Malice at the Gates of Eden: current and future distribution of *Agrilus mali* threatening wild and domestic apples

Zhaozhi Lu[1,2] (ID), Xiaoxian Liu[3,4,5], Ting Wang[1,2], Ping Zhang[3,4,5],
Zhenlin Wang[3,4,5], Yanlong Zhang[6], Darren J. Kriticos[7,8] and Myron P. Zalucki[8]

[1]College of Plant Health and Medicine of Qingdao Agriculture University, Qingdao 266109, China; [2]Shandong Engineering Research Center for Environment-Friendly Agricultural Pest Management, College of Plant Health and Medicine, Qingdao Agricultural University, Qingdao 266109, China; [3]Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, China; [4]University of Chinese Academy of Sciences, Beijing 100049, China; [5]Research Center for Ecology and Environment of Central Asia, CAS, Urumqi 830011, China; [6]Ecology and Nature Conservation Institute, Chinese Academy of Forestry, Beijing 100091, China; [7]CSIRO Health & Biosecurity, Canberra ACT, Australia 2601 and [8]School of Biological Sciences, The University of Queensland, Brisbane, Australia 4072

Abstract

The apple buprestid, *Agrilus mali* Matsumura, that was widespread in north-eastern China, was accidently introduced to the wild apple forest ecosystem in mountainous areas of Xinjiang, China. This invasive beetle feeds on domesticated apples and many species of *Malus* and presents a serious threat to ancestral apple germplasm sources and apple production worldwide. Estimating the potential area at risk of colonization by *A. mali* is crucial for instigating appropriate preventative management strategies, especially under global warming. We developed a CLIMEX model of *A. mali* to project this pest's potential distribution under current and future climatic scenarios in 2100 using CSIRO-Mk 3.0 GCM running the SRES A1B emissions scenario. Under current climate, *A. mali* could potentially invade neighbouring central Asia and eventually the mid-latitude temperate zone, and some subtropical areas and Pampas Steppe in the Southern Hemisphere. This potential distribution encompasses wild apples species, the ancestral germplasm for domesticated apples. With global warming, the potential distribution shifts to higher latitudes, with the potential range expanding slightly, though the overall suitability could decline in both hemispheres. In 2100, the length of the growing season of this pest in the mid-latitude temperature zone could increase by 1–2 weeks, with higher growth rates in most sites compared with current climate in mid-latitudes, at least in China. Our work highlights the need for strategies to prevent the spread of this pest, managing the threats to wild apples in Tian Shan Mountain forests in Central Asia, and commercial apple production globally. We discuss practical management tactics to reduce the spread of this pest and mitigate its impacts.

Introduction

The spread of invasive destructive pests has been causing damage to the environment as well as agricultural production, with consequent socio-economic impacts that need to be confronted by the public, policy-makers, governments and international agencies (Vitousek *et al.*, 1997; Pimentel *et al.*, 2000; Poland and Mccullough, 2006; Kovacs *et al.*, 2010; Aljaryian and Kumar, 2016; Hulme, 2017; Staentzel *et al.*, 2019). Recent high profile examples include emerald ash borer (*Agrilus planipennis* Fairmaire) in the USA (Poland and Mccullough, 2006), tomato pinworm (*Tuta absoluta* (Meyrick)) across the world (Biondi *et al.*, 2018), brown marmorated stink bug (*Halyomorpha halys* (Stål)) in the USA (Kistner, 2017; Kriticos *et al.*, 2017) and fall armyworm (*Spodoptera frugiperda* (J.E. Smith)) in Africa (Goergen *et al.*, 2016) and Asia (Baloch *et al.*, 2020; Li *et al.*, 2020). Being able to accurately estimate the potential geographical ranges under current conditions and estimate how they might shift with global warming between now and 2100 will enable mitigation strategies for such pests to be better informed and prepared (Kriticos *et al.*, 2013).

As climates warm, empirical evidence on herbivorous insects indicates a higher frequency of outbreaks for some species (Ayres and Lombardero, 2000; Logan *et al.*, 2003), expansion of geographical range (Battisti *et al.*, 2005; Engelkes *et al.*, 2008; Bebber *et al.*, 2013), phenological asynchrony between some plant hosts and herbivores (Singer and Parmesan, 2010; Foster *et al.*, 2013) and increasing prevalence of insect viral vectors and plant disease epidemics (Kriticos *et al.*, 2020). However, some consequences of climate change for herbivores are unpredictable due to cryptic biological characteristics (Deutsch *et al.*, 2008; Jaric *et al.*, 2019), resistant responses to global warming (due to behaviour, physiological fitness or

immigration) (Li et al., 2016) and changes in interactions between trophic levels (Furlong and Zalucki, 2017). Thus, while there are general patterns (Sutherst et al., 2007), there may be uncertainty in how an individual invasive pest's geographical range might shift due to global warming (Chaves, 2016; Gillard et al., 2017; Hulme, 2017).

The apple buprestid, Agrilus mali Matsumura (Coleoptera: Buprestidae), was originally described as restricted to the Russian Far East (Amur Province, Primorskii and Khabarovskii territories), north-eastern China and Korea (Sun et al., 1979; Zhang et al., 2021). Around the 1950s, A. mali established and became locally distributed in Liaoning, Jilin, Gansu, Heilongjiang, Hebei, Shannxi, Inner Mongolia, Shandong, Henan, Sichuan and Hubei provinces in China (fig. 1), where it was considered a secondary pest of domesticated apples, causing little damage in well-managed orchards (Sun et al., 1979). Agrilus mali continued to spread from north-eastern China in 1950s–1990s to southern China in 1990s–2000s (fig. 1); it was accidently introduced to orchards in the Yili valley, Xinjiang Uyghur Autonomous Region (XUAR) in north-west China with apple seedlings in the 1990s. Catastrophically, it moved from local domestic apple orchards into natural populations of wild apple, Malus sieversii (Ledeb.) Roem (Yi et al., 2016; Zhang et al., 2018). Agrilus mali is now widespread in wild apple forests in the Tian Shan Mountains in XUAR (Cui et al., 2015; Zhang et al., 2019). It has caused severe damage to M. sieversii populations, posing a threat to this rare and valuable source of apple germplasm in XUAR and central Asia (Zhang et al., 2019). Agrilus mali is oligophagous, and utilizes numerous species in the genus Malus (Li and Zhang, 2017). Other wild apple species at risk if this pest continues to spread include M. orientalis Uglitzk. in Armenia and Turkey, M. baccata Borkh. across Siberia and South Asia (India, Pakistan and Nepal) and M. sylvestris Mill. in Europe. All four wild apple species are the ancestors of domestic apples, with the major genetic contribution from M. sieversii (Harris et al., 2002; Velasco et al., 2010; Cornille et al., 2012).

The spread of A. mali within XAUR had disastrous consequences and cascading effects in the local forest ecosystems. More than 95% of the wild apple forest in the Yili valley became infested, and 40–50% of trees in this valley were killed (Cui et al., 2018). Following the invasion by A. mali, production of wild apple fruits per hectare was reduced from 9 tonnes in healthy areas to 1.5 tonnes in infested areas, greatly reducing the forest seed bank. This insect pest is of economic importance in domesticated apple varieties and ornamental Malus plants in parks, windbreak forest, hedge-rows and gardens (Li and Zhang, 2017).

Worldwide, more than 8 million ha of apples are harvested annually, yielding 124 million tonnes, with more than 30% of the apple production from China (http://www.fao.org/faostat/en/). The USA, Poland, Turkey, India, Iran and Italy are also major apple producers. Elsewhere, for example, Australia and New Zealand, apple production is an important contributor to national or regional economies. Given the severe impacts observed in China from the invasion of A. mali, understanding the potential distribution of this pest in relation to apple production areas is likely to be of global interest to many bio-security agencies and horticultural industries.

Climate change has produced global temperature increases of approximately 0.7°C throughout the 20th century, with temperatures expected to continue to increase throughout the 21st century (Walther et al., 2002). The effect of climate change on the distribution of invasive pests such as A. mali will be crucial, especially for the prosperity of apple production and associated industries at risk. Bioclimatic niche modelling exercises have repeatedly found that the potential distribution of invasive organisms is sensitive to climate change scenarios for the 21st century (Kriticos et al., 2003, 2011; Sutherst et al., 2007; Olfert et al., 2011; Guichard et al., 2014), with the potential to affect biosecurity policies in nations and states that are at the margins of climatic suitability under historical climate conditions.

In this study, we assess the geographic area at risk of invasion by this pest under historical climate conditions and a business-as-usual global climate scenario, with special emphasis on China, the world's largest producer of apples. We use the results to highlight areas of current and emerging biosecurity concern to domesticated apple industries and for conservation of apple germplasm resources.

Methods and materials

Agrilus mali: background biology and ecology

Agrilus mali has a univoltine life cycle with an obligatory diapause for overwintering in China. There are five larval instars with diapausing larvae (mostly first-second instars) occurring in the shallow phloem of Malus spp. (Sun et al., 1979; Li and Zhang, 2017). The first-four instars feed on phloem and cambium. Pupation occurs when the fifth instar drills into the shallow xylem (Wang et al., 2013). In China, adults emerge at the start of May and persist until the end of August or September depending on pupal development, and the peak time for adults is mid-July in most regions in China (Li and Zhang, 2017; Cui et al., 2018). Adults are active flyers, mating around noon (Liu, 2010). Their feeding on leaves causes minor damage to the tree. Females prefer to oviposit in the scar crevices of younger branches and buds, and a female usually lays 40–60 eggs over her life time (Bozorov et al., 2019).

A distinctive feature of this pest is that it only infests a narrow range of branch sizes (diameter ranges: 2–9 cm) in the field (Zhang et al., 2021). Similar to other Agrilus species (Haack and Benjamin, 1982; Poland and McCullough, 2006), it feeds in the cambial region on phloem and outer sapwood forming S-shaped or irregular galleries that disrupt nutrient and water flow within the host plant. High infestations can result in the death of trees after 3–5 years, usually because of water and nutrient deficiencies (Zhang et al., 2020). Early larval instars are cryptic, and the movement of infested seedling apple trees is regarded as the main means by which A. mali has spread within China (Cui et al., 2018; Zhang et al., 2019).

Location records

Geographical locations of A. mali, as well as the year it was reported, were sourced from GBIF (https://www.gbif.org), CABI (https://www.cabi.org/) and references and reports in China (Cornille et al., 2013; Kumar et al., 2018; Zhang et al., 2020). In addition, our colleagues across China offered new sites and our team recorded sites based on field surveys. In total, 95 sites were used in this study (fig. 1, Supplementary table 1).

Meteorological data

We used the CM10 1975H dataset within the CliMond database (Kriticos et al., 2012), comprising 30-year averages centred on 1975 at 10′ spatial resolution of monthly mean values for daily minimum and maximum temperature (°C), relative humidity (%) at 09:00 and 15:00 and monthly rainfall total.
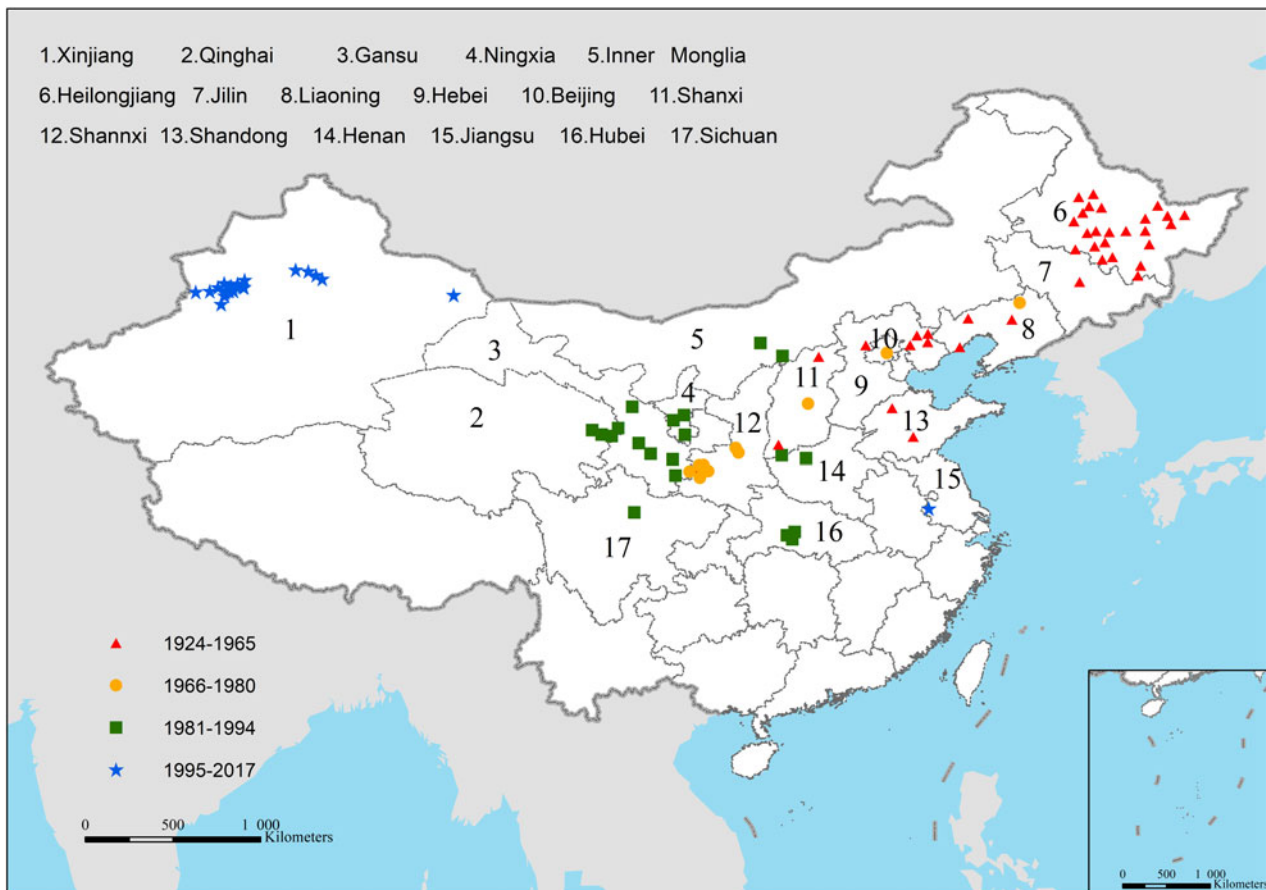
Figure 1. The current distribution of *Agrilus mali* and invasion history in China from 1920′s to date based on GBIF, published papers (Zhang *et al*., 2019) and our own collections. Key provinces mentioned in the text are numbered.

The A1B greenhouse gas emissions scenario describes a world with a balanced use of fossil and renewable resources resulting in an estimated temperature rise of 2.8°C (range from 1.7 to 4.4°C) (Nakicenovic *et al*., 2000). In this study, we use the results of a model forced with the A1B greenhouse gas emissions scenario for global climate change in current and 2100 obtained from the CliMond dataset (https://www.climond.org) to project the species potential distribution worldwide. This emission scenario was chosen because it represents a 'business as usual' emissions scenario, similar to the RCP 8.5 scenario in CMIP5 (Taylor *et al*., 2012). Its inclusion in this analysis is not intended to support a *prediction* of what will happen in the future. Rather, it is used here as a means of *stress-testing* the baseline potential distribution model, to highlight areas of concern for future potential range expansion by *A. mali*.

Modelling strategy

Based on the known distribution records and its biology from our own field studies during 2016–2018 (Cui *et al*., 2019), a CLIMEX model (Sutherst and Maywald, 1985; Kriticos *et al*., 2015) was developed for the potential distribution of *A. mali*. The stress-related parameter values were adjusted to fit the known distribution records of *A. mali* in China, bearing in mind the need for parameters to be biologically reasonable (Kriticos *et al*., 2015). The aim was to achieve perfect model sensitivity and good specificity using parameters that were consistent with the known

biology of *A. mali*. The Ecoclimatic Index (EI) was classified into four arbitrary classes to display potential geographic distributions for mapping in ArcGIS (ESRI company, version 10.2): not suitable (EI = 0), marginal (0 < EI< 5), low suitability (5 < EI< 15) and highly suitable (EI > 15). Plots of the weekly growth index (GI_W) with time of year indicated seasonal suitability for the species. By comparing these to assessments of phenology, we are cross-validating the model growth parameters.

Model fitting

The CLIMEX parameter set (table 1) was iteratively fitted to the current known distribution based on the biology of this pest (Cui *et al*., 2019; Zhang *et al*., 2019). The EI describes the potential geographical distribution of persistent populations, while the GI_W describes the potential for population growth seasonally. The details of equations and parameters are described in the CLIMEX User Manual (Kriticos *et al*., 2015). In brief, the EI is a function of the GI_W, and the combined stresses, where the stresses can be thought of as growth losses. If stresses reach a value of 100, they are lethal, though if the potential growth during the year is limited, then little stress is needed to make the location unsuitable for population persistence. The stress indices (and special requirements such as diapause and the minimum annual heat sum (PDD)) play the largest role in defining the potential range for establishment, while the growth indices define the relative climate suitability patterns within this range (Kriticos *et al*., 2015).

Table 1. The fitted CLIMEX parameters for *Agrilus mali* (see text for details)

Parameter	Description	A. mali	Unit
Temperature			
DV0	Lower temperature threshold for growth	10	°C
DV1	Lower optimum temperature	24	°C
DV2	Upper optimum temperature	30	°C
DV3	Upper temperature threshold for growth	35	°C
PDD	Degree-day threshold (base DV0)	450	°C days
Diapause			
DPD0	Diapause induction daylength	12	Hour
DPT0	Diapause induction temperature	6	°C
DPT1	Diapause termination temperature	2	°C
DPD	Diapause development days	30	Day
DPSW	Summer/winter diapauses indicator	0	Winter
Cold stress			
TTCS	Temperature threshold for cold stress	−34	°C
THCS	Cold stress accumulation rate	−0.05	°C
DTCS	Cold stress degree-day	15	Degree-day
DHCS	Cold stress degree-day rate	−0.0001	$Week^{-1}$
Heat stress			
TTHS	Temperature threshold for heat stress	35	°C
THHS	Heat stress accumulation rate	0.001	$Week^{-1}$
Dry stress			
SMDS	Soil moisture threshold for heat stress	0.1	
HDS	Dry stress accumulation rate	−0.05	$Week^{-1}$
Wet stress			
SMWS	Soil moisture threshold for wet stress	1.75	
HWS	Wet stress accumulation rate	0.02	$Week^{-1}$
Moisture index[a]			
SM0	Limiting low moisture	0.1a	
SM1	Lower optimal moisture	0.4	
SM2	Upper optimal moisture	1	
SM3	Limiting high moisture	1.75	

[a]Threshold expressed as a proportion of soil moisture holding capacity (0, oven dry; and 1, field capacity [saturation]). Values > 1.0 indicate the possibility of excessive amounts of rainfall and soil moisture. 0.1 is wilting point for most plants.

The parameter fitting method aims to define the species potential range in terms of a positive EI, using parameters that are biologically plausible (Kriticos *et al.*, 2015). In practice, this means adjusting the parameters, and assessing the fit of the result with known distribution points for the species being modelled. If biologically implausible parameters are required to fit distribution outliers, the modeller is alerted to investigate the discrepancy, considering the veracity, and meaning of the outlying record, the relevance and reliability of the climate data point(s), the presence of synthetic habitat modifying factors such as glasshouses or irrigation, the suitability of the stress or special requirement, and the basis of the biologically reasonable bounds. All the evidence is assessed using the method of multiple competing hypotheses (Chamberlin, 1965).

In our simulations, an irrigation scenario of 1.1 mm day^{-1} in summer was added as top-up to rainfall to capture agricultural practices in arid areas. This level of irrigation is typical in the area inhabited by wild apple (Tao *et al.*, 2019).

Growth indices

The temperature parameters were initially set to values estimated for the closely related species *A. planipennis* (Duan *et al.*, 2013); the lower and upper temperature limits for optimal development (DV1 and DV2) were set to 24 and 30°C and upper temperature limit for development (DV3) was set to 35°C. The minimum temperature for development (DV0) was lowered to 10°C to better fit the known distribution in southern China.

The lower soil moisture for growth (SM0) was set to 0.1 to approximate permanent wilting point. The upper soil moisture level for optimal growth (SM2) was set to 1, indicating that apple trees can grow optimally up to field capacity, with growth diminishing under flooding conditions. SM1 (the lower limit for optimal growth) was set to 0.4, indicating a moist soil.

Stresses

Cold stress

Two types of cold stress were included in the model (lethal low temperature cold stress and a degree-day cold stress). The lethal low temperature cold stress represents direct chilling damage and accumulates relatively quickly. The threshold temperature was set to −34°C which was based on the observed super-cooling point for the closely-related *A. planipennis* (Mathers, 2005). The stress accumulation rate (TTCS) was set at a high rate (−0.05 week^{-1}). The degree day cold stress function was also used. The degree day threshold (DTCS) was set to 15°C days above a base temperature of 10°C (DV0), and the stress accumulation rate (DHCS) was set to −0.0001 week^{-1} to make sites north of 'known' northern locations (fig. 1) barely suitable. This stress mechanism acts slowly as it represents the effects of constraints on the ability of the *Malus* spp. plants to produce photosynthate that can be co-opted by *A. mali*. In essence, it simulates how quickly *A. mali* will starve when it cannot forage sufficiently to meet its basal metabolic needs.

Heat stress

Above 35°C (the upper thermal limit for population growth = TTHS), heat stress accumulated was adjusted to a rate of 0.001 week^{-1} to accord with our field observation on the demography and simulation iteration on parameters increment to fit the present known distribution of *A. mali*.

Dry stress

Below the SM0 dry stress accumulated at a high rate (0.05 week^{-1}) to account for absence of records in non-irrigated desert areas.

Wet stress

Wet stress was accumulated above the upper moisture level (1.75) and adjusted to a rate of 0.02 week^{-1} to capture the condition such as over irrigation or flood.

Diapause

An obligate diapause function was used to allow *A. mali* to avoid otherwise lethal low temperature conditions. DPSW was set to 0, indicating a winter diapause. DPD0, the diapause induction daylength was set to 12 h, and the diapause induction temperature (DPT0) was set to 6°C, DPT1 (diapause termination temperature) to 2°C with a minimum duration of 30 days (DPD) to capture the approximate time and indicated that this is an obligate diapause. The development of larvae was observed in the field in our study during 2016–2017 (Supplementary fig. 2).

Minimum annual heat accumulation (PDD)

The minimum annual heat sum (PDD) was set to 450°C days above DV0 (10°C). The PDD limits accord well with the known distribution sites in our simulation and validation.

Model assessment

Due to the limited geographical distribution of *A. mali*, the modelled potential distribution could not be validated presently using independent data. Hence, we were limited to verifying the model, checking the sensitivity and specificity instead. We were also able to cross-validate the growth index by comparing the species modelled phenology with field observations. This process tests the temperature and soil moisture growth indices and the diapause index.

Sensitivity and uncertainty analysis

Automated sensitivity and uncertainty analyses were introduced in version 4 of CLIMEX (Kriticos *et al.*, 2015). The sensitivity analysis highlights the parameters that are of most concern, and the uncertainty analysis provides a measure of the overall robustness of the model given typical parameter uncertainty. The sensitivity analysis systematically adjusts each parameter in turn, in a pairwise manner (upward and downward in relation to the fitted values), assessing the effects of the difference in results for each state variable. The resulting table allows the relative sensitivity for each parameter to be gauged. Some sensitivity patterns are unremarkable (e.g., wet stress is highly sensitive to the wet stress parameters). The sensitivity relationships of concern are those affecting the species potential range (number of locations where EI ≥ 1), the EI and GI$_A$. Parameters for which these state variables are sensitive, and where their estimated values are not known confidently are parameters of concern. The uncertainty analysis is superficially similar to the sensitivity analysis but applies generic confidence limits to each parameter and then samples from uncertainty distributions using an efficient Latin hypercube method to generate a distribution of maps (Kriticos *et al.*, 2015). The resulting map portrays the level of agreement between the sampled model parameter sets. High levels of model agreement indicate areas of high likelihood of the climate being suitable for establishment. The parameter increments in this analysis are presented in table 2.

In the map figures, the EI values have been classified arbitrarily, though in a manner that accords with the knowledge of some of the authors of the population dynamics patterns of *A. mali* in its native range. It is possible to fit a classification scheme based on the density of distribution records. However, these records are notoriously biased and incomplete (Hortal *et al.*, 2008), and hence a numerically fitted classification scheme would be fruit of this poison tree. By focussing model-fitting attention on the distribution records on the climatic periphery, CLIMEX is unaffected by biases in distribution data. Likewise, some knowledge of a species biology can overcome limitations from incomplete distribution datasets.

Results

Historical distribution of A. mali *and verification of biological parameters*

Agrilus mali, having historically been concentrated in northeastern regions, has expanded its range to mid-China in the 1980s and then to orchards in Xinjiang via seedlings from Shandong province in the 1990s, before invading mountain areas in the Yili Valley and devastating wild apple forests (fig. 1). After many iterations based on biological parameters from our field work, our CLIMEX model (table 1) fits the

Table 2. CLIMEX parameter sensitivity values for *Agrilus mali* parameters listed in Table 1, as applied to the CM10 1975 V1.1 global dataset under a natural rainfall scenario

Parameter	Mnemonic	Parameter values			Proportional change in state variables (%)									
		Low	Default	High	Geographical range Change	EI	Core dist'n	TI	MI	GI	HS	DS	CS	WS
Dry stress Threshold	SMDS	0	0.1	0.2	2.16	1.9	11.04	0	0	0	0	70.15	0	0
Limiting low temperature	DV0	9	10	11	1.88	1.6	0	1.9	0	1.1	0	0	0	0
Degree-days per Generation	PDD	360	450	540	1.73	1.2	0	0	0	0	0	0	0	0
Limiting low moisture	SM0	0	0.1	0.2	0.99	1.4	0	0	16.24	2.7	0	0	0	0
Diapause Induction Temperature	DPT0	5	6	7	0.45	1.9	0	0	0	3.3	0	0	0	0
Diapause Termination Temperature	DPT1	1	2	3	0.4	1.8	0	0	0	1.9	0	0	0	0
Diapause Development Days	DPD	24	30	36	0.3	1.7	0	0	0	1.8	0	0	0	0
Dry stress rate	HDS	−0.06	−0.05	−0.04	0.23	0.3	0.14	0	0	0	0	7.73	0	0
Lower optimal moisture	SM1	0.3	0.4	0.5	0.19	1.3	0	0	12.29	2	0	0	0	0
Cold stress Temperature Threshold	TTCS	−35	−34	−33	0.08	0.3	1.54	0	0	0	0	0	18	0
Lower optimal temperature	DV1	25	26	27	0.04	0.7	0	2.8	0	1.3	0	0	0	0
Diapause Induction Daylength	DPD0	11.5	12	12.5	0.03	0.3	0	0	0	0.3	0	0	0	0
Cold stress Temperature Rate	THCS	−0.06	−0.05	−0.04	0.01	0	0.02	0	0	0	0	0	2.44	0
Wet stress Threshold	SMWS	1.65	1.75	1.85	0.01	0.1	1.31	0	0	0	0	0	0	9.12
Limiting high temperature	DV3	34	35	36	0.01	0.2	0	5.2	0	2.3	0	0	0	0
Upper optimal temperature	DV2	29	30	31	0.01	0.4	0	6.9	0	3	0	0	0	0
Heat stress Temperature Threshold	TTHS	34	35	36	0	0	0.23	0	0	0	12.34	0	0	0
Limiting high moisture	SM3	1.65	1.75	1.85	0	0.4	0	0	4.02	2.4	0	0	0	0
Wet stress rate	HWS	0.016	0.02	0.024	0	0	0.06	0	0	0	0	0	0	2.31
Upper optimal moisture	SM2	0.9	1	1.1	0	0.5	0	0	6.89	1.9	0	0	0	0
Heat stress Temperature Rate	THHS	0.0008	0.001	0.0012	0	0	0.01	0	0	0	4.61	0	0	0

Core dist'n, core distribution area; TI, temperature index; MI, moisture index; GI, growth index; HS, heat stress; DS, drought stress; CS, coldness stress; WS, wet stress.
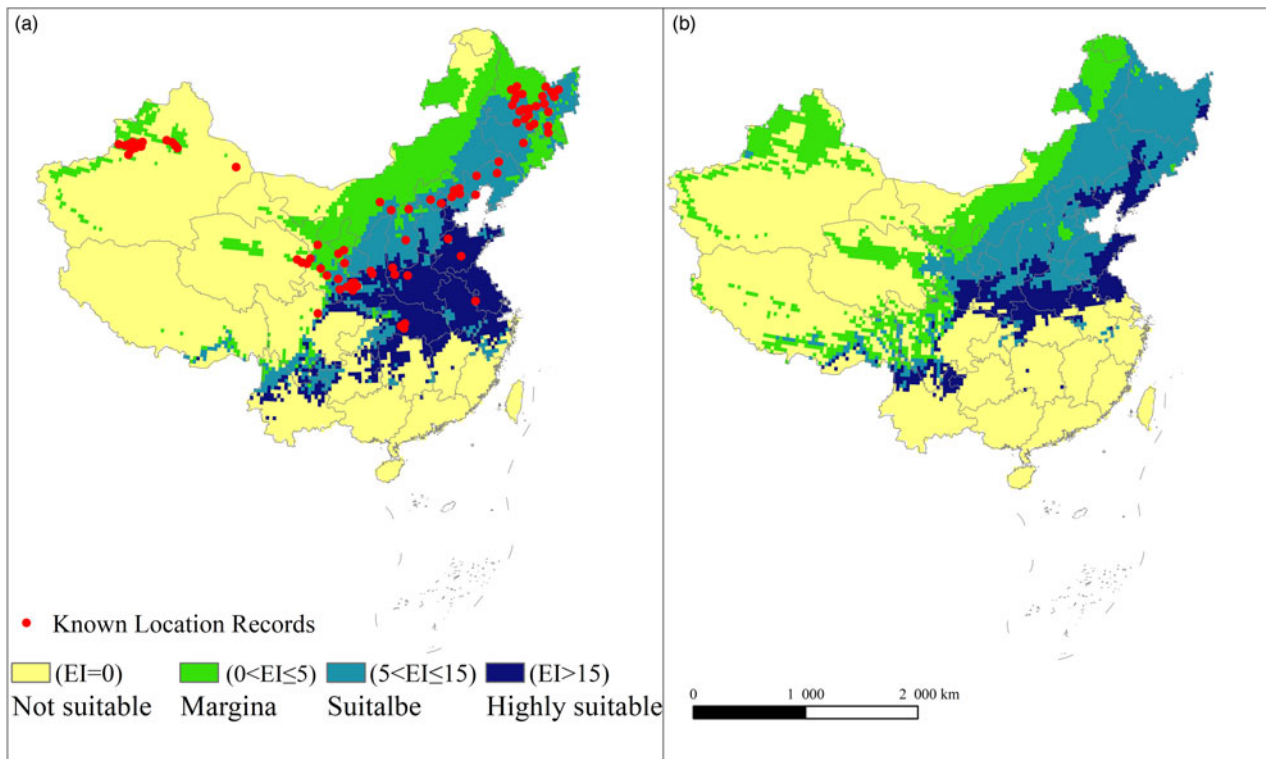
Figure 2. The change of Ecoclimatic suitability (EI) for *Agrilus mali* with global warming in China from current conditions (a) and 2100 (d) under CSIRO-Mk 3.0 GCM running the SRES A1B. Points show the known location records of *A. mali*.

known distribution sites (figs 1 and 2a). All known distribution records fall within areas that are modelled as suitable to marginally suitable. Simulation with those parameters suggests the species has the potential to become more widespread in the southern mountainous areas of China, as well as north-eastern China, the Huang-Huai-Hai Plain (including Shandong, Henan, Anhui and Jiangsu provinces), parts of the Loess Plateau (Gansu, Qinghai, Shaanxi, Ningxia and Shanxi provinces), some areas of Sichuan basin (including Sichuan and Chongqing), southern areas of Tibet and northern Xinjiang (fig. 2a), if hosts are available. *Agrilus mali* has not yet been reported from central Asia, though it has been reported spreading towards areas at risk in Kazakhstan (see below).

Current population phenology and the distribution in China under climate change

Overall, the potential distribution of this pest lies between latitudes 30° and 50° North, which overlaps with the apple production belt in China. With increasing temperatures to the year 2100, the potential distribution of this pest will likely shift northwards, especially to the northeast, while contracting its distribution in the south (fig. 2). The suitable areas will likely become more extensive in northern Xinjiang and encompass all known wild apple forests (fig. 2 and Supplementary fig. 1).

The phenology of *A. mali* varies geographically within China (fig. 3), conditions being suitable from the end of March and April (fig. 3) to mid-September and the end of November (site 7, 8 and 9; fig. 3) based on modelled GI_W values. The observed phenology is mostly consistent with our projection in various sites (fig. 3). Larvae are present from the previous

September to Mid-June, and pupae from mid-June to mid-July in Yili valley. Adults emerge from the start of July to mid-July in site 1 and site 2 (fig. 3). The modelled phenology for site 1, where the phenology of *A. mali* was assessed in wild apple forest areas during 2016–2017, is similar to our field data (Supplementary fig. 2).

The population growth index (GI_A) shows the highest potential in Shandong, one of the biggest apple production areas in China. Under the future climate scenario, the modelled growth potential in most sites in China is higher in 2100 except at sites 7 and 8, and the species phenology starts earlier by 1–2 weeks in spring (mostly in March) and persists longer into autumn (ending in November) (fig. 3).

The potential worldwide distribution of Agrilus mali

Under current climate conditions, *A. mali* could potentially expand its distribution in mid-latitudes across the temperate zone in the northern hemisphere (latitudes: 30°N to 50°N) and in some areas of the subtropical, Mediterranean and Temperate zones in the southern hemisphere (latitudes: 23.5°S to 40°S). Suitable areas for this pest occur around the Mediterranean, most of Europe, parts of the Middle East and central Asia, North China Plain, and large areas North America, as well as New Zealand, parts of Australia, parts of southern Africa and the Pampas Steppe alongside the Andes Mountains in the Southern Hemisphere (fig. 4). This potential distribution overlaps known apple production areas (Supplementary fig. 1). Additionally, areas projected to be suitable for *A. mali* overlap with wild apples in central Asia (*M. sieversii*), Europe (*M. sylvestris*), Turkey (*M. orientalis*) and Siberia (*M. baccata*) (see Supplementary fig. 1).
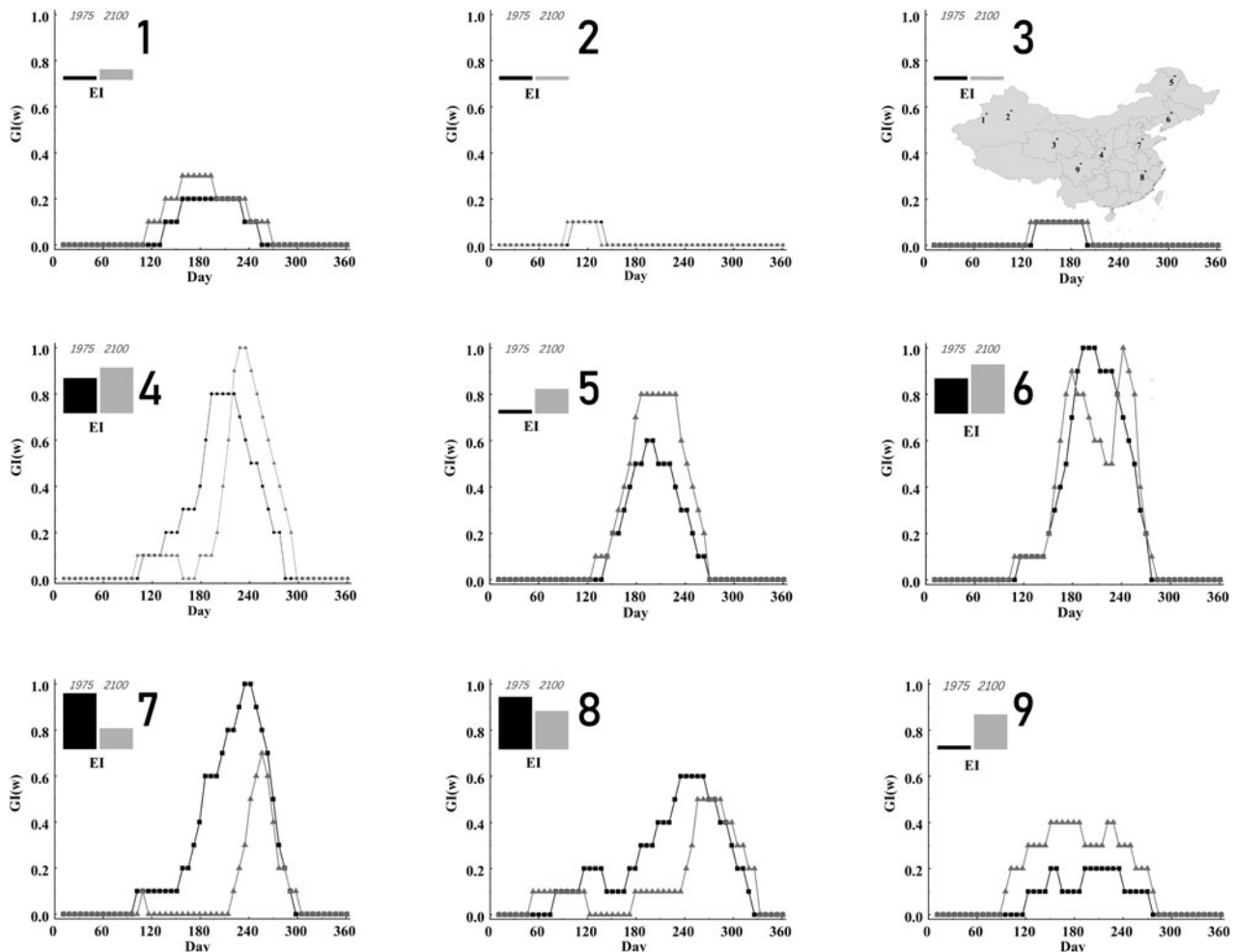
Figure 3. The modelled phenology of *Agrilus mali* based on weekly CLIMEX growth index (GI$_W$) values under current climate and in the 2100 scenario across nine sites where the species is known to occur in China. The relative EI values are also shown.

Under the global warming scenario, the potential distribution of *A. mali* shifted to higher altitudes and latitudes in both hemispheres. The unsuitable area declined by 4%, as did the highly suitable area by 0.8% in both hemispheres (fig. 5). At the same time, the marginally suitable areas (EI < 5) increased by 3.6% with global warming, as did the low suitability area by 2.1% in the same period (fig. 5). The low suitability area in the Northern Hemisphere is more sensitive to global warming, and will increase in the future, especially in the northern Xinjiang, northern Europe and Russia (fig. 5).

Sensitivity and uncertainty analysis

The parametric uncertainty analysis indicated that the potential geographical range is most sensitive to dry stress threshold (SMDS, 2.16%), limiting low temperature for growth (DV0, 1.88%) and minimum annual heat sum (PDD, 1.73%) values, indicating that the model is quite insensitive to variation in all parameters (table 2). The uncertainty around SMDS is likely quite low, as it is guided by the permanent wilting point. Our estimate of DV0 was guided by the model fitting, and in the absence of further corroborating information, should be considered an educated guess. For the EI, no parameters had a sensitivity greater than 1.9% (Supplementary fig. 4). The uncertainty map based on

the natural rainfall scenario revealed that the areas of greatest confidence in the model are the temperate climate areas (Supplementary fig. 4). The low agreement areas extended into the lower rainfall areas.

Discussion

Based on our modelling, *A. mali* presents a serious threat to *Malus* spp. with the projected geographical range of *A. mali* overlapping not only all domestic apple production areas, but also wild apple ecosystems – the Garden of Eden of apples in central Asia, Europe, Armenia, Turkey and Siberia (Supplementary fig. 1) (Velasco *et al.*, 2010). With global warming, the projected range of *A. mali* could extend to higher latitudes and altitudes and possibly lead to greater potential commercial and biodiversity impacts. Improvements in projections for areas with high topographic relief could be achieved by using a finer scale grid for climate variables, though the overall picture will remain similar.

Our simulations and validation fit well the known distribution of this pest, which overlaps with the distribution of domesticated and wild apples across the world (fig. 4 and Supplementary fig. 1). The model growth indices capture known seasonal phenology. Moreover, the parametric uncertainty analysis reveals the model is quite insensitive to variation in most parameters (table 2),
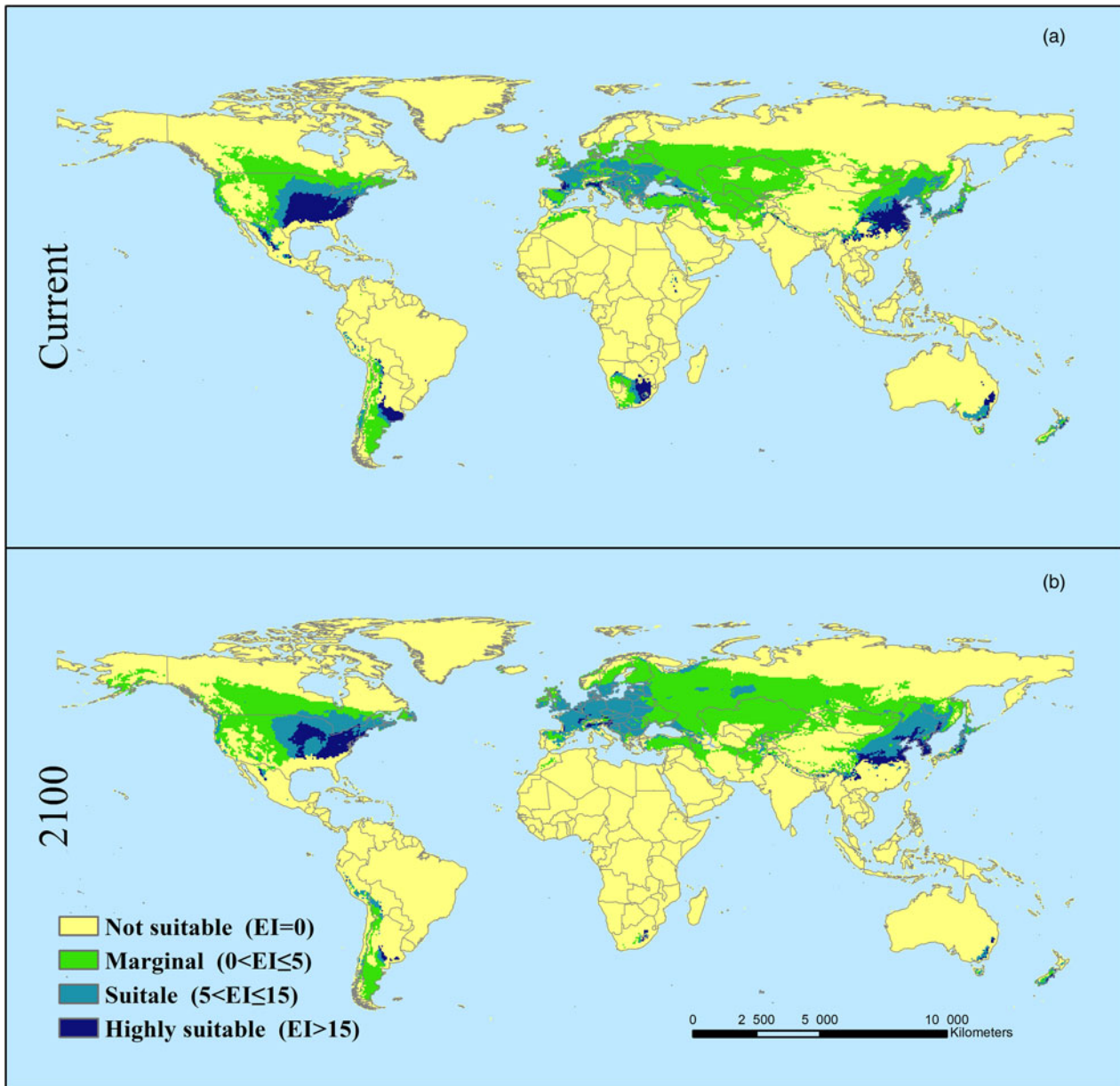
Figure 4. The potential global distribution of *Agrilus mali* under current and future climate scenarios in 2100 under CSIRO-Mk 3.0 GCM running the SRES A1B.

perhaps reflecting this insect being buffered by its feeding within host trees. The potential geographical range was most sensitive to dry stress threshold (SMDS). This implies that soil moisture should directly influence the survival of *Malus* spp. and indirectly determine the distribution of this pest. The obligate diapause in *A. mali* precludes it from expanding its range into low latitude, mid-altitude areas that may be suitable for Apple production (e.g., southern China and Kenya, Supplementary fig. 1).

Agrilus mali can infest many *Malus* spp., domesticated varieties as horticultural crops and as ornamental plants in agriculture lands, national parks, gardens and cities across world. Of particular concern are the *Malus* species ancestors of domesticated apples. Their distribution overlaps with the areas projected to be suitable for *A. mali* establishment (fig. 4). One interesting feature of this pest is that it prefers feeding on the younger branches or twigs (Zhang *et al.*, 2021). Consequently, columnar

apple trees and trellis orchards may be at greater risk than standard apple trees.

Climate change is expected to cause most insect species to shift their range to higher altitudes and latitudes (Sutherst *et al.*, 2007; Bebber *et al.*, 2013; Virkkala and Lehikoinen, 2014). In both hemispheres, increasing temperatures are likely to enable *A. mali* to extend its range into higher latitudes, with suitability declining in lower latitudes (fig. 3 such as site 7 and site 8, and fig. 4). This is similar to previous findings for various species of butterflies, beetles, midges, weeds and birds (Parmesan *et al.*, 1999; Guichard *et al.*, 2014; Virkkala and Lehikoinen, 2014; Lehmann *et al.*, 2015).

Key drivers for *A. mali* appear to be the obligatory diapause driven by cold temperatures, daylength and the minimum annual heat sum. This implies that milder winters due to global warming will relax diapause conditions, and hence the constraints on
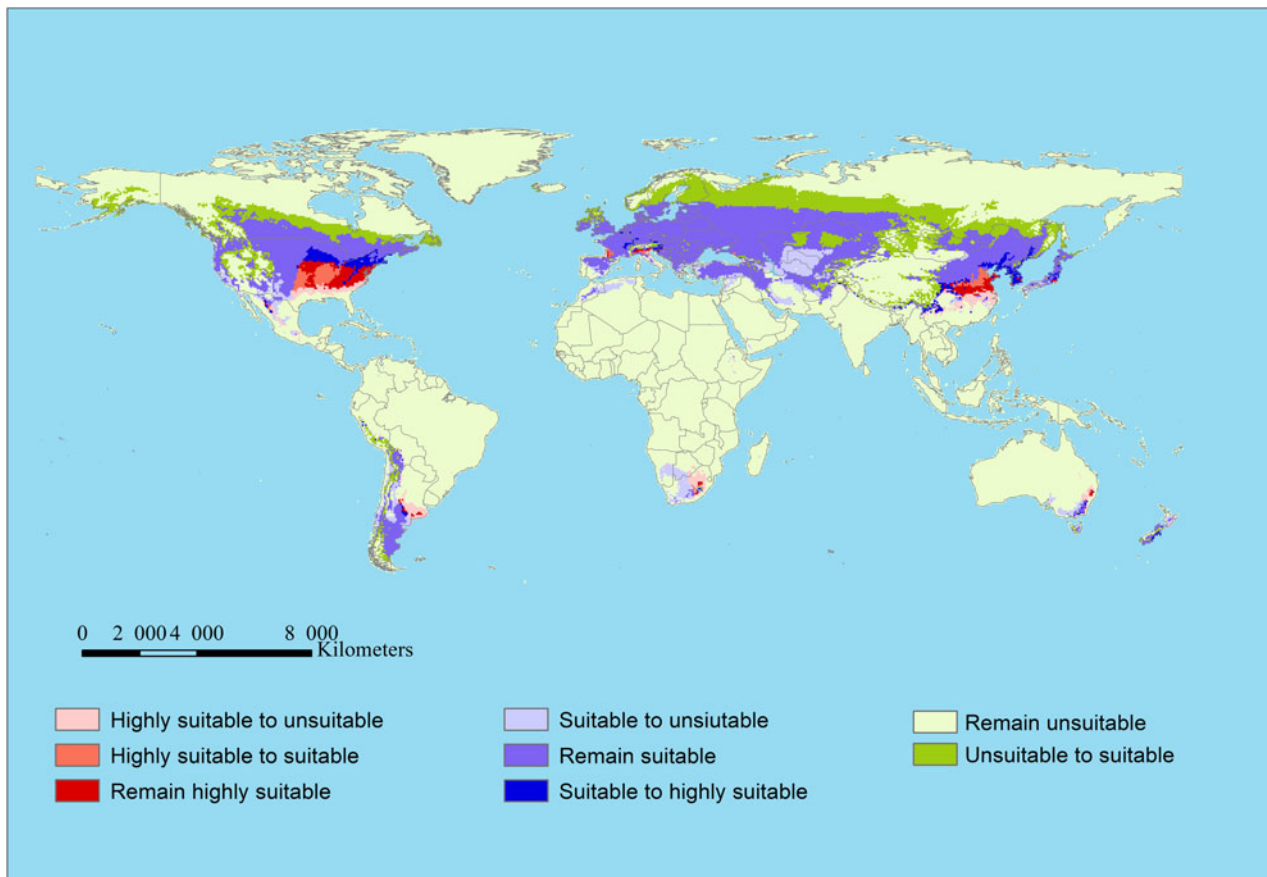
Figure 5. The relative change in suitability of *Agrilus mail* under the climate change scenario (comparison between current and 2100).

A. mali's cold range limits, especially in the marginal subtropical zones (fig. 4b). Diapause intensity has been found to be variable between animal strains and geographic locations which are probably genetically determined (e.g., Kimura, 1988; Koveos *et al.*, 1993; Huang *et al.*, 2020) and may have adaptive significance for this pest to spread southward. Furthermore, if global warming positively affects the prevalence of Valsa canker in wild apple, the combination of impacts from *A. mali* and Valse canker could be an extra cause for concern for apple production and conservation of wild apple diversity in infested areas.

Our confidence in the model could be improved with validation against independent data sets and further cross-validation with independent measures of biological parameters. Those parameters that had to be borrowed from closely related species or iteratively fitted should be measured as a matter of course. Diapause is particularly understudied in buprestids (Duan *et al.*, 2021) and in terms of species distribution modelling in general (Kriticos *et al.*, 2017). In addition, the uncertainty of variability in temperature and rainfall (such as the amplitude and frequency of extreme events) is likely to impact the distribution of species at range margins directly, and indirectly by impacting the health of host plants, especially for wild apple, and lead to range shifts.

Because of the potential current threat to apple production and ancestors of domesticated apples worldwide posed by *A. mali* (Supplementary fig. 3), mitigation measures need to be designed and implemented for the conservation of wild apple forests as a priority. *Agrilus mali* and other woodborers can rapidly become

more widespread where dead trees are harvested and moved as firewood (Haack *et al.*, 2010; Kovacs *et al.*, 2010; Jacobi *et al.*, 2012; Dodds *et al.*, 2017). Consequently, controlling the movement of firewood from infested areas locally, as well as developing suitable phytosanitary protocols for disinfesting seedlings of *Malus* spp. in national and international trade, has the potential to reduce the spread of *A. mali*. To protect the biodiversity of *Malus* spp. and resilience of forest ecosystems, education campaigns targeting the consequences of moving potentially contaminated cuttings and the need for phytosanitation in relation to *Malus* spp. may be a useful adjunct to local eradication or slow the spread campaigns. Doubtless, there will be a need to monitor these spread pathways and to develop rapid response capabilities in areas at risk of invasion.

Our CLIMEX model is easily reproducible by simply applying the parameters in table 1 to the same climatology and irrigation scenario we used. The reliability of the model should be judged in terms of the description of the fitting procedure, where the rationale for each parameter is described. The justification for each parameter can come from distribution data, phenological observations, experimental data or theoretical expectations. The parameters and functions constitute testable hypotheses about the response of *A. mali* to each climate variable. In the future, if more distribution, ecophysiological or phenological data become available, the model can be refined. Indeed, the less robust aspects of the parameter selection can guide future research prioritization. The sensitivity analysis however suggests

that there may be little to be gained in terms of refining the pest risk area because the most sensitive parameters are well-defined.

Agrilus mali is a clear and present threat to both domestic apples and the ancestral wild apple species in Eurasia, especially in China and in central Asia (Zhang *et al.*, 2021). This invasive species seems to be set to join the pantheon of other recently invasive buprestids (*A. planipennis*, *Agrilus biguttatus*, *Agrilus roscidus*) in devastating forest ecosystems in vulnerable regions (Brown *et al.*, 2017; Digirolomo *et al.*, 2019; Poole *et al.*, 2019) worldwide. Measures to mitigate the spread of *A. mali* need to be implemented sooner rather than later for the conservation of wild apple forests, especially in central Asia.

References

Aljaryian R and Kumar L (2016) Changing global risk of invading greenbug *Schizaphis graminum* under climate change. *Crop Protection* **88**, 137–148.

Ayres MP and Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* **262**, 263–286.

Baloch MN, Fan J, Haseeb M and Zhang RZ (2020) Mapping potential distribution of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Central Asia. *Insects* **11**, 172.

Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A and Larsson S (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications* **15**, 2084–2096.

Bebber DP, Ramotowski MAT and Gurr SJ (2013) Crop pests and pathogens move polewards in a warming world. *Nature Climate Change* **3**, 985–988.

Biondi A, Guedes RNC, Wan F and Desneux N (2018) Ecology, worldwide spread, and management of the invasive south American tomato pinworm, *Tuta absoluta*: past, present, and future. *Annual Review of Entomology* **63**, 239–258.

Bozorov TA, Luo Z, Li X and Zhang D (2019) *Agrilus mali* Matsumara (Coleoptera: Buprestidae), a new invasive pest of wild apple in western China: DNA barcoding and life cycle. *Ecology and Evolution* **9**, 1160–1172.

Brown N, Jeger M, Kirk S, Williams D, Xu X, Pautasso M and Denman S (2017) Acute oak decline and *Agrilus biguttatus*: the co-occurrence of stem bleeding and D-shaped emergence holes in Great Britain. *Forests* **8**, 1–17.

Chamberlin TC (1965) The method of multiple working hypotheses. *Science (New York, N.Y.)* **148**, 754–759.

Chaves LF (2016) Globally invasive, withdrawing at home: *Aedes albopictus* and *Aedes japonicus* facing the rise of *Aedes flavopictus*. *International Journal of Biometeorology* **60**, 1727–1738.

Cornille A, Gladieux P, Smulders MJM, Roldán-Ruiz I, Laurens F, Le Cam B, Nersesyan A, Clavel J, Olonova M, Feugey L, Gabrielyan I, Zhang XG, Tenaillon MI and Giraud T (2012) New insight into the history of domesticated apple: secondary contribution of the European wild apple to the genome of cultivated varieties. *PLoS Genetics* **8**, e1002703.

Cornille A, Giraud T, Bellard C, Tellier A, Le Cam B, Smulders MJM, Kleinschmit J, Roldan-Ruiz I and Gladieux P (2013) Postglacial recolonization history of the European crab apple (*Malus sylvestris* Mill.), a wild contributor to the domesticated apple. *Molecular Ecology* **22**, 2249–2263.

Cui XN, Liu DG and Liu AH (2015) Research progress in integrated management of *Agrilus mali*. *Plant Protection* **41**, 16–23.

Cui ZJ, Zhang YL, Luo ZH, Ma HL and Lu ZZ (2018) Damage of *Agrilus mali* Matsumura in wild apple forest and its assessment. *Arid Zone Research* **35**, 1153–1159.

Cui ZJ, Zhang YL, Zhang X, Luo ZH, Zhang P, Golec J, Poland TM, Zalucki MP, Han P and Lu ZZ (2019) Life history and mortality factors of *Agrilus mali* Matsumura (Coleoptera: Buprestidae) in wild apples in Northwestern China: life history and mortality factors of *Agrilus mali* Matsumura. *Agricultural and Forest Entomology* **21**, 309–317.

Deutsch C, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC and Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the USA* **105**, 6668–6672.

Digirolomo MF, Jendek E, Grebennikov VV and Nakladal O (2019) First North American record of an unnamed West Palaearctic *Agrilus* (Coleoptera: Buprestidae) infesting European beech (*Fagus sylvatica*) in New York City, USA. *European Journal of Entomology* **116**, 244–252.

Dodds KJ, Hanavan RP and DiGirolomo MF (2017) Firewood collected after a catastrophic wind event: the bark beetle (Scolytinae) and woodborer (Buprestidae, Cerambycidae) community present over a 3-year period. *Agricultural & Forest Entomology* **19**, 309–320.

Duan JJ, Tim W, Phil T, Kristi L and Lelito JP (2013) Effects of ambient temperature on egg and larval development of the invasive emerald ash borer (Coleoptera: Buprestidae): implications for laboratory rearing. *Journal of Economic Entomology* **106**, 2101–2108.

Duan JJ, Schmude JM and Larson KM (2021) Effects of low temperature exposure on diapause, development, and reproductive fitness of the emerald ash borer (Coleoptera: Buprestidae): implications for voltinism and laboratory rearing. *Journal of Economic Entomology* **114**, 201–208.

Engelkes T, Morrieen E, Verhoeven KJF, Bezemer TM, Biere A, Harvey JA, McIntyre LM, Tamis WLM and van der Putten WH (2008) Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature* **456**, 946–948.

Foster JR, Townsend PA and Mladenoff DJ (2013) Mapping asynchrony between gypsy moth egg-hatch and forest leaf-out: putting the phenological window hypothesis in a spatial context. *Forest Ecology and Management* **287**, 67–76.

Furlong MJ and Zalucki MP (2017) Climate change and biological control: the consequences of increasing temperatures on host–parasitoid interactions. *Current Opinion in Insect Science* **20**, 39–44.

Gillard M, Thiebaut G, Deleu C and Leroy B (2017) Present and future distribution of three aquatic plants taxa across the world: decrease in native and increase in invasive ranges. *Biological Invasions* **19**, 2159–2170.

Goergen G, Kumar PL, Sankung SB, Togola A and Tamo M (2016) First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in west and central Africa. *PLoS ONE* **11**, 1–9.

Guichard S, Guis H, Tran A, Garros C, Balenghien T and Kriticos DJ (2014) Worldwide niche and future potential distribution of *Culicoides imicola*, a major vector of bluetongue and African horse sickness viruses. *PLoS ONE* **9**, e112491.

Haack RA and Benjamin DM (1982) The biology and ecology of the twolined chestnut borer, *Agrilus bilineatus* (Coleoptera: Buprestidae), on oaks, *Quercus* spp., in Wisconsin. *Canadian Entomologist* **114**, 385–396.

Haack RA, Petrice TR and Wiedenhoeft AC (2010) Incidence of bark- and wood-boring insects in firewood: a survey at Michigan's Mackinac bridge. *Journal of Economic Entomology* **103**, 1682–1692.

Harris SA, Robinson JP and Juniper BE (2002) Genetic clues to the origin of the apple. *Trends in Genetics* **18**, 426–430.

Hortal J, Jiménez-Valverde A, Gómez JF, Lobo JM and Baselga A (2008) Historical bias in biodiversity inventories affects the observed environmental niche of the species. *Oikos* **6**, 847–858.

Huang L, Tang J, Chen C, He H, Gao Y and Xue F (2020) Diapause incidence and critical day length of Asian corn borer (*Ostrinia furnacalis*)

populations exhibit a latitudinal cline in both pure and hybrid strains. *Journal of Pest Science* **93**, 559–568.

Hulme PE (2017) Climate change and biological invasions: evidence, expectations, and response options. *Biological Reviews* **92**, 1297–1313.

Jacobi WR, Hardin JG, Goodrich BA and Cleaver CM (2012) Retail firewood can transport live tree pests. *Journal of Economic Entomology* **105**, 1645–1658.

Jaric I, Heger T, Monzon FC, Jeschke JM, Kowarik I, Mcconkey KR, Pysek P, Sagouis A and Essl F (2019) Crypticity in biological invasions. *Trends in Ecology and Evolution* **34**, 291–302.

Kimura MT (1988) Interspecific and geographic variation of diapause intensity and seasonal adaptation in the *Drosophila auraria* species complex (Diptera: Drosophilidae). *Functional Ecology* **2**, 177–183.

Kistner EJ (2017) Climate change impacts on the potential distribution and abundance of the brown marmorated stink bug (Hemiptera: Pentatomidae) with special reference to North America and Europe. *Environmental Entomology* **46**, 1212–1224.

Kovacs KF, Haight RG, McCullough DG, Mercader RJ, Siegert NW and Liebhold AM (2010) Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecological Economics* **69**, 569–578.

Koveos DS, Kroon A and Veerman A (1993) Geographic variation of diapause intensity in the spider mite *Tetranychus urticae*. *Physiological Entomology* **18**, 50–56.

Kriticos DJ, Sutherst RW, Brown JR, Adkins SW and Maywald GF (2003) Climate change and biotic invasions: a case history of a tropical woody vine. *Biological Invasions* **5**, 147–165.

Kriticos DJ, Watt MS, Potter KJB, Manning LK, Alexander NS and Tallent-Halsell N (2011) Managing invasive weeds under climate change: considering the current and potential future distribution of *Buddleja davidii*. *Weed Research* **51**, 85–96.

Kriticos DJ, Webber BL, Leriche A, Ota N, Macadam I, Bathols J and Scott JK (2012) CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution* **3**, 53–64.

Kriticos DJ, Agathe L, Palmer DJ, Cook DC, Brockerhoff EG, Stephens AEA, Watt MS and Alex SM (2013) Linking climate suitability, spread rates and host-impact when estimating the potential costs of invasive pests. *PLoS ONE* **8**, e54861.

Kriticos DJ, Ota N, Hutchison WD, Beddow J, Walsh T, Tay WT, Borchert DM, Paula-Moreas SV, Czepak C and Zalucki MP (2015) The potential distribution of invading *Helicoverpa armigera* in North America: is it just a matter of time? *PLoS ONE* **10**, e0119618.

Kriticos DJ, Kean JM, Phillips CB, Senay SD, Acosta H and Haye T (2017) The potential global distribution of the brown marmorated stink bug, *Halyomorpha halys*, a critical threat to plant biosecurity. *Journal of Pest Science* **90**, 1033–1043.

Kriticos DJ, Darnell RE, Yonow T, Ota N, Boykin LM, Sutherst RW, Parry HR, Mugerwa H, Maruthi MN, Seal S, Colvin J, Macfadyen SA, Kalyebi A, Hulthen A and De Barro PJ (2020) Improving climate suitability for *Bemisia tabaci* in East and Central Africa correlates with increased prevalence of whiteflies and cassava diseases. *Scientific Reports* **10**, 22049.

Kumar C, Singh SK, Pramanick KK, Verma MK, Srivastav M, Singh R, Bharadwaj C and Naga KC (2018) Morphological and biochemical diversity among the *Malus* species including indigenous Himalayan wild apples. *Scientia Horticulturae* **233**, 204–219.

Lehmann P, Lyytinen A, Piiroinen S and Lindström L (2015) Latitudinal differences in diapause related photoperiodic responses of European Colorado potato beetles (*Leptinotarsa decemlineata*). *Evolutionary Ecology* **29**, 269–282.

Li ML and Zhang ZQ (2017) Discussion on biology and life history associated with *Agrilus mali* Matsumura. *Journal of Northwest Forestry University* **32**, 139–146.

Li ZY, Feng X, Liu SS, You M and Furlong MJ (2016) Biology, ecology, and management of the diamondback moth in China. *Annual Review of Entomology* **61**, 277–296.

Li X, Wu MF, Ma J, Gao BY, Wu QL, Chen AD, Liu J, Jiang YY, Zhai BP, Early R, Chapman JW and Hu G (2020) Prediction of migratory routes of the invasive fall armyworm in eastern China using a trajectory analytical approach. *Pest Management Science* **76**, 454–463.

Liu AH (2010) *Biology and Ecology of Agrilus mali and its Dominant Natural Enemies in Wild Fruit Forests in Xinjiang*. Xinjiang: China Xinjiang Agricultural University.

Logan JA, Reniere J and Powell JA (2003) Assessing the impacts of global climate change on forest pests. *Frontiers in Ecology* **1**, 130–137.

Mathers HM (2005) Screening *Malus* seedlings for cold hardiness. *Hortscience A Publication of the American Society for Horticultural Science* **40**, 318–322.

Nakicenovic N, Alcamo J, Grubler A, Riahi K, Roehrl RA, Rogner H-H and Victor N (2000) *Special Report on Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University, Press.

Olfert O, Weiss RM and Kriticos D (2011) Application of general circulation models to assess the potential impact of climate change on potential distribution and relative abundance of *Melanoplus sanguinipes* (Fabricius) (Orthoptera: Acrididae) in North America. *Psyche: A Journal of Entomology* **2011**, 1–9.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA and Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579–583.

Pimentel D, Lach L, Zuniga R and Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience* **50**, 53–65.

Poland TM and Mccullough DG (2006) Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry* **104**, 118–124.

Poole EM, Ulyshen MD, Horn S, Cram M, Olatinwo R and Fraedrich S (2019) Biology and distribution of *Agrilus macer* LeConte (Coleoptera: Buprestidae), a species associated with sugarberry (*Celtis laevigata* Willd.) mortality in the southeastern USA. *Annals of Forest Science* **76**, 1–14.

Singer MC and Parmesan C (2010) Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society of London* **365**, 3161–3176.

Staentzel C, Combroux I, Barillier A, Grac C, Chanez E and Beisel J (2019) Effects of a river restoration project along the Old Rhine River (France-Germany): response of macroinvertebrate communities. *Ecological Engineering* **127**, 114–124.

Sun YZ, Liang YY and Sun H (1979) Studies apple buprestid (*Agrilus mali* Mats.) in Shanxi. *Journal of Northwest A & F University (Natural Science Edition)* **2**, 47–56.

Sutherst RW and Maywald GF (1985) A computerised system for matching climates in ecology. *Agriculture Ecosystems & Environment* **13**, 281–299.

Sutherst RW, Baker RHA, Coakley SM, Harrington R and Scherm H (2007) *Pests Under Global Change – Meeting Your Future Landlords?* New York: Springer, Berlin Heidelberg.

Tao Y, Li Q, Chen X, Philippe DM, Xue Y, Liu Y, Zhao TB and Li LH (2019) Spatiotemporal variability of the precipitation concentration and diversity in Central Asia. *Atmospheric Research* **241**, 1–28.

Taylor KE, Stouffer RJ and Meehl GA (2012) An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society* **93**, 485–498.

Velasco R, Zharkikh A, Affourtit J, Dhingra A, Cestaro A, Kalyanaraman A, Fontana P, Bhatnagar SK, Troggio M and Pruss D (2010) The genome of the domesticated apple (*Malus × domestica* Borkh.). *Nature Genetics* **42**, 833–839.

Virkkala R and Lehikoinen A (2014) Patterns of climate-induced density shifts of species: poleward shifts faster in northern boreal birds than in southern birds. *Global Change Biology* **20**, 2995–3003.

Vitousek PM, Dantonio CM, Loope LL, Rejmanek M and Westbrooks R (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* **21**, 1–16.

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O and Bairlein F (2002) Ecological responses to recent climate change. *Nature* **416**, 389–395.

Wang ZY, Zhang YL, Yang ZQ and Wang XY (2013) Determination of larval instars of *Agrilus mali* Matsumura (Coleoptera: Buprestidae). *Forest Research* **26**, 786–789.

Yi ZH, Liu DG, Cui XN and Shang ZM (2016) Morphology and ultrastructure of antennal sensilla in male and female *Agrilus mali* (Coleoptera: Buprestidae). *Journal of Insect Science* **16**, 86, 81–10.

Zhang ZQ, Jiao S, Li XH and Li ML (2018) Bacterial and fungal gut communities of *Agrilus mali* at different developmental stages and fed different diets. *Scientific Reports* **8**, 1–11.

Zhang P, Lu ZZ, Zhang X, Zhao XP, Zhang YG, Tanabeko G, Bagila M, Zhanera A and Cui ZJ (2019) Age structure of *Malus sieversii* population in Ili of Xinjiang and Kazakhstan. *Arid Zone Research* **36**, 844–853.

Zhang P, Cui ZJ, Xu H, Ali A and Lu ZZ (2020) Thirst or malnutrition: the impacts of invasive insect *Agrilus mali* on the physiological status of wild apple tree. *Forests* **11**, 440.

Zhang X, Zhang YL, Zhang P, Cui ZJ, Han P, Gao GZ, Poland TM, Zalucki MP and Lu ZZ (2021) *Agrilus mali* Matsumura (Coleoptera: Buprestidae) density and damage in wild apple *Malus sieversii* (Rosales: Rosaceae) forests in Central Eurasia under four different management strategies. *Entomologia Generalis* **41**, 257–266.