Key tropical crops at risk from pollinator biodiversity loss due to climate change and land use

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One sentence summary

Pollinator abundance losses from agriculture and climate change risk production of key crops in the tropics, especially cocoa

Short title

Pollinator changes and pollination risk

Abstract

Recent studies have highlighted rapid ongoing changes in insect biodiversity, in part driven by the interaction of land-use and climate change. Insect pollinator biodiversity specifically has been shown to be changing rapidly, with potential consequences for the provision of crop pollination. The role of land-use-climate interactions in pollinator biodiversity changes remains poorly understood. Here, we present a global assessment of the interactive effects of climate change and land use on pollinator abundance, and predictions of the risk to crop pollination worldwide from the inferred abundance changes. We show that the interactive combination of agricultural land use and recent climate change is associated with particularly large reductions in the abundance of insect pollinators. As a result, it is expected that the tropics will likely experience the greatest risk to crop production from pollinator biodiversity losses. The risk to these crops is highest, and predicted to increase most rapidly, in regions of sub-Saharan Africa and northern South America, especially in areas used to produce cocoa, mango, pumpkin, melon, watermelon, and coffee. The health, well-being, and livelihoods of billions of people rely to some extent upon the availability and affordability of crops dependent on animal pollination. Climate change and agricultural land use could put these people's wellbeing at high risk, if loss of pollinator abundance translates into crop pollination shortfalls.

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Introduction

Recent studies have highlighted rapid ongoing changes in terrestrial insect biodiversity (*1–3*), including among pollinating species (*4–8*). Some of these studies have reported net declines (*1, 3*), while others have shown mixtures of gains and losses (*2*). Pollinator biodiversity changes have potential consequences for the provision of pollination to wild plants and crops. Importantly, evidence for insect biodiversity trends has been biased toward Western Europe and North America (*9, 10*), with little coverage of tropical and subtropical regions (*11, 12*). Although a few studies have shown steep declines of insects in the tropics (*3*), evidence about insect biodiversity trends there often remains anecdotal (*13*), with global syntheses (*1, 2*) having strong geographic biases towards non-tropical regions.

Among the drivers of insect and pollinator biodiversity changes, human-driven land-use changes and climate change are prominent (*5, 10, 14–17*). Climate change, in particular, is emerging as an increasingly important driver (*8, 14, 18–21*), while synergistic interactive effects of land-use and climate change are associated with further reductions in insect biodiversity compared to if the pressures acted in isolation (*22–26*). A key mechanism underpinning interactive land use and climate effects is the altered microclimatic conditions in areas where vegetation has been modified for human land use (*22*). Tropical insects are expected to be more susceptible to climate change, including interactive effects with land use, given their narrower physiological tolerance compared to non-tropical species (*27*). Indeed, recent studies show greater effects in tropical than non-tropical insect biodiversity (*26*).

Changes in the biodiversity and composition of pollinator communities are expected to have large effects on the provision of pollination services. Pollen limitation from animal pollinator losses has already been shown to reduce the reproductive success of wild plants (*4, 28*), and the productivity of certain crops (*29–32*), although there is no clear evidence that pollen limitation is yet causing wholesale reductions in yields of crops that rely on animal pollination (*33*). Evidence that insect biodiversity responds to human pressures more strongly in the tropics than elsewhere (*17, 26*) is noteworthy, given that the majority of animal-pollination-dependent crops are grown there (*34*). However, it is not only tropical countries that will experience the effects of pollinator losses and subsequent pollen limitation, with high income countries benefiting from imports of animal-pollination-dependent foods from tropical areas (*35*). Abundance, species diversity, and functional diversity of pollinators have all been implicated as determinants of the delivery of pollination service (*32, 36–40*). Previous attempts to model the provision of crop pollination service are often based on predictions of pollinator abundance, which bears a direct relation to pollination of plants, and has been shown to give a reasonable approximation of pollen deposition in at least some study systems (*41*). A key uncertainty however relates to the shape of the functional relationship between pollinator abundance and crop production (*41*).

Here, we present a global assessment of the interactive effects of climate change and land use on pollinator abundance, and predictions of how the inferred abundance changes might translate into risk to crop pollination worldwide based on a range of possible abundance-pollination relationships. Our underlying analyses are based on the PREDICTS database of biodiversity comparisons in different land uses (*42*), together with a list of species identified in the literature as likely pollinators (*17*). We use mixed-effects models to fit total pollinator community abundance as a function of land use (primary vegetation versus cropland) and a measure of historical temperature change between a baseline period (1901-1930) and the year prior to biodiversity sampling, standardized by monthly temperature variability in the baseline period (*26*). We standardised temperature changes in this way to capture where temperatures have exceeded ordinary seasonal variation, a consideration that has previously been identified as important for insects in general (*26*). We then apply these models to predict which locations and crops are likely to be exposed to the greatest losses of pollinator abundance, and thus to face the greatest risk of pollination shortfalls. We moderate estimates of risk according to estimates of where crops are grown (*43*), how dependent these crops are on animal pollination (*34*), projections of historical and future climate change, and a set of assumptions for the relationship between local pollinator abundance and crop pollination (from linear to highly convex or concave). We focus on future climate projections under two Representative Concentration Pathways (RCP) scenarios: RCP 2.6, which has a multi-model-median predicted 1.5°C increase in global average temperatures by 2100 compared to the pre-industrial climate; and RCP 8.5, which has a multi-model-median predicted

85 4.9°C increase in global average temperatures (*44*). Finally, we combine projected pollination risk with
86 estimates of the trade in pollination-dependent crop production (*35*), to predict regions of the world that
87 may be vulnerable to the indirect consequences of crop pollination risk via trade connections.

Results and Discussion

89 The abundance of insect pollinators responded strongly to the interaction of recent climate change and land
90 use (Figure 1). Within cropland experiencing novel temperatures (Standardized Temperature Anomaly =
91 1), pollinator abundance is 38.9% that in natural habitat that has not experienced temperature increases.
92 The causal mechanism underpinning this interaction is unclear, but the alteration and homogenisation of
93 microclimatic conditions in croplands (*45*) is likely to be partly responsible. Our results are qualitatively
94 consistent with recent results for a sample of all insects (*26*), but importantly we show that responses to the
95 interactive effects of climate change and land use are stronger for pollinating than non-pollinating insects
96 (Figure 1). We also show that the strength of the interactive effect varies among taxonomic groups, with
97 the strongest effects seen in dipteran and hymenopteran pollinators (Figure S5). Whether the sensitivity of
98 pollinating insects to the interaction of climate change and land use relates directly to their reliance on floral
99 resources, or to other correlated traits typical of pollinators, is unclear, and a combination of both factors
100 is likely to operate. For example, selection of animal pollinated plants is thought to be highly sensitive to
101 climatic conditions (*46*), suggesting that plant-pollinator interactions are highly sensitive to thermal changes.
102 Pollinator pilosity (i.e. hairiness), on the other hand, likely affects an insect's ability to adapt to changes
103 in climate (*47*), and given its nature as a trait typical of bees and hoverflies, tends to be correlated with a
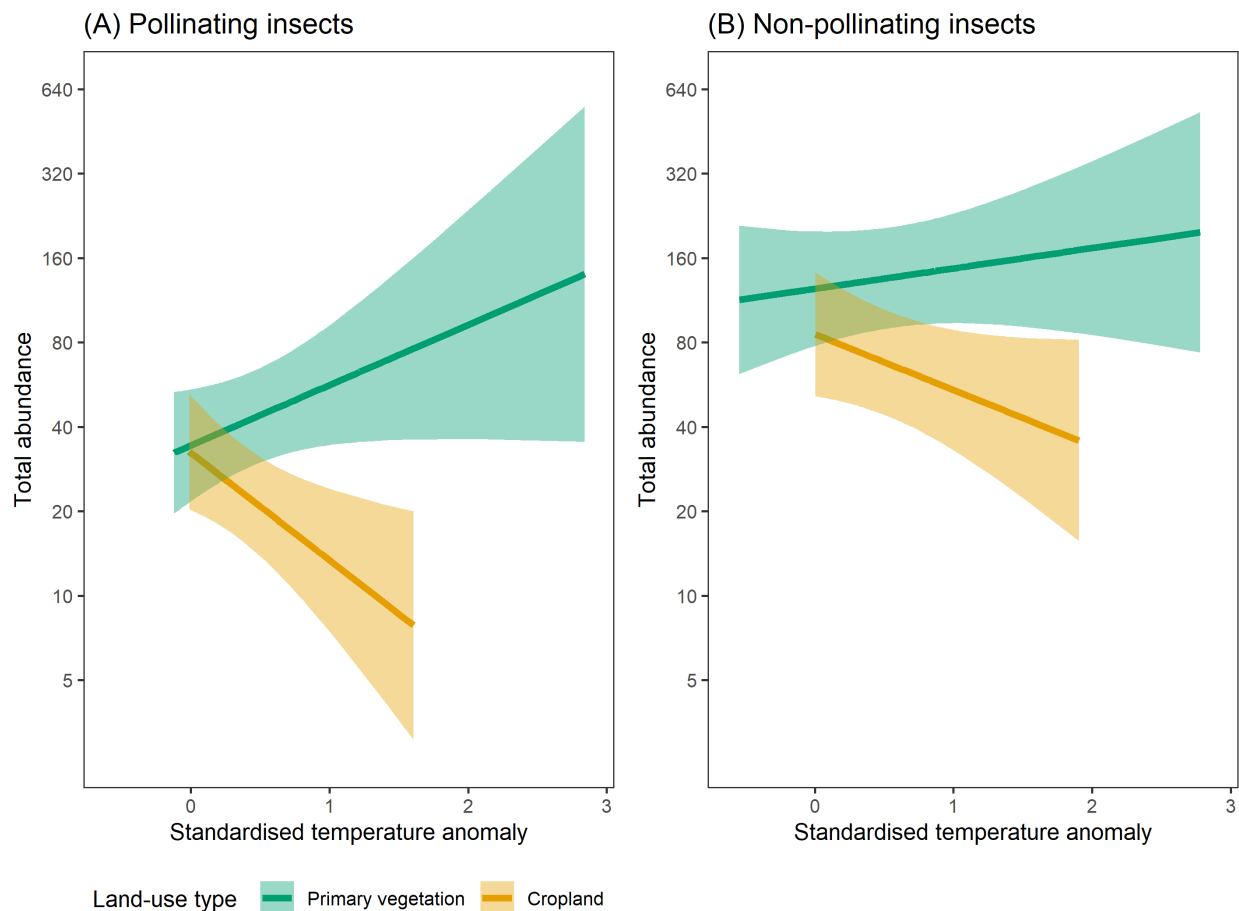**104** reliance on floral resources (*48*).

Figure 1: Response of pollinating (A) and non-pollinating (B) insect total abundance to the interactive effect of standardised temperature anomaly and land use (primary vegetation versus cropland) (A: F = 22.4068, p < 0.001; B: F = 10.7520, p < 0.01). Note that abundance is plotted on a $\log_e$ scale. Results are based on linear mixed-effects models. Site numbers are as follows (see also Table S2): insects known to pollinate (primary vegetation = 1166, cropland = 1507); insects not known to pollinate (primary vegetation = 1747, cropland = 922). Shading represents 95% confidence intervals around the mean fitted effect. Green = primary vegetation; yellow = cropland.

We predict that total pollination production risk will increase under all climate scenarios (Figure 2). For all scenarios, our projections use change in pollinating insect abundance as a proxy for the relative risk to the production of crops dependent on insects, incorporating information on where crops are grown worldwide (43) as well as the fractional dependence of crops on animal pollination (34). Our estimates of both relative risk as well as absolute production risk should be interpreted as indices of risk, rather than predictions of the actual amount of production likely to be lost, given the very high uncertainty in how pollinator abundance changes will translate into actual production losses. Increases in risk are seen for all assumed relationships between abundance loss and production risk, although the magnitude of changes in relative risk and especially absolute production risk varied widely (Figure 2 and S13). The predicted rate of increase in average production risk was substantially higher under RCP (Representative Concentration Pathway) 6.0 than RCP 2.6, suggesting that efforts to mitigate climate change will reduce the risk to future crop production, alongside the many other benefits (49). Relative production risk varied strongly between years under the convex abundance-production relationships (Figure 2 and S13). This volatility may be explained by way in which the non-linearity of abundance/production relationships interacts with inter-annual climate

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variability caused by the El Nino Southern Oscillation (*50*). While increasingly convex assumed relationships between insect abundance loss and crop production risk led to steeper increases in relative production risk with future climate change, absolute production risk was markedly lower, owing to a lower baseline in the present day (Figure 2). Our estimates of risk are based on the distribution of crops as grown in 2000, meaning we do not account for changes in the distribution of crops over time, which are likely to occur as a result of the direct impacts of climate change, indirect effects through the loss of pollinator biodiversity, and socio-economic factors such as price changes in the global markets for particular crops. The modelled effects of land-use-climate interactions on pollinator abundance are robust to dropping individual taxonomic families from the model dataset (Figure S10), and to using threshold temperatures to restrict the months considered to those in which insects are likely to be active (Figure S11 and S12). The projections of crop production risk are robust to variation in climate predictions under different individual climate models (Figure S6), do not change markedly when abundance loss is capped at the maximum model-fitted value (Figure S2), and do not change markedly when tested for sensitivity to the quality of mapped estimates of crop production (Figure S4).
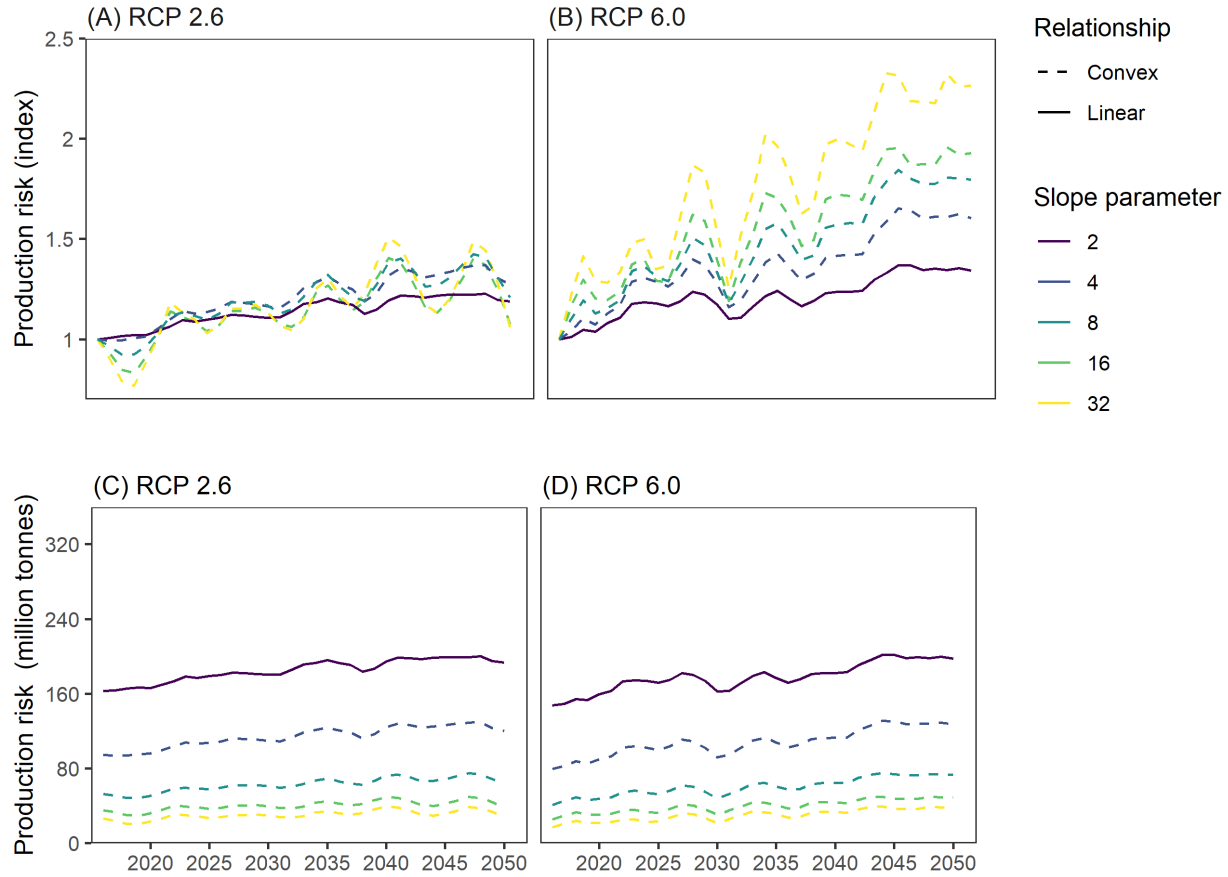
Figure 2: Projected change in total production risk under two RCP scenarios (2.6 and 6.0) and a set of hypothetical relationships between pollinator abundance and crop production (linear and varying degrees of convexity). Results are shown both for an index of change in relative risk (A and B) and for the total production potentially at risk (in tonnes) (C and D). For each year into the future, the standardised temperature anomaly was projected globally for all cells with production of crops dependent on animal pollination, using a 3-year rolling average of temperature anomaly estimates in each cell, from an ensemble of different climate models. We used data on crop production from the year 2000 (the latest year when such data are available for all crops). For each annual projection of standardised temperature anomaly, insect pollinator abundance on cropland was predicted according to the model shown in Figure 1A, and then expressed as proportional abundance loss compared to cropland that has experienced no warming (i.e. standardised temperature anomaly of 0). In each cell, the total production of each crop (43) was multiplied by dependence on animal pollination (34), and then adjusted for the predicted percentage reduction in insect pollinator abundance in that cell. These estimates of crop production at risk were summed across crops, and then across all terrestrial cells globally. Lines show different assumed relationships between insect pollinator abundance and crop production: dashed = convex relationships (of differing degrees, indicated by different colours: yellow = most convex; purple/blue = least convex); and solid = linear relationship.

Projected risk to crop production in 2050 from insect pollinator abundance losses, as a proportion of all production in a given location, is highest in the tropical regions of sub-Saharan Africa, South America, and southeast Asia (Figure 3A; see Figure S7 for underlying maps). In terms of total production potentially at risk, China, India, Indonesia, Brazil, and the Philippines emerge as being most at risk (Figure 3B). Among crops, cocoa is estimated to be at highest risk, by a large margin, especially in Africa, followed by

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138 mango (particularly in India) and watermelon (notably in China) (Figure 3B; Figure S1). The risk to cocoa
139 production is particularly significant in light of the social and economic context, as most cocoa is produced
140 on small farms (two to four hectares) that provide income to between 40 and 50 million people globally (*51*).
141 Coffee is also expected to have a combination of relatively high production risk (Figure 3B) and high value,
142 suggesting that regions in which it is grown may experience economic difficulties, unless the pollination
143 service can be replaced cost effectively. Similarly to cocoa, coffee production provides income to millions of
144 small-scale farmers and their families in the tropics (*52*). Therefore, the increased production risk due to
145 loss of pollinators could lead to increased income insecurity for some of the most vulnerable people globally.
146 Projections of local crop production risk are sensitive to the assumed abundance-production relationship
147 (Figure S8), with the exception of South East Asia, which is consistently projected to have high risk, and
148 the temperate realm, which is consistently projected to have low risk (Figure S9).

149 It is impossible to predict exactly how our estimates of production risk measure will translate into actual
150 crop production losses. There are multiple uncertainties associated with predicting pollinator biodiversity
151 changes and how this impacts crop production, some of which we explore here (e.g. the relationship between
152 pollinator abundance and crop production), but many of which we do not or cannot (e.g. the changing
153 distribution of crops, the economic viability of hand pollination, the buffering effects of managed pollinators,
154 the effects of climate change alone, and other technological solutions such as the breeding or engineering
155 of pollinator-independent cultivars). Regardless, at the global scale, the changes to pollinator biodiversity
156 that we estimate are likely to be reflected in changes in the risk to production of crops dependent on animal
157 pollination. For cocoa, recent research has focused on the direct effects of climate change on crop production
158 (*53*, *54*), often overlooking those that might be pollinator-mediated, probably because the direct effects
159 of climate change are easier to capture. Importantly, solutions to direct and pollinator-mediated effects
160 of climate change may differ. For example, shade trees might protect crops from extreme temperatures
161 (*53*), but might not for the ceratopogonid fly pollinators on which cocoa pollination depends. The focus in
162 previous research on direct climate impacts rather than pollinator-mediated effects is a key gap given that
163 some cocoa varieties are limited more by pollination availability then resource availability (*55*).
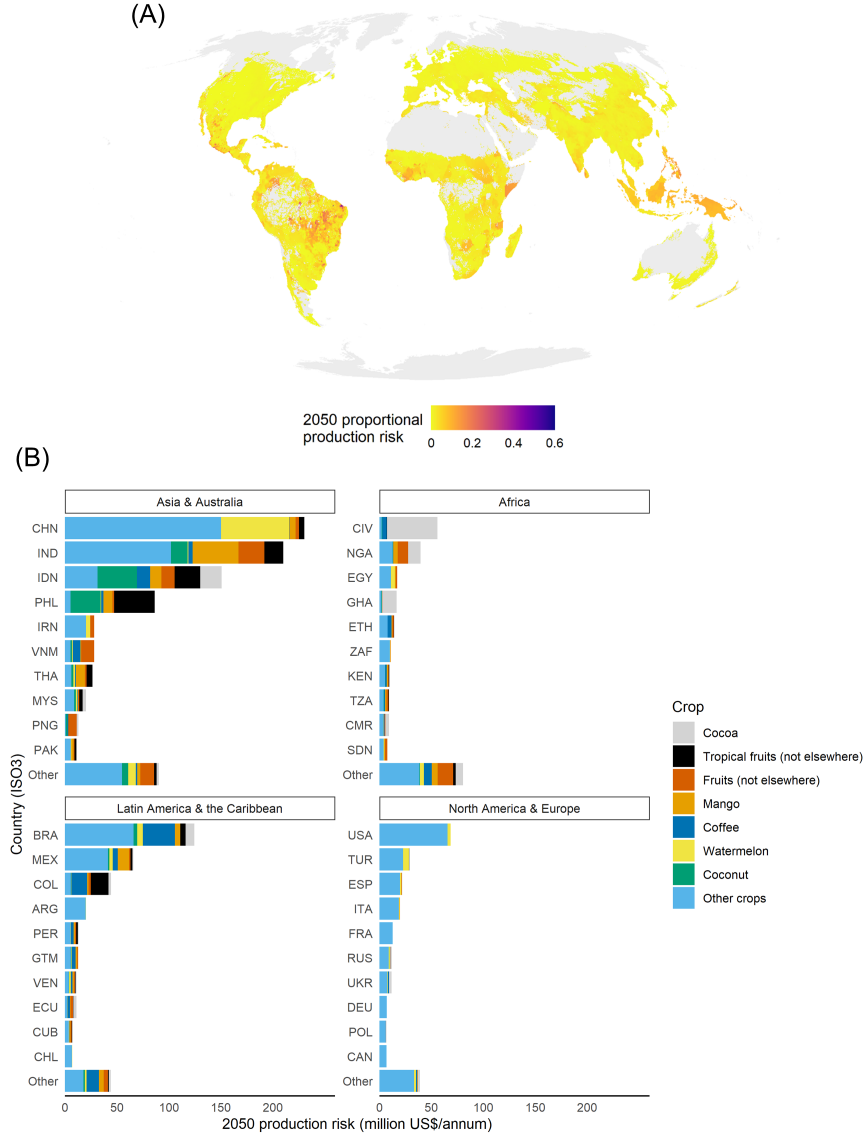
Figure 3: Projected change globally in the fraction of crop production estimated to be at risk in 2050 under the RCP 6.0 climate scenario, assuming a linear relationship between insect pollinator abundance loss and production loss for crops dependent on animal pollination. All projections are based on mean projections of the standardized temperature anomaly based on temperature estimates from an ensemble of individual climate models. (A) The sum of crop production at risk across all crops with some dependence on animal pollination, as a proportion of the production of all crops grown in a location ('proportional production risk'). (B) Proportional production risk for the 20 crops with the highest total pollination dependent production globally (see Figure S01 for the top 20 crops). Overall risk here is the median of proportional production risk for all spatial cells in which that crop appears, whilst change in risk is the difference in overall risk between the start and the end of the series. Point size represents an estimation of the per kg value of each crop for the years 2015-2019, calculated from (56). (C) Proportional production risk at the level of each country. Here overall risk is the median of proportional production risk for all cells of that country, whilst change in risk is the difference in overall risk between the start and the end of the series. Point size here represents the total value of the pollination dependent production in that country adjusted for GDP, calculated from the product of total pollination dependent production per annum according to (43) and (34), and the per kg value of each crop (56). Colour represents the geographic region of each country, distinguishing between regions within a panel: Blue, Africa; orange, Asia; black, Australia; green, Europe; yellow, North America; dark blue, South America; grey, the Caribbean.

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Countries besides those with high production risk will feel the impact of losses of pollinator biodiversity and the crops that depend on them, through disruption to imports, especially as the most vulnerable crops tend to be valuable export products such as coffee and cocoa. In absolute terms, large countries such as China and the United States have the highest total import risks (Figure 4B). The Netherlands emerges has having surprisingly high risk given its size, the third largest overall import risk (Figure 4B), consistent with its status as the greatest importer of cocoa beans worldwide (*57*). Import risk per capita (Figure 4A) highlights the challenges that could be faced by nations with limited agricultural production capacity, such as many island countries (e.g. Cayman Islands, Aruba, Singapore, the first, second and fourth highest import risk per capita, respectively) or countries with unfavourable environmental conditions for agriculture (e.g., Mongolia, with the 19th highest import risk per capita). Total import risk per capita tends to be high also in northern and high-income countries, particularly continental western Europe, which has large processing industries for crops such as coffee and cocoa. High income and unfavourable environment for agriculture could both account for high import risk per capita for some countries in the Middle East (United Arab Emirates, Kuwait, Saudi Arabia, which have the 5th, 8th and 27th highest estimated pollination import risk per capita). Our predictions of import risk are based on trade patterns in the present day (*35*), meaning we do not account for changes in trade flows that will likely occur in the future.
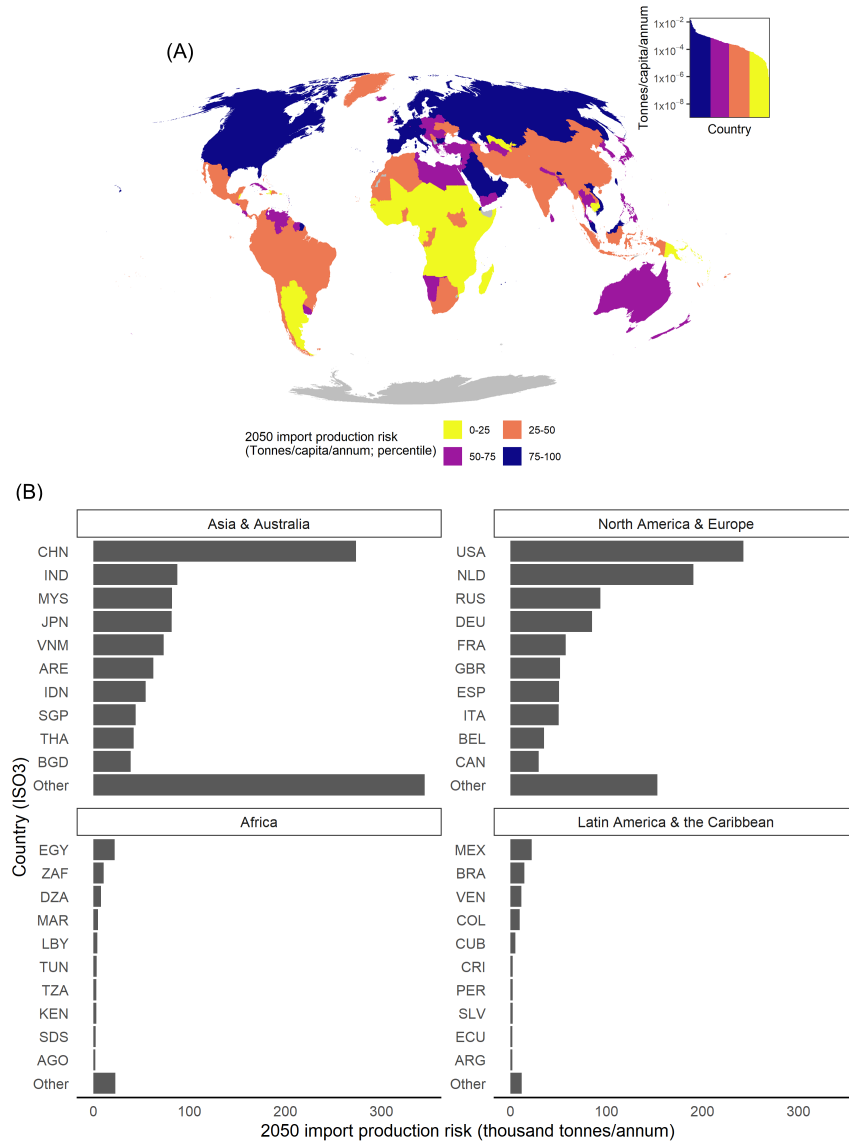
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Figure 4: Projected total import risk for 2050 under the RCP 6.0 scenario, assuming a linear relationship between insect pollinator abundance loss and production loss. Projections are based on changes in the mean standardized temperature anomaly based on projections from an ensemble of individual climate models. Import risk is a measure of how the effects of localised production risk might be distributed among other countries, calculated using trade flow data from (*35*). For each yearly time step into the future, local production risk in each spatial cell is attributed to importers according to the quantity of pollination trade imported from each country. For example, if an importer is dependent on 3 countries for imports, at a proportion of 30%, 50%, and 20%, then any change in import risk should scale as a function of the local production risk aggregated at those same proportions. Total import risk here has been adjusted for country population size and then converted to a percentile. Colours represent each percentile grouping: yellow, 0-25th percentile; orange, 25-50th; purple, 50-75th; dark blue, 75-100th.

180 Interacting effects of climate change and anthropogenic land use are rapidly restructuring biodiversity (*26*,
181 *58*). Here we show that the combination of agricultural land use and recent climate change is associated
182 with particularly large reductions in the abundance of insect pollinators. As a result, we predict that the
183 tropics will likely experience the greatest risk of future pollination shortfalls, putting at risk the production

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of crops that depend on insect pollination. Future pollination risk is estimated to be highest in areas used to produce cocoa, mango, watermelon, and coffee. Given the many factors that determine crop production and crop price (*59*), the likely effects of insect pollinator losses on crop production are unclear, and even if they do occur, conclusive attribution is likely to be challenging. Such complications likely in part explain why identifying a strong effect of pollinator losses on global crop yield and price has thus far been so difficult (*33*, *60*, *61*). Regardless, there is sufficient evidence to suggest that declining insect pollinator abundance will influence crop production risk, particularly for those in the global south (*62*). Such risk could manifest in the form of direct and immediate losses to crop production through pollinator shortfall, fluctuations in the stability of production, or through decreased resilience to changes that will happen in conjunction (e.g. the effects of extreme temperature and drought on crop growth). The health, well-being, and livelihoods of a high proportion of the global population, from small farmers to consumers, relies to some extent upon the availability and affordability of crops dependent on animal pollination, which is likely to be put at greater risk as a result of future pollinator losses as land-use and climate changes intensify.

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Competing interests

All authors declare that they have no competing interests.

Data and materials availability

All data will be made available on FigShare, and all code on both Zenodo and GitHub.

Supplementary Materials

Materials and Methods

Figs. S1-S13

Tables

References