



Abundance and richness of invertebrates in shade-grown versus sun-exposed coffee home gardens in Indonesia

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Abstract Complex agroforestry systems are suggested as a possible solution to reduce the effects of deforestation in the tropics while enhancing the livelihoods of local human populations. Coffee (*Coffea* spp.) is one of the most important commodity crops in the world that can easily be cultivated in complex agroforestry systems. Coffee agroforestry systems usually sustain higher biodiversity levels than sun-exposed fields while keeping similar levels of

productivity considering the several benefits of growing coffee under a complex system. We aim to explore the richness and abundance of invertebrates in coffee home gardens in West Java, Indonesia by comparing 14 sun-exposed and 14 shade-grown gardens. We collected data in March/April 2019 via pitfall traps, pan traps, and beating tray in each field. We ran generalised linear models to assess whether the number of species and the number of individuals of insects differed between sun-exposed vs. shade-grown coffee gardens, and tested associations between main taxa. Overall, there was no difference in the richness (sun-exposed: $19.86 \pm \text{SE}1.19$; shade-grown: $19.71 \pm \text{SE}1.19$; $Z\text{-value}=0.12$, $p\text{ value}=0.904$) and abundance (sun-exposed: $141.93 \pm \text{SE} 3.18$; shade-grown: $139.93 \pm \text{SE}3.16$; $Z\text{-value}=0.35$, $p\text{ value}=0.706$) of invertebrates in coffee gardens, although taxa specific differences were present. Sun-exposed fields had a higher abundance of invertebrates considered as pests (Blattodea: Rhinotermitidae, Ectobiidae; Coleoptera: Scarabaeidae, Lycidae and Tenebrionidae; Diptera: Anisolabididae, Drosophilidae and Sarcophagidae). *Camponotus* spp. were the most dominant ants in shade-grown gardens while *Dolichoderus* spp. and *Myrmecaria* spp. were more abundant in sun-exposed gardens. Despite the fact that sun-exposed coffee fields registered higher abundance of invertebrate pests than shade-grown coffee fields, the richness of invertebrates did not substantially vary between sun-exposed and shade-grown coffee, suggesting that the matrix of gardens offers

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advanced ecosystem services. It is important to keep the complexity of agroforestry systems that provide key habitats for biodiversity.

Keywords Spider · Ant · Land sharing · Agroforestry · Insects · Pest

Introduction

Tropical forests are heavily impacted by the increased need for food production and the consequent expansion of agricultural land (Foley et al. 2011). The complexity of agricultural systems, in terms of ecological and crop diversity, are also reduced, with intensive monocultures becoming more abundant than complex agroforestry systems, to meet the high food demand (Laurence et al. 2014). Agroforestry systems (i.e., complexes of crops and shade trees) are suggested as a possible solution to reduce the effects of deforestation of tropical forests, while also enhancing the livelihoods of local communities (Bhagwat et al. 2008). Agroforestry systems can sustain similar biodiversity of natural habitats for some taxa (Bhagwat et al. 2008; De Beenhouwer et al. 2013; Santos-Heredia et al. 2018) and can partially restore the soil structure after conversion of forests to monocultures (Saputra et al. 2020). They are, however, likely to conserve little functional diversity unless the adjacent natural habitat is also protected (Cannon et al. 2019). Thus, land sparing agriculture (i.e., intensification of existing farmlands and expansion of protected natural habitats) is often preferred to land sharing agriculture (i.e., agroforestry systems) (Cannon et al. 2019). To show the conservation potential of land sharing system, more data are needed, especially in the tropics since some regions of high biodiversity outside the Neotropics are less studied.

Coffee (*Coffea* spp.) is one of the most important commodity crops in the world (DaMatta et al. 2019), with around 25 million people estimated to depend on its production for their livelihoods (Bunn et al. 2015). Coffee, together with cocoa (*Theobroma cacao*), are the best examples of crops that can easily be cultivated in complex agroforestry systems. Traditionally cultivated under dense and diverse shade canopy (Moguel and Toledo 1999), these crops can sustain high biodiversity of various taxa when under shade trees (e.g., invertebrates: Armbrrecht

and Perfecto 2003; Perfecto et al. 2003; Borkhataria et al. 2012; birds: Perfecto et al. 2003; Gordon et al. 2007; Borkhataria et al. 2012; Philpott and Bichier 2012; mammals: Gordon et al. 2007; Caudill et al. 2015). The presence of shade trees in coffee agroforestry systems can also enhance carbon sequestration, drought resistance, functional biodiversity, soil fertility, as well as provide natural solutions for weed and biological pest control (reviewed in Tscharnkte et al. 2011). In addition, coffee agroforestry systems show smaller temperature fluctuations (López-Bravo et al. 2012; Mariño et al. 2016), improve microclimate conditions and deep-water drainage (De Carvalho et al. 2021), and can provide key resources for wildlife (Perfecto et al. 1996) when compared to sun-exposed coffee fields.

Several taxa of insects are considered as bioindicators for assessing the state of agroforestry systems (Kevan 1999; Andersen et al. 2002; Jimenez-Soto et al. 2019). Many insects are known to be sensitive to land use changes despite their important roles in the ecosystem as pollinators, pest control agents and nutrient cyclers (Peck et al. 1998; Rainio and Niemela 2003; Losey and Vaughan 2006). For example, ants (Formicidae) can be important biological control agents in coffee fields as they predate the main coffee pest borer, *Hypothenemus hampei*, a beetle (Family Curculionidae) that severely damages coffee seeds (Morris et al. 2018; Jimenez-Soto et al. 2019). Soil insects such as ants and termites (Isoptera) can move particles in the soils and favour the mobilisation of nutrients (Dangles et al. 2012) as well as hasten organic matter decomposition (Crespo-Pérez et al. 2020). Pollinators from different orders (e.g., Lepidoptera, Hymenoptera, and Diptera) are important bioindicators as most of the crops benefit from cross-pollination by producing more fruits, increasing fruit quality and maintaining high genetic variability (Klein et al. 2007; Garibaldi et al. 2011).

The question about changes in invertebrate richness and abundance between different agroforestry systems remains elusive. Ant species richness and abundance, for example, is higher either in shade-grown coffee (Armbrrecht and Perfecto 2003; Perfecto et al. 2003) or in sun-exposed coffee (Arenas-Clavijo and Armbrrecht 2019). Borkhataria et al. (2012) found higher abundance of Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera in shade-grown than in sun-exposed coffee fields and a

higher abundance of Orthoptera in sun-exposed coffee fields. Pollinators are expected to be more abundant in shade-grown coffee as flowers from other plant species can attract them, but the abundance of some species do not differ between sun-exposed and shade-grown coffee (e.g., bees, Classen et al. 2014). Moreover, Prado et al. (2021) found no influence of flower availability on shade trees or type of coffee field (shade vs. sun-exposed) on the frequency of bee visitation. The response is therefore taxon specific, with the need to consider regional and environmental variables (Smith et al. 2015).

We aimed to explore the richness and abundance of invertebrates in coffee home gardens in West Java, Indonesia by comparing sun-exposed and shade-grown gardens. Indonesia is one of the 17 megadiverse countries in the World and a biodiversity hotspot, with many endemic species under a constant threat of extinction (von Rintelen et al. 2017). The study area is a good model to test the effect of sun vs. shade home gardens without the influence of environmental variables as it is subject to dry periods of around 5 months but still maintains similar ambient temperatures. In addition, there are relatively few studies on the impact of different management practices on coffee fields in Indonesia, despite being the fourth largest coffee producer in the world (Szenthe 2020). Despite evidence of regional differences in animal diversity between sun and shade coffee fields from neotropical studies, few researchers have investigated this in the Asian context, including Indonesia. Coffee production in Indonesia has increased since 2010, both in terms of local and exported coffee markets (Prajanti et al. 2020). With the increase in these markets, we expect an intensification in the management of coffee fields and a consequent increase in sun exposed fields. It is therefore key to understand the implications of shifting cultivation to sun fields in this biodiversity hotspot. We predict an overall decrease in richness and abundance of invertebrates in sun-exposed coffee, compared with shade-grown coffee, although we expect taxon specific differences on the response. We predict that shade-grown coffee would favour the presence and abundance of invertebrates with important ecological roles for the ecosystem, while sun-exposed coffee fields would host higher abundances of invertebrates typically regarded as pests.

Materials and methods

Study area

We collected data in 28 coffee home gardens in the municipalities of Cipaganti and Pangauban, West Java, Indonesia (7.2786°S, 107.7577°E; elevation ~1350 m a.s.l.; Fig. 1). The area consists of an agroforestry system of interconnected crops usually separated by trees alongside trees planted inside gardens (Nekaris et al. 2017; Campera et al. 2021b). This agroforestry system lies in the foothills of Mount Puntang, which is part of the mountain range containing the active volcano Mount Papandayan. The forests on Mount Papandayan are protected in part as a watershed (hutan lindung) and in part to protect its unique biodiversity (cagar alam), but the agroforestry system is not included in the protected area. The climate is ever-wet, with a mean annual precipitation exceeding 2500 mm and a drier period between April and September (Nekaris et al. 2017). In addition to coffee (*Coffea arabica*), there are other yielding crops such as tea (*Camellia sinensis*), chayote (*Sechium edule*), carrot (*Daucus carota*), white cabbage (*Pieris brassicae*), tomato (*Solanum lycopersicum*), cassava (*Manihot esculenta*), and potato (*Solanum tuberosum*). The agroforestry systems is on a mixture of clay soil and sandy soil.

Data collection

Out of the estimated 400 small-holder coffee gardens present in the area, we sampled only a subset of gardens randomly chosen to have an equal number of sun-exposed and shade-grown gardens. Coffee gardens surveyed covered a mean area of $1,216 \pm \text{SD } 877 \text{ m}^2$, for a total of 34,055 m². The sampled coffee gardens were at a distance of $1734 \pm \text{SD } 371 \text{ m}$ (range = 1296–2505 m) from the edge of the continuous forest from which they were connected by a series of home gardens and bamboo forest patches. We divided coffee gardens into sun vs. shade depending on the shade cover and the variety of shade trees. To determine shade cover, we used the Canopeo App, which calculates the proportion of area shaded from photographs (Patrignani and Ochsner 2015). We took four random and independent photographs and calculated the mean value for each coffee garden. The minimum distance between points of photo capture

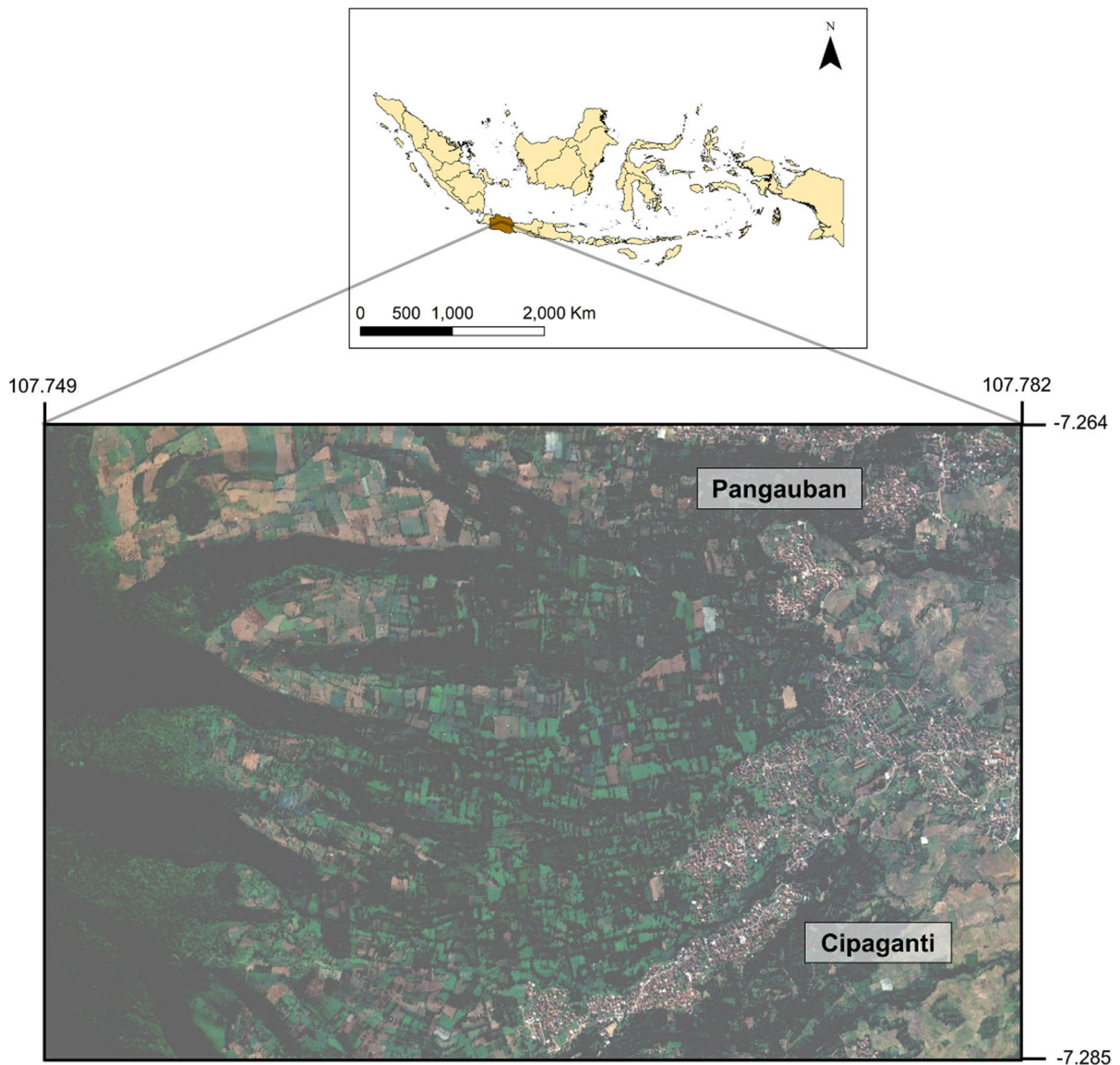


Fig. 1 Location of the study area. The coffee gardens are included in an agroforestry system connected to a protected forest and in proximity of the villages Cipaganati and Pangauban (West Java, Indonesia). Coordinates are decimal degrees. (Color figure online)

was 10 m, and the minimum distance from field edge was 5 m. We ensured that the photos did not include understory canopy such as banana leaves, which would have biased the calculation of the tree shade cover. We recorded the tree species that were used as shade trees in the sampled gardens. The main shade trees in coffee gardens were *Grevillea robusta*, *Mesopsis eminii*, *Manglietia glauca*, *Melaleuca cajuputi*, *Persea americana*, and *Toona sureni*. We divided sun-exposed gardens ($n=14$) and shade-grown gardens

($n=14$). We recorded the temperature and humidity via a weather station (HOBO RX3000) in proximity to the gardens to represent the general weather conditions during the data collection period and not the weather conditions at the garden *per se*.

We collected data during the beginning of the dry period (March/April 2019) at times where there was no rain or wind that could have affected the presence of invertebrates. The mean temperature during the data collection varied little (mean = $21.4 \pm$ SD

0.8 °C). We installed the traps between 0600 and 0700 h in a single 12.25 m² plot in the middle of each coffee garden. We installed six pitfall traps (diameter: 11 cm) set along the diagonal keeping 1 m spacing between traps and positioned pan traps (inner dimensions: 37 × 27 × 2 cm) in opposite corners of the plot at a height of one meter (Fig. 2) (Woodcock 2005). We used two colours (blue and yellow) for pan traps as there can be a colour preference in some taxa of pollinators (Heneberg and Bogusch 2014). We filled pitfalls to one third and pan traps to the brim with a solution of clean water and a few drops of detergent. After installing the traps, we used the beating tray method on three random coffee plants in the garden. We placed a white tray of 1 m² below the plant, and then shook the whole plant for 5 s and collected all the insects dropped on the tray using an insect aspirator (Ozanne 2005). We then left the garden and came back 6 h after installing the traps to collect the samples. We substituted the solution of water and detergent with 70% ethanol and put in the freezer to preserve the samples and allow subsequent counting and identification. The identification was done to the genus level when possible, and we considered morphospecies. We used taxonomic keys and Olympus SZ61 microscope to perform the identification. For an easier representation of the results, we first present the data grouped by Order and then make additional separations within the main orders detected. For the Formicidae, we present the results at genus level as they were the most abundant taxa.

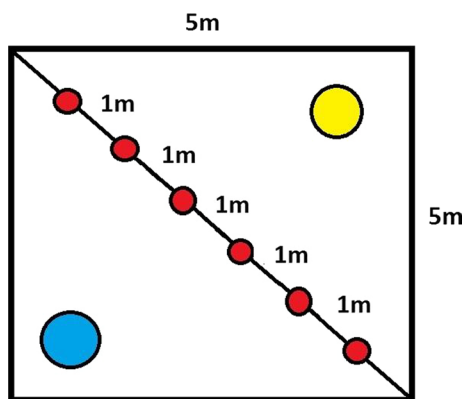


Fig. 2 Representation of the plots used to collect data on insects in coffee home gardens. Yellow and blue circles represent pan traps, red circles represent pitfall traps. (Color figure online)

Data analysis

We ran generalised linear models to assess whether the number of species and the number of individuals of insects differed between sun-exposed vs. shade-grown coffee gardens. We fit the dependent variables with Poisson distributions for count data. We additionally ran generalised linear models considering each Family separately (and genera of the Family Formicidae) for the families for which we found at least ten individuals to better understand the differences between taxa. We used the function “glm” in R 4.0.4 for the analysis. We considered $p=0.05$ as threshold level for significance. For the species that were present in at least ten gardens, we run a correlation matrix via “cor.mest” function in the package “corrplot” and corrected p-value via Bonferroni-Holm method in “p.adjust” function (Wei and Simko 2021).

Results

Sun-exposed gardens had a shade cover < 10% and with shade mainly given by trees at the border of gardens. Shade-grown gardens had a shade cover > 15% and had higher richness of shade trees in the middle of the coffee gardens (Table 1). The other parameters relative to the coffee gardens and the data collection did not change between sun-exposed and shade-grown gardens.

In total, we recorded 3,962 individuals from 111 species of invertebrates in coffee gardens (Table 2). With the pitfall trap method, we collected the highest abundance of invertebrates (3,114 specimens from 49 species), although the beating tray method resulted in the highest number of species (538 specimens from 66 species). The pan traps collected only 211 specimens from 22 species (yellow) and 99 specimens from 18 species (blue) but were more efficient in collecting data on Hymenoptera not belonging to the Family Formicidae, and on Diptera.

The total number of species of invertebrates did not vary significantly between sun-exposed and shade-grown coffee gardens (Z -value=0.12, p value=0.904; Table 3). The overall abundance of invertebrates also did not vary (Z -value=0.35, p value=0.706), but significant differences occurred at the Order level. The abundance of

Table 1 Parameters of the coffee home gardens (median and quartiles) selected for the invertebrate surveys between 20 March and 4 April 2019

Parameter	Sun-exposed (n = 14)	Shade-grown (n = 14)	Mann-Whitney U
Shade cover (%)	2.8 (0.4–5.1)	23.5 (18.1–31.1)	4.505**
Shade tree richness	1.00 (0.00–2.00)	3.50 (2.00–6.25)	3.868**
Richness of other crops	1.00 (0.75–2.00)	1.50 (1.00–2.00)	0.409
Elevation (m a.s.l.)	1304 (1254–1342)	1334 (1314–1346)	1.471
Size (m ²)	733 (413–1604)	1065 (696–1975)	1.057
Distance from village (m)	84 (2–315)	216 (186–406)	1.820
Distance from forest (m)	1798 (1512–2135)	1516 (1481–1687)	1.019
Humidity (%)	77.5 (72.8–80.0)	78.0 (74.1–80.3)	0.255
Temperature (°C)	21.2 (20.9–21.8)	21.4 (20.7–21.9)	0.529

Humidity and temperature are averages during the data collection period in the area, not at the coffee home gardens. Mann-Whitney U values are standardised values

* $p < 0.05$; ** $p < 0.001$

Table 2 Number of species (and total individuals) of invertebrates censused using four different methods in 28 coffee home gardens in Indonesia

Order	Pitfall trap	Blue pan trap	Yellow pan trap	Beating tray	Total
Araneae	4 (195)	2 (2)	3 (6)	25 (229)	28 (432)
Blattodea	5 (240)	0 (0)	0 (0)	2 (15)	5 (255)
Coleoptera	8 (26)	1 (13)	2 (2)	8 (50)	14 (91)
Dermoptera	4 (147)	0 (0)	0 (0)	2 (25)	4 (172)
Diptera	5 (20)	7 (34)	6 (133)	4 (6)	11 (193)
Hemiptera	2 (8)	0 (0)	0 (0)	3 (4)	5 (12)
Hymenoptera	10 (2285)	8 (50)	9 (68)	12 (172)	26 (2575)
>>>Formicidae	9 (2283)	2 (3)	1 (2)	7 (167)	11 (2455)
Julida	1 (1)	0 (0)	0 (0)	0 (0)	1 (1)
Lepidoptera	4 (7)	0 (0)	1 (1)	4 (9)	7 (17)
Odonata	0 (0)	0 (0)	1 (1)	0 (0)	1 (1)
Orthoptera	5 (168)	0 (0)	0 (0)	6 (28)	8 (196)
Scolopendridae	1 (17)	0 (0)	0 (0)	0 (0)	1 (17)
Total	49 (3114)	18 (99)	22 (211)	66 (538)	111 (3962)

Blattodea (Z -value = 8.69, p value < 0.001) and Diptera (Z -value = 3.78, p value < 0.001) was significantly higher in sun-exposed gardens, while the abundance of Orthoptera was significantly higher in shade-grown gardens (Z -value = -4.05, p value < 0.001). When investigating differences at Family levels, we found additional significant results. Within the Araneae, the individuals of the Family Lycosidae were more abundant in shade-grown gardens (Z -value = -2.30, p value = 0.021), while Linyphiidae were more abundant in sun-exposed gardens (Z -value = -2.78, p value = 0.005) (Fig. 3). Within the Blattodea, Rhinotermitidae (Z -value = 8.12,

p value < 0.001) and Ectobiidae (Z -value = 2.59, p value = 0.010) were more abundant in sun-exposed gardens. Coleoptera of the Families Scarabaeidae (Z -value = 2.46, p -value = 0.014), Lycidae (Z -value = 2.22, p -value = 0.026) and Tenebrionidae (Z -value = 1.97, p value = 0.049), and Diptera of the families Culicidae (Z -value = 2.31, p value = 0.021), Sarcophagidae (Z -value = 2.91, p value = 0.004) and Drosophilidae (Z -value = 1.96, p value = 0.050) were more abundant in sun-exposed gardens. Within the Family Formicidae, we found variability among genera with higher abundance of *Camponotus* spp. (Z -value = -10.14, p -value < 0.001) in shade-grown

Table 3 Number of species and individuals in 28 coffee home gardens (14 sun-exposed and 14 shade-grown) in Indonesia. Estimated model means and beta coefficients based on generalised linear models. Values in brackets are standard errors

Order	Number of species per garden			Number of individuals per garden		
	Sun	Shade	Beta	Sun	Shade	Beta
Araneae	4.29 (0.55)	4.86 (0.59)	− 0.13 (0.18)	15.07 (1.04)	15.79 (1.06)	− 0.05 (0.10)
Blattodea	1.57 (0.34)	0.79 (0.24)	0.69 (0.37)	14.36 (1.01)	3.86 (0.52)	1.31 (0.15)**
Coleoptera	1.36 (0.31)	1.79 (0.36)	− 0.27 (0.30)	3.00 (0.46)	3.50 (0.50)	− 0.15 (0.21)
Dermaptera	1.86 (0.36)	1.71 (0.35)	0.08 (0.28)	7.00 (0.71)	5.29 (0.61)	0.28 (0.15)
Diptera	2.79 (0.45)	2.36 (0.41)	0.17 (0.24)	8.86 (0.80)	5.00 (0.60)	0.57 (0.15)**
Hemiptera	0.43 (0.17)	0.29 (0.14)	0.41 (0.65)	0.64 (0.21)	0.29 (0.14)	0.81 (0.60)
Hymenoptera	5.50 (0.63)	5.21 (0.61)	0.05 (0.16)	88.79 (2.51)	95.14 (2.61)	− 0.07 (0.04)
Lepidoptera	0.50 (0.19)	0.57 (0.20)	− 0.13 (0.52)	0.64 (0.21)	0.57 (0.20)	0.12 (0.49)
Orthoptera	1.50 (0.33)	2.07 (0.38)	− 0.32 (0.29)	4.93 (0.59)	9.07 (0.80)	− 0.61 (0.15)**
Scolopendridae	0.29 (0.14)	0.36 (0.16)	− 0.22 (0.67)	0.64 (0.21)	0.57 (0.20)	0.12 (0.49)
Total	19.86 (1.19)	19.71 (1.19)	0.01 (0.09)	141.93 (3.18)	139.93 (3.16)	0.01 (0.03)

* $p < 0.05$; ** $p < 0.01$

gardens and higher abundance of *Myrmecaria* spp. (Z -value = 10.10, p value < 0.001) and *Dolichoderus* spp. (Z -value = 5.17, p value < 0.001) in sun-exposed gardens. The abundance of *Camponotus* spp. was negatively correlated to the abundance of *Dolichoderus* spp. ($r = -0.53$, $p = 0.003$) and *Myrmecaria* spp. ($r = -0.53$, $p = 0.004$) (Fig. 4). The abundance of *Paratrechina* spp. was positively correlated to the abundance of *Zodariidae* (Araneae) ($r = 0.53$, $p = 0.004$), *Chelisochidae* (Dermaptera) ($r = 0.60$, $p < 0.001$), and *Gryllidae* (Orthoptera) ($r = 0.59$, $p < 0.001$). We also found a positive correlation between the abundance of *Rhinotermitidae* (Blattodea) and *Sarcophagidae* (Diptera) ($r = 0.62$, $p < 0.001$) and between the abundance of *Anisolabididae* (Dermaptera) and *Drosophilidae* (Diptera) ($r = 0.57$, $p = 0.002$).

Discussion

We found that the complexity of coffee home gardens, evaluated by comparing sun-exposed and shade-grown gardens, influenced the abundance of several taxa of invertebrates, although overall there was no difference in terms of richness and abundance of invertebrates between the two types of gardens. This finding can be dependent on the fact that the sun-exposed home gardens in the study area were included in a matrix of other home gardens with shade cover. Despite this factor, the abundance

of several taxa that can be considered as pests were still more abundant in sun-exposed fields. Termites of the Family *Rhinotermitidae*, for example, are known to cause severe damage to mature trees and can bring about a reduction in crop productivity (Cowie et al. 1989; Fajar et al. 2021). Cockroaches of the Family *Ectobiidae* (*Blattella* sp. in the study site) are omnivores and can damage crops by eating leaves and pre-dating on eggs of *Lepidoptera* and *Hemiptera* (Capinera 2020). Beetles of Families *Lycidae* (*Cautires* sp. and *Scarelus* sp. in the study site) and *Tenebrionidae* (*Euhemicera* sp. in the study site) also eat leaves and are predators of larvae (Lundgren et al. 2014; Capinera 2020), although they can bring benefits to coffee production as they are occasional pollinators of coffee flowers (Hipólito et al. 2018) and are agents of organic matter decomposition (Crespo-Pérez et al. 2020). Sun-exposed gardens also had a higher abundance of parasites from the Family *Diptera*. Shade-grown gardens had a higher abundance of *Orthoptera*, and this is somehow unexpected since *Orthoptera* are expected to prefer areas with bare ground used for basking and oviposition (Fartmann et al. 2012; Rahman et al. 2012), however, also found a higher abundance of *Orthoptera* in agroforestry systems than in monocultures. Considering additional factors such as diversity of other crops and ground vegetation can help better understand this pattern.

We revealed some interesting associations between taxa. In ant communities, the dominant genera were

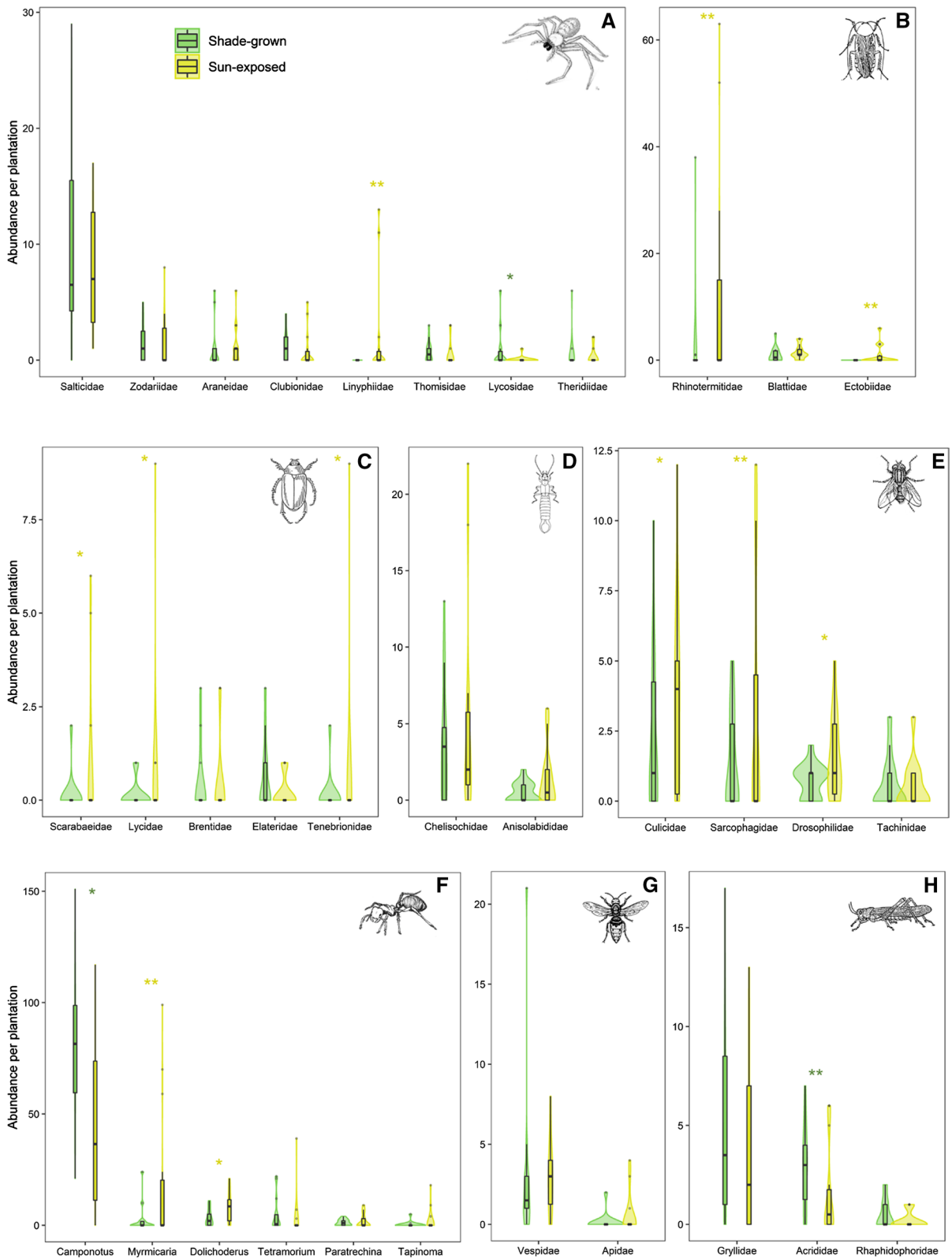


Fig. 3 Abundance of invertebrates in 28 coffee home gardens (14 sun-exposed and 14 shade-grown) in Indonesia. Plots show raw data represented via box plots embedded in violin plots. A: Araneae; B: Blattodea; C: Coleoptera; D: Dermaptera; E: Diptera; F: Formicidae; G: other Hymenoptera; H: Orthoptera. * $p < 0.05$; ** $p < 0.01$ based on generalised linear models. The colour of the * indicates whether values are significantly higher in sun-exposed (yellow) or shade-grown (green) gardens. A: Araneae; B: Blattodea; C: Coleoptera; D: Dermaptera; E: Diptera; F: Formicidae; G: Hymenoptera (other); H: Orthoptera. (Color figure online)

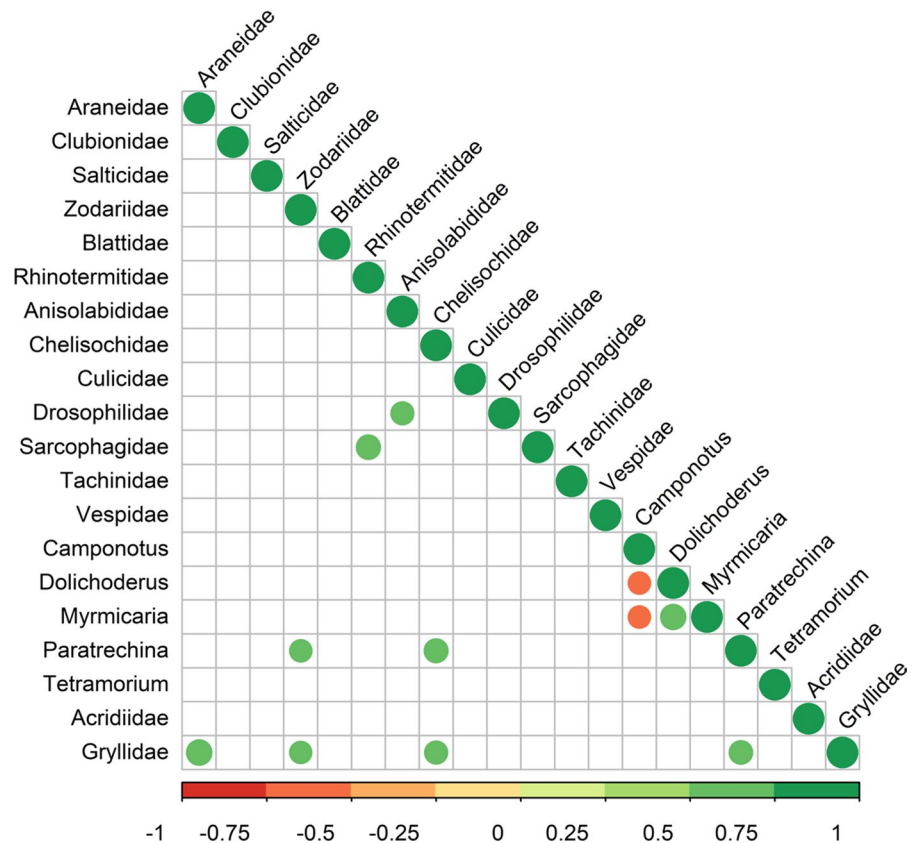
Camponotus spp. in shade-grown gardens and *Dolichoderus* spp. and *Myrmecaria* spp. in sun-exposed gardens. This pattern of exclusion of dominant species in relation to the complexity of the coffee field was also found in Puerto Rico (Perfecto and Vandermeer 2020). *Paratrechina* spp., a predator of several invertebrate larvae that are both pests and important pollinators (Romeis et al. 1995; Silva et al. 2015), were associated with the ant mimicking spiders from the Family Zodariidae, suggesting that the detected species of Zodariidae were highly specialised on hunting *Paratrechina* spp. (Pekár et al. 2018). Anisolabididae was positively associated with Drosophilidae, suggesting that the detected earwigs are predators of the larvae of flies (Garcia et al. 2020). Eggs or larvae of Gryllidae might also be target of predator spiders and earwigs (Midega et al. 2004), although we would need more experimental support to draw conclusions on the associations revealed via the correlation matrix.

There are a series of limitations and additional considerations based on our results. First, there are additional predictors to invertebrate abundance that were not considered in our investigation. For example, invertebrate abundance and richness can be shaped by the use of agrochemicals (Iwasaki and Hoogendorn 2021; Manson et al. 2022), shade tree richness (Campera et al. 2021a), soil moisture content (Staley et al. 2007), fire (Swengel 2001), and climate change (Barnett and Facey 2016). Second, the methods used were mainly effective in detecting ground-dwelling invertebrates, although pan traps and beating trays were effective in detecting other taxa. Given the methods used, the results are probably more accurate for some taxa (e.g., Araneae, Blattodea, Coleoptera, Formicidae) and less accurate for other taxa that require additional methods for data collection (e.g., Hemiptera, Hymenoptera not Formicidae,

Lepidoptera, Odonata). For example, pan traps are commonly used to assess the communities of flower-visiting insects in an area (Heneberg and Bogusch 2014), but other methods (e.g., net sampling) can perform better or be complementary (Popic et al. 2013). The reduced number of flower-visiting insects might also be due to the temporal limitation of our sampling that was not done in the peak of the flowering season in coffee gardens (usually July–August), although other plants were flowering at the time of data collection. These methodological issues, however, do not limit the importance of our findings since our scope is to present the variations in invertebrate abundance and richness between sun-exposed and shade-grown gardens.

Our findings suggest that sun-exposed coffee fields host a higher abundance of invertebrate pests than shade-grown coffee fields. Still, the abundance of functional invertebrates such as ants and spiders were very high compared to the abundance of pests. In addition, the diversity of invertebrates was not different between the two field types, suggesting the ecosystem services offered by the agroforestry environment are efficient. The agroforestry environment is particularly important as it is an important habitat for the conservation of threatened mammal and bird species (Nekaris et al. 2020; Campera et al. 2021b). Coffee farmers in the area mainly use organic practices, favoured by extensive training for organic fertilisers and pesticides and conservation education initiatives (Campera et al. 2021b). We also promoted the planting of shade tree saplings (~30,000) in the circa 400 coffee gardens present in the study area that could provide long-term benefits (Campera et al. 2021b), considering the increase in the coffee market in Indonesia (Prajanji et al. 2020) and the possible intensification in crop management in the near future (Schroth et al. 2015). Accordingly, a land sharing agroforestry environment can also enhance the credibility of sustainable coffee production that is wildlife-friendly and contributes to the food security of local communities (Duffy et al. 2021). This is also potentially important to consumers seeking sustainable brands that are authentic in their conservation actions. Considering the constant decline of terrestrial invertebrates (van Klink et al. 2020), birds and mammals (Spooner et al. 2018), the efforts in conservation should focus on maintaining and promoting complex agroforestry systems that might represent the future of conservation

Fig. 4 Correlation matrix with the abundance of the main taxa present in home coffee gardens in Indonesia. We only show significant results after a corrected p value (Bonferroni–Holm). (Color figure online)



for some threatened species that prefer human-modified habitats.

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Availability of data and material The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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