	28,0	Egg	42,44	-81,89	CR	Invasive	146	5,5	7,9	11,4	13,5
virgifera	,_	-33	,	- ,				-,-	.,.	, .	
Popillia	27,5	Larva	39,96	-75,19	UN, HA	Invasive	147	10,4	12,3	15,1	16,7
japonica	,		,	,	,			,	,	,	,
Eldana	29,0	Egg to adult	-25,46	31,58	CR	Invasive	148	19,3	20,2	22,3	24,1
saccharina		00		-					-		
Leucoptera	30,0	Larva	9,95	-84,01	CR	Native	149	25,4	26,2	28,0	29,3
coffeella											
Marmara	29,0	Egg to pupa	36,60	-119,51	CR	Invasive	150	13,8	15,4	18,0	19,1
gulosa											
Phyllocnistis	30,0	Adult	36,99	35,34	CR	Invasive	151	12,2	13,4	16,2	17,7
citrella											
Chilo	32,0	Larva	4,43	39,31	UN, HA	Invasive	117	21,4	22,6	24,8	26,0
partellus											

Chilo	32,0	Larva	8,40	39,35	UN, HA	Invasive	152	16,5	17,6	20,1	21,6
partellus											
Chilo	32,0	Larva	28,64	77,16	UN, HA	Invasive	153	21,0	21,6	23,4	25,0
partellus											
Myzus	26,5	Egg to pupa	30,30	120,12	CR	Native	154	14,1	14,8	18,0	19,4
persicae											

CR = Core range, UN, HA = Unknown position in range, but occurring in high abundance. For some pests there are several thermal

performance studies available. Here we chose the most comprehensive (in terms of methodology, temperature range, and life-stages analysed), and for two species (Choristoneura fumiferana and Chilo partellus) we included several populations that had been investigated.

bioRxiv preprint doi: https://doi.org/10.1101/425488; this version posted September 24, 2018. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission. **Table S4** Coefficients of variation in phylogenetically controlled generalized least square

Table S4 Coefficients of variation in phylogenetically controlled generalized least square models (pgls) testing the relationship between temperature suitability and latitude in four different time-periods (past: 1960-1969, present: 2005-2015, near future: 2056-2065 and future: 2070-2079).

Effect	Estimate	Std. Error	t value	Significance
Past				
Intercept	0.741	0.078	9.464	< 0.001
Latitude	-0.008	0.002	-3.879	< 0.001
Present				
Intercept	0.768	0.073	10.475	< 0.001
Latitude	-0.007	0.001	-3.788	0.001
Near future				
Intercept	0.831	0.079	10.514	< 0.001
Latitude	-0.006	0.002	-2.980	0.007
Future				
Intercept	0.878	0.081	10.872	< 0.001
Latitude	-0.006	0.002	-2.790	0.011

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1 Supplement 2

2

3 Complex responses of global insect pests to climate change

4

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59 1. Eastern spruce budworm (*Choristoneura fumiferana*) Lepidoptera: Tortricidae60 (Clemens 1865)

61

The eastern spruce budworm Choristoneura fumiferana is a native defoliator of 62 63 North American conifer forests. The main host of the eastern spruce budworm is 64 balsam fir, Abies balsamea, though it may also utilize white, red and to some extent black spruce, Picea glauca, P. rubens and P. mariana. The eastern spruce 65 budworm causes considerably more damage than any other defoliating insect in 66 North America's boreal forests (Volney and Fleming 2000). The northern range of 67 the eastern spruce budworm is predicted to shift towards north and higher 68 elevations under projected climate change. The expansions are predicted to be 69 spatially non-uniform depending on the distribution of the main host species, but 70 temperate regions are expected to be most affected (Réniere et al. 2012). 71 72 Climate change and forest composition are predicted to influence the outbreak characteristics of the eastern spruce budworm in Canada (Gray et al. 2000, Gray 73 2013). Outbreak duration has been shown to be most strongly influenced by 74 75 spring accumulation of degree days and outbreak severity most influenced by the 76 extreme maximum temperatures of spring (Gray 2013). Forest characteristics (tree species composition, basal area) influence the outbreaks duration and 77 severity. In Pennsylvania increased temperature with increasing precipitation is 78 predicted to increase defoliation area whereas increased temperature alone or 79 combined with low precipitation decreased the defoliation area (Williams and 80 Liebhold 1995). 81



82

Distribution map from: CABI, 2018. *Choristoneura fumiferana*. In: Invasive

- 84 Species Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>.
- 85 Printed with permission.

86 87 2. Gypsy moth (*Lymantria dispar*) Lepidoptera: Erebidae (Linnaeus 1758)

The major insect pest of temperate central European and eastern North 88 American forests is the gypsy moth, Lymantria dispar. The gypsy moth is native 89 to southern Europe, northern Africa, central and southern Asia and Japan. The 90 European strain has been introduced to the United States (in 1869) and Canada 91 and is now present in most of northeastern N. America but its range is expanding 92 to the south and west. In its caterpillar stage, the gypsy moth can feed on more 93 than 500 different species of trees and shrubs. In N. America the preferred hosts 94 include oak, cherry white birch, maple, alder, willow, elm and trembling aspen. 95 Defoliations may change oak dominated forest to maple dominated forests thus 96 causing considerable forest ecosystem changes (Fajyan and Wood 1996). In 97 eastern N. America current climate change forecasts are expected to increase 98 99 the area of climatic suitability for the gypsy moth (Regniere et al. 2009). Williams and Liebhold (1995) modeled that in Pennsylvania increased temperature alone 100 or with increasing precipitation are expected to increase defoliation areas 101 whereas increasing temperature with decreasing precipitation is expected to 102 103 decrease defoliation area. Control of gypsy moth populations by the fungal pathogen Entomaphaga maimaiga has decreased damage in N. America during 104 the last decades (Oswalt & Smith 2014). In Europe climate change is expected to 105 increase range shift towards north (e.g. Vanhanen et al. 2007, Fält-Nardmann et 106 al. 2018a, b, c). Also Asian gypsy moth populations are modeled to have 107 potential to expand towards north and west under changing climate (Peterson et 108 al. 2007). Finally, the Nun moth, Lymantria monacha, has been shown to spread 109 northwards in Europe probably due to increased winter survival because of 110 reduced thermal constraints (Fält-Nardmann et al. 2018a, b). 111



- 112
- Distribution map from: CABI, 2018. *Lymantria dispar*. In: Invasive Species
- 114 Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>. Printed with
- 115 permission. Reviewed by: Patrick Tobin, School of Environmental and Forest
- 116 Sciences, University of Washington, Seattle, USA

3. Winter moth (*Operophtera brumata*) Lepidoptera: Geometridae (Linnaeus 1758)

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The winter moth (Operopthera brumata) is distributed in temperate, boreal and 120 121 sub-arctic forests throughout Europe, western Russia, south-east Russia and parts of Asia (Tenow 1972). In North America it has been accidentally introduced 122 to both eastern and western Canada. From the latest introduction in Nova Scotia 123 124 it has spread into the north-eastern coastal states of the US (Elkinton et al. 2014). The species is univoltine with overwintering eggs and spring-feeding larvae. 125 which feed on a variety of mostly deciduous trees. In northern regions it displays 126 a pronounced cyclic dynamics with decadal outbreaks of varying amplitude. In 127 temperate Europe the winter moth is an important pest in orchards and natural 128 oak forest, while in northern Fennoscandia, outbreaks by winter moth and 129 130 autumnal moth (see elsewhere) have defoliated 1 mill ha of birch forest during the 2000's (Jepsen et al. 2009a) and caused ecosystem levels changes in the 131 birch forest system (Jepsen et al. 2013, Kaukonen et al. 2013). At its northern 132 range the winter moth has spread northwards and inland during the last few 133 134 decades (Jepsen et al. 2008) probably due both to a release from climatic constraints on eggs survival in winter (Ammunet et al. 2012), and a better 135 phenological synchrony with the main host tree, mountain birch (Jepsen et al. 136 2009b). In temperate Europe, a disrupted phenological synchrony between winter 137 moth and oak caused by warming temperatures (Visser and Holleman 2001) 138 appears to have been restored by a hereditary change in egg hatching dates in 139 response to the altered selection pressure . In the Netherlands observations of 140 winter moth damage have increased over the last 50 years (Moraal & Jagers op 141 Akkerhuis, 2011). 142



143

144 Distribution map from: CABI, 2018. *Operophtera brumata*. In: Invasive Species 145 Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>. Printed with

145 Compendiur146 permission.

4. Autumnal moth (*Epirrita autumnata*) Lepidoptera: Geometridae (Borkhausen
148 1794)

149

The autumnal moth (*Epirrita autumnata*) is distributed mainly in boreal, alpine and 150 sub-arctic forests throughout the northern hemisphere (Tenow 1972). The 151 species is univoltine with overwintering eggs and spring-feeding larvae, which 152 feed on a variety of mostly deciduous trees. As the winter moth, it displays 153 pronounced cyclic dynamics with decadal outbreaks of varying amplitude in 154 Fennoscandia, causing large-scale and severe damage to alpine and sub-arctic 155 mountain birch forests (Jepsen et al. 2013, Karlsen et al. 2013). At its northern 156 range the species has recently spread into colder and more continental areas 157 (Jepsen et al. 2008), probably due to a release from climatic constraints on egg 158 survival in winter (Ammunet et al. 2012). The autumnal moth is a widespread 159 species but outbreaks occur mainly near the northern margin of its distribution 160 (Tenow 1972, Neuvonen et al. 1999). Therefore, it seems plausible that at least 161 one reason behind this pattern is higher numbers or efficiency of natural enemies 162 in more southern areas, and there is evidence that the efficiency of the 163 parasitoids of the autumnal moth is higher in warmer temperatures (Virtanen & 164 Neuvonen 1999). Finally, in a seven-year field experiment, Svensson et al. 165 (2018) showed links between habitat warming and trophic shifts in herbivore-166 plant interactions leading to more severe pest outbreaks. 167



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Distribution map from: CABI, 2018. *Epirrita autumnata*. In: Invasive Species
 Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>. Printed with

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- 5. Pine processionary moth (*Thaumetopoea pityocampa*) Lepidoptera:
- 173 Thaumetopoeidae (Denis & Shiffermüller 1775)
- 174

The pine processionary moth (*Thaumetopoea pityocampa*) native to the western 175 Mediterranean basin (Kerdelhué et al. 2009). It is currently extending its 176 distribution northwards and into higher elevations and breeds as far north as the 177 Paris basin (Rogues 2014). The species has a univoltine life cycle, with larvae 178 that feed gregariously during winter on coniferous tree species. The main hosts 179 are *Pinus* spp., in particular *P. nigra*, but the species can also attack other 180 conifers such as Cedrus ssp. Adoption of new native and non-native hosts (P. 181 mugo, Pseudotsuga menziesii) has been observed, although female host choice 182 appears conservative (Stastny et al. 2006). The range expansion in pine 183 processionary moth has been shown to be facilitated by an increase of winter 184 temperatures, resulting in better thermal conditions for both female dispersal 185 (Battisti et al. 2006, 2017), and for larval feeding activity in winter, the latter 186 resulting in higher probabilities of winter survival (Battisti et al. 2005; Buffo et al. 187 2007; Robinet et al. 2007, Toigo et al. 2017). However, accidental human-188 mediated dispersal is likely to have contributed to the establishment of recent 189 pioneer colonies north of Paris and in eastern France (Robinet et al. 2012). 190



191

192 Distribution map from: CABI, 2018. *Thaumetopoea pityocampa*. In: Invasive

- 193 Species Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>.
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6. Colorado potato beetle (*Leptinotarsa decemlineata*) Coleoptera:
Chrysomelidae (Say 1824)

196 197

The major insect pest of cultivated potato is the Colorado potato beetle. 198 199 Leptinotarsa decemlineata. This species has spread from native habitats in northern Mexico to cover a range of over 16M km² in North America, Europe and 200 Asia (Alyokhin 2009). The species differs in voltinism and generation time across 201 202 latitude (Hsiao 1985) and increasing mean temperatures associated with climate change have been observed to increase the range of L. decemlineata in 203 temperate regions, due to ecological release of thermal constraints as well as a 204 lengthening growth season (Boman et al. 2008, Valosaari et al. 2008, Lyytinen et 205 al. 2009, Piiroinen et al. 2011, Lehmann et al. 2014, 2015). The species has been 206 shown to be able to adaptively synchronize its life-cycle with novel environments 207 (Danilevskii 1965). However, due to the low scale of potato cultivation at higher 208 latitudes than the current range limit, net socioeconomic effects of range 209 expansion might be negligible. Instead a larger socioeconomic impact might be 210 seen at lower latitudes, where the species likely instead will increase in voltinism 211 212 (Jönsson et al. 2013, Pulatov et al. 2016, Wang et al. 2017). Potential desertification at low latitudes (e.g. the Mediterranean region) is unlikely to 213 constrain L. decemlineata since adults can aestivate over periods of harshness 214 during summer (Tauber et al. 1986). In conclusion, as long as the host plant is 215 cultivated, climate change is likely to have net positive effects on L. 216 decemlineata, leading to an increase in socioeconomic impact of this important 217 pest species. 218



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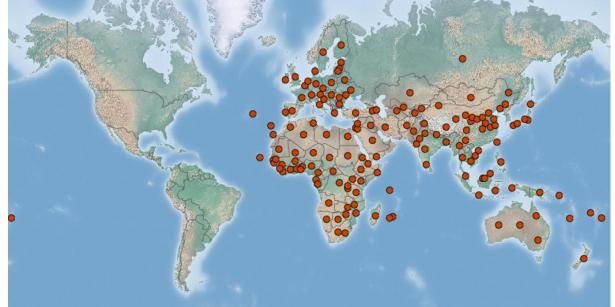
220 Distribution map from: CABI, 2018. *Leptinotarsa decemlineata*. In: Invasive

- 221 Species Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>.
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7. Oriental migratory locust (*Locusta migratoria manilensis*) Orthoptera: Acrididae(Meyen 1835)

225

The migratory locust is an important polyphagous defoliator of crops occurring in 226 227 a wide area across Africa, Asia, Australia, New Zeeland and occasionally in 228 Europe (e.g. Brázdil et al 2014). Due to its large geographical range the species has been divided into a number of subspecies (see Chapuis et al. 2008). In Asia 229 230 the primary subspecies is Locusta migratoria manilensis, sometimes referred to as L. migratoria migratorioides, a pest with a very long history in the region 231 (Uvarov 1936). Indeed, the first records are over 3500 years old (Tian 2011). The 232 species is generally guite harmless and exists in low-density populations along 233 the coastal and sub-coastal regions. However, changes in local climatic 234 conditions can rapidly cause locusts to shift into a high-density, gregarious, 235 migratory phase, with profound negative impact on local ecosystems (Uvarov 236 1936). What triggers outbreaks is still a matter of debate, with on the one hand, 237 warm temperatures and dry conditions (Ma 1958) and on the other hand, 238 239 droughts/floods (Stige et al. 2007; Liu et al. 2008; Zhang et al. 2009, see also 240 Brázdil et al. 2014 for an European example) suggested to act as outbreak triggers. Due to the long history of record-keeping in the region, Tian and 241 colleagues (2011) correlated historical records of locust outbreaks in China with 242 historical meteorological records and found that across a 1900-year period, 243 outbreaks are positively associated with dry conditions and low temperatures. 244 Since climate change scenarios in the region suggest increasing temperatures 245 and a decreasing frequency of droughts and floods (Zhang et al. 2009) these 246 findings suggest that net effects of climate change on the Oriental migratory 247 locust are negative, with the pest decreasing in severity due to reduced outbreak 248 frequency. 249



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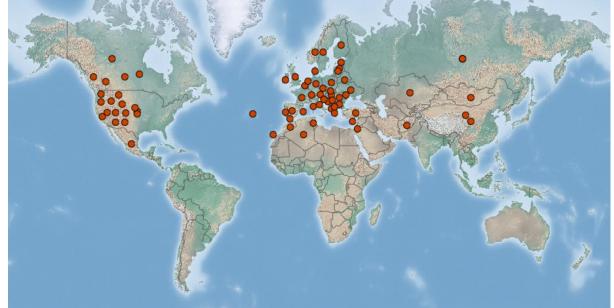
251 Distribution map from: CABI, 2018. *Locusta migratoria*. In: Invasive Species

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8. Pollen beetle (Meligethes aeneus) Coleoptera: Nitidulidae (Fabricius 1775)

254 255

The rape beetle, *Meligethes aeneus* is a common beetle occurring in most of the 256 Holarctic region (Alford 2003). It feeds on a range of naturally occurring plants, 257 especially Brassica and Sinapis species where it is not considered particularly 258 harmful (Alford 2003). However, since it also feeds on commercially grown rape 259 crops, it might become a serious pest with a large regional economic impact. 260 Populations of *M. aeneus* are generally univoltine, and adults overwinter in 261 woodlands (Tiilikainen and Hokkanen 2008). Rape is one of the most important 262 crop plants in Europe with a total production volume of 19 x 10⁶ tonnes grown 263 during 2010-2011 in the EU (Covette et al. 2012). An increasing utilization of rape 264 has led to the development of winter hardy high latitude variants which can be 265 found in northern Europe (Mäkelä et al. 2011). Increasing the growing areas of 266 rape crops has also resulted in positive effects on *M. aeneus*, which has 267 increased in abundance in concert with its host plant (Tiilikainen and Hokkanen 268 2008). In case populations are not controlled, yield losses in commercial rape 269 270 crops can be up to seventy percent (Nilsson 1987). Populations of *M. aeneus* are 271 widely controlled both through biological (Veromann et al. 2006), and more commonly, chemical means (Smatas et al. 2012). Chemical management is 272 complicated by high levels of pesticide resistance (Tiilikainen and Hokkainen 273 2008; Smatas et al. 2012) which is exacerbated by host shifts of *M. aeneus* 274 individuals from commercially grown rape crops to wild relatives (Hokkanen 275 2000). The shift of host plants can increase spatial heterogeneity and contribute 276 to the maintenance of large potential genetic variation in the populations. The 277 effect of climate change is difficult to estimate in *M. aeneus* since this univoltine 278 species already has a more northern distribution than its crop host plants. 279 Therefore climate change effects will likely act indirectly as warming affects the 280 range of its host plant if rape is going to be cultured at higher latitudes and in 281 larger areas. According to Bebber et al. (2013) M. aeneus has not shifted or 282 enlarged its range during the last 60 years; however its severity has increased, 283 284 primarily through an enlargement of host plant planting areas and increasing pesticide resistance (Tiilikainen and Hokkainen 2008; Smatas et al. 2012). 285 According to Hakala et al. (2011) climate change might make cultivation of 286 different rape variants possible even above the Arctic Circle (65°N). If this is the 287 case, *M. aeneus* most likely will transition along with its host, and further increase 288 in severity as pest. A similar scenario has been outlined for the bean beetle 289 Cerotoma trifurcata, where it is the response of the primary host, Glycine max, to 290 climate change, that will determine the changes of the pest as well (Berzitis et al. 291 292 2014).



293

Distribution map from: CABI, 2018. *Meligethes aeneus*. In: Invasive Species
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9. The diamondback moth (*Plutella xylostella*) Lepidoptera: Plutellidae (Linnaeus
1758)

299

The diamondback moth (Plutella xylostella) has an European origin, but has now 300 301 spread all over the world where its Brassicaceae hosts are cultivated or it can feed on native Brassicaceae plants (Talekar & Shelton 1993). This 302 microlepidopteran starts its lifecycle as a leaf miner in the first two instars, after 303 which it is a free-moving defoliator. The larvae cause severe damage on flowers, 304 leaves, buds and seed pods (siliguae) when numerous and management costs 305 are estimated to be between 4 and 5 billion USD per year (Zalucki et al. 2012). 306 The diamondback moth is the first crop pest known to have developed resistance 307 against DDT. It is also the first insect known to develop resistance against 308 biological control by Bt toxin (Bacillius thuringiensis) (Shelton et al. 1993, Talekar 309 310 & Shelton 1993). The thermal developmental range is very wide (4-37°C) and in the tropics and subtropics the diamondback moth occurs throughout the year 311 (Zalucki et al. 2011; Li et al. 2012, Marchioro & Foerster 2012; Nguyen et al. 312 313 2014, Li et al. 2016). The number of generations is dependent on temperature 314 and varies from 4 in the northern latitudes to 12 in the south. The high number of generations has probably influenced the development of resistance. Migration 315 and southern air currents allow the species to be found all the way up to Svalbard 316 (Coulson et al. 2002) and yearly migration (exceeding 3000 km) allows for 317 growing season invasions in areas too cold during the winter while the moth 318 overwinters in more southern areas (Dosdall et al. 2001; Chapman et al. 2002; 319 Gu, 2009; Wei et al. 2013). Drought has a positive effect on the diamondback 320 moth survival (Talekar, Lee & Huang 1988; http://eap.mcgill.ca/CPCM_3.htm). 321 While a modeling study suggested an increase in voltinism over time in several 322 replicated locations at the northern range limit of the species with increasing 323 324 temperature (Collier et al. 2008), a similar study at tropical latitudes suggested 325 more variable, both severity increasing and decreasing effects (Ngowi et al. 326 2017).



327

Distribution map from: CABI, 2018. *Plutella xylostella*. In: Invasive Species

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331 Research Centre, The University of British Columbia, 4200-6270 University Blvd.,

332 Vancouver, British Columbia, Canada V6T 1Z4

10. Bird cherry oat aphid (*Rhopalosiphum padi*) Hemiptera: Aphididae (Linnaeus1758)

335

The bird cherry oat aphid Rhopalosiphum padi is a principal pest and vector of 336 337 Barley yellow dwarf virus in wheat and other cereals in UK, NA, Europe, but also attacks other plant species. The species is thought to have originated in North 338 America (Halbert & Voegtlin 1998), but now has a cosmopolitan distribution. It is 339 340 one of the 14 most important aphid species worldwide because of its impacts on globally significant staple grasses. As a result it has been extensively studied on 341 various aspects of its biology. Across this range it is primarily heteroecious 342 holocyclic with the predominant primary host *Prunus padus* or other *Prunus* 343 species, but where winters are mild and primary hosts rare, it is anholocyclic, 344 moving from wild grasses to cultivated cereals (Williams and Dixon 2007). Its 345 pest status is amplified in some regions where it is a vector of viruses affecting 346 noncereals, potato, where its transient movements and transient feeding makes 347 is a vector for Potato virus Y (Katis and Gibson 1985). Outside of cropping 348 systems, the ecological impact of the bird cherry oat aphid is likely minimal. 349 350 Nonetheless as a vector of cereal yellow dwarf viruses, it contributes to complex interactions among competing grasses, including invasive and native ones 351 (Malmstrom et al. 2006). In many areas, these viruses can readily be found in 352 perennial grasses (Ingwell et al. 2012) with implications for the functioning of 353 these systems. Potentially, the bird cherry oat aphid could respond to climate 354 change directly, due to the constraints of its optimal thermal range and indirectly 355 due to changes in the quality of its host plants under climate related stress, or 356 changes in its natural enemy complex. Finally, climatic conditions could influence 357 the bird cherry oat aphid as a vector of viruses. As is true for most aphid species 358 (Awmack and Leather, 2007), increases in temperature accelerates development 359 and the potential number of generations that can be achieved within a single 360 growing season. A number of laboratory studies have delineated the temperature 361 envelope for the bird cherry oat aphid (reviewed in Finlay and Luck 2011). There 362 appears to be an optimum near 26°C, above which development is retarded and 363 below which it declines to around 10°C. Developmental thresholds range 364 between 4° and 6°C. Thus, as climates in particular regions warm, as is generally 365 projected, the aphid could exhibit extended seasons of viability and more rapid 366 growth where lower temperatures are currently limiting, and reductions where 367 higher temperatures are limiting. Since there is considerable variation among 368 clones of bird cherry oat aphid that have been investigated in the laboratory (e.g. 369 Valenzuela et al. 2008), the potential responses to climate trends are difficult to 370 371 project. Despite several laboratory studies of bird cherry oat aphid responses to climatic drivers, and the significance of this aphid as a pest worldwide, there are 372 few studies and no evidence that its populations respond to documented trends 373 in temperature or other drivers (Newman et al. 2003; Hoover and Newman 2004, 374 but see Andrade et al. 2016). In the Pacific Northwest of the USA, a network of 375 376 28 suction traps acquired extensive data on flights and inferred abundance of bird

cherry oat aphid abundances over a 17-year trapping period. Interannual 377 abundance exhibited evidence for biotic feedback, but was unrelated to trends or 378 variability in temperature and precipitation throughout the sampled period (Davis 379 et al. 2014). In Sweden, trends in temperature and precipitation explained a small 380 amount (1-9%) of the variation in abundance of bird cherry oat aphids from four 381 trap locations over a 20-year period and do not support any robust projections of 382 responses of the aphid to climate trends (Bommarco et al. 2007). Long-term data 383 sets do not exist for the bird cherry oat aphid in other regions or have not been 384 analyzed. Although climate related stress on the first and higher trophic levels 385 could affect populations of the bird cherry oat aphid, current data do not allow 386 robust projections about the effects of climate change on the bird cherry oat 387 aphid (Newman et al. 2003; Hoover and Newman 2004; Finlay and Luck 2011, 388 but see Andrade et al. 2016 and Wade et al. 2017). 389

390



391

392 Distribution map from: CABI, 2018. *Choristoneura fumiferana*. In: Invasive

- 393 Species Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>.
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11. Russian wheat aphid (*Diuraphis noxia*) Hemiptera: Aphididae (Kurdjumov 1913)

396 397

395

This aphid is a pest of wheat in North America, Africa, and Eurasia, Central Asia, 398 Middle East, North Africa, Kenya, South Africa, Chile, Argentina, North America 399 (first record 1986, Shufran et al. 2007) and South America (first records for Chile 400 1988, Argentina 1992; Clua et al. 2004). The species is well studied because of 401 its global distribution and potential for causing significant direct injury to wheat 402 and other cereal crops. The species impact on natural systems is probably 403 minimal. Potentially, *Diuraphis noxia* could respond to climate change directly, 404 due to the constraints of its optimal thermal range and indirectly due to changes 405 in the quality of its host plants under climate related stress, or changes in its 406 natural enemy complex. The species is relatively well studied because of its 407 408 global distribution and potential for causing direct injury to wheat and other cereal crops. This has included assessments of its development and mortality under 409 varving thermal regimes (Michels and Behle 1988), which appeared to show 410 411 reproductive an optimum at a relatively cool 20°C (see also Scott and Yeoh, 412 1999). Thus, like other aphid species responses to warming trends will likely be complex and dependent upon baselines. There are few long-term data sets that 413 could be used to develop projections of *D. noxia* responses to climatic drivers. In 414 the Pacific Northwest of the USA, a network of 28 suction traps acquired 415 extensive data on flights of *D. noxia* abundances over a 17-year trapping period. 416 Interannual abundance exhibited evidence for biotic feedback, but in addition 417 populations of the aphid were negatively correlated with increasing temperatures 418 during the sampled period in the absence of density-dependent effect (i.e., 419 420 considering residuals after accounting for feedbacks) (Davis et al. 2014). Coupled with the relatively cool documented temperature optimum for this species 421 422 (Michels and Behle 1988), this suggests warming trends would be associated with reduced abundance and therefore pest pressure from *D. noxia*, although this 423 inference has not been fully substantiated. However, in Australia, a CLIMEX 424 425 modeling approach suggested high suitability of dry inland wheat growing regions would be highly favorable for *D. noxia* infestation (Hughes and Maywald, 1990). 426 Therefore, responses are likely to vary locally. 427



428

- 429 Distribution map from: CABI, 2018. *Diuraphis noxia*. In: Invasive Species
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- 431 permission. Reviewed by: Monanimad Reza Nematoliani, Assistant Professor o 432 Entomology, Department of Plant Protection, Isfahan Research Center for
- 433 Agriculture and Natural Resources, Isfahan, Iran.

434 12. Hemlock woolly adelgid (*Adelges tsugae*) Hemiptera: Adelgidae (Annand435 1928)

436

The hemlock woolly adelgid (Adelges tsugae) is endemic to Eastern Asia and 437 438 became a pest on the eastern hemlock (Tsuga canadensis) in N. America, causing extensive tree mortality in natural forests. It has extended its distribution 439 range into north-eastern USA from the site of introduction in Virginia (Evans and 440 Gregoire, 2007; Paradis et al., 2008). The limiting factor is winter temperature, 441 which can be lethal for the overwintering stages (Paradis et al., 2008). With the 442 increase in mean minimum winter temperature accompanying climate change, 443 the aphid has progressively expanded to the north and simultaneously built up 444 high densities in the already colonized areas, contributing greatly to hemlock 445 dieback (Fitzpatrick et al., 2012, Leppanen & Simberloff 2017, McAvoy et al. 446 2017). In this view, the temperature-dependent spreading occurs from the south 447 to the north, leaving behind dead trees on which the insect cannot persist. 448 However, there are indications that at the southern edge of the range the young 449 450 nymphs suffer increased mortality because of summer heat, allowing the trees to 451 survive (University of Georgia, personal communication).



452

Distribution map from: CABI, 2018. *Adelges tsugae* (original text by National

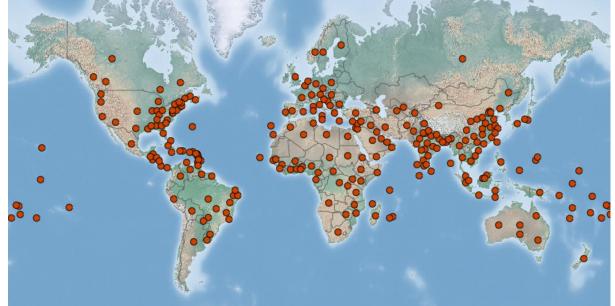
- 454 Biological Information Infrastructure (NBII) & IUCN/SSC Invasive Species
- 455 Specialist Group (ISSG)). In: Invasive Species Compendium. Wallingford, UK:
- 456 CAB International. <u>www.cabi.org/isc</u>. Printed with permission.

13. Sweet potato whitefly or Silverleaf whitefly (*Bemisia tabaci*) Hemiptera: Aleyrodidae (Gennadius 1889)

458 459

457

Although Bemisia tabaci is now recognized as a probable species complex (De 460 Barro et al. 2011), collectively the group includes significant pests, including two 461 species (now referred to as MEAM1 and Med) that are serious pests in the 462 tropics and subtropics worldwide. Other members of the complex are regional 463 pests. The pests cause direct injury and act as vectors of viruses affecting 464 several important tropical crops, including cassava. The ecological impact of 465 these species is little studied. As vectors of several plant viruses, they could 466 affect natural communities and otherwise contribute to the stability of foodwebs. 467 The general expectation for the Sweet potato whitefly is an expansion of range 468 northward with warming, which would exacerbate its importance as a pest 469 470 worldwide. This would presumably be most important in more temperate zones where its range could be currently constrained by cooler temperatures. In 471 Europe, where Bemisia is currently confined to southern coastal environments, 472 473 expansion of the pest northwards is thought to be prevented by lower 474 temperatures. A process-based modeling exercise, with inputs from the extensive literature on the life history of the species and hypothetical uniform temperature 475 changes of 1°C and 2°C project range expansions of *B. tabaci* into northern 476 Spain, central France, Italy, Greece and along the Adriatic coast of the Balkans, 477 but not into northern parts of Europe (Gilioli et al. 2014). Similar patterns are 478 possible in other temperate regions (e.g. Zidon et al. 2016). Ongoing studies are 479 examining responses to temperature and CO2 increases have detected 480 constraints at higher temperatures (between 28°C and 33°C) (Curnutte et al. 481 2014), which may indicate reductions in pressure from the Sweet potato whitefly 482 in certain regions as temperatures increase. These inferences pertain to the 483 Sweet potato whitefly species that have been most widely studied. It is possible 484 that other species within the complex and almost certain that other Bemisia 485 species will respond differently to changing climate. 486



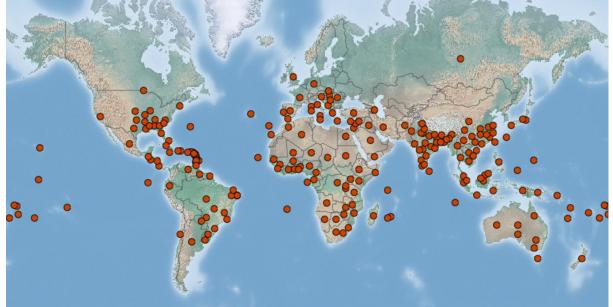
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- 488 Distribution map from: CABI, 2018. *Bemisia tabaci*. In: Invasive Species
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 Agency, Sand Hutton, York, UK

492 14. Southern green stink bug (*Nezara viridula*) Hemiptera: Pentatomidae493 (Linnaeus 1758)

494

The southern green stink bug (*Nezara viridula*) is a cosmopolitan pest of fruits 495 and seeds, especially on herbaceous crops, with multiple generations per year 496 and overwintering as an adult in a number of shelters, including buildings where it 497 can become a nuisance. In Japan N. viridula is progressively occupying areas 498 located outside the historic northern edge of the range, because of more 499 favourable winter temperature for the adults (Musolin and Saulich 2012). 500 Interestingly, the expansion has resulted in a displacement of a native bug of the 501 same genus (N. antennata) (Tougou et al. 2009). Laboratory studies reveal a 502 sensitivity to thermal conditions during development, with higher temperatures 503 leading to an increase in development rates and higher voltinism, though these 504 responses were coupled with increased adult mortality (Musolin et al. 2010). It is 505 therefore difficult to predict how warming temperature will affect the phenology, 506 voltinism and survival of *N. viridula* in the field (Panizzi & Lucini 2016). 507



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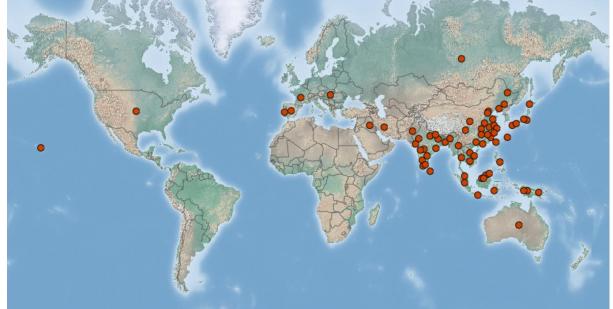
509 Distribution map from: CABI, 2018. *Nezara viridula*. In: Invasive Species

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512 15. The Asiatic rice borer (*Chilo suppressalis*) Lepidoptera: Crambidae (Walker513 1863)

514

The Asiatic rice borer, Chilo suppressalis, is a widely distributed and serious pest 515 516 of rice. It occurs in large parts of the world but the main area is East Asia. Accidental introductions into Australia, North America, Hawaii and Europe have 517 been observed but there are yet no records from Africa (Bleszynski 1970, 518 519 Waterhouse 1993). Under favourable conditions the borer can have up to six generations per year but two is most common. The cold hardiness of the larvae 520 seems to be independent of the diapause state of the insect (Lu et al. 2013), 521 indicating that climate-induced changes in the life cycle will not lead to decreased 522 risks for damage. The heat tolerance of the species is generally high and is better 523 among larvae than adults, which translates into effects especially on fertility and 524 less on survival (Lu et al. 2014). Analysis of 50-year annual light trap data from 525 Japan indicates an increase in trap catches in years following winters with 526 increasing temperatures (Yamamura et al. 2006). However, it is unlikely that 527 climate warming will bring C. suppressalis back to its former pest status that 528 529 peaked in the 1950's and early 1960's in Japan (Kiritani 2006). Observed increase in damage in later years in a closely related rice borer, Tryporyza 530 incertulas, corroborates the findings of Yamamura et al. (2006) and has been 531 attributed to warmer winters but also changes in cropping systems and cultivation 532 practices together with decreased parasitism are considered to be of importance 533 (Sun et al. 2003). 534



535

536 Distribution map from: CABI, 2018. *Chilo suppressalis*. In: Invasive Species

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539 16. The European corn borer (*Ostrinia nubilalis*) Lepidoptera: Crambidae (Hübner540 1796)

541

The European corn borer, Ostrinia nubilalis, is one of the most important pests on 542 543 corn but cause damage also in potato and cotton. Its main distribution is in Europe, North America and some parts of northern Africa. In northern regions it 544 has one generation per year but may have more than two in warm areas 545 (Showers 1981, 1993). The ecological impact of O. nubilalis may be indirect and 546 'positive'; an increased use of Bt-resistant GM-corn reduces the need for 547 insecticides but the positive effect may be reversed and worsened if the pest 548 develops resistance to Bt and non-target organisms are hit (Medvinsky et al. 549 2004; Speiser at al. 2013). The development and voltinism of O. nubilalis seems 550 to be particularly sensitive to climatic conditions (Onstad and Brewer 1996), 551 552 making it suitable to use in climatic modeling efforts (Svobodova et al. 2014). However, the outcome of modeling efforts may vary considerably (Maiorano 553 2012). The directly observed evidence of a climatic response include 554 555 observations from Czech Republic of a sudden increase in infestation during the 556 unusually warm period 1991-2000 (Trnka et al. 2007). In addition, analysis of light trap data from Hungary indicates an increase in number and damage, probably 557 partly as a consequence of the appearance and spread of a bivoltine strain. 558 connected to warming (Radin 1990; Keszthelyi 2010). A trend for decreasing 559 damage during a cold period during the 1960's in Minnesota was broken in the 560 warm year 1970 when the highest population densities since the peaks in early 561 1950's were observed (Chiang and Hudson 1972). Further, in a series of 562 experiments, Xiao et al. (2017) were able to link poor spring performance to 563 warm winter climates, indicating that future warming could have negative effects 564 on this pest, this however remains unsubstantiated in the field. 565



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567 Distribution map from: CABI, 2018. Ostrinia nubilalis. In: Invasive Species

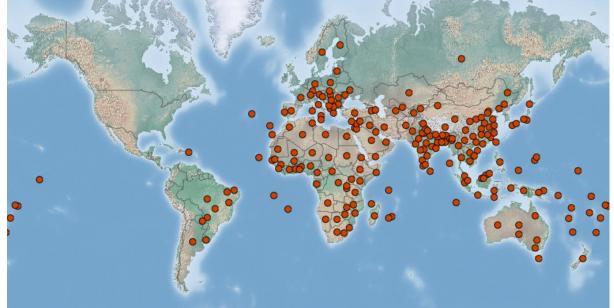
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570 17. The Cotton bollworm (*Helicoverpa armigera*) Lepidoptera: Noctuidae (Hübner 571 1808)

572

The Cotton bollworm, Helicoverpa armigera, is a polyphagous pest causing 573 574 damage on 200 plant species. It is a cosmopolitan pest mainly occurring in central and southern Europe, temperate parts of Asia, Africa Oceania, and 575 Australia and has recently invaded South America (Kriticos et al. 2015). Beyond 576 577 its present range, as a migrant, in Europe, it may reach northern regions where it cannot overwinter at present climatic conditions outdoors but still causes severe 578 damage, particularly in glasshouses (Smith 1999). The damage in some core 579 areas, such as India, has shown a general decline (Dhaliwal et al. 2010) but 580 increases in damage has also been observed, as in for instance Japan (Kiritani 581 2006). The density and damage of the species have been observed to increase 582 583 in later years in China (after analyzing the period 1975 - 2011) due to increased temperature, declining rainfall and agricultural intensification (Lu et al. 2013), 584 resulting in weakened negative density dependence, in turn, leading to the 585 population equilibrium increasing to a higher level (Ouyang et al. 2014, 2016). In 586 587 Hungary H. armigera was first observed in 1993 and had by 2001 spread over 94 % of the country; the spread – and the level of damage – seems to be connected 588 to moderately dry and warm weather conditions (Keszthelyi 2013). In Australia, a 589 series of studies suggest that rainfall, rather than temperature is the major driver 590 of population dynamics during summer, with early winter rainfall exerting positive 591 and spring rainfalls negative effects on *H. armigera* and *H. punctigera* summer 592 population sizes (Maelzer et al. 1996; Maelzer and Zalucki, 2000, Zalucki and 593 Furlong, 2005). 594



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596 Distribution map from: CABI, 2018. *Helicoverpa armigera*. In: Invasive Species

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18. Mountain pine beetle (*Dendroctonus ponderosae*) Coleoptera: Curculionidae (Hopkins 1902)

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The Mountain pine beetle, Dendroctonus ponderosae, is the most destructive 602 603 insect pest of lodgepole pine (Pinus contorta) and other pine forests in the mountains of western North America. During the last decades vast Mountain pine 604 beetle outbreaks have destroyed millions of hectares of pine forests in USA and 605 Canada. The species has generally one generation per year at low elevations 606 and the generation time is one or two years at high elevations (Bentz et al., 607 2014). Changing climate affects Mountain pine beetles at least in three main 608 ways: 1) summer temperatures affect the timing of life history events which is 609 important for the phenological synchrony of adult emergence – a necessary 610 condition for mass attacks; 2) cold winter temperatures cause high mortality of 611 overwintering beetles in some areas but not in all (Weed et al. 2015); 3) there are 612 also indirect effects of weather on Mountain pine beetle dynamics via different 613 mechanisms, especially via drought-altered changes in the defensive capacity of 614 host trees. There appears to be genetic variability among Mountain pine beetle 615 616 populations in their sensitivity to weather factors. Degree days required for the development of one generation are clearly less in populations living in cooler than 617 warmer locations (Bentz et al., 2011). At higher summer temperatures 618 populations at the warmer edge of the distribution mostly remain univoltine, but in 619 the north the generation time shortens from two years to one, which increases 620 the growth rate of these populations. At the cooler edge of its distribution, 621 increasing winter temperatures (decreased winter mortality) also have facilitated 622 range expansion northwards and to higher elevations than recorded previously. 623 Due to this climatically driven range expansion, Mountain pine beetle encounters 624 naïve (and less well defended) host populations and species (Cudmore et al., 625 2010; Raffa et al., 2013). There is also concern about the potential for the 626 Mountain pine beetle to expand its range over the jack pine forests of central and 627 628 eastern North America. Modeling work, however, suggests that the probability of 629 this remains low to moderate during this century (Benz et al., 2010, 2016).



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631 Distribution map from: CABI, 2018. *Dendroctonus ponderosae*. In: Invasive

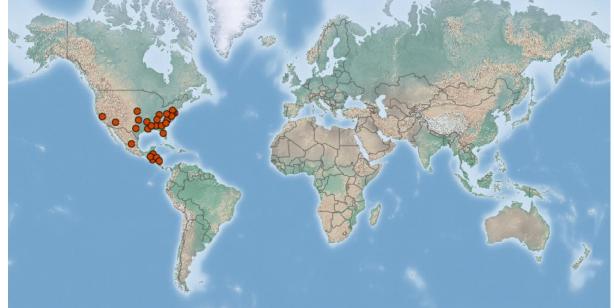
- 632 Species Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>.
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19. Southern pine beetle (*Dendroctonus frontalis*) Coleoptera: Curculionidae (Zimmermann 1868)

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The southern pine beetle, Dendroctonus frontalis Zimmermann, is the 637 638 economically most important pest insect of pines (primarily loblolly, Pinus taeda, 639 and shortleaf, P. echinata, pines) from Central America to southern USA. Most of the time the Southern pine beetle lives on trees weakened or damaged by e.g. 640 lightning strikes, storms or diseases, but during occasional outbreaks (normally 641 lasting 2-3 years) these beetles can kill thousands of healthy pines. The annual 642 economic losses due to the Southern pine beetle can exceed \$200 million in US. 643 Depending on temperature the Southern pine beetle can have from one to nine 644 generations per year. The relationships between climatic variables and Southern 645 pine beetle outbreaks are complex and these may interact with other 646 environmental effects and management activities (McNulty et al., 1997; Gumpertz 647 et al., 1999; Ungerer et al., 1999; Williams & Liebhold 2002; Gan, 2004; Tran et 648 al. 2007; Friedenberg et al, 2008; Duehl et al., 2011, Marini et al. 2017). The most 649 important factor limiting the northern distribution limit of Southern pine beetle 650 651 outbreaks is minimum winter temperatures, as air temperatures of -16°C cause almost total mortality of the Southern pine beetle. Recently, Southern pine beetle 652 outbreaks have been observed in New Jersey and even further north, of the 653 historical outbreak range (Weed et al. 2013, Dodds et al. 2018). As climate 654 warms further, the outbreak range is predicted to increase to large areas in 655 northeast USA and southern Canada (Lesk et al. 2017). 656



657

Distribution map from: CABI, 2018. *Dendroctonus frontalis*. In: Invasive Species

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20. Eurasian spruce bark beetle (*lps typographus*) Coleoptera: Curculionidae (Linnaeus 1758)

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The Eurasian spruce bark beetle (Ips typographus) is a major insect pest of 664 spruce forests in Europe and some regions in Asia, mass-attacking and killing 665 spruces over extensive areas during outbreaks (Grégoire and Evans 2004, 666 Økland et al. 2012). More frequent extreme damages and drier and warmer 667 summer climate may trigger both population growth and susceptibility of spruce 668 stands to attack (Økland & Bjørnstad 2006, Marini et al. 2012, Netherer et al. 669 2015). In northern areas, global warming may increase the productivity of host 670 trees and indirectly the beetle populations due to more access to breeding 671 substrates and enhanced conditions for flight and attacks. A warmer climate is 672 expected to give a northern expansion of the area experiencing two generations 673 674 per year (Lange et al. 2006, Jönsson et al. 2012), and more cases of bivoltinism have been observed in Finland and southern Scandinavia during the last years 675 (Pouttu & Annila 2010). There have been few bark beetle outbreaks in the 676 677 extensive areas of spruce forest in Finland and the northern part of Scandinavia, 678 but increasing bark beetle populations and infestations have been reported in these areas during warm years in the last decades (Økland et al. 2009). 679 Increased frequency of drought periods due to global warming may extend the 680 areas of bark beetle infestations in Southern and Central Europe, since lower 681 than average precipitation seems to generally favour bark beetle infestations at 682 the southern margin of the spruce distribution in Europe (Marini et al. 2012, 683 Netherer et al. 2015). While the optimal areas for spruce are in northern Europe 684 and the mountain ranges of Central Europe, even-aged plantations outside the 685 natural range of Norway spruce are highly susceptible to disturbance events such 686 as wind throw and bark beetle attacks. 687



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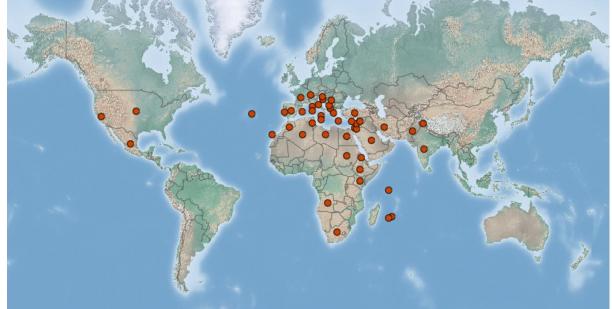
Distribution map from: CABI, 2018. *Ips typographus*. In: Invasive Species

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- 21. Olive fruit fly (Bactrocera oleae) Diptera: Tephritidae (Rossi 1790)
- 692 693

Bactrocera oleae is a specialized fruit feeder associated with the olive tree (Olea 694 europaea) in most of its cultivation range. It is active all year long, depending on 695 temperature and availability of fruits, with multiple generations. Gutierrez et al. 696 (2009) suggest that the range of the olive fly will retract in the south and expand 697 in the northern part of the range, both in North America and Europe, due to the 698 effect of high temperature during summer and milder winter on the adult flies, 699 respectively. Ponti et al. (2014) predict that in the Mediterranean region the 700 damage of the pest will change dramatically in the near future as a consequence 701 of climate change, with large socio-economic impacts on farmers. This effect was 702 documented by Marchi et al. (2016) using a 13 year dataset from central Italy, 703 suggesting that mild winter temperature is the main driver of high infestation 704 705 rates.



706 707

Distribution map from: CABI, 2018. *Bactrocera oleae*. In: Invasive Species

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710 711 22. Codling moth (*Cydia pomonella*) Lepidoptera: Tortricidae (Linnaeus 1758)

The Codling moth (*Cydia pomonella*) is a major polyphagous pest of fruit trees 712 including apple, pear and walnut, and impacts the economies of many countries 713 across the globe (Dorn et al., 1999). The species is native to Europe, but it can 714 now be found in nearly all temperate fruit-growing regions across the world 715 (generally above 30°N and below 30°S; (Willett et al., 2009). The Codling moth 716 undergoes a facultative diapause in the larval stage, and across its range 717 voltinism varies, generally decreasing at higher latitudes. In walnut orchards 718 across California rising temperatures over the past 50 years have been 719 associated with increases in the number of generations completed each season 720 (Luedeling et al., 2011). These patterns are also reflected in modeling studies 721 that consider Codling moth populations in Switzerland (Stoeckli et al., 2012), 722 723 Norway (Rafoss and Saethre, 2003), Poland (Juszczak et al., 2013) and Marocco (El Iraqui and Hmimina 2016). By driving these models with data of future climate 724 change scenarios, the authors consistently predict further increases in voltinism, 725 726 as well as an expansion in distribution into higher latitudes (Rafoss and Saethre, 727 2003). The boundary of this species range at low latitudes, however, is currently constrained by winter temperatures that fail to induce larval diapause 728 (Sheldeshova, 1967; Willett et al., 2009). Therefore, a contraction in this species' 729 range boundary at low latitudes due to increasingly warmer winters may also 730 occur, leading to an overall shift in this species' distribution. As such, changes in 731 crop damage caused by the Codling moth under future climate change scenarios 732 are likely to vary among different fruit growing regions. 733



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Distribution map from: CABI, 2018. *Cydia pomonella*. In: Invasive Species

- 736 Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>.
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23. Coffee Berry Borer (*Hypothenemus hampei*) Coleoptera: Curculionidae (Ferrari 1867)

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The Coffee berry borer (Hypothenemus hampei) is an important global pest of 741 Coffea species including C. arabica and, to a lesser extent, C. canephora, 742 causing global economic losses of up to \$US 500 million per annum (Vega et al. 743 2003; Vega & Hofstetter 2015). The species is thought to originate in Eastern and 744 Central Africa (Le Pelley 1968); however it has spread through human-mediated 745 dispersal to all coffee growing regions across Africa. Asia and the Americas 746 (Jaramillo et al. 2006). All life-history stages of H. hampei inhabit and feed on 747 coffee berries and so, across its distribution, the number of generations 748 completed per year varies from one to nine depending on the duration of the local 749 fruiting season (Damon 2000). Survival and performance of this species are 750 751 directly affected by temperature (Jaramillo et al. 2009), and recent warming conditions have been associated with an expansion of its range into higher 752 elevations, where it was previously thought to be too cold for the beetle to inhabit 753 754 (Jaramillo et al. 2009). For example, in comparison to 1984 when there were no 755 infestations of the Coffee berry borer at Jimma in Ethiopia, current conditions allow for the completion of one to two generations per year (Mendesil et al. 2003; 756 Jaramillo et al. 2009). Increases in voltinism of this species in Kenya and 757 Colombia have also been linked to rises in temperature over recent decades 758 (Jaramillo et al. 2009). As such, future increases in temperature are predicted to 759 have an overall positive effect on this species (Jaramillo et al. 2011). The income 760 from coffee production sustains an estimated 20 million families (Vega et al. 761 2003), and so the increasing voltinism and expanding distribution of this pest 762 under future climates will likely have substantial socio-economic impacts on a 763 global scale. 764



Distribution map from: CABI, 2018. *Hypothenemus hampei*. In: Invasive Species
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Lane, Egham, Surrey TW20 9TY, UK

771 24. Western corn rootworm (*Diabrotica virgifera virgifera*) Coleoptera:

772 773

Chrysomelidae (LeConte 1868)

The western corn rootworm *Diabrotica virgifera virgifera* is a chrysomelid beetle 774 775 native to Central America and an oligophagous pest of maize and other cereals. 776 While it has been one of the most important insect pest species in the US for many decades (coined "one billion dollar bug" in the 1980ies - Gassmann 2012), 777 starting early in the 1990s the Western corn rootworm was accidentally 778 introduced to Europe by a series of invasion events (Miller et al. 2005, Ciosi et al. 779 2008) where it now causes extensive damage to European maize crops. A 780 northward range expansion is indicated by the repeated introductions at 781 increasing latitudes in Europe (Miller et al. 2005, Ciosi et al. 2008, Bermond et al. 782 2012). Establishment in many parts of Central Europe seems to be likely (e.g. 783 784 Baufeld et al. 1996) and further northward range expansion due to advancement of the upper physiological limit has been modelled (Aragón and Lobo 2012, see 785 also Haridas et al. 2016). As a vector of the Maize chlorotic mottle virus, known to 786 infect a range of naturally occurring grasses of the family Poaceae (Scheets 787 788 2004), the Western corn rootworm has the potential to cause significant ecological damage. 789



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791 Distribution map from: CABI, 2018. *Diabrotica virgifera virgifera*. In: Invasive

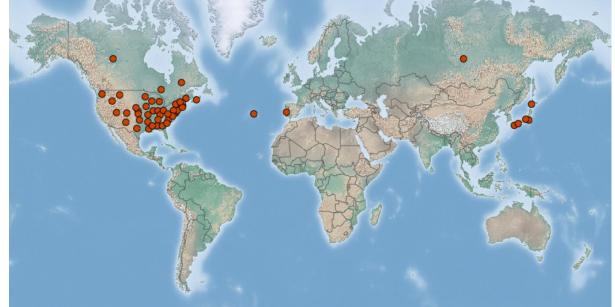
- 792 Species Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>.
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25. Japanese beetle (*Popillia japonica*) Coleoptera: Scarabaeidae (Newman 1841)

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The Japanese beetle *Popillia japonica* is a scarabaeid beetle native to the main 797 islands of the Japanese archipelago where this species is not considered a pest 798 799 due to a lack of suitable habitats, effective control by its natural enemies and regular shortages of its main resources (Fleming 1972, 1976). After its 800 introduction into the United States in the early 20th century, however, it became a 801 very successful pest species of high socioeconomic impact in large parts of the 802 eastern US while its potential distribution includes many other humid, temperate 803 regions globally (Allsopp 1996). Popillia japonica is a generalist considered one 804 of the most polyphagous of plant-feeding insects and it is known to feed on more 805 than 300 species of wild and cultivated plants (Fleming 1972, Potter and Held 806 807 2002, Lemoine et al. 2013). Amongst these many potential beetle-plant interactions the effects of *P. japonica* on soy bean appear to be covered best by 808 recent, climate-change related research (e.g. Hamilton et al. 2005, DeLucia et al. 809 810 2012, Niziolek et al. 2013, but see Lemoine et al. 2013). The root feeding grubs 811 are important turf pests in parks, gardens or golf courses (Fleming 1972, Potter and Held 2002). Generally, economic damage caused by *P. japonica* is mainly 812 attributed to defoliating adults but fruit and flower feeding also has considerable 813 impact (Held and Potter 2004). While there is little information about climate 814 change effects on the damage potential of *P. japonica* root feeding grubs, there 815 are considerably more studies analyzing climate change effects on the feeding 816 damage caused by adult beetles. For instance several studies demonstrate a 817 high potential for enhanced foliar damage in soy bean related to elevated CO₂-818 levels and/or higher temperatures (Hamilton et al. 2005, Zavala et al. 2008, 819 O'Neill et al. 2008, Dermody et al. 2008, Niziolek et al. 2013). On the contrary 820 821 DeLucia et al (2012) report that earlier emergence of *P. japonica* caused by progressively warmer winters and spring should reduce the potential for 822 defoliation-induced yield losses in the interaction with this particular host species. 823 824 Finally, there is one recent study that has looked at the impact of rising temperatures on diet composition in *P. japonica* by testing nine different plant 825 species: Lemoine et al (2013, 2017) found that (1) consumption generally 826 increases with rising temperature while (2) diet breadth is reduced. These 827 findings suggest that the consequences related to climate change are highly 828 crop-species specific and predictions at the global socio-economic scale are 829 complex and hard to make. 830



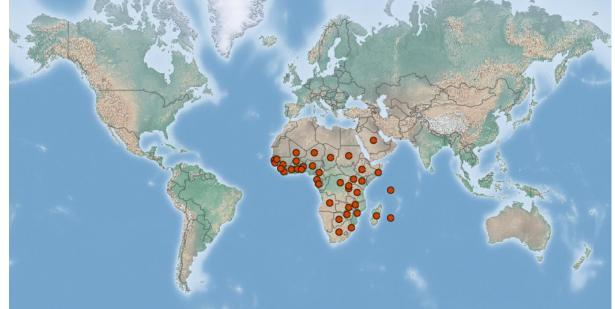
- 831
- B32 Distribution map from: CABI, 2018. *Popillia japonica*. In: Invasive Species
- 833 Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>.
- 834 Printed with permission. Reviewed by: Michael Klein, Ohio Agricultural Research
- and Development Center, Adjunct Associate Professor, 1680 Madison Avenue,
- 836 Wooster, OH 44691, USA

26. African sugarcane stalk borer (*Eldana saccharina*) Lepidoptera: Pyralidae (Walker 1865)

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The African sugarcane stalk borer (Eldana saccharina) is a multivoltine 840 841 Lepidopteran pest that infests a wide range or crops including sugar cane, maize and sorghum (Assefa et al., 2006). The larval stage of this pest infests its host by 842 boring into its stalks, resulting in major tissue damage and economic losses. This 843 species originated in western Africa, but is now found broadly across sub-844 Saharan Africa (from 15°N to 30°S). Since its initial invasion into South Africa in 845 the 1930's the species has more recently spread from coastal to inland regions 846 which were previously thought to be too cold to inhabit (Dick, 1945; Way, 1994). 847 Studies suggest that this range expansion has been facilitated by a switch in host 848 plant from sugar cane to maize (Assefa et al., 2008; Assefa et al., 2006), and an 849 850 adaptation in the lower critical temperature threshold (Kleynhans et al., 2014a; Kleynhans et al., 2014b). The species also exhibits phenotypic plasticity in 851 response to variation in rearing conditions: warmer temperatures induce faster 852 853 development and growth (Atkinson, 1980; Way, 1995), but adults emerge with a 854 smaller body size, increased rates of water loss and reduced longevity and fecundity (Kleynhans et al., 2014b). These laboratory findings suggest that as 855 temperatures in the field continue to warm, we may expect an increase in 856 voltinism across the range of the African sugarcane stalk borer. However, given 857 that higher temperatures also lead to smaller adults and reduced performance of 858 size-related traits (Kleynhans et al., 2014c), any likely changes in crop damage 859 caused by this pest remain difficult to predict. Making such predictions is further 860 complicated by the high rates of adaptation observed in this species (Assefa et 861 al., 2006; Kleynhans et al., 2014b). Further work that compares recent changes 862 in local temperature and rainfall with the expansion of this species into central 863 South Africa may, nonetheless, provide valuable insights into the role that climate 864 plays in limiting the distribution, phenology and damage caused by this invasive 865 866 pest.



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868 Distribution map from: CABI, 2018. *Eldana saccharina*. In: Invasive Species

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27. Coffee leaf miner (*Leucoptera coffeella*) Lepidoptera: Lyonetiidae (Guérin Méneville 1842)

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The larvae of the Coffee leaf miner (Leucoptera coffeella) damage the 874 assimilative parenchyma of Coffea species (Pereira et al. 2007) during 9-40 days 875 confined within the leaf, and then form pupae on the outside of the leaf. The 876 damage may extend to 37% of the cultivated coffee plantations leading to 877 reduced flower formation, fructification and consequently up to a yearly loss of 878 40-80% in yield. The damage was considered to occur only during the dry season 879 up to 1970, but recently the leaf miner has caused damage in both dry and wet 880 seasons in areas of Sao Paolo in Brazil (Ghini et al. 2008). Studies indicate that 881 temperature and precipitation are significant factors in the pest population 882 dynamics. Currently approximately 8-12 overlapping generations may occur 883 during the year. However, more generations of the coffee leaf miner per year 884 would be possible to achieve in the predicted climate change scenarios (Ghini et 885 al. 2008). As the performance of the coffee leaf miner is limited at high elevation 886 in Mexico (Lomelí-Flores et al. 2010), mainly because of reduced temperature, it 887 seems likely that climate change will facilitate range expansion into areas which 888 at the moment are unaffected or only affected to a small degree. 889



890

891 Distribution map from: CABI, 2018. *Leucoptera coffeella*. In: Invasive Species

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28. Citrus peel miner (*Marmara gulosa*) Lepidoptera: Gracillariidae (Guillén & Davis 2001)

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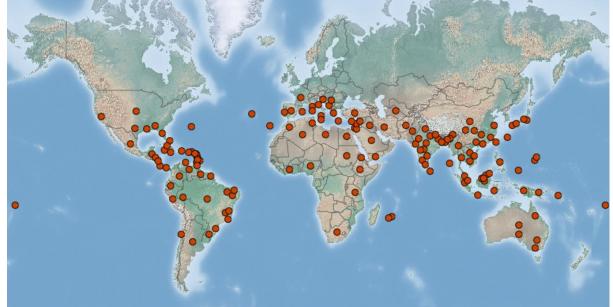
The peel mining moth, Marmara gulosa, feeds on and damages the peel of the 897 898 fruit of more than 31 families of plants. These include grapefruit, lemon, oranges and citrus, but also other orchard fruit such as apple and avocado and 899 ornamental trees such as oleander and willow (Guillén et al. 2003). The wide host 900 901 range allows the moth to switch hosts according to availability during the growing season (Grafton-Cardwell et al. 2008). The damage on the commercial citrus 902 fruits is economically important only in California, Arizona, Mexico and Cuba, 903 although the species occurs throughout the United States (Guillén et al. 2003). 904 Two to three mines per fruit renders the fruit commercially unacceptable. On 905 occasion, the damage may cause up to 80-90% fruit loss (Guillén et al. 2003). 906 The temperature range for development is between 12-33°C and the average 907 degree days required for the development of one generation is 309-375. 908 depending on the host species (O'Neal et al. 2011). The peel miner is fairly 909 efficiently controlled by a biocontrol agent (*Cirrospilus coachellae*). However, this 910 911 parasitoid wasp does not tolerate as cold temperatures as the peel miner (Grafton-Cardwell et al. 2008). 912 913

No distribution map available at CABI, but the species is restricted to California,
 Arizona, Texas, Florida and Cuba according to Jones et al. 2001.

29. Citrus leaf miner (*Phyllocnistis citrella*) Lepidoptera: Gracillariidae (Stainton1856)

917 918

The citrus leaf miner is native to Asia, but currently occupies a global distribution 919 920 range from Japan to Australia to India and Africa to South and North America (Grafton-Cardwell et al. 2008). The larvae mine the leaves of citrus trees, such as 921 mandarins, lemons, limes and grapefruit. Damage on the leaves is most notable 922 923 in the nurseries, but does not kill the trees. More severe damage is caused by a bacterial disease, the citrus bacterial canker (Xanthomonas axonopodis pv. citri), 924 facilitated by the feeding damage done by the leaf miner. The citrus bacterial 925 canker, while primarily a pathogen of cultivated plants, is known to infect a range 926 of natural plants in the family Rutaceae. The annual losses due to the disease 927 and consequent costs of eradication during 20 years after discovering, have been 928 929 estimated at 28 million USD in the USA (Gottwald 2000). Efficient management of the disease involves eradication of the host within a radius from the infestation 930 point. The leaf miner completes 5-6 generations in Asia (Grafton-Cardwell et al. 931 932 2008) with a generation time between 11.4 to 32.8 days (at 32°C and 18°C 933 respectively), and shows no significant reduction in survival within a temperature range from 18 to 32°C (Chagas & Parra 2000). Furthermore, the Citrus leaf miner 934 does not enter diapause in the colder months of the year, but instead slows down 935 development (Lim and Hoy 2006). Therefore, it may be hypothesized that a 936 warming climate allows for faster development and a consequent increase in the 937 number of generations. It can be noted that ongoing climate warming is 938 suggested to be an important factor in facilitating northward range expansion in 939 the closely related species Phyllonorycter leucographella (Gröbler & Lewis 2008). 940



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942 Distribution map from: CABI, 2018. *Phyllocnistis citrella*. In: Invasive Species

- 943 Compendium. Wallingford, UK: CAB International. <u>www.cabi.org/isc</u>.
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945 946 30. Spotted stem borer (*Chilo partellus*) Lepidoptera: Crambidae (Swinhoe 1885)

The spotted stem borer (Chilo partellus) is one of a complex of stem borer 947 species that severely constrain maize production in Africa (de Groote 2002, Kfir 948 949 et al. 2002). It is unique amongst these species in that it is invasive across the continent, having originated in India. Thus, there has been considerable interest 950 in this invasion process and the role of climatic factors in determining its current 951 and potential range (Kfir et al. 2002, Overholt et al. 2000), which, as of 2002 952 included Ethiopia, Sudan, Somalia, Kenya, Tanzania, Uganda, Mozambigue, 953 South Africa, Swaziland, Lesotho, Zimbabwe, Zambia, Malawi, and Botswana. 954 This species alone can account for 50% yield losses in sorghum and it is a major 955 target of pest management efforts, including the development of 'push-pull' 956 technologies, which have proven successful in many contexts (Pickett et al. 957 958 2014). The ecological impact of this species is little studied. There is evidence that this invasive species has displaced native borers in native grasses in Kenya 959 (Kfir 1997, Overholt 2008) raising the possibility that it could disrupt native 960 grassland communities elsewhere in its invaded range (Mutamiswa et al. 2017). 961 962 Overall, the climatic niche of this species appears to be well validated and supported by current distributions. Climatic models employed in 2000 predicted 963 its eventual establishment in Namibia, Angola and parts of Nigeria, Cameroon, 964 Togo, Benin, Ghana and Ivory Coast (Overholt et al. 2000), which has come to 965 pass in some of these areas. Climate models predict that warming temperatures 966 will facilitate its invasion and establishment at higher elevations where it does not 967 occur presently (see also Tamir et al. 2012), but that it also could disappear from 968 low lying regions where higher temperatures will constrain it ecologically (Khadioli 969 970 et al. 2014). In some areas, warming will facilitate an increase in the number of generations of the pest per year (Khadioli et al. 2014). Although the pest has 971 972 expanded its range to some uplands where it previously did not occur (Ong'amo 973 et al. 2006), it is not clear whether this has been facilitated by the warming trend 974 in the continent, or is the result of continued invasion with possible local 975 adaptation by spotted stem borer populations.



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977 Distribution map from: CABI, 2018. *Chilo partellus*. In: Invasive Species

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- 31. Green peach aphid (Myzus persicae) Hemiptera: Aphididae (Sulzer 1776)
- 980 981

The Green peach aphid, *Myzus persicae*, is a global pest of Asian origin which 982 occurs on over 40 different plant families (including many economically important 983 plants). It has a complex geographically varying life-history strategy which varies 984 between Heteroecious holocyclic in temperate climates and anholocylclic in most 985 tropical climates (Blackman 1974). Holocyclic populations reproduce sexually and 986 987 overwinter on *Prunus* species, while summer generations reproduce asexually on a wide variety of hosts. The overwintering eggs are extremely cold tolerant 988 (Strathdee et al. 1995). Anholocyclic populations exist where winters are mild and 989 mostly reproduce asexually on a variety of hosts; however also sexual 990 reproduction exists to some degree in most populations (Blackman 1974). The 991 most detrimental feature of *M. persicae* is its role as a virus vector, as it can 992 993 transmit over 100 plant virus diseases which affect plants from over 30 families. Mild climates are directly linked to increased population densities, increasing 994 numbers of generations and outbreak frequencies which lead to increased overall 995 996 damage (Bale and Hayward 2010) and have been documented during the past 997 60 years in northern Europe (Harrington et al. 2007). While not studied to the same degree, absence of an equal effect on the predators of the aphids suggests 998 decreased predation pressure under warmer climates (Bale and Hayward 2010). 999



1000 1001

Distribution map from: CABI, 2018. *Myzus persicae*. In: Invasive Species

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1004References for Supplement 2

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