

Global threat to agriculture from invasive species

Dean R. Paini^{a,b,1}, Andy W. Sheppard^a, David C. Cook^{c,d}, Paul J. De Barro^e, Susan P. Worner^f, and Matthew B. Thomas^{g,h}

^aCommonwealth Scientific and Industrial Research Organization, Canberra, ACT 2601, Australia; ^bPlant Biosecurity Cooperative Research Centre, Bruce, ACT 2617, Australia; ^cDepartment of Agriculture and Food, Western Australia, Bunbury, WA 6230, Australia; ^dSchool of Agricultural and Resource Economics, The University of Western Australia, Crawley, WA 6009, Australia; ^eCommonwealth Scientific and Industrial Research Organization, Brisbane, QLD 4001, Australia; ^fBio-Protection Research Centre, Lincoln University, Lincoln 7647, New Zealand; ^gDepartment of Entomology, Penn State University, State College, PA 16802; and ^hCenter for Infectious Disease Dynamics, Penn State University, State College, PA 16802

Edited by Harold A. Mooney, Stanford University, Stanford, CA, and approved April 28, 2016 (received for review February 13, 2016)

Invasive species present significant threats to global agriculture, although how the magnitude and distribution of the threats vary between countries and regions remains unclear. Here, we present an analysis of almost 1,300 known invasive insect pests and pathogens, calculating the total potential cost of these species invading each of 124 countries of the world, as well as determining which countries present the greatest threat to the rest of the world given their trading partners and incumbent pool of invasive species. We find that countries vary in terms of potential threat from invasive species and also their role as potential sources, with apparently similar countries sometimes varying markedly depending on specifics of agricultural commodities and trade patterns. Overall, the biggest agricultural producers (China and the United States) could experience the greatest absolute cost from further species invasions. However, developing countries, in particular, Sub-Saharan African countries, appear most vulnerable in relative terms. Furthermore, China and the United States represent the greatest potential sources of invasive species for the rest of the world. The analysis reveals considerable scope for ongoing redistribution of known invasive pests and highlights the need for international cooperation to slow their spread.

NIS | insect pests | fungal pathogens | trade

Invasive species are a major cause of crop loss and can adversely affect food security (1). In the United States alone, crop and forest production losses from invasive insects and pathogens have been estimated at almost US\$40 billion per year (2). With increased globalization and connectedness via world trade, the threat from invasive species arriving to countries in which they were previously absent is expected to increase (3, 4). To quantify this threat and develop effective biosecurity policy requires an understanding of the sources of potential pests and pathogens, their likelihood of arriving at a particular location, their likelihood of establishment upon arrival, and an estimate of their possible impact. Numerous studies have modeled arrival and/or establishment (5, 6) of invasive species, often with a focus on the threat from individual species to a particular country. A few studies have considered establishment of broader species assemblages (7–11) but, again, typically from an individual country-level perspective. To date, there has been no evaluation of total invasion threat and its potential cost to agricultural crop production from a global pool of potential invasive species considering all countries at risk. Such an analysis would be valuable as it not only identifies those countries most vulnerable to invasion by this global pool of invasive species but also those countries that present the greatest threat to the rest of the world given their current trade patterns and the pests they already have present.

We define invasion threat as the product of arrival likelihood (i.e., the chances of a particular pest or pathogen arriving in a new location) and establishment likelihood (i.e., the chances of a particular pest or pathogen establishing in a new location once it has arrived). Quantifying the many potential pathways by which multiple invasive species could arrive at a particular country is extremely challenging. However, the numbers of invasive species in a region or country have consistently been shown to be related to gross levels of trade (4, 12–16). Accordingly, we used the value

of each country's annual mean (2000–2009) importation (in millions of US dollars) from each trading partner as a proportion of total imports from all trading partners (17) as a proxy for species arrival likelihood. For establishment likelihood, we analyzed the worldwide distribution of the almost 1,300 insect pests and fungal pathogens (18) using a self-organizing map (SOM), which analyses pest assemblages and pest associations to generate establishment indices for all species, for all countries included in the dataset (8, 10). The pest assemblage present in a location captures the biotic and abiotic characteristics of that location and serves as a proxy measure for those variables. To illustrate, a location that has a humid climate will have present a collection of pests and pathogens that can only survive there because the abiotic characteristics (such as temperature and humidity) are suitable. If two locations (A and B) have similar assemblages, then they are likely to have similar biotic and abiotic conditions. If location A has species 1–10 and location B has species 1–9, then it is reasonable to assume that species 10 has a high likelihood of establishing in location B. The SOM is able to assess the similarity between locations (in this case, countries) based on species assemblages for all countries simultaneously, generating establishment indices for all species in all locations in which they are not currently present. This method has been shown to be resilient to significant errors in species distributional data (19) and highly effective at ranking those species that can establish in a region above those that cannot (20).

For each country, we obtained mean annual crop production values (2000–2009) (21) for the most important crops grown (i.e., those crops that comprised approximately the top 75% of the total value of agricultural production for the country). For every

Significance

A key scientific and policy challenge relating to invasive species at the world level is to understand and predict which countries are most vulnerable to the threat of invasive species. We present an analysis of the threat from almost 1,300 agricultural invasive species to the world (124 countries). The analysis examines the global distribution of these species, international trade flows, and each country's main agricultural production crops, to determine potential invasion and impact of these invasive species. We found the most vulnerable countries to be from Sub-Saharan Africa, while those countries representing the greatest threat to the rest of the world (given the invasive species they already contain, and their trade patterns) to be the United States and China.

Author contributions: D.R.P., A.W.S., D.C.C., P.J.D.B., S.P.W., and M.B.T. designed research; D.R.P. performed research; D.R.P. and D.C.C. contributed new reagents/analytic tools; D.R.P. analyzed data; and D.R.P., A.W.S., D.C.C., P.J.D.B., S.P.W., and M.B.T. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

¹To whom correspondence should be addressed. Email: Dean.Paini@csiro.au.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1602205113/-DCSupplemental.

pest and pathogen species in the analysis, we calculated the invasion threat to a particular country only if that country grew an agricultural crop that was a known host of that pest or pathogen species and that species was not already present in the country. The invasion threat (IT_{ps}) of one species, p , from one source country, s , to a recipient (or threatened) country, t , was calculated as the product of the arrival and establishment indices. We calculated the total invasion threat (TT_{tp}) of one species, p , from all possible source countries to a given threatened country, t (*SI Appendix, Fig. S1*). We then combined the TT values for all species to calculate an overall invasion threat (OT_t) to a country, t , incorporating all pests and pathogens from all possible source countries (trading partners).

Having defined the threat from invasive species to a country, we then calculated the potential cost from invasive pests and pathogens on each crop, c , in each country, t (crop invasion cost— CIC_{tc}). It was not possible to determine the potential impact of all species in all countries as such data are not available. As an alternative, we obtained the maximum reported percentage impact for 140 species (of the 1,297 species in our analysis) on one of its main agricultural hosts. We assumed this represented the range of possible impacts of all species in our dataset. For each species, p , and each crop, c , and in each country, t , we sampled from this range 100 times (with replacement) to get a mean potential impact (MI_{pct}). We therefore generated more than 37,000 unique mean potential impact values, for each possible combination of species, crop, and country. The mean was then multiplied by the TT_{tp} and the value of the crop in that country to generate the potential financial impact of that pest on that crop in that country. This was

subsequently summed over all pests and all crops to determine the total invasion cost (TIC_t) to that country.

We were also able to identify not just threatened countries, which have the most to lose from these invasive species, but also those countries that represent the greatest threat to the rest of the world, given their trade patterns and the invasive species they already have present within their borders. To estimate source-TIC (TIC_s) for an individual source country, s , we followed a similar method used to generate TIC_t for threatened countries, except we used the crop data of countries they export to and those invasive species present within their own country, which could spread to trading countries.

Results

Invasion Threat. We found that 40 of the 124 countries assessed (32%) had a likelihood index of being invaded (OT_t) by any one insect or pathogen species greater than 0.80 (Fig. 1A and *SI Appendix, Table S1*). Only 10 countries (8%) had OT_t values <0.4 .

Invasion Cost. As expected, countries that are large agricultural producers such as China, United States, India, and Brazil exhibit the highest potential cost from these 1,297 invasive species (Fig. 1B and *SI Appendix, Table S2*). However, the economic significance of an invasive species following introduction will likely depend not only on the value of the threatened commodity but also the ability to manage or mitigate the impact via means such as pest management, plant breeding, crop substitutions, imports, or subsidies (22). To provide an estimate of this relative cost, we divided a country's TIC_t by its mean gross domestic product

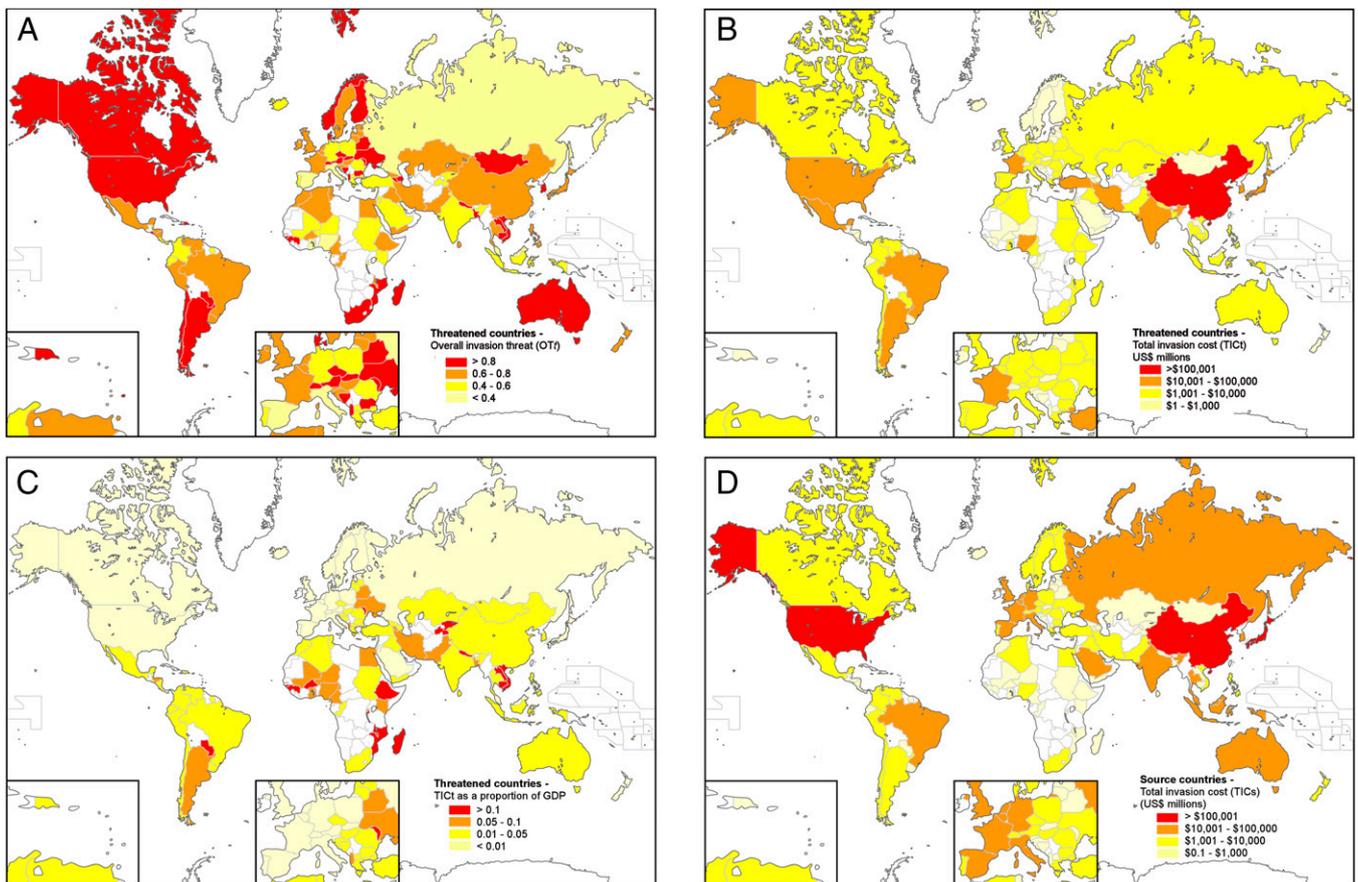


Fig. 1. World map representation of model outputs. (A) The overall invasion threat (OT_t) to each threatened country, t ; (B) the total invasion cost (TIC_t) (in millions of US dollars) to threatened countries; (C) the total invasion cost (TIC_t) (in millions of US dollars) to threatened countries, as a proportion of GDP; and (D) the total invasion cost (TIC_s) (in millions of US dollars) from source countries, s . Those countries without color were not included in the analysis.

(GDP) (2000–2009) (23) [our assumption being that countries in which TIC_i represents a larger proportion of GDP will be more vulnerable to invasive species impacts (22)]. Countries with the largest TIC_i values relative to GDP (countries in red, Fig. 1C) were all developing countries, with the top 6 countries most at risk (and 11 of the top 20) all located in Sub-Saharan Africa (Fig. 1C and *SI Appendix, Table S3*).

Source Countries. As with the rankings by TIC_s , we found that China and the United States ranked first and second as potential source countries (Fig. 1D and *SI Appendix, Table S4*). Furthermore, exactly one-half (10) of the countries ranked in the top 20 source countries were also ranked in the top 20 for threatened countries (Fig. 1B and *SI Appendix, Table S2*).

Discussion

We saw little pattern in which countries had higher or lower OT_i values, indicating the complex interplay between the types of crops grown in a country, the level of trade with other countries, and the particular invasive species present in those trading countries. For example, neighboring countries can have surprisingly different OT_i values. Italy has a low OT_i , whereas its immediate neighbors, Switzerland and Austria, both have high OT_i values (Fig. 1A and *SI Appendix, Table S1*), despite Italy's importing approximately twice the value of either Switzerland or Austria (IT = \$371,349M, CH = \$151,835M, AT = \$188,494M). This is partly driven by the fact that fewer invasive species threaten Italy (IT = 147, CH = 170, AT = 264), but also by the particular species that are threatening (and their establishment indices), as well as the different trading partners of these countries. Furthermore, although it would be expected that import dollars will strongly influence a country's TIC_s , we found a number of examples where this is not the case. India and Sweden have similar mean import dollars (\$138,542M and \$109,479M, respectively), but very different TIC_s values (Fig. 1B and *SI Appendix, Table S2*), as a result of the number of species threatening each country (190 and 58, respectively), which is a function of the crops grown and the invasive species present in trading countries. Finally, examining TIC_s shows that, although export dollars can influence a country's TIC_s value, it can also be the number of threatening invasive species. Mexico and Pakistan have very different TIC_s values (Fig. 1D and *SI Appendix, Table S4*) but similar numbers of invasive species present (379 and 377, respectively). The difference in TIC_s values for these two countries is influenced by the large differences in mean export dollars (\$217,484M and \$12,464M, respectively). Alternatively, India and Czech Republic have similar mean export dollars (\$97,034M and \$86,478M), yet different TIC_s values (Fig. 1D and *SI Appendix, Table S4*), driven by large differences in the number of invasive species present in each country (627 and 212, respectively).

Despite these apparent complex interactions, when examining TIC_i as a proportion of GDP, countries in Sub-Saharan Africa were clearly identified as the most vulnerable to the potential impact of invasion by the agricultural pests and pathogens included in this analysis. These countries (and many of the highly ranked developing countries) generally do not have diverse economic industries and are subsequently disproportionately more dependent on agriculture (24). As a result, any threat from invasive species can potentially have a greater relative impact on these countries. Wealthy regions where agricultural activity represents a smaller proportion of GDP have a much smaller relative TIC_i , even where invasion threat is large. To illustrate, North American and Scandinavian countries all have a high OT_i (Fig. 1A), yet, when potential impact (TIC_i) as a proportion of GDP is considered (Fig. 1C), these countries are placed in the lowest category.

The United States and China were identified as the two most important source countries to the rest of the world. These countries are characterized by large and diverse trade volumes and

have been confirmed as network hubs in the international agro-food trade network (25). They also have diverse agroecosystems and host a substantial number (52% and 56%, respectively) of the pool of invasive pests and pathogens, more than any other country in this analysis. As such, they can be considered central nodes in the worldwide network of invasive species spread. Other countries, such as Japan, Germany, France, and Republic of Korea, also ranked highly as potential source countries [Germany and France have also been identified as network hubs (25)]. At the other end of the scale, numerous developing countries ranked low as potential sources of invasive species. This contrasts to their position as generally the most vulnerable countries to invasion as a function of GDP (Fig. 1C).

Uncertainties are an intrinsic feature of any model-based assessment of ecological invasions (26), and it is important to quantify the impact of these uncertainties in any model outputs. There were four key parameters in our model (arrival index, establishment index, mean potential impact, and crop production value), and we examined their impact on TIC for both threatened and source countries (TIC_i and TIC_s , respectively).

We found little change in the rankings with the introduction of these errors (*SI Appendix, Figs. S2–S9*). We also found only small changes in TIC_i and TIC_s values. The largest change was a decrease in TIC_i for Mongolia by 16% with the introduction of uncertainty to mean annual crop value, although this country's ranking only dropped by one place as a result (from 111 to 112). Overall, the mean change in TIC_i and TIC_s varied from 0.24% to 3.94% depending on the type of uncertainty introduced (i.e., arrival index, establishment index, mean potential impact, or mean annual crop value) (*SI Appendix, Table S5*).

Predicting invasion by a species with no known invasion history or with no previous pest impact is extremely challenging because they are likely to be unknown before invasion of the new region. However, the invasive species assessed here are a substantial subset of the known global species pool of economically significant pests. We would therefore expect the patterns revealed in this analysis to be robust to the inclusion of more species.

The presence/absence data used in the Centre for Agriculture and Bioscience International (CABI) Crop Protection Compendium (CPC) include species that may be recorded in a country from a restricted range (one location only) up to a widespread range. As such, we have not been able to consider whether a species establishes and does not spread or if there is a lag phase before spread. Our predictions therefore only consider whether a species can establish in a country and not the more complex dynamic invasion processes that could follow. Furthermore, predicting the impact of an individual pest species is extremely challenging due to spatial and temporal uncertainty. The same pest species can have a major impact in one location yet a minor impact in another. The rate of spread of a pest species will also influence any economic impact assessment. Accordingly, we feel our use of mean potential impact drawn from the range of reported impacts for a subsample of species in this analysis is a parsimonious approach to analyzing global patterns.

To our knowledge, this is the first analysis summarizing the invasive species threat to global crop production on a country-by-country basis. We find that far from being “saturated” or “homogenized,” many countries are open to substantial ongoing threat of invasion from known pests and/or pathogens. Countries that are large crop producers are most at risk in absolute terms, whereas numerous developing countries are disproportionately vulnerable to invasion in relative terms. Countries with diverse commodities and/or large trade volumes are likely the greatest source of invasive pests and pathogens, whereas countries with developing economies likely play less of a role as sources of invasion. As trade volumes continue to increase and more trade connections are made between countries, the pressures from invasive species will only intensify. The formation of an international

body responsible for invasive species could not only enable the management of invasive species at the global scale but also provide those countries identified here as most vulnerable, with the information, and possibly the resources necessary to protect their borders and limit the further spread of invasive species (27).

Materials and Methods

Species and Country Data. Species data were extracted from the CABI CPC (18). Species in this database fall into one of two categories in terms of the quality of data (basic data sheets and full data sheets). Basic data sheets are generated by a process of data mining and have not been manually checked. Full data sheets have been written specifically for the compendium by a range of specialists. These full data sheets are then edited and checked by additional experts. Only those insect and fungal pathogen species in the database with a full data sheet available were extracted.

Countries were included in the analysis only if both crop data from the Food and Agriculture Organization of the United Nations (FAO) (21) and direction of trade data from the International Monetary Fund (17) were available. For some country-to-country combinations, no direction of trade data were available (e.g., Burkina Faso and Azerbaijan). These were relatively infrequent, and rather than remove both countries from the analysis, we assumed the value of trade between the two countries was zero.

Arrival Index. An arrival index was generated from direction of trade data (17), which has consistently been shown to be related to the number of invasive species in a country or region (4, 12–16). For each country, we generated a mean importation value (in millions of US dollars—normalized to 2011) from each trading partner over the period of 2000–2009. For each country, a proportion was generated by dividing the mean import value from the trading country by the mean total import value from all trading countries. This proportion was used as a proxy for likelihood of a species arriving at the threatened country over the course of 1 y.

Establishment Index. The species distribution for each of the 1,297 invasive species in 124 countries was extracted (18) and placed into a $124 \times 1,297$ matrix of 1's and 0's in which 1 represented a species being present in a country and 0 represented absence.

An SOM (28) was used to analyze this matrix. An SOM is a type of artificial neural network capable of converting high-dimensional data into a 2D map, pictorially showing which data points are most similar. The SOM therefore is a clustering method and full details can be obtained from refs. 10 and 28, but essentially each region occupies a multidimensional space determined by a vector of the presence/absence data. In this case, there are 1,297 species, so each region will have a 1,297 element vector made up of 1's (present) and 0's (absent) to determine its position in a 1,297-dimension space. The SOM is an elastic network of neurons that are projected into this multidimensional space and which interact with the regions. The vector that determines each neuron's position in this space is termed the neuron weight vector. The number of neurons in an SOM is partially determined by the heuristic rule, $5\sqrt{n}$, where n is the number of samples (in our case, this is 124 countries) (29). In addition, the two largest eigenvalues are calculated from the dataset, and the ratio of length and width of the SOM is set to those eigenvalues. Given this ratio, the final number of neurons is set as close as possible to the heuristic rule. The size of the map in this analysis was 9×6 (54 neurons), with the standard hexagonal configuration.

Although the initial projection of these neurons into the multidimensional space can be done randomly, a linear initialization is recommended, which aligns the SOM corresponding to the first two eigenvalues discussed above. This linear initialization significantly reduces the time required to complete the analysis because the neurons are arranged in a way that is more representative of the raw data (28).

When the analysis is initiated, each country is assessed and the closest neuron to this country in multidimensional space is identified as the best matching unit (BMU). The neuron weight vector of the BMU is adjusted so the neuron moves closer to the country. All countries are assessed simultaneously (batch algorithm). Because all neurons in the SOM are connected together similar to a large "elastic net," the process of one neuron moving closer to a country exerts a gravitational force that drags other neurons in the SOM with it. This gravitational effect is strongest on the nearest neurons to the BMU and decreases with neurons further away. The simultaneous analysis of all countries completes one iteration, and the recommended number of iterations is $500 \times$ number of neurons (for this analysis, $500 \times 54 = 27,000$). With each iteration, the gravitational effect of one neuron on neighboring neurons decreases and the distance a BMU is moved closer to a country also

decreases. As the analysis approaches the final iterations, the SOM spreads out to occupy approximately the same area that the countries occupy in the multidimensional space. When the analysis is complete, each country will be assigned to a BMU that is its closest neuron. Some countries will have the same BMU, because they have similar assemblages of invasive species and hence are found close to each other in the multidimensional space. Each of the 1,297 elements of the neuron weight vector of a BMU corresponds to each of the 1,297 invasive species in the analysis and will have a value between 0 and 1, which is a measure of the strength of association of the invasive species with the assemblage of invasive species of any country assigned to that BMU. The strength of association for a species can be interpreted as an index of establishment likelihood for that species in a region (10, 19, 20). On completion of the analysis, an establishment index can be determined for every species in every country included in the analysis.

Mean Crop Value. The mean annual value (2000–2009) of each agricultural crop (in millions of US dollars), for each of the 124 countries, was obtained from the FAO (21). For each country, crop categories were ranked by value and those crops that comprised the top 75% of total agricultural production were used. For each crop category, a list of the insect pests and fungal pathogens using that crop as a host was extracted from the CABI CPC (18). Some crop categories were too general to determine what species of crop was included (e.g., dry beans), whereas for other crop categories there was no information available in the CABI CPC (e.g., mushrooms and truffles). These crops were therefore omitted in the calculation of the top 75% of agricultural production.

Invasion Threat. The invasion threat, IT_{tps} , for each threatened country, t , for each invasive species, p , from each source country, s , conducting trade with the threatened country was calculated only if that invasive species was present in the source country, absent from the threatened country, and a known pest or pathogen of a crop grown in the threatened country:

$$IT_{tps} = A_{ts} E_{tp} \quad [1]$$

where A_{ts} is the arrival index of a species to a threatened country, t , from source country, s , and E_{tp} is the establishment index of species, p , in threatened country, t .

Threatened Countries. The TT_{tp} for a threatened country was calculated for one species, p , from all possible source countries, s , to a given threatened country, t :

$$TT_{tp} = 1 - \prod_s [1 - IT_{tps}] \quad [2]$$

In addition, the total invasion threat, TT_{tc} , from all species known to be a threat to a particular crop, c , grown in a threatened country, t , was calculated as follows:

$$TT_{tc} = 1 - \prod_p [1 - IT_{tps}] \quad [3]$$

The overall invasion threat, OT_t , was calculated for all species threatening any agricultural crop of a threatened country, t :

$$OT_t = 1 - \prod_p [1 - TT_{tp}] \quad [4]$$

Threatened Countries—Invasion Cost. Before estimating the invasion cost, we first estimated the potential impact of species, p , on crop, c , in country t . To do this, we searched the CABI CPC (30) and found the maximum reported percentage impact on crop production for 140 species. Damage estimates are not reported for most species and the 140 species were selected to include a representative diversity of pest taxa from the complete list, and to span the range of possible impacts any species could have on any crop in any country (*SI Appendix, Table S6*). For each species on each crop in each country, we sampled from this range 100 times (with replacement) and calculated the mean potential impact, MI_{pct} , generating more than 37,000 unique mean potential impact values.

The crop invasion cost, CIC_{tc} , of all invasive species that are known pests or pathogens of an agricultural crop, c , grown in a threatened country, t , was then calculated as follows:

$$CIC_{tc} = TT_{tc} MI_{pct} CV_{tc} \quad [5]$$

where CV_{tc} is the mean annual value of crop, c , in threatened country, t .

The total invasion cost for each threatened country, TIC_t , was calculated from the sum of CIC_{tc} , of all crops grown in the threatened country:

$$TIC_t = \sum_c [CIC_{tc}]. \quad [6]$$

Source Countries. The total invasion threat from all species found in a source country, TT_{sc} , to a particular crop, c , grown in a threatened country, t , was calculated as follows:

$$TT_{sc} = 1 - \prod_p [1 - IT_{tps}]. \quad [7]$$

Source Countries—Invasion Cost. The crop invasion cost from a source country, CIC_{sc} , of all invasive species that are known pests or pathogens found in the source country, s , and threatening an agricultural crop, c , grown in a threatened country, t was calculated as follows:

$$CIC_{sc} = TT_{sc} MI_{pct} CV_{tc}, \quad [8]$$

where CV_{tc} is the mean annual value of crop, c , in threatened country, t .

The total invasion cost from each source country, TIC_s , was calculated from the sum of CIC_{sc} , of all crops, c , grown in threatened countries:

$$TIC_s = \sum_c [CIC_{sc}]. \quad [9]$$

Uncertainty Analysis. We introduced an error rate separately to the four parameters used in the analysis (arrival index, establishment index, mean potential impact, and mean annual crop value) by multiplying the parameter value for each species in each country, by a randomly selected value from a uniform distribution between -0.2 and $+0.2$ and measured the change in TIC_t (for threatened countries) and TIC_s (for source countries). We compared the rankings of countries by TIC_t and TIC_s when these errors were introduced with the original rankings, using Spearman rank correlation.

ACKNOWLEDGMENTS. We thank Liam Thammavongsa and Richard Lamont for data processing and extraction; and Tom Harwood, Michael Hirsch, Sunil Singh, and Peter Caley for helpful discussions. Louise Morin, Mark Lonsdale, and Russ Wise made helpful comments on earlier versions of the manuscript. D.R.P. acknowledges the support of the Australian Government's Cooperative Research Centres Program (Grant CRCNPB 10184).

- Cook DC, et al. (2011) Biosecurity and yield improvement technologies are strategic complements in the fight against food insecurity. *PLoS One* 6(10):e26084.
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econ* 52(3):273–288.
- Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *J Appl Ecol* 46(1):10–18.
- Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. *Conserv Biol* 17(1):322–326.
- Bourdot GW, Lamoureaux SL, Watt MS, Manning LK, Kriticos DJ (2012) The potential global distribution of the invasive weed *Nassella neesiana* under current and future climates. *Biol Invasions* 14(8):1545–1556.
- Hill MP, Hoffmann AA, Macfadyen S, Umina PA, Elith J (2012) Understanding niche shifts: Using current and historical data to model the invasive redlegged earth mite, *Halotydeus destructor*. *Divers Distrib* 18(2):191–203.
- Bomford M, Kraus F, Barry SC, Lawrence E (2009) Predicting establishment success for alien reptiles and amphibians: A role for climate matching. *Biol Invasions* 11(3): 713–724.
- Paini DR, Worner SP, Cook DC, De Barro PJ, Thomas MB (2010) Threat of invasive pests from within national borders. *Nat Commun* 1:115.
- Thuiller W (2003) BIOMOD—optimizing predictions of species distributions and projecting potential future shifts under global change. *Glob Change Biol* 9(10):1353–1362.
- Worner SP, Gevrey M (2006) Modelling global insect pest species assemblages to determine risk of invasion. *J Appl Ecol* 43(5):858–867.
- Thuiller W, et al. (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Glob Change Biol* 11(12):2234–2250.
- Dalmazzone S (2000) Economic factors affecting the vulnerability to biological invasions. *The Economics of Biological Invasions*, eds Perrings C, Williamson MH, Dalmazzone S (Edward Elgar, Cheltenham, UK), pp 17–30.
- Vila M, Pujadas J (2001) Land-use and socio-economic correlates of plant invasions in European and North African countries. *Biol Conserv* 100(3):397–401.
- Westphal MI, Browne M, MacKinnon K, Noble I (2008) The link between international trade and the global distribution of invasive alien species. *Biol Invasions* 10(4):391–398.
- Marini L, et al. (2011) Exploring associations between international trade and environmental factors with establishment patterns of exotic Scolytinae. *Biol Invasions* 13(10):2275–2288.
- Desprez-Loustau ML (2009) Alien fungi of Europe. *Handbook of Alien Species in Europe*, ed Drake JA (Springer, Berlin).
- International Monetary Fund (2011) *IMF Direction of Trade Statistics* (International Monetary Fund, Washington, DC).
- Centre for Agriculture and Bioscience International (2007) *CAB International Crop Protection Compendium* (Centre for Agriculture and Bioscience International, Wallingford, Oxfordshire, UK).
- Paini DR, Worner SP, Cook DC, De Barro PJ, Thomas MB (2010) Using a self organising map to predict invasive species: Sensitivity to data errors and a comparison with expert opinion. *J Appl Ecol* 47(2):290–298.
- Paini DR, Bianchi FJ, Northfield TD, De Barro PJ (2011) Predicting invasive fungal pathogens using invasive pest assemblages: Testing model predictions in a virtual world. *PLoS One* 6(10):e25695.
- Food and Agriculture Organization of the United Nations (2012) *FAOSTAT Database* (Food and Agriculture Organization of the United Nations, Rome). Available at faostat3.fao.org/home/E. Accessed February 1, 2012.
- Perrings C (2007) Pests, pathogens and poverty: Biological invasions and agricultural dependence. *Biodiversity Economics: Principles, Methods and Applications*, eds Kontoleon A, Pascual U, Swanson T (Cambridge Univ Press, Cambridge, UK).
- World Bank (2013) Data. Available at data.worldbank.org/. Accessed May 20, 2013.
- Organisation for Economic Co-operation and Development/United Nations (2011) *Economic Diversification in Africa. A Review of Selected Countries* (Organisation for Economic Co-operation and Development/United Nations, Paris).
- Ercey-Ravasz M, Toroczka Z, Lakner Z, Baranyi J (2012) Complexity of the international agro-food trade network and its impact on food safety. *PLoS One* 7(5): e37810.
- Andrews CJ, Hassenzähl DM, Johnson BB (2004) Accommodating uncertainty in comparative risk. *Risk Anal* 24(5):1323–1335.
- Perrings C, Burgiel S, Lonsdale M, Mooney H, Williamson M (2010) International co-operation in the solution to trade-related invasive species risks. *Ann NY Acad Sci* 1195: 198–212.
- Kohonen T (2001) *Self-Organizing Maps* (Springer, Berlin), 3rd Ed.
- Vesanto J, Himberg J, Alhoniemi E, Parhankangas J (2000) *SOM Toolbox for Matlab 5* (Helsinki University of Technology, Helsinki).
- Centre for Agriculture and Bioscience International (2011) *CAB International Crop Protection Compendium* (Centre for Agriculture and Bioscience International, Wallingford, Oxfordshire, UK).