



Coupling of pollination services and coffee suitability under climate change

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Climate change will cause geographic range shifts for pollinators and major crops, with global implications for food security and rural livelihoods. However, little is known about the potential for coupled impacts of climate change on pollinators and crops. Coffee production exemplifies this issue, because large losses in areas suitable for coffee production have been projected due to climate change and because coffee production is dependent on bee pollination. We modeled the potential distributions of coffee and coffee pollinators under current and future climates in Latin America to understand whether future coffee-suitable areas will also be suitable for pollinators. Our results suggest that coffee-suitable areas will be reduced 73–88% by 2050 across warming scenarios, a decline 46–76% greater than estimated by global assessments. Mean bee richness will decline 8–18% within future coffee-suitable areas, but all are predicted to contain at least 5 bee species, and 46–59% of future coffee-suitable areas will contain 10 or more species. In our models, coffee suitability and bee richness each increase (i.e., positive coupling) in 10–22% of future coffee-suitable areas. Diminished coffee suitability and bee richness (i.e., negative coupling), however, occur in 34–51% of other areas. Finally, in 31–33% of the future coffee distribution areas, bee richness decreases and coffee suitability increases. Assessing coupled effects of climate change on crop suitability and pollination can help target appropriate management practices, including forest conservation, shade adjustment, crop rotation, or status quo, in different regions.

coffee | adaptation strategies | smallholder farms | suitability modeling | pollination

Climate change impact assessments suggest a significant reduction, up to 50% (1, 2), in the global area suitable for coffee farming by midcentury. Such losses will affect the livelihoods of 100 million people in the coffee industry (2). The direct effect of climate change on the climatic suitability of coffee farms may be mitigated or accentuated by further effect on pollinators (3). These coupled effects have not been examined in coffee climate studies.

Pollinator activity at flowers has a positive effect on coffee yield (4), fruit set (5–7), and berry weight (4, 7). Significant fruit set increases occur on coffee farms as the number of bee species increases from 3 to 20 (5). Native bee species are often more effective coffee pollinators than nonnative honey bees (8), and maximizing their diversity can help provide continuous pollination over time (9). The number of flower visits and pollen deposition on flowers are higher for coffee plants close to the forest (5, 9–11) because food and nesting sites maintain pollinator populations year-round (9). Native bee foraging activity declines within hundreds of meters (up to 1,600 m) from forests where bees nest (9), making forest proximity an important determinant of pollination service. In tropical forest regions where coffee is grown, the abundant native bees are meliponines (Meliponini, subfamily Apinae), colonial stingless bees that require nesting

cavities (11) and year-round resources. Naturalized Western hive bees (*Apis mellifera*) also are important coffee pollinators (4); they forage considerably farther and rely less on forests for nesting (11), but they readily relocate or abscond (12) and can be dangerous.

Climate change can affect the geographic distribution of pollinators (13, 14), and thus the effectiveness of pollination. Therefore, coffee production will likely be affected by climate change in two ways: directly, through the effects of changes in temperature, rainfall, or extreme events on coffee production, and indirectly, through changes in pollination services. However, it is not clear whether climate effects on pollinators will accentuate or offset future losses of coffee-producing areas, particularly in the complex montane topographies that produce coffee of high quality. Assessing the coupling between the dual factors that drive coffee yield is critical for developing management responses for a crop that depends on pollinators and supports many farming communities worldwide. A detailed spatial assessment of climate change effects on both coffee suitability and bee diversity is required for effective planning and management.

Significance

Coffee production supports the livelihoods of millions of smallholder farmers around the world, and bees provide coffee farms with pollination. Climate change will modify coffee and bee distributions, and thus coffee production. We modeled impacts for the largest coffee-growing region, Latin America, under global warming scenarios. Although we found reduced coffee suitability and bee species diversity for more than one-third of the future coffee-suitable areas, all future coffee-suitable areas will potentially host at least five bee species, indicating continued pollination services. Bee diversity also can be expected to offset farmers' losses from reduced coffee suitability. In other areas, bee diversity losses offset increased coffee suitability. Our results highlight the need for responsive management strategies tailored to bee pollination, coffee suitability, and potential coupled effects.

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Here we estimate the degree of coupling between the potential responses of coffee and pollinators to climate change in Latin America, the world's largest coffee-producing region [$>80\%$ of global arabica coffee production (15)]. More than 80% of Latin America's coffee is from smallholder farms of less than 4 ha (16), making the region a good case study for examining the effects of climate change on smallholders of relatively low income. We identified areas across the continent (tropical or subtropical North and South America) that may experience either positive coupling (areas with an increase in both bee richness and coffee suitability) or negative coupling (areas with joint decrease in bee richness and coffee suitability) under future climate scenarios. We also mapped areas where there will be a decoupling of coffee pollination services and suitability (areas where coffee suitability and bee richness change in opposite directions). Our analysis allows improved understanding of the combined effects of climate change on coffee production and helps identify specific management needs for areas that will experience either coupled or decoupled impacts.

We estimated the spatial changes in coffee and pollinator suitability under climate change, using a machine-learning modeling approach [Maxent algorithm (17)] for arabica coffee (*Coffea arabica*) and 39 coffee-pollinating bee species (including the Old World and naturalized honey bee; Table S1). For both bee species and coffee, we used 19 climate variables (at $\approx 1 \text{ km}^2$ resolution; Table S2) to predict species range distributions for reference (1950–2000) and future (2041–2060) mean climate conditions (18) under representative concentration pathways (RCP) 4.5 and 8.5 (Wm^{-2} of radiative forcing) with 19 and 17 downscaled Coupled Model Intercomparison Project 5 (CMIP5) general circulation models, respectively.

Results

Our models predict that the total current suitable areas for coffee production in Latin America will be reduced by 73% and 88% for mid and high warming scenarios, respectively (hereafter, ranges indicate results from RCP4.5 and RCP8.5 scenarios) (Fig. 1). These estimates are larger than those reported in studies using coarser resolution approaches, which yield $<30\%$ reductions for Latin America (1) using 2.5 arc-minute resolution. The higher resolution of our model in mountainous regions, and differences between climate model generations [i.e., Special Report on Emission Scenarios (SRES)/CMIP3 vs. RCP/CMIP5] used here account for the different results (1, 2). Most of the future suitable range for coffee will occur in areas currently suitable for coffee. However, some future coffee-suitable areas (12–30%) will occur in new areas.

We also found a general reduction in future bee richness over 65% of the continent (for both RCP4.5 and RCP8.5). An increase in bee richness occurred on only 4–5% of the continent (Fig. 2). Coffee-suitable areas are concentrated in areas of high pollinator

diversity (mean, 13.0 bee species per 1 km^2 pixel) compared with the continent overall (mean, 4.8 species per 1 km^2 pixel) (Fig. 1). In future coffee-suitable areas, mean bee species diversity fell to 10.7–12.0 species/pixel, while continental mean bee diversity reached 2.5–2.6 species. Continental bee richness was mostly explained by species persisting in sites, rather than being redistributed into new areas. Future species distributions have a median persistence area (i.e., suitable under both current and future climates) of 76–96% across genera. Although future areas suitable for coffee show a general loss in bee species richness, about 16% of coffee-suitable areas will gain bee richness relative to their current state.

Despite these overall losses, coffee-suitable areas under future climate scenarios will retain significant bee diversity. Mean bee richness will decline 8–18% within future coffee-suitable areas, but all are predicted to contain at least 5 bee species, and 46–59% of future coffee-suitable areas will contain 10 or more species (Fig. 3).

Positive coupling (e.g., areas showing an increase in both future coffee suitability and bee richness) occurred in 10–22% of future coffee-suitable areas. Most positive coupling occurred in Central America (Fig. 4). In contrast, 34–51% of the future coffee distribution showed widely distributed negative coupling, and thus, decreases in both coffee suitability and bee richness (Fig. 4). Decoupling occurs in much of the region, and most was a result of bee richness loss in areas where coffee suitability increases (31–33% across future coffee-suitable areas). Between 8% and 10% of future coffee-suitable areas gained bee richness but lost suitability for coffee (Fig. 4).

Most of the current and future suitable areas (91% and 97%, respectively) for coffee were within 1,600 m of forest, a distance that may allow at least some pollination services from forest-dependent bees (9). Such areas, therefore, will remain central for native pollinators, assuming forests continue to be conserved in these areas.

Discussion

Our findings concur with previous studies indicating large declines in future areas suitable for the production of high-quality coffee because of their sensitivity to increased temperatures (2). The small areas of increased coffee suitability generally occur in higher-elevation areas, as suitability moves upslope to compensate for increased temperature (1, 19). This explains the significant loss in total suitable area in less montane areas (Nicaragua, Honduras, and Venezuela) and slight expansion in other areas (Mexico, Guatemala, Colombia, and Costa Rica). Areas of new coffee-suitability face new deforestation threats (1) as coffee potentially expands into areas that are currently forested. The magnitude of those changes depends on the level of warming under future scenarios (2).

We also found that declines in coffee suitability were combined with potential declines in bee richness, with consequent reduced benefits in productivity from pollination. Nevertheless, future coffee distribution will cover areas with high bee richness

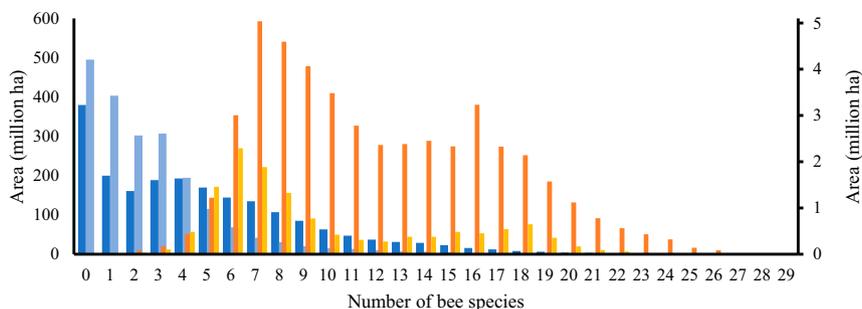


Fig. 1. Area histogram for bee richness across the continent and coffee-suitable areas under current and future climate (mid global warming). Distribution of area per number of bee species for the continent (left axis): dark blue under current climate and light blue under future scenarios, and for coffee-suitable areas (right axis): dark orange for current distribution and light orange under future climate.

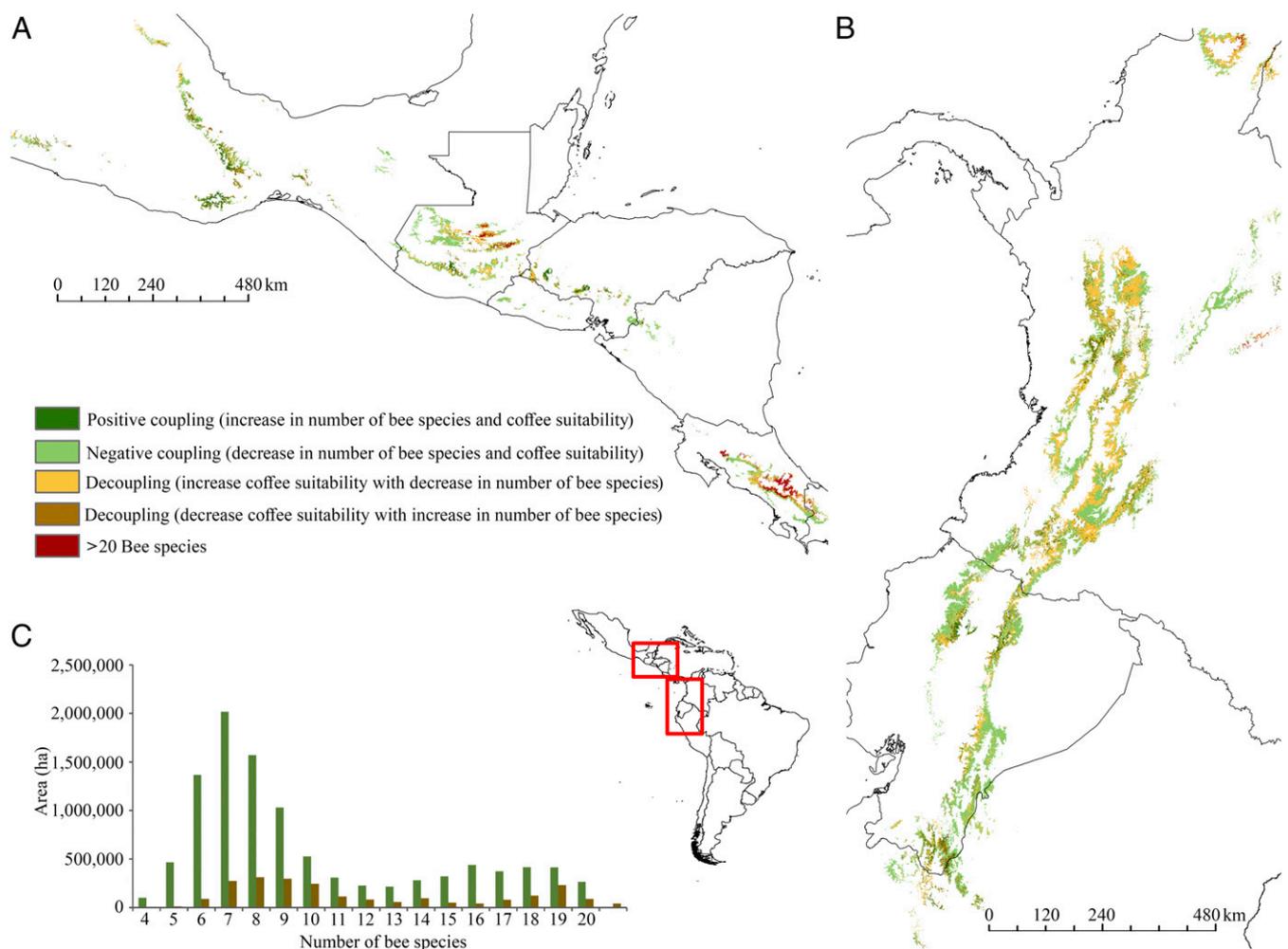


Fig. 4. Coupling of changes in pollination services and coffee suitability under climate change scenarios (RCP4.5). (A and B) Dark green denotes positive coupling (increase in both bee richness and coffee suitability), and light green denotes negative coupling (decrease in both bee richness and coffee suitability) occurring over 10% and 51% of future coffee distribution areas in Latin America, respectively. Decoupling occurs because increased coffee suitability potentially offsets positive effects of increased bee species (brown, 8%). Red areas (1%) indicate high bee richness (>20 species) regardless of climate change impacts. (C) Histograms indicate the total number of bee species over areas showing declined (green bars) and increased (brown bars) number of bee species over future coffee-suitable areas with pollination services (>3 bee species).

in areas where bee diversity is expected to decrease, while coffee suitability will increase, adaptation strategies should prioritize implementing coffee plot and farm management that increases bee habitat and helps ensure native bees are continuously maintained. Conversely, in areas where bee diversity is expected to increase while suitability for coffee cultivation decreases, coffee and farm management practices that minimize the effects of climate change on coffee production should be a priority. Finally, in locations where coffee suitability and bee suitability will both increase in the future, there is no current need for adaptation action, as the future conditions will become more favorable for coffee production.

Forest conservation and the maintenance of heterogeneous agricultural landscapes, with shade trees, windbreaks, live fences, weed strips, and protection of native plants that provide food resources and nesting sites and materials, are no-regret adaptation strategies. These strategies not only support future pollination service but also conserve biodiversity (23) and provide multiple ecosystem services today (24), such as water regulation and climate change mitigation (25, 26). Managing a diverse, complex shade canopy could be a double-win that allows coffee to adjust to changes in climate while improving bee habitat. Additional research is needed, given the complex relation between shade and

coffee under different climate conditions, but as bees and their host crops converge on smaller habitat area, an active and flexible human management role is vital to crops and their productivity.

Our study has highlighted the existence of coupled impacts of climate change on coffee production through effects on both coffee suitability and bee diversity. This enhanced understanding of coupled impacts can help target adaptation strategies and prioritize adaptation policies for a globally important crop that supports millions of households in some of the most biodiverse regions on earth.

Methods

Coffee and Bee Species Observational Data. Coffee-pollinating species were selected based on literature review (Table S1). Historical observations for the 39 selected bee species were obtained from global (Global Biodiversity Information Facility, www.gbif.org; Integrated Taxonomic Information System, www.itis.gov; Bee Database Project, www.discoverlife.org) and national databases (National Institute of Biodiversity in Costa Rica, www.inbio.ac.cr). We selected species with a total of >25 observations across datasets. Repeated observations (on the same site) across databases were removed. A total of 3,767 observations were used for all species with a minimum/median/maximum number of observations of 27/59/826, respectively (Table S1). Coffee observations made up a global coverage of 2,194 presence location points of *Coffea arabica* selected from a larger data collection effort (of >65,000 observations), literature review, and additional sites provided by coffee research institutes from 19 countries (1).

Potential Climate Niche Modeling. We used the Maxent tool (17) to model species distribution ranges using species' presence records and environmental data. The modeling approach has shown improved outputs compared with other common methods used to predict species distribution ranges (27). The tool calculates a function describing the probability of species presence based on environmental variables (determinants) and tests for their interactions (e.g., between precipitation and temperature layers over the dry season that might be important for defining species distribution ranges) and variable transformations (27). The function is based on comparing the density of the determinants (i.e., climate layers) between species-presence sites and the background area (i.e., the whole study area). To reduce errors from spatially biased bee species records, we used a sample point selection within a buffered minimum convex polygon (28) from the Species Distribution Models Toolbox (28) to correct the background sampling of the determinants performed over a randomly selected set of 10,000 pseudoabsence sites. Coffee presence data had extensive coverage (1), so the background sampling area was not corrected. Model validation was performed using a sample of randomly selected observations (10% of total observations) not used to train the model, and based on the area under the curve of the receiver operating characteristic (29). Maxent output provides a continuous probability map of species presence. We selected a threshold value to define suitable and unsuitable areas for bee species based on equal errors in sensitivity (proportion of accurately predicted presences) and specificity (proportion of absences accurately predicted; Table S1), as recommended by comparative studies (30).

Potential niche models allow estimating current and future suitable environmental conditions ("climate envelopes") for a species assuming that: its climate envelope remains constant (31) (no in situ adaptation or rapid evolutionary response) and ignoring the effect of new determinants (i.e., increased CO₂); and more important, that species can freely migrate and colonize new landscapes without accounting for dispersal limitations or landscape barriers (17). Current potential niche distributions might differ

from realized niches as a result of topographic barriers, species competition (31), pests, predators, diseases, new variety developments, or novel climates (32), which can affect the capacity to simulate future ranges of individual species.

Climate Change Scenarios. We used WorldClim (18) high-resolution (1 arc-second or ~1 km²) climatology representing means of monthly precipitation and temperature (mean, maximum, and minimum) for 1950–2000. The database has global coverage and was generated by interpolating weather station data, elevation, latitude, and longitude as independent variables. Future climate scenarios were developed using a simple statistical method based on adding coarse-scale future climate anomalies, simulated by general circulation models, to a high-resolution reference climatology (18). Future climate anomalies were derived from 19 of the latest generation of general circulation model simulations from the CMIP5 (33) under a representative concentration pathway of greenhouse gases leading to 4.5 and 8.5 Wm⁻² global warming (RCP4.5 and RCP8.5).

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