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Natural parasitism of the coffee leaf miner: climate factors, insecticide, and landscape affecting parasitoid diversity and their ecosystem services in coffee agroecosystems

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Abstract

Climate factors, pesticides, and landscape in coffee agroecosystems directly affect the populations of the coffee leaf miner and its parasitoids. This study aimed to investigate the effects of climate factors, insecticide use, and landscape on natural parasitism, parasitoid diversity, and infestation of *L. coffeella* in coffee plantations in the Planalto region, Bahia, Brazil. Mined leaves were collected monthly in six coffee plantations with varying edge density, vegetation cover, landscape diversity in scales of 500 to 3000 m of radius, insecticide use, and climate factors. *Closterocerus coffeellae*, and *Proacrias coffeae* (Eulophidae) predominated in the pest's natural parasitism. Our record is the first for the occurrence of *Stiropius reticulatus*, *Neochrysocharis* sp. 1, *Neochrysocharis* sp. 2, and *Zagrammosoma* sp. in Bahia. Higher temperature and larger forest cover increased the coffee leaf miner infestation. Higher rainfall values, insecticide use, and landscape diversity decreased the pest infestations. Natural parasitism and species diversity are favoured by increase in temperature, forest cover, and edge density, while increase in rainfall, insecticide use, and landscape diversity lead them to decrease.The natural parasitism and diversity of parasitoid species of the coffee leaf miner have been enhancing in the areas with greater forest cover and edge density associated with low use of insecticides. The areas composed of different lands with annual croplands surrounding the coffee plantations showed less natural parasitism and parasitoid species diversity. The ecosystem services provided by *C. coffeellae* and *P. coffeae* in coffee crops areas require conservation and these species are potential bioproducts for applied biological control programmes.

Introduction

Biological control using wasps and parasitoids is an important method to reduce economic losses caused by *L. coffeella* (David-Rueda *et al.*, 2016; Tomazella *et al.*, 2018; Medeiros *et al.*, 2019*a*, 2019*b*; Rezende *et al.*, 2021; Rosado *et al.*, 2021; Venzon, 2021). It has been increasingly used in recent years with insecticide application, causing problems such as the selection of resistant populations and biological imbalances (Fragoso *et al.*, 2002; Vega *et al.*, 2007; Costa *et al.*, 2016; Leite *et al.*, 2020*a*, 2021, 2022; Rocha *et al.*, 2022). At least 28 species of parasitoids from the families Eulophidae and Braconidae (Hymenoptera) (Parra and Reis, 2013; David-Rueda *et al.*, 2016) have been associated with the coffee leaf miner. The most important species include *Closterocerus coffeellae* Ihering, 1914; *Proacrias coffeae* Ihering, 1914; *Cirrospilus neotropicus* Diez & Fidalgo, 2003; and *Horismenus aeneicolis* Ashmead, 1904 (Eulophidae); *Stiropius reticulatus* Penteado-Dias, 1999, and *Orgilus niger* Penteado-Dias, 1999 (Braconidae) (Parra *et al.*, 1977; Penteado-Dias, 1999; Melo *et al.*, 2007; Lomelí-Flores *et al.*, 2009, Tango *et al.*, 2014; Marques *et al.*, 2022; Calderón-Arroyo *et al.*, 2023).

Parasitoids are responsible for about 15 and 30% of the coffee leaf miner biological control (Parra and Reis, 2013) and up to over 50% in organic crops (Ecole *et al.*, 2010). The coffee leaf miner control potential by parasitoids is underestimated due to the lack of knowledge on the interactions between natural enemies and the coffee leaf miner, in addition to the aspects that may affect trophic relationships (Reis *et al.*, 2000). Among these aspects, climate factors directly affect the populations of *L. coffeella*, which are favoured in hot and dry seasons at low altitudes (Tuelher *et al.*, 2003; Pereira *et al.*, 2007*a*, 2007*b*; Lomelí-Flores *et al.*, 2010;

Dantas *et al.*, 2021). Intensive use of non-selective insecticides increases selection pressure on pest populations that rapidly recolonise the habitat. Meanwhile, their natural enemies take longer to reestablish their populations since a large proportion of individuals is usually eliminated (Fragoso *et al.*, 2001; Perfecto *et al.*, 2010; Fernandes *et al.*, 2014; Harelimana *et al.*, 2022).

Furthermore, the characteristics of the agroecosystem landscape directly affect natural enemies (Iverson *et al.*, 2019; Stüber *et al.*, 2021). They include biodiversity reservoirs of beneficial species, which disperse to coffee plantations exploiting resources in time and space, regulating the growth of pest populations (Vandermeer *et al.*, 2010; Aristizábal and Metzger, 2019; Medeiros *et al.*, 2019*a*, 2019*b*; Hohlenwerger *et al.*, 2022). However, this information is restricted to the role of predatory wasps and does not measure the advantages of the coffee leaf miner parasitoids.

Thus, current hypotheses cover that coffee leaf miner infestations, natural parasitism, and parasitoid diversity increase with forest cover and the presence of natural landscape habitats that provided resources and space for natural parasitism to occur in coffee plantations. In addition, both coffee leaf miner and parasitoid populations would be influenced by climatic conditions. This study aimed to investigate the effects of climate factors, intensity of insecticide use, and multiscale landscape on natural parasitism, parasitoid diversity, and infestation of *L. coffeella* on coffee plantations in the Planalto region, Bahia, Brazil.

Materials and methods

Study area

This study was conducted at commercial coffee plantations in the Planalto region. The experimental period ranged from December 2020 to November 2021.

Six coffee plantations were selected for sampling, two belonging to the municipality of Barra do Choça (BCH1 and BCH2) (Y: 14°55′11.54″S; X: 40°35′53.81″W and Y: 14°50′26.59″S; X: 40°31′17.5″W), three located in Mucugê (MUC1 – Y: 13°5′48.68″S; X: 41°26′58.39″W, MUC2 – Y: 13°7′30.04″S; X: 41°29′34.43″W, and MUC3 – Y: 13°6′52.59″S; X: 41°27′32.66″W) in the Chapada Diamantina region, and one crop in Vitória da Conquista (VDC1) (Y: 15°0′2.28″S; X: 40°45′55.5″W) (fig. 1).

The coffee plantations in Barra do Choça and Vitória da Conquista were 34.5 km from each other, which were, in turn, 222 and 226 km from the coffee plantations in Mucugê.

The coffee plantations located in the municipalities of Barra do Choça and Vitória da Conquista are inserted in a transition area between the Atlantic Forest and Caatinga biomes (CONAB, 2022). Their vegetation belong to the Semideciduous Seasonal Forest type, popularly known as ‘Mata de cipó’ (SEI, 2015). According to Köppen’s classification, the climate is type Cwb, also classified as sub-humid to dry by Thornthwaite (SEI, 1998). The two coffee plantations in Barra do Choça and the one in Vitória da Conquista were planted with the Catuaí 144 cultivar, which is more than 30 years old.

The Caatinga biome predominates in the Chapada Diamantina, where the municipality of Mucugê is located, and the vegetation typology is shrubby Caatinga (SEI, 2015). The climate of Mucugê is classified as Am by Köppen and semi-arid by Thornthwaite (SEI, 2015). The coffee plantations were planted with the Topázio and Catuaí 144 cultivars around 18 years ago. The large territorial extent of the Planalto coffee region reflects different contexts of the coffee tree and coffee leaf miner management, climate, and landscape structure, especially insecticide use to manage the pest (Leite *et al.*, 2020*b*).

The coffee plantations in Barra do Choça and Vitória da Conquista are rainfed, while those in Mucugê are fully irrigated through a centre pivot (MUC1 and MUC3) and drip irrigation (MUC2).

The history of insecticide use is different according to each coffee farm (table S1 see Supplementary Material), for example, VDC1 (Vitória da Conquista) has not used insecticides to control the coffee leaf miner for about 15 years.

Natural parasitism assessment and parasitoid species identification

We installed four rectangular sampling units of 2.7 hectares each (fig. S1 of the supplementary material) in each coffee plantation selected, each comprising 30 sampling points. The collection points were equally spaced at 30 m, each corresponding to a set of the four closest coffee plants within a 5-m radius.

Two leaves per plagiotropic branch located in the upper third of the coffee tree were randomly collected monthly from each sampling point, numbering six coffee leaves per point, 240 leaves per sampling unit, and 960 leaves per coffee plantation. The two leaves were collected at the third or fourth plagiotropic branch from the apical end of the branch (Melo *et al.*, 2007; Rosado *et al.*, 2021).

We opened the mines and recorded the presence of live caterpillars of the coffee leaf miner and pupae, larvae, and exuvia of the parasitoids and parasitised coffee leaf miner caterpillars.

All parasitised caterpillars, parasitoid pupae and larvae were placed in 2 ml microcentrifuge tubes (Eppendorf®). These tubes were stored in a controlled environment (25 ± 3°C *T*; 65 ± 5% RH; and 12-h photophase) until the emergence of the adults. Then, the adults were fixed in 95°GL alcohol for preservation and forwarded for identification.

We have identified parasitoids of the families Braconidae and Eulophidae at the generic and specific levels (Ihering, 1914; Schauff *et al.*, 1997; Wharton *et al.*, 1997; Penteado-Dias, 1999). Part of the material was deposited in the Invertebrate Collection of the National Institute of Amazonian Research, Manaus, Amazonas, Brazil (INPA) (Y: 3°5′28.25″W; X: 59°59′21.08″S).

Parasitism percentages were determined by the equation: TPN (%) = [(No. of emerged parasitoids/Total number of parasitoids collected) × 100]. Infestations were identified by the equation: ML (%) = [(No. of intact mined leaves/total number of leaves with mines) × 100] (Melo *et al.*, 2019).

Climate data collection

Throughout the experimental period (December 2020 to November 2021), the following variables were recorded daily in the coffee plantations: mean, maximum, and minimum air temperature (°C), relative humidity (%), rainfall (mm), and wind speed (m s^{-1}).

The data were stored in databases of weather stations (Vantage Pro2 Davis Instruments, Hayward, California, USA, and TFA Nexus, Reicholzheim, Germany) located at the MUC1 property in Mucugê and BCH2 in Barra do Choça. We obtained the climate data for Vitória da Conquista from the database of the Integrated Environmental Data System (SINDA) of the National Institute for Space Research (INPE) (INPE, 2022a).

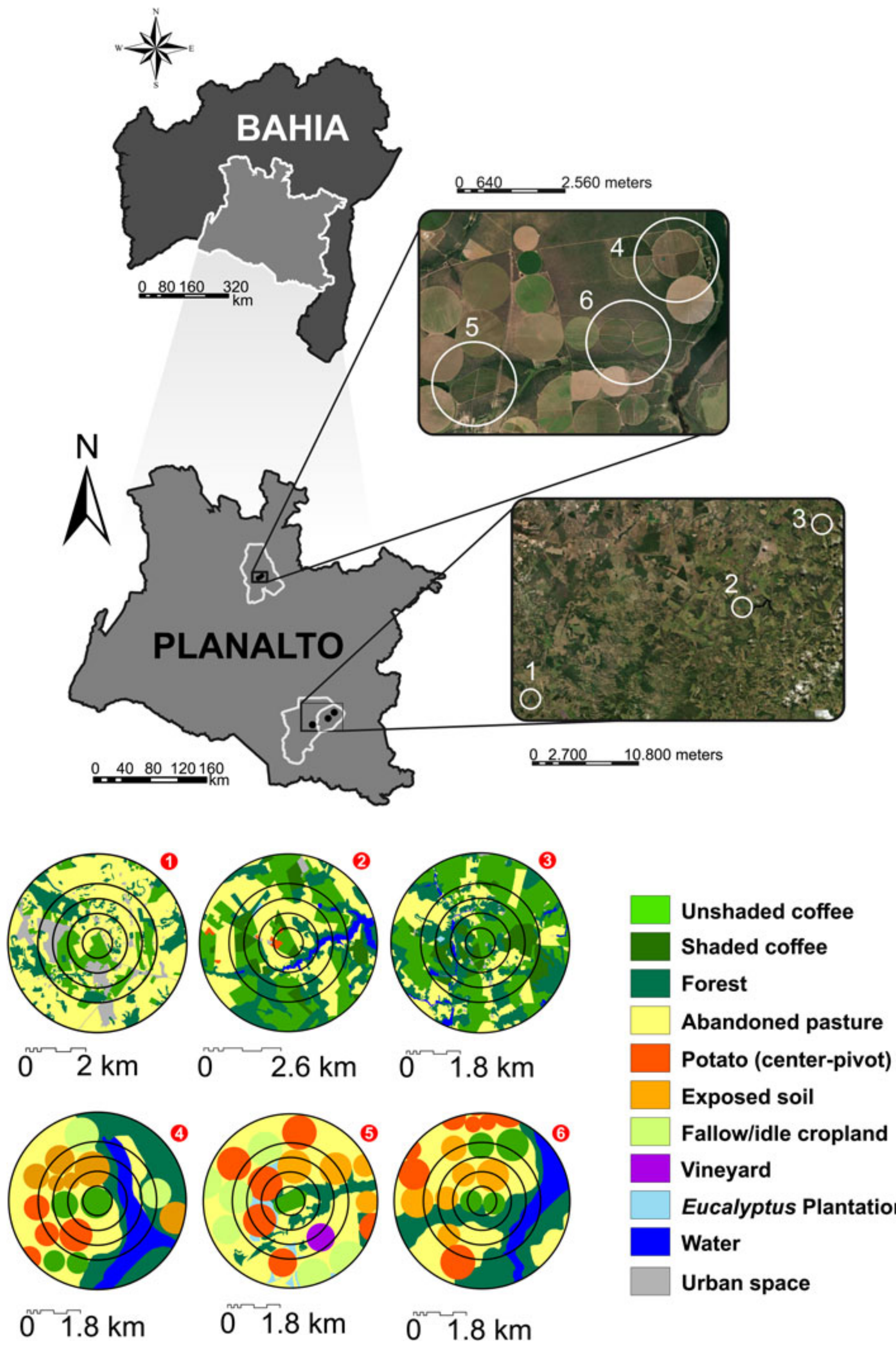

Figure 1. Sampling sites in coffee plantations in the Planalto region, Bahia, Brazil. 1 = VDC1 (Vitória da Conquista); 2 = BCH1 (Barra do Choça); 3 = BCH2 (Barra do Choça); 4 = MUC1 (Mucugê); 5 = MUC2 (Mucugê); 6 = MUC3 (Mucugê). Four repetitions (sampling units) comprising 30 leaf collection points were established at each site. The buffers represent the estimated local landscape within a 500, 1000, 1500, 2000, and 3000 m radius of each coffee plantation. Coordinate System: SIRGAS 2000.

Insecticide use intensity assessment

We calculated the insecticide application frequency index (Gravesen, 2003; Bakker *et al.*, 2021) and gathered information on the insecticides used on the crops during the study period through questionnaires to the landowners (table S1 in the supplementary material). The following equation determined the insecticide application frequency index:

$$\mathrm{IAFI} = \Sigma(\mathrm{DA}_i/\mathrm{MD}_i) \quad (1)$$

where AD is the applied dose of the commercial product, and MD is the maximum dose of the commercial product recommended by the manufacturer.

Landscape metrics

Each of the six coffee plantations was georeferenced for characterising the local landscape using a GPS receiver (Gramin eTrex 20, Garmin International, Inc., Kansas, USA). Based on the coordinates surveyed, we mapped the coffee plantations to determine land use and vegetation cover classes using high-resolution images from the CBERS 04A satellite (2-m panchromatic spatial resolution) (INPE, 2022*b*).

The images were processed in ArcGIS 10.8 (ESRI – Environmental System Research Institute, California, USA) at a 1:5000 scale. The area around each set of coffee plantations was assessed within five landscape radii: 500, 1000, 1500, 2000 and 3000 m (Aristizábal and Metzger, 2019; Medeiros *et al.*, 2019*a*) (fig. 1). Each land cover determined in the buffers through image processing was vectorised for forest cover estimation, edge density, and Shannon index of landscape diversity (McGarigal and Marks, 1995). The metrics were estimated using the Patch Analyst for ArcGIS tool (Rempel *et al*., 2012).

Statistical analyses

The data were analysed using generalised linear models (GLM) with a Poisson error distribution to verify variations in natural parasitism and infestations as a function of the wet and dry seasons in the region. The model selection criterion was based on the smallest values according to the Akaike's information criterion, corrected for small samples (AICc) (Burnham and Anderson, 2004; Medeiros *et al*., 2019*a*).

We calculated the faunal richness (fig. S2, supplementary material) and Shannon–Wiener diversity indexes (H′) (Krebs, 2014), which were analysed along with parasitism and infestation rates, climatic factors (maximum, mean, minimum temperature, relative humidity, rainfall, and wind speed), insecticide use intensity (application frequency index) by Canonical Correlation Analysis, with the PROC CANCOR procedure on the SAS Software (Statistical Analysis System) (SAS Institute, 2011).

We used generalised linear mixed models (GLMM) with a Gaussian distribution to analyse the data on the effects of agroecosystem landscape on biological control services (natural parasitism and parasitoid species diversity) and coffee leaf miner infestation using (Zuur *et al*., 2009; Aristizábal and Metzger, 2019; Hohlenwerger *et al*., 2022). All analyses were performed using the 'glmer' function of the 'lme4' (Bates *et al*., 2015) and 'emmeans' (Lenth, 2020) packages.

We used the hypothesis-based modelling to identify the predictive factors that affect the biological variables of insect populations at landscape scales. According to these approaches, the models were ranked and selected for testing the hypotheses for each biological variable (table S2, supplementary material). We built and tested models for each response variable, considering the explanatory variables as fixed effects in the model and a null model represented by the absence of effects ($y \sim 1$). We added the experimental unit and collection site variables to the models as random effects.

Model selection was based on the Akaike's information criterion, with correction for small samples (AICc) ($P < 0.05$). The ΔAICc parameters were considered for ranking the models (Burnham and Anderson, 2004). The ΔAICc values represent the difference between the best model and each model tested. Therefore, the models whose ΔAICc values were less than or equal to 2.0 were selected ($P < 0.05$) for being adequate to explain the effects of the predictor variables on the dependents. The estimation of these parameters was performed by the 'AICctab' function of the 'bbmle' package (Bolker, 2010). All statistical analyses were run on the R 4.0.4 Lost Library Book software (R Development Core Team, 2020).

Results

Coffee leaf miner natural parasitism and infestation rates

We collected 2662 parasitoids from the Eulophidae and Braconidae families (table 1). The eulophid species found included *C. coffeellae* Ihering, 1914; *P. coffeae* Ihering, 1914; *Neochrysocharis* sp. 1; *Neochrysocharis* sp. 2; *Cirrospilus* sp.; *Horismenus* sp.; and *Zagrammosoma* sp. The braconids collected included *S. reticulatus* Penteado-Dias, 1999, and *Stiropius* sp.1.

Species richness was sufficient regarding the number of samples taken (see fig. S2 of the supplementary material), varying according to the coffee plant studied, with the lowest values found for MUC1 and the highest for BCH2. *C. coffeellae* and *P. coffeae* were constant and dominant in all sampled coffee plantations, representing more than 84% of the total parasitoids collected. The coffee plantations with the highest richness and diversity of parasitoids were BCH2 and VDC1. Abundance was higher in BCH2 and MUC3.

Coffee leaf miner natural parasitism and infestations varied in the dry and wet seasons (figs 2 and 3), with higher rates and temperatures during the wettest months (fig. 3) (see fig. S3 in the supplementary material). In this period, coffee leaf miner infestations exceeded the threshold of control established for the region, which is 20% infestation in areas with higher temperatures and 30% in regions with mild temperatures (Souza and Reis, 2000).

Peak infestations occurred twice. The first peak occurred between December 2020 and March 2021. The second peak occurred between September and November 2021 for BCH1 and BCH2 (fig. 2b and c), with percentages ranging from 7.18 to 42.90%. For the VDC1 coffee plantation, the peak infestation occurred from March to June 2021, with an average of 24.15%. We found an increase in the number of mined leaves starting in October 2021 (fig. 2a).

Two infestation peaks occurred from December 2020 to January 2021 and from September to November 2021 on the MUC1, MUC2, and MUC3 properties (fig. 2d–f).

The species *C. coffeellae* and *P. coffeae* showed the highest parasitism percentages among the parasitoids collected in all the coffee plants studied (fig. 2). For VDC1, *C. coffeellae* and *P. coffeae* had maximum parasitism rates (4.75 to 24.30% and 3.21 to 20.73%, respectively). However, peaks occurred at the end of the wet season for *P. coffeae* and at the end of the dry season for *C. coffeellae*. Mean parasitism rates for *Neochrysocharis* sp.1, *Neochrysocharis* sp.2, *Cirrospilus* sp., *S. reticulatus*, and *Horismenus* sp. ranged from 0.40 to 5.88%.

Maximum parasitism rates of *C. coffeellae* and *P. coffeae* for BCH1 and BCH2 occurred during the wet season (March 2021) (fig. 2). In MUC3, *P. coffeae* and *C. coffeellae* parasitism were higher during the wet season. In MUC2, parasitism by *P. coffeae* occurred in the wet season (February 2021) and by *C. coffeellae* in the dry season (September 2021). For the other coffee plantations studied, the parasitism rates for the other parasitoids did not exceed 20%, with rates ranging from 0.31 to 10.12%.

Climatic factors and insecticides effects on the infestations of coffee leaf miners and natural parasitism

The canonical correlation analysis indicated that the first two canonical axes were significant (table 2), showing the effects of climatic factors and the use of insecticides on crops, both for infestations and for natural parasitism of the coffee leaf miner. The first canonical axis for coffee leaf miner infestations explained 97% of the variation, while for natural parasitism, about 99% of all variation was explained by the first canonical axis. The values of the absolute canonical coefficient reveal that the average temperature and precipitation were strongly correlated with infestations; however, positively for temperature and negatively for precipitation (canonical axis 1, table 2). As to the natural

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Table 1. Parasitoid communities of *Leucoptera coffeella* on coffee farms in the Planalto region, Bahia, Brazil

Property	Species (Family)	No. of individuals (Constancy[a]/Dominance[b])
VC1	*Closterocerus coffeellae* Ihering, 1914 (Eulophidae)	188 (W/D)
	Proacrias coffeae Ihering, 1914 (Eulophidae)	92 (W/D)
	Neochrysocharis sp. 1 (Eulophidae)	27 (W/nd)
	Neochrysocharis sp. 2 (Eulophidae)	32 (W/nd)
	Cirrospilus sp. (Eulophidae)	12 (Y/nd)
	Stiropius reticulatus Penteado-Dias, 1999 (Braconidae)	5 (Y/nd)
	Horismenus sp. (Eulophidae)	1 (Z/nd)
BCH1	*Closterocerus coffeellae* Ihering, 1914 (Eulophidae)	191 (W/D)
	Proacrias coffeae Ihering, 1914 (Eulophidae)	127 (W/D)
	Neochrysocharis sp. 1 (Eulophidae)	13 (W/nd)
	Neochrysocharis sp. 2 (Eulophidae)	27 (W/nd)
	Cirrospilus sp. (Eulophidae)	6 (W/nd)
	Horismenus sp. (Eulophidae)	1 (Z/nd)
BCH2	*Closterocerus coffeellae* Ihering, 1914 (Eulophidae)	260 (W/D)
	Proacrias coffeae Ihering, 1914 (Eulophidae)	120 (W/D)
	Neochrysocharis sp. 1 (Eulophidae)	12 (Y/nd)
	Neochrysocharis sp. 2 (Eulophidae)	27 (W/nd)
	Cirrospilus sp. (Eulophidae)	3 (Y/nd)
	Stiropius reticulatus Penteado-Dias, 1999 (Braconidae)	6 (Y/nd)
	Stiropius sp.1 (Braconidae)	4 (Y/nd)
	Horismenus sp. (Eulophidae)	1 (Z/nd)
	Zagrammosoma sp. (Eulophidae)	1 (Z/nd)
MUC1	*Closterocerus coffeellae* Ihering, 1914 (Eulophidae)	117 (W/D)
	Proacrias coffeae Ihering, 1914 (Eulophidae)	151 (W/D)
	Neochrysocharis sp. 2 (Eulophidae)	44 (Y/nd)
MUC2	*Closterocerus coffeellae* Ihering, 1914 (Eulophidae)	238 (W/D)
	Proacrias coffeae Ihering, 1914 (Eulophidae)	214 (W/D)
	Neochrysocharis sp. 2 (Eulophidae)	81 (W/nd)
	Cirrospilus sp. (Eulophidae)	3 (Y/nd)
	Horismenus sp. (Eulophidae)	3 (Y/nd)
MUC3	*Closterocerus coffeellae* Ihering, 1914 (Eulophidae)	275 (W/D)
	Proacrias coffeae Ihering, 1914 (Eulophidae)	246 (W/D)
	Neochrysocharis sp. 1 (Eulophidae)	6 (Y/nd)
	Neochrysocharis sp. 2 (Eulophidae)	79 (Y/nd)
	Cirrospilus sp. (Eulophidae)	9 (Y/nd)

VDC1, Vitória da Conquista; BCH1, Barra do Choça; BCH2, Barra do Choça; MUC1, Mucugê; MUC2, Mucugê; MUC3, Mucugê.
[a]Constancy and Dominance, according to Basha *et al.* (2021), representing the presence of species as: W – in more than 50% of the collections; Y – from 25 to 50% of the collections; and Z – in less than 25% of the collections.
[b]D: dominant species with a frequency greater than 1/*S*, where *S* is the total number of species and nd is the non-dominant species with a frequency lower than 1/*S*.

parasitism of coffee leaf miners, the variables precipitation and insecticide showed the strongest negative correlations in the two canonical axes (table 2). The other climatic variables showed moderate and weak correlation values (table 2) for infestations and natural parasitism.

Landscape effects on the coffee leaf miner infestations, natural parasitism, and species diversity

The coffee plantations studied varied regarding landscape contexts (see table S3 in the supplementary material). The significant

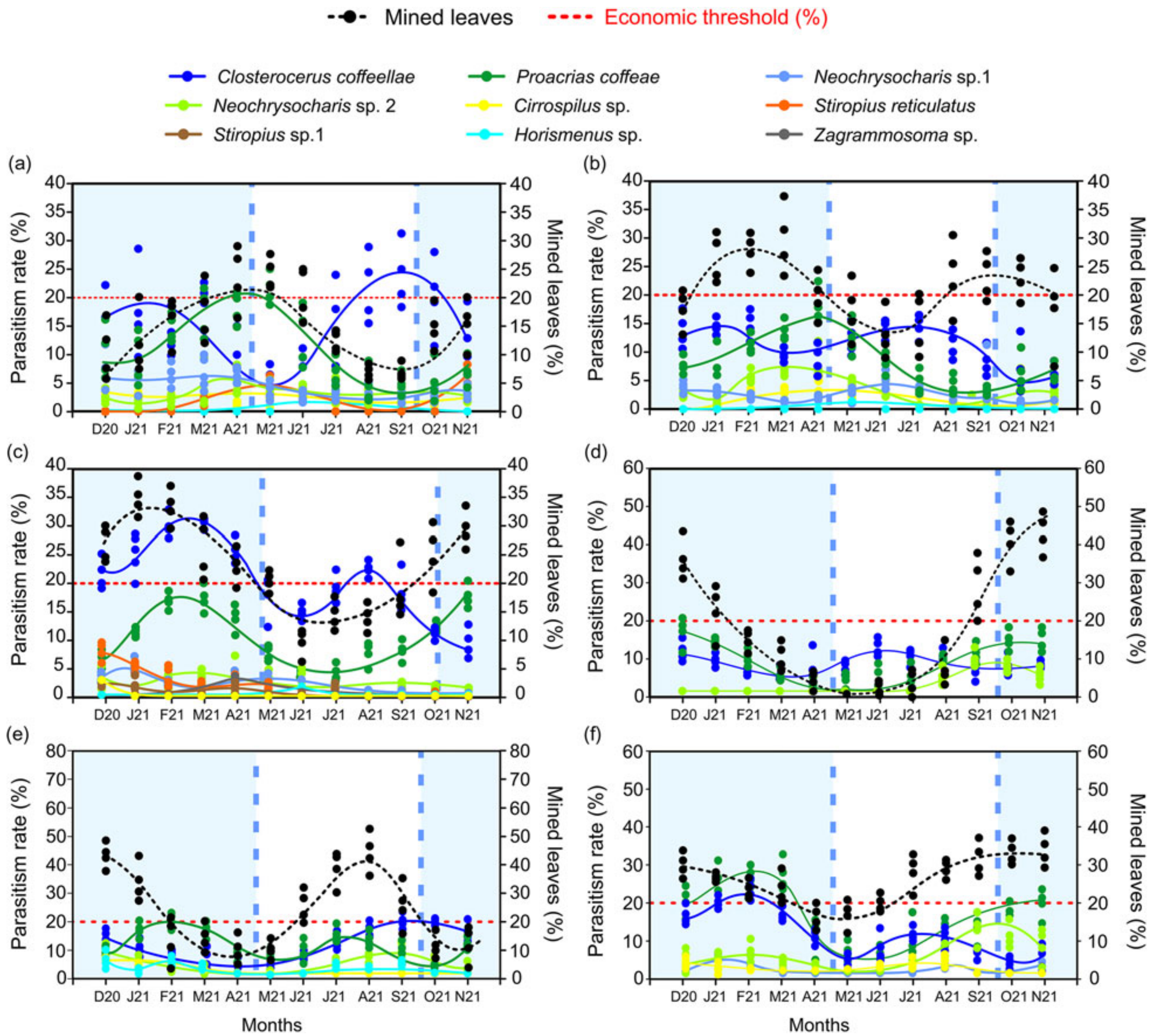

Figure 2. Temporal variation of natural parasitism and infestations of the coffee leaf miner in six coffee plantations in the Planalto region, Bahia, Brazil, from December 2020 to November 2021. The blue areas indicate the wet season in the region. The white areas represent the dry season. The red dashed lines indicate the threshold of control adopted for the leaf miner in the region. Properties: (a) VDC1 = Vitória da Conquista; (b) BCH1 = Barra do Choça; (c) BCH2 = Barra do Choça; (d) MUC1 = Mucugê; (e) MUC2 = Mucugê; (f) MUC3 = Mucugê.

models for each landscape scale had the lowest AICc value, more than 2 AICc and lower than the null model (table 3).

The coffee leaf miner infestations were significantly favoured by increases in forest cover (table 3; Fig. 3a, c, e and f) in all landscape scales, in addition to a greater diversity of the agroecosystem landscape at 2000 m (table 3; Fig. 3d). In a 500 m of radius, the coffee leaf miner infestations increased with the landscape diversity (table 3; Fig. 3b).

The relationship between natural parasitism and edge density (table 3; Fig. 4a, d, g, i and g) in all landscape scales was significant and positive. Greater landscape diversification in 500, 1500, and 3000 m scales (table 3; Fig. 4b, e and k) led to reductions in the pest's natural parasitism. Forest cover and increased natural parasitism were verified at all landscape scales (fig. 4c, f, h and l), except for 500 m since the predictor model was not significant.

Regarding species diversity, we found that increases in forest cover generated greater diversity (table 3; Fig. 5a, d, g, j and m) in all landscape scales. We observed the same effect for edge density (table 3, fig. 5b, e, h, k and n); however, we found a diversity decrease with landscape diversity increase (table 3; Fig. 5c, f, i and l). For 500 m of radius landscape, the predictor model was not significant.

Discussion

We have introduced relevant evidence on the effect of landscape, climate, and insecticide use on ecosystem services provided by coffee leaf miner parasitoids at landscape scales in coffee farms. Direct negative effects occurred on the ecosystem services provided by natural enemies, primarily due to rainfall, insecticide use intensity, and landscape diversity.

The parasitoid community associated with *L. coffeella* presents high diversity and wide geographic species distribution (Lomelí-Flores *et al.*, 2009; David-Rueda *et al.*, 2016). The

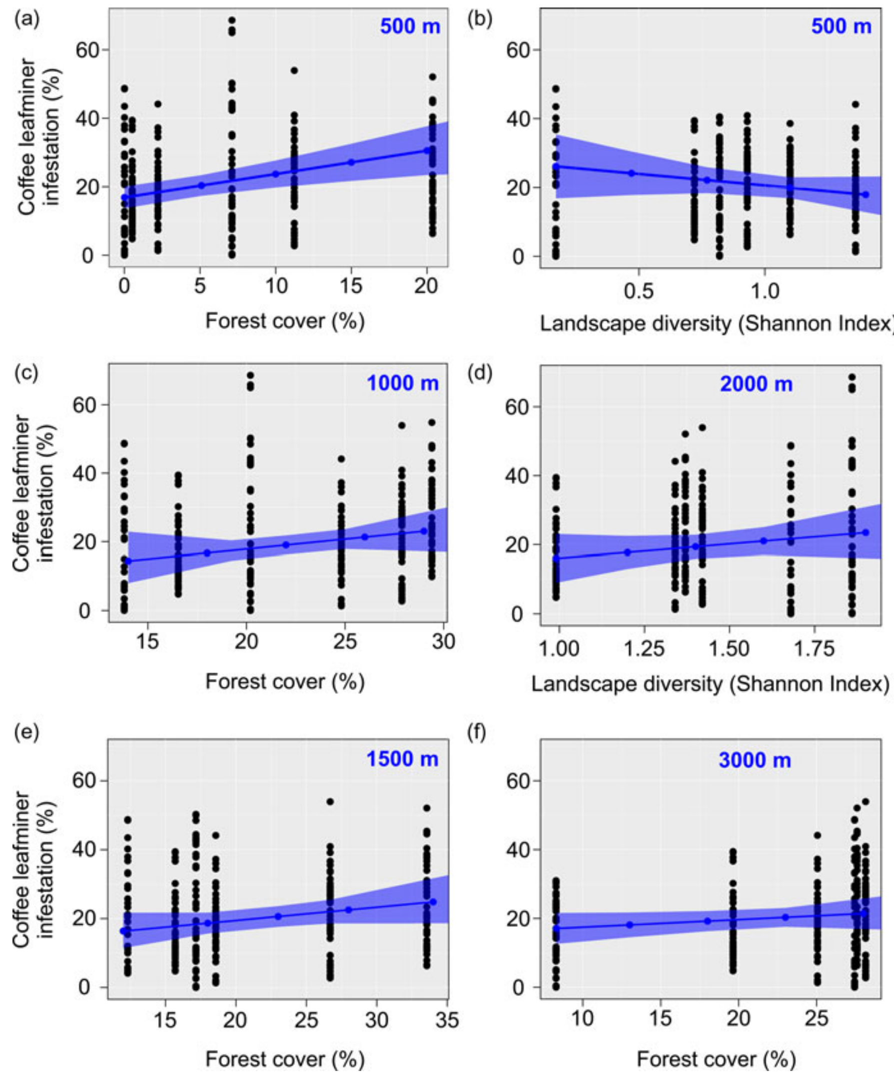

Figure 3. The relationships between coffee leaf miner infestations, forest cover, and local landscape diversity are explained by the best model predictors. Blue areas represent 95% confidence intervals. 500 (a, b), 1000 (c), 1500, 2000 (d), 1500 (e), and 3000 (f). The GLMM models were selected according to the ΔAICc ≤ 2.0 values (table 3).

Table 2. Canonical correlation between the climatic factors, insecticides, and the populations of coffee leaf miner and their natural parasitism in Planalto coffee region, Bahia, Brazil

	Canonical axes			
	Coffee leaf miner infestation		Natural parasitism	
Variable	1	2	1	2
Maximum temperature	0.175	0.223	0.441	0.417
Mean temperature	0.951	0.624	0.002	0.026
Minimum temperature	0.149	0.482	0.066	0.298
Rainfall	−0.967	−0.789	−0.843	−0.695
Relative humidity	−0.169	−0.339	0.204	0.192
Wind speed	−0.104	−0.573	−0.001	−0.014
Insecticide frequency index	−0.227	−0.052	−0.928	−0.8762
F	132.51	19.67	188.82	6.13
DF (num.; den)	10;28	10;28	7; 28	7; 28
P	<0.0001	<0.0001	< 0.01	< 0.01
Canonical squared correlation	0.97	0.52	0.99	0.63

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Table 3. The GLMM models selected to explain the effects of landscape on coffee leaf miner infestation and natural parasitism

Model	Parameter	Landscape-scale	AICc	ΔAICc	Adj R^2
Null	Y ~ 1	N/A	2309.01	2.43	
Infestation of coffee leaf miner					
Global	Y ~ Forest cover + Edge density + Landscape diversity	500	2310.01	2.7	0.12
Forest cover	Y ~ Forest cover (+)	500	2307.30	0.8	0.77
Edge density	Y ~ Edge density	500	2313.97	4.2	0.08
Landscape diversity	Y ~ Landscape diversity (–)	500	2308.04	1.1	0.83
Global	Y ~ Forest cover + Edge density + Landscape diversity	1000	2316.64	6.5	0.01
Forest cover	Y ~ Forest cover (+)	1000	2306.50	0.2	0.73
Edge density	Y ~ Edge density	1000	2315.92	3.5	0.07
Landscape diversity	Y ~ Landscape diversity	1000	2314.10	2.8	0.26
Global	Y ~ Forest cover + Edge density + Landscape diversity	1500	2312.00	3.5	0.09
Forest cover	Y ~ Forest cover (+)	1500	2311.40	1.2	0.56
Edge density	Y ~ Edge density	1500	2313.30	2.8	0.12
Landscape diversity	Y ~ Landscape diversity	1500	2314.60	5.9	0.02
Global	Y ~ Forest cover + Edge density + Landscape diversity	2000	2318.30	7.6	0.001
Forest cover	Y ~ Forest cover	2000	2310.00	3.5	0.10
Edge density	Y ~ Edge density	2000	2314.10	7.6	0.01
Landscape diversity	Y ~ Landscape diversity (–)	2000	2306.52	0.0	0.58
Global	Y ~ Forest cover + Edge density + Landscape diversity	3000	2318.06	10.9	0.001
Forest cover	Y ~ Forest cover (+)	3000	2307.10	0.1	0.68
Edge density	Y ~ Edge density (+)	3000	2309.71	1.6	0.54
Landscape diversity	Y ~ Landscape diversity (–)	3000	2309.66	1.5	0.52
Natural parasitism					
Global	Y ~ Forest cover + Edge density + Landscape diversity	500	2433.60	4.3	0.22
Forest cover	Y ~ Forest cover (+)	500	2333.10	0.5	0.88
Edge density	Y ~ Edge density (+)	500	2334.54	0.8	0.73
Landscape diversity	Y ~ Landscape diversity (–)	500	2338.20	0.1	0.91
Global	Y ~ Forest cover + Edge density + Landscape diversity	1000	2437.80	4.1	0.02
Forest cover	Y ~ Forest cover (+)	1000	2433.70	0.1	0.75
Edge density	Y ~ Edge density (+)	1000	2433.80	1.2	0.48
Landscape diversity	Y ~ Landscape diversity	1000	2433.90	2.8	0.15
Global	Y ~ Forest cover + Edge density + Landscape diversity	1500	2437.80	4.0	0.03
Forest cover	Y ~ Forest cover (+)	1500	2435.40	1.7	0.81
Edge density	Y ~ Edge density (+)	1500	2434.80	1.7	0.78
Landscape diversity	Y ~ Landscape diversity (–)	1500	2435.30	1.6	0.87
Global	Y ~ Forest cover + Edge density + Landscape diversity	2000	2436.65	3.8	0.01
Forest cover	Y ~ Forest cover (+)	2000	2433.80	0.6	0.42
Edge density	Y ~ Edge density (+)	2000	2433.62	0.8	0.64
Landscape diversity	Y ~ Landscape diversity (–)	2000	2433.60	0.8	0.64
Global	Y ~ Forest cover + Edge density + Landscape diversity	3000	2437.80	4.1	0.02
Forest cover	Y ~ Forest cover (+)	3000	2433.7	0.3	0.85
Edge density	Y ~ Edge density (+)	3000	2433.8	0.4	0.85
Landscape diversity	Y ~ Landscape diversity (–)	3000	2433.8	0.4	0.85

(*Continued*)

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Table 3. (*Continued.*)

Model	Parameter	Landscape-scale	AICc	ΔAICc	Adj R^2
Species diversity					
Global	Y ~ Forest cover + Edge density + Landscape diversity	500	2477.50	12.8	0.01
Forest cover	Y ~ Forest cover (+)	500	2309.12	1.0	0.67
Edge density	Y ~ Edge density (+)	500	2307.59	0.9	0.54
Landscape diversity	Y ~ Landscape diversity (–)	500	2307.13	0.8	0.65
Global	Y ~ Forest cover + Edge density + Landscape diversity	1000	2435.20	17.6	0.09
Forest cover	Y ~ Forest cover (+)	1000	2429.70	0.7	0.89
Edge density	Y ~ Edge density (+)	1000	2429.70	0.8	0.86
Landscape diversity	Y ~ Landscape diversity (–)	1000	2428.90	1.1	0.80
Global	Y ~ Forest cover + Edge density + Landscape diversity	1500	2485.80	17.0	0.01
Forest cover	Y ~ Forest cover (+)	1500	2406.78	0.7	0.90
Edge density	Y ~ Edge density (+)	1500	2406.65	0.7	0.89
Landscape diversity	Y ~ Landscape diversity (–)	1500	2409.13	0.9	0.81
Global	Y ~ Forest cover + Edge density + Landscape diversity	2000	2487.91	13.6	0.01
Forest cover	Y ~ Forest cover (+)	2000	2403.75	1.3	0.77
Edge density	Y ~ Edge density (+)	2000	2403.50	1.2	0.74
Landscape diversity	Y ~ Landscape diversity (–)	2000	2401.23	0.9	0.84
Global	Y ~ Forest cover + Edge density + Landscape diversity	3000	2433.9	18.8	0.001
Forest cover	Y ~ Forest cover (+)	3000	2401.92	1.02	0.81
Edge density	Y ~ Edge density (+)	3000	2401.03	1.14	0.75
Landscape diversity	Y ~ Landscape diversity (–)	3000	2401.03	1.14	0.75

Model selection criteria = ΔAICc ≤ 2.0. The signs in parentheses indicate the direction of the correlation found for the model, where (+) indicates a positive correlation and (–) indicates a negative correlation.
The difference in AICc values from the lowest value is indicated by ΔAICc.

Eulophidae family, the most abundant and richest parasitoid species, predominates throughout Neotropical America, mainly in countries such as Mexico, Colombia, Costa Rica, and Brazil (Lomelí-Flores *et al*., 2010; David-Rueda *et al*., 2016).

Among the 28 species of coffee leaf miner parasitoids that occur in Brazil, *C. coffeellae* and *P. coffeae* are the most abundant in coffee plantations in the states of São Paulo, Minas Gerais, Paraná, and Bahia. These species were the most abundant in the coffee plantations of the Planalto region, where coffee is grown through different management systems, including pesticide use. Thus, they are a promising species to be bred and released in coffee plantations, in addition to their wide geographical distribution (Melo *et al*., 2007).

Growing conditions, especially pesticide use, led to different richness values among the studied properties. Some eulophid species, such as *C. coffeellae* and *P. coffeae*, showed ecological plasticity and were present in sites with insecticide selection pressure (Melo *et al*., 2007). Thus, they could exhibit higher parasitism rates than other species, such as braconids, which were not collected on farms with higher insecticide use. The hypothesis of competition between the species can also be considered since eulophid have the habit of parasitising coffee leaf miner caterpillars in the early instars. Meanwhile, braconids prefer to parasitise caterpillars in advanced instars, and adult emergence occurs in the chrysalis stage (Melo, 2005).

This study recorded the *S. reticulatus* species for the first time in the state of Bahia. This species had only been recorded in the states of São Paulo (Penteado-Dias, 1999) and Minas Gerais (Ecole *et al*., 2010; Marques *et al*., 2022), showing coffee leaf miner parasitism percentages of around 8.8%. Furthermore, we also recorded the *Zagrammosoma* sp. species for the first time in Bahia, whose occurrence had been reported only in the state of São Paulo (Gravena, 1983). Its participation in controlling the coffee leaf miner in the region was very low, with only one specimen collected in Barra do Choça. However, the species of this genus do not seem to have significant efficiency in controlling the coffee leaf miner, as verified in Colombia, where *Zagrammosoma multilineatum* Ashmead, 1888 (Hymenoptera: Eulophidae) occurred in low abundance (David-Rueda *et al*., 2016).

There are controversies regarding parasitoids' role in the coffee leaf miner's biological control in Brazil since parasitism rates are generally considered low (Reis and Souza, 1996; Parra and Reis, 2013). It has been attributed to the constant phytosanitary treatments in coffee plantations and antagonistic interactions with predatory wasps that can prey on the parasitised caterpillars of the coffee leaf miner indiscriminately (Reis *et al*., 2000).

There have been discussions on the effects of climate conditions on infestations and parasitism of the coffee leaf miner, especially temperature and rainfall (Pereira *et al*., 2007*a*; Lomelí-Flores *et al*., 2009; Amaral *et al*., 2010; Jaramillo *et al*., 2019). Under higher temperature conditions, infestations are favoured and parasitism also increases since species benefit from the availability of hosts and the greater allocation of food resources from plant

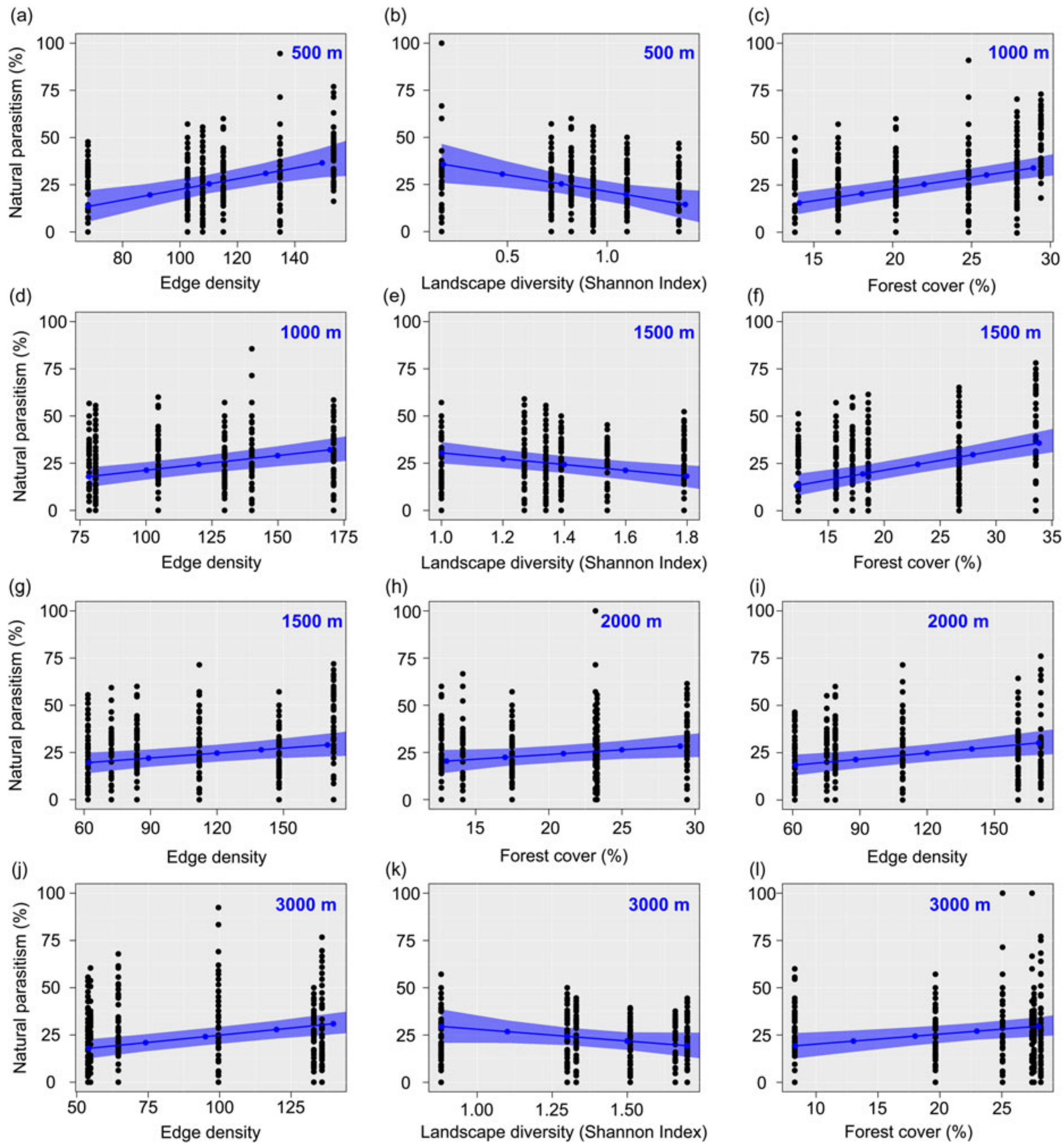

Figure 4. The relationships between the natural parasitism of the coffee leaf miner, edge density, local landscape diversity, and forest cover are explained by the best model predictors. Blue areas represent 95% confidence intervals. 500 (a, b), 1000 (c, d), 1500 (e, f, g), 2000 (h, i), and 3000 (j, k, l). The GLMM models were selected according to the ΔAICc ≤ 2.0 values (table 3).

species that produce nectar and pollen (Rosado *et al.*, 2021; Venzon, 2021).

Rainfall is one of the main factors in the coffee leaf miner's natural mortality. Droplets concentrating on leaves can drown caterpillars inside the mines (Nestel *et al.*, 1994; Fernandes *et al.*, 2009) and increase moisture on the plant tissue surface, leading to decreased oviposition. Mortality of pest adults can also occur when directly hit by raindrops (Pereira *et al.*, 2007*a*, 2007*b*). Since the parasitoids are small, they also reduce their movement during the wet season (Ecole *et al.*, 2010; Lomelí-Flores *et al.*, 2010). Thus, high humidity and rainfall conditions, either natural or artificial, through irrigation (Custódio *et al.*, 2009), affect population dynamics and the correlation between the coffee leaf miner and its natural enemies (Fernandes *et al.*, 2009).

Insecticide use intensity led to reduced pest infestations, natural parasitism, and parasitoid diversity of the coffee leaf miner. Morgan *et al.* (2017) demonstrated that insecticide use directly affects the dependency relationship of parasitoid densities. Therefore, selective insecticides that kill pests without causing negative effects on parasitoids should be searched to allow the conservation of these natural enemies in coffee plantations (Fernandes *et al.*, 2014; Carvalho *et al.*, 2019). Studies have shown that coffee leaf miner parasitoids are more sensitive to the effects of insecticides than predatory wasps (Gusmão *et al.*, 2000; Carvalho *et al.*, 2004; Bacci *et al.*, 2006, Picanço *et al.*,

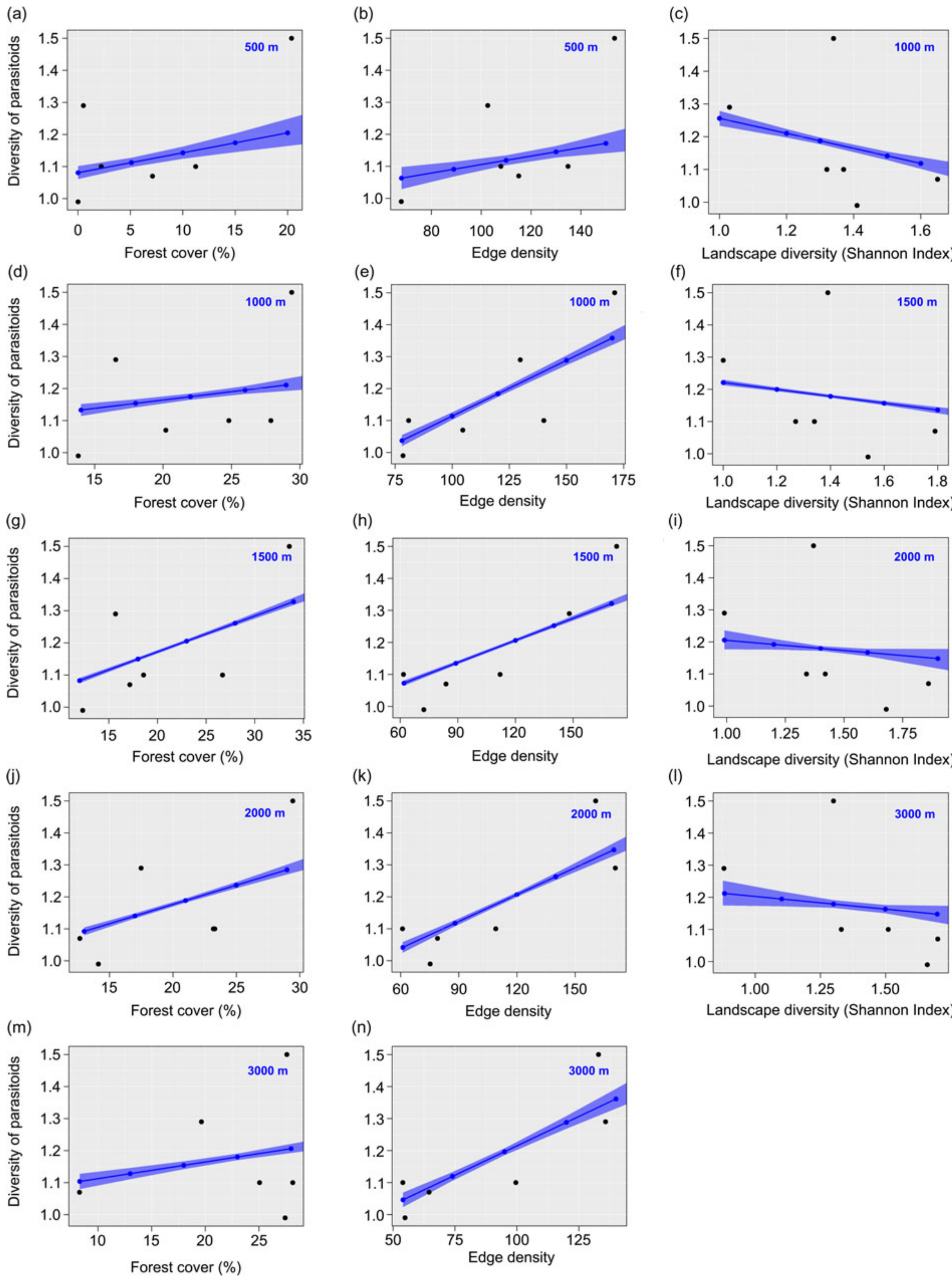

Figure 5. The relationships between parasitoid species diversity of the coffee leaf miner, forest cover, edge density, and local landscape diversity are explained by the best model predictors. Blue areas represent 95% confidence intervals. 500 (a, b), 1000 (c, d, e), 1500 (f, g, h), 2000 (i, j, k), and 3000 (l, m, n). The GLMM models were selected according to the ΔAICc ≤ 2.0 values (table 3).

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2012). Organophosphate insecticides, neonicotinoids, and some pyrethroids present toxicity to parasitoids in coffee plantations (Carvalho *et al*., 2004, 2005).

In the coffee plantations of Mucugê, the use of neonicotinoid, pyrethroid, and organophosphate insecticides (Leite *et al*., 2020*b*) may be associated with the lower diversity of parasitoids found. These results indicate the need for selectivity studies and clarifying the impacts of the compounds on the parasitoids' bioecology. Therefore, the dependence on pesticides in coffee crops should be reduced for MUC1, MUC2, and MUC3. A more sustainable practice would the intercropping with no-cultivated pollen-producing plants between the coffee lines, as they provide food and shelter for parasitoids and other enemies, which are important natural resources to control the coffee leaf miner (Rosado *et al*., 2021; Calderón-Arroyo *et al*., 2023). In addition, reforestation programmes on surrounding coffee crops can also contribute to the increase in natural parasitism in these areas.

In regenerative coffee farming, the search for diversifying coffee plantations has proven to be an important tool for pest management for conserving ecosystem services provided by parasitoids and predators (Rezende *et al*., 2014; Rosado *et al*., 2021; Venzon, 2021). Natural vegetation areas, forest remnants, and ecological corridors are true biodiversity deposits of natural enemies in agroecosystems (Librán-Embid *et al*., 2017; Villa *et al*., 2020; Vilchez-Mendoza *et al*., 2022).

According to Medeiros *et al*. (2019*a*), natural enemies exploit crop resources under certain temporal and spatial circumstances. Our results showed that the multi-scaling structure of the landscape edge is a spatial factor that favours the natural parasitism of the coffee leaf miner and the diversity and richness of parasitoids in coffee plantations. The resource abundance at the edges of vegetation near coffee plantations allows the parasitoids to explore more than one habitat. Thus, their stay at these sites is favoured and allows for increased parasitism.

Forest cover is positively associated with higher diversity and abundance of natural enemies in coffee agroecosystems (De la Mora *et al*., 2015; Allinne *et al*., 2016). This study showed that the forest cover favours coffee leaf miner infestations and natural parasitism. However, it is worth noting that the landscapes varied across the regions where coffee was grown. In the proprieties of Mucugê, for example, there is landscape diversification (table S3, supplementary material), where landcover predominates with annual crops such as potatoes, vineyards, and areas of exposed soil prepared for new plantings surrounding the coffee crops. Normally, the pressure exerted by pesticides in these areas is intense and can lead to, in addition to the management of the coffee crop itself, negative impacts such as sublethal effects on populations of natural enemies (Carvalho *et al*., 2005).

These conditions decrease the natural parasitism and the diversity of parasitoid species of the coffee leaf miner. Moreover, the coffee leaf miner is considered a monophagous pest, attacking exclusively the coffee tree, which indicates that the surrounding landscape impacts their populations at a much lower level than their natural enemies. Thus, in such conditions, their populations decrease mainly due to the use of insecticides, both inside and outside the coffee crops. It has been shown that the simplification of natural areas into agricultural areas is associated with a decrease in biological control in coffee plantations (Righi *et al*., 2013; Medeiros *et al*., 2019*b*).

Further studies should focus on the *C. coffeellae* and *P. coffeae* species since their effective participation in the biological control of the coffee leaf miner indicates their great potential for exploitation in rearing and massive release programmes in coffee crops. The occurrence of *S. reticulatus* and *Zagrammosoma* sp. expands the species diversity of the parasitoid communities present in coffee plantations in Bahia. However, further studies should address species surveys in other locations and coffee-growing regions in Bahia, such as the Atlantic (South and Far South of the state), and types of coffee management, such as organic, intercropping, and agroforestry systems, among others. In the case of the BCH1 and BCH2 properties, management recommendations to producers would be the cultivation of no-intercropping pollen-producing plants, as well as the use of semiochemicals (Bacca *et al*., 2006), which could help in monitoring, especially in a season of coffee leaf miner outbreaks. In addition, the reduction of pesticide use is important to avoid the problems of resistant population selection.

Coffee farms may present different conditions for the aforementioned factors, thus affecting population dynamics. Therefore, these scenarios should be further explored based on the effects of the temperature, rainfall, insecticide use, and landscape characteristics in the coffee leaf miner and its parasitoid populations.

We have introduced new insights into the natural parasitism of the coffee leaf miner, in addition to demonstrating that natural parasitism occurs in all seasons. The *C. coffeellae* and *P. coffeae* species are highlighted for being abundant in all the studied areas. We report the unprecedented occurrence of *S. reticulatus*, *Neochrysocharis* sp. 1, *Neocrhysocharis* sp. 2, and *Zagrammosoma* sp. in Bahia. We emphasise the *C. coffeellae* and *P. coffeae* as potential species for the development of novel commercial bioproducts that are still not available for coffee crops, but are proven necessary to reduce dependence on pesticides in coffee leaf miner management.

The forest cover and edge density increase the natural parasitism of the coffee leaf miner. The diversity of crops around coffee plantations reduces natural parasitism, which also occurs in coffee areas with greater use of pesticides in coffee plantations. Thus, we recommend that coffee growers pay attention to the role of the forest cover close to the coffee plantations. It enhances the biological control provided by the parasitoids and maintains the diversity of species and their valuable ecosystem service. Furthermore, incorporating cultural techniques with pollen-producing non-cultivated plants may be a more sustainable option to be adopted in coffee crops.

Such an information should be used to develop coffee leaf miner management programmes with parasitoids in the region, adopting conservation practices of the natural landscape and habitat, and reducing the use of insecticides to contribute to the sustainability of coffee production.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485323000482.

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