


# Fragmented landscapes affect honey bee colony strength at diverse spatial scales in agroecological landscapes in Kenya

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**Abstract.** Landscape fragmentation and habitat loss at multiple scales directly affect species abundance, diversity, and productivity. There is a paucity of information about the effect of the landscape structure and diversity on honey bee colony strength in Africa. Here, we present new insights into the relationship between landscape metrics such as patch size, shape, connectivity, composition, and configuration and honey bee (*Apis mellifera*) colony strength characteristics. Remote-sensing-based landscape variables were linked to honey bee colony strength variables in a typical highly fragmented smallholder agroecological region in Kenya. We examined colonies in six sites with varying degrees of land degradation during the period from 2017 to 2018. Landscape structure was first mapped using medium resolution bitemporal Sentinel-1 and Sentinel-2 satellite imagery with an optimized random forest model. The influence of the surrounding landscape matrix was then constrained to two buffer distances, i.e., 1 km representing the local foraging scale and 2.5 km representing the wider foraging scale around each investigated apiary and for each of the six sites. The results of zero-inflated negative binomial regression with mixed effects showed that lower complexity of patch geometries represented by fractal dimension and reduced proportions of croplands were most influential at local foraging scales (1 km) from the apiary. In addition, higher proportions of woody vegetation and hedges resulted in higher colony strength at longer distances from the apiary (2.5 km). Honey bees in moderately degraded landscapes demonstrated the most consistently strong colonies throughout the study period. Efforts towards improving beekeeper livelihoods, through higher hive productivity, should target moderately degraded and heterogeneous landscapes, which provide forage from diverse land covers.

**Key words:** honey bees; Kenya; landscape fragmentation; Sentinel-1; Sentinel-2; zero-inflated negative binomial regression.

## INTRODUCTION

Globally, pervasive anthropogenic activities have resulted in habitat loss and consequently fragmentation of the natural landscapes (Defries and Foley 2004, Foley et al. 2005, Morris 2010). Such habitat modifications often hinder fundamental ecosystem functions leading to reduction of global biodiversity (Ewers and Didham 2006, Haddad et al. 2015). For instance, forest fragmentation from human activities has been shown to modify plant species composition, subsequently influencing carbon sequestration and water production characteristics

adversely (Edwards et al. 2014, Putz et al. 2014). Furthermore, fragmentation lessens animal and plant mobility across landscapes, hence interfering with their ability to forage, migrate, breed, and disperse (Fischer and Lindenmayer 2006). In addition, fragmented patches are smaller, with greater edge effects, and therefore support smaller species populations and affect their overall persistence (Harper et al. 2005, Dobson 2006).

Fragmentation of landscapes can lead to nutritional deficiency and thus lower survival rates of honey bees from a lack of flora in the habitat (Naug 2009). Additionally, honey bee colony productivity is correlated with the surrounding landscape composition, therefore influencing the well-being of honey bees (Donkersley et al. 2014, Sponsler and Johnson 2015). Also, honey bee colonies located near natural/seminatural landscapes have higher hive productivity and survival rates (Brosi

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2009, Sande et al. 2009, Smart et al. 2016). In some instances, however, the surrounding landscapes have not displayed any strong effect on honey bee colony strength (Vaudo et al. 2012). Further studies on the effects of landscape on honey bee colony performance are therefore required.

In Africa, the livelihoods of a significant proportion of the rural population is dependent on beekeeping as an income-generating activity, mainly from sales of honey (Bradbear 2009). Furthermore, in Western Kenya, honey bees together with other pollinators are estimated to contribute US\$3.2 million in ecosystem services to numerous crops in the region (Macharia and Raina 2007, Kasina et al. 2009). Populations of wild honey bee swarms are regularly trapped into hives to establish “domesticated” honey bee stocks in the region (Dietemann and Pirk 2009) and beekeepers typically only interfere with the colonies during honey harvesting (Carroll 2006). Given the “wild” nature of honey bees in Kenya, they are greatly affected by habitat fragmentation especially with regard to their food sources (Macharia et al. 2007). This poses a tangible threat to the honey bees particularly because human population growth is increasing in Africa faster than any other place in the world (Cohen 2003), subsequently resulting in increased habitat degradation and fragmentation. Likewise, beekeepers in the region are aware that small honey bee colonies result in low productivity and such colonies are frequently discarded (Muli 2014). This demonstrates that honey bee colony strength variables can be associated with its productivity (Muli et al. 2014). However, there is a paucity of empirical studies that specifically address the association between landscape fragmentation and honey bees colony strength in Africa, unlike in European and North American countries where several studies exist (Aizen and Feinsinger 1994, Brosi et al. 2008). Understanding the effects of landscape fragmentation on honey bees in Africa could guide the selection of optimal locations of honey bee apiaries within the landscape, similar to the practice of commercial beekeepers in the United States who purposively select apiary locations in order to ensure abundant forage for the colonies throughout the year (Otto et al. 2016).

In this study, we investigated the effects of landscape fragmentation at both the landscape and landcover class level, on honey bee colony strength parameters in a semiarid agroecological landscape in eastern Kenya, an area characterized by variable landscape degradation levels. Specifically, we utilized landscape fragmentation metrics that were derived from a comprehensive landcover mapping of honey bee habitats at the study site using medium resolution fused Sentinel-1 (S1) and Sentinel-2 (S2) data sets (Ochungo et al. 2019). The present study is unique since it links remote sensing-based landscape variables to in situ determined honey bee colony strength variables using a novel data integration approach. We hypothesized that honey bee colonies

situated in landscapes with a greater proportion of natural and seminatural vegetation, as well as larger patch sizes, would exhibit higher colony strength than colonies located in landscapes with very little natural and seminatural vegetation, due to greater availability of pollen and nectar provided by different plant species in such ecosystems. Our specific objectives were to (1) assess the influence of landscape fragmentation metrics on honey bee colony strength parameters and productivity and (2) to identify landscape fragmentation metrics that are strongly associated with honey bee colony strength and productivity.

## METHODS

### *Study area and study sites*

We carried out our study in Mwingi sub-county within Kitui County in the southeastern part of Kenya (Fig. 1). Mwingi is an important honey-bee-keeping area in the country, and its beekeepers have a long association with agricultural researchers. The area exhibits a semiarid climatic pattern with average annual rainfall amounts of ~700 mm. Temperatures typically range from ~15°C during the cold season to ~30°C during the hot months. The study area is made up of variable and heterogeneous landscape types, from highly vegetated zones in the northwestern region to degraded and sparsely vegetated drier areas towards the southeast. The study area is predominantly an agroecological mosaic, consisting of maize and sorghum as the main crops (Landmann et al. 2015), which flower mainly in January, while the natural woodlands, chiefly *Acacia* spp., flower from February to April (Nagarajan et al. 2007), predominantly driven by the short rainy period from November to December.

Six study sites were selected across various land-degradation-severity gradients. These sites were predefined from field observations and consisted of sites with plenty of natural vegetation, i.e., higher proportions of woody vegetation, grasslands, and hedges compared to croplands (Mumoni and Kathiani), sites consisting of mixed natural and cropland areas, i.e., proportions of woody vegetation, grasslands, and hedges occupied almost an equal share of the landscape as croplands (Kasanga and Itiva Nzou), and sites with scant natural vegetation, i.e., the proportion of croplands was greater than proportion of woody vegetation, grasslands, and croplands (Nguni and Imba), and each were at least >3 km from each other (Fig. 1 and Table 1). Hedges in this context refers to linear features that are traditionally established to provide boundary demarcations between fields.

Ten 10-frame hives were placed in each of the six study sites (apiaries) where the hives were placed singly on stands and were at least 1 m or more apart from each other. Colonization was let to occur naturally through swarming, as is typical in Africa. A multiseasonal data collection was thereafter carried out.

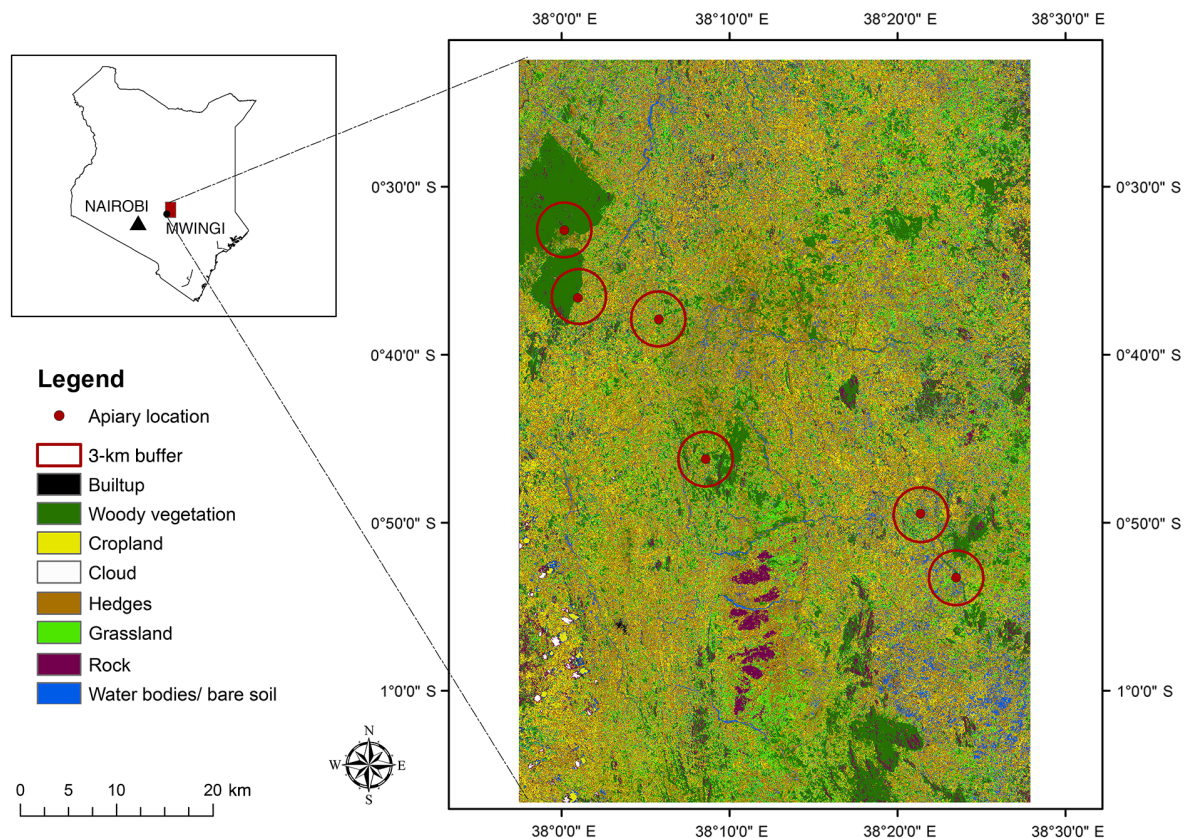


FIG. 1. Location of the study region in Kenya (left) with the hives located in each of the six study sites, marked by red dots. A classified landcover map of the study site is shown. Buffer zones from 500 m to 3 km were generated around the sites but for clarity, only the 3-km buffer zones are displayed here as red circles.

TABLE 1. Landscape characteristics of the experimental apiaries (the six study sites) in Mwingi study area.

Study site	Latitude (°E)	Longitude (°S)	Woody vegetation (%)	Grassland (%)	Hedges (%)	Croplands (%)
Nguni	38.3561	0.821710	08.52	16.09	6.94	46.69
Imba	38.39139	0.887838	10.76	16.14	03.8	49.37
Itiva	38.09649	0.631461	18.61	16.72	11.04	45.43
Kasanga	38.14273	0.770265	31.13	15.72	04.09	43.71
Kathiani	38.01603	0.610229	41.64	09.46	05.05	39.43
Mumoni	38.00261	0.543050	76.97	01.58	00.0	19.24

Note: Landscape composition comprising proportions of woody vegetation, grasslands, hedges, and croplands for each apiary site is calculated within a 3-km buffer zone.

*Honey bee colony strength measurements*

Standard Langstroth hives were used for this study. Each of the hives were labeled randomly from 1 to 10 in each apiary and subsequently the frames in the hives labeled 1–10 with each side of the frame labeled A or B. Initially, 60 hives were setup for this study, i.e., 10 hives per site. However, throughout the study period, we only inspected and sampled 30 hives (i.e., colonies), which were the only ones occupied by natural swarms as observed during our first field data collection. Visual

estimates from two observers were used, as this method is less disruptive compared to using empirical measurements such as mass of the honey bees (Delaplane et al. 2013). All the data measurements were conducted during the early hours around 07:00 and 08:00 local time (Greenwich Mean Time: GMT + 3) of the day to control for the foraging activities of honey bees, which might affect the observations, especially of the adult honey bee population. Each of the occupied hives was lightly smoked, opened, and frames containing combs were sequentially removed and examined. The percent

coverage of each frame side by the target resource (adult population, sealed and open brood, eggs, honey, and pollen) was visually estimated. Honey bee colony strength was estimated following Delaplane et al. (2013) and Imdorf and Gerig (2001) Liebefeld protocol. When using this method, the type of hive and frame determines the approximation of these metrics. Appendix S2: Table S1 shows the guiding values used for estimating the various comb types.

We adopted parameters for the Langstroth hive (Appendix S2:Table S1) and used estimates of the African honey bee body size from Buco et al. (1987), whereby the African honey bee is approximately 3% smaller than the Africanized honey bees in South America (1.75 bees/cm<sup>2</sup>). We therefore logically used a value of 1.8025 honey bees/cm<sup>2</sup> as the approximated size of the African honey bee. Further, we physically sampled 12 different combs from the six study sites and manually counted the number of cells in a 2 × 2 cm size comb area, to come up with the number of cells in a 1 × 1 cm comb area for each comb. The mean value of this exercise was 4.8 cells/1 cm<sup>2</sup> of comb for our study area. These values were then used to convert the proportions of honey, brood, pollen, and eggs on each side of a comb into count values of these parameters. Primary parameters of colony strength, i.e., adult population and brood (including eggs) and secondary parameters consisting of amount of stored pollen and honey were systematically collected in each hived colony over the entire study period (i.e., May 2017–November 2018). These primary and secondary parameters were deliberately selected to match different seasons in the region. In specific, each of the 30 sampled hives were inspected five times over a sampling period of five seasons, i.e., two rainy (May and November) and three dry ones (January, February, and June).

#### *Landscape characteristics measurements*

Remote-sensing-based landscape metrics were computed by analyzing habitat fragmentation at a maximum

radius of 3 km around each georeferenced apiary, using concentric circles around the middle point of the apiaries. This radius was selected based on estimated honey bee foraging distance, which is on average within 3 km from an apiary (Roubik 1989, Hepburn and Radloff 1998). Similarly, Vaudo et al. (2012) indicated that African races of honey bees typically forage within 1 km of the hive, and this further informed our selection of the 3-km radius. These landscape metrics can be used for estimating landscape composition and configuration, shape, heterogeneity, and connectedness and subsequently assessing their impact on honey bee colony strength. None of the apiaries were less than 3 km from each other.

In order to generate the landscape fragmentation indices, a honey bee habitat map was generated from a fused bitemporal Sentinel-1 and a single-season Sentinel-2 data set (European Space Association (ESA) 2017), which had an overall accuracy of 86% (Ochungo et al. 2019; Fig. 1). The readers are referred to Ochungo et al. (2019) for a detailed methodological description and results of the honey bee habitat map. Fragmentation indices were thereafter generated from the habitat map at various spatial scales ranging from 0.5 to 3 km (Table 2). Selection of these metrics was done based on their relevance to insects population and community ecology (Hunter 2002). We derived an index that we called fractional cover of seminatural vegetation to croplands (FNC) as an additional fragmentation index since honey bees have shown improved performance with increased proximity to seminatural areas (Sande et al. 2009, Patrício-Roberto and Campos 2014). The FNC index essentially calculates the proportion of seminatural vegetation compared to croplands in each of the study sites. A lower FNC indicates a lower proportion of seminatural vegetation in a site, while a higher FNC indicates a greater proportion of seminatural vegetation in a site. Furthermore, to quantify landscape heterogeneity, the splitting index (SI) (Jaeger 2000) was used. This index measures the number of equal-sized patches of a

TABLE 2. Class and landscape fragmentation indices used in this study (Mcgarigal 2014).

Index type	Fragstat index	Description
Landscape composition	percentage of landscape (PLAND)	proportional abundance (PLAND) for each of the patch types across the landscape
Landscape configuration	largest patch index (LPI)	index used to quantify the percentage of total landscape area characterized by the largest patch
Landscape shape	landscape shape index (LSI)	index used to reflect the complexity of the landscape patches; a greater value indicates more complexity
Landscape composition	splitting index (SI)	number of equal-sized patches of a specific class needed to produce a desired degree of landscape division
Landscape shape	fractal dimension (FD)	measures the degree of shape complexity
Landscape composition	Shannon diversity index (SHDI)	measures the number of landscape elements as well as their proportional changes, and the abundance of landscape types
Landscape connectivity	contagion (CONTAG)	a measure of the degree of adjacency of classes within a map
Landscape composition	fractional cover of natural to croplands (FNC)	index that measures the proportion of seminatural vegetation to croplands

particular class needed to produce a desired degree of landscape division (Jaeger 2000). The Shannon diversity index (SHDI), which is a measure of the number of landscape elements together with their proportional changes, was also computed. This index considers the abundance of the types of landscapes or landscape heterogeneity. The selection of SHDI was made on the basis of Morris (2014) who demonstrated that simpler indices like SHDI were slightly preferable when detecting effects of land use on diversity. When comparing two or more landscapes, those with lower SHDI values are typically more homogeneous than those with higher SHDI values. Further, the contagion index (CONTAG) was selected to measure landscape connectivity, while the fractal dimension index (FD) represented complexity of patch geometry. To quantify class level of fragmentation, the percentage of landscape (PLAND) measured the proportional abundance for each of the patch types across the landscape, whilst the landscape shape index (LSI) was selected to measure shape complexity at the class level. Finally, the landscape patch index (LPI) was used to quantify the percentage of total landscape area characterized by the largest patch (Mcgarigal 2014).

#### *Data analysis*

*Assessing multicollinearity and variable selection optimization.*—Two methods were utilized to assess multicollinearity in the fragmentation variables. The findCorrelation and the Recursive Feature Elimination (RFE) bootstrapping methods (Yan and Zhang 2015) were used concurrently to account for collinearity and disregard those indices that were highly correlated. As part of the findCorrelation method, first, a Spearman's rank-order correlation test was conducted at each buffer distance scale between all the fragmentation parameters (Table 2) to determine whether there were relationships among them with the intention of eliminating multicollinearity. There was a total of 96 landscape fragmentation metrics at both the class and landscape-level and most of these metrics were found to be highly correlated. Therefore, the findCorrelation function in the caret package in R (Kuhn 2019) was used to exclude highly correlated variables using the mean absolute error score. The caret package has demonstrated robustness in the selection of predictor variables (Kyalo et al. 2018, Mudreri et al. 2020). A threshold correlation coefficient of  $|r| > 0.75$  was set to indicate variable collinearity that would influence the outcome of our model (Dormann 2013). Fragmentation parameters that were highly correlated were then eliminated. Further, the RFE bootstrapping method was also used for automatic feature selection at every buffer distance. The RFE is a feature-ranking algorithm that performs optimization algorithms to achieve an optimal subset of variables (Pullanagari and Kereszturi 2018). Variables are ranked according to their importance after a process whereby

every variable in the out-of-bag data is randomly rearranged. A 10-fold cross validation is used to achieve optimization of the variable selection, after which the root mean squared error (RMSE) values are evaluated by the algorithm and those with large values are eliminated. This process is recursively exercised until the best variables with the lowest RMSE are identified (Pullanagari et al. 2018). The caret package in R (Kuhn 2019) was once again used to conduct the RFE on the landscape variables.

Landscape fragmentation variables that were selected by both the findCorrelation and the RFE functions were chosen for use in the regression analysis. In instances where there was no commonality between the selections from the two feature elimination functions, the RFE selection was used. Further, two radii were selected, i.e., the 1 km radius to represent a typical honey bee foraging distance (Vaudo et al. 2012) and the 2.5 km to represent the larger landscape in which the apiaries were situated (Roubik 1989, Hepburn and Radloff 1998). The following variables were selected at the 1 km radius: fractal dimension, percentage of landscape under cropland, landscape shape index for woody vegetation, landscape patch index for cropland class and fractional cover of natural to cropland. Further, the following variables were selected at the 2.5 km radius: percentage of landscape under grassland, percentage of landscape under woody vegetation, largest patch index for hedges class, percentage of land under hedges, and fractional cover of natural to cropland.

*Linking landscape variables and honey bee colony strength metrics.*—The uncorrelated landscape fragmentation characteristics at the two selected radii (1 and 2.5 km) were compared with the field-collected honey bee colony data (adult bee population, brood, honey, pollen, and eggs) at hive level. Zero-inflated negative binomial (ZINB) mixed models were used to analyze for each of the response variables (i.e., colony strength parameters and productivity). Due to the hierarchical quality of the data collection, which involved repeated in situ data collections within each of the sites and colonies, mixed effects involving random and fixed effects were also applied, with colony nested within site as random effects. Mixed-effects models allow for the use of all the data, while avoiding the use of individual colonies as pseudo-replicates (Crawley 2002, Chaves 2010). All the data analyses were carried out within the R statistical programming language (R Development Core Team, 2019) using the glmmTMB package (Brooks et al. 2017). Additionally, backward stepwise variable elimination was carried out on the predictor variables using AIC values to remove variables whose  $P$  value was non-significant in the regression outcome (NCSS Statistical Software 2014). Residuals for each response variable were then plotted using R package DHARMA (Hartig 2020).

RESULTS

*Honey bee colony strength measurements*

Data distributions of the honey bee colony strength response variables displayed large proportions of zero counts. Appendix S1: Fig. S1, shows the distributions of adult honey bee populations and number of cells of honey only since the distributions for the rest of the colony strength parameters exhibit a similar pattern. Further, honey bee colony strength characteristics summed across the five data collection periods showed that the two study sites in the moderately degraded areas (Kasanga and Itiva) displayed the highest colony strength parameters throughout the data collection period whereas the two study sites in the highly degraded areas (Nguni and Imba) showed the lowest values (Appendix S1: Fig. S2).

*Landscape fragmentation variables vs. honey bee colony strength*

Examination of the count component model coefficients and *P* values (Table 3) at the 1-km scale showed that FD was the most important variable since it was significant in both the count and zero components of the models. Lower FD values resulted in higher adult honey bee counts and cells of honey and conversely, higher FD values resulted in zero adult honey bee population counts, cells of honey and cells of pollen. Furthermore, higher landscape shape index of woody vegetation (LSW) resulted in higher adult honey bee counts and higher number of cells of honey, whereas lower proportion of cropland (PLC) and lower fractional cover of natural to croplands (FNC) resulted in higher adult honey bee population. The complete models for each response variable at the 1-km scale are shown in the following expressions:

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$$\begin{aligned} \text{Popbees1km} <- \text{glmmTMB}(\text{Popbees} \sim \text{FD1km} &+ \text{PLANDCropland1km} + \text{LSIwoody1km} + \\ &\text{FCNC1km} + (1|\text{Site/Colony}), \text{zi} \sim \text{FD1km} + \\ &\text{PLANDCropland1km} + \text{LSIwoody1km} + \\ &\text{FCNC1km}, \text{family}=\text{nbinom2}, \\ &\text{data}=\text{hivedata1km}) \end{aligned} \tag{1}$$

$$\begin{aligned} \text{Brood1km} <- \text{glmmTMB}(\text{Cellsbrood} \sim &\text{FD1km} + \text{PLANDCropland1km} + \\ &(1|\text{Site/Colony}), \text{zi} \sim \text{FD1km} + \\ &\text{PLANDCropland1km}, \text{family}=\text{nbinom2}, \\ &\text{data}=\text{hivedata1km}) \end{aligned} \tag{2}$$

$$\begin{aligned} \text{Honey1km} <- \text{glmmTMB}(\text{Cellshoney} \sim \text{FD1km} &+ \\ &\text{PLANDCropland1km} + \text{LSIwoody1km} + \\ &\text{FCNC1km} + (1|\text{Site/Colony}), \text{zi} \sim \text{FD1km} + \\ &\text{PLANDCropland1km} + \text{LSIwoody1km} + \\ &\text{FCNC1km}, \text{family}=\text{nbinom2}, \text{data}=\text{hivedata1km}) \end{aligned} \tag{3}$$


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$$\begin{aligned} \text{Pollen1km} <- \text{glmmTMB}(\text{Cellspollen} \sim \text{FD1km} &+ \\ &\text{PLANDCropland1km} + \text{LSIwoody1km} + \\ &\text{FCNC1km} + (1|\text{Site/Colony}), \text{zi} \sim \text{FD1km} + \\ &\text{PLANDCropland1km} + \text{LSIwoody1km} + \\ &\text{FCNC1km}, \text{family}=\text{nbinom2}, \text{data}=\text{hivedata1km}) \end{aligned} \tag{4}$$

$$\begin{aligned} \text{eggs1km} <- \text{glmmTMB}(\text{Cellseggs} \sim \text{FD1km} &+ \\ &(1|\text{Site/Colony}), \text{zi} \sim \text{FD1km}, \text{family}=\text{nbinom2}, \\ &\text{data}=\text{hivedata1km}). \end{aligned} \tag{5}$$


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At the 2.5-km scale, the proportion of woody vegetation (PLW) was the most important variable since it was significant in both the count and zero components of the models for most of the honey bee colony strength variables. A higher PLW resulted in higher adult honey bee populations, higher number of cells of brood, honey, and pollen, whereas a lower PLW resulted in zero counts of adult honey bee populations, cells of brood, honey, pollen, and eggs. Additionally, lower proportions of grasslands (PLG) and hedges (PLH) resulted in zero adult honey bee populations, cells of brood, honey, pollen, and eggs, while larger patch size index of hedges (LPH) resulted in zero values for all the honey bee colony strength parameters (Table 3). The complete models for each response variable at the 2.5-km scale are shown in the following expressions:

---


$$\begin{aligned} \text{Popbees2.5km} <- \text{glmmTMB}(\text{Popbees} \sim &\text{PLANDgrass2.5} + \text{PLANDwoody2.5} + \\ &\text{LPIhedges2.5} + \text{PLANDhedges2.5} + \\ &(1|\text{Site/Colony}), \text{zi} \sim \text{PLANDgrass2.5} + \\ &\text{PLANDwoody2.5} + \text{LPIhedges2.5} + \\ &\text{PLANDhedges2.5}, \text{family}=\text{nbinom2}, \\ &\text{data}=\text{hivedata2.5km}) \end{aligned} \tag{6}$$

$$\begin{aligned} \text{Brood2.5km} <- \text{glmmTMB}(\text{Cellsbrood} \sim &\text{PLANDgrass2.5} + \text{PLANDwoody2.5} + \\ &\text{LPIhedges2.5} + \text{PLANDhedges2.5} + \\ &(1|\text{Site/Colony}), \text{zi} \sim \text{PLANDgrass2.5} + \\ &\text{PLANDwoody2.5} + \text{LPIhedges2.5} + \\ &\text{PLANDhedges2.5}, \text{family}=\text{nbinom2}, \\ &\text{data}=\text{hivedata2.5km}) \end{aligned} \tag{7}$$

$$\begin{aligned} \text{Honey2.5km} <- \text{glmmTMB}(\text{Cellshoney} \sim &\text{PLANDgrass2.5} + \text{PLANDwoody2.5} + \\ &\text{LPIhedges2.5} + \text{PLANDhedges2.5} + \\ &(1|\text{Site/Colony}), \text{zi} \sim \text{PLANDgrass2.5} + \\ &\text{PLANDwoody2.5} + \text{LPIhedges2.5} + \\ &\text{PLANDhedges2.5}, \text{family}=\text{nbinom2}, \\ &\text{data}=\text{hivedata2.5km}) \end{aligned} \tag{8}$$

$$\begin{aligned} \text{Pollen2.5km} <- \text{glmmTMB}(\text{Cellspollen} \sim &\text{PLANDgrass2.5} + \text{PLANDwoody2.5} + \\ &\text{LPIhedges2.5} + \text{PLANDhedges2.5} + \\ &(1|\text{Site/Colony}), \text{zi} \sim \text{PLANDgrass2.5} + \\ &\text{PLANDwoody2.5} + \text{LPIhedges2.5} + \\ &\text{PLANDhedges2.5}, \text{family}=\text{nbinom2}, \\ &\text{data}=\text{hivedata2.5km}) \end{aligned} \tag{9}$$


---

```
eggs2.5km <- glmmTMB(Cellseggs ~
  PLANDgrass2.5 + PLANDwoody2.5 +
  LPIhedges2.5 + PLANDhedges2.5 +
  (1|Site/Colony), zi=~ PLANDgrass2.5 +
  PLANDwoody2.5 + LPIhedges2.5 +
  PLANDhedges2.5, family=nbinom2,
  data=hivedata2.5km)
```

(10) indicating good model fits as shown in Appendix S1: Figs. S3 and S4, respectively.

DISCUSSION

The main objective of our study was to assess the effect of landscape fragmentation on the colony strength of honey bees within a short foraging range of the apiary (1 km) and within the larger landscape (2.5 km) in a semiarid region of Kenya. The influence of spatial scale on the well-being of honey bees has also been demonstrated in this study, similar to another that found that landscape factors at different spatial scales affected crop yields by both managed and wild pollinators (Taki et al.

Effect plots showing the main findings are shown in Figs. 2 and 3. Further, scaled residuals for each of the response variables at the 1- and 2.5-km scales indicated that overall deviations from the expected distribution, including tests for accurate distribution (KS test), dispersion, and outliers were not significant, therefore

TABLE 3. Zero-inflated negative binomial (ZINB) model parameters of the response of population of all the honey bee colony strength parameters ( $n = 150$ ) to landscape fragmentation predictors at 1 and 2.5 km radii.

Variable	Zero component			Count component		
	Estimate	SE	<i>z</i>	Estimate	SE	<i>z</i>
1 km						
Adult worker bee population						
FD	48.25	20.99	2.30*	-22.08	10.09	-2.19*
PLC	0.03	0.33	0.10	-0.36	0.16	-2.31*
LSW	-0.64	0.34	-1.86	0.42	0.15	2.76*
FNC	0.51	2.77	0.18	-3.05	1.35	-2.26*
Cells of honey						
LSW	-0.65	0.33	-1.93	0.27	0.13	2.11*
FD	48.70	20.09	2.42*	-9.26	7.44	-1.25
Cells of pollen						
FD	44.67	18.94	2.36*	-13.14	10.64	-1.24
PLG	-0.26	0.11	-2.34*	0.08	0.05	1.66
2.5 km						
Adult worker bee population						
PLW	-0.15	0.05	-3.09*	0.04	0.02	2.13*
LPH	0.30	0.11	2.63*	-0.08	0.06	-1.42
PLH	-1.24	0.41	-3.05*	0.23	0.16	1.43
Cells of brood						
PLG	-0.34	0.12	-2.90*	0.18	0.06	2.86*
PLW	-0.21	0.05	-3.76*	0.07	0.03	2.36*
LPH	0.49	0.16	2.95*	-0.05	0.10	-0.54
PLH	-1.66	0.48	-3.49*	0.27	0.27	1.01
Cells of honey						
PLG	-0.26	0.11	-2.34*	0.09	0.08	1.22
PLW	-0.16	0.05	-3.26*	0.06	0.03	2.29*
LPH	0.21	0.12	1.80	-0.07	0.09	-0.75
PLH	-1.22	0.41	-2.95*	0.35	0.24	1.49
Cells of pollen						
PLW	-0.13	0.05	-2.90*	0.09	0.03	3.19*
PLH	-1.03	0.38	-2.69*	0.48	0.22	2.14
Cells of eggs						
PLG	-0.27	0.13	-2.12*	0.07	0.06	1.05
PLW	-0.20	0.07	-2.96*	0.05	0.04	1.41
LPH	0.57	0.22	2.64*	-0.21	0.12	-1.78
PLH	-1.83	0.60	-3.04*	0.46	0.32	1.43

Notes: Zero-component results show how predictors affect the odds of observing excess zeros in adult honey bee populations while count-component results show how predictors affect the population of adult honey bees. Only significant variables are shown. SE is the standard error and *z* is the regression coefficient divided by standard error.  
\* $P < 0.05$ .

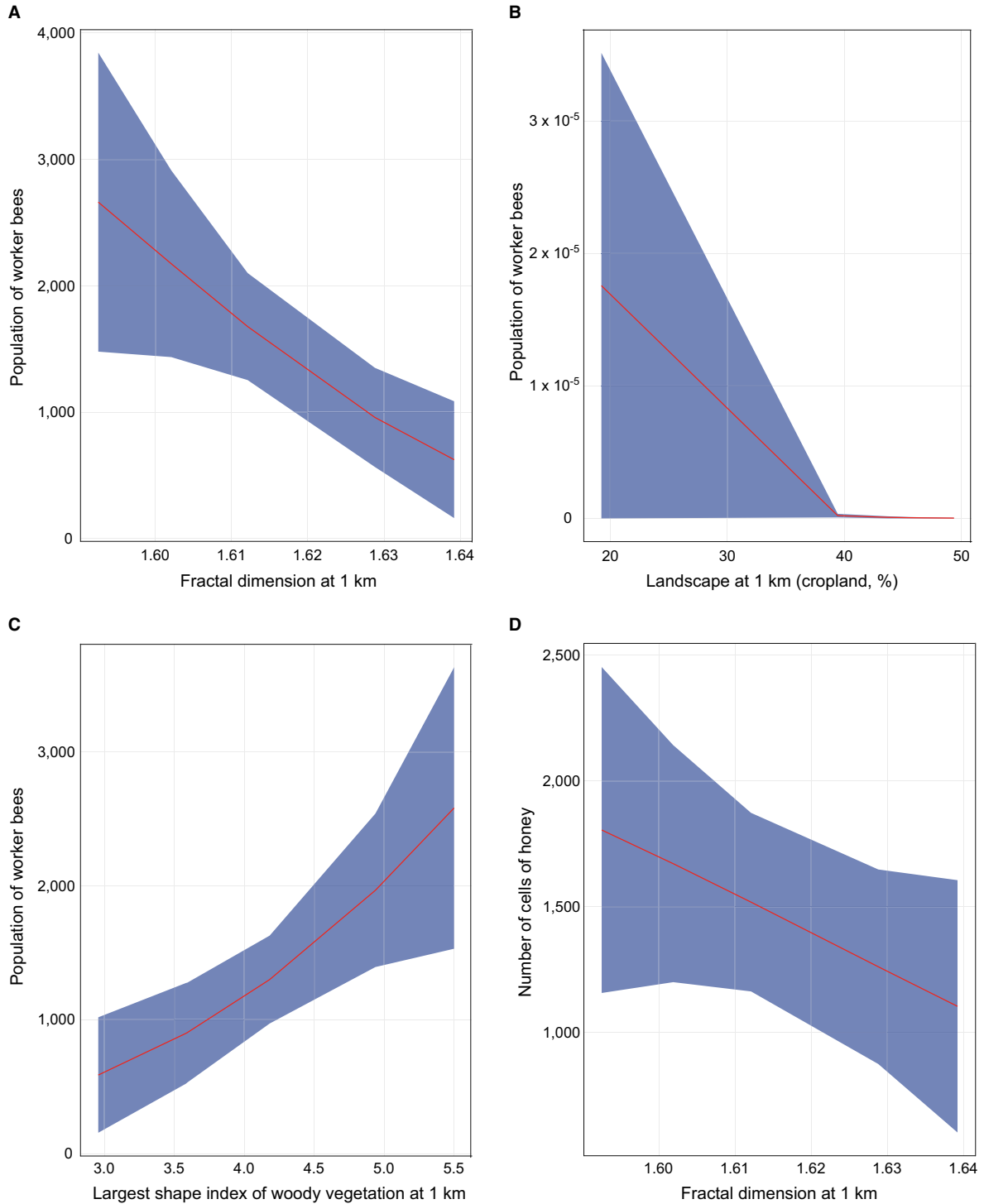


FIG. 2. Marginal effects of landscape fragmentation indices on honey bee colony strength at 1 km scale. (A) Fractal dimension vs. population of bees, (B) proportion of cropland (%) vs. population of bees, (C) landscape shape index of woody vegetation vs. population of bees, and (D) fractal dimension vs. number of cells of honey. Predicted values are conditioned on the fixed effects and components of the zero-inflation model. The shaded gray area represents 95% confidence intervals.

2010). Overall, the negative effect of the fractal dimension variable for the count component of the model at the 1-km scale indicates that patch geometries that were

less complex had a positive effect on adult honey bee population, brood, honey, and pollen. Our results are in agreement with Brosi (2009) who found that forest



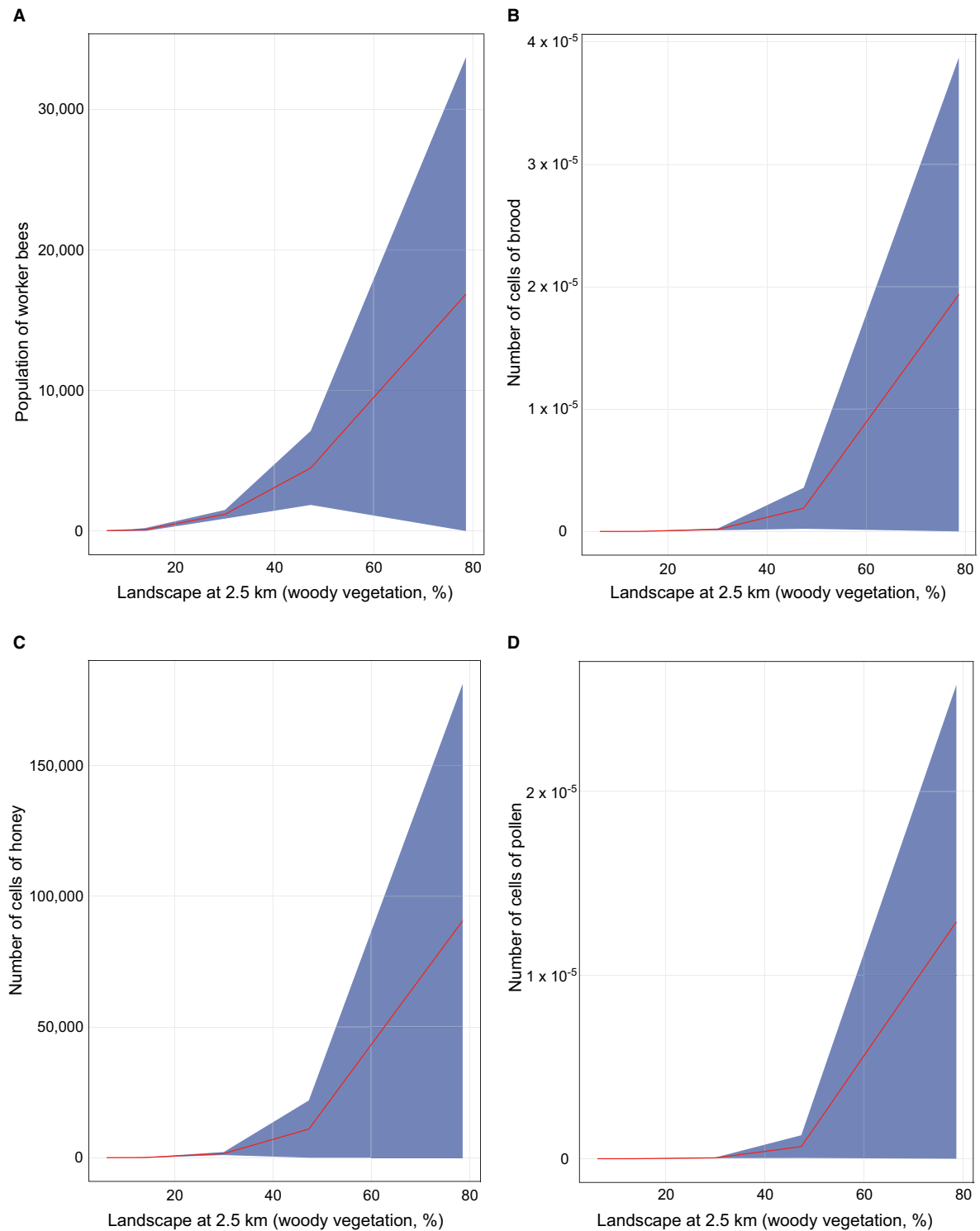


FIG. 3. Marginal effect of proportion of woody vegetation (%) on honey bee colony strength at 2.5 km scale. (A) Population of bees, (B) number of cells with brood, (C) number of cells with pollen, and (D) number of cells with honey. Predicted values are conditioned on the fixed effects and components of the zero-inflation model. The shaded gray area represents 95% confidence intervals.

fragment shape was the most important landscape factor affecting euglossine bee's abundance and species richness. Moreover, Reynolds et al. (2007) demonstrated

that honey bees search for the most optimal and efficient paths to return to their hives after foraging. Complex patch geometries would hypothetically lead to inefficient

use of the honey bee's energy and consequently weaker adult workers who cannot forage effectively for pollen and nectar. Further, simpler patch shapes are also associated with lower landscape fragmentation, which can be important for different ecological processes (Forman 1995). Similarly, the positive effect of the fractal dimension variable on the probability of occurrence of zero values for nearly all the honey bee colony strength parameters agrees with our finding that complex shapes negatively affected the colonies.

Further, the negative effect of the proportion of croplands variable in the count component of the model at the 1 km radius from the apiary on adult honey bee population is similar to studies that found that agricultural lands were associated with honey bee colony losses probably due to reduced foraging resources from seminatural land covers (Vandame and Palacio 2010, Vaudo et al. 2012, Clermont et al. 2015, Otto et al. 2016).

Our results demonstrate that honey bee colonies in landscapes with abundant woody vegetation will demonstrate greater colony strength (i.e., large colonies that persist overtime and are more resistant to disease). This finding was expected since woody vegetation provide foraging resources for the honey bees at different times of the year depending on their floral cycle (Potts et al. 2010). Further, our findings corresponded with others who demonstrated the importance of woody vegetation for densities of feral honey bees as well as the improvement of the abundance and richness of domesticated honey bees, mainly due to the availability of floral resources for the honey bees (Arthur et al. 2010, Schrader et al. 2018). Similarly, higher amounts of stored honey and pollen have also been linked to shorter distances to woody vegetation (Sande et al. 2009, Bertrand et al. 2019).

Interestingly, there was a strong positive effect of the proportion of hedges in the landscape at the 2.5km scale on number of honey bee cells with stored pollen. Hedgerows have been shown to support a diverse herbaceous flora that forms a key foraging habitat for bees (Hannon and Sisk 2009). Similarly, hedgerows should be included in farmlands because they have been shown to improve visitation to crops by pollinators (Winfree et al. 2008), which further strengthens our results. Additionally, hedges have also demonstrated their necessity in facilitating pollinator movement between habitat fragments (Cranmer and McCollin 2012). Likewise, a lower proportion of hedges in the landscape increased the probability that honey bee hives would be unoccupied.

Our results further demonstrated that presence of grasslands would result in stronger honey bee colonies, similar to studies that found that grasslands supported pollen amounts and quality, therefore directly influencing honey bee colony strength (Otto et al. 2016, Simonok and Otto 2020). In addition, our result showed that the fractional cover of natural over cropland (FNC) variable had a negative effect on the population of adult honey bees at the 1-km scale was unexpected

but could point toward the need for diverse landscapes closer to the hive rather than homogeneous natural landscapes. Furthermore, in subtropical Africa, agroecological landscapes are typically heterogeneous and these types of landscapes have been shown to enhance pollinator richness and abundance due to the landscape diversity (Steckel et al. 2014, Aguirre-Gutiérrez et al. 2015).

While we had hypothesized that apiaries in the least degraded sites would have the strongest colonies, we established that the apiaries in the moderately degraded sites had the most consistently strong colonies throughout the study period (Appendix S1: Fig. S2). This pattern is similar to the intermediate disturbance hypothesis, whereby pollinator species and abundance have been found to be higher in moderately disturbed landscapes compared to completely undisturbed habitats (Hinnens and Kearns 2012, Coulin and Aizen 2019). Such areas are composed of heterogeneous landscapes with different types of crops and, consequently, a diversity of weeds and grasses. These crops, weeds, and grasses have been shown to provide honey bee forage during periods when the seminatural woody areas are not flowering (Odoux et al. 2012, Bretagnolle and Gaba 2015). Also, the abundance of weeds has been shown to enhance pollination services and consequently improved honey yields (Bretagnolle and Gaba 2015). On the other hand, apiaries in the two least-degraded sites experienced the most absconding, again contrary to our postulation. During the periods when the honey bees had absconded in these areas; we found several (>20) large hive beetles (*Oplostomus fuliginus*) inside these empty hives and speculated that these pests could have caused absconding. These beetles have been reported to cause significant damage to colonies by chewing on the comb, brood, honey, and pollen (Oldroyd and Allsopp 2017, Wambua et al. 2019). Further, a study by Makori (2017) showed that honey bee pests occurred more in areas with higher proportion of natural vegetation, which is in agreement with our observation in this study. Such areas should therefore be targeted for pest control exercises if honey bee colonies are to have maximal productivity and strength.

## CONCLUSIONS

This study demonstrates the importance of landscape fragmentation on honey bee colony performance variables at various buffer scales. Therefore, it is recommended that optimal hive placement should consider the landscape structure of sites at various spatial scales in our study region. The study also revealed that heterogeneous landscapes in moderately degraded areas were more favorable for beekeeping compared to the least degraded areas. The likely reason for this is that landscapes with patches of croplands can contain a variety of weeds and grasses that could supply forage for the honey bee colonies even during seasons when the seminatural

vegetations were not flowering. Suitability mapping for purposes of scaling up could therefore be carried out in the country with the aim of encouraging beekeeping activities in similar areas.

Moreover, highly degraded areas exhibited the lowest honey bee colony strength parameters throughout the study period, and it is recommended that supplemental feeding of the colonies during dry seasons could be carried out to support honey bee colonies in these areas. This will improve honey bee colony performance in degraded areas and consequently beekeepers' livelihoods and food security.

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## SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2483/full>

## OPEN RESEARCH

Data (Ochungo et al. 2021) is available in the Dryad digital repository: <https://doi.org/10.5061/dryad.j3tx95xdj>.