



Biogeography of pollination under climate change: integrating pollinator effectiveness into species distribution models for mango in South Africa

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Abstract

Pollination by wild insects is vital for maintaining ecosystems and food security, but climate change is altering the biogeography of many pollinator species. While progress has been made in assessing climate-driven range shifts using species distribution models (SDMs), most assume all pollinators are functionally equivalent. Here, we introduce a biogeographic approach that integrates Pollen Deposition Effectiveness (PDE), a quantitative metric of species pollination function, with SDMs by summing PDE values of co-occurring pollinators to assess climate-driven changes in both pollinator distributions and their capacity to deliver pollination services. We demonstrate this approach using mango (*Mangifera indica*) pollinators in South Africa. We identified 61 mango flower visitors, quantified PDE for 38 pollinating species and projected changes in climatically suitable habitat under two climate scenarios (RCP4.5 and RCP8.5) using SDMs. Both species richness and PDE-weighted pollination provision are predicted to decline across core mango-growing regions, alongside substantial species turnover. We find similar spatial patterns of PDE-weighted and unweighted SDMs, indicating high functional redundancy and identify some over-performing pollinators which could be the focus of targeted conservation efforts. We believe this functional approach enhances SDM outputs and provides greater insight for assessing climate change impacts on ecosystem services.

South Africa (Limpopo, Mpumalanga and KwaZulu-Natal provinces).

- We identified members of Hymenoptera and Diptera as the most common mango pollinators, while members of Coleoptera, Lepidoptera and Hemiptera do not transfer mango pollen or there are insufficient data to assess them.
- We identified smaller species such as those belonging to Calliphoridae and small bees like *Liotrigona* species were the most efficient mango pollinators.
- We identified 38 mango-pollinating insects and found an overall decrease in their future suitable habitat under RCP4.5 and RCP8.5 climate scenarios.
- A decrease in mango pollination could decrease mango production, affecting more than 10,000 people working in mango processing and support industries, many smallholder farmers who operate in the informal market and those who grow mango for personal consumption.

Keywords

climate change, ecosystem services, *Mangifera indica*, pollination, pollinator effectiveness, species distribution models

Highlights

- We used pollination efficiency calculations and species distribution models (SDMs) to assess potential declines of important mango pollinators in

Introduction

Pollination is vital for agriculture, yet pollinators are in decline globally (Potts et al. 2010). Worldwide, over 75% of major crops rely on animal pollination, primarily by insects, for yield and quality (Potts et al. 2016). It is a service valued from US\$195 billion up to US\$657 billion per year

(Porto et al. 2020). Pollinators also sustain most of the world's plant diversity and the people and ecological communities relying on it, by assisting in plant reproduction (Ollerton 2017). Pollinators are, therefore, necessary for maintaining both ecosystems and food security.

Climate change is a contributing factor to pollinator shifts, driving many species towards higher latitudes and elevation where possible (Forrest 2017). While substantial progress has been made in mapping pollinator distributions and assessing climate-driven range shifts using species distribution models (SDMs), most assume all pollinators are functionally equivalent, each contributing equally to pollination. This assumption overlooks variation in morphology and behaviour which determine how effectively a species deposits pollen and, therefore, how well it contributes to pollination services. This is especially important in generalist crops which attract a myriad of visitors to mango flowers not specialised for pollinating them (Jiron and Hedstrom 1985).

To address this issue, our study combines SDMs with Pollen Deposition Effectiveness (PDE). This measure is based on the modular approach for comparing pollinator performance described by Ne'eman et al. (2017), which calculates pollen deposition as the product of single-visit pollen deposition (SVD) and frequency of visits. We incorporate an additional module, the effective visit percentage (proportion of visits involving contact with flower reproductive organs), to better account for morphological differences. The product of these modules is PDE, an estimate of the number of pollen grains deposited by a species per minute. Combining SDMs with PDE then requires replacing binary presences of SDM results with each species' corresponding PDE value and summing the PDE of co-occurring species. By incorporating PDE into SDM results, our study provides a framework that improves upon presence-based or richness-based estimates, allowing us to evaluate how climate change may differentially affect functionally important species versus less effective ones. It may be especially important in identifying cases where species numbers remain stable, but the total functional capacity of pollinator communities is reduced by the replacement of effective pollinators by less effective ones.

To demonstrate the utility of this framework, we apply it to a case study of mango (*Mangifera indica*) pollinators in South Africa. We use South Africa as a case study as we can build upon previous SDM methodologies (climate projection selection, SDM algorithms) by Groner et al. (2021) and Shen et al. (2023). Mango provides a useful system because studies of mango pollinators typically lack distinction between legitimate pollinators and visitors that do not transfer pollen (Ramírez and Davenport 2016). While several studies have compiled mango flower visitor lists, quantitative data on pollination effectiveness remain scarce. Mango also depends on pollinators for flower fertilisation, fruit production (Marcacci et al. 2023) and preventing fruit

malformation (Severiano-Galeana et al. 2024) and final fruit set and fruit weight are affected by pollinator type, abundance and species richness (Dag and Gazit 2000; Cabrera-Asencio and Meléndez-Ackerman 2021). Mango production, an important industry in South Africa, is therefore potentially at risk due to pollinator declines.

Mango processing and support industries employed 13,650 people in 2019 (DALRRD 2020) and provide indirect employment for communities near production sites. Mango production has been valued at over US\$25 million annually, with > 95% consumed within-country in 2020 (Grové 2022). However, these figures do not include mango sold by smallholder farmers in the informal market, nor mango often grown for personal consumption (C. Munyai pers. comm.). These lower-income farmers rely mostly on wild pollinators for crop production (Tibesigwa et al. 2019), are vulnerable to production disruptions (Ndlovu and Masuku 2021) and are amongst the most food-insecure populations in South Africa (Zondi et al. 2022). It is, therefore, vital to estimate the current and future distributions of effective pollinators and to understand the likely availability of pollination within South Africa in the coming decades. However, we emphasise that the primary aim of this study is to illustrate the value of integrating PDE into SDMs, rather than to provide definitive forecasts of mango pollination outcomes.

Based on previous studies predicting insect declines (e.g. Giannini et al. (2017)), we expected our raw SDM results to predict species' suitable habitat declines, species turnover and species richness losses. However, we hypothesised that the spatial patterns of pollination provision estimated by PDE would differ from raw SDM results and highlight regions where losses of highly effective pollinators may disproportionately reduce pollination provision. Using this framework, we deepen our understanding of the likely impacts of climate-change on crop pollination, which can guide more targeted conservation and agricultural strategies.

Materials and methods

Pollen deposition effectiveness framework

Our framework integrates a quantitative measure of pollinator function, PDE, with SDMs to evaluate the impacts of climate change on the functional capacity of pollinator communities. We utilised the framework to: (i) compile mango flower visitors present in South Africa and distinguish pollinators from non-pollinating visitors using PDE; (ii) conduct SDMs for pollinator species to estimate their climatically suitable area under present and future scenarios; (iii) calculate both species richness changes and potential pollination provision changes (PDE-weighted presence); and (iv) calculate species turnover to examine the functional consequences of community reassembly.

Study system and region

We used *Mangifera indica* in South Africa as a case study. Mango is a generalist, mass flowering crop which attracts a myriad of visitors to its flowers that are not specialised for pollinating them (Jiron and Hedstrom 1985; Halder et al. 2019). The generalist strategy ensures pollination occurs even if some pollinators fail to visit. However, visiting pollinators vary in their effectiveness, with many not transferring any pollen. This is largely due to the relationship of body size and tongue length: mango nectar is easily available to insects of all tongue lengths, but body size and tongue length together dictate the contact between the insect and the reproductive organs of the tiny mango flower. Feeding often results in contact with flower reproductive organs for medium-tongued honeybees (Sung et al. 2006), Diptera and Coleoptera (Jiron and Hedstrom 1985); however, Lepidopterans' height combined with a long proboscis allows them to feed on nectar without touching the flower's reproductive organs, resulting in no pollen transfer (Jiron and Hedstrom 1985). In Australia, short-tongued insects carrying pollen grains on their thoraces were the most efficient mango pollinators (Anderson et al. 1982). Due to these differences, estimating pollinator effectiveness is critical for distinguishing pollinators from non-pollinators and for identifying the most efficient pollinators.

We focused on the Limpopo, Mpumalanga and KwaZulu-Natal provinces in South Africa where mango production is concentrated (Fig. 1). The majority of mango production in South Africa by hectares of mango trees planted occurs in Limpopo (74%), followed by Mpumalanga (24%) and KwaZulu-Natal (0.15%) (SAMGA 2024), though informal production is not included in these figures and is widespread throughout.

This region is ecologically diverse, encompassing several climates (largely temperate, with arid regions further north and tropical regions in the south) with rainfall mostly during the summer (except in tropical zones) and temperatures typical of the Southern Hemisphere, though lowered in high-altitude regions. These provinces support mango production at commercial, smallholder and personal scales, allowing us to illustrate the framework's policy relevance, while emphasising that our primary aim is methodological.

Mango visitor data

We searched the literature to identify insect species that visit mango flowers around the world (Suppl. material 1: table S1) and then used the Global Biodiversity Information Facility (GBIF) to identify those species with at least 20 occurrence records since 1970 also present in South Africa (at least one record in-country) (Derived dataset GBIF.org 2025). We used a minimum of 20 occurrence records to limit model errors and allow k-fold cross validation (van Proosdij et al. 2016) and we used an earliest date of 1970 to avoid records that do not represent recent distributions and, therefore, do not coincide with recent climate data. Occurrence records were evaluated for signs of automated or erroneous data, including alignment with capital or centroid coordinates, identical latitude and longitude, proximity within one degree of GBIF headquarters or major biodiversity institutions, offshore records and records with plain zeros using the CoordinateCleaner package version 3.0.1 (Zizka et al. 2019). Of 14,670 records, 1,383 failed these checks and were removed (median 70 records per species). The final visitor list included 61 species (Suppl. material 1: table S1).

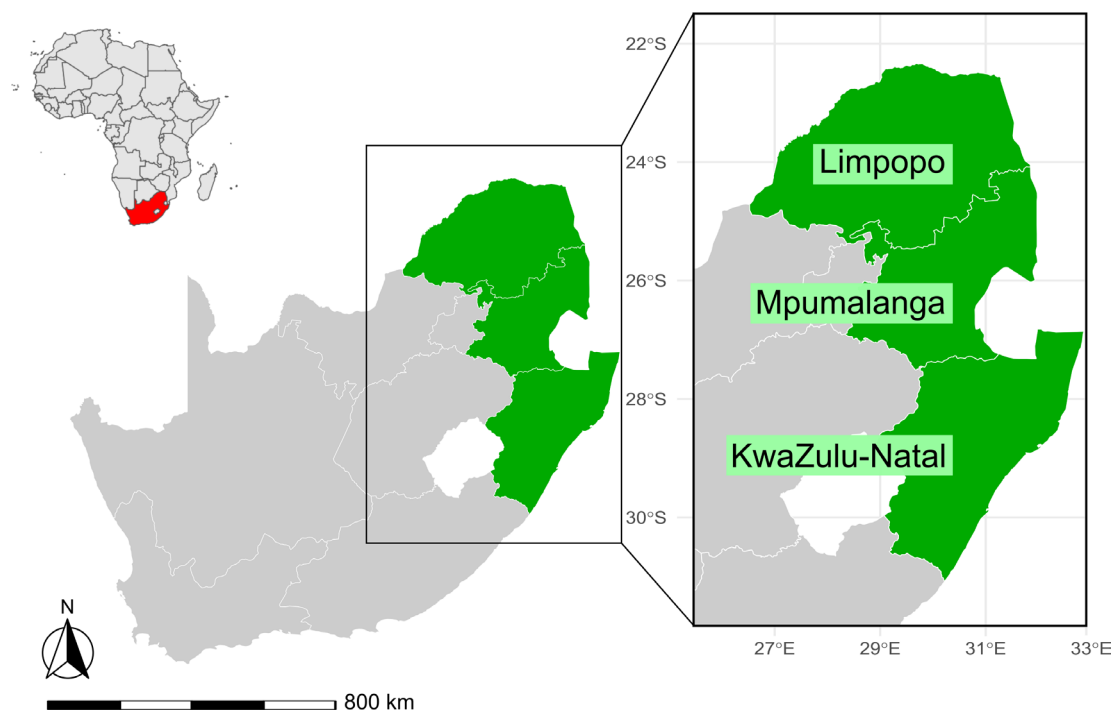


Figure 1. Study region: Limpopo, Mpumalanga and KwaZulu-Natal provinces within South Africa.

While not encompassing all pollinators, the presence of data within GBIF suggests that this list likely includes the most common species. Ant species were not included because mango production is thought to require cross-pollination and non-flying insects primarily drive self-pollination due to limited mobility, resulting in fruit abortion in self-incompatible cultivars (Carvalho et al. 2012).

Calculating pollen deposition effectiveness (PDE)

To distinguish pollinators from non-pollinating visitors and to weight species by function, we calculated PDE as:

$$PDE = \text{Visitation frequency} * \text{Effective visit \%} * \text{Single-visit pollen deposition}$$

The values for each component of the PDE formula were sourced by averaging values in the published literature (electronic supplementary material). For each species, a value of each component was assigned, based on the taxonomically closest value (Suppl. material 1: fig. S2). For example, there was no species-specific measure of mango flower visitation rate for *Allograpta calopa*, so the average value for its family (Syrphidae) was assigned. Species with PDE greater than zero were deemed pollinators, while species with a PDE of zero were considered non-pollinating visitors.

It is difficult to understand the significance of PDE, beyond recognising that larger values are better for pollination. For added context, Sánchez et al. (2022) demonstrated a positive relationship between pollen grains deposited by syrphid flies and flower fertilisation in the Osteen mango cultivar. Flowers that received over 10 pollen grains reached over 70% fruit set. In comparison, an average of 9.2, 5.2, 3.8, 2.6 and 0.1 pollen grains deposited across a tree's flowers resulted in fertilisation of 54.6%, 28.4%, 22.7% and 4% of flowers, respectively. Additional grains increase competition between pollen tubes, increasing their growth speed (Sánchez et al. 2022). While flower fertilisation is not linearly proportional to final fruit yield due to complex mechanisms of final fruit set and variation between cultivars, higher fertilisation has been found to produce higher yields in several studies (Deuri et al. 2018; Ela et al. 2021; Sánchez et al. 2022; Chauhan 2023). A higher PDE value indicates that less time is required to increase average flower fertilisation and, therefore, suggests higher yields. This is especially important in a mass flowering plant like mango, where thousands of flowers per tree must be pollinated in a few weeks.

Species distribution models

SDMs estimate the suitable climatic habitat (abiotic niche) of species through the relationship between occurrence points and current climatic conditions, which can then be projected under future climatic scenarios (Elith and Leathwick 2009; Peterson et al. 2011). We used SDMs

of pollinators to determine changes in species richness, potential pollination provision, species turnover and magnitude of climatic suitable area changes. Species richness positively affects mango yield (Cabrera-Asencio and Meléndez-Ackerman 2021) and is important in estimating functional diversity and redundancy that impact ecosystem resilience and recovery (Biggs et al. 2020). Species turnover reveals changes in species composition, which may be important considering pollinators have different PDEs. The magnitude of suitable area changes uncovers pollination availability changes and how climate change differentially impacts species. Important characteristics of mango pollinators which could not be quantified, but were considered when determining important pollinators, include mango flower attraction, species effects on fruit set, foraging distance, diet and nesting specialisation.

We selected climate variables for each species by searching literature for information on abiotic factors affecting their survival. Variables used by SDM studies on these or similar species were adopted if the rationale was adequately explained (Suppl. material 1: table S1). Present (1979–2013) and future (2061–2080) variables were sourced from CHELSA at a horizontal resolution of 30 arcseconds (Karger et al. 2017). Two representative concentration pathways (RCPs) were selected, RCP4.5 and RCP8.5, describing greenhouse gas levels and their effect on radiative forcing. RCP4.5 is an intermediate scenario where emissions increase until 2040 and RCP8.5 is a scenario of high emissions with no mitigation measures. We used projections generated by the HadGEM2-CC General Circulation Model (Martin et al. 2011) because Shen et al. (2023) found this model to predict well for South Africa.

Due to the variety of SDM algorithms and variability in their outcomes (Pearson et al. 2006), three contrasting algorithms were used and incorporated into an ensemble model following Araujo and New (2007). The selected algorithms were: Bioclimate Envelopes (a simple bioclimate envelope) and Generalised Linear Models (statistical regression), both implemented using the dismo package version 1.3-4 (Hijmans et al. 2015) and Random Forests (a machine-learning model), implemented using the RandomForest package version 4.7-1.1 (Liaw and Wiener 2002). These algorithms were implemented using package defaults. We emphasise that this choice was made to support a proof-of-concept demonstration and does not represent best practices for optimised, decision-ready predictions reviewed elsewhere (e.g. Guisan et al. (2025)). Each algorithm's outputs were averaged and values weighted by the area under the received operator curve (AUC-ROC) from 4-fold cross validation. AUC describes model performance in relation to observed occurrence records and ranges from 0.5 (no predictive ability) to 1.0 (perfect performance). Across all species, ensemble AUCs ranged from 0.636 to 0.979, with an average of 0.787 (0.1 standard deviation; Suppl. material 1: table S1). We note that, lacking true absence data, AUC-ROC can favour models that predict broader suitable areas, because pseudo-absences may include locations that are environmentally suitable, but unsampled (Lobo et al. 2008).

This is especially true for studies involving large regions, strong sampling bias and less-prevalent species. Therefore, our results may over-estimate climatically suitable areas and associated pollination provision.

For species richness calculations, continuous SDM outputs were converted to binary 'absence' and 'presence' by selecting a threshold to maximise the True Skill Statistic (TSS) (Liu et al. 2013). TSS better reflects true ecological phenomena in respect to its response to prevalence, compared to other methods, such as kappa, thus reducing the effects of spatial bias (Allouche et al. 2006). This threshold corresponds to the value where the sum of specificity (true negative rate) and sensitivity (true positive rate) are maximised. In cases where few occurrences resulted in zero or miniscule suitable area predicted, in contrast to occurrence records, the highest threshold at which there is no omission of occurrences was selected, to account for all datapoints. We acknowledge this thresholding criteria may result in over-estimation of suitable area for a few species where no occurrences are omitted and under-estimation for others due to the lack of true absence data. We then summed predicted presences across all species in each cell to give an estimate of species richness. We calculated the potential pollination provision at each locality as the sum of PDE of species located at the site by replacing each species' presence (1) with its PDE value.

Change in species composition (β -diversity) was calculated using Sørensen's dissimilarity with the betapart package version 1.6 (Baselga and Orme 2012). We calculated change in species composition for two components, species turnover and nestedness, to better understand underlying processes of community changes (Baselga 2010). Species turnover, calculated as Simpson's dissimilarity (following González-Orozco et al. (2014)), highlights regions of species loss with replacement. Nestedness highlights loss without replacement. We calculated percentage change and absolute change (km²) of suitable area using the terra package version 1.7-71 (Hijmans et al. 2025). Suitable habitat changes were classified into 'loss' (< -10%), 'gain' (> 10%) and 'no change' (-10% to 10%).

Importantly, our SDMs estimate climatically suitable area, not realised habitat. We did not include land use, land cover or phenology in our calculations. As a result, some areas deemed climatically suitable may not support populations and seasonal mismatches with mango flowering are not captured.

Results

Visitors versus pollinators

Of the 61 visiting species, 38 had a non-zero PDE and were classified as pollinators (Fig. 2). Pollinators corresponded exclusively to Diptera and Hymenoptera (flies, bees and wasps), particularly of the Apidae, Syrphidae, Calliphoridae and Rhiniidae families. Lepidoptera, Coleoptera and Hemiptera were not classified as pollinators due to 0%

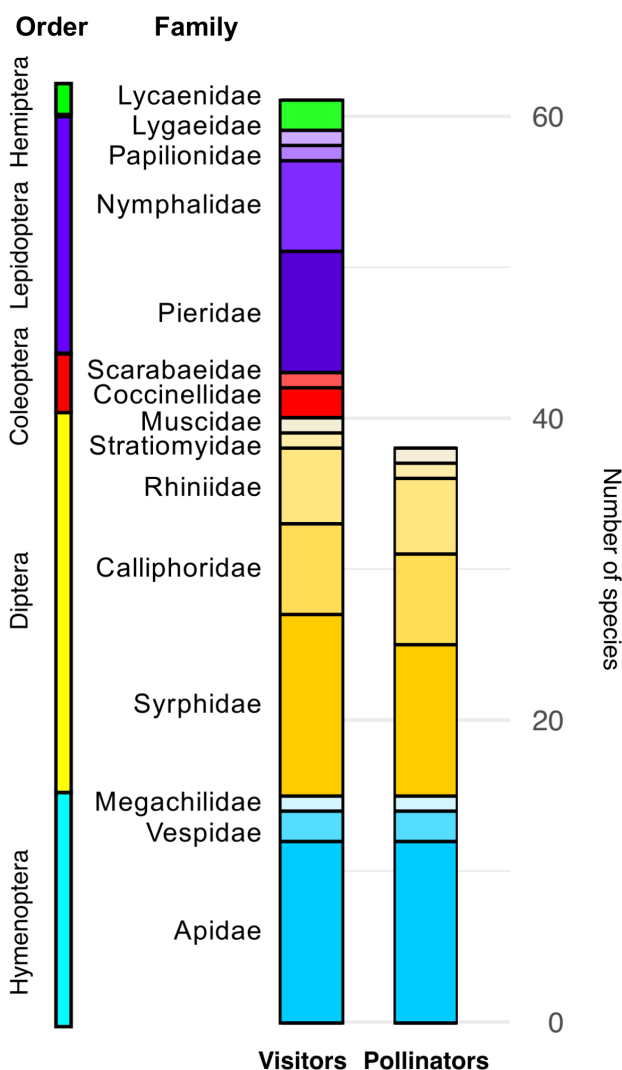


Figure 2. Visiting vs. pollinating species of mango in South Africa. Insect visitors of mango in South Africa (61), composed of five orders and 15 families ('Visitors'). Compiled from global studies describing visitors to mango flowers, which are also present in South Africa with at least 20 occurrence records on GBIF. Thirty-eight of these are pollinators (pollen deposition effectiveness > 0), belonging to two orders and eight families ('Pollinators').

effective visitation rate (Lepidoptera), no SVD data (Coleoptera) and no data for all components (Hemiptera).

Pollen deposition effectiveness

Of all pollinators identified, calliphorids, *Liotrigona bottegoi* (stingless bee), *Ornidia obesa* and *Musca domestica* (housefly) are found to have the highest PDE (Fig. 3). Other bees, wasps and syrphid flies were less effective. Higher efficiency for smaller, short-tongued pollinators is expected, given the role of body size and proboscis length. However, Syrphidae is an outlier, likely caused by data inconsistencies as several studies found opposing effective visit percentages due to low sample size (many 100% (e.g. *O. obesa*) and 0% values averaged to 43%).

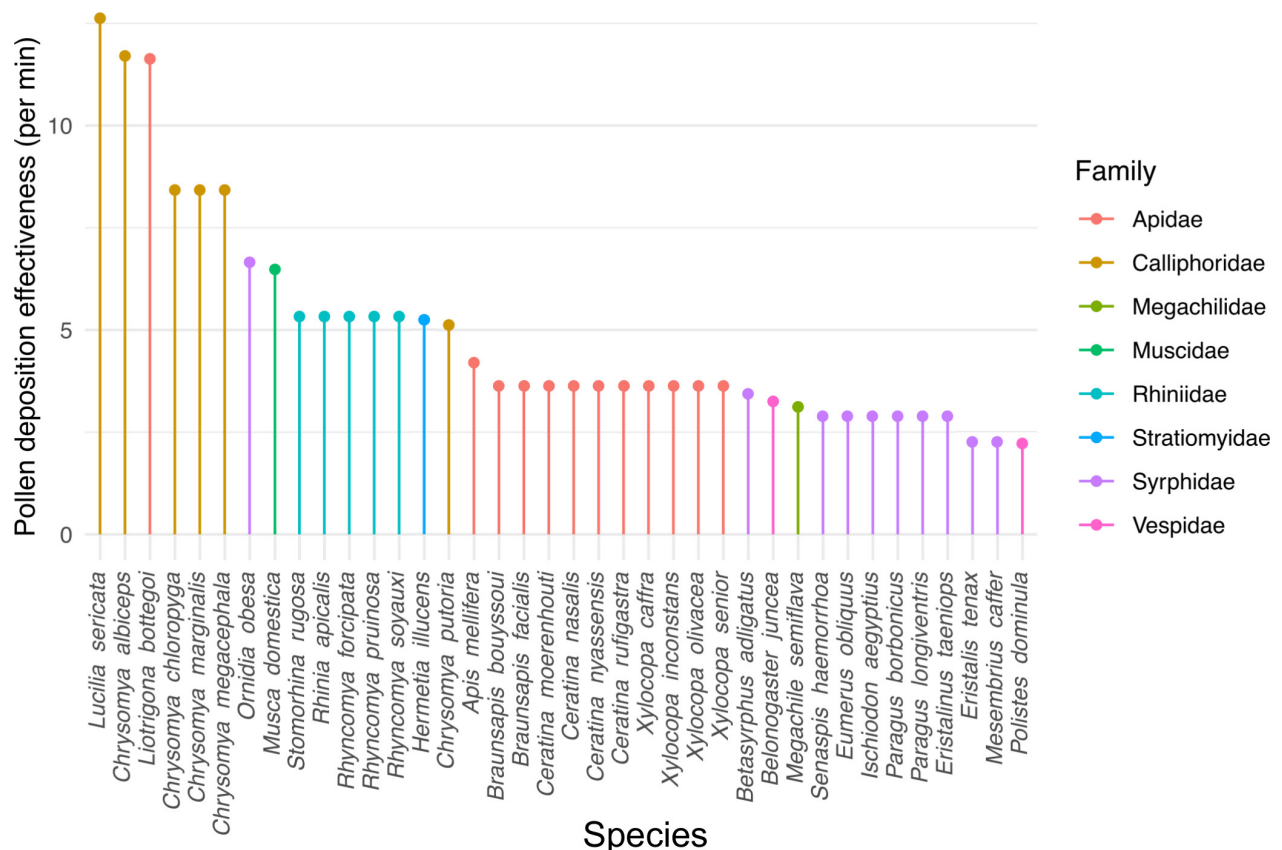


Figure 3. Pollen deposition effectiveness (PDE) of mango pollinators. PDE of mango pollinators, coloured by family (line and dot). PDE module values are sourced from global literature studying single-visit deposition, visitation frequency and effective visit percentage of insect visitors on mango flowers.

Rhiniidae values are also not likely representative of true PDE, as no visit effectiveness values were found for the family, meaning we had to rely on the Diptera average.

Overall, PDE differences are not extreme. If we assume the relationship between pollen grains deposited and fruit set described by Sánchez et al. (2022) is reasonable, then the top three species would achieve 70% fruit set, the following three around 50% and the remaining 32 would average around 25%. This distribution suggests a community without a single keystone pollinator, with several species contributing moderate effectiveness.

We explicitly acknowledge uncertainty from taxonomic extrapolation, sparse SVD or effective visit estimates for some families and possible context dependence of behaviour across habitats or regions. We, therefore, interpret PDE as a best-available, conservative index of relative function and will highlight data gaps where additional measurements are required.

Species richness and pollination changes

Pollinator species richness is estimated to be as high as 27 within the study area, particularly in KwaZulu-Natal (Fig. 4). Under both future climate scenarios, richness is mostly expected to decline or remain unchanged, with estimated gains limited to small, fragmented regions (southern Kwa-

Zulu-Natal) (Fig. 4). Diptera are predicted to overwhelmingly experience losses, while Hymenoptera gain species within Mpumalanga and KwaZulu-Natal (Suppl. material 1: fig. S3). RCP4.5 and RCP8.5 conditions show similar patterns, but RCP8.5 shows larger losses and gains for all measures.

Spatial patterns of potential pollination provision (PDE-weighted) and species richness do not differ substantially. This could be indicative of a community where functional contributions are relatively evenly distributed amongst species with moderate PDE metrics. This functional redundancy balances pollination provision, such that losses in species richness translate proportionally into reductions in functional capacity. Nevertheless, the loss of the most effective species may still have some impact, especially in regions with low species richness. Amongst them, *Lucilia sericata*, all *Chrysomya* species and both *Braunsapis* bees experience significant reductions in suitable climatic habitat even under RCP4.5 conditions. On the other hand, *Ceratina nyassensis* gains substantial suitable climatic habitat.

Species turnover and suitable habitat changes

Sørensen's dissimilarity shows most regions are likely to experience substantial changes in species composition (Fig. 5). Simpson's dissimilarity was highest in the centre

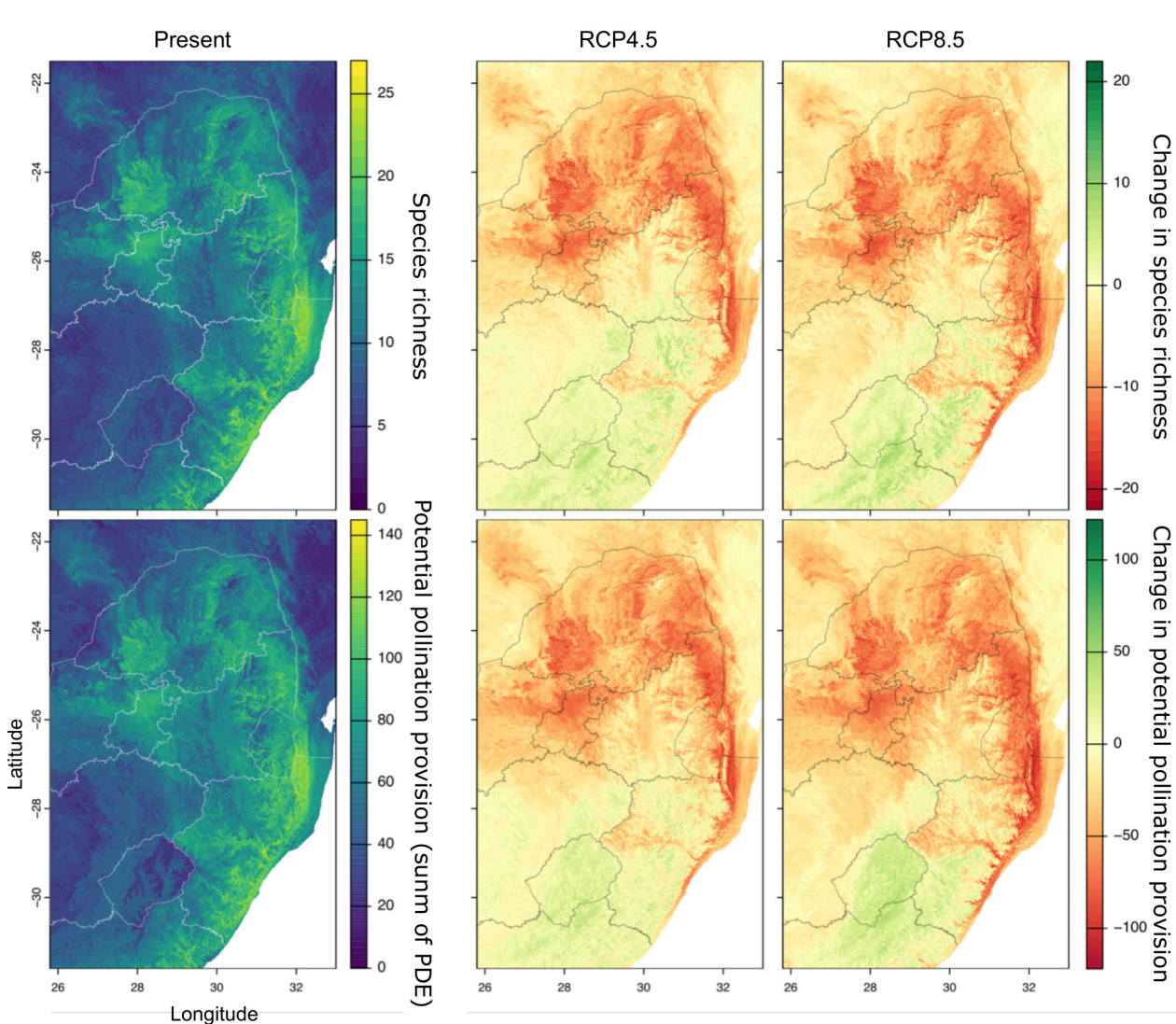


Figure 4. Mango pollinator species richness and potential pollination provision. Species richness and potential pollination provision under present-day climate (left column) and SDM-predicted changes under two climate change scenarios (right columns).

of the study region and in some of the northernmost areas. The nestedness component's highest values occur mainly in Limpopo and north-eastern Mpumalanga, indicating loss without replacement. Losses in the north and turnover elsewhere indicate that pollinators currently found in South Africa may be driven pole-wards by the changing climate. Given the relatively even PDE distribution amongst species, we infer turnover (replacement) will not generally produce sharp functional decline, but data-poor families remain a concern in drawing conclusions.

Across all pollinators, an average loss in suitable habitat of 66,663 km² (RCP4.5) and 73,608 km² (RCP8.5) is predicted, representing 41.67% and 43.49% of total habitat, respectively. Diptera are predicted to experience the most negative biogeographic changes, both in terms of percentage change and total area lost. Three species switch from 'loss' to 'no change' or vice versa under differing RCP scenarios, but *Xylocopa olivacea* is the only pollinator predicted to lose habitat (-31.76%) under RCP4.5 conditions and

gain it (54.03%) under RCP8.5 conditions. Of the most effective pollinators, *Lucilia sericata*, *Chrysomya albiceps*, *C. chloropyga*, *C. marginalis* and *Braunsapis facialis* lose the most climatic habitat in total area (RCP4.5), ranging from 102,056 km² to 372,888 km² (mean 215,086 km²). *Ceratina nyassensis* gains 165,469 km² of suitable climatic habitat.

Discussion

We introduce and demonstrate a methodology that integrates SDMs with a quantifiable measure of pollinator performance, PDE, to evaluate climate-driven change in wild pollination services. Our study predicts that climate change will likely drive current pollinators of mango south, with potential for losses of suitable climatic habitat where mango is most commonly grown. PDE integration suggests mango pollinators similarly contribute to pollination, meaning richness declines may produce a proportional

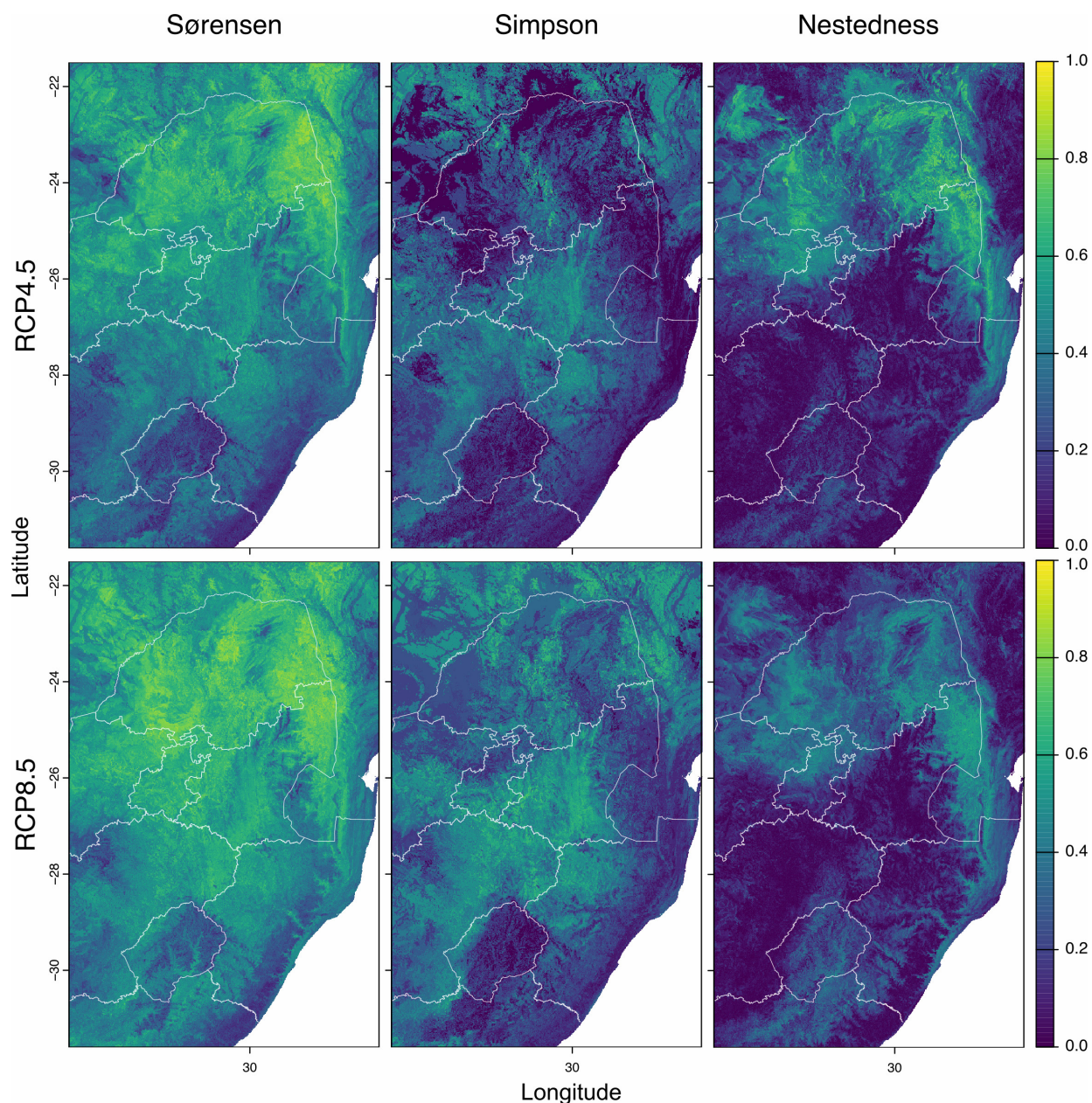


Figure 5. Mango pollinator species composition changes. Sørensen's dissimilarity (left), Simpson's dissimilarity (middle) and the nestedness component of Sørensen's dissimilarity (right) for mango pollinators under two climate change scenarios.

decrease in pollination services. Nevertheless, PDE integration also identifies highly effective key species to guide more targeted conservation efforts and highlights important data gaps to address. Though the primary aim of this study is to present a new methodology, our results could serve as an initial estimation of potential economic and food-security issues that South African mango farmers could face in light of wild pollinator declines.

Which pollinators are the most important?

While calculated PDE largely concurs with the expectation that smaller, short-tongued pollinators are more effective, a lack of visit effectiveness data affects some results.

Small flies were more effective than bees on average, barring *Liotrigona bottegoi* (Fig. 3). From Diptera, Calliphoridae had the highest PDE, in part due to its 83% visit effectiveness, followed by Muscidae (84%). Rhiniidae and Syrphidae values are likely inaccurate, with further data collection required for estimating their pollination effectiveness. Apidae's PDE largely lies between Calliphoridae and Syrphidae, with equal values for 10 species of three genera. This is due to limited visitation rates, effective visit percentages and SVDs for bee genera outside *Apis* and the Meliponini tribe (stingless bees), which do not represent the sizes of all bee pollinators.

All bees, except for *L. bottegoi*, *Megachile semiflava* and the honeybee, were assigned the average Apidae effective visit percentage and SVD, based on values from

honeybees and stingless bees. However, the sizes of these bees are highly variable. *Ceratina* bees are small in length (3–8 mm), with pollen adhering to their hind legs and under their abdomen where it is available for pollination. Larger bees like the honeybee (10–15 mm) collect pollen on the hind leg (less available), with grains elsewhere on its body adhering accidentally and less frequently (Eardley and Mansell 1994). This is evidenced by the high PDE of *L. bottegoid* (2.1–4.2 mm) (Fig. 3), based on its tribe's high 5.18 SVD estimate (underlying data, *Frieseomelitta nigra*: 6 mm), compared to the honeybees' 1.65. The PDE of small *Ceratina* and *Braunsapis* (5–6 mm) bees should, therefore, be similar to Calliphoridae, *L. bottegoid* and Muscidae, above honeybees and large *Xylocopa* (> 20 mm) and *Megachile* (10 mm) bees. However, further species-specific SVD and effective visit percentage data are required to confirm size as the main factor in these measures.

Effective visit percentage and SVD measures, however, do not account for behavioural factors which also contribute to pollinator efficiency. For example, the honeybee used to supplement pollination in South Africa may behave in a way that undermines its effectiveness. Managed honeybees are not often attracted by mango flowers, except in cases of food stress (Jiron and Hedstrom 1985), as they provide insufficient nutrition for mass foraging (Dag and Gazit 2000; Sung et al. 2006; Carvalheiro et al. 2010; Ela et al. 2021). Managed honeybees may have no effect on fruit set (South Africa (Carvalheiro et al. 2010)) or reduce it by transferring less compatible pollen or negatively affecting other pollinator's behaviour (Severiano-Galeana et al. 2024). Further study is required to assess these effects in wild South African honeybees, which do visit mango flowers (Eardley and Mansell 1994; Carvalheiro et al. 2010). Conversely, honeybees are widespread and resilient to environmental change as they can colonise many habitats through high nesting adaptability (as opposed to solitary or small-colony bees like *Ceratina* and *Braunsapis*), generalist feeding (unlike specialist *Xylocopa* bees) and a 9 km foraging range (surpassing Diptera) (Ballantyne et al. 2017; Mukundamago et al. 2023; Munyuli et al. 2024; Severiano-Galeana et al. 2024). A lack of flight range and specialisation data for most mango pollinators exists (Severiano-Galeana et al. 2024) and should be addressed, given their importance for conservation efforts.

From this analysis, we can infer that calliphorid flies, Muscidae and the small bee species of *Ceratina*, *Braunsapis* and *Liotrigona* are the most efficient pollinators of mango in South Africa. Wild honeybees may be important, but issues with mango flower attraction and fruit set must be investigated. More accurate PDE data are also required for Rhiniidae and Syrphidae. Identifying the most impactful pollinators is useful for guiding limited conservation efforts, but establishing that the majority of mango pollinators (32/38) are functionally equivalent is also a positive outcome in regard to potential species turnover and resulting changes in pollination provision.

Species richness and pollination provision

Predicted species richness declines could negatively impact mango production, as yield increases with species richness (Cabrera-Asencio 2021; Severiano-Galeana et al. 2024). Species richness is thought to modify the behaviour of pollinators through interspecific interactions, increasing visit effectiveness and fruit set (Brittain et al. 2013). For example, it may drive pollinators to move between flowers more quickly (Carvalheiro et al. 2010). Species richness losses are, thus, likely to result in decreased mango yield.

Lower species richness may also reduce functional redundancy, which supports resilience and stability in many ecosystems (Biggs et al. 2020), compromising pollination services. Though our results suggest that this community has high functional redundancy, the loss of a great number of species throughout the study area compromises this resilience in the near future. Redundancy is also important because mango pollinators are not all temporally consistent; for instance, several visitor species may be present one year and absent the next (Ela et al. 2021; Severiano-Galeana et al. 2024). Visitation throughout the flowering period can also differ between pollinator species (Annoh et al. 2017). These factors suggest a need to conserve mango pollinator diversity. While hymenopterans species richness may increase in some regions (Suppl. material 1: fig. S3), the accompanying dipteran decline may still affect mango production. However, there remains potential for pollinating species currently distributed north of South Africa to move into the region and replace the function of species driven south, which was not captured in our modelling and would ameliorate the predicted losses.

We found no substantial difference between potential pollination provision and species richness patterns (Fig. 4). This result implies high functional redundancy, where multiple species contribute moderate levels of pollen deposition and no single species dominates (increasing stability of pollination). Though pollination services will still decline with species richness loss, high redundancy prevents high species turnover from causing immediate wild pollination service collapse in areas with sufficient species replacement. High functional redundancy also highlights species richness as a useful metric for analysing this pollinator community. These metrics may have been distinct if sufficient data were available for PDE calculations per species or if only a few species were contributing towards pollination. Nevertheless, this framework could be an important metric to consider elsewhere, for example to identify cases where species loss has not affected pollination services (because highly efficient pollinators remain) or where pollination services are reduced by an inflow of inefficient pollinators. Potential pollination provision could also be useful to estimate pollination levels if combined with species abundance data. PDE might be improved in future research by taking into account body size, though we found there are currently insufficient data to do this.

Species turnover and magnitude of habitat changes

Species turnover, which we predicted to be high throughout the study region (Fig. 5), is not inherently negative. Species better-suited to the changing conditions, such as heat-tolerant species, are likely to replace less well-adapted ones. Pollination is not likely to decrease in areas with sufficient species replacement due to high functional redundancy. In some cases, new biotic interactions could drive behavioural changes that increase pollination (Brittain et al. 2013). However, replacement may diminish mango production if new species are not compatible, less efficient or phenologically misaligned with mango flowering. Furthermore, redundancy is not infinite. Large regions of the study area will face species loss without replacement (Fig. 5) and are key areas where conservation efforts should focus.

Overall, the magnitude of suitable habitat changes is greater under RCP8.5 conditions than RCP4.5. Interestingly, some bees responded more positively to the more extreme climate scenario: *Braunsapis bouyssoui* and *Ceratina rufigastra* lost less suitable habitat (14.4% and 12.9%, respectively) under RCP8.5 than RCP4.5 conditions. However, these predictions may be misleading due to limitations of SDMs (Pearson and Dawson 2003) and complexities that are not currently captured. For instance, the complexity of pollinator life cycles, whereby climatic conditions may differentially affect distinct life stages (e.g. larvae versus adult) make predictions of suitable habitat and pollination provision difficult. This is especially true if climate change alters the timing of peak pollinator populations and mango flowering, as mass flowering plants require high pollinator visits within a short period for fruit set (Reddy et al. 2023). Our study is also limited in that we could not incorporate the seasonality of the presence, abundance and activity of mango pollinators in our calculations. Though many identified species were observed visiting flowers in South Africa at the correct time, we cannot estimate how the timing of their behaviour will be affected by climate change. Species phenology is rarely included in ecological modelling, but steps such as modelling pollinator phenophases (such as reproduction and metamorphosis) could make calculations more realistic (Ponti and Sannolo 2023). It is also important to acknowledge uncertainties in using GBIF records, especially concerning regions and taxonomic groups with fewer resources and interest, respectively (García-Roselló et al. 2023). A larger number of species could have been considered if there were sufficient occurrence records for calculations. Future research would benefit from models utilising more occurrence records from diverse sources. Our study gives only first-pass estimates of future impacts, yet is strongly suggestive that conservation actions are important to protect vital ecosystem services.

Future prospects for mango production

The projected decreases in mango pollinators within eastern South Africa may have far-reaching consequences, as decreases in yield are expected. Smallholder farmers are likely to be the most impacted, as they are less able to afford managed pollinators to supplement those lost and are reliant on production for income and, therefore, food security. For example, changes in pollinator habitats reduced crop revenue by as much as 29% (mean) for smallholder farmers of pollinator-dependent crops in Tanzania (Tibesigwa et al. 2019). Decreased production in large commercial orchards or increased costs incurred due to the need for managed pollinators, might also affect the employment prospects of many thousands of workers involved in collecting and processing mango (DALRRD 2020), affecting food security and well-being.

The effects of climate change on mango trees themselves have not been explored here, but include reduced yield and quality of fruit due to wind and sunburn (Oosthuizen et al. 2016). These impacts could be mitigated using shade nets to reduce sun damage, tree stress and evapotranspiration. However, nets are expensive even for commercial orchards and so would likely be unaffordable for smallholders. Additionally, a predicted 8% annual increase in irrigation will be required to maintain present yields in the future (Oosthuizen et al. 2016). Both smallholders and large commercial orchards may also be impacted by shifts in mango season. Aside from potential flowering and pollinator peak mismatches which would significantly affect mango production, shifting seasons by one or two weeks could result in 30–40% decreases in sale price (Oosthuizen et al. 2016). This is due to price peaks between Christmas and New Year when demand is highest. This primarily affects the commonly grown ‘Tommy Atkins’ cultivar, such that it may be necessary to switch cultivars to avoid this.

Conservation actions can be taken to increase current wild pollinator populations and increase yield, which may diminish predicted effects of climate change. For instance, reducing pesticide and herbicide use (Carvalho et al. 2012; Marcacci et al. 2023), adopting low-cost methods to attract calliphorid flies (e.g. ‘stink stations’ (Finch et al. 2023)), introducing small native flower patches or allowing weed growth in mango orchards to provide food sources and nesting sites (Carvalho et al. 2012; Kleiman et al. 2021) and increasing plant diversity in orchards (Ebeling et al. 2008) can support pollinator communities.

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Supplementary materials

Supplementary material 1

Additional information (.zip)

Link: <https://doi.org/10.21425/fob.19.180771.suppl1>

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.

No AI tools were used in the preparation of this manuscript.

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Author contributions

All authors contributed to the study's conception, design and editing. Data curation, formal analysis and original draft writing were conducted by Matthew Phillips Sánchez. Supervision, review and funding acquisition were conducted by Richard Pearson. All authors read and approved the final manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.