

Range-Expanding Pests and Pathogens in a Warming World

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Annu. Rev. Phytopathol. 2015. 53:335–56

First published online as a Review in Advance on
May 27, 2015

The *Annual Review of Phytopathology* is online at
phyto.annualreviews.org

This article's doi:
10.1146/annurev-phyto-080614-120207

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Keywords

climate change, species distribution model, Colorado potato beetle, CLIMEX, agricultural crops

Abstract

Crop pests and pathogens (CPPs) present a growing threat to food security and ecosystem management. The interactions between plants and their natural enemies are influenced by environmental conditions and thus global warming and climate change could affect CPP ranges and impact. Observations of changing CPP distributions over the twentieth century suggest that growing agricultural production and trade have been most important in disseminating CPPs, but there is some evidence for a latitudinal bias in range shifts that indicates a global warming signal. Species distribution models using climatic variables as drivers suggest that ranges will shift latitudinally in the future. The rapid spread of the Colorado potato beetle across Eurasia illustrates the importance of evolutionary adaptation, host distribution, and migration patterns in affecting the predictions of climate-based species distribution models. Understanding species range shifts in the framework of ecological niche theory may help to direct future research needs.

INTRODUCTION

Agricultural crops and forestry plantations around the world are threatened by growing numbers of plant pests and pathogens (11, 42). The challenge posed by these destructive organisms to food security and land management has prompted research into why these organisms are spreading, where they are likely to establish next, what damage they are likely to do, and what can be done to reduce their impact. Humans provide crop pests and pathogens (CPPs) with vast areas of genetically uniform host plants, often lacking the natural defenses of their wild ancestors, and, through increasing flows of trade and transport, the means to reach their host crops. Efforts to protect crops with genetic resistance or chemistry have repeatedly been thwarted by rapid adaptation, and quarantine measures are frequently breached. Only rarely, and with great effort, have established pests been eradicated. We are thus engaged in an arms race with mobile, highly adaptable enemies on a growing number of fronts.

The fight against CPPs is played out in a changing world. As crop production has expanded, now covering one tenth of the global land surface, forests have been felled, wetlands drained, rivers dammed, roads built, the atmosphere polluted, fossil fuels burned, and the climate altered (153). Climate change in particular has the potential to dramatically alter the Earth system (62). The strong interrelationship between plants, their natural enemies, and the environment (the disease triangle) has motivated numerous reviews on the potential impact of climate change on CPP distributions and impact (25, 38, 47, 48, 69, 91, 146, 156, 169). However, even recently the lack of a clear synthesis of novel principles and conclusions to guide future research has been identified (24). In the first part of this review, I summarize recent observations and analyses of changing CPP distributions, considering the evidence for a climate change signal in these observations. In the second part, I investigate tools for modeling the effect of climate change on CPP distributions and provide case studies for illustration of the principles of CPP distribution modeling. Finally, I propose that framing the discussion of changing CPP distributions in current ecological niche theory could help reveal gaps in knowledge and clarify the direction of future research.

The review focuses on changing distributions and their causes, rather than on the potential effect of climate change on plant-pest or plant-pathogen interactions, while acknowledging that these processes are related: When conditions promoting population growth arise, establishment becomes possible. Although interactions between CPPs and their natural enemies may alter range-shift dynamics, primarily due to the escape into enemy-free space by dispersing CPPs (160), full consideration of tritrophic interactions is beyond the scope of this review. Most examples refer to agricultural CPPs, although forestry studies are used to illustrate the principles where required. CPPs comprising viruses, bacteria, fungi, oomycetes, nematodes, and arthropods are all considered, given their common ecological function, although most work has been undertaken for insects and fungi. The review is restricted, as far as possible, to the literature published in the past five years. Interested readers can consult the sources listed above for syntheses of the earlier literature.

RECENT RANGE EXPANSIONS

Since 1994, the ProMED initiative has gathered reports on infectious diseases of humans, animals, and plants from the academic, practitioner, and popular literature, and distributed these as email alerts with an online archive (<http://www.promedmail.org/>). These alerts have previously been interrogated to elucidate general patterns of pest and pathogen emergence (4). The majority of reports relate to outbreaks of CPPs already present in a region, but the first cases of recently arrived organisms or newly evolved strains are also included. Between January 2010 and the time

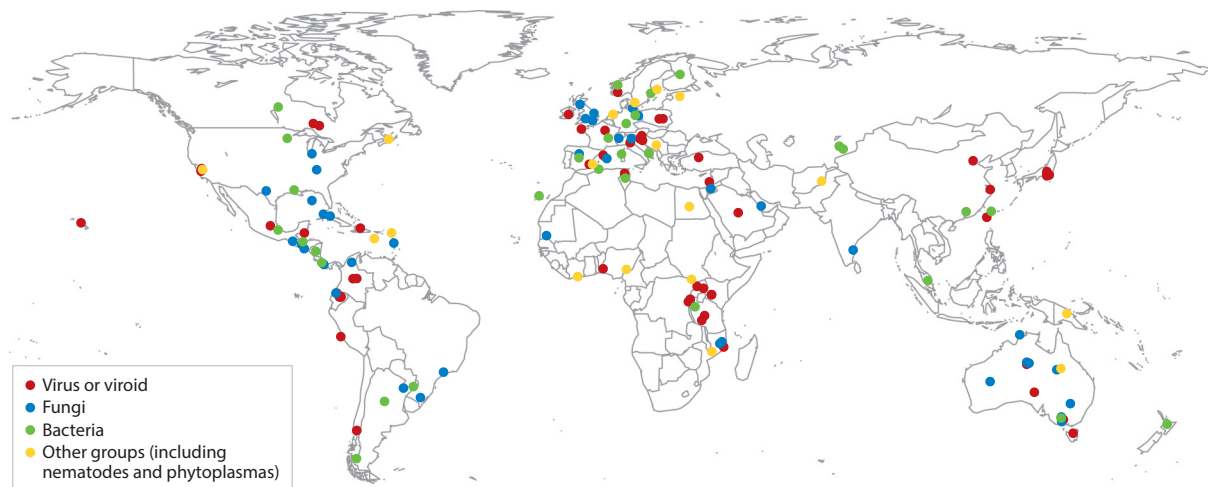


Figure 1

First reports of crop pathogens in 2010–2015 from ProMED email alerts. Hot spots of new reports include Europe, Central America, East Africa, and Australia.

of this writing, ProMED listed approximately 140 of these first reports, i.e., around two per month globally. Most common are reports of newly arrived viruses and viroids (36.6%), followed by fungi (28.2%). ProMED reports primarily on infectious diseases, including plant-pathogenic nematodes, and thus new reports of insect pests are rare. The majority of new observations are in the Northern Hemisphere, although several are from Australia (**Figure 1**). The most commonly affected crops are maize (9.1%), bananas (8.5%), citrus (7.7%), and potato (7.0%). For maize, among the most concerning reports is the emergence of a syndrome known as maize lethal necrosis (MLN) in Africa. MLN was first identified in Kenya in 2011 (163) and appears to have spread to Mozambique, Uganda, Rwanda, Tanzania, and, most recently, the Democratic Republic of Congo (92). Plants are infected by *Maize chlorotic mottle virus* plus a potyvirus such as *Maize dwarf mosaic virus* or *Wheat streak mosaic virus* (1). Transmission appears to be via an insect vector, perhaps the *Frankliniella williamsi* thrip (163). Interestingly, this syndrome has emerged several times independently, with the first identification in Kansas in 1976 (106).

Other first reports for maize include the spread of Goss's Wilt (*Clavibacter michiganensis* subsp. *nebraskensis*) to Minnesota and Manitoba from Nebraska and surrounding states, the spread of Stewart's Wilt (*Pantoea stewartii* subsp. *stewartii*) to Argentina (126), and the emergence of a new disease, *Maize rough dwarf virus*, in Uganda and its subsequent spread to Kenya (122). The main emerging threat to bananas, particularly the ubiquitous Cavendish variety, is the emergence of the TR4 (tropical race 4) strain of Panama disease (*Fusarium oxysporum* f. sp. *cubense*), recently reported in Mozambique (128) and Jordan (127), with the evolution of another strain virulent on Cavendish in India (119). Other emerging diseases of banana include Black Sigatoka (*Mycosphaerella fijiensis*) reported for the first time in the several Caribbean states (121), Freckle disease (*Phyllosticta* sp.) in parts of Australia (125), Moko disease (*Ralstonia solanacearum*) in Peninsular Malaysia (170) and Ecuador (32), bacterial wilt (*Xanthomonas campestris* pv. *musacearum*) in Burundi (120), and *Banana bunchy top virus* in Benin (90).

First reports of diseases spread by insect vectors are common. For example, citrus greening disease, or Huanglongbing (*Candidatus Liberibacter asiaticus*), has further spread across Central and South America, with a single report from California (124). The African psyllid vector of

Huanglongbing, *Trioza erytrae*, has recently been found in Spain (135). Xylella leaf scorch (*Xylella fastidiosa*) of olives, spread by various leafhoppers, has been detected in Italy and France (134).

Virulent new strains are frequently reported. Septoria tritici blotch (*Zymoseptoria tritici*) of wheat has developed azole fungicide resistance in Australia (131) and strobilurin resistance in New Zealand (132), as has Cercospora leaf spot (*Cercospora beticola*) of sugar beet in Michigan (123). A virulent new population of Coffee leaf rust (*Hemileia vestatrix*) able to attack Arabica coffee in cooler, high altitude plantations was discovered in Guatemala in 2012, and heavy rainfall in Central America has fostered outbreaks of this disease in the region in recent years (130). In a few cases, changes in management have been suggested as drivers for emergence. Yellow mottle disease of rice, caused by a sobemovirus, was first detected in the Democratic Republic of Congo in 2012. A shift from low intensity upland agriculture to lowland irrigated systems may have facilitated establishment of the disease through increased vector density or alternative host plant availability (61). Although economic losses are generally of the most concern, social impacts can also be great. Plum pox virus, which causes the sharka disease that originated in Eastern Europe, was detected for the first time in Tokyo in 2010 (95). In April 2014, all 1,266 plum trees in Umeno Park, Ome, were felled to prevent the spread of the disease. The plum blossom in Umeno Park had been one of Japan's most popular tourist attractions.

Many of these reports come from the popular press and, although usually featuring expert opinions, require peer-reviewed verification. In some cases, this verification can take several years. For example, a new disease termed leaf stripe and stem rot of maize, caused by *Burkholderia gladioli*, appeared in Veracruz, Mexico, in 2003 and was published in peer-reviewed literature eight years later (49). Bearing these caveats in mind, we can tentatively conclude from the ProMED reports that first establishments of plant diseases appear to be primarily due to introductions, spread from neighboring areas, and evolution of new virulent genotypes. There is little suggestion of a climate change signal in the ProMED reports. Weather is cited as a possible reason for emergence in only a handful of cases. The Barley yellow dwarf virus PAS isolate spread rapidly in wheat in Turkey following heavy rains in 2014. Black Sigatoka was blown to Martinique by strong winds and subsequently thrived due to heavy rain (129). Warm autumn and winter weather increased aphid vector populations of *Beet western yellows virus* in Australia (133). The first outbreak of *Puccinia graminis* f. sp. *tritici* in Germany in several decades was related to warm weather in 2013. These examples contrast with reports of outbreaks of established diseases, which are often cited as caused by weather conditions (4).

PATTERNS AND PROCESSES OF CHANGING DISTRIBUTIONS

Occasionally, a time series of observational data is available for a particular CPP, allowing patterns and processes of range expansion to be studied. For example, subnational historical observations allowed the rates of spread of the invasive woodwasp *Sirex noctilio* across parts of South America, South Africa, and Australia to be related to high-resolution climate data, showing that dispersal rate increased with mean annual temperature and isothermality (78). The most intense spatiotemporal monitoring of any plant disease is the US network of soybean sentinel plots for soybean rust (*Phakopsora pachyrhizi*) (158). Such intensive monitoring will be invaluable in understanding the roles of different drivers of range expansion in the future, particularly if the technology and tools to positively identify CPPs become more affordable. The increasing use of molecular tools has allowed the population structure of plant pathogens to be analyzed, enabling reconstruction of dispersal history in the absence of historical records. For example, microsatellite genotyping revealed that six major geographical clusters comprise the global population of wheat yellow rust

fungus (*Puccinia striiformis* f. sp. *tritici*) and the Himalayas to be the center of origin for this pathogen, with human activities as the most likely cause of spread (2).

Perhaps the most comprehensive global data set on CPP distributions has been compiled by the organization CABI, which synthesizes and curates distribution data from multiple academic and practitioner sources (111). CABI data have been used in numerous studies of CPP distributions (7, 8, 11–13, 42, 107, 108, 166). Analyses of global patterns of hundreds of CPP distributions have revealed that the number of CPPs present in a country increases with the quantity and diversity of crop production and with the mean annual rainfall, and is greater on islands (12). Globally, more than one-tenth of CPPs are present in more than half of the countries in which host plants are grown, although pest assemblages remain strongly regionalized (11). The rate of dispersal increases with host range within taxa, although fungi generally have the narrowest host range but are the most widely dispersed of CPPs (11).

In Europe, the number of countries invaded by a fungus increases with the length of time that the fungus has been present in Europe, and the number of alien fungi present in a country is correlated with the area of the country, the population density, and the amount of rainfall (33). The powdery mildews (Erysiphales) appear to be spreading most rapidly, a finding confirmed on a global scale (11). This may be because powdery mildews are biotrophic pathogens and are therefore being spread by increasing trade in live plants, or that their symptoms are conspicuous and thus they are easy to detect and report, or that they release large numbers of airborne spores (33). The probability of quarantined arthropod invasions into Europe increases with host availability, climatic suitability, and the volume of trade of host crops entering a country from countries where the CPP is present (7). The number of invasive forest pathogens in Europe has grown rapidly, apparently through introductions on living plants (144). Invasive forest pathogen assemblages are similar in countries with similar climates and GDP, and invasiveness tends to increase with host range.

Historical observations of invasive species within countries permit higher resolution analyses of drivers of range shifts. CPP reporting systems in the United States allow analysis at the county level and comparison with high-resolution forest inventory and census data (6). Exotic forest pests and pathogens have established at a roughly uniform rate in the United States since the mid-nineteenth century, with at least 450 insect pests and 16 pathogens establishing since 1860 (6). The number of forest pests and pathogens per county is greatest in the Northeast and, to a lesser extent, on the Pacific coast, which has been linked to the forest cover, to population density, and also to their being historical centers of trade (87), which includes the import of live plants (86). Alien species (mainly plant pests and pathogens) invasions into China follow a similar pattern to those into the United States, with more reported from coastal provinces with greater commerce, trade, and economic development (60).

The majority of observations suggest that CPP ranges only expand, and this is expected because crops have been exported around the world and their natural enemies eventually follow (11, 30). There are a small number of examples in which particular CPPs become insignificant in part of their range. A trivial case is where production of the host crop is simply abandoned. Alternatively, environmental conditions can alter suitability for different species. For example, in the United Kingdom, the relative abundance of two wheat pathogens, *Parastaganospora nodurum* and *Z. tritici*, appears to vary with air quality (45).

CLIMATE CHANGE AND RANGE EXPANSION

We have seen that recent first reports and syntheses of historical observations provide little indication for effects of climate change on changing species distributions, although climatic factors have

been connected with establishment risk. Theoretically, species ranges should shift in response to changing climate, as the geographic region with a climate suitable for population growth is altered (21, 27). As a first approximation, global warming leads to a poleward shift in isotherms, which populations should track, and observed changes in the distributions of wild species have been cited as among the strongest evidence for the biological impact of climate change (27, 34, 110). However, the presence of oceans, atmosphere, and complex landforms leads to complex and highly dynamic patterns of climate change (22). Since 1950, terrestrial temperatures have risen most rapidly in the boreal regions of North America and Asia, the Himalayas, parts of the Middle East, southern Brazil, and Sudan, although data are missing from large parts of Africa (67). Mean land-surface air temperature has increased by approximately 0.18°C per decade since 1950 (62). Warming since 1960 has resulted in a median velocity of isotherms of 27.3 km per decade at a spatial scale of $1^\circ \times 1^\circ$ (21). The spatial scale of analysis is important because short-range influences of topographic features such as mountain ranges, for example, can be masked by averaging (22, 36, 89). Thus, the European Alps, the Pyrenees, and the Carpathians act as climatic attractors, disrupting the poleward trajectories (22). Mean annual temperature, although often used in analyses of climate change velocity, can be a relatively poor indicator of biological response. Plant distributions, for example, are governed strongly by measures such as actual evapotranspiration (AET), climatic water deficit (D), and annual minimum temperature (T_{\min}) (36). Analysis of changes in these variables across the United States at a range of spatial resolutions (30 arcseconds to 1°) has revealed great spatial variability and slower velocities than suggested by mean annual temperature (36). The mean velocity across the United States is 5.1 km per decade from 1976 to 2005 based on T_{\min} , 2.2 km per decade based on AET, and 2.5 km per decade based on D. Importantly, the direction of velocity vectors became more coherent as the scale of analysis was coarsened, i.e., a stronger northward signal was detected as the data were aggregated. Velocities based on T_{\min} tend to be greater in the eastern half of the United States, whereas only the central regions, particularly the Northern Plains states of North and South Dakota, show significant increases in northward velocities when using AET and D (36). Considerations of spatial scale and biologically relevant climate variables may explain the lack of evidence for poleward range shifts for many tree species in the eastern United States, which instead primarily show range contractions (168). Nevertheless, at a large scale, the expected shift in distributions should be poleward.

Huang et al. (59) compiled data from 1900–2005 of first occurrence dates of invasive alien species, mainly CPPs, in China, the United States, and the United Kingdom from the academic literature and other sources. These data suggest that, broadly speaking, both land-surface temperature and establishment rate increase over time, perhaps suggesting that warming has promoted establishment. However, certain statistical issues and the plausibility of other explanations, such as historical variation in observation capacity, preclude a robust conclusion regarding the effect of global warming.

Bebber et al. (13) used the likely latitudinal bias in CPP observations (see sidebar, Observational Biases in Crop Pest and Pathogen Distributions) as an alternative hypothesis when investigating whether global warming is likely to have influenced range shifts of CPPs on a global scale. Under the global warming hypothesis, latitudinal ranges should shift poleward away from the Equator, tracking the changing distributions of habitable climates (21, 27). Under the observational bias hypothesis, wealthy countries with high scientific and technical capacity, which are generally further from the Equator (12, 77), should detect and report invasive species earlier than developing countries near the Equator. This would bias the perceived range shift toward the Equator, i.e., the opposite trend to what would be expected under global warming. For most insect pest groups and fungal pathogens, the mean within-species latitudinal shift was significantly positive, but for other groups, e.g., oomycetes, the mean rate could not be differentiated from zero, and for the viruses

OBSERVATIONAL BIASES IN CROP PEST AND PATHOGEN DISTRIBUTIONS

Our knowledge of CPP distributions appears to be highly biased by varying observational capacity around the world, and this bias must be considered in the interpretation of distributional data (12). Bias is related to latitude because tropical countries tend to be poorer and have weaker scientific infrastructure (12), but monitoring can be lacking even in scientifically advanced nations (33). Similar patterns of species detection have been noted in invasive species in general (138) and interpreted as the signal of historical trade (43, 137). Present CPPs are more likely to go unobserved than absent CPPs are to be reported because of the burden of evidence required to establish a positive identification. Another issue is that of delay between establishment and reporting. This delay is likely to be longer in countries with poor scientific capacity, leading to potential biases in the interpretation of distribution shifts (13). For example, the emerald ash borer (*Agrilus planipennis*) is likely to have been in the United States for approximately a decade before its official identification (147). In some cases, reports are forgotten and CPPs are “discovered” decades later (33). Comprehensive data mining of the historical literature is required to reduce these errors and provide a better understanding of historical changes in distributions (24, 66).

and nematodes, the latitudinal shift was significantly negative, i.e., toward the Equator. Compared with insects, viruses and nematodes are difficult to identify and their symptoms can be mistaken for abiotic stress (35), and so it is plausible that observational bias applies most strongly to these groups, whereas the effects of global warming are detected in the more mobile, easily identifiable groups. Guo et al. (53) argue that positive latitudinal shifts of invasive species could also occur because temperate regions are more invasible than the tropics or because tropical species are more likely to have been restricted on tropical islands (which are more numerous at low latitudes) and thus could rapidly expand their ranges when exported, or because particular climates are found at different latitudes around the world. However, it is difficult to postulate reasons why these mechanisms give rise to opposing trends for mobile, visible CPPs compared with soilborne and more cryptic CPPs.

The data used by Bebbler et al. (13) were at the coarsest possible spatial resolution and likely contain large errors and biases in observation dates, but the relatively large amount of data does allow tentative conclusions regarding the role of global warming in CPP range expansion to be drawn (46). Further studies using high-resolution data will be required to test the validity of these conclusions, but this will require intensive monitoring across all latitudes, not just in the developed world.

MODELING RESPONSES OF DISTRIBUTIONS TO CLIMATE CHANGE

The statistical and mathematical tools collectively known as species distribution models (SDMs) aim to predict potential species distributions by matching species’ environmental (primarily climatic) preferences with conditions in physical space (37, 39, 162). Thus, estimation of the species’ niche (see below) and climate data (see sidebar, Improved Climate Data and Models) are required. There are two paradigms or approaches to SDMs, which can be broadly characterized as statistical or correlative, versus mechanistic or process-based (37, 155). In both cases, geographic areas are classified as being more or less suitable and potential presence is assumed when suitability exceeds a particular threshold. Advocates of these two paradigms have engaged in heated debate (73, 145) and the use of forceful language (154), but there appears to be no reason to elevate one over the other so long as the strengths and weaknesses of each are understood and appreciated (37).

The correlative approach, exemplified by methods such as MaxEnt (114) and BIOCLIM (17), uses statistical relationships between the known species distribution and environmental (often

IMPROVED CLIMATE DATA AND MODELS

Bioclimatic species distribution models require climate observations and projections at high spatial and temporal resolutions. Updated versions of existing gridded climate data sets and new products include CRUTEM4 (67), HadCRUT4 (101), CRU TS3.10 (55), GISTEMP (54), and Global Precipitation Climatology Center (GPCC) precipitation data (14). The Global Historical Climatology Network (GHCN) used in many gridded products was itself updated in 2011 (80). The European Center for Medium-Range Weather Forecasts (ECMWF) ERA-Interim reanalysis provides high-resolution four-dimensional (i.e., including atmospheric layers) data, incorporating many ground-based, airborne, and satellite-derived data sets (31). A 30-arcsecond climatology has been published by researchers at the University of Oregon (100, 103). The new CliMond climatology database using 10-arcminute and 30-arcminute resolution (76) has improved on the popular WorldClim database (58) by incorporating an additional set of 16 BIOCLIM variables, including radiation and moisture measures. CliMond also provides projections of future climates to 2080, using outputs of two older global circulation models (GCMs). However, GCMs and future greenhouse gas emissions scenarios have now been updated for publication in the IPCC Fifth Assessment Report (62). Four new representative concentration pathways (RCPs) have replaced the Special Report on Emissions Scenarios (SRES) (104, 141). Interested readers can find information on the growing number of climate databases available in the Climate Data Guide (105).

climatic) variables to estimate the suitability of other sites based on their similarity to regions where the species already exists. Projections of changing climates can then be used to estimate how suitable different regions will become and how ranges are likely to develop (39, 40). However, extrapolation from nonequilibrium distributions must be treated with caution because the current distribution may not accurately reflect that of the potential distribution (39). Broad-scale climate classifications, like the Köppen-Geiger climate zones (143), could indicate where the largest changes are likely to occur. For example, the Cfb (warm temperate, fully humid, warm summer) climate zone found primarily in western Europe and southern Australia covered 2.46% of the global land surface around 1900, 2.62% around the year 2000, and under a high emissions scenario could cover 2.54% by 2100 (143).

The mechanistic approach uses ecophysiological models of varying complexity, describing organismal responses to environmental conditions that can either be determined experimentally or inferred from known distributions (75), and have been widely applied to CPPs (19, 50, 79, 83). For example, the CLIMEX model uses 19 parameters describing growth and stress responses to temperature and moisture (75), whereas a model of fungal infection probability uses three temperature variables and one moisture variable (97). CLIMEX has proved particularly popular in the projections of climate change impacts on CPP range shifts (16, 72, 75, 109).

Fungal pathogen responses to climate change are commonly studied because of the great importance of this group to agriculture (44). For plant-pathogenic fungi and oomycetes, moisture is critical to the infection process and, in particular, for foliar pathogens that require certain durations of leaf wetness in order to develop and invade the host (51, 79, 97). This introduces greater uncertainty into projections, first because of the greater complexity in modeling the global water cycle than in modeling temperature change (62) and second because leaf wetness duration (LWD) is not an output of observational data sets or climate models and must be inferred from temperature, humidity, and precipitation (20). Further, infection models require LWD at subdaily, usually hourly, resolutions, and so climate data at coarser resolutions require downscaling (e.g., 79). As an example, *Puccinia psidii*, the fungus that causes guava rust (also known as eucalyptus rust or myrtle rust) (75), has been modeled with both correlative and mechanistic approaches.

The NAPPFAST (NCSU APHIS Plant Pest Forecasting System) model used an average daily temperature of 13–33°C and 5–25 wet days per month, with suitability expected if three or more months met these conditions (96). MaxEnt models were fitted to seven temperature and humidity parameters for different taxonomic subsets of the *P. psidii* species complex (41). CLIMEX model parameters derived from the known distribution (excluding Asian and Australian observations for model validation) were supplemented by ecophysiological observations and laboratory data on the temperature response of spore germination (75). All three approaches gave qualitatively similar results, predicting that *P. psidii* could establish and persist in central and parts of southern Africa, Southeast Asia, and the eastern coast of Australia, as well as the native range. Kriticos et al. (75) pondered the lack of *P. psidii* observations in central Africa, given the large areas that appear to be climatically suitable. In fact, *P. psidii* was discovered on a garden plant in KwaZulu-Natal Province, South Africa, in the same month that their study was published (142).

SDMs give varying results for future distributions of CPPs, depending on the climatic preferences of the model species and the climate projections employed for mapping. Unfortunately, many model results are presented without estimates of uncertainties or sensitivity analyses to test how outputs respond to variation in parameters (18). Models are often validated by perceived congruity between the output and the known distribution, without formal statistical model comparison between models of differing complexity or parameterization. For example, recent projections for six soilborne fungal pathogens in Europe did not consider uncertainty in climate projections or in model parameterization, gave no estimates of uncertainty in model outputs, and did not compare outputs with current distributions (99). Such tests are vital if SDMs are to provide an honest assessment of the likely future ranges of CPPs.

CLIMATE CHANGE AND THE COLORADO POTATO BEETLE

As a case study of observational data and modeling, I review recent research on the Colorado potato beetle (CPB; *Leptinotarsa decemlineata*, Chrysomelidae), an important pest of potato crops that has spread across much of the Northern Hemisphere (3). The latitudinal spread of the CPB has been linked to global warming (116, 148), and the beetle therefore serves as an example of how climate change could affect CPP distributions. The CPB likely originated in the mountainous regions of the southwestern United States, expanded its host range to potato early in the nineteenth century, and by 1880 had reached the East Coast of the United States. The CPB arrived in France in 1922 and invaded most European and Central Asian countries by 1950. The CPB reached China from Kazakhstan in the 1990s and by 2010 was found across the whole of Russia, as far east as the Kamchatka Peninsula (88). The CPB has migrated eastward across China at peak dispersal rates of up to 226 km per year (mean: up to 45 km per year), perhaps assisted by strong westerly winds during the beetle's migration period (88).

Although the longitudinal spread of the CPB across both North America and Asia has been rapid and is essentially complete, the distribution appears to be latitudinally restricted. The United Kingdom, Scandinavia, and Russian territory above 61°N remain free of the beetle, despite evidence of numerous unsuccessful invasions and perhaps because of rigorous quarantine and eradication efforts (52). Beetle survival does not appear to be affected by cold weather during the growing season (93). Rather, the number of generations per year increases with temperature, with each generation requiring around 400 growing degree days (>10°C) (68, 116, 164). In Estonia, for example, the CPB produced a distinct second generation during 2010, perhaps for the first time since entering the country in 1965 (57). The beetle has historically caused little significant economic loss in Estonia due to the cold winters, but by the 1980s some beetles were able to overwinter in the southern part of the country, and by 2002 a permanent overwintering population

was established. Very hot weather also limits the distribution. In China, the boundary between presence and absence closely follows the -8°C isotherm of mean monthly minimum temperature in winter, whereas very high summer temperatures appear to have limited spread in some parts of Xinjiang Province (85).

The temperature dependence of the CPB has motivated numerous studies on the potential effect of climate change on future distributions (68, 72, 116, 136, 159). In general, models predict an increase in the number of generations per year as the planet warms and consequently a poleward shift in the distribution in Eurasia, but results are highly sensitive to the climate model used. However, there is a universal lack of rigorous sensitivity analyses, which are required to quantify the reliability of the projections (74). The rapid spread of the CPB allows comparison of model projections with reality. Almost a quarter of a century ago, Sutherst et al. (157) modeled the potential range and voltinism (the number of generations per year) across Europe and Asia, using the known North American distribution to derive growth and stress parameters for the CLIMEX model. The model suggested that, under the current climate, southern Europe should support up to six generations and central Europe one or two generations, with Scandinavia being largely unsuitable for the CPB. These predictions have been largely borne out, except that the greatest number of generations observed in warmer parts of Italy and the Caucasus is three rather than six (164). The potential distribution in East Asia, specifically China, was also estimated (**Figure 2**). In this case, the deviation of the observed spread of the CPB from the model projections is great. Sutherst et al. (136) predicted that the CPB would be unable to establish in Turkey, Iran, and Iraq, with low suitability values in Turkmenistan, Uzbekistan, and Tajikistan. Kazakhstan, southern Russia, northwest China, and Mongolia were also found to be unsuitable, but the Himalayas, parts of southern India, eastern and southern China, and much of Southeast Asia were predicted to be highly suitable. In reality, the beetle has spread rapidly through Central Asia, including Kazakhstan and southern Russia, and entered Xinjiang Province, China, from Kazakhstan around 1992 (85, 88).

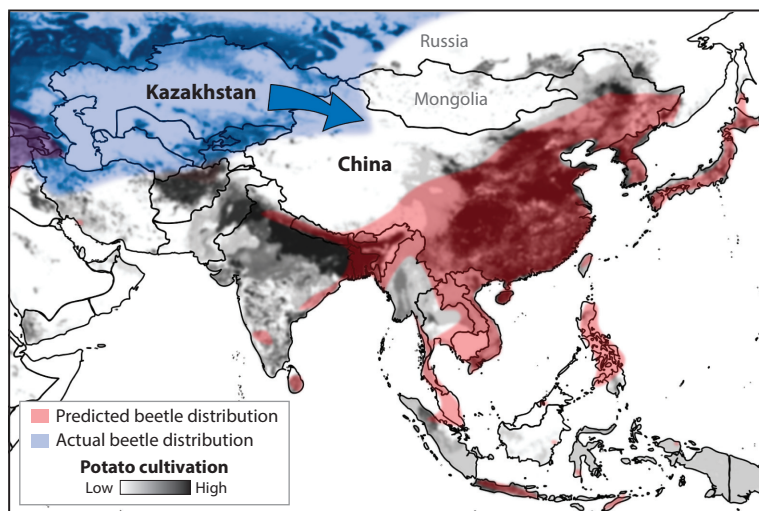


Figure 2

Invasion of the Colorado potato beetle (CPB) into China (CN) from Kazakhstan (KH) occurred around 1992 (*blue arrow*). A CLIMEX model (157) predicted high suitability of eastern China and other parts of Asia for the CPB (*red zones*), excluding Kazakhstan and western China. The actual distribution of the beetle (*blue zone*) did not overlap with these predictions.

Use of the CLIMEX model for pest risk assessment would have led to entirely erroneous targeting of monitoring or quarantine measures in this instance, as the predicted ecoclimatic suitability zone barely overlaps with the realized distribution. This example illustrates that, for an adaptable species like the CPB, the results of even sophisticated process-based models like CLIMEX must be treated with caution.

One reason for the difficulty in projecting future distributions is that the CPB has shown itself to be highly adaptable, rapidly evolving resistance to pesticides and the ability to thrive in novel climates. An important outcome of experimental studies has been the key role of behavioral, rather than physiological, adaptation to cooler conditions. A key feature of the CPB life cycle is the winter diapause, or hibernation, triggered by low temperatures or short days (57, 63, 81, 115). Mature larvae then fall to the ground and burrow into the soil, pupating and overwintering at depths of up to 50 cm. This behavior is triggered by either cooler temperatures or shorter day lengths. In Scandinavia, for example, diapause in the model is triggered by a day length threshold of 15 h or mean daily temperature less than 12°C for longer than one week, and the critical day length for diapause increases with latitude (68). Early entry into diapause is important for survival at the northern range limit (115) but is a recent adaptation apparently absent from beetles in the native range (64). Although beetles from different regions do not differ in the temperature at which they freeze, beetles from the native range (Mexico) climbed out of the soil when buried at the start of winter, and subsequently perished, whereas those from further north dug deeper and survived (64). Behavioral differentiation has also been found in Eurasian populations. Beetles sampled from Italy burrow less frequently than those sampled from Poland and Russia (81). Some differentiation in the physiological response to day length has been detected between Italian and Russian populations. In particular, expression of genes related to energy metabolism and stress tolerance indicates that Russian beetles prepare for diapause even under long day lengths (82).

Host effects must also be considered. For example, potato plants exposed to short day cycles (eight hours of light) contained more nitrogen, and beetles feeding on these plants were more likely to enter diapause even when kept at long day lengths (63). Whether this effect is driven by recognition of a short day length biochemical signal by the beetle or due to the altered nutritional quality of the host is not known.

Although models have suggested a likely increase in the damage wrought by the CPB, there have been enough surprises to warn that future impacts cannot be easily predicted. In terms of expanding range, warm regions may become inhospitable, but the potential impact of further ingress into China is grave. It is hoped that a region known as the Hexi Corridor in neighboring Gansu Province, which has very cold winter soil temperatures, will help to block the spread of the CPB to the warmer east (85). Northward spread is of less concern; less than 0.5% of the world's potato growing area is found above 61°N (118), and permafrost is likely to prevent further northern expansion of potato production in the near future. Hence, future changes in CPB activity, specifically voltinicity, at lower latitudes are likely to be of greater importance than further latitudinal range expansion.

BIOGEOGRAPHY AND THE ECOLOGICAL NICHE

Statistical analyses of observed distributions and predictive models have investigated the many different drivers and interactions determining CPP distributions and threat, but a heuristic framework for synthesis has been lacking (24). Here, I suggest that recent advances in ecological niche theory and biogeography may provide this framework. Biogeography is the study of species distributions in time and space. CPP distributions are therefore the proper subject of biogeographical

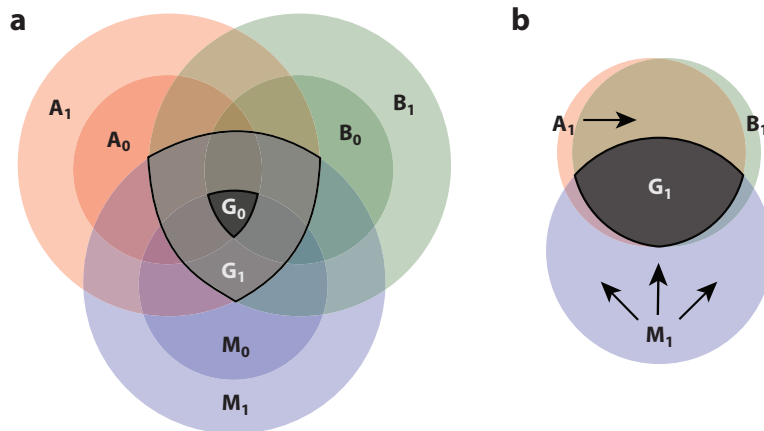


Figure 3

The biotic-abiotic-migration (BAM) framework relating niches to geographic distributions of crop pests and pathogens (CPPs) (149–151). (a) The region A_0 represents the geographic area in which abiotic conditions required for population growth occur. If the species adapts to new conditions, this region can evolve (A_1). B_0 represents the geographic region in which biotic conditions required for population growth occur. In the case of crop pests and pathogens (CPPs), this can be interpreted as the distribution of the host crops. If more crops are planted, or the CPP evolves a wider host range, then this region grows (B_1). M_0 represents the region that a species is capable of reaching by dispersal. Human activities have increased dispersal for many CPPs (M_1). G_0 is actual geographical distribution of the CPP species, defined by $A_0 \cap B_0 \cap M_0$. If the species adapts, increases its host range, and is introduced to a wider area, the distribution increases to G_1 . (b) The climatic preferences of a pest are likely to evolve toward those of a host, such that A_1 and B_1 will eventually overlap. Eventually, anthropogenic introductions introduce a pest to all regions, such that M_1 completely covers $A_1 \cap B_1$.

analysis, and recent developments in the theory of biogeography may help to frame discussion on how climate change can affect CPP distributions.

The relationships between climate, resource availability, ecological interactions, and dispersal in determining distributions have been distilled in the biotic-abiotic-migration (BAM) framework of Soberón and colleagues (149–151). In the BAM framework, A is defined as the region in geographic space where abiotic conditions that define the species' fundamental niche exist (**Figure 3**). These abiotic conditions are determined by nonconsumable, noninteractive environmental factors that generally vary over large spatial scales and are primarily climatic variables (113). Soberón and colleagues equate these abiotic factors with G . Evelyn Hutchinson's scenopoetic variables that describe a multidimensional space of environmental conditions, and the determinants of Joseph Grinnell's niche concept as a habitat requirement. B is defined as the geographical region where biotic conditions, such as competition, availability of prey, and predation, allow the existence of viable populations. These biotic conditions tend to vary over smaller spatial scales and can be dynamically dependent on the species itself, as would be the case for a consumable resource (113). Soberón and colleagues relate B to Charles Elton's niche concept as the interactions of a species with other species, and to Hutchinson's bionomic variables that describe resources affected by the species. M is defined as the region accessible to colonization. The intersection $A \cap B \cap M$ is the region that is actually occupied, and changes in the size or shape of any component can alter the geographical range of the species. The intersection $A \cap B \cap M$, when projected back into niche space, will give a subset of the fundamental niche termed the realized niche, i.e., those environmental conditions actually experienced by a species in nature. BAM therefore clarifies the relationship between

the ecological niche and geographic space, i.e., Hutchinson's duality (29), and provides a useful conceptual model for considering how climate change and other factors might limit distribution.

The most important outcome of considering CPP distributions in the BAM framework is the acknowledgment that SDMs, in particular those parameterized from known distributions, cannot recover the fundamental niche, as reprojection of conditions in the current distribution are likely a small subset of the abiotic conditions conducive to population growth (29, 150). Reprojecting the realized niche back into geographic space, particularly for future climates, is unlikely to give an unbiased estimate of the distribution. Process-based models should be parameterized from experimental data or from biophysical first principles if the fundamental niche is to be estimated (70). However, there is no guarantee that the resulting model is an accurate reflection of the fundamental niche, as there may be several models that equally fit the data (37). Another consideration, rarely acknowledged in SDM, is that species evolve and adapt to new conditions. This can happen very quickly with CPPs. The fungal pathogen *Z. tritici*, for example, has shown rapid temperature acclimation across geographic regions (167). Parameterization of the CLIMEX model from the native and invaded distributions of an invasive weed gave widely differing results for the potential range (162). In terms of BAM, this means that when M expands to overlap more of B, adaptation increases the area of A to match. Expansion of M can alter understanding of A and B. For example, establishment of *P. psidii* in Australia has added more than one hundred species, primarily *Eucalyptus* spp. in family Myrtaceae, to the known host range of the pathogen (23, 102).

For most wild species, the ecological milieu of competition, predation, parasitism, and food availability is highly complex and variable in space and time. Estimation of B is thus extremely difficult and rarely attempted (149, 150). In contrast, CPPs inhabit simplified agricultural ecosystems in which biological diversity has been reduced by management, most obviously in plants and animals, but also potentially in soil microbes (84). Therefore, the network of biotic interactions in which CPPs take part is also likely to be simplified. Although there are some records of successful biological control of agricultural pests, these are rare, and we can therefore approximate the CPP population as being controlled from the bottom up by their host crops. B is large for CPPs that attack widely grown hosts or have wide host ranges but could reduce in size if management, pesticides, or resistant varieties reduce host availability, and could grow again if virulence emerges. In a few cases, we have seen B decrease in size owing to the impact of CPPs, for example, in the cessation of coffee cultivation in Sri Lanka in the nineteenth century following devastation by coffee rust (*Hemileia vastatrix*). B will also change if agricultural crop ranges shift in response to climate change (15, 161) or atmospheric carbon dioxide concentration (5). So far, few studies have attempted to integrate host availability into CPP distribution models under climate change. Combined projections for the soybean and the bean leaf beetle (*Cerotoma trifurcata*) using the CLIMEX model indicate that host distribution will limit the potential pest distribution (16). This is because, despite the wide climatic tolerances of soybean (due in part to breeding of cultivars for different climates), the temperature range of the beetle, a generalist feeding on numerous hosts, is even wider. A useful feature of CLIMEX is the ability to consider both potential for growth during the growing season and survival during stressful periods (e.g., 75), because CPPs must endure overwintering conditions, whereas annual crops are replanted each year. This may prevent A from evolving to overlap B.

The region M is that which is accessible to a species, and consideration of the effect of M on A and B is crucial to SDM but widely ignored (10). For many pests, pathogens, and other invasive species, M has grown because of human activities like trade and transport (7, 11) but can be restricted by careful quarantine and sanitation measures (94). Epidemiological models of likely spread have been developed and could be further refined by inclusion of data on trade and transport routes, wind direction, and dispersal behavior (140).

CONCLUSIONS

Although the evidence for global warming and climate change is undeniable, and latitudinal range shifts have been observed for many species over the twentieth century, the impact on the ranges of CPPs remains largely speculative. There appear to be no studies that compare modeled changes in CPP distributions over the twentieth century with climate change and other drivers, but given that average global temperature has increased by nearly 1°C over the past century it is surprising that the scientific evidence for an effect of warming on CPP distributions is not stronger. Increased migration via human activities is establishing CPPs wherever their hosts are found, assisted by adaptive evolution to exploit novel conditions. This may be because of the lack of a high-quality historical time series of distributions (24, 66). The BAM framework linking ecological niche theory to biogeography illustrates the gap between current SDM approaches to predicting future distributions, with the requirement to estimate dispersal (M) and biotic factors (B) in order to obtain the intersection of these three elements. The responses of crops and crop-pest interactions to climate change and carbon dioxide enrichment are likely to be great and should not be ignored. The ability of the CPB to adapt and its unexpected route of migration into China illustrate the necessity of considering all three BAM dimensions simultaneously. The relative simplicity of agroecosystems and the availability of data on dispersal drivers (e.g., trade routes) make this an achievable goal. The ability of CPPs to evolve tolerance to novel climates has been investigated in a few species but has not been considered in distribution models. Further research on the limits of adaptation, particularly on overwintering survival when crops are not present, is required. Improvements in monitoring and identification of CPPs, particularly in the developing world, are urgently required both for research and to secure food production.

SUMMARY POINTS

1. The distributions of pests and pathogens of agricultural crops are expanding rapidly.
2. Range expansion is primarily due to increased dispersal through human activities.
3. Despite significant global warming over the twentieth century, the evidence for latitudinal range shifts of pests and pathogens remains largely speculative, in part because of incomplete and biased historical data sets.
4. SDMs based on bioclimatic variables predict significant changes in potential distributions in the coming century but give an incomplete understanding because they ignore host ranges, adaptation, and dispersal patterns.
5. Rapid behavioral adaptation and unexpected migration routes of the Colorado potato beetle across Eurasia illustrate the need to extend SDMs beyond climate.
6. The BAM framework provides a heuristic tool for improved projections of future distributions and likely routes of spread.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Errata

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