RESEARCH ARTICLE

Agricultural intensification with seasonal fallow land promotes high bee diversity in Afrotropical drylands

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Abstract

1. The exponential increase in the human population in tandem with increased food demand has caused agriculture to be the global-dominant form of land use. Afrotropical drylands are currently facing the loss of natural savannah habitats and agricultural intensification with largely unknown consequences for bees. Here we investigate the effects of agricultural intensification on bee assemblages in the Afrotropical drylands of northern Tanzania. We disentangled the direct effects of agricultural intensification and temperature on bee richness from indirect effects mediated by changes in floral resources.

2. We collected data from 24 study sites representing three levels of management intensity (natural savannah, moderate intensive and highly intensive agriculture) spanning an extensive gradient of mean annual temperature (MAT) in northern Tanzania. We used ordinary linear models and path analysis to test the effects of agricultural intensity and MAT on bee species richness, bee species composition and body-size variation of bee communities.

3. We found that bee species richness increased with agricultural intensity and with increasing temperature. The effects of agricultural intensity and temperature on bee species richness were mediated by the positive effects of agriculture and temperature on the richness of floral resources used by bees. During the off-growing season, agricultural land was characterized by an extensive period of fallow land holding a very high density of flowering plants with unique bee species composition. The increase in bee diversity in agricultural habitats paralleled an increasing variation of bee body sizes with agricultural intensification that, however, diminished in environments with higher temperatures.

4. *Synthesis and applications*. Our study reveals that bee assemblages in Afrotropical drylands benefit from agricultural intensification in the way it is currently practiced. However, further land-use intensification, including year-round irrigated crop monocultures and excessive use of agrochemicals, is likely to exert a negative impact on bee diversity and pollination services, as reported in temperate regions. Moreover, several bee species were restricted to natural savannah

habitats. To conserve bee communities and guarantee pollination services in the region, a mixture of savannah and agriculture, with long periods of fallow land should be maintained.

KEYWORDS

bee abundance, bee body size, bee species richness, forage resources, inter-tegular distance, mean annual temperature, northern Tanzania, species community composition

1 | INTRODUCTION

Eighty-five to ninety percent of the major food crops and 35% of global food production benefit from animal pollination and in particular on bees (Klein et al., 2007). There is great concern regarding the global decline of bees with a negative upshot for pollination services (Dainese et al., 2019; Potts et al., 2016). Land-use intensification, particularly agriculture expansion, is assumed to be a major driver (Potts et al., 2010). The exponential increase in the human population in tandem with increased food demand has caused agriculture to be the global-prevalent form of land use (Ramankutty et al., 2018). Global agriculture expansion has been associated with the loss of natural habitats and intensified agricultural practices, resulting in the loss of bee diversity and its associated ecosystem services (Goulson et al., 2015; Potts et al., 2016; Steffan-Dewenter & Westphal, 2008). Intensification of agriculture through increased field sizes, agricultural mechanization, external inputs such as pesticides and chemical fertilizers, and decreased crop diversity are among practices performed to increase food production (Almusaed, 2016; Palma et al., 2015). On the other hand, these practices are increasingly becoming one of the cardinal pressures that directly and indirectly affect bee survival (Sanchez-Bayo & Goka, 2014). Some direct effects of agricultural intensification on bees are evidenced through the use of pesticides that cause direct intoxication (Potts et al., 2016), ploughing and compaction that destroys nests of ground-nesting bees (Kim et al., 2006), or impairing nests in branches or twigs of non-crop plants (Sutter et al., 2017). Conversely, agricultural intensification could indirectly affect bees through decreasing floral resource availability via reduced weed cover and loss of non-crop habitats (Langlois et al., 2020; Tommasi et al., 2021). These habitats provide forage resources and nesting sites for bees; hence, their loss interrupts bee–plant interactions (Roulston & Goodell, 2011). Some highly intensive agricultural practices could also limit the availability of floral resources for bees (Dicks et al., 2021). The scenario that could trigger changes in bees morphological functional traits such as body size reduction due to low food supplied to larvae (Filipiak, 2018; Tommasi et al., 2021). Understanding the variation of bee body size is crucial for its conservation efforts as it correlates with many ecological relevant variables such as foraging range and thermoregulatory characteristics (Greenleaf et al., 2007).

Most studies on the impacts of agricultural intensification on bee assemblages were conducted in temperate regions, while consequences for bees in tropical regions are still little understood. This is particularly true for tropical dryland habitats that host a large diversity of bees, show a rather small ecological resilience (Millard et al., 2021; Peters et al., 2019), and in which temperatures are increasingly approaching the critical thermal limits of ectothermic insects (Deutsch et al., 2008; Sunday et al., 2014). A special concern regarding the impact of agricultural intensification on bees is how agricultural intensification interacts with higher temperatures in the course of global change. Bees are ectotherms and their body metabolism and activity pattern are increasing with ambient temperature (Classen et al., 2015; Deutsch et al., 2008; Soroye et al., 2020). However, some terrestrial habitats in the tropics hold temperatures that already surpass optimum temperatures and even critical thermal limits of species (Deutsch et al., 2008; Sunday et al., 2014). Therefore, both negative and positive effects of temperature on bee assemblage can be contemplated (Classen et al., 2015; Hamblin et al., 2018; Mayr et al., 2020). Temperature may also interact with the effects of agricultural intensification, that is, stronger effects of intensification in warmer habitats may lead to a synergistic effect on the bee assemblage (Millard et al., 2021). Such synergistic effects of global change drivers are of high concern, as they are little incorporated in the estimations of global change effects (Oliver & Morecroft, 2014; Peters et al., 2019).

Although agriculture is a major land-use type on earth (Lasway, 2022; Ramankutty et al., 2018) and is expected to increase in Afrotropical drylands (Laurance et al., 2014; Millard et al., 2021; Newbold et al., 2017), few studies have attempted to elucidate the effect of agricultural intensification on bee species assemblage and functional traits (body size) in the region (Hagen & Kraemer, 2010; Otieno et al., 2015; Stein et al., 2018; Tommasi et al., 2021). Hitherto, most studies have been conducted in temperate Europe and America (Saunders et al., 2020), which is unlike to be globally representative, and leaves the knowledge of the effects of agriculture on bee assemblage in tropical East African drylands largely unknown. Additionally, studies on wild bee communities that shift from considering single stressors to quantifying multiple, compounding pressures such as agricultural intensification and temperature are even scarcer (Kammerer et al., 2021).

Therefore, in this study, we investigated the effects of local agricultural intensification on bee diversity, community composition and body size distributions along a temperature gradient in the Afrotropical dryland of northern Tanzania. Furthermore, the study aimed at understanding the drivers of bee species richness by disentangling the direct effects of agricultural intensification and temperature on bee species richness from indirect effects that are mediated by a change in floral resources. We hypothesized that:

1. Highly intense agriculture negatively affects bee species richness and abundance.
2. Bee richness increases with the increment in temperature. The effects of temperature and agriculture are interactive, that is, stronger effects of agricultural intensity on bee species richness are supposed to occur in warmer habitats.
3. The effect of agriculture on bee species richness is indirect, that is, mediated by a change in their potential floral resources (plant species richness). Alternatively, agricultural practices (e.g. ploughing, weeding or pesticide application) directly, rather than indirectly, impact bee species richness.
4. Increases in temperature and agricultural intensity lead to a change (increase or decrease) in the mean and the variation of bee body sizes.

2 | MATERIALS AND METHODS

2.1 | Description of the study area

We conducted this study in northern Tanzania, in the lowlands of Mt. Kilimanjaro and Mt. Meru, and the areas of Tarangire National Park in Kilimanjaro, Arusha and Manyara regions, respectively (Figure 1). The study area is characterized by a tropical climate with extensive dry periods (Gebrechorkos et al., 2019). Study area elevation ranges between 702 m and 1708 m above sea level (a.s.l.) with the mean annual temperature (MAT) spanning from 18°C to 26°C (depending on elevation) with maxima temperatures regularly exceeding 40°C (own unpublished data). The area experiences a bimodal rainfall with a long rainy season between March and May and a short rainy season typically in November and December (Foley & Faust, 2010). The dominant natural vegetation of this dryland is a tropical savannah composed of grasses interspersed with herbs and scattered trees (dominated by *Commiphora* sp., *Vachellia* sp. and *Senegalia* sp.).

There are several non-native trees outside the protected areas, including *Acrocarpus fraxinifolius* Wight et. Arn (Fabaceae), *Leucaena leucocephala* (Lam.) de Wit (Fabaceae) and *Grevillea robusta* A. Cunn. exR. Br. (Proteaceae). Planting and harvesting calendar of typical crops (wheat, maize, barley, sorghum, beans and sunflower) in the study area follow the rainfall patterns (Rowhani et al., 2011). Planting is usually made after the first rains, in early March, and harvest is carried out at the end of the long rainy season, between mid-July and early August (Rowhani et al., 2011). Following crop harvesting, fields are customarily abandoned until the next coming annual rain season. During this period, the fields are dominated by proliferated herbs. However, due to the relatively low use of herbicides, even during the planting and when the crops are in the fields (growing season), flowering weeds can be found in fields.

2.2 | Data collection

We collected data from August 2018 to March 2020 on 24 replicate study sites distributed equally among three selected habitats following a gradient of agricultural intensification (Figure 1). The first habitat was natural savannah, which was situated in the protected areas of the Tarangire National Park, Arusha National Park and Lake Challa wildlife area with a distance of >500 m from study sites to any border of the protected area. This habitat is characterized by rolling grassland with native scattered trees, shrubs and herbs. It served as a natural control site with no agricultural activities and a minimum of human-modified physical environment. The second habitat type consists of moderate intensive agriculture, composed of subsistence farming characterized by small field sizes (mostly less than 1 ha) of mixed crops such as maize, beans and sunflower. Crop areas were surrounded by patches of savannah habitats, and typically only small agriculture machines such as small tractors and planters are used. The third habitat type was defined as highly intensive agriculture.
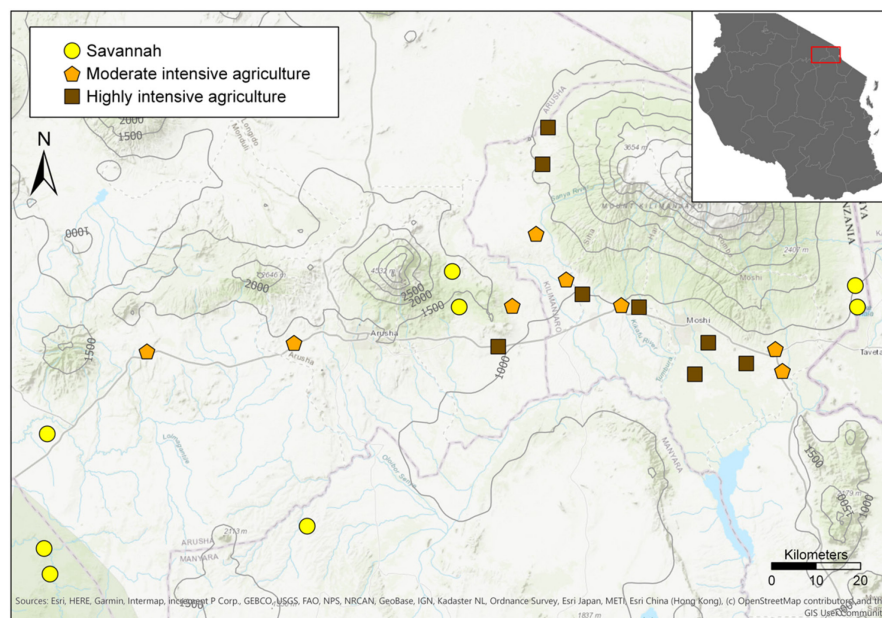

FIGURE 1 A map of the study area. The map shows the distribution of study sites with different colors and symbols representing different land use intensity classes (see legend). The two big mountains on the map are Mt. Meru (center) and Mt. Kilimanjaro (upper right). In the upper right corner, the small map shows the location of the study area in northern Tanzania.

This habitat type was characterized by large monoculture fields (ca. 50–100ha) of wheat, maize or barley as the major crops. Heavy agricultural machines and chemical fertilizers are regularly used during the growing time of the crops.

Distances between study sites were at least 3 km, which is far larger than the flying distance of most bee species (Wright et al., 2015; Zurbuchen et al., 2010). Eight replicates of each different habitat were distributed along the elevation gradient of the entire study region (mean ± SD elevation of study sites: savannah: 1140 ±226m a.s.l.; moderate intensive agriculture: 1140 ±259m a.s.l.; intensive agriculture: 1062 ±364m a.s.l.). Each study site was composed of two study plots positioned ca. 150m apart. Each study plot had a size of 50×50m, where bees and floral resources were sampled and quantified. The two plots were placed in a way to approximately capture the overall structural heterogeneity of the respective habitat by placing the two plots in contrasting microhabitats where possible. For example, in moderate intensive agriculture, both areas with and without tree or shrub cover were selected. Research permit No:2019-631-NA-2019-235 was obtained from Tanzania Commission for Science and Technology (COSTECH) to conduct field data collection. No Ethical approval was required.

2.2.1 | Bee sampling

Two standardized sampling methods (UV-reflecting coloured pan traps and standardized random walks) were employed to sample bees (Lasway et al., 2021; Prendergast et al., 2020). In all, 12 pan traps in four clusters (each cluster with three different UV-reflecting colours: white, yellow and blue) were installed in each plot to passively collect bees (Figure A1a in Appendix; Classen et al., 2020; Elzay & Baum, 2021). Pan trap clusters at different heights (two with 120cm height poles and two with 35cm) were positioned diagonally on two 50m parallel transects separated by 30m interspatial distance (Figure A1b in Appendix). The height differences in the pan traps were aimed to maximize capturing bees flying at different heights: at the shrub layer level (120cm above-ground distance) and the herbaceous layer level (35cm from the ground). Pan traps were filled with unscented soapy water and left in the field for 48 h to passively collect bees (Classen et al., 2020). A drop of scentless liquid soap per ca. 1 L was used to break the surface tension of water so that bees landing on the pan trap were more likely to be captured. Scentless soap was used to avoid attraction of insects to certain olfactory cues. Bees were collected from the pan traps after 48 h and temporarily preserved in 70% ethanol before being further processed in the laboratory. In each study site, we conducted pan trap sampling in three different main seasons of the year; long rainy season, dry season and short rain season. The pan trap sampling effort summed up to 3456 h per study site and 82,944 h for the entire study.

Besides pan trap sampling, we used a standardized random walk method to sample bees. This method involves random slow pace walks within plots using a hand net to actively collect bees that are foraging on flowers. Using this method, we collected bees for 2 h on each study site (1 h per each 50×50m study plot), excluding handling and recording time. Random walks were conducted anytime between 9:00am and 5:00pm when bees are expected to be highly active (Classen et al., 2020). On each study site, a 2-h random walk was conducted in three main seasons of the year (long rainy season, dry season and short rainy season). This summed up to 6 h of active bee collection for each study site and in total 144 h for the whole study. We restricted random walk sampling to days with no or very little rainfall and low wind speed. All specimens collected were temporarily preserved in 70% ethanol before being mounted and identified. All bees were identified following the nomenclatural system established by Michener (2007) with exception of the Halictidae family. Bee identification to species levels was mainly performed by two experts on Afrotropical bees (C.E. and A.P.). However, few were identified by J.V.L. We calculated the species richness per study site by summing up the cumulative number of bee species collected by both sampling methods across all three sampling seasons. Because we intended to measure the cumulative species richness on study sites across the year (which integrates the temporal turnover in species communities), we pooled the data from all sampling rounds for calculating the total species richness per study site.

2.2.2 | Quantification of bee-visited plants

In each study site, all plant species visited by bees during random walks were recorded. This measure corresponds to the plant species used by foraging bees as an alternative to the assessment of the total number of plant species on sites (Classen et al., 2020; Lasway, Steffan-Dewenter, et al., 2022; Tucker & Rehan, 2017). Plant species were recorded as bees visited blooms of flowering plants, that is, in case, we observed a bee walking or landing on a flower (not just flying over it) (Tucker & Rehan, 2017). Flowering plant species that could not be identified in the field were taken to the National Herbarium of Tanzania for morphological identification. Other plants could have been visited by bees outside our random walks time; hence, this survey method may not recover all plant species which are principally attracting bees and for that reason, for each study site, floral resource richness was counted as the cumulative number of plant species visited by the foraging bee community throughout the three sampling rounds.

2.2.3 | Body size measurement

The inter-tegular distance (ITD; in mm) was measured as a proxy for bees' body size (Classen et al., 2017) using a digital microscope (Dino-Lite digital handheld microscope Taiwan, with a precision of 0.001mm). The ITD measures the miniature distance between the two tegulae, that is, the small-scale-like sclerites covering the base of the fore wing in bees (Figure A4 in Appendix). For each study site,

we calculated the mean and the coefficient of variation of the ITD using the data of all sampled individuals.

2.2.4 | Mean annual temperature

Data on temperature on study sites were recorded using temperature sensors (iButton) (Classen et al., 2015). For each study site, a Thermochron iButton data logger (DS1921G; ±0.5°C resolution; Maxim Integrated Products, USA) was placed at 2 m height above the ground (on a branch of a shrub/tree) to continuously record temperatures through the study time (Classen et al., 2015). An overlay plastic funnel was hung 10 cm above the sensor for protecting it from direct solar radiation (Figure A1c in Appendix). Temperature sensors were set to take records in 60-min intervals. Sensors were left in the field for the entire year and visited every 3 months for data reading and maintenance. MAT per study site was obtained by averaging all individual temperature measurements. As an alternative to MAT, we also tested mean maximum temperature for explaining the variation in bee species richness. While the results and conclusions derived from this analysis were the same as for MAT, the explained variation was lower for models including mean maximum temperature than for those including MAT as an explanatory variable (for bee species richness: $R^2 = 0.41$ for mean maximum temperature versus $R^2 = 0.52$ for MAT).

2.3 | Statistical analyses

We analysed the data using R version 4.0.3 (R Core Team 2016). Ordinary linear models were used to explore the effect of agricultural intensity (AI) and MAT on bee species richness and abundance. MAT was added as a first- and second-degree polynomial term to model potential monotonic or unimodal relationships between MAT and the species richness and abundance of bees. We tested for both additive and interactive effects of temperature and agriculture intensity on bee species richness. The *dredge* function in the MuMIn R package version 1.7.2 (Barton, 2012) was used to select the best-supported model based on Akaike information criterion (AIC) values (Burnham & Anderson, 2004). Our sample size was relatively low, a situation that compelled the use of AIC with a second-order bias correction (AICc) instead of the normal AIC. The obtained *p*-value from the best model summary *F* test was used to evaluate the significance level of estimated parameters. Residuals of final models were checked for violation of the assumption of normality using the Shapiro–Wilk test on normality and with normal quantile–quantile plots.

As sampling incompleteness, a typical problem in studies of tropical insect communities, could lead to biases in the number of observed species on study sites, we additionally calculated estimates of asymptotic species richness using the Chao-1 richness estimator and performed the same tests mentioned above using the chao1-index of asymptotic species richness as a response variable. As the

chao1-estimated species richness was strongly correlated to the observed species richness of bees ($r = 0.86$, $p < 0.01$; Figure A3a in Appendix) and test on the influence of agricultural intensification and MAT on the chao1-estimated species richness revealed similar effects like those found for the observed data but with lower explained variation, we mainly focused on observed species richness patterns and report results on chao1-estimated species richness patterns in Figure A3 in Appendix.

Path analysis following Shipley (2016) was used to examine causal relationships and to disentangle the direct effect from the indirect effects of MAT and AI on floral resource richness and bee species richness. Direct causal effects represent effects that go directly from one variable to another, while indirect effects occur when the relationship between two or more variables is mediated by one or two variables (Shipley, 2016). We postulated and constructed a conceptual path diagram (Figure 3b), based on the ecological understanding of bees, assuming both direct and indirect effects of AI and MAT on bee species richness. Possible path combinations were pre-selected by analysing two endogenous variables of the path model (bee species richness and floral resource richness) with all explaining variables, that is, AI, MAT and MAT^2. Squared MAT (MAT^2) was used to model potential unimodal relationships between MAT and bee species richness. The most inclusive full model for bee species richness was:

$$SD_b \sim AI + MAT + MAT^2 + AI : MAT + AI : MAT^2 + \text{floral resource richness.}$$

For floral resource richness, the following full model was constructed:

$$SD_p \sim AI + MAT + MAT^2 + AI : MAT + AI : MAT^2.$$

The *dredge* function of the MuMIn R package version 1.7.2 (Barton, 2012) was used to rank models based on the AIC_C. For all combinations of competitive models ($\Delta AIC_C < 2$), we conducted a formal path analysis and derived path coefficients, their statistical significance and multiple coefficients of determination (R^2) for the two response variables. For formal path analysis, the R package PIECEWISESEM version 1.1.3 (Lefcheck, 2016) was used.

A Venn diagram was constructed using VENNDIAGRAM R package version 1.6.16 (Chen & Boutros, 2011) to visualize the number of species that were shared and unshared between habitats of different agricultural intensities. To visualize the effect of MAT and AI on the species composition of bee communities, non-metric multidimensional scaling (NMDS) was applied based on a dissimilarity matrix calculated with the Sorensen index of dissimilarity (Holland, 2008). Using the *ordisurf* function of the R package VEGAN (Oksanen et al., 2018), we modelled MAT isotherms to be plotted in the ordination graph. To test the effect of MAT, AI and their interaction on the bee species community composition, a permutational multivariate analysis of variance (MANOVA) (i.e. the *adonis* function of the R package VEGAN) was used. The test was based on

the same dissimilarity matrix used for the NMDS. The permutational MANOVA calculates the statistical significance for effects of explanatory variables through a permutation procedure (Anderson, 2001; McArdle & Anderson, 2001) with the number of permutations set to 999. We started with permutational MANOVA model testing for an interactive effect of MAT and AI and successively simplified it by deleting non-significant explanatory variables from the model. We used the *beta. pair* function in the BETAPART package version 1.5.2 (Baselga et al., 2021) to partition the Sorensen dissimilarity matrix into species turnover and nestedness components and compared their overall contribution with boxplots.

Finally, we performed a linear model to explore the effect of AI and MAT on the mean ITD and the coefficient of variation of the ITD. Similar to species richness, MAT was added as a first- and second-degree polynomial term to model potential unimodal relationships between MAT and ITD parameters. We tested for both additive and interaction effects of the two predictor variables on the mean ITD and the coefficient of variation of the ITD.

3 | RESULTS

We sampled a cumulative total of 3428 bee individuals and sorted them into 219 species representing 58 genera and six families: Andrenidae (5 species), Apidae (76 species), Colletidae (4 species), Halictidae (86 species), Megachilidae (47 species) and Melittidae (1 species). Habitats experiencing highly intensive agriculture had the highest cumulative bee species richness (146 species) and abundance (1639 individuals). Species richness values were relatively similar in habitats experiencing moderate intensive agriculture (140 species and 1098 individuals) but higher than in savannah habitats with no agricultural activities (105 species and 691 individuals; Figure 2a, Table A1 in Appendix). Additionally, Venn diagram results showed unique bee species in both agricultural habitats (with 17% each) and

savannah habitats (12%) (Figure A2 in Appendix). Nonetheless, there were overlaps in bee species, with 16 species overlapping between savannah and highly intensive agriculture, 11 species between savannah and moderate intensive agriculture, and 39 species overlapping between moderate and highly intensive agriculture.

Agricultural intensity and MAT showed significant additive effects on bee species richness and abundance. Bee species richness was, on average, higher in high and moderate intensive agricultural habitats, while the savannah habitat showed a lower mean number of species (Figure 2b). Conversely, bee species richness showed a linear increase with MAT from 18.5°C to 25.5°C (Figure 2c). Besides, multi-model inference revealed no significant support for models assuming an interactive effect of AI and MAT, suggesting that the effect of agriculture on bee species richness was consistent along the temperature gradient (and vice versa). We additionally tested how far results were influenced by the methods used for collecting bees: Both pan trap sampling and sweep netting on random walks revealed individually the same results as found for the pooled dataset but the number of species detected per study site was strongly reduced, indicating complementarity in the bee species communities being sampled by the two methods (Figure A5 in Appendix). The change in bee species richness with agricultural intensification was mirrored by an increase in bee abundance with agricultural intensity and MAT ($R^2 = 0.52$, $F_{3,20} = 7.125$, $p = 0.002$; $p_{AI} = 0.0003$; $p_{MAT} = 0.01$).

Results from path analysis suggest that agricultural intensity and climate determined bee diversity mainly by modifying the floral resource richness across habitats. Temperature and agriculture intensity were both significant predictors of the floral resource richness: Floral resource richness increased significantly with agricultural intensity (Figure 3, Figure A1 and Table A2 in Appendix) and MAT (Figure 3, Figure A2; $R^2 = 0.52$, $F_{3,20} = 4.963$; $p_{AI} = 0.004$; $p_{MAT} = 0.05$). Bee species richness (and similarly the chao-1 estimated species richness, Figure A3d in Appendix) linearly increased with the
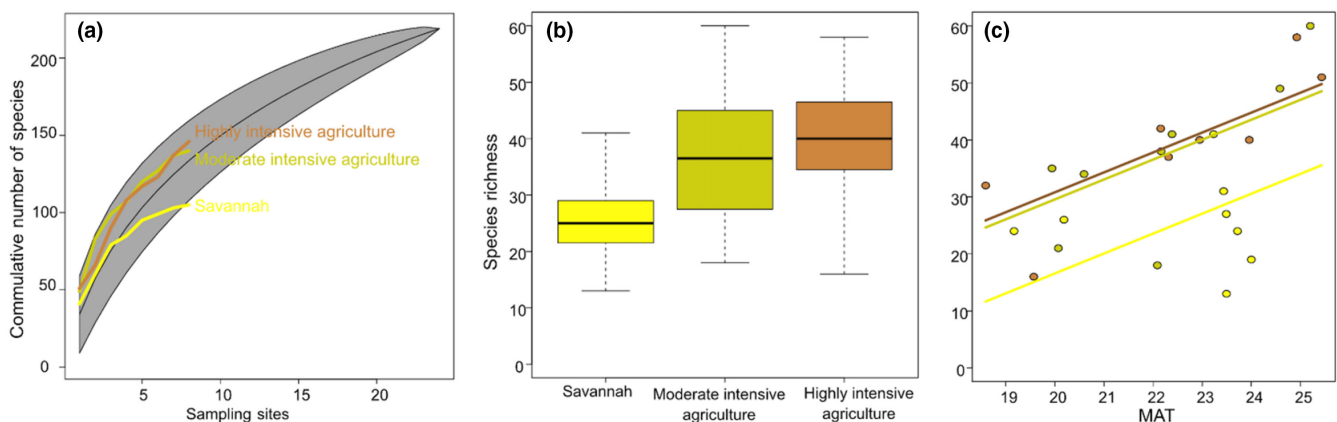

FIGURE 2 Bee species richness changes with agricultural intensification. (A) Cumulative number of bee species richness increases with the number of sampled study sites but did not reach an asymptote. Species accumulation curves were shown by the bold black line across all study sites (grey polygon: 95% CI). Individual habitat type values were shown by shorter colored lines. (B) Mean bee species richness per study site in three different habitats (ANOVA, $F_{2,21} = 3.18$, $p = 0.062$). (C) Species richness as a function of agricultural intensity and mean annual temperature ($R^2 = 0.53$, $F_{3,20} = 7.465$, $p = 0.001$; $p_{AI} = 0.007$; $p_{MAT} = 0.002$)

floral resource richness (Figure 3, Figure A4; $R^2 = 0.57$, $F_{2,21} = 13.65$; $p_{Sdp} = 0.001$). Data also support a direct positive effect of MAT on bee species richness (Figure 3, Figure A3; $R^2 = 0.57$, $F_{2,21} = 13.65$; $p_{MAT} = 0.04$). However, we did not detect a direct effect of AI on the bees' species richness. A competitive (second-best supported) path model ($\Delta AIC = 0.32$) was highly similar to the best-supported path model (Figure 3) but did not include a positive effect of MAT on bee species richness.

A permutational MANOVA on a distance matrix calculated using the Sorensen index revealed a significant interactive effect of agricultural intensity and MAT on the composition of bee communities (effect of AI: $F = 1.96$, $p = 0.003$; MAT: $F = 4.31$, $p = 0.001$; AI×MAT: $F = 1.72$, $p = 0.011$; Figure 4). Study sites situated in warmer environments (MAT >23°C) showed more distinct species communities along the agricultural intensity gradient ($p = 0.008$) than those in colder (MAT >23°C) environments ($p = 0.079$; Figure 4). Partitioning the dissimilarity between species

communities in turnover and nestedness components revealed that species turnover was much more important mechanisms of community changes than nestedness.

Agricultural intensity and MAT had no significant effects on the mean ITD ($R^2 = 0.04$, $F_{3,20} = 0.299$; $p_{AI} = 0.381$; $p_{MAT} = 0.834$), but the variation the coefficient of variation in ITD significantly increased with agricultural intensification and decreased with increasing MAT (Figure 5).

4 | DISCUSSION

Contrary to our expectation, we found that agricultural intensification in the tropical drylands of the studied region was associated with an increase in bee species richness and abundance, and an increased variation of bee body sizes in cooler temperature. Bee species richness and abundance also increased with increasing temperature,
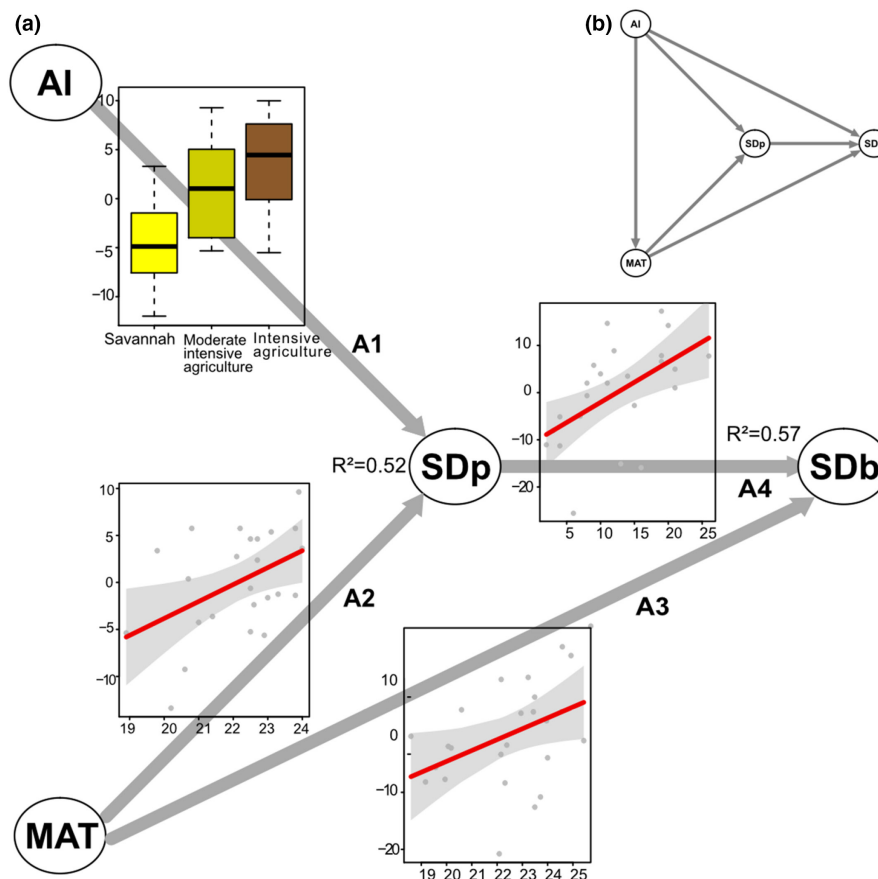

FIGURE 3 Path model showing the direct and indirect effects of MAT and AI on floral resource richness and species richness of bees. (A) The best-supported path model shows that the effect of mean annual temperature (MAT) and agriculture intensity (AI) on species richness of bees (SDb) is mainly mediated by floral resource richness (SDp). In addition, MAT exerts a direct effect on bee species richness. The inlet figures on arrows depict the relationships between AI and residual SDp (A1), MAT and residual SDp (A2), MAT and residual SDb (A3), and SDp and residual SDb (A4). In all figures, the explanatory variable is shown on the x-axis and the response variable on the y-axis. Inlet Figures A1–A4 show relationships between the response and explanatory variable after controlling for all other effects in the model. Grey dots show data points while red lines and grey polygons show predictions of ordinary linear models and 95% confidence intervals, respectively. (B) Conceptual path diagram (the most inclusive path model) illustrating all considered relationships among exogenous and endogenous variables.
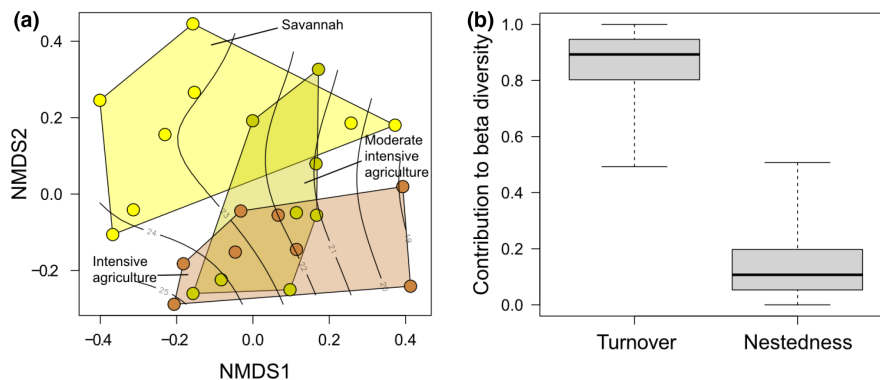
FIGURE 4 Variation in the composition of bee species communities. (A) The ordination shows the results of non-metric multidimensional scaling of a dissimilarity matrix based on the Sorensen dissimilarity measure. Bee communities from study sites in natural savannah are shown in yellow, those from sites with moderate intensive agriculture in dark yellow, and those from sites with intensive agriculture in brown. In the background, contour lines of MAT are displayed (isotherms; in °C). The curvature suggests that agricultural intensity leads to stronger changes in the composition of species communities at high than at low temperatures, illustrating the significant interaction between MAT and AI. (B) Decomposing overall Sorensen dissimilarity into two components (turnover and nestedness), reveals that in the study system, species turnover is more relevant for changes in species communities than nestedness.

FIGURE 5 Bee body mass changes with agriculture intensification and temperature. (A) Mean ITD was similar across the land use intensity gradient. (B) The coefficient of variation in bee body size (ITD) was affected by both agriculture and temperature (ANOVA, $F_{3,20} = 11.57$, $p < 0.001$; $p_{AI:MAT} = 0.038$)
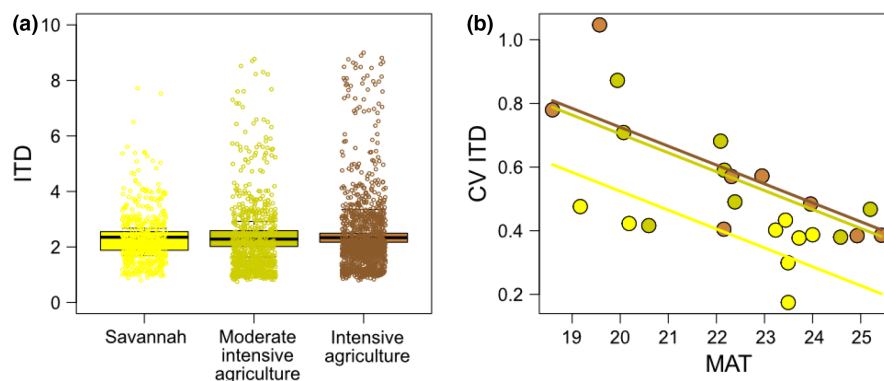
but we detected no evidence for an interactive effect of temperature and agricultural intensification on bee species richness. Changes in bee species richness along temperature and land-use gradients were mediated by the positive effects of agriculture and temperature on the floral resources that are used by bees.

Our findings that overall bee species richness and abundance increased with agricultural intensification was unexpected and is inconsistent with most studies conducted along agricultural intensification gradients in temperate Europe (Coutinho et al., 2018; Le Féon et al., 2010; Steffan-Dewenter & Westphal, 2008). However, a similar pattern was reported by Classen et al. (2015) on the foothill of Mt. Kilimanjaro and Vogel et al. (2021) in Mzimba district, Northern Malawi. The authors observed that habitat disturbance through agriculture did not negatively impact bee species richness patterns. The response of pollinators to agricultural intensification is diverse, and differs between taxonomic groups, landscape types, climatic regions and specificities of agriculture systems (De Palma et al., 2016).

Changes in bee species richness with agricultural intensity were mediated by the positive effect of agriculture and temperature on the floral resources used by bees. A high diversity and abundance of floral resources in agricultural landscapes is often correlated with more abundant and diverse bee communities, as revealed by

studies from temperate (Kleijn & van Langevelde, 2006; Scheper et al., 2015) and tropical agricultural systems (Escobedo-Kenefic et al., 2020; Landaverde-González et al., 2017). Eighty percent of global agriculture depends on rainfall (Kijne et al., 2003), and most parts of Tanzania consist of drought-prone ecosystems (Gebrechorkos et al., 2019). Therefore, crop cultivation in the study area is practiced mainly during the long rainy season when water is available for crop growth and development. Following crop harvesting (between mid-July and early August), the land is left fallow for several months until the next annual rain season (Abass et al., 2014). Over this time, fallow fields are dominated by proliferated annual herbs and grass cover (Massante et al., 2019; Verhulst et al., 2004), which can flourish even with small amounts of rainfall, and thus provide forage resources for bees (Tucker & Rehan, 2017). Long period of fallow land may promote a high floral resource richness in agricultural habitats that promote high bee diversity (Boetzl et al., 2021; Westphal et al., 2009). Besides, abandoned agriculture fields increase bee nesting substrates, offering higher spatial–temporal stability of food resources and nesting sites from which bees could benefit (Landaverde-González et al., 2017; Nicholls & Altieri, 2013; Requier & Leonhardt, 2020; Steffan-Dewenter & Tscharntke, 2001).

A long period of fallow land with climate fostering bee activity strongly contrasts with the conditions of intensified agriculture in many temperate regions (Figure A6 in Appendix). Here, crops are cultivated from spring to summer, that is, in the time of the year when the temperature is high enough for crop production (Sloat et al., 2020). Before and after the harvesting period, low temperatures do not support the activity of ectothermic bees and the growth of their floral resources (Borghi et al., 2019).

The farming practices of the studied agricultural system in East Africa resemble traditional *milpa*. A local form of agriculture management in Mesoamerica where fallow areas between intensive agriculture periods allow plant heterogeneity and therefore high floral resource availability (Escobedo-Kenefic et al., 2020; Landaverde-González et al., 2017) that attract high bee diversity. The major difference between traditional farming practices in East Africa and the traditional *milpa* system is that in the latter forests are cut and burned, and the resulting fields are used for crop cultivation for ca. 2–5 years before being abandoned, after which secondary forest reestablishes (Escobedo-Kenefic et al., 2020; Landaverde-González et al., 2017). However, both tropical agricultural systems reveal a very high number of bee species.

Unexpectedly, natural savannah habitats showed, on average, a lower number of bee species than agricultural habitats. The relatively low bee species richness in the savannah habitat can be explained by a lower floral resource richness and a high cover of grasses, that do not provide pollen and nectar resources to bees (Ratnam et al., 2011). The lower amount of food resources may limit the number of bee species to coexist in the area (Moylett et al., 2020; Ratnam et al., 2011). Nonetheless, both habitats (savannah and agricultural) showed to contain unique bee species and complementary species communities. Therefore, conservation of savannah natural ecosystem is also necessary for conserving bee communities of Afrotropical drylands.

We did not observe a direct effect of agricultural intensification on bee species richness. Such a relationship would be plausible if ploughing or weed extirpating would lead to the destruction of bee nesting sites for both ground and pith nesting bees or if pesticides application would cause species extinctions on sites. Conversely to intensive agricultural practices in temperate latitudes, many smallholder and intensive farmers in Tanzania still manually extirpate weeds (Classen et al., 2015; Tommasi et al., 2021). This practice reduces the impact of soil compaction on ground-nesting bees (Classen et al., 2015) and avoids agrochemical run-offs (Tommasi et al., 2021). These practices conserve habitats of ground-nesting bees and reduce the potential direct impact of pesticides on insects that may lead to their mortality. Moreover, manually weeding practice contributes to the maintenance of diverse floral resources that probably leaves more resources to bees compared to herbicides treated fields (Tommasi et al., 2021).

Our study shows that the current agriculture practice of a major cultivation time in the rainy season followed by a prolonged periods of fallow land promotes high bee diversity. However, we expect that future intensification, including year-round crop monoculture with artificial water supply (irrigation), could subsequently result in the loss of long periods of fallow land, lowering floral resource availability, which may result in a strong decline in bee diversity. Also increased use of pesticides and heavy machines would potentially have a strong negative impact on bee diversity and pollination services as reported in temperate latitudes where the decline in bee species richness and abundance due to agriculture intensification is alarming (Potts et al., 2010).

The study indicates temperature to have a positive influence on bee species richness. Mean bee species richness sharply increased from 18.5°C to 25.5°C. However, increases in bee species richness with temperature are in line with the metabolic theory of ecology. Under warm temperatures, metabolic rates, foraging activities and net energy gain are higher than in cold temperatures (Brown et al., 2004; Classen et al., 2015). Additionally, biological processes that shape species richness such as species interactions and evolutionary rates in ectothermic organisms depend on temperature (Puurtinen et al., 2016). In that regard, temperature-mediated speciation rates or enhanced negative density-dependent mortality at higher temperatures may increase the pool of coexisting species of warm ecosystems. Despite the high temperatures which are already reached in East African dryland habitats in parts of the year, no decrease in bee species richness was observed even in the hottest study sites. A decrease was expected because day temperatures in the East African drylands, in particular at the soil level, already approach the upper thermal limits of insects (Deutsch et al., 2008; Sunday et al., 2014). One reason for the lack of a negative effect of temperature on species richness in the upper thermal range could be shading of the soil by a relatively continuous plant cover provided by the field crops during the cultivation time and a herb cover during periods of fallow land. Nevertheless, future warming of these ecosystems may push temperatures beyond the critical thermal limits of even the warm-adapted bees. In addition, it should be noted that the temporal resolution of the temperature and species richness data of this study was very coarse such that the effect of extreme temperatures that might occur over time periods of days or seasons could not be analysed in detail.

We found the variation in body size of bees increased with agricultural intensification in the cooler sites. This observation parallels that of Le Féon et al. (2010), who observed large-bodied size bees (bumblebees) increased in frequency with agriculture intensification. Increased floral resource diversity with agricultural intensity offers a higher amount of forage resources and nesting sites that attract a diverse bee fauna with various morphological traits (Laha et al., 2020; Rollin et al., 2019), including small-sized bees, and large-bodied size bees that require more food resources for their offspring (Müller et al., 2006). Observed large-sized bees in highly intensive agriculture sites could also be explained by their larger foraging range and flight ability (Greenleaf et al., 2007). This trait enables large-sized bees to fly to far proximity looking for rewards obtained from diverse floral resources. Because of this, it is probable that the observed large-sized bees are non-resident of the area. In addition,

we found that the variation in body size decreased with increasing temperatures, which, together with the finding of no effect of temperature on mean body size, suggests filtering of bees species with extreme body sizes in warmer climates.

One potential caveat of this study is that the methodology of sampling bees and plants could have biased some of the resulting patterns. The distribution of flowering plants in the savannah can be extremely patchy, as the scarce flowering trees or bushes (e.g. *Vachellia* and *Senegalia* trees) between grasses attract a very high diversity of bees but only flower over a very short time period (Stone et al., 1998) such that some important flowering plant species could have been missed during random walks. In contrast, the distribution of flowers in the fallow land on agricultural sites is rather homogeneous and less patchy in space and time. This could have also facilitated the sampling of a larger number of bees in the agricultural habitats than in the savannah. Results were highly consistent for subsets of data that were either based on pan trap sampling or random walks with sweep netting, underscoring that the selection of specific sampling methods or pooling of the data from two sampling methods did not strongly bias resulting patterns.

This study only considered the impact of agriculture intensification on bee diversity at the local scale. Incorporating the surrounding landscape structure in models could potentially contribute to explaining the variation in bee species richness observed in this study. While our results suggest that intensive agriculture with long periods of fallow land can sustain a high diversity of bees, the lack of a dense temporal sampling of both flowering plants and bee species throughout a year did not allow us to conduct a precise estimate of bee and flower diversity during and after the cultivation time. Studies with a higher temporal resolution in the sampling of bees and flowering plants could contribute to a better understanding of the contribution of the cultivation time and periods of fallow land for sustaining bee communities.

5 | CONCLUSION

Our study concludes that the positive effect of agriculture on bee species richness with varying body sizes was largely driven by the fact that agricultural habitats showed higher levels of floral resource richness. This may largely be a consequence of a prolonged period of fallow land in this agricultural system, which facilitates the growth of diverse herbaceous flowering plant communities. Our study, therefore, supports the view that the impact of agriculture intensification on bee communities depends on the studied region and the reference practiced agricultural system. The monotonic increase in bee species richness with temperature underscores a positive effect of temperatures within the range of temperatures currently reached in the East African study region. Nonetheless, an unbounded increase in temperature, as a consequence of ongoing climate change, may lead to undesirable consequences such as species loss of bee communities and floral resources with consequent negative impacts on pollination services.

AUTHOR CONTRIBUTIONS

Ingolf Steffan-Dewenter, Marcell K. Peters and Henry K. Njovu conceived the ideas and designed the methodology; Julius V. Lasway collected the data; Connal Eardley, Alain Pauly and Julius V. Lasway identified the collected bee specimens; Marcell K. Peters and Julius V. Lasway analysed the data; Julius V. Lasway led the writing of the manuscript with input from Marcell K. Peters, Ingolf Steffan-Dewenter and Henry K. Njovu. All authors contributed substantially to the drafts and gave final approval for the publication.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Figshare Digital Repository https://doi.org/10.6084/m9.figshare.21126001.v1 (Lasway, Peters, et al., 2022).

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