



Impact of forest fragments on bee visits and fruit set in rain-fed and irrigated coffee agro-forests

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ARTICLE INFO

Article history:

Received 13 October 2010

Received in revised form 14 April 2012

Accepted 9 May 2012

Available online 2 June 2012

Keywords:

Coffea canephora

Forest remnants

India

Pollinators

Shade tree species richness

ABSTRACT

Forest fragments in agricultural landscapes are recognised to provide a variety of ecosystem services, several of which benefit neighbouring agricultural land uses. Pollination of crops is one such service that has attracted much research and public attention, yet the dependency of crops on pollinators, and the role of forest fragments in providing this service, remains contentious. Indeed, the trend towards increasing crop production through intensification is at odds with the expected concurrent decline in pollination. We investigated the combined effect of distance from forest and forest size on pollinator abundance at coffee agro-forests in Kodagu District, India, under two contrasting flowering scenarios: irrigation triggered flowering in a single agro-forest, and rain triggered flowering at all the remaining agro-forests that received rain but were not previously irrigated. Three social bee species, *Apis dorsata*, *Apis cerana* and *Tetragonula iridipennis* were the main flower visitors. In rain-fed agro-forests, the total visitor abundance at coffee flowers decreased with increasing distance to the nearest forest. When the three main pollinators were analysed separately, the abundances of *A. dorsata* and *T. iridipennis* decreased with increasing distance from a neighbouring forest patch but this distance effect was reduced with an increase in size of the nearby forest. An increase in pollinator abundance at coffee flowers increased coffee fruit set in rain-fed agro-forests. Irrigated agro-forests had far higher pollinator abundance and fruit set than rain-fed agro-forests. We attribute this to the small-scale staggered flowering of irrigated agro-forests resulting in the concentration of pollinators at these sites regardless of its proximity to forests or the size of nearby forest. Agro-forest shade tree species richness also negatively affected pollinator abundance in rain-fed agro-forests. Although our results show that distance to forest and size of neighbouring forest fragments do affect the abundance of pollinators at coffee, at least in rain-fed agro-forests, justifying the conservation of large forest remnants is problematic on this account as there was no direct effect of forest on coffee fruit set. This is likely to be because there remains a high density of forest remnants within Kodagu, and a threshold of forest cover at which crop fruit set begins to be affected by pollinator scarcity has yet to be reached. By controlling the timing of flowering through irrigation or managing domesticated bee hives, farmers effectively reduce the dependency on nearby forest cover for pollinator services irrespective of the distance between forests and agro-forests, but these management practices incur costs that not every farmer can cover.

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1. Introduction

Conversion of forested lands for agriculture has increasingly fragmented natural habitats leading to loss of suitable pollinator

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habitat (Kearns et al., 1998). Although fragmentation could lead to spatial isolation of habitats, the presence of a matrix (such as coffee grown under native shade) that is conducive for biodiversity around forest fragments may lessen the overall effect of fragmentation and could facilitate movement of forest-dependent species between forest fragments (Simberloff et al., 1992; Ricketts, 2001). Under such circumstances, forest fragments interspersed in an agricultural landscape may support a number of ecosystem services, including pollination (Ricketts, 2004; Julier and Roulston, 2009). In the tropics, coffee agro-forests retain varying degrees of shade and shade tree diversity, which in turn support high diversities of vertebrates, invertebrates and plants (Perfecto et al., 2007). This is expected to have a positive effect

on ecosystem services such as pollinator services (see study on coffee by Jha and Vandermeer, 2009). In the event that pollinator abundance promotes higher crop fruit set, then pollination services can be used as an economic justification for conserving remnant forests and traditional shade trees within coffee agro-forests.

In addition to loss of pollinator habitats, an increasing demand for pollination services due to ever expanding agricultural fruit set could cause a deficit in pollination services for many crops (Ghazoul, 2005). Several studies on a variety of crop species demonstrated the importance of entomophilous pollination service for initial fruit set (Blanche et al., 2006; Klein et al., 2007) or crop fruit set (De Marco and Coelho, 2004), even in some self-fertile species (De Marco and Coelho, 2004; Degrandi-Hoffman and Chambers, 2006). Other studies showed that proximity to forests increases pollinator abundance and diversity within agricultural crops, even in biodiversity rich areas (Perfecto and Vandermeer, 2002; Klein et al., 2003a,b; Ricketts, 2004; Blanche and Cunningham, 2005; Blanche et al., 2006; Chacoff and Aizen, 2006; Carvalheiro et al., 2010). Most of the studies on coffee, however, have investigated the effects of only a few forest remnants on fruit set (e.g. Klein et al., 2003a,b: one fragment of undetermined size, but exceeding 100,000 ha; Ricketts, 2004: three fragments of 34, 46 and 111 ha) and have not explored the effects of forest fragments of varying size and distances to agro-forests on pollinator abundance and final crop fruit set. Furthermore, the role of very small forest fragments (i.e. less than 5 ha) as sources of pollinators is often ignored. Larger landscape scale studies on pollination services and their contribution to crop fruit set are needed, not least to bridge the gap between the many local scale studies that indicate the dependency of crop fruit set on pollinators which are supported by natural habitats (see studies on various crops including coffee by Klein et al., 2003b; Ricketts, 2004; Blanche and Cunningham, 2005; Chacoff and Aizen, 2006; Carvalheiro et al., 2010), and global studies that show that fruit set of pollinator-dependent crops has kept up with other crops despite habitat degradation (Aizen et al., 2008; Ghazoul and Koh, 2010).

In recent years farmers have been increasingly relying on irrigation to induce flowering due to irregular rainfall patterns. Irrigation triggers flowering in individual agro-forests (i.e. only the agro-forest that has been irrigated) leading to staggered flowering at a small-scale while rainfall leads to synchronous flowering across the landscape at all the remaining agro-forests (i.e. the ones that were not irrigated previously) that receives rain. Since irrigation and rain create different scenarios in terms of distribution of flowering resources, it could influence pollinator abundance especially since coffee flowers remain fresh for only 1 day. Other characteristics of coffee agro-forests, such as shade tree species richness and density, shade cover (which is not necessarily correlated with shade tree density), as well as relative humidity which reportedly influences visitor abundance (Jha and Vandermeer, 2009; Vergara and Badano, 2009), were also included in the study. Since the foraging ranges and nesting preferences vary among the three main coffee pollinators in southern India, namely *Apis dorsata* F., *Apis cerana* Fabr. and *Tetragonula iridipennis* (Wille, 1983; Dyer and Seeley, 1991), we expected to find species specific responses to landscape attributes.

This study investigates the following objectives under irrigated and rain-fed agro-forests: (1) the effects of distance and size of the nearest forest fragment on pollinator abundance at coffee flowers and final fruit set (2) the influence of agro-forest characteristics (relative air humidity, shade, density of non-native shade trees, shade tree species richness) on pollinator abundance at coffee flowers and fruit set (3) the role of pollinator abundance on coffee fruit set.

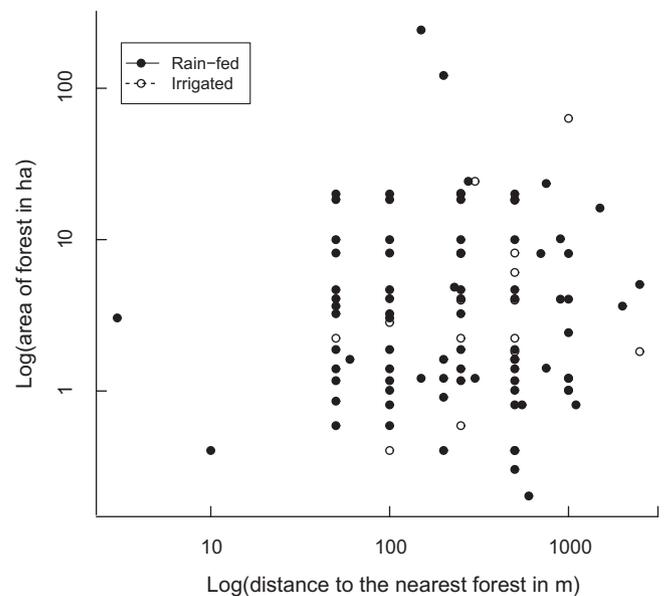


Fig. 1. Distribution of distance and size of nearest forest across irrigated and rain-fed sites. Filled circles represent rain-fed agro-forests, while empty circles represent irrigated agro-forests.

2. Materials and methods

2.1. Study area

The study was carried out in the district of Kodagu, south India, along the Western Ghats. The main agricultural product in Kodagu is coffee, grown mainly on hill slopes and covering 33% of the district's land area, with *Coffea canephora* Pierre ex Froehner comprising three quarters of the coffee cultivated area, the remaining being *C. arabica* L. Other major land uses include rice fields (21% of land area) in valley bottoms, and 'forests' (46%) (Elouard, 2000; Garcia et al., 2010), the designation of which is ambiguous. Two-thirds of the forested area (accounting for 30% of land area) is government-owned 'reserve forests' located in large blocks at the edge of the district political boundaries. About 16% of total land area is composed of over a thousand forests fragments scattered within the coffee and paddy matrix, the size of most being less than 1 ha to around 20 ha (Kalam and Thanuja, 2000).

The original vegetation in this area consisted of moist-deciduous to evergreen forests. The coffee agro-forests are shaded by either native trees (e.g. *Aporosa lindleyana* (Wt.) Baill, *Artocarpus heterophyllus* Lam., *Syzygium cumini* (L.) Skeels., *Dalbergia latifolia* Roxb., listed in declining order of abundance), or a mixture of native and exotic trees (the latter being mainly *Grevillea robusta* A. Cunn. ex R. Br.). Most coffee farmers grow pepper vines as a secondary crop and shade trees are often used as a trellis for pepper vines. *Grevillea robusta* is a fast growing exotic tree species which provides a better trellis for pepper vines than most native shade tree species and can also be harvested for timber. Prior permission from the government is not required to harvest this tree species since it is a non-native species. In light of these perceived benefits coffee farmers are gradually replacing native tree species with *G. robusta*, hence reducing shade tree species diversity within coffee agro-forests (Garcia et al., 2010).

2.2. Characteristics of the coffee agro-forests

In 2008, we selected 126 coffee agro-forests for our study. We used the size and distance from the edge of the nearest forest to quantify the impact of forest on coffee pollination (see Fig. 1). The

Table 1
Characteristics of environmental variables of rain-fed and irrigated agro-forests with means and standard errors.

	Rain-fed scenario <i>n</i> = 94	Irrigated scenario <i>n</i> = 32
Distance to nearest forest (m)	394 ± 45 (SE)	639 ± 146 (SE)
Size of nearest forest (ha)	52 ± 13 (SE)	207 ± 35 (SE)
Shade tree density (trees ha ⁻¹)	261 ± 14 (SE)	279 ± 27 (SE)
Density of <i>G. robusta</i> (trees ha ⁻¹)	50 ± 6 (SE)	90 ± 18 (SE)
Shade tree species richness	9 ± 0.4 (SE)	7 ± 0.4 (SE)
Shade (%)	41 ± 1 (SE)	45 ± 2 (SE)

use of satellite imagery was not possible due to the difficulty of separating agro-forests from natural forest when classifying vegetation cover. The distance from each coffee agro-forest to the nearest forest fragment and the size of the forest fragment were either measured using a GPS (Garmin 60CSx), or determined through interviews with farmers. The forests adjoining some of these coffee agro-forests were state-designated 'Reserve forests', 'Wildlife Sanctuaries' or 'National Parks', all of which covered large areas exceeding 100 km². For this study, the forests were classified as 650 ha, the vast majority of other forest fragments being considerably smaller than this. We are treating 650 ha as the size at which larger forest fragments will not have an impact on bee abundance, since the usual foraging range of the pollinators in this study is not larger than two kilometres (Dyer and Seeley, 1991). A bee foraging up to 2 km would cover a circular area of approximately 1300 ha around its hive. We are considering only one half of it (i.e. 650 ha) as we are interested in the direction towards the coffee agro-forests from the hive.

Data on shade cover, shade tree density and shade tree species richness were collected in each of 126 agro-forests (Table 1). The percentage canopy cover (henceforth 'shade') was measured using a densiometer (Lemmon, 1956). Five or six readings adjacent to the selected coffee bushes were taken before or immediately after coffee flowering and before the shade trees were pruned. Species richness and density of shade trees (trees per ha, differentiating between *Grevillea* and non-*Grevillea*) with diameter at breast height (DBH) greater than 10 cm were recorded over a 600 m² area centred on the coffee bushes surveyed for coffee fruit set. Non-*Grevillea* shade tree density was correlated with shade tree species richness (correlation coefficient of 0.7, *p*-value < 0.001) and therefore not included in the analysis.

The coffee agro-forests were also classified into two management classes: rain-fed (94 agro-forests) and irrigated (32 agro-forests) which led to contrasting flowering scenarios. Although the extent of flowering across the landscape when an irrigated agro-forest was flowering was not documented, it is very less compared to when mass-flowering occurs following rain (VB, SK, pers. obs.).

2.3. Coffee flower visitation and fruit set

Flowering in *Coffea canephora* is initiated 8 days after the first summer rain (or after irrigation) which occur between February and March. In 2008, we observed bees visiting coffee flowers in 126 agro-forests. The sampled agro-forests were dispersed across 625 km² in which two episodes of mass-flowering (following rainfall events) occurred in mid-February and mid-March. Most agro-forests were holdings of <10 ha, with a median of 6.5 ha (interquartile range of 5.8). At each agro-forest, three to eight coffee bushes were selected, each being separated from the next by at least 7 m. When many agro-forests flowered simultaneously, we limited observations to three plants per agro-forest to maximise the number of agro-forests that could be sampled. On each plant, five branches with six inflorescences per branch (i.e. 30

inflorescences per plant) were observed simultaneously for 15 min. On occasions with high bee activity, three branches were initially observed for 15 min, following which the remaining two were observed for 15 min, and the data from the two observations periods were summed. Observations were carried out on sunny days, though sometimes with occasional light cloud cover, from 9 am to 5 pm. During each observation period, we recorded the abundance of flower visitors and identified each floral visitor to genus or species. All the social bees were easily identified to species on the field. We were able to identify the solitary bees only to their respective genus, however, they were not included in the analysis due to their low occurrences. Since all observed trees were used in the analysis, to compensate for variations in the number of trees, visitation data of all observed trees were averaged to a 45 min observation period (the minimum period of observation at any one site). The relative humidity (RH) was measured at the time of observation, under shade and at an approximate height of 1 m above ground.

On each bush, five branches were selected and marked using tie-wraps on either end such that six inflorescences were encompassed between them. Since we sampled varying numbers of bushes, we averaged the flower and fruit counts per branch. The number of flower buds on each branch was counted 1–3 days prior to flowering (henceforth 'number of flowers'). Final fruit set (henceforth 'fruit set') on the same marked branches was counted just before fruit harvest (around 10 months after flowering) when the coffee berries were ripe.

2.4. Statistical analysis

Due to unbalanced data structure, we separated the data into two datasets, one with irrigated agro-forests and the second with rain-fed agro-forests. Independent variables were not correlated (Table 2). The variable 'distance from forest' was log transformed to obtain normal error distributions and 'size of the forest' was considered continuous in all analyses despite considering forests larger than 650 ha as 650 ha. We arrived at the final models by step-wise elimination of the least significant variables (variables with *p*-values < 0.05 were eliminated) and retained the model with the lowest Akaike information criteria (AIC). The statistical software 'R' was used for all the analyses (The R Project for Statistical Computing).

2.5. Visitor abundance

In rain-fed agro-forests, four models with visitor abundances (total pollinator abundance, abundance of *A. dorsata*, abundance of *A. cerana* and abundance of *T. iridipennis*, all within 45 min observation periods) as response variables were analysed using zero inflated negative binomial (ZINB) models. ZINB models were used due to occurrences of high number of zero values as well as the large over-dispersion in the observed visitor abundances. In irrigated agro-forests, multiple linear regressions (MLR) were used on the same dependent variables. Visitor abundances were log-transformed to meet the conditions of normality. The independent variables used for irrigated and rain-fed agro-forests were consistent in all the models, and included the interaction of distance to the nearest forest (m) and size (ha) of the nearest forest, shade tree species richness, *G. robusta* density (trees per ha), shade (%) and relative humidity (%).

2.6. Fruit set

Multiple linear regressions were used to determine which independent variables best explained final fruit set. Independent variables included the effect of interaction of pollinator abundance

Table 2

Correlation matrix of agro-forest variables (relative humidity, percent canopy cover, density of exotic shade tree species *Grevillea robusta*—silver oak) and forest variables (size and distance from agro-forest). Spearman's correlation coefficient values and *p*-values for rain-fed and irrigated agro-forests are presented in separate tables.

Spearman's correlation	Distance	RH	Shade	<i>G. robusta</i>	Forest size	Bee abundance	<i>A. dorsata</i> abundance	<i>A. cerana</i> abundance	<i>T. iridipennis</i> abundance
Rain-fed (n = 94)									
RH	-0.0456								
Shade	0.1637	0.0839							
Density of <i>G. robusta</i>	-0.0102	0.0141	-0.0574						
Forest size	-0.0597	-0.0009	0.0454	0.1741					
Bee abundance	-0.1937	-0.2325*	0.1452	-0.0518	0.0371				
<i>A. dorsata</i> abundance	-0.2260*	-0.0543	0.1453	-0.0953	0.1185	0.6239***			
<i>A. cerana</i> abundance	-0.0319	-0.0722	0.1690	-0.0376	0.0812	0.5978***	0.3182**		
<i>T. iridipennis</i> abundance	-0.0991	0.2396*	0.1653	-0.0558	0.0017	0.8006***	0.4299***	0.3500***	
Shade tree species richness	0.0405	-0.0683	0.2458*	0.2534*	-0.0564	-0.1381	-0.1312	-0.1259	-0.0235
Irrigated (n = 32)									
RH	-0.0916								
Shade	0.2557	0.1222							
Density of <i>G. robusta</i>	-0.0138	-0.0366	0.1600						
Forest size	0.1102	-0.2331	0.1557	0.0249					
Bee abundance	0.1289	0.0585	-0.3564*	-0.0306	-0.2523				
<i>A. dorsata</i> abundance	0.1045	0.3075	-0.3492*	-0.1256	-0.2578	0.8517***			
<i>A. cerana</i> abundance	0.3616*	-0.0187	0.0390	-0.0270	-0.0684	0.6284***	0.3087		
<i>T. iridipennis</i> abundance	0.098	-0.4434*	-0.1468	0.2975	-0.0193	0.4892**	0.0978	0.4148*	
Shade tree species richness	-0.1482	0.3498	0.0860	0.0317	-0.3635*	-0.0023	0.0171	0.0081	-0.2892

† Significance level: $P < 0.1$.

* Significance level: $P < 0.05$.

** Significance level: $P < 0.01$.

*** Significance level: $P < 0.001$.

and initial number of flowers, interaction of distance to the nearest forest (m) and size (ha) of the nearest forest, shade tree species richness, *G. robusta* density (trees per ha), shade (%) and relative humidity (%) on final fruit set (number of coffee berries per branch) for both irrigated and rain-fed agro-forests separately.

3. Results

3.1. Environmental variables

The distance between the coffee agro-forests and the nearest forest fragment varied from 3 to 3500 m and the size of the forests varied from very small fragments of 0.1 ha to large forests greater than 650 ha in size (see Fig. 1). Shade cover within the coffee agro-forests ranged from 15 to 90%, and shade tree density was between 32 and 817 trees ha⁻¹. The density of *Grevillea robusta* as shade trees ranged from 0 to 383 trees ha⁻¹. Thirty-nine of the 126 agro-forests (31%) had no *G. robusta* and in 15 (12%) agro-forests, *G. robusta* accounted for more than 50% of shade trees. Shade tree species richness was between 2 and 17 species in 600 m² of agro-forest, with a total of 140 tree species across all 126 agro-forests (Table 1).

3.2. Coffee flower visitors

Of all the visitors recorded at coffee flowers, 56% were *A. dorsata*, 21% *A. cerana* and 22% *T. iridipennis*, which collectively accounted for 99% of all flower visitors. Total visitor abundance in irrigated agro-forests was approximately four times higher than that in rain-fed agro-forests (Fig. 2), driven primarily by a six-fold increase in the abundance of *A. dorsata* and smaller increases in *A. cerana* (2.6-fold increase) and *T. iridipennis* (2-fold increase). In rain-fed mass-flowering agro-forests, 48% of the agro-forests did not have any bee visits.

3.3. Variables influencing pollinator abundance and coffee fruit set

In rain-fed agro-forests, although distance to the nearest forest habitat and size of the adjoining remnant forest did not significantly

influence total pollinator abundance at coffee flowers, there was a positive interaction effect between distance and forest size on *A. dorsata* and *T. iridipennis* (Table 3). In other words, at increasing distance from a forest, larger fragments support higher populations of *A. dorsata* and *T. iridipennis* at coffee flowers than smaller ones. Shade had a positive influence on pollinator abundance while shade tree species richness and relative air humidity negatively affected pollinator abundance (Table 3). An increase in the abundance of the non-native shade tree species *Grevillea robusta* increased the abundance of *A. dorsata* in rain-fed agro-forests.

In irrigated agro-forests, none of the variables influenced the abundance of the three bee species except for relative humidity which significantly increased the abundance of *A. dorsata* and decreased that of *T. iridipennis* (Table 3).

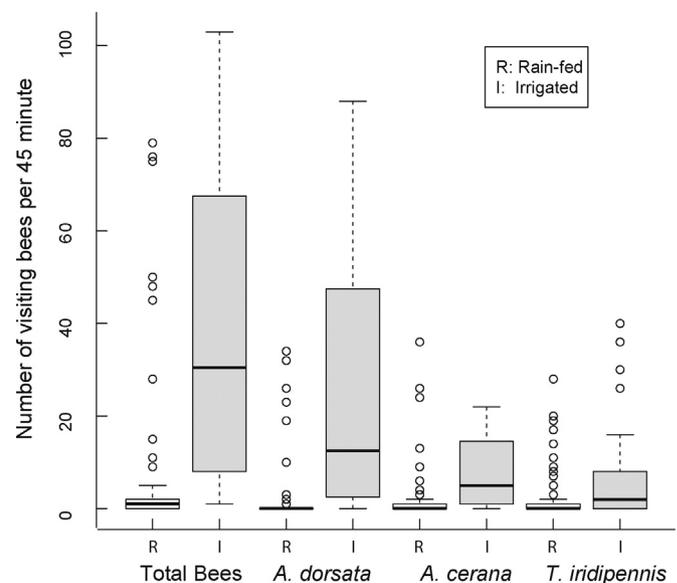


Fig. 2. Comparison of the effect of rain and irrigation on abundance of total bees, *A. dorsata*, *A. cerana* and *T. iridipennis*. In this study 126 agro-forests were observed of which 94 received rain and 32 were irrigated.

Table 3

Effects of plantation and landscape variables on abundance of bees (total pollinators and each bee species) at coffee flowers and final fruit set in rain-fed and irrigated agro-forests.

Rain-fed agro-forests (ZINB model) ^a					
	Estimate	Std. error	z-Value	p-Value	
Response: Total pollinators ^c					
Distance to forest (m)	-0.30	0.154	-1.95	0.051	
Shade tree species richness	-0.26	0.061	-4.30	<0.001	
Shade (%) 0.09	0.09	0.022	4.03	<0.001	
Relative air humidity (%)	-0.06	0.019	-3.33	<0.001	
Response: <i>A. dorsata</i> ^d					
Distance to forest (m)	-1.17	0.321	-3.66	<0.001	
Forest size (ha)	0.01	0.002	1.35	0.177	
Shade tree species richness	-0.72	0.177	-4.07	<0.001	
Density of <i>G. robusta</i> (tree ha ⁻¹)	0.01	0.009	1.57	0.116	
Shade (%)	0.24	0.059	4.02	<0.001	
Distance to forest (m): Forest size (ha)	0.01	0.002	2.60	0.009	
Response: <i>A. cerana</i> ^e					
Shade tree species richness	-0.48	0.102	-4.73	<0.001	
Density of <i>G. robusta</i> (tree ha ⁻¹)	0.01	0.005	1.31	0.189	
Shade (%)	0.07	0.026	2.83	0.005	
Response: <i>T. iridipennis</i> ^f					
Distance to forest (m)	0.05	0.170	0.30	0.764	
Forest size (ha)	0.01	0.001	1.24	0.215	
Shade tree species richness	-0.30	0.077	-3.88	<0.001	
Shade (%)	0.05	0.025	2.17	0.030	
Distance to forest (m):Forest size (ha)	0.01	0.001	2.90	0.004	
Irrigated agro-forests (MLR models) ^{a,b}					
	Estimate	Std. error	t-Value	p-Value	R ²
Response: <i>A. dorsata</i> ^g					
Relative air humidity (%)	0.29	0.013	2.18	0.039	0.12
Response: <i>T. iridipennis</i> ^h					
Relative air humidity (%)	-0.02	0.010	-2.07	0.048	0.11

^a All variables from the final models have been displayed.

^b In irrigated agro-forests none of the independent variables were correlated with either total bee abundance or *A. cerana* abundance, so these models are not presented in the table.

^c Variables dropped with step-wise elimination: Distance to forest (m): Forest size (ha), Forest size (ha), Density of *G. robusta* (trees per ha).

^d Variables dropped with step-wise elimination: Relative air humidity (%).

^e Variables dropped with step-wise elimination: Distance to forest (m) × Forest size (ha), Relative air humidity (%).

^f Variables dropped with step-wise elimination: Density of *G. robusta* (trees per ha), Relative air humidity (%).

^g Variables dropped with step-wise elimination: Distance to forest (m) × Forest size (ha), Shade tree species richness, Density of *G. robusta* (trees per ha), Shade (%).

^h Variables dropped with step-wise elimination: Distance to forest (m) × Forest size (ha), Shade tree species richness, Density of *G. robusta* (trees per ha), Shade (%).

Distance to forest and size of the adjoining forest did not affect final fruit set in either rain-fed or irrigated agro-forests. In rain-fed agro-forests (and not in irrigated agro-forests) there was, however, a significant positive interaction effect of bee abundance and the number of flowers on coffee fruit set (Table 4 and Fig. 3).

4. Discussion

In Kodagu, two contrasting flowering scenarios affect the provision of pollinator services to coffee and coffee fruit set differentially. In irrigated agro-forests, environmental variables did not influence visitor abundance, while in rain-fed agro-forests, the three main pollinators, all social bees, were influenced by various features of the agro-forest and landscape. Hence, it is imperative to understand the drivers of visitor abundance in coffee agro-forests in order to implement improved management practices that account for pollinator services and thus increase crop productivity even in the event of mass-flowering in coffee agro-forests.

Table 4

Effects of plantation, bees and landscape variables on final fruit set in rain-fed and irrigated agro-forests. All variables from the final models have been displayed.

	Estimate	Std. error	z-Value	p-Value
Rain-fed agro-forests (MLR model)				
Response: Final fruit set, R ² = 0.11 ^a				
Pollinator abundance	0.71	0.211	3.37	0.001
Number of flowers	0.17	0.097	1.80	0.075
Pollinator abundance: Number of flowers	0.03	0.010	3.36	0.001
Irrigated agro-forests (MLR model)				
Response: Final fruit set, R ² = 0.27 ^b				
Number of flowers	0.33	0.103	3.18	0.004
Relative air humidity (%)	-0.25	0.180	-1.39	0.177

^a Variables dropped with step-wise elimination: Distance to forest (m) × Forest size (ha), Shade tree species richness, Density of *G. robusta* (trees per ha), Shade (%), Relative air humidity (%).

^b Variables dropped with step-wise elimination: Pollinator abundance × Number of flowers, Distance to forest (m) × Forest size (ha), Shade tree species richness, Density of *G. robusta* (trees per ha), Shade (%).

4.1. Contrasting flowering scenarios

A severe pollinator deficit was observed in mass-flowering coffee agro-forests, while staggered small-scale flowering events triggered by irrigation attracted pollinators in very large numbers. This suggests a dilution effect whereby pollinators are distributed across many agro-forests during a mass-flowering event, as opposed to being concentrated at one (or a few) irrigated agro-forests. Such a dilution effect in mass flowering coffee agro-forests was observed by Jha and Vandermeer (2009) amongst native social and solitary bees. Veddeler et al. (2006) demonstrates a similar dilution effect at a coffee field scale, and a concentration effect at smaller scales (tree and branch).

Coffee fruit set increased with an increase in bees and flowers in rain-fed agro-forests even though the overall bee abundance in rain-fed agro-forests was low (Table 4). In irrigated agro-forests where bee abundances were high there was no such relationship. The abundance of bees in all irrigated agro-forests might exceed

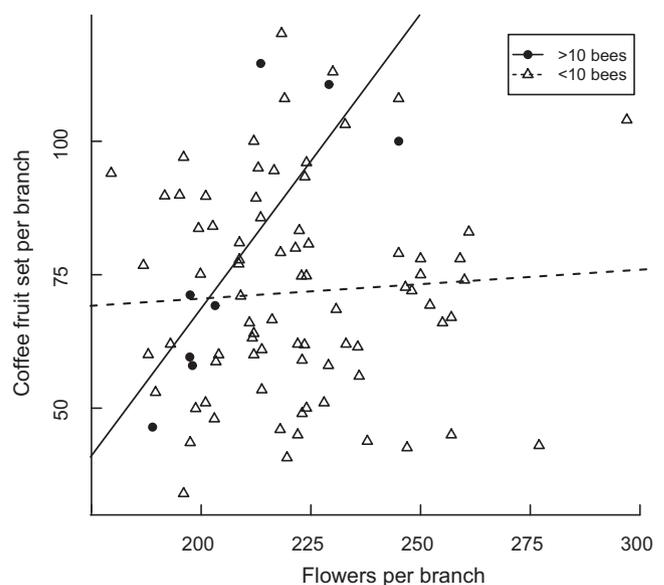


Fig. 3. Influence of flowers on the final fruit set of coffee for two categories of total bee abundance (>10 bees and ≤10 bees). Flowers and fruit set were recorded on the same branches. Filled circles represent low number of bees and triangles represent high number of bees.

the threshold beyond which coffee fruit set is no longer limited by pollination but rather by other factors (e.g. nutrients). Rain-fed agro forests are pollinator deficient, while irrigated agro-forests have more than adequate pollinators. Further research is necessary to evaluate the extent of pollinators required to successfully pollinate the flowers so as to reap maximum benefits from pollination services.

4.2. Distance from forest and forest size

Visitor abundance at coffee flowers decreased with increasing distance to the nearest forest in mass-flowering agro-forests. Many studies on a wide range of agricultural crops, amongst which coffee, have shown a reduction in pollinator visits with increasing distance from natural habitats (Klein et al., 2002; Ricketts, 2004; Blanche et al., 2006; Greenleaf and Kremen, 2006; Carvalheiro et al., 2010) with only a few showing no effects of forest proximity (see Chacoff et al., 2008; Winfree et al., 2008). While in Costa Rica (Ricketts, 2004), forest remnants were large and relatively isolated, in Kodagu, forests fragments ranged from very small to large forests and were found at a high density in the landscape. Moreover, these forests are dispersed within a complex matrix of coffee agro-forests characterised by a high diversity and density of native shade trees, making it conducive for a wide range of organisms (Bhagwat et al., 2005, 2008). The low pollinator visitation at coffee, even in a landscape with a high density of forest fragments emphasises the dearth in pollinators in mass-flowering agricultural landscapes.

Bee species respond differentially to both distance from and size of surrounding forest fragments. Although abundance of *A. dorsata* at coffee flowers declined as distance to forest remnants increased, this effect is reduced with an increase in size of the nearest forest. Colonies of *A. dorsata* are usually found in large old trees with a wide crown (Roubik, 2005). Availability of such nesting sites is often limited to forest remnants or large protected forests, and only seldom present in agro-forests (only four nesting trees were found across more than 400 agro-forests visited between 2006 and 2009, VB, SK pers. obs.) since shade trees in coffee agro-forests are often pruned, thus retaining only a very small crown. A large forest fragment potentially provides greater nesting opportunities which might increase the overall population of *A. dorsata* in such forests. *A. cerana* does not depend on forests for nesting as it can also establish in tree holes and old termite mounds (Raffiudin and Crozier, 2007), both of which are often found in coffee agro-forests as well as forests. Additionally, *A. cerana* is a domesticated species that is maintained by some coffee farmers. For these reasons its abundance in coffee agro-forests is less likely to be influenced by size of or distance to neighbouring forest fragments, as is likely the case for *A. dorsata*.

Although our results illustrate the importance of retaining large forest remnants to reduce the distance effect on pollinator abundances (see Table 3), especially in mass-flowering insect pollinated crops, it is hard to convincingly substantiate the need to protect them since size or distance from forests did not influence coffee fruit set (Table 4). Although we have an unprecedented sample size for this kind of study (126 coffee agro-forests), most of our agro-forests are located less than 1000 m from a forest, and a distance effect on coffee fruit set (if it exists at all) might not be apparent at such scales.

4.3. Shade trees and shade cover

In addition to forests as important forage providers, shade trees provide additional floral resources to bees. In our study, however, shade tree species richness negatively affected visitation at coffee flowers across all three species. Although high densities of flowering shade trees are thought to support higher pollinator abundance and diversity throughout the year (Jha and Vandermeer, 2010), the

availability of alternative (shade tree) floral resources might reduce the effectiveness of pollination services by directly competing for pollinators with the crop plants (Krishnan, 2011).

On the other hand, shade has a consistent positive effect on visitation by all three bee species, as noted in recent studies on *C. arabica* (Jha and Vandermeer, 2009). Even so, there remains lack of consensus on the impact of shade on coffee fruit set (see DaMatta, 2004; Soto-Pinto et al., 2002; Muschler, 2008). A recent study by Lin (2009) demonstrated that even under high shade conditions (60–80%) coffee productivity was comparable to coffee agro-forests under low shade cover (30–65%). Hence, increasing shade would augment pollinator abundance at coffee, but, at least at Kodagu, this does not appear to directly affect final fruit set. Furthermore, given the interaction between flower production and pollinator abundance on coffee fruit set, the role of shade needs to be determined in consideration of how light affects flower production, and not just total bee abundance alone. It should be recognised, of course, that shade has other benefits such as buffering against microclimatic extremes (Beer et al., 1998).

Simplified agro-forestry systems are believed to have a negative impact on visitor abundance (Jha and Vandermeer, 2009), in particular among social bees (Klein et al., 2002). Our study shows that an increase in the density of *G. robusta*, which simplifies the shade tree cover in terms of diversity, increases the abundance of *A. dorsata* locally. The increase in *G. robusta* is at the expense of native shade trees. Thus, availability of fewer attractive floral resources at shade trees might explain the increase in pollinators observed at coffee flowers in agro-forests with higher densities of *G. robusta*. Increasing the number of *G. robusta* at the expense of native trees would, however, reduce the availability of floral resources at other times of the year, which might undermine the long term survival of bee populations (Jha and Vandermeer, 2010). Although loss of shade tree diversity brings definite benefits to farmers in terms of the timber value of *G. robusta*, continued intensification across many agro-forests in the region could result in a landscape that is denuded of native trees and forest cover to an extent that pollinator availability does begin to become limiting, affecting fruit set. Determining what such thresholds are remains challenging.

4.4. Management recommendations and conservation implications

Pollinators need to be integrated in the management of agro-forests. Many studies including our own have shown that *Coffea canephora* fruit set is significantly enhanced by insect pollination (Klein et al., 2003a; Boreux, 2010; Krishnan et al., 2012). Since coffee is a mass-flowering species and the flowers remain fresh for only 1 day, the number of pollinators required within this short time is large, and when many rain-fed agro-forests flower simultaneously there appears to be a 'dilution effect' that depresses the number of pollinators at any one plant. Continued conversion of natural forests to crop lands could exacerbate such a pollinator deficit. Loss of forests might also adversely affect some pollinators more than others. *A. dorsata*, for example, is currently mainly dependent on forest trees for nesting. To increase the availability of suitable nest locations within agro-forests, farmers could maintain a few bee-preferred trees (see Thomas et al., 2009 for details), without pruning. *A. cerana* is found in the wild, but it also a domesticated species, albeit many domestic colonies have in recent decades been lost through disease. Farmers can potentially increase the abundance of *A. cerana* colonies by integrating bees resistant to diseases such as the Thai sac brood virus (Thomas et al., 2002) into the agroforestry system.

Since shade acts as a buffer which helps maintain cooler temperatures and moister soils (Beer et al., 1998), farmers in areas with insufficient access to water resources might benefit from

maintaining canopy cover so as to reduce water and heat stress till the onset of rain. Where farmers have access to water resources irrigation can greatly increase bee visits, particularly if the timing of irrigation is coordinated with neighbours to promote non-synchronous (staggered) flowering. The current high density of forest fragments combined with the possibility of farmers to manage the timing of flowering, and hence pollinator attraction, suggests that coffee fruit set need not be limited by pollinator abundance. Yet it should also be recognised that the Kodagu landscape is undergoing rapid change. Many forest fragments are being lost to agricultural encroachment, and many agro-forests are being intensified by reduction in the extent of native tree cover (Garcia et al., 2010). Irrigation reduces farmers' dependency on nearby forest cover for pollinator services, and hence encourages farmers to further accelerate landscape transformation. It is not yet clear whether, this continued landscape transformation will negatively impact coffee fruit set in Kodagu for rain-fed and irrigated agro-forests. We therefore suggest that farmers explore options for coordinated use of irrigation, support bee populations by increasing nesting and foraging resources within agro-forests, increase the population of managed bees, and protect forest remnants.

Acknowledgements

We would like to thank the College of Forestry, Ponnampet, Kodagu for the support that they provided throughout the study and in particular the students who helped with the field work. This work would have been impossible without the cooperation of the farmers and the assistance of the field staff. This study was funded by the North-South Centre, ETH Zürich and the Professorship of Ecosystem Management, ETH Zürich. We would like to thank Dr. Philippe Vaast and Prof. Harald Bugmann, as well as three anonymous reviewers for their comments which helped us improve our manuscript considerably.

References

- Aizen, M.A., Garibaldi, L.A., Cunningham, S.A., Klein, A.M., 2008. Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Curr. Biol.* 18, 1572–1575.
- Beer, J., Muschler, R., Kass, D., Somarriba, E., 1998. Shade management in coffee and cacao plantations. *Agrofor. Syst.* 38, 139–164.
- Bhagwat, S.A., Kushalappa, C.G., Williams, P.H., Brown, N.D., 2005. Landscape approach to biodiversity conservation of sacred groves in the Western Ghats of India. *Conserv. Biol.* 19, 1853–1862.
- Bhagwat, S.A., Willis, K.J., Birks, H.J.B., Whittaker, R.J., 2008. Agroforestry: a refuge for tropical biodiversity? *Trends Ecol. Evol.* 23, 261–267.
- Blanche, K.R., Ludwig, J.A., Cunningham, S.A., 2006. Proximity to rainforest enhances pollination and fruit set in orchards. *J. Appl. Ecol.* 43, 1182–1187.
- Blanche, R., Cunningham, S.A., 2005. Rain forest provides pollinating beetles for atemoya crops. *J. Econ. Entomol.* 98, 1193–1201.
- Boreux, V.E., 2010. An Ecosystem Service Approach to Coffee Production in a Complex Landscape Mosaic. Department of Environmental Sciences, ETH Zurich.
- Carvalho, L.G., Seymour, C.L., Veldtman, R., Nicolson, S.W., 2010. Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *J. Appl. Ecol.* 47, 810–820.
- Chacoff, N.P., Aizen, M.A., 2006. Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *J. Appl. Ecol.* 43, 18–27.
- Chacoff, N.P., Aizen, M.A., Aschero, V., 2008. Proximity to forest edge does not affect crop production despite pollen limitation. *Proc. R. Soc. B: Biol. Sci.* 275, 907–991.
- DaMatta, F.M., 2004. Ecophysiological constraints on the production of shaded and unshaded coffee: a review. *Field Crops Research* 86, 99–114.
- De Marco, P., Coelho, F.M., 2004. Services performed by the ecosystem: forest remnants influence agricultural cultures' pollination and production. *Biodivers. Conserv.* 13, 1245–1255.
- Degrandi-Hoffman, G., Chambers, M., 2006. Effects of honey bee (*Hymenoptera: Apidae*) foraging on seed set in self-fertile sunflowers (*Helianthus annuus* L.). *Environ. Entomol.* 35, 1103–1108.
- Dyer, F.C., Seeley, T.D., 1991. Dance dialects and foraging range in three Asian honey bee species. *Behav. Ecol. Sociobiol.* 28, 227–233.
- Elouard, C., 2000. Landscape and society: vegetation features in relation to biogeography. In: Ramakrishnan, P.S., Chandrashekhara, U.M., Elouard, C., Guilmo, C.Z., Maikhuri, R.K., Rao, K.S., Sankar, S., Saxena, K.G. (Eds.), *Mountain Biodiversity, Land Use Dynamics and Traditional Ecological Knowledge*. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi, Calcutta, pp. 25–42.
- Garcia, C.A., Bhagwat, S.A., Ghazoul, J., Nath, C.D., Nanaya, K.M., Kushalappa, C.G., Raghuramulu, Y., Nasi, R., Vaast, P., 2010. Biodiversity conservation in agricultural landscapes: challenges and opportunities of coffee agroforests in the Western Ghats, India. *Conserv. Biol.* 24, 479–488.
- Ghazoul, J., 2005. Buzziness as usual? Questioning the global pollination crisis. *Trends Ecol. Evol.* 20, 367–373.
- Ghazoul, J., Koh, L.P., 2010. Food security not (yet) threatened by declining pollination. *Front. Ecol. Environ.* 8, 9–10.
- Greenleaf, S.S., Kremen, C., 2006. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biol. Conserv.* 133, 81–87.
- Jha, S., Vandermeer, J.H., 2009. Contrasting bee foraging in response to resource scale and local habitat management. *Oikos* 118, 1174–1180.
- Jha, S., Vandermeer, J.H., 2010. Impacts of coffee agroforestry management on tropical bee communities. *Biol. Conserv.* 143, 1423–1431.
- Julier, H.E., Roulston, T.H., 2009. Wild bee abundance and pollination service in cultivated pumpkins: farm management, nesting behavior and landscape effects. *J. Econ. Entomol.* 102, 563–573.
- Kalam, M.A., Thanuja, M., 2000. The dynamics of land use—Devarakadus (Sacred Groves) and encroachments. In: Ramakrishnan, P.S., Chandrashekhara, U.M., Elouard, C., Guilmo, C.Z., Maikhuri, R.K., Rao, K.S., Sankar, S., Saxena, K.G. (Eds.), *Mountain Biodiversity, Land Use Dynamics and Traditional Ecological Knowledge*. Oxford and IBH Publishers, New Delhi, Calcutta, pp. 98–119.
- Kearns, C.A., Inouye, D.W., Waser, N.M., 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. *Annu. Rev. Ecol. Syst.* 29, 83–112.
- Klein, A.M., Steffan-Dewenter, I., Buchori, D., Tschardtke, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trapping bees and wasps. *Conserv. Biol.* 16, 1003–1014.
- Klein, A.M., Steffan-Dewenter, I., Tschardtke, T., 2003a. Bee pollination and fruit set of *Coffea arabica* and *C. canephora* (Rubiaceae). *Am. J. Bot.* 90, 153–157.
- Klein, A.M., Steffan-Dewenter, I., Tschardtke, T., 2003b. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *J. Appl. Ecol.* 40, 837–845.
- Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschardtke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B: Biol. Sci.* 274, 303–331.
- Krishnan, S., 2011. Pollinator Services and Coffee Production in a Forested Landscape Mosaic. Department of Environmental Sciences, ETH Zurich.
- Krishnan, S., Kushalappa, C.G., Uma Shaanker, R., Ghazoul, J., et al., 2012. Status of pollinators and their efficiency in coffee fruit set in a fragmented landscape mosaic in South India. *Basic and Applied Ecology*, in press <http://dx.doi.org/10.1016/j.bae.2012.03.007>.
- Lemmon, P.E., 1956. A spherical densiometer for estimating forest overstory density. *For. Sci.* 2, 314–320.
- Lin, B., 2009. Coffee (*Coffea arabica* var. Bourbon) fruit growth and development under varying shade levels in the Soconusco Region of Chiapas, Mexico. *J. Sust. Agric.* 33, 51–65.
- Muschler, R.G., 2008. Shade management and its effect on coffee growth and quality. In: Wintgens, J.N. (Ed.), *Coffee: Growing, processing, sustainable production: A guidebook for growers, processors, traders, and researchers*. Wiley-VCH, Verlag GmbH, pp. 391–418.
- Perfecto, I., Armbrecht, I., Philpott, S.M., Soto-Pinto, L., Dietsch, T.V., 2007. Shaded coffee and the stability of rainforest margins in northern Latin America. In: *Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation*, pp. 227–263.
- Perfecto, I., Vandermeer, J., 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conserv. Biol.* 16, 174–182.
- Raffudin, R., Crozier, R.H., 2007. Phylogenetic analysis of honey bee behavioral evolution. *Mol. Phylogenet. Evol.* 43, 543–552.
- Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 158, 87–99.
- Ricketts, T.H., 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv. Biol.* 18, 1262–1271.
- Roubik, D.W., 2005. Honeybees in Borneo. *Pollination Ecology and the Rainforest*. Sarawak Studies, 174, pp. 89–103.
- Simberloff, D., Farr, J.A., Cox, J., Mehlman, D.W., 1992. Movement corridors—conservation bargains or poor investments. *Conserv. Biol.* 6, 493–504.
- Soto-Pinto, L., Perfecto, I., Caballero-Nieto, J., 2002. Shade over coffee: Its effects on berry borer, leaf rust and spontaneous herbs in Chiapas, 55. *Agroforestry Systems, Mexico*, pp. 37–45.
- Thomas, D., Pal, N., Rao, K.S., 2002. Bee management and productivity of Indian honeybees. *Apiacta* 3.
- Thomas, S.G., Varghese, A., Roy, P., Bradbear, N., Potts, S.G., Davidar, P., 2009. Characteristics of trees used as nest sites by *Apis dorsata* (Hymenoptera, Apidae) in the Nilgiri Biosphere Reserve, India. *J. Trop. Ecol.* 25, 559–562.
- Veddeler, D., Klein, A.-M., Tschardtke, T., 2006. Contrasting responses of bee communities to coffee flowering at different spatial scales. *Oikos* 112, 594–601.
- Vergara, C.H., Badano, E.I., 2009. Pollinator diversity increases fruit production in Mexican coffee plantations. The importance of rustic management systems. *Agric. Ecosyst. Environ.* 129, 117–123.
- Wille, A., 1983. Biology of the stingless bees. *Annu. Rev. Entomol.* 28, 41–64.
- Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S., Kremen, C., 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J. Appl. Ecol.* 45, 793–802.