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# Research investment implications of shifts in the global geography of wheat stripe rust

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**Breeding new crop varieties with resistance to the biotic stresses that undermine crop yields is tantamount to increasing the amount and quality of biological capital in agriculture. However, the success of genes that confer resistance to pests induces a co-evolutionary response that depreciates the biological capital embodied in the crop, as pests evolve the capacity to overcome the crop's new defences. Thus, simply maintaining this biological capital, and the beneficial production and economic outcomes it bestows, requires continual reinvestment in new crop defences. Here we use observed and modelled data on stripe rust occurrence to gauge changes in the geographic spread of the disease over recent decades. We document a significant increase in the spread of stripe rust since 1960, with 88% of the world's wheat production now susceptible to infection. Using a probabilistic Monte Carlo simulation model we estimate that 5.47 million tonnes of wheat are lost to the pathogen each year, equivalent to a loss of US$979 million per year. Comparing the cost of developing stripe-rust-resistant varieties of wheat with the cost of stripe-rust-induced yield losses, we estimate that a sustained annual research investment of at least US$32 million into stripe rust resistance is economically justified.**

Global average wheat yields grew by 2.95% per year from 1961 to 1990, but grew at less than a third that rate (0.85% per year) for 1990–2012 (ref. 1). Changes in how, where and when crops are grown affect the pace of crop yield and output growth[2]. These changes can induce or be induced by breeding new crop varieties with resistance to the biotic (pests and diseases) and abiotic (soil, terrain and climate) stresses that affect crop yields. In such a light, genes conferring resistance can be viewed as a form of biological capital that enhances the production and economic outcomes of farmers. For genes conferring resistance to pests and diseases, the durability of this biological capital is challenged by the ensuing co-evolutionary dance their deployment triggers. Pests facing the new selection pressure evolve the capacity to overcome the plant's defences, effectively depreciating the biological capital, possibly to the point of biological obsolescence.

The case of stripe rust on wheat, caused by *Puccinia striiformis* f. sp. *tritici* (hereafter '*Pst*'), graphically illustrates the problem of biological obsolescence in crop production. Until 30 years or so ago, wheat yield and production losses attributed to stripe rust were considered much less of a global problem than those attributed to stem rust (*Puccinia graminis* f. sp. *tritici*), another fungal disease that affects wheat production[3,4], although notable stripe rust losses have been observed historically. However, given the expanding geographical extent and increased production losses associated with stripe rust, it has been suggested that stripe rust is now the most damaging of all the cereal rusts[5–7].

The empirical basis for these claims seems fragile, or not especially apparent, with many questions remaining. Specifically, what are the past, present and prospective geographical extents of stripe rust occurrence worldwide and their associated crop losses? Given these losses, what is the economically justified amount of investment in breeding new wheat varieties that retain resistance to ever-evolving variants of *Pst* and thus maintain the world's biological capital that would otherwise be lost to this disease?

The geographic occurrence of stripe rust is changing. Historically, stripe rust was mainly endemic in cooler—often higher elevation—and somewhat moister regions (see ref. 8 and the Supplementary Material). More recently, the footprint of stripe rust epidemics appears to be moving into non-traditional, warmer and dryer areas suggesting a wider range of adaption. Using ostensibly representative isolates of *Pst* collected before and after 2000 in the United States (and genetically similar isolates from Denmark, Mexico and Eritrea)[7], the newer isolates appeared to have become more aggressive in the sense that they were capable of producing more urediniospores in a shorter time period at higher temperatures. In contrast, the new pathotype of *Pst* introduced into Australia in 2002 did not show evidence of adaptation to high temperature, suggesting that other factors contributed to the increased aggressiveness[9]. Increased parasitic fitness[10] has been put forward as an explanation for the spread of *Pst* populations in Australia and the United States[9].

For whatever reason, the pathogen has been mobile and its genetic geography has changed and expanded, especially beginning around 2000. Multiple new incursions of the pathogen have been reported in Australia and South Africa[11,12] and attributed to the international movement of stripe rust spores from Europe (in 1979) and North America (in 2002) on the clothing of travellers[6]. A previous study has provided molecular evidence of frequent migration of spores throughout northwestern Europe[13] (likely to be by wind and, perhaps other, including human-mediated, means).

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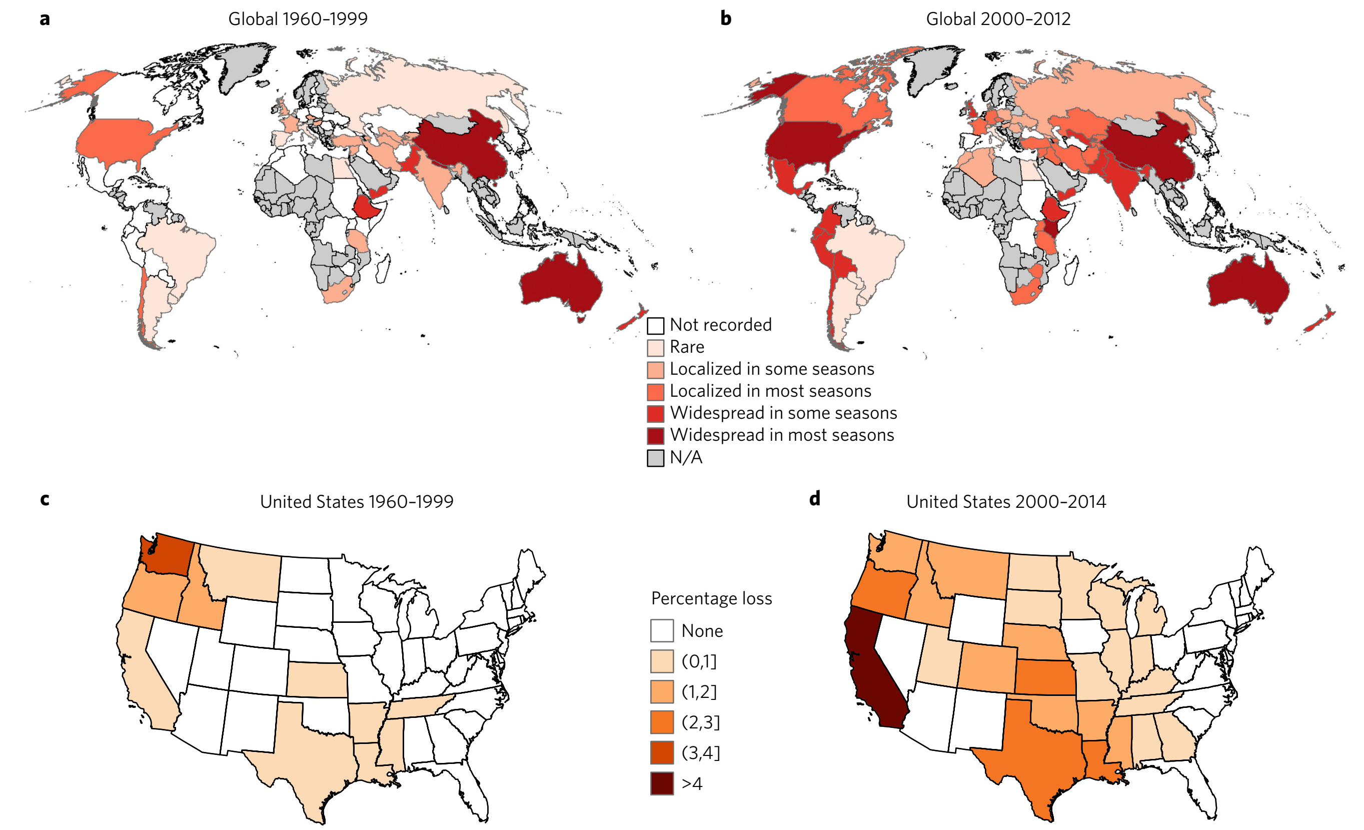


**Figure 1 | The expanding geography of crop losses attributable to stripe rust, before and after 2000.** **a**, Global 1960–1999; **b**, Global 2000–2012; **c**, United States 1960–1999; **d**, United States 2000–2014. Data for **a**,**b** are country-level data from ref. 6 and references detailed in the Supplementary Information. Data for **c**,**d** are US state-level data from ref. 14; **c**,**d** show the average percentage losses to stripe rust over the indicated periods.

## Results

Using responses received from 43 of the world's foremost wheat rust scientists engaged in the Borlaug Global Rust Initiative, in conjunction with reports from the Cereal Disease Laboratory of the United States Department of Agriculture (USDA)[14], D. Hodson (personal communication), Wellings[6], and others (Supplementary Material), we have found reports of substantive commercial crop losses associated with stripe rust in 35 (55%) of the 64 countries for which we have information between 2000 and 2012 (Fig. 1b). These 35 countries constituted 76.8% of the world's wheat crop in 2012. Prior to 2000, substantive losses were reported for just nine (14%) of the countries (Fig. 1a). State-specific data compiled by the USDA's Cereal Disease Laboratory reinforces the notion that the spatial extent of losses from stripe rust has expanded substantially in recent decades compared with the historical prevalence of the disease. For the entire period 1960–1999, just 11 of the 48 conterminous US states reported losses from stripe rust; for 2000 and beyond, the disease showed up in a total of 26 states (Fig. 1c,d).

**Implications for wheat production.** Figure 2 shows areas that are climatically suitable to the occurrence and persistence of stripe rust worldwide based on previously reported results derived from an ecological model of the disease[15]. Areas in the figure shown in green are, on average, suitable for the emergence of stripe rust infection, whereas areas shown in red have temperature and moisture profiles that enable the pathogen to persist from year to year (for example both during winter and during summer). To validate the model results that underpin our estimates, we assembled a more spatially explicit database of reported stripe rust occurrences using county-specific data from the USDA's Cereal Disease Laboratory for the United States (1959–2014); African, Indian, Pakistani and Western European data (2007–2014) (D. Hodson, personal communication); and the University of Sydney's Plant Breeding Institute for Australia (1980–2014) (R.F.P., C. Wellings and W.S.C., unpublished data). Plots comparing these observed points against the model results are provided in the Supplementary Materials (Supplementary Fig. 3a–d)—96.3% of the points fall within modelled suitable areas.

Although the model[15] reveals all areas of the world in which stripe rust can, on average, occur and, possibly, persist, Fig. 2 shows the geographic range of the pathogen within the estimated footprint of wheat production in 2005. We estimate that almost 88.0% of the world's wheat production is now vulnerable to the disease and about 38.2% of that production lies in regions where the pathogen is likely to persist from year to year (Table 1). Effectively all of the wheat production in Europe is seasonally susceptible to the disease and it could persist in areas accounting for 89% of the region's production, which makes up a large share of the world's wheat crop. The Asia and Pacific region (including China, India and Pakistan) also accounted for a substantial share of the world's wheat production in 2012 (36.8%), and 85.4% of that region's production was susceptible to infection from stripe rust. This means that 54.5% of the entire world's wheat crop is susceptible to stripe rust infections that occur only in these two regions. In contrast, although large shares of the wheat production in sub-Saharan Africa (SSA; 79.8%), Latin America and the Caribbean (LAC; 90.3%), and Australasia (90.2%) are vulnerable to the pathogen, losses in these three regions are of less consequence to global food supplies because together they accounted for less than 9% of the world's wheat production in 2012.

There is a large spatial disconnect between production in areas where the wheat crop is vulnerable to seasonal incursions of the pathogen and those areas where, once infected, it is likely to persist. For example, only 8.6% of the wheat crop area (and 13.1%

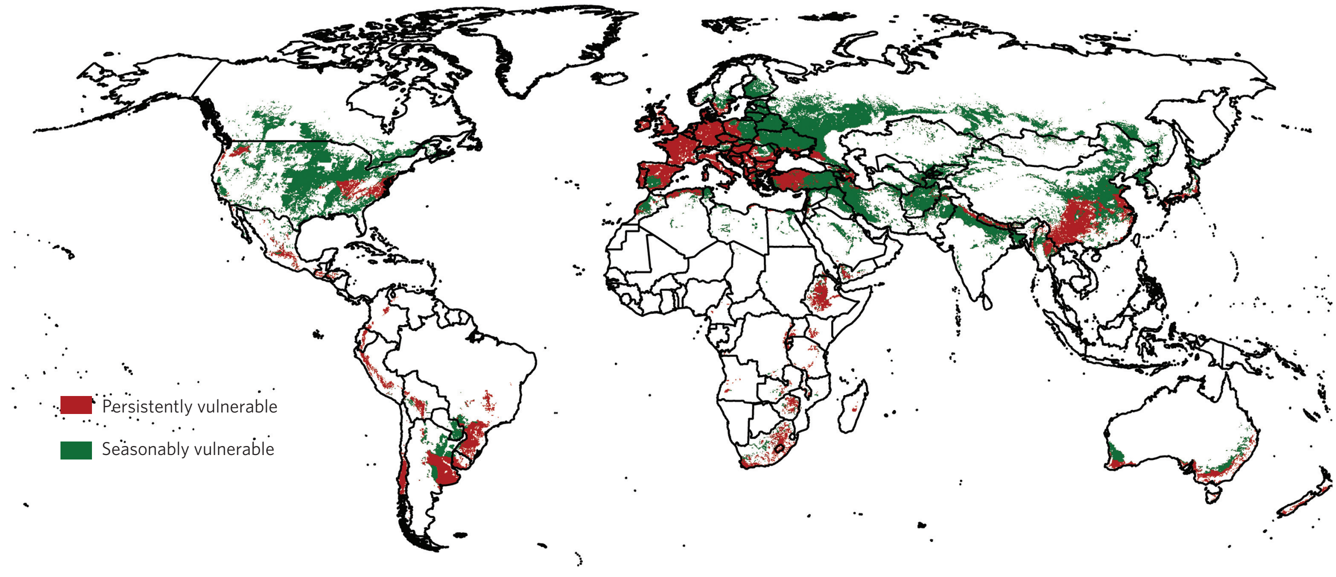


**Figure 2 | Modelled global climate vulnerability for stripe rust.** Red areas are modelled as being persistently vulnerable to stripe rust; green areas are modelled as being seasonally vulnerable. Vulnerability areas from ref. 15.

of the wheat production) of the United States is in areas where the disease is likely to persist (versus 93.6% of the US area that is suitable for the disease). In stark contrast, stripe rust can persist in almost all (95.6%) of the wheat area in sub-Saharan Africa that is also suitable for infection from the pathogen. As a consequence, in any given season, African farmers are more exposed to production risk owing to stripe rust losses than are American farmers. Thus the realities of stripe rust infection for the livelihoods of wheat farmers can be quite different than the implications for global food security. Losses to African farmers are much more likely, but of much less consequence, for global wheat supplies (and thus the price of wheat to consumers) than losses incurred by farmers in, say, the United States or Europe.

**Valuing biological capital for stripe rust resistance.** Growing wheat in a locale that is vulnerable to stripe rust infection is not the same as incurring losses from the disease. If a crop gets infected when the weather is unfavourable to the development of the disease, the rust will cause less damage. For example, crops infected later rather than earlier in the growing season tend to suffer less damage[16], as do crops endowed with genes that confer resistance to the disease or that are treated with fungicide. Therefore, choice of sowing date, seed variety and fungicide use are among the crop management practices that can mitigate losses from stripe rust.

**Table 1 | The vulnerability of the world's wheat crop to stripe rust.**

| | Vulnerability | | Production | |
|---|---|---|---|---|
| | Seasonal | Persistent | Amount (million tonnes) | Share of global total (%) |
| | (% of production) | | | |
| China | 99.8 | 24.3 | 120.6 | 18.0 |
| India | 68.6 | 0.2 | 91.5 | 13.6 |
| Pakistan | 74.7 | 0.7 | 27.3 | 4.1 |
| Rest of Asia and Pacific | 97.5 | 9.8 | 8.0 | 1.2 |
| Russia | 74.7 | 9.8 | 42.1 | 6.3 |
| Europe (incl. Turkey) | 99.9 | 89.0 | 154.5 | 23.0 |
| N. America | 80.9 | 9.0 | 89.0 | 13.3 |
| LAC | 90.3 | 73.9 | 19.8 | 2.9 |
| SSA | 79.8 | 75.6 | 6.9 | 1.0 |
| Australasia | 90.2 | 47.6 | 30.4 | 4.5 |
| Other areas | 87.4 | 13.6 | 81.3 | 12.1 |
| **World** | **88.0** | **33.6** | 671.5 | 100.0 |

Developed from data in refs 1, 15 and 20.

Additionally, in areas where the disease can grow but not persist from year to year, a source of inoculum is required for an infection to develop. Given that aerial dispersion is a major source of inoculum flow for *Pst*, the amount, timing of infection and virulence of any particular race of *Pst* in a particular locale, and especially in locales where the disease cannot persist, is highly stochastic. Thus we expect and observe substantial year-to-year variation in the local crop production losses attributed to stripe rust. This makes the losses in any particular locale or particular year not representative of the losses one might expect, on average, over a period of time for a more encompassing epidemiological area.

These realities were the key motivation in our decision to develop and deploy a probabilistic Monte Carlo simulation model to assess the global losses attributable to stripe rust (see Supplementary Material for details). The model uses 15 epidemiological zones throughout the world, and is calibrated with long-run US crop loss data compiled by the USDA's Cereal Disease Laboratory and our estimate of the global climate suitability of the pathogen within the 2005 extent of world wheat production. Using these empirical and analytical approaches, we estimated the probabilistic global losses benchmarked on US data for two different periods, juxtaposed against various counterfactual scenarios. The first period, spanning 1961–1984, is representative of an era in which crop losses attributed to stripe rust were typically confined to cooler, moister areas. The second period, spanning 2000–2014, is representative of the present era, wherein the stripe rust footprint expanded beyond the cooler and wetter areas of historical commercial consequence to also become more problematic for farmers in warmer and dryer areas.

Here we report estimates of the global wheat losses to be expected from two eras that represent past and present patterns of global losses attributable to stripe rust. Losses for both eras are assessed relative to the low-loss counterfactual, which is taken to be the more realistic (and conservative) benchmark for comparison; results for a no-loss counterfactual are reported in the Supplementary Material. To calibrate the low-loss counterfactual we used the reported US losses for the 1985–1999 period, when stripe rust was being partially controlled by use of fungicides and a series of resistant wheat varieties.

**Table 2 | Global annual average wheat loss estimates attributed to stripe rust.**

| Probability of loss (%) | Limited area extent | | Extended area extent | |
|---|---|---|---|---|
| | Amount (million tonnes) | Value (US$ million) | Amount (million tonnes) | Value (US$ million) |
| 90 | ≥0.73 | ≥130 | ≥4.70 | ≥840 |
| 50 | ≥0.88 | ≥157 | ≥5.45 | ≥975 |
| 20 | ≥0.98 | ≥176 | ≥5.98 | ≥1,071 |
| 5 | ≥1.09 | ≥195 | ≥6.54 | ≥1,170 |
| Mean | ≥0.88 | ≥158 | ≥5.47 | ≥979 |

Estimated by authors.
Values reflect annual losses against the low loss counterfactual. That is, they are benchmarked relative to 1985–1999 US losses. Supplementary Table 4 also reports values benchmarked against a no loss counterfactual. The limited area extent is characterized by US losses for 1959–1984 and the extended area extent is characterized by US losses for 2000–2014. Values are derived using the 2009–2010 average US wheat price.

Table 2 summarizes our results. When stripe rust losses were more limited to cooler areas, we estimate that on average at least 0.88 million tonnes per year was lost globally to the pathogen—a negligible share of the 2012 total tonnage of 671 million tonnes, and equivalent to a relatively modest monetary loss of at least US$158 million per year valued in 2009–2010 average US wheat prices—with a 90% chance that at least 0.73 million tonnes of wheat per year was lost. Now that the disease occurs in many more, including warmer and dryer locations, the losses on average have jumped dramatically to an estimated 5.47 million tonnes annually (equivalent to a loss of US$979 million per year), with a 90% chance of at least 4.70 million tonnes being lost each year.

## Research to renew depleted biological capital

These losses are an estimate of the value of the biological capital that has been lost from a breakdown in resistance to stripe rust. How much money should be invested in restoring this lost value (and to preserving those gains) by breeding a stream of new wheat varieties that keep the inevitable succession of ever-evolving genetic variants of stripe rust at bay?

Investing in stripe rust research has an opportunity cost (for example, the potential loss in the productive value of biological capital from failing to retain resistance to ever-evolving variants of the other fungal diseases, such as leaf rust and stem rust, that also affect wheat). Thus an economic approach to determining the socially optimal amount of investment in stripe rust research is to compare the worldwide costs of research into developing varieties resistant to stripe rust against the global benefits of averting the yield losses attributable to this disease. If this particular benefit–cost ratio exceeds the ratio realized from using these same resources in other ways, then it argues for more investment in stripe rust research. This economic balance can best be struck by reference to the modified internal rate of return (MIRR), which reflects the annual rate of return from a stream of investment benefits over time[17].

Taking the estimated stream of counterfactual global losses attributable to stripe rust from 2000 to 2050 as indicative of the potential benefits from successful stripe-rust-resistance research for the period 1990–2050 (allowing a 10 year lag from initiating this research to realizing its benefits, see Supplementary Materials), we estimate that a sustained investment of US$32.0 million per year (2009–2010 US prices) in stripe rust research is justified economically. With such a sustained investment, there is a 95% chance that the MIRR would exceed 10% per year, conditional on the success of the funded research.

To be clear, this is not a one-off investment, it is a steady-state investment stream in research that is economically justified based on a continuance of the new, more expansive, pattern of losses observed in the 2000–2014 period. If the extent of the spread and the magnitude of the crop losses associated with this disease continue to increase, then this would be a conservative estimate of the annual investment justified in alleviating stripe rust losses globally.

## Discussion

This study uses long-term US crop loss data in conjunction with modelled climate suitability for stripe rust to simulate a probabilistic pattern of global losses from this pathogen. Our simulations reveal that damage caused by the expansion of the geographical footprint of this pathogen in recent decades has substantial wheat production and economic consequences. We find that the economically justified annual, global research and development (R&D) investment in stripe rust (US$32.0 million) is more than three-fifths of the recurring investment that can be economically justified for stem rust research (Supplementary Material). That said, there is a major distinction between the crop loss estimates for these two diseases. The estimated stem rust losses assume a failure to forestall the spread of newer variants of the disease around the world; in other words these are prospective not realized losses for all but a handful of countries (mainly those in sub-Saharan Africa). In stark contrast, the estimated 5.47 million tonnes of wheat production lost every year to stripe rust, on average, are a continuation of the pattern of recently observed losses. These are not hypothetical losses, but are actually being incurred at present. Thus although many of the new investments into stem rust research are targeted at avoiding losses that are yet to be realized, stripe rust research is targeted at mitigating losses that are presently occurring around the world.

The contemporary losses reflect an increase in both virulence and geographic scope of the losses to stripe rust. Thus, to contextualize these results, we consider the research investment implications of failing to take account of these changes. Specifically, we took the 1959–1984 US loss structure—a period in which the disease tended to be more geographically limited—to represent the earlier era of more circumscribed global losses. Had we assumed this loss structure, we would have found an average justifiable investment into stripe rust research of just US$9.5 million per year, compared with US$32.0 million deemed justifiable under the contemporary pattern of losses. This implies that the changing structure of losses justifies an additional annual investment of at least US$22.5 million.

Allowing biological capital to depreciate is especially costly. Notwithstanding the broadening geographic distribution of stripe rust, the lack of funding increases targeted to stripe rust relative to stem rust has been noted by others[18]. R&D on wheat rusts in general waned after the Cold War era. Although the appearance of the Ug99 *Puccinia graminis* variants spurred renewed donor attention into stem rust[19], the more expansive stripe rust footprint has not induced a comparable response. Failure to maintain the stock of biological capital by means of a sustained flow of funding for rust research has important economic consequences. In the present case, more consistent historical investments are likely to have shortened the gestation lag. For instance, if the lag were halved (for example from 10 to 5 years), benefits would begin to flow sooner and the justifiable annual investment would increase by some 61%, from US$32.0 million to US$51.6 million. The practical policy and investment implication is that sustaining biological capital stocks via stop–start funding models is expensive relative to sustaining the flow of investments into recurring crop health problems.

## Methods

**Probabilistic Monte Carlo simulation.** We estimated the potential spatial distribution of stripe rust using the CLIMEX Compare Locations model, incorporating information on the ecology, phenology and known occurrence of the pathogen[15]. The resulting modelled suitability indicators were then spatially intersected with the 2005 wheat crop geography estimates previously reported[20] to derive an integrated global map of the production risk associated with stripe rust.

Drawing on the notion of epidemiological zones[8], we delineated 15 epidemiological zones worldwide for stripe rust. We then calculated the share of each zone's wheat area that is suitable for the disease, and applied our estimates of stripe rust losses to those areas. Probabilistic estimates of the wheat production losses attributable to stripe rust were obtained using 50,000 repeated, independent random draws for each epidemiological zone from a beta distribution fitted to long-run reported loss data for the United States. Separate beta distributions were estimated for each of the time periods 1959–1984, 1985–1999 and 2000–2014.

**Economically justified annual, global wheat R&D in stripe rust control.** We applied the MIRR concept[17] to estimate the economically justifiable annual global investment into stripe rust R&D. It typically takes around 10 years to breed, bulk and release a new wheat variety. Thus, we assume there is a 10-year lag between investments in stripe rust research and realizing the loss-mitigating effects of those investments through the adoption of rust-resistant varieties. We assume that investments into stripe rust research will reduce losses to levels seen in the low-loss counterfactual era (1985–1999). Under that assumption, we calculate the annual investment amount for 1990–2050 that achieves a MIRR of at least 10% per year with a probability of 95%, given a reinvestment rate of 3% per year, a cost of capital of 10% per year, and forecasted wheat production[21].

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## Author contributions

P.G.P., J.M.B. and T.M.H. designed the study and methods; D.J.K., J.M.B., Y.C., R.F.P., H.J.B., T.Y. and W.S.C. compiled and interpreted distribution data and developed the species niche model; Y.C. and T.M.H. undertook the probabilistic assessment; J.M.B. implemented the spatial assessment; P.G.P., J.M.B., T.M.H., Y.C., R.F.P. and W.S.C. wrote the paper.

## Additional information

Supplementary information is available online. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.M.B.

## Competing interests

The authors declare no competing financial interests.