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Shade tree diversity may not drive prey-predator interaction in coffee agroforests of the Western Ghats biodiversity hotspot, India

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HIGHLIGHTS

- Shade simplification is a manifestation of agricultural intensification.
- Coffee is grown under natural shade and under silver oak shade.
- Predatory function in coffee agroforests of two shade types is studied.
- Predatory function is not affected by shade type in coffee.

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ABSTRACT

Agricultural intensification can decrease biodiversity and ecosystem services they deliver to agroecosystems. Diverse trees-shaded coffee is structurally and functionally complex and has biodiversity adequate for sustainable production of coffee and mitigation of biodiversity loss due to deforestation. However, shade tree simplification is intense in coffee agroforests worldwide, threatening their economic and environmental targets. In south India, native trees have been replaced by silver oak (*Grevillea robusta*) trees. Native trees-shaded coffee is floristically complex and diverse than oak-shaded coffee. We hypothesize that the natural prey removal fares better in native trees-shaded coffee than in oak-shaded coffee. Artificial caterpillar models of three colors were installed rotationally on leaves, stems, and branches of coffee plants in native trees-shaded- and oak-shaded coffee, and assessed the predation rates for fruiting and leaf-flushing periods of coffee to test this. Forty-four percent of the caterpillars were predated. Arthropods, and in particular the ants, were the predominant predators. Lizards followed by birds, and mammals were second, third, and fourth important predators of coffee agroforests. Overall, predation rates did not differ with the shade diversity, but lizard predation rates were higher in diverse trees-shaded coffee than in oak-shaded coffee. The predation rates were slightly higher in the fruiting season of coffee. Predation rates of any predator taxa were higher for the caterpillars placed on stems and branches than on leaves. The study does not support the hypothesis that the natural predation rates might be higher in floristically complex coffee agroforests, but highlights the biocontrol potential of lizards in diverse-shaded coffee.

1. Introduction

Globally, land-use change and crop plantations are threats to native forests and biodiversity (Foley et al., 2011; Ramankutty et al., 2008). It is estimated that about 40% of the land on the earth is used for agriculture, including plantation crops (Ramankutty et al., 2008). While forest plantations – oak, spruce, birch, eucalyptus, and so on – are a threat to native forests and woodlands in temperate parts of the world (Bremer and Farley, 2010), the cash crops – tea, coffee, oil-palm, rubber, and so on – are the reasons for deforestation and biodiversity loss in the tropics (Phillips et al., 2017). Although plantations have reduced the net loss of green cover and tree cover due to the whopping rate of deforestation in the tropics, the dynamic land-use policies in underdeveloped countries can destabilize their environmental goals (Brockerhoff et al., 2008). The impact of plantations on native biodiversity varies by continent, the nature of species cultivated, and the taxa involved in the

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study (Phillips et al., 2017). Although conservationists have methods to manage plantations for profiting native biodiversity, biotic functions, and sustainable production of crops (Tscharntke et al., 2011), very few systems have adopted them (Sandker et al. 2012).

Not all managed habitats are detrimental for biodiversity (Pimentel et al., 1992). For instance, the conventional shaded coffee is a managed land having high floristic diversity and structural complexity (Jha et al., 2014; Nesper et al., 2017; Perfecto and Vandermeer, 1996). Biodiversity studies suggest that they can have biodiversity at par or much higher than on the well-protected tropical forests (Phillips et al., 2017; De la Mora et al., 2013; Philpott et al., 2008). Coffee is now cultivated on over ten million hectares of land globally (FAO, 2017). Coffee plantations are a direct and indirect source of revenue for many households in Latin America, peninsular India, East Africa, and Southeast Asia. They are a significant source of foreign exchange for countries that are growing it. Therefore, coffee is an influential industry for many underdeveloped tropical countries. Its policies on habitat management can affect biodiversity conservation and sustainable crop production targets of several biodiversity hotspots that harbor this industry.

While biodiversity conservation is the environmental goal of agroforests and cash crop plantations in the tropics, how biodiversity can contribute to the sustainable production of the crop is the economic goal. Pollination and pest control are the two natural services coffee plants require from the biodiversity harbored in coffee agroforests. Several studies have documented pollinators and pollination in coffee agroforests and have analyzed the relationship between coffee habitat and pollination services (e.g.: Boreux et al., 2013; Klein et al., 2003; Krishnan et al., 2012). However, only a few empirical studies have investigated natural prey-predator or host-parasitoid interaction in coffee; almost all these studies have come from Latin America (Morris et al., 2018 and references therein; Morris et al., 2015; Morris and Perfecto, 2016; Philpott et al., 2009) or Africa (Milligan et al., 2016). Arthropods, particularly ants, and birds have been identified as significant predators of coffee pests (Chain-Guadarrama et al., 2019; Morris et al., 2018 and references therein; Milligan et al., 2016). Morris et al. (2018) reviewed the role of different species of ants in coffee pest management. While some ants may favor the population rise of some minor coffee pests, such as Coffee green scale insects, many of them found reducing the population of major pests, such as coffee berry borer (Morris et al., 2018 and references therein).

It is suggested that the local factors rather than the landscape factors drive biodiversity patterns and biotic functions in managed agroecosystems (Daily et al., 2001; Dauber et al., 2005; De la Mora et al., 2013; Jha and Vandermeer, 2010; Klein et al., 2003; Philpott et al., 2006; Sinu, 2011). De la Mora et al. (2013) documented higher diversity of species- and functional guilds of ants in the native trees-shaded coffee in Latin America. Perfecto et al. (1996) found that the ant diversity of shade trees can even be different from one shade tree species to another in shaded coffee of Mexico (Perfecto et al., 1996). It suggests that the shaded coffee has many niches and microhabitats that can sustain a greater diversity of arthropods and other lesser-known taxa beneficial for the plantations. Shade coffee in Mexico has about three times more arboreal ant colonies and species than in the forests. The abundance and richness of ants on tree trunks are higher in heavily shaded coffee than in the intensively cultivated or sun coffee (De la Mora et al., 2015, 2013).

A moderate shade (60–70%) is required for optimum production of coffee berries (Soto-Pinto et al., 2000). Traditionally, farmers around the globe have raised coffee under the shade of evergreen and moist deciduous forests. These wild shade trees have gradually been substituted by fruit trees and later by timber trees, such as *Grevillea robusta* – Australian silver oak (Gaucherel et al., 2017). This simplifaction in shade tree diversity has reduced the overall floristic and functional diversity of coffee agroforests (Jha et al., 2014; Nesper et al., 2017; Perfecto et al., 1996; Philpott et al., 2008), affected the services the biodiversity rendered for sustainable production of coffee (Perfecto et al., 2014, 2005; Philpott et al., 2009; Tscharntke et al., 2011; Vandermeer et al., 2010, 2002), and increased the pest incidence in coffee (Mariño et al. 2016). Mariño et al. (2016) found significantly more number of female borers and borer-infected berries in sun coffee than in shaded coffee in Peru. De la Mora et al. (2015) demonstrate that prey removal by ants on coffee plants is high in floristically diverse agroforests. Several other studies have recorded higher abundance and diversity of predatory ants in shaded coffee (Morris and Perfecto, 2016; Milligan et al., 2016; Morris et al., 2018). Conversely, some studies from Africa and Asia have shown that sun coffee has a greater diversity and a good community of insectivorous birds than shaded coffee (Milligan et al., 2016; Morris et al., 2018; Smith et al., 2015). Philpott et al. (2009) has shown that arthropod removal by insectivorous birds is not predicted by the vegetation complexity of the coffee agroforests.

In south India, coffee plantations and agroforests, despite encroached a large number of private forests, sacred groves, and reserve forests (Gaucherel et al., 2017), serve as a refugia for native biodiversity (Wordley et al., 2017, and references therein; Anil Kumar et al., 2019). Coffee in India is primarily cultivated in the Western Ghats biodiversity hotspot (Gaucherel et al., 2017; Myers et al., 2000). When cultivation began during the 1860 s, coffee was grown fully under the shade of diverse natural moist-deciduous and evergreen forests. Although it is still a practice in large-scale plantations owned by companies, the small growers have replaced native trees with silver oak (*Grevillea robusta*) and raised under the shade of this monodominant species. In Kodagu, a small district that produces 2% of the coffee the world produces, Gaucherel et al. (2017) predicted further expansion of coffee in private lands, but under the shade of silver oak. While coffee foliage is damaged by a range of herbivores including caterpillar pests and coffee locusts, the coffee berry-borer damages the fruits during fruiting season.

It has been suggested that the diversity of natural enemies and biological control of insect pests are fared better in the floristically diverse agroecosystems than in the intensive agroecosystems (Chaplin-Kramer et al. 2011 and references therein). We tested this hypothesis by assessing the prey removal by predators in native trees-shaded coffee (a floristically diverse habitat) and oak-shaded coffee (a floristically simple habitat). We expected that the prey removal was higher in native trees-shaded coffee than in oak-shaded coffee. Specifically, we examined whether the predation rates by overall predators and different predator taxa were different on coffee (*Coffea robusta*) plants 1) raised under the shade of diverse native-trees and monodominant silver-oak, 2) during leaf-flushing and fruiting seasons, and 3) by the position of prey on coffee plants and by an interaction of prey position and coffee habitat type?

Quantifying predation using live preys is arduous (Howe et al., 2009). We used artificial caterpillars to examine predation rates. Despite having potential limitations (Howe et al., 2009), studies suggest that artificial caterpillars can provide quick, easy, and reliable information on diversity and community of predators and predation rates in managed and natural habitats (Howe et al., 2009; Low et al., 2014; Posa et al., 2007; Sam et al., 2015; Seifert et al., 2015; Tvardikova and Novotny, 2012; Hariraveendra et al., 2020). The bite and predation marks are distinct for different predator taxa (Howe et al., 2009; Hariraveendra et al., 2020). Studies have used artificial caterpillars to estimate arthropod, bird, reptile, and mammal predation rates of caterpillars. Among arthropods, the predation by ants is easily distinguishable by the mandible marks on model caterpillars (Howe et al., 2009; Low et al., 2014; Posa et al., 2007; Sam et al., 2015; Seifert et al., 2015; Tvardikova and Novotny, 2012; Hariraveendra et al., 2020). Although caterpillar pests are relatively poor for coffee plants, this method can reveal the community of predators of coffee pests, predominantly generalists, such as ants and birds (Morris et al., 2018).

2. Material and methods

2.1. Study area

We conducted this study in Kodagu district of Karnataka State in south India. Kodagu is located on the eastern slope of the Western Ghats biodiversity hotspot between the latitudes 11°57′N and 12°48′N and between the longitudes 74°55′E and 76°00′E at the altitude 800–1500 m asl. The temperature in Kodagu district varies from 10 °C to 28 °C with an average of 15 °C. The district receives an average annual rainfall of 3500 mm; 80% of that falls during the southwest monsoon (June-September). The district has an area of 4102 square km. Although 82% of this area was under the cover of forests and sacred groves until 1960 s, today, only about 50% of the total area is under the cover of forests (Garcia et al., 2010). During this period, the coffee area has increased four folds; today, about 35% of the district is under coffee agroforests.

Coffee is cultivated both as large plantations (200–500 ha) and smallholdings (1–20 ha) by individual households in Kodagu. Smallholdings represent a continuum with large plantations on the forested landscape. While large plantations maintain coffee under the thick cover of forests and sacred groves, the coffee in smallholdings is grown under the shade of wild and edible native trees and silver oak. Both of them have silver oak but in different proportions (see below).

2.2. Sampling

This study was conducted in Virajpet taluk (12°00′ – 12°29′N and 75°39′–76°33′E) of Kodagu district. Eight (fruiting period) to ten sites (leaf-flushing period), each with one pair of coffee types – one under the shade of wild and native plants (hereafter, native trees-shaded coffee) and another under the shade of silver oak (hereafter, oak-shaded coffee) – were selected (Fig. 1). The sites were spaced out by an average of 15 km from each other. We counted the shade trees on a 500 m × 100 m transect in each plantation and identified species/morphospecies for all trees. The Girth at Breast Height (GBH) of shade trees – measured at the height of 1.3 m above the ground – in native coffee (89 ± 18 cm) was higher than in oak coffee (45 ± 12 cm) ($t = 6.91$, $DF = 18$, $p < 0.0005$). Shade cover – measured on a visual scale at all focal plant levels (Bellow and Nair, 2003) – in native coffee is higher (38 ± 5%) than in oak coffee (21 ± 3%) ($t = 10.38$, $DF = 18$, $p < 0.0005$). Shade tree density in the Kodagu coffee landscape ranged between 248 and 567 per ha. The percent of silver oak in native trees-shaded coffee is lesser (12.9 ± 15%) than in oak-shaded coffee (93 ± 3%) ($t = 18.6$, $DF = 18$, $p < 0.0005$). The shade tree diversity of native trees-shaded coffee (Shannon-diversity = 2.4–2.7; Number of species = 24–29) was different from the oak-shaded coffee (Shannon-diversity = 0.2–0.4; Number of species = 1–4) (Shannon-diversity: $t = 14.4$, $DF = 18$, $p < 0.0005$). All the focal coffee plants that have artificial caterpillars in native trees-shaded coffee were selected in the local vicinity of native trees. All the focal coffee plants with artificial caterpillars in the oak-shaded coffee were selected in the local vicinity of oak trees.

We sampled predation rates in two phenological phases of coffee: the fruit ripening period (October-November 2019) and the leaf-flushing period (January-March 2020). During fruiting season, fifteen caterpillars were installed on five randomly selected plants in each plantation. During leaf-flushing season, forty-five caterpillars were installed on fifteen randomly selected coffee plants in each plantation. The focal coffee plants were spaced out by about 150 m in both seasons. On each coffee plant, three caterpillars of three colors were placed, one on three parts of the plants – new leaf with some herbivory marks, stem, and branch; the color of caterpillars placed on plant parts was rotated among plants. All the caterpillars on stems and branches were at about 1.5 m – 2 m above the ground.

We used non-toxic oil-based non-hardening modeling clay (Peacock brand) to make caterpillars (Howe et al., 2009; Hariraveendra et al., 2020). The size of each caterpillar was about 30 mm long and 5 mm in diameter. We used simple smooth caterpillars in this study. We used Fevicol (MR brand) to glue them on plant parts (Hariraveendra et al., 2020). We installed the caterpillars at around 7 AM and retrieved them after 48 h. The retrieved caterpillars were grouped into different predator taxa based on the bite marks of predators (Howe et al., 2009; Hariraveendra et al., 2020) (Fig. 2). If a caterpillar had bite marks of more than one predator group, we included that into both the group of predators during analyses. (Hariraveendra et al. 2020).

2.3. Data analyses

The predation rates by overall predators and by different predator taxa – arthropods, birds, reptiles, and mammals – were used as the response variables throughout the models used in the present study. To test the hypothesis that coffee habitat type predicts predation rates, we used a generalized linear mixed-effect model (GLMM) with predation rates as the response variable, coffee type as a fixed effect, and tree ID nested in sites and seasons as a random effect. Binomial distribution was used as the error type in the models (model: m1 < -glmer(predation.rates ~ coffee.type+(1|season/sites/plant.ID),family = binomial)). To examine for the effect of season on predation rates, we constructed another GLMM with the season as a fixed effect and tree ID nested in sites and coffee type as a random effect (model: m1 < -glmer(predation.rates ~ season+(1|coffee.type/sites/plant.ID),family = binomial).

To examine whether the predation rates were affected by the interaction of the position of caterpillars on different parts of coffee plants and the habitat type, we used a GLMM with binomial distribution as an error type, and coffee plant ID nested in sites as a random effect in the models. In this model, the coffee habitat type and position of caterpillars on coffee plants in interaction terms were used as the fixed effect (model: m1 < -glmer(predation.rates ~ coffee.type*position+(1|sites/plant.ID),family = binomial). R^2 values were calculated for all the

Fig. 1. (A) A native tree-shaded and (B) a silver oak-shaded coffee plantation of Kodagu in the Western Ghats biodiversity hotspot. (Print in gray-scale).

Fig. 2. Predation marks of different taxa on artificial caterpillars. A&B) mammal predation marks; C&D) reptile predation marks; E) a group of *Oecophyla smaragdina* is predating on a caterpillar model; F) predation marks of ants; G) predation marks of birds.

GLMMs using the R-package MuMIn. The significance of the overall models was tested using ANOVA or Wald's Chisquare tests available in the R-package, car. All the analyses were performed in R 4.02 (R Core Team, 2018).

3. Results

We retrieved 1129 caterpillars out of 1140 used in the whole study. We lost one and ten caterpillars, respectively, while sampling during fruiting and leaf flushing seasons. The nature of remains of some lost

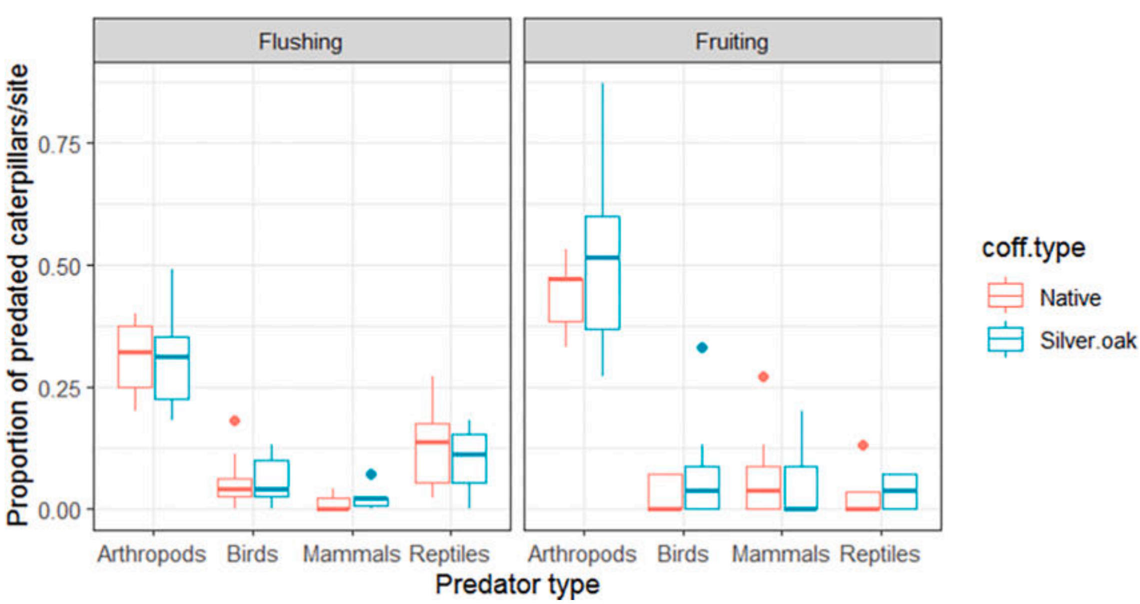

Fig. 3. Box plots show the predation rates of caterpillars by different predators in diverse native-trees shaded and monodominant silver-oak shaded coffee during leaf-flushing and fruiting periods of coffee plants. The arthropod predation rates of caterpillars were significantly higher during fruiting season of coffee than in leaf-flushing season ($p < 0.0005$). In the box plots, median, quartile 1 and 3, whiskers (1.5 times the inter-quartile range), and outliers are plotted.

caterpillars on the plant parts suggests that they were lost to some predators rather than to people (pers. observ.); however, we did not use any of the lost caterpillars in analyses. In the retrieved caterpillars, 44% had predation marks of one or more predator taxa. Fifty-four percent (N = 239) and forty-one percent (N = 890) of the caterpillars retrieved during fruiting season and leaf-flushing season, respectively, had predation marks. In the fruiting season, the predation rates in native trees-shaded coffee and oak-shaded coffee were 47% and 54%, respectively. During leaf-flushing season, these were 51% and 49%, respectively, for native trees-shaded and oak-shaded coffee. On average, arthropod predation was higher (34%; N = 1129) than reptile- (10%; N = 1129), bird- (6%; N = 1129), and mammalian predation (3%; N = 1129). The difference in the proportion of predated caterpillars by four different taxa was significant ($\chi^2 = 15.8$, DF = 3, p = 0.001) (Fig. 3).

The predation rates for overall predators (−0.17 ± 0.23, -z = 0.72, p = 0.47; $R^2 = 0.06$), arthropods predators (−0.31 ± 0.27, z = −1.11, p = 0.27; $R^2 = 0.03$), avian predators (0.24 ± 0.42, z = 0.58p = 0.6; $R^2 = 0.005$), and mammalian predators (−0.03 ± 0.6, z = −0.05, p = 0.95; $R^2 = 0.0005$) were not different between coffee habitats, but were significantly lesser in oak-shaded coffee than in native trees-shaded coffee for reptile predators (−1.34 ± 0.65, z = −2.04, p = 0.041; $R^2 = 0.12$). The overall predation rates (−0.66 ± 0.26, z = −2.49, p = 0.01; $R^2 = 0.06$) and arthropod predation rates (−1.01 ± 0.26, z = −3.83, p = 0.0001, $R^2 = 0.05$) were lesser during leaf-flushing season than fruiting season (Fig. 3).

On average, 45%, 39%, and 47% of brown, green, and grey caterpillars, respectively, were predated by the overall predators (Table 1), suggesting that the predation may not be confined to one particular type of caterpillar species. Although the rates of predation were different for different taxa, the patterns were similar to overall predation rates (Table 1). The pattern of predation rates by caterpillar color was similar for the two coffee habitats ($\chi^2 = 0.47$, DF = 2, p = 0.79; Fig. 4). The predation rates, however, varied for the caterpillars kept on different parts of coffee plants. On average, 50% and 51% of the caterpillars placed on branches and stems, respectively, were predated; only 28% of the caterpillars placed on the leaves were predated. The predation rates were significantly lower for the caterpillars placed on leaves than for the caterpillars placed on other parts of plants for overall predators (−0.94 ± 0.25, z = −3.8, p = 0.0001; $R^2 = 0.07$), arthropod predators (−0.8 ± 0.3, z = −2.9, p = 0.003; $R^2 = 0.05$), reptile predators (−1.1 ± 0.38, z = −2.61, p = 0.009; $R^2 = 0.21$), and bird predators (−1.7 ± 0.8, z = −2.15, p = 0.03; $R^2 = 0.23$). The patterns of predation rates for overall predators and different predator taxa were similar for the two coffee habitats (Table 2; Fig. 4)

4. Discussion

A good number of studies have examined the biodiversity inside coffee agroforests (e.g. Anand et al., 2008; Dolia et al., 2008; Donald, 2004; Gordon et al., 2007; Komar, 2006; Nesper et al., 2017; Perfecto et al., 1997; Perfecto and Vandermeer, 1996; Philpott et al., 2008; Raman, 2006; Greenberg et al., 1997; Petit and Petit, 2003; Wordley et al., 2017) and appraised the conservation potential of conventional shaded coffee around the world (Jha et al., 2014; Moguel and Toledo, 1999; Perfecto et al., 1996; Phillips et al., 2017). However, how beneficial the biodiversity inside coffee plantations is for sustainable production of coffee has received very little global attention or mainly studied in parts of Latin America and Africa (De la Mora et al., 2015; Mariño et al., 2016; Perfecto and Vandermeer, 2006; Philpott et al., 2009 for studies from Latin America).

Natural shade, pollination, and pest control are the three critical functions coffee plants need from biodiversity inside coffee plantations (Chain-Guadarrama et al., 2019). Shade level and diversity can be critical for pest infestation, natural pest control, pollination, and yield (Armbrecht and Perfecto, 2003; Boreux et al., 2016, 2013; Krishnan et al., 2012; Morris and Perfecto, 2016; Milligan et al., 2016; Nesper et al., 2017; Rigal et al., 2020; Smith et al., 2015). Interestingly, some studies find adverse effects of shade tree diversity and shade level on biotic functions and yield. Boreux et al. (2013) reveal that bee visits on coffee flowers have been decreased with the proportion of native trees in the plantations in our study area. Smith et al. (2015) reveal that sun coffee has high diversity and community of insectivorous birds in coffee plantations of Kenya. Mariño et al. (2016) find that the pest infestation rates of berries decrease with the amount of shade in coffee agroforests of Peru. Rigal et al. (2020) find that coffee flower-setting and bean production are less in shaded coffee.

Our study did not support the hypothesis that the conversion of multi-species native trees-shade into the silver-oak-dominated shade in coffee plantations adversely affects the natural prey removal on coffee (Philpott et al. 2009). Predation rates for overall predators and different taxa, but reptiles, were similar in native trees-shaded and oak-shaded coffee. The two coffee habitats in the present study are different in terms of shade, diversity of shade trees, GBH of shade trees, and abundance of silver oak. Our results agree partially with the findings of Boreux et al. (2013), Dolia et al. (2008), Krishnan et al. (2012), and Nesper et al. (2017), who have studied butterfly diversity, pollination services, and yield of coffee under the two circumstances in our study area or nearby coffee-growing districts. Nesper et al. (2017) found that neither coffee production nor coffee berry borer infestation was affected by coffee cultivation methods – conventional coffee and organic coffee. These two farming practices are different in terms of physical characteristics, including shade trees' composition and diversity. However, they found that coffee production increases with the Shannon diversity of shade trees in both the farming types, reiterating that shade tree diversity is vital for optimum production of quality coffee beans.

Similarly, Boreux et al. (2013) showed that shade tree density negatively affects coffee pollination during the massive general flowering event of coffee plants. Krishnan et al. (2012) suggested that local factors, instead of the landscape factors, may predict the probability of coffee pollination success. Dolia et al. (2008) documented 86 species of butterflies in coffee agroforests of Bhadra region. However, they reveal that silver oak composition was not a driver of butterfly species richness or abundance in coffee agroforests. Our study agrees with the findings of a *meta*-analysis (Philpott et al., 2009) that suggest that vegetation complexity of shade trees has no specific effect on arthropod reduction and bird predation of arthropods in coffee plants. However, our results disagree with Perfecto et al. (2004), who got evidences for greater rate of predation of caterpillar pests in heavily-shaded coffee farms (represented by a thick shade of about 200 species of plants) than in poorly-shaded coffee farms (represented by relatively open farms with the dominance of *Inga* spp) in Mexico. However, the major predator in their site was insectivorous birds, and not arthropods.

We encountered predation marks on caterpillar models in all the study sites in both the critical phenological phases of coffee–fruiting and leaf flushing periods, demonstrating the methodology's success in

Table 1
Proportion (mean ± S.D.) of predated caterpillars by overall predators and individual predator taxa.

Caterpillar color	N	Overall	Arthropods	Reptiles	Mammals	Birds
Brown	376	0.47 ± 0.12	0.36 ± 0.10	0.09 ± 0.05	0.04 ± 0.06	0.08 ± 0.08
Green	380	0.41 ± 0.14	0.31 ± 0.13	0.10 ± 0.06	0.03 ± 0.03	0.03 ± 0.02
Gray	372	0.47 ± 0.08	0.37 ± 0.09	0.09 ± 0.07	0.04 ± 0.05	0.06 ± 0.06
F(2,30)		1.06	1.15	0.02	0.2	3.08
R^2		0.005	0.005	0.0002	0.009	0.06
p-value		0.3	0.3	0.9	0.8	0.06

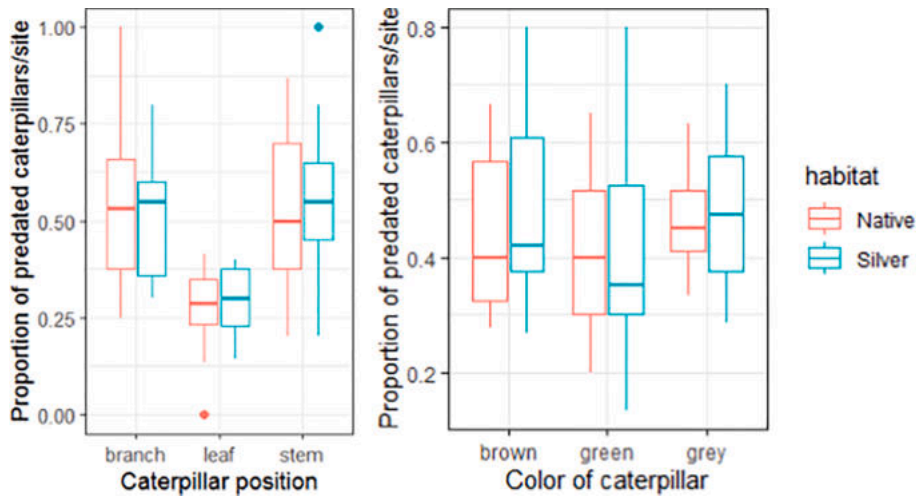

Fig. 4. Box plots show the predation rates of caterpillars by the position on coffee plants and color of caterpillars. Caterpillars on leaves are less predated in both diverse native-trees shaded and monodominant silver-oak shaded coffee.

Table 2
The model (GLMM) results show that the predation rates were different by the position of caterpillars on plants for all predator taxa but mammalian predators. It also shows that the predation rates by caterpillar positions were not affected by the coffee habitat type. The values given are χ^2. ***p < 0.00005; **p < 0.005; *p < 0.05.

Effect type	DF	Overall	Arthropods	Reptiles	Mammals	Birds
Caterpillar position	2	37.97***	23.46***	15.04**	1.86	7.24*
Coffee type × Position	2	0.11	0.24	3.5	1.01	0.97

estimating predation rates in coffee plantations. While coffee berry borer (*Hypothenemus hampei*) is an important pest of coffee during fruiting stage, coffee locusts, coffee green scale insects, hemipteran bugs, and caterpillar pests are the critical herbivores in the leaf-flushing stage of coffee. The native trees maintained in the coffee plantations also have several Lepidoptera species as herbivores (pers. observ.). Although we assessed the predation rates by using artificial caterpillar models, our results are comparable to similar studies that followed different strategies – sentinel preys or frozen prays – for examining predation rates (Armbrecht and Perfecto, 2003; De la Mora et al., 2015). The model caterpillars had predation marks of four major predator taxa, as illustrated by Howe et al. (2009), Low et al. (2014), and Hariraveendra et al. (2020).

Regardless of regions, ants and birds have been illustrated as major natural enemies of coffee pests (see a review by Morris et al., 2018; a *meta*-analysis by Milligan et al., 2016; Philpott et al., 2009). As the reports from Latin America and Africa, ants are crucial and predominant predators in the coffee agroforests of India. However, unlike the other studies, birds are only second to reptiles as natural predators. This pattern remained the same both in the native trees-shaded and silver oak-shaded coffee and during fruiting and leaf flushing seasons. The role of insectivorous reptiles, such as lizards in prey removal, however, has received little attention in coffee agroforests (but see, Borkhataria et al. 2006). Borkhataria et al. (2006) find that the abundance of large insects in coffee plants increased when the lizards and birds were excluded from the plants, and suggest that lizards can give an additive effect on avian predation of coffee herbivores. The predation rates by reptiles in the present study are higher in native trees-shade coffee than in oak-shaded coffee, suggesting that the native trees-shaded coffee might support the diversity and abundance of insectivorous lizards.

The arthropod predation contributes mainly (34%) to the overall predation of caterpillars in the present investigation. *Oecophylla smaragdina* (red weaver ant) was encountered most on coffee plants among arthropod predators. Most of the predated caterpillars had bite marks of *O. smaragdina*, which we often have personally experienced. Farmers agree that this ant is a voracious predator of coffee berry borer - a major pest of coffee in the study area - and nests on coffee plants and shade trees. Their using coffee plants for nesting might be a reason for the weak effect of habitat on overall predation rates of caterpillars. However, the study found that the overall predation rates, and the arthropod predation rates, in particular, were higher during the fruiting season than the leaf-flushing season. The farms are kept undisturbed during the fruit maturing period of coffee and abundance of coffee-berry borers during fruting seasons are the likely reasons why the predation rates are higher during fruiting period of coffee. The biocontrol potential of *O. smaragdina* has been tested in several crop systems, including Cacao, Cashew, and Mango, and in several parts of Asia-Pacific region (Forbes and Northfield, 2017 and references therein). One implication of this study is that farmers may take immediate steps to promote the density of this ant in coffee plantations. This ant, because, is a significant source of protein for the local households of highlands of Karnataka (pers. observ.), farmers are maintaining them on their coffee plantations.

We also had different numbers and colors of caterpillars placed on various plant parts for assessing predation rates in two different seasons. We shuffled the position of caterpillars by colors so that each sampled coffee plant has three caterpillars belong to three different colors. The results that emerged from the study clearly showed that caterpillar color does not predict the probability of predation by any of the predator taxa, suggesting that the predation is more generalized and not confined by any particular type of caterpillar pest species. However, birds prefer brown caterpillars over caterpillars of the other two colors (Table 2). Similarly, caterpillars on branches and stems are predated more than on leaves. Therefore, caterpillar position is a crucial predictor of predation rates in coffee agroforests. Apart from ants, the lizards and dominant insectivorous birds, such as Oriental White-Eye (*Zosterops palpebrosus*), Oriental Magpie-Robin (*Copsychus saularis*), and Velvet-Fronted Nuthatch (*Sitta frontalis*), are active on coffee stem and branches. Our results corroborate the findings of Philpott et al. (2009), who found that the richness of small birds active at the understory layer of plantations is crucial for pest reduction in coffee.

5. Conclusions

It is generally believed that the diverse agroecosystem supports a greater diversity of natural enemies and better pest control as a diverse system provides adequate microhabitats and resources for supporting diversity and density of natural enemies (Chaplin-Kramer et al. 2011, and references therein). Although we have not directly studied the diversity of natural enemies in two types of coffee habitats that are differed by the shade characteristics, we assessed it by examining the predation rates and bite marks of predators on caterpillar models. Our results do not support this hypothesis. The predation rates of artificial caterpillars were alike for the diverse native-trees-shaded and monodominant oak-shaded coffee plantations of Kodagu. However, the predation rates by lizards were slightly higher in the former type of coffee plantations than in the latter kind of coffee. Unlike similar studies from Latin America (Greenberg et al., 2000; Perfecto et al., 2004), the predators of coffee plantations of diverse tree-shaded and monodominant species-shaded coffee of our sites were generalist ants, which use coffee foliage for building large nests. Our results also highlight the biocontrol potential of the lizards in diverse-shaded coffee agroforests (Borkhataria et al., 2006).

Management decisions in production landscapes are made to increase productivity and not essentially to maintain ecosystem services *per se*, even though the latter plays a crucial role in agricultural productivity. The coffee production landscape in the tropics has both the economic and environmental targets because coffee has replaced a tremendous amount of tropical evergreen forests. Agronomic investigations recommend less or no shade in coffee as their interest is to increase coffee flowering and productivity (Cerdán et al., 2012; Rigal et al., 2020). Shade tree diversity is, however, critical for delivering essential pollination service and natural pest control (Mariño et al., 2016; Nesper et al., 2017).

Unlike Latin America – a leading coffee producer globally, India is far behind in documenting biodiversity and biotic functions in coffee agroforests. Although our present study suggests that shade tree simplification has little effect on pest control, taking a policy decision on conversion of the composition of shade trees from native trees to silver oaks may be discouraged. Coffee agroforests are a production landscape and a lung and a wildlife refuge for tropical biodiversity in the era of climate change (Chain-Guadarrama et al., 2019; Nesper et al., 2017).

CRediT authorship contribution statement

Palatty Allesh Sinu: Conceptualization, Data curation and analyses, Manuscript writing, Overall administration, and Funding acquisition. **Gopika Viswan:** Data collection and curation. **P.P. Fahira:** Data collection and curation. **T.P. Rajesh:** Data collection and curation. **K. Manoj:** Data collection and curation. **M. Hariraveendra:** Data collection and curation. **Thomas Jose:** Data collection and curation.

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