

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

Joseph Millard^{1,2*}, Charlotte L. Outhwaite³, Lynn V. Dicks⁴, Jeff Ollerton⁵, Silvia Ceausu³,
Tim Newbold³

¹ Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK

² Leverhulme Centre for Demographic Science, Nuffield College, University of Oxford, Oxford OX1 3UQ, United Kingdom

³ Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, WC1E 6BT, UK

⁴ Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

⁵ Faculty of Arts, Science & Technology, University of Northampton. University Drive, Northampton, NN1 5PH UK

*Corresponding author. Email: joseph.millard@nhm.ac.uk

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.

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.

88 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 homogenisation of microclimatic
93 conditions in croplands (45) may be partly responsible. Our results are qualitatively consistent with recent
94 results for a sample of all functional groups of 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 S05). 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).

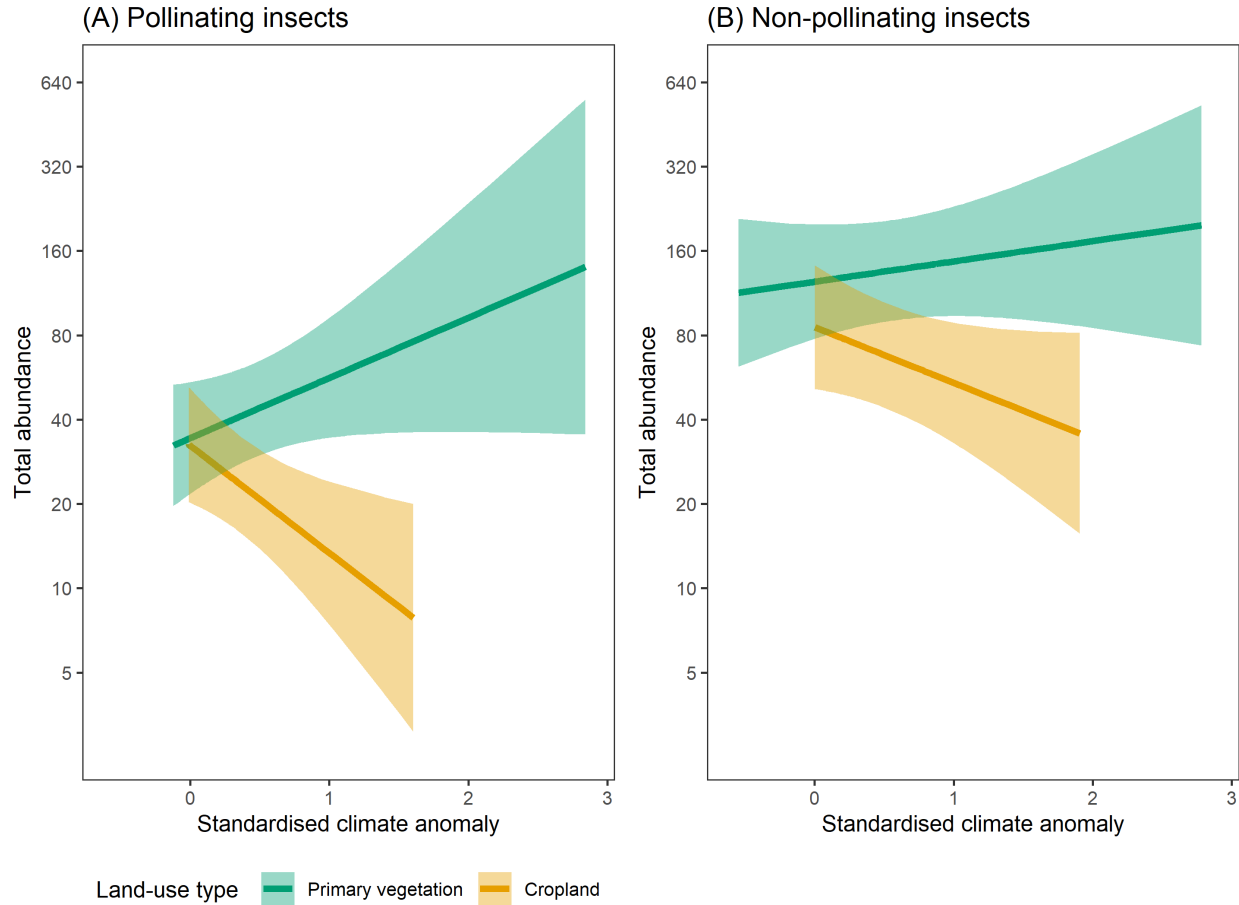


Figure 1: Response of pollinating (A) and non-pollinating (B) insect total abundance to the interactive effect of standardised temperature anomaly and land use (primary vegetation versus cropland) (A: $F = 22.4068$, $p < 0.001$; B: $F = 10.7520$, $p < 0.01$). Note that abundance is plotted on a \log_e scale. Results are based on linear mixed-effects models. Site numbers are as follows (also see Supplementary Material Table 2): 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.

105 We predict that total pollination production risk will increase under all climate scenarios (Figure 2). For all
 106 scenarios, our projections use change in pollinating insect abundance as a proxy for the relative risk to the
 107 production of crops dependent on insects, incorporating information on where crops are grown worldwide
 108 (43) as well as the fractional dependence of crops on animal pollination (34). Our estimates of risk are based
 109 on the distribution of crops as grown in 2000, meaning we do not account for changes in the distribution of
 110 crops over time, which are likely to occur as a result of the direct impacts of climate change, indirect effects
 111 through the loss of pollinator biodiversity, and socio-economic factors such as price changes in the global
 112 markets for particular crops. Our estimates of both relative risk as well as absolute production risk should
 113 be interpreted as indices of risk, rather than predictions of the actual amount of production likely to be lost,
 114 given the very high uncertainty in how pollinator abundance changes will translate into actual production
 115 losses.

116 Increases in risk are seen for all assumed relationships between abundance loss and production risk, although
 117 the magnitude of changes in relative risk and especially absolute production risk varied widely. The predicted
 118 rate of increase in average production risk was substantially higher under RCP (Representative Concentration
 119 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 variability caused by the El Nino Southern Oscillation (50), although at present this is unclear. Such climate effects would be some seen to some extent under all abundance-production relationships, but magnified under highly convex scenarios as regions undergo marked shifts from high to low production. 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). Results were robust to variation in climate predictions under different individual climate models (Figure S06), do not change markedly when abundance loss is capped at the maximum model-fitted value (Figure S02), do not change markedly when tested for sensitivity to data quality (Figure S04), and likely hold across a set of plausible active season temperature thresholds (fitted through two different approaches, see Figures S11 and S12) and abundance change slopes (Figure S10).

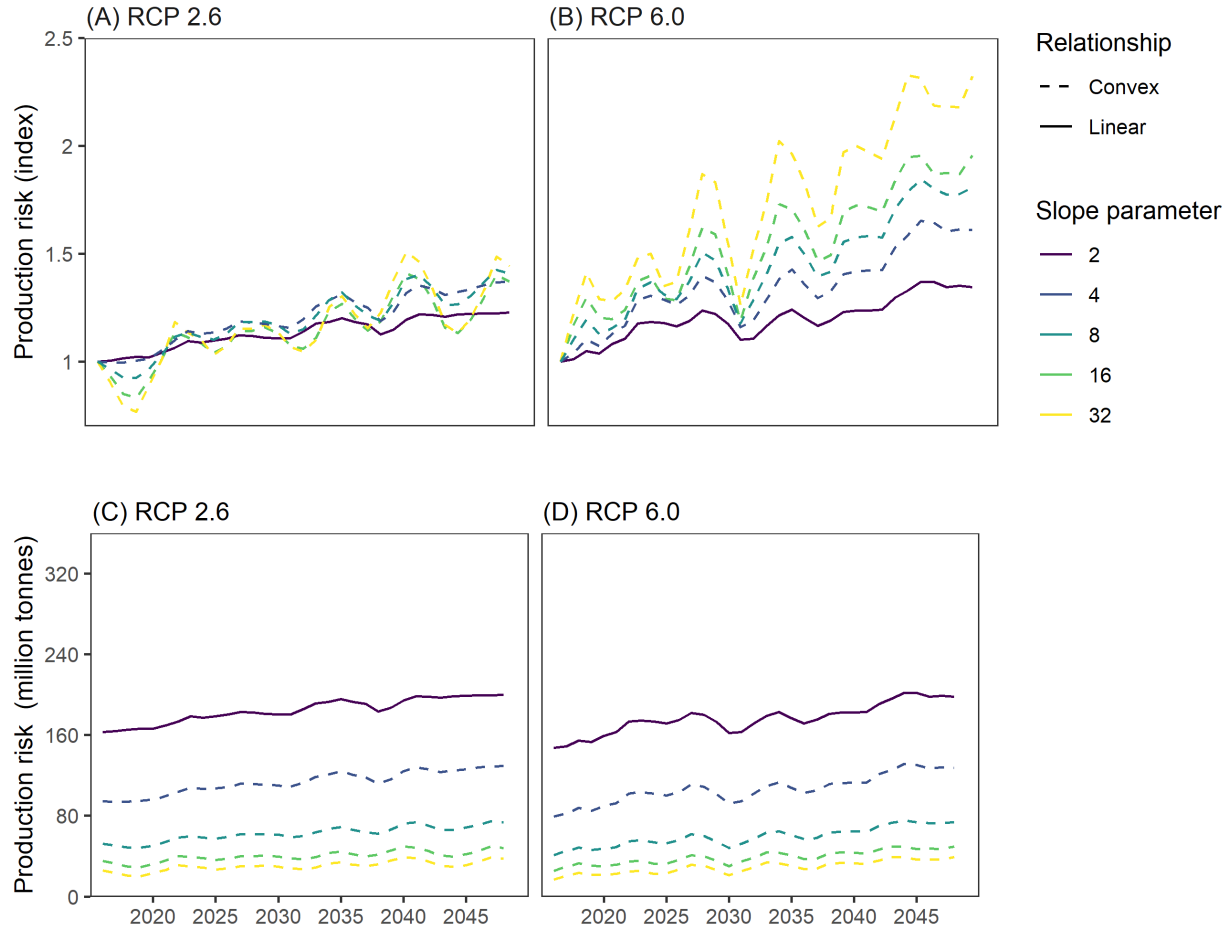


Figure 2: Projected change in total production risk under two RCP scenarios (2.6 and 6.0) and a set of different pollinator abundance-crop production relationships (linear and varying degrees of convexity). Results are shown both for an index of change in relative risk (A and B) and for absolute total production 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.

134 Production risk from insect pollinator abundance losses is highest, and predicted to increase most rapidly,
 135 in regions of sub-Saharan Africa, northern South America, and southeast Asia (Figure 3A and Figure 3C).
 136 Somalia, Guinea Bissau, and Ivory Coast emerge as particularly vulnerable, given their high and increasing
 137 production risk, and the high dependence of their economy on agriculture (Figure 3C). A number of countries

138 in Asia, South America, and the Caribbean have high and increasing levels of production risk, but lower levels
139 of agricultural dependence, making their economies less vulnerable overall. For example, the Philippines,
140 Indonesia, Papua New Guinea, Puerto Rico, Haiti, and Suriname all have high and increasing levels of
141 production risk (Figure 3C), but relatively low GDP adjusted pollination dependent production. Among
142 crops, cocoa is estimated to be at highest risk by a large margin, followed by mango and watermelon (Figure
143 3B). The risk to cocoa production is all the more significant from a social and economic perspective, as
144 most cocoa is produced on small farms (two to four hectares) that provide income to between 40 and 50
145 million people globally (51). Coffee is also expected to have a combination of relatively high production risk
146 and high value, suggesting that regions in which it is grown may experience economic difficulties, unless the
147 pollination service can be replaced cost effectively. Similarly to cocoa, coffee production provides income to
148 millions of small-scale farmers and their families in the tropics (52). Therefore, the increased production
149 risk due to loss of pollinators could lead to increased income insecurity for some of the most vulnerable
150 people globally. Projections of local crop production risk are sensitive to the assumed abundance-production
151 relationship (Figure S08), with the exception of South East Asia which is consistently resolved as high risk,
152 and the temperate realm which is consistently predicted as low risk (Figure S09).

153 For both countries and crops it is difficult to predict how the consequences of our production risk measure will
154 play out in the real world. In part this is due to the push and pull of multiple uncertainties, some of which
155 we do explore here (e.g. the relationship between pollinator abundance and crop production), but many of
156 which we do not or cannot (e.g. the changing distribution of crops, the economic viability of hand pollination,
157 the buffering effects of managed pollinators, the effects of climate change alone, and other technological
158 solutions such as the breeding or engineering of pollinator independent cultivars). Regardless, at the global
159 scale independent of changes in agricultural intensity, it's not unreasonable to state that the distribution
160 of standardised temperature anomaly and animal-pollinator dependent crop production should predict a
161 substantial portion of the variation in pollinator-mediated losses to crop production. For cocoa, recent
162 research has focused on the direct effects of climate change on crop production (53, 54), often overlooking
163 those that might be pollinator-mediated. Given the difficulties in teasing these mechanisms apart, and that
164 the direct effects of climate change are easier to intuit, it is probable that this trend continues. However, and
165 importantly, solutions to direct and pollinator-mediated effects will differ. For example, shade trees might
166 protect crops from extreme temperatures (53), but might not for the ceratopogonid fly pollinators on which
167 cocoa pollination depends. This is particularly pertinent given that some cocoa varieties are limited more
168 by pollination availability than resource availability (55).

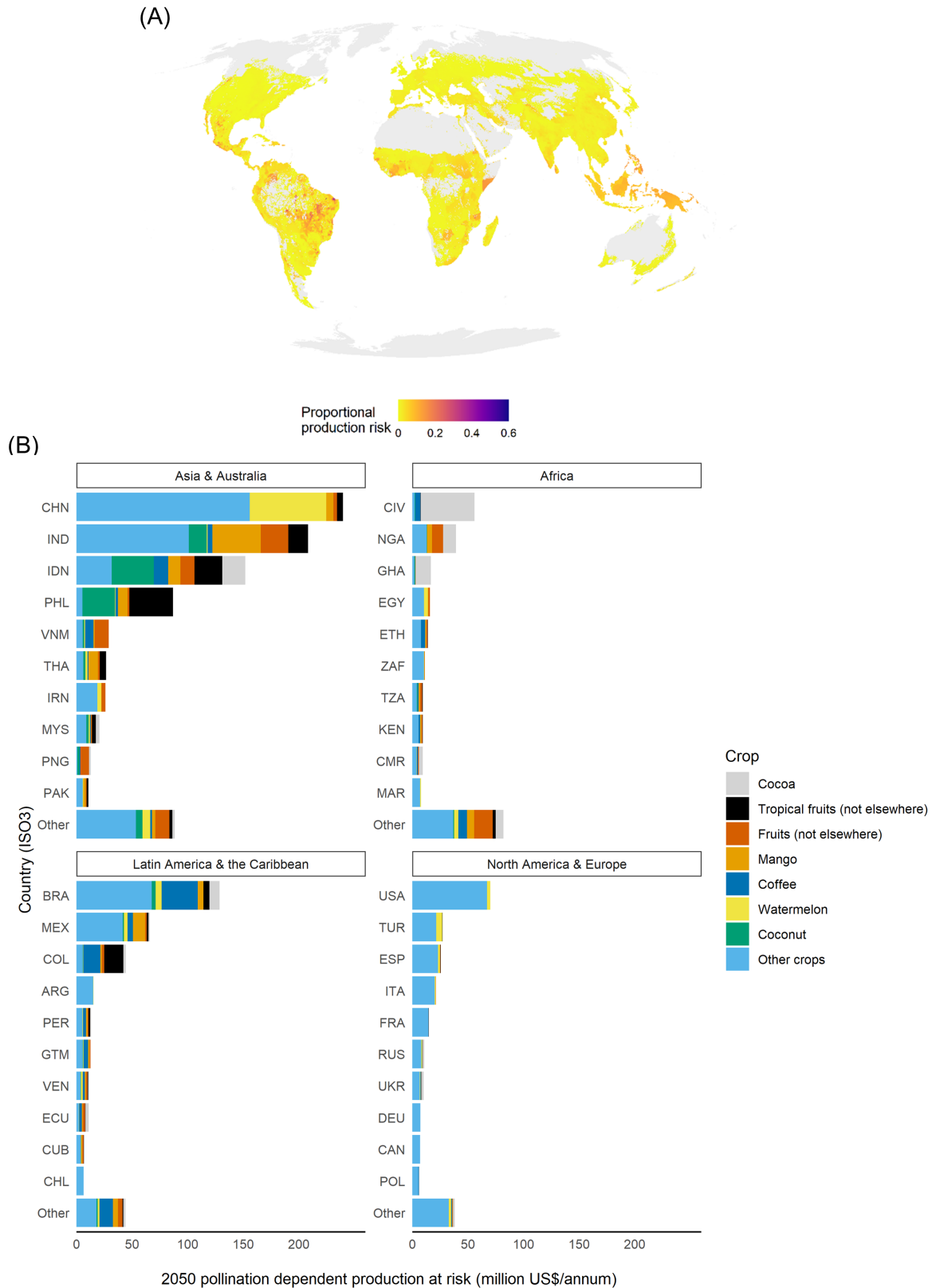


Figure 3: Projected change globally in the fraction of crop production estimated to be at risk in 2050 under the RCP 6.0 climate scenario, assuming a linear relationship between insect pollinator abundance loss and production loss for crops dependent on animal pollination. All projections are based on mean projections of the standardized temperature anomaly⁸ 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 (in each spatial cell), as a proportion of the production of all crops grown in that spatial cell (i.e. proportional production risk; see Figure S08 to see how cell-level risk differs among abundance-

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. The exception is the Netherlands which has the third largest overall import risk, much higher than expected based on its size but consistent with its status as the greatest importer of cocoa beans worldwide (57). Import risk per capita 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, 19th in 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 are 5th, 8th and 27th highest pollination import risk per capita). Our predictions of import risk are based on trade patterns from the present day (35), meaning we do not account for changes in trade flows that will likely occur in the future.

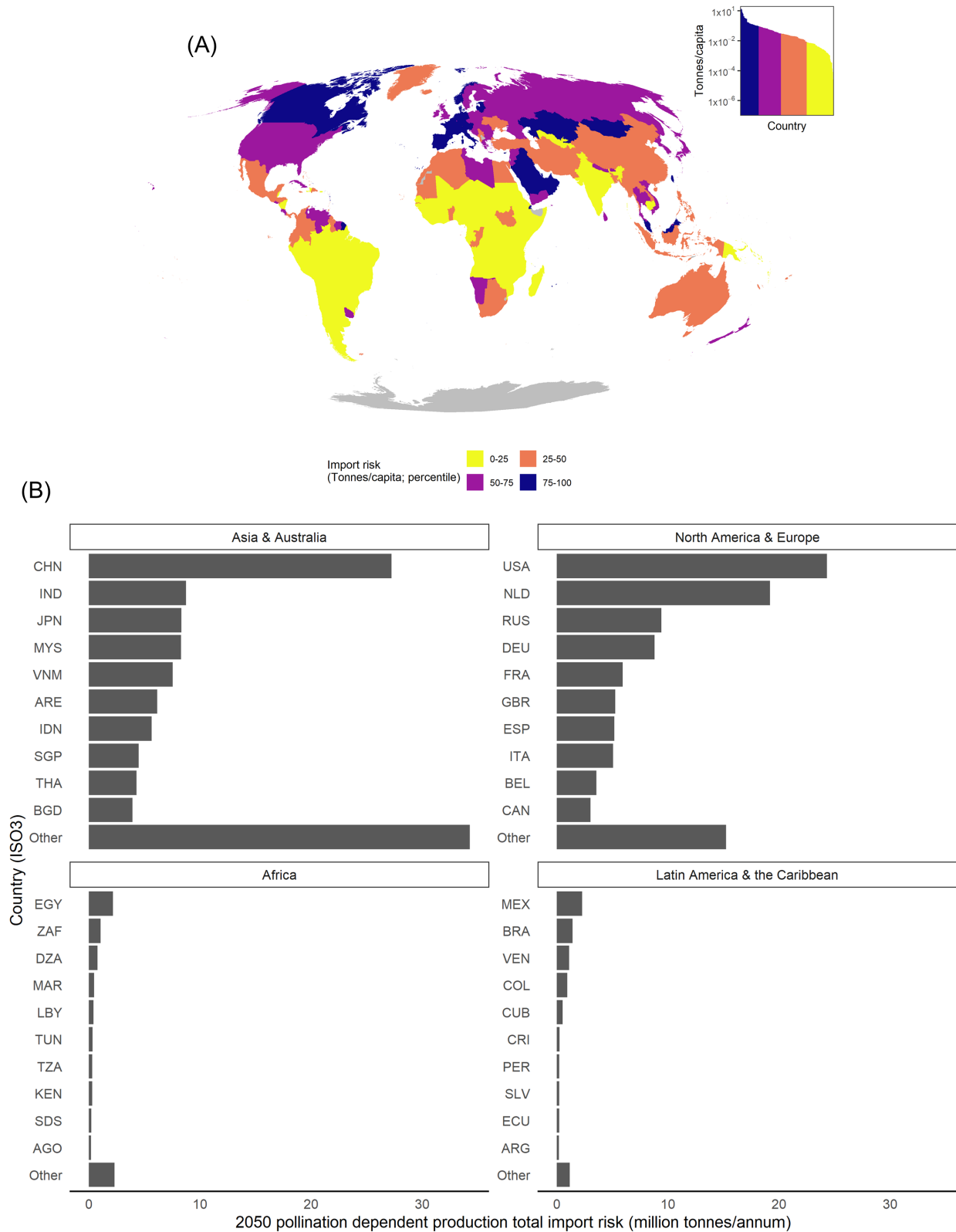


Figure 4: Projected total import risk for 2050 under the RCP 6.0 scenario, assuming a linear relationship between insect pollinator abundance loss and production loss. Projections are based on changes in the mean standardized temperature anomaly based on projections from an ensemble of individual climate 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

185 Interacting effects of climate change and anthropogenic land use are rapidly restructuring biodiversity (26,
 186 58). Here we show that the combination of agricultural land use and recent climate change is associated
 187 with particularly large reductions in the abundance of insect pollinators. We further show that the tropics
 188 will likely experience the greatest risk of future pollination shortfalls, putting at risk the production of crops
 189 that depend on insect pollination. The risk to these crops is highest, and predicted to increase most rapidly,
 190 in regions of sub-Saharan Africa and northern South America, especially in areas used to produce cocoa,
 191 mango, pumpkin, melon, watermelon, and coffee. Given the many factors that determine crop production
 192 and crop price (59), the likely effects of insect pollinator losses on crop production are unclear, and even if
 193 they do occur, conclusive attribution is likely to be challenging. Such complications likely in part explain
 194 why identifying a strong effect of pollinator losses on global crop yield and price has thus far been so
 195 difficult (33, 60, 61). Regardless, there is sufficient evidence to suggest that declining insect pollinator
 196 abundance will influence crop production risk, particularly for those in the global south (62). Such risk
 197 could manifest in the form of direct and immediate losses to crop production through pollinator shortfall
 198 and fluctuations in the stability of production, as well through decreased resilience to changes that will
 199 happen in conjunction (e.g. the effects of extreme temperature and drought on crop growth). The health,
 200 well-being, and livelihoods of billions of people, from small farmers to consumers, relies to some extent upon
 201 the availability and affordability of crops dependent on animal pollination, and therefore on those pollinators
 202 (63). Climate change and agricultural land use could put these people’s well-being at very high risk.

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Author contributions

Conceptualization: JM, TN

Methodology: JM, CO, TN, LD, JO

342 Investigation: JM, SC
343 Visualization: JM
344 Supervision: TN
345 Writing – original draft: JM, TN
346 Writing – review & editing: JM, TN, CO, LD, JO, SC

347 **Competing interests**

348 All authors declare that they have no competing interests.

349 **Data and materials availability**

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

351 **Supplementary Materials**

352 Materials and Methods
353 Figs. S1-S13
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