



Local-scale tree and shrub diversity improves pollination services to shea trees in tropical West African parklands

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Abstract

1. Shea *Vitellaria paradoxa* trees bear fruit and seeds of considerable economic, nutritional and cultural value in the African Sudano-Sahelian zone. In much of West Africa, shea exists within an agroforestry system referred to as 'parkland', where social changes, including migration, have resulted in expanding areas of crop cultivation, reductions in both the area of fallow land and the duration of fallow periods, and reduced diversity of habitats and woody species. Shea benefits strongly from pollination by bees and the loss of Parkland biodiversity may reduce the availability of pollinators, leading to pollen limitation and reductions in fruit yields.
2. We investigated whether shea trees in southern Burkina Faso experienced pollination limitation, and whether local- and landscape-scale diversity were linked to visitation by bees, the degree of limitation observed and the weight of fruit produced.
3. Honeybees *Apis mellifera* were observed more frequently in diverse sites, whereas *non-Apis* species were generally widespread but visited trees in greater numbers at diverse sites.
4. We found that shea fruit production was significantly limited due to lack of pollination and that the degree of pollination limitation was greater in sites with lower levels of tree and shrub diversity.
5. *Synthesis and applications.* Sites with greater diversity of tree and shrub species had more bee visits and less extreme pollination limitation than less diverse sites, indicating that small-scale diversity is associated with more efficient pollination services. Consequently, shea yields are likely to benefit from retention of a range of different tree and shrub species in parklands. We recommend that when fallows are cleared for cultivation, such beneficial plants are retained within cultivated fields, and that measures to conserve pollinators in the region should target both *A. mellifera* and *non-Apis* bee species.

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KEYWORDS

agro-ecology, biodiversity, ecosystem services, parkland, pollination limitation, pollination services, shea, tropical

1 | INTRODUCTION

An estimated 96% of flowering plants in the tropics benefit from animal-mediated pollination (Ollerton, Winfree, & Tarrant, 2011). On a global scale, there is concern about decline of pollinating insects, particularly bees, although most evidence for pollinator decline comes from North America and Europe. Despite their cultural, nutritional and economic value (IPBES, 2016), relatively little is known of the status of pollinators and pollination services in lower latitudes (Brown & Paxton, 2009). Pollinator declines are frequently linked to land use (Potts et al., 2010), and agriculture has expanded and intensified in the tropics in recent decades (Gibbs et al., 2010; Stéphenne & Lambin, 2001). Landscape changes, particularly landscape homogenization, have been shown to affect pollinator abundance and diversity in tropical systems, with negative effects on certain crop yields (Dainese et al., 2019; Klein et al., 2012).

Loss and fragmentation of natural habitat in the landscape affects the availability of resources such as food and shelter, alters the impacts of competing species and pathogens (Kremen et al., 2007) and, ultimately, influences the communities of pollinating insects. Impacts of reduced area of natural habitats can lead to reduced delivery of pollination service (Banks et al., 2013). Furthermore, in highly modified landscapes with few natural areas, mobile, generalist species such as honeybees tend to persist, while smaller or less mobile bee species are scarcer (Klein et al., 2012).

On a local scale, relationships between floral diversity and pollinator abundance and diversity in subtropical and tropical systems are inconsistent, particularly where woody species grow in mixed cropping systems. Norfolk, Eichhorn, and Gilbert (2016) found a positive relationship between ground flora diversity, pollinator density and yield within almond orchards in Egypt, but no relationship between flower visitors and proximity to natural habitats. Here, orchards provide more resources for pollinating insects than the arid habitats surrounding them, demonstrating the importance of landscape context. Conversely, higher species richness of non-crop trees has been linked with lower pollinator abundance in coffee farms, possibly due to competition for pollinators (Boreux, Krishnan, Cheppudira, & Ghazoul, 2013). On a landscape scale, maintaining natural habitats close to agricultural areas has been shown to increase pollinator diversity by supporting non-*Apis* bees (Klein, Steffan-Dewenter, & Tschardtke, 2003), an important factor influencing the effectiveness of pollination services (Garibaldi et al., 2011; Woodcock et al., 2019). The importance of local- and landscape-scale factors in delivery of pollination services can be linked, for example Motzke, Klein, Saleh, Wanger, and Tschardtke (2016) found that bee abundance in home gardens in Indonesia was greatest when flower cover within the garden was high and distance to a forest fragment was <100 m.

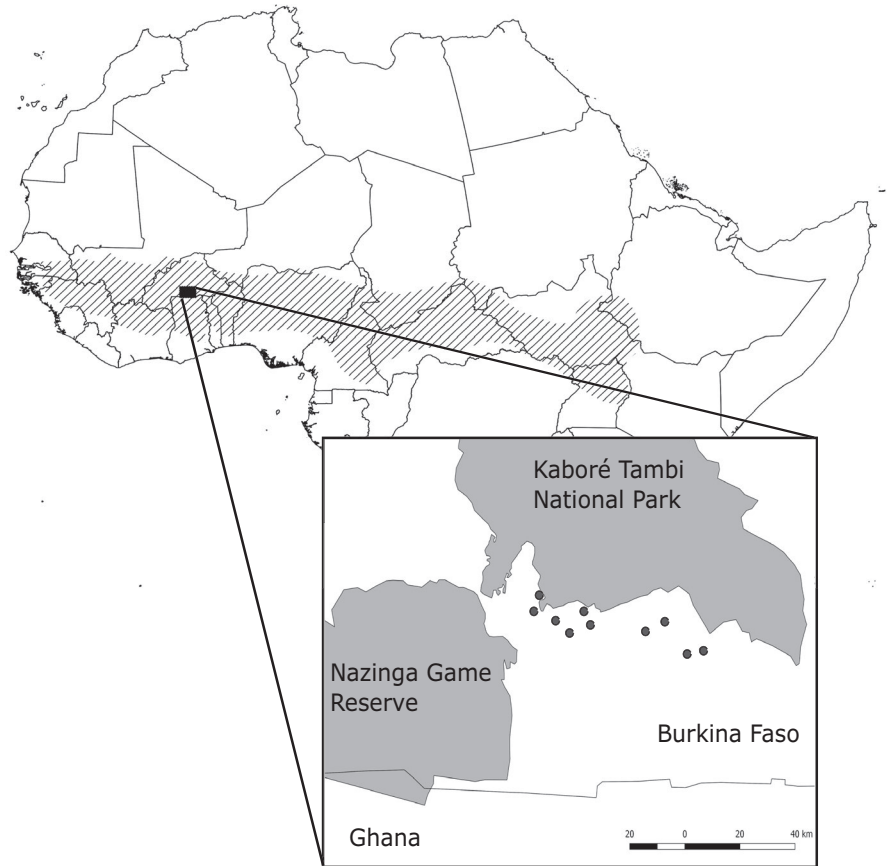
In the West African Sudano-Sahel, shea parkland is a traditional agroforestry system practised from Senegal in the west to Kenya in the east (Figure 1). The parkland is composed of cultivated fields where trees valued by local communities, primarily shea *Vitellaria paradoxa* Gaertn, are planted or regenerate naturally during fallow periods (Boffa, 2015; Gijssbers, Kessler, & Knevel, 1994). Shea is nutritionally valuable to people as the fruits ripen when food is scarce, and the pulp is a source of protein, fibre, calcium and potassium (Maranz, Kpikpi, Wiesman, De Saint Sauveur, & Chapagain, 2004). Shea nuts are also commonly processed to produce shea butter, which is an important source of dietary fats (Victoria & Ajay, 2015). The nuts and butter are commercially valuable: traded locally providing women with a rare source of cash income and internationally for use in the cosmetics and confectionary industries (Pouliot, 2012). Shea is heavily dependent on bees for pollination, and a range of bee species have been recorded visiting flowers, although honeybees are thought to be more effective pollinators than smaller bees (Lassen, Nielsen, Lompo, Dupont, & Kjær, 2016; Stout et al., 2018).

Agricultural intensification and expansion in shea parklands in recent decades (Stéphenne & Lambin, 2001) has resulted in longer cultivation periods within fields, shorter fallow periods and, in some cases, abandonment of the practice of fallowing (Augusseau, Nikiéma, & Torquebiau, 2006). Trees regenerate during fallow periods, and these changes have led to reduced diversity and abundance of trees in parkland fields (Kaboré, Bastide, Traoré, & Boussim, 2012), and loss of semi-natural habitats including scrub and woodland from parklands (Gijssbers et al., 1994). Such environmental perturbations can result in changes to plant–pollinator interactions, few pollination events or the transfer of less pollen, and thus pollination limitation and decreases in fruit and/or seed production (Knight et al., 2005).

Given the intensification of agriculture and encroachment on natural areas in West African shea parklands, and the association between habitat loss and fragmentation with decreased pollinator abundance and diversity, pollination services in shea parklands may be negatively affected by human activities. As shea relies heavily on bees for pollination (Lassen et al., 2016; Stout et al., 2018), changes in agricultural practices may have a negative effect on pollinating insects, which could contribute to threats to food security and the economic well-being of an estimated 45.1 million rural people living in the shea belt (Naughton, Lovett, & Mihelcic, 2015). We aimed to quantify the relationship between species diversity in fields in shea parkland, the area of semi-natural habitat in the wider landscape and provision of pollination services to shea trees by testing the following hypotheses:

1. Shea trees in West Africa are pollination limited.
2. The proportion of natural habitat surrounding sites and plant diversity within sites influence the visitation rate of bee species that

FIGURE 1 Northern Africa with shea parkland adapted from Naughton et al. (2015) represented by hatching (main map). The inset shows the 10 study sites in southern Burkina Faso. Unshaded areas are primarily managed as agroforestry while shaded areas are under management for conservation



visit shea flowers, the degree of limitation and the number and weight of fruit set by naturally pollinated flowers.

Pollination limitation, bee visitation, and fruit set and weight were used as proxies to measure the effectiveness of pollination services.

2 | MATERIALS AND METHODS

2.1 | Study species

Shea, or *Vitellaria paradoxa*, is the only member of its genus in the family Sapotaceae. Its range is restricted to the Sudano-Sahelian zone of western and central Africa (Figure 1) and it comprises two subspecies: *Vitellaria paradoxa* ssp. *nilotica* in the east and *Vitellaria paradoxa* ssp. *paradoxa* in the central and western parts of its range (Naughton et al., 2015). Shea trees bloom during the dry season, between January and April, with peak fruiting occurring by the end of July, although anecdotal evidence suggests flowering and fruiting periods can vary yearly. Flowers are born on inflorescences located at the tips of branches. The flowers are short lived, but buds, receptive flowers and older blooms occur simultaneously over a long flowering period (Stout et al., 2018). The flowers are protogynous, with the stigma emerging from the bud and becoming receptive before the sepals part to reveal the petals and stamens (Hall,

Aebischer, Tomlinson, Osei-Amaning, & Hindle, 1996). Although this reduces the likelihood of a flower self-pollinating, the presence of flowers at different stages of maturity on the same inflorescence indicates that within-inflorescence pollination is possible. The success of pollination by flowers on the same inflorescence is not well understood. Shea produces fruit with sweet pulp surrounding a large seed (the shea 'nut'), and occasionally more than one nut may be produced in a single fruit.

2.2 | Site selection

This study was conducted in the Centre-Sud region of Burkina Faso, south of the Kaboré Tambi National Park (KTNP) and east of Nazinga Game Ranch (Figure 1). All data were recorded between February and June 2017.

We selected ten 1-ha sites (100 m × 100 m) in fields which had been cultivated during the previous rainy season. Sites were organized into five pairs located 2–3.5 km apart, and the minimum distance between pairs was 4 km. The paired design allowed us to minimize the impacts of external factors (e.g. distance to a large town or nature reserve). Within each pair, we selected one site with low diversity of woody species and one site with higher diversity. All trees and shrubs, including shea, >3 m in height were identified and counted in each site, and the mean inverse Simpson's index (1/D) was calculated to represent site diversity.

We did not include small trees and shrubs (<3 m in height) because local knowledge indicated they were unlikely to flower (an observation that proved true). Herbaceous species were also excluded from site diversity calculations because we worked in ploughed fields that were open to grazing animals, with low cover of herbaceous plants (<0.01% cover). We mapped and calculated the area of semi-natural habitat within a radius of 1 km from the centre of each site in ArcMap 10.4 using satellite imagery provided by ESRI world maps and Google Earth (accessed in September 2017, photographs dated to 2013). Restricting the radius to 1 km avoided an overlap in mapped habitat between sites. Although the foraging range of *A. mellifera* can greatly exceed this distance, studies based on waggle dances and mark-recapture indicate that African honeybee races, including *A. mellifera adansonii*, focus the majority of their foraging within distances of 1 km of the hive or previous feeding stations (Roubik, 1999; Schneider, 1989). Diversity ($1/D$) of woody species within our 10 sites (site diversity) and area of semi-natural habitats then acted as the independent variables (see data analysis).

We collected data regarding pollination services from 10 shea trees within each site that met the following criteria: selected trees had a single trunk, were >3 m tall, appeared healthy and had developing flower buds. If more than 10 trees in a site met the criteria, the 10 selected trees were distributed as evenly as possible through each site.

2.3 | Pollination limitation

Supplemental hand pollination was carried out over the course of three visits to each site during the flowering period. We selected up to three pairs of inflorescences that had a similar number of flowers with receptive stigmas on each tree. The flowers with receptive stigmas on one inflorescence per pair were marked for fruit counts later in the season and were left open to natural pollination (untreated flowers). The other inflorescence per pair was also marked and left

open, but in addition was hand pollinated with pollen from another tree (pollen supplementation).

The number of trees and inflorescences varied between sites because three comparable pairs of inflorescences were not present on every tree (Table 1). In total, 2,248 flowers were included in the analysis: 1,096 untreated flowers and 1,152 flowers with pollen supplementation by hand. On average, the difference in the number of hand pollinated and control flowers at each site was 2.4%. The greatest difference was 8.6%. All results relating to flowers and fruit set are from these selected flowers.

2.4 | Flower visitors

We surveyed flower visitors during two 10-min recording episodes per tree, one between 6 and 8 a.m. and another between 4 and 6 p.m., when insect visitors are most active, on each of three dates during the flowering season (January–March 2017; Stout et al., 2018). If there were no receptive flowers on a tree, no attempt was made to record visitation (Table 1). All bees observed visiting inflorescences during recording episodes were caught. The native honeybee, *Apis mellifera adansonii* Latreille could be identified easily, but other bees were placed in 70% alcohol solution and sent for expert identification.

2.5 | Fruit set

We counted fruit set in early May 2017, when the selected flowers had developed small fruits, but before fruits ripened and fell. Ripe fruits were collected and their nuts were weighed in the field in June to August 2017. Initially, fruits were hand harvested ($n = 35$), but proved to be unripe. The remaining ($n = 133$) fruits were collected by placing bags around them, so they could fall naturally as they ripened without being lost. Only the ripe fruits collected in bags were included in the analysis of fruit weight.

Site name	Diversity	Pollen supplementation		Flower visitors	
		Trees	Total inflorescences	Trees	Recording episodes
Dongo	High	8	46	9	38
Gho	Low	9	44	10	40
Mationgo 1	High	9	38	9	34
Mationgo 2	Low	8	48	9	42
Pighyiri	High	9	50	10	51
Po	Low	9	52	10	52
Torem 1	High	9	46	10	37
Torem 2	Low	8	42	10	37
Yaro 1	High	7	42	9	46
Yaro 2	Low	9	50	10	45

TABLE 1 Recording effort for flower visitors and pollen supplementation at each site. Fewer trees were included in pollination supplementation experiment as comparable inflorescences were not present on some trees during site visits

2.6 | Data analysis

2.6.1 | Pollination limitation

We assessed pollination limitation in a mixed effects model using the proportion of flowers that formed fruit per inflorescence ('fruit set') as the dependent variable and pollen supplementation as a fixed factor (expressed as pollen supplementation = 1, no pollen supplementation = 0). Site was specified as a random factor, the binomial distribution was used and the model was weighted by the number of flowers originally selected on each inflorescence (Table 2).

2.6.2 | Spatial autocorrelation and correlation among independent variables

We tested the relationship between pollination limitation and distance between sites using the Incremental Spatial Autocorrelation tool in ArcMap 10.4. This tool indicates the minimum distance between independent sites by comparing the Moran's index of spatial correlation for data recorded over a range of distances with the expected values if no clustering occurs. Spatial autocorrelation was

detected in sites <4 km apart ($I = 0.85, z = 2.2, p = 0.03$) but not in sites >4 km apart ($I < 0.05, z < 0.4, p = 0.35$). Because the distance between pairs of sites was >4 km, each pair can be considered independent of the others. There was no evidence of correlation between area of semi-natural habitat and site diversity (data not shown).

2.6.3 | Influence of site diversity and area of semi-natural habitat on pollination services

Five mixed effects models were used to assess the influence of site diversity and area of semi-natural habitat on pollination services (as assessed through bee visitation, degree of pollen limitation and fruit set; Table 2). *Apis mellifera* and non-*Apis* bees have been shown to act as two different functional groups in Burkina Faso (Lassen et al., 2016), and were treated separately in the analysis. The visitation rate (number of bees recorded/number of recording episodes per tree) was therefore assessed in separate models for *Apis mellifera* and non-*Apis* bees. The degree of pollination limitation was expressed as the difference between the proportion of pollen-supplemented and untreated flowers that set fruit per tree (proportional difference). This approach reduced zero inflation and

TABLE 2 Design of mixed effects models used in the analysis. Hurdle models were used for the models investigating *Apis mellifera* visitation, non-*Apis* visitation and fruit set. In these two-part models, the dependent variable is broken into presence/absence and a quantitative measure for non-zero values before the analysis is conducted

Model	Dependent variable	Fixed effect 1	Fixed effect 2	Random effects	Distribution
Limitation	Proportion of selected flowers that bore fruit	Pollen supplementation		Site	Gaussian (log link)
<i>A. mellifera</i> visitation	Part 1: Presence of <i>A. mellifera</i>	Diversity	Semi-natural area	Site nested within pair	Binomial (weighted by number of recording episodes)
	Part 2: <i>A. mellifera</i> visitation rate at sites where they occurred	Diversity	Semi-natural area	Site nested within pair	Gamma (inverse link)
Non- <i>Apis</i> bee visitation	Part 1: Presence of non- <i>Apis</i> bees	Diversity	Semi-natural area	Site nested within pair	Binomial (weighted by number of recording episodes)
	Part 2: Non- <i>Apis</i> bee visitation rate at sites where they occurred	Diversity	Semi-natural area	Site nested within pair	Gamma (log link)
Degree of limitation	Fruit set of flowers with supplementary pollen–fruit set of untreated flowers	Diversity	Semi-natural area	Site nested within pair	Gaussian (log link)
Fruit set	Part 1: Presence of fruit on untreated flowers	Diversity	Semi-natural area	Site nested within pair	Binomial (weighted by number of flowers selected)
	Part 2: Proportion of untreated flowers that bore fruit	Diversity	Semi-natural area	Site nested within pair	Gamma (inverse link)
Nut weight	Weight of nuts	Pollination method (pollen supplemented or untreated)		Site nested within pair	Gamma (log link)

allowed calculations to be made when none of the flowers with supplementary pollen bore fruit. Fruit set was expressed as the mean proportion of untreated flowers that bore fruit per tree. The impact of pollen supplementation on nuts was assessed by comparing the weights of nuts from treated and untreated flowers ($n = 133$). In each of the five models addressing the influence of site diversity and area of semi-natural habitat on pollination services, site diversity (expressed as diverse = 1, less diverse = 0) and area of semi-natural habitat were specified as fixed effects. The area of semi-natural habitats was expressed as a proportion of the total area within 1 km of the site and scaled (the mean was subtracted from each value and the result was divided by the standard deviation) to enable the data to meet the requirements of the analysis. Site was placed within pair as a random factor to account for the paired design.

As the data collected for bee visitation and fruit set contained a large proportion of zeros and were over-dispersed, hurdle models were the most appropriate tool for these analyses. In a hurdle model, the dependent variable is broken into two components: (a) presence/absence in sites and (b) a quantitative measure where it is present (i.e. instances where the dependent variable scored zero are removed from this component). The relationship of the independent variables with presence/absence was assessed in a mixed effects model using the binomial distribution. The quantitative component (e.g. visitation rate, nut weight) was then assessed in a mixed effects model using an appropriate distribution (Table 2). Because the model has two parts, two p -values are generated per hurdle model.

In accordance with Zuur, Ieno, and Smith (2007), AIC values were used in model selection. Residual distributions were checked to ensure they met the assumptions of the analysis. Analyses were carried out in R (R Core Team, 2019) using the GLMMTMB (Bates, Mächler, Bolker, & Walker, 2015; Brooks et al., 2017), lme4 (Bates et al., 2015), DHARMA (Hartig, 2019) and CAR packages (Fox & Weisberg, 2010).

3 | RESULTS

3.1 | Limitation

A significantly greater proportion of flowers with supplementary pollen bore fruit (0.35 ± 0.35) than untreated flowers (0.03 ± 0.11 ; $\beta = 2.88 \pm 0.19$, $p < 0.001$, Figure 2). Mean values are shown \pm standard error throughout this section.

3.2 | Environmental variables

In total, 285 trees and shrubs >3 m tall, belonging to 19 species, were found in the sites (range: 1–7 species per site). Shea was the commonest tree (222 individuals), followed by *Parkia biglobosa*

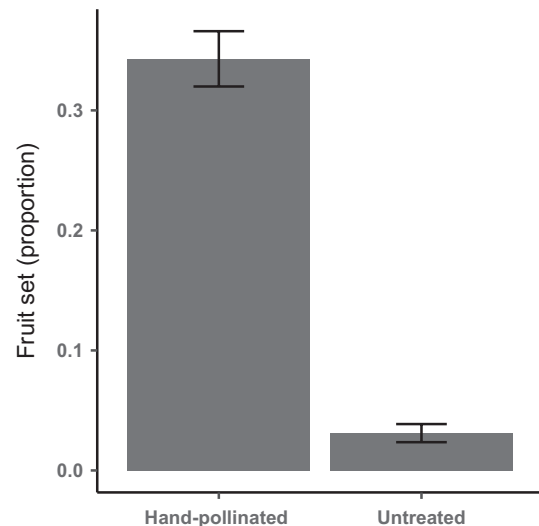


FIGURE 2 Proportion of marked flowers that bore fruit ('Fruit set') on pollen-supplemented and untreated inflorescences (mean proportion per inflorescence \pm SE)

(27 individuals) and *Lannea microcarpa* (seven individuals). The area of semi-natural habitats surrounding each site ranged from 6% to 48% with an average of 31% (Table 3).

3.3 | Influence of diversity and area of semi-natural habitat on pollination services

3.3.1 | Visitation by *Apis mellifera* and non-*Apis* bees

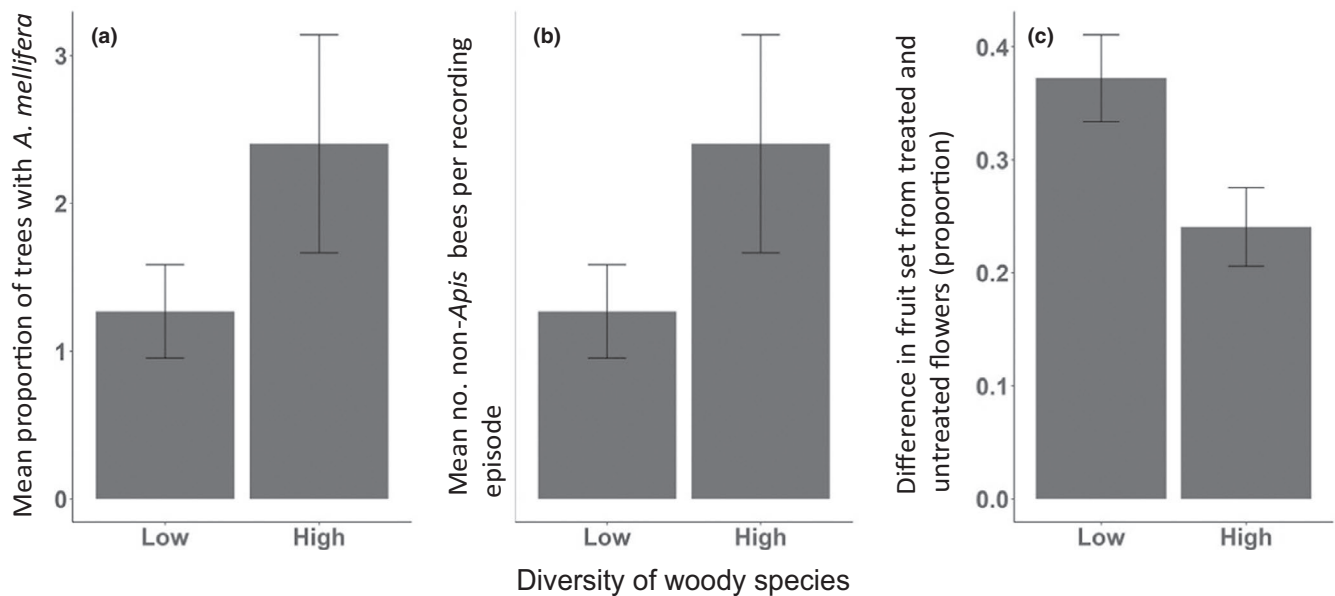
We recorded 57 *A. mellifera* and 511 individuals of other bee species visiting shea flowers over a total of 69 hr of observations. Of the 511 non-*Apis* bees recorded, 456 were identified to species and these comprised *Hypotrigona ruspoli* (439 individuals), *Compsomelissa* sp. (seven individuals), *Lasioglossum* sp. (eight individuals) and *Braunsapis* sp. (two individuals).

At diverse sites, 42 *A. mellifera* were recorded, compared to 15 at less diverse sites. The best fit model for *A. mellifera* visitation included site diversity and omitted the area of semi-natural habitat. Inspection of both parts of the model showed that while *A. mellifera* were significantly more likely to be present at more diverse sites ($\beta = 1.8 \pm 0.62$, $p = 0.005$, Figure 3), site diversity was not significantly related to the rate of visitation when *A. mellifera* were present ($\beta = -0.21 \pm 0.69$, $p = 0.76$).

In total, 347 non-*Apis* bees were caught at diverse sites and 164 were caught at less diverse sites. The best fit model for non-*Apis* bee visitation included diversity and omitted the area of semi-natural habitat, as for *A. mellifera*. However, for non-*Apis* bees, diversity was not related to the likelihood of bees being present at trees ($\beta = 0.14 \pm 0.62$, $p = 0.82$), while visitation rate where non-*Apis* bees were present was significantly related to diversity ($\beta = 0.57 \pm 0.28$, $p = 0.04$, Figure 3).

TABLE 3 Summary of variables recorded at study sites. Degree of limitation is the mean of the proportion of fruit set of flowers with supplementary pollen minus that of untreated flowers per tree

Site	Diversity (1/D)	Area semi-natural habitat (%)	Degree of limitation	<i>Apis mellifera</i> per recording episode	Non- <i>Apis</i> per recording episode	Selected flowers	Number of fruit	Mean nut weight (g)
Dongo	1.95	32.8	0.24	0	0.56	302	49	21.6
Gho	1	40	0.39	0	0.46	235	50	13.9
Mationgo 1	1.78	20.8	0.26	0.32	0.73	232	39	18.1
Mationgo 2	1.1	5.8	0.35	0.2	0.72	221	45	22.4
Pighyiri	2.6	41	0.31	0.22	1.33	270	33	13.1
Po	1.55	42.6	0.45	0	0.89	211	50	14.6
Torem 1	2.45	27.4	0.19	0.02	2.12	203	26	15.3
Torem 2	1.62	27.1	0.37	0.03	1.45	159	36	13.7
Yaro 1	1.74	47.8	0.19	0.38	3.43	205	34	n/a
Yaro 2	1.27	26.5	0.31	0.07	0.23	210	20	13.3

**FIGURE 3** Mean (\pm SE) (a) proportion of trees where *Apis mellifera* were recorded per site, (b) number of non-*Apis* bees per recording episode and (c) degree of limitation per tree expressed as the difference in the proportion of fruits from treated and untreated flowers at sites with low and high diversity

3.3.2 | Degree of pollination limitation

Pollination limitation was greater at less diverse sites ($\beta = 0.44 \pm 0.18$, $p = 0.015$, Figure 3), but area of semi-natural habitat was not related to the degree of limitation observed. The best fit model included diversity but not area of semi-natural habitat.

3.3.3 | Fruit set and nut weight

Area of semi-natural habitat (but not diversity) had a significant relationship with the presence of fruit on untreated flowers ($\beta = -0.95 \pm 0.31$, $p = 0.003$, Figure 4). The best fit model included area of semi-natural habitat but not diversity. Fruit abundance

was not related to site diversity or area of semi-natural habitat, but a power analysis indicated that an effect size comparable to that observed for the degree of limitation was unlikely to be detected.

Of the 413 fruits that were counted in May 2017, 168 matured to collection. Fruit loss was attributed primarily to fructivory, although late-acting self-abortion is also possible, and some fruits may simply have matured and fallen before collection. Thirty-five fruits were harvested before they had reached maturity (see Section 2). Only 22 fruits of untreated inflorescences were collected for weighing and the remaining 111 fruits were from flowers that received supplementary pollen (Table 3). Mean weight of nuts of flowers with supplementary pollen was 18.4 g and of 16.6 g for untreated flowers, but the difference was not significant.

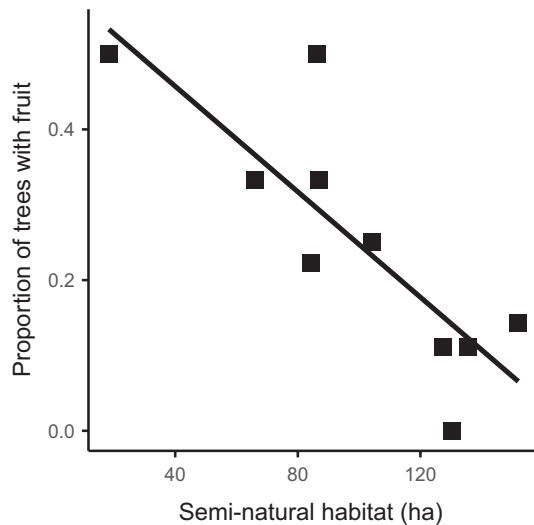


FIGURE 4 Proportion of trees which bore fruit on untreated flowers compared to area of semi-natural habitat within 1 km of the site

4 | DISCUSSION

We found strong evidence of pollination limitation in production of shea fruits. More visitation by bee species (the proportion of trees visited by *A. mellifera* and the number of non-*Apis* bees recorded per recording episode) was observed in sites with greater diversity of woody species, and pollination limitation was lower in these sites. Additionally, we found a negative relationship between the proportion of untreated inflorescences that bore fruit on trees and the area of semi-natural habitat within 1 km.

Pollen limitation of fruit set is common and can be a consequence of habitat degradation (Knight et al., 2005) causing declines in the abundance of pollinators (e.g. through lack of food or shelter, pesticide use). The intensification of agriculture in Burkina Faso and, in particular, changes to the practice of fallowing have reduced the opportunities for regeneration of native woody species in agricultural fields. The importance of maintaining plant diversity to support pollinators was demonstrated by Nombé, Schweitzer, Sawadogo, Issaka Boussim, and Millogo-Rasolodimby (2009) who showed that honeybees from domestic hives foraged from at least 97 plant species in 1 year and that the plant species visited varied from month to month. Our results provide evidence that reduced diversity of woody species affects the provision of pollination services as assessed via (a) visitation by pollinating species and (b) the degree of pollination limitation observed.

Although *A. mellifera* occurred at more trees in diverse sites, their abundance where they occurred was not related to site diversity or area of semi-natural habitat. This may relate to foraging behaviour: *A. mellifera* tended to be abundant on only one tree at a site, even when other trees had a profusion of receptive flowers. This focus on a single tree may result from the within-nest recruitment of foragers to specific floral resources and the use of attractant scent marks on flowers (Free & Williams, 1983; Stout & Goulson, 2001).

Non-*Apis* bees were widespread in occurrence, but more abundant in more diverse sites. *H. ruspoli* was the bee species recorded most

frequently and they drove this relationship. Lobreau-Callen, Le Thomas, Darchen, Darchen, and D'Amico (1990) observed that in Cote-d'Ivoire, colonies of another *Hypotrigena* species (*H. pothieri*) were more successful in food collection and brood production when located in open situations. This preference may explain why *Hypotrigena* are abundant in landscapes modified by human activities (Lassen, Ræbild, Hansen, Brødsgaard, & Eriksen, 2012; Stein et al., 2018), and we noted that *H. ruspoli* colonies were very numerous at our sites (>200 were noted within 10 m of study plots, data not shown). However, Lobreau-Callen et al. (1990) also found that *H. pothieri* tended to preferentially collect nectar and pollen from a restricted number of flowering species and suggested their preference may be based on the alkaloid content of nectar. If *H. ruspoli* have similar preferences, more diverse sites may be more likely to include their preferred species, explaining their increased abundance in these sites.

Apis mellifera and non-*Apis* bees probably provide complimentary pollination services in shea parklands. Although *A. mellifera* were seen less frequently, they tend to forage over longer distances and, at an individual level, are more effective pollinators of shea (Lassen et al., 2016). Conversely, *H. ruspoli* occurred widely and may deliver pollination services to shea in the absence of *A. mellifera*. Thus, as has been demonstrated in other systems (e.g. Brittain, Williams, Kremen, & Klein, 2013; Sapir et al., 2017), both *A. mellifera* and non-*Apis* bees are likely to be important.

Site diversity was strongly related to shea pollination: flowers received more visitors in diverse sites and were less pollination limited. Diverse sites might be expected to support greater abundances of pollinating insects by improving ecological complexity at the site level, including: (a) providing floral resources over an extended period due to non-synchronous flowering among different species; (b) increasing the likelihood of pollinating insects' preferred species being present and (c) providing a diversity of nesting opportunities (Schuldt et al., 2019).

Site diversity was not related to fruit set, but area of semi-natural habitat in the surrounding landscape was negatively related to the presence of fruit on untreated flowers. Although other studies have shown that more natural areas in the surrounding landscape can positively influence pollinators (e.g. Cusser, Neff, & Jha, 2016), in our study, levels of fruit set may be explained by biological factors other than pollination. Several lines of evidence of herbivory by insect larvae, mammals and birds were commonly observed (personal observations), but it is not clear if herbivores were attracted from nearby semi-natural habitats to developing shea fruit. This deserves further investigation, and the contribution of shea to supporting overall biodiversity in parklands should be taken into account when establishing a sustainable level of exploitation.

The lack of a relationship between semi-natural habitats and either bee visitation or pollination limitation could be due to the quality or fragmented nature of semi-natural habitats (fallow fields and fragments on rocky hills or in river corridors), which may have limited their value for pollinators. Alternatively, shea may not have been attractive enough floral resource to draw bees from semi-natural areas, particularly during the dry season, when bees prefer to forage in more natural habitats, moving to agricultural ones during the rainy season (Stein et al., 2018). In addition, we only looked at landscape composition, and

as landscape configuration is important for pollinators elsewhere (e.g. Freitas et al., 2014), this deserves further attention.

5 | CONCLUSIONS

Our results show that woody species diversity in shea parklands supports pollination services of shea. We recommend that a range of native woody species are retained or planted into cultivated fields when fallows are cleared to support pollinators and pollination services. Fragments of semi-natural habitat in the surrounding landscape may not be sufficient to provide the necessary pollination services. Shea is one of several insect-pollinated species that provide non-timber forest products and flower during the dry season in shea parklands. In a region that is subject to nutritional poverty and where the finance required to supplement local foods is lacking for most families, maintaining natural ecosystem services that support food provision must be a priority.

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AUTHORS' CONTRIBUTIONS

J.C.S. developed the methodology, with intellectual contributions from I.N., E.M., J.V., C.T. and A.D.; A.D., F.G.L., A.N. and A.D. contributed to the field methodology; A.D. and F.G.L. carried out the field work; F.G.L. and I.N. facilitated plant species identification; A.D. carried out the data analysis and wrote the manuscript with J.C.S. and E.M. All the authors have given final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.69p8cz8z0> (Delaney et al., 2020).

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