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ORIGINAL ARTICLE

Spread of *Bambusa bambos* (L.) Voss influences litter-dwelling arthropod communities in native forests: a case study from Sri Lanka

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Abstract

- Both native and non-native bamboo populations can expand their distributions in a rather irregular manner, inflicting changes in native vegetation with potential consequences for litter-dwelling arthropod communities. To our knowledge, no studies have been undertaken to explore the impacts of bamboo spread on litter-dwelling arthropods.
- 2. This study examined the impacts of *Bambusa bambos*, a spreading native bamboo species, on abundance and order richness of litter-dwelling arthropods in tropical moist evergreen forests. Bamboo-rich and non-bamboo forests were compared in three study sites at Moragahakanda in the Central Province of Sri Lanka. Arthropods were sampled from leaf litter and individuals were categorised into their respective orders.
- 3. Arthropod abundance and order richness were higher in bamboo-rich forests than in non-bamboo forests across all sites, indicating more hospitable micro-habitat conditions following bamboo spread. Litter-dwelling arthropods belonging to orders Blattodea, Hymenoptera, Diptera, Lepidoptera and Orthoptera were either more prevalent or more frequently associated with bamboo-rich forests than nonbamboo forests, suggesting a potential shift in community structure.
- 4. The abundance and order richness of litter-dwelling arthropods in non-bamboo forests was explained by environmental variables, whilst no such associations were observed in bamboo-rich forests.
- 5. The overall findings indicate that the spread of bamboo may facilitate litter-dwelling arthropods and cause a compositional shift in taxonomic assemblages, perhaps as a result of changes in the micro-habitat conditions on the forest floor.

KEYWORDS

bamboo dominance, environmental variables, litter fall, tree mortality, tropical moist evergreen forests

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INTRODUCTION

Litter-dwelling arthropods contribute significantly to the arthropod diversity in tropical forests (Bardgett et al., 2005; Novotny et al., 2006; Stork & Grimbacher, 2006), and play a key role in ecosystem functions such as nutrient cycling and carbon sequestration (Costanza et al., 2017; deVries et al., 2013; Jeffery et al., 2010). They are well-known drivers of many functions in forest ecosystems and are influenced by natural/semi-natural disturbances (fire, invasion, etc.,) and forest management activities (logging, harvesting and restoration), emphasising their pivotal role as bio-indicators in monitoring forest health (Hartshorn, 2021; Oliver et al., 2000; Perry et al., 2021). Litter-dwelling arthropods are involved in the primary decomposition that facilitates the subsequent microbial breakdown of organic matter (Cardenas et al., 2017; Grandy et al., 2016). Therefore, any changes to communities of litter-dwelling arthropods could trigger a significant impact on ecosystem functions and their stability (Wolters, 2001).

Ground-dwelling insect communities are highly sensitive to environmental changes (Levings & Windsor, 1984), thus making them vital bio-indicators of ecosystem dynamics and disturbances (Moldenke et al., 2000). Any deviations to the above-ground vegetation could impose changes in the micro-environment of the forest floor (light intensity, temperature and soil moisture), for example through changes in the quantity and quality of litter fall and canopy openness. (Frey et al., 2016; Liu et al., 2019). These micro-environmental changes in turn influence the movement, distribution and reproductive success of litter-dwelling arthropods (Schirmel et al., 2011; Talley et al., 2012; Wolkovich et al., 2009). The litter-dwelling arthropod abundance and richness are best described using the upper soil layer and forest floor characteristics. Vegetation characteristics are also known to affect arthropod communities (Richards & Windsor, 2007; Hartshorn, 2021). As litter-dwelling arthropods show specific preferences for different substrates for their feeding and breeding, any changes to above-ground vegetation could lead to modifications in their species composition and assemblage structure (Bernays & Graham, 1988).

Until recently, invaders were defined as alien/exotic species that colonise and expand their distributions in habitats to which they are introduced. Since there is growing evidence that some native species have the potential to expand their populations in a way similar to that of exotic invaders, Simberloff (2012) termed them as 'native invaders' to avoid unnecessary confusion in terminology. In bamboos, some native and exotic species show great tendencies to expand their populations inflicting profound impacts on their resident forest communities (Tian et al., 2020) in terms of the forest structure (Kobayashi et al., 2015; Kudo et al., 2011; Lima et al., 2012), composition (Rother et al., 2016; Wijewickrama et al., 2020) and functions (Dutta & Reddy, 2016; Suzuki, 2015; Tokuoka et al., 2015; Yang et al., 2015). Bambusa bambos (L.) Voss. has drawn our attention as its population started expanding in a rather erratic manner, with the potential of altering the structure and composition of native forests in Sri Lanka (Wijewickrama et al., 2020). It is a thorny bamboo species native to south and south-east Asia, belonging to a genus that contains both

exotic and native invaders (Canavan et al., 2017). *B. bambos* prefers areas with a humid tropical climate with a low to moderate elevation (<1000 m) and a rainfall of 2000–2500 mm (Sarojam & Kumar, 2001). In Sri Lanka, it is distributed from the outer parts of the intermediate climatic zone (lies in-between the wet and dry zones) to the immediate margins of the dry zone. Due to its ability to expand rapidly under resource-poor conditions (Duriyaprapan & Jansen, 1995; Ohrnberger, 1999), *B. bambos* has been identified as a problematic plant despite its native status (Gunatilleke et al., 2008). However, due to many commercial uses, bamboos and their likely impacts garnered little attention from researchers and conservationists until recently.

In bamboo-dominated forests, mass flowering/death events and the clumped distribution of bamboo allow soil fauna to receive resources in a temporally and spatially heterogeneous manner (Griscom & Ashton, 2006; Olivier, 2008). While the highly dynamic nature of bamboo forests is relatively well understood, it is still not clear how bamboo-dominated forests re-structure their soil faunal communities (Jacobs et al., 2018). A study carried out in the southwestern Amazon discovered a modified community structure of ground-dwelling beetles in bamboo forests in comparison to terra firme forests (Jacobs et al., 2018), while another study noted thriving ant colonies due to increased nest sites in dead bamboo culms (jointed hollow stems of bamboos) (Davidson et al., 2006). Chica et al. (2013) observed a slightly higher diversity of nematodes following bamboo invasion of broadleaf forests. However, no studies have been undertaken to evaluate the impacts of the bamboo dominance on litterdwelling arthropods. The present study was designed to investigate if and how the spread of native bamboo restructures the litter-dwelling arthropod assemblages, thus causing potential impacts on functional aspects of native forests. We hypothesized that the bamboo dominance increases the abundance and order richness of litter-dwelling arthropods through bamboo-driven modifications to the forest floor leading to an increased complexity of microhabitats that are likely to favour their survival.

MATERIALS AND METHODS

Study area

The study was conducted in Tropical Moist Evergreen forests (TMEFs) in the Intermediate Zone of Sri Lanka. It is the dominant native forest type in the study area and consists of three vertical strata including a canopy (20–25 m), a sub-canopy/shrub layer (5–10 m), and ground vegetation. This region of Sri Lanka is dominated by secondary forests that were repeatedly disturbed due to, for example, shifting cultivation and logging. TMEFs are located along the northern borders of the Central Province of Sri Lanka that belong to the northern intermediate floristic region of the island (Ashton and Gunatilleke, 1987), and are dominated by tree species such as Mangifera zeylanica, Canarium zeylanicum, Filicium decipiens, Dimorcarpus longan, Nothopegia beddomei and Gironniera parvifolia (Gunatilleke et al., 2008). The mean annual temperature in

the area is in the range of 22.5–25.0°C with an annual rainfall of 2000–2500 mm (Kulawardhana et al., 2004). The study area receives a significant portion of its annual rainfall from the northeast monsoons from November to February. There is a long dry spell from May to September. According to Wijenayake (2016), *B. bambos* was introduced to forest reserves (dominated by Tropical Dry Mixed Evergreen forests) in the Dry Zone of Sri Lanka a few decades ago as a source of raw material for paper manufacturing, though they have never been utilised for this purpose. Over time, the bamboo populations have gradually expanded, leading to the formation of highly localised bamboo-rich forest patches (Gunatilleke et al., 2008; Wijewickrama et al., 2020).

The study was conducted in forest patches with a high prevalence of *B. bambos* (BM; with a bamboo cover of more than 50%) from three localities, Galboda (7.6177°N 80.7208°E), Moragolla (7.6516°N 80.7100°E) and Maragomuwa (7.7088° N 80.7133° E) that are situated approximately 4–13 km from each other. Bamboo-rich forests can be easily recognised from their physiognomy. For comparison, three forest patches without bamboo (NB) were also selected from respective localities. In these forests, a few bamboo bushes were still noted, but they formed a very minor component of the vegetation. The tree canopy height at BM was 10–15 m and 3404 \pm 1875 stems per ha (in terms of all non-bamboo individuals higher than 2 m in height) while it was 8–20 m in height and 3352 \pm 1255 stems/ha at NB forests (Wijewickrama et al., 2022). The study sites are described in detail in Wijewickrama et al. (2020).

Sampling of litter-dwelling arthropods

Litter sampling was carried out from September to November in 2018, just before the onset of north-east monsoons. Each sampling event was approximately 5 hr (from 9.00 a.m. to 2.00 p.m.) per forest type (BM/NB) in each study site (Galboda, GAL; Moragolla, MOR and Maragamuwa, MAR). Eighteen litter samples were collected from each forest type per study site using a $1 \text{ m} \times 1 \text{ m}$ wooden quadrat along three transects (located approximately parallel to each other and running from the forest edge towards the forest interior) at different distances of 0, 20, 40, 60, 80 and 100 m, totaling 108 samples [6 distances \times 3 transects \times 2 forest types (BM/NB) \times 3 study sites (GAL/MOR/MAR)]. The arthropods were extracted from litter samples using the Winkler extraction method (Bestelmeyer et al., 2000) and preserved in 70% ethyl alcohol until identified to their respective orders based on morphological characters using keys and identification guides. Abundance (number of individuals per sq. m) and order richness (number of orders per sq. m) were calculated based on the number of individuals and orders for each plot (Jacobs et al., 2015).

Environmental variables

A parallel study was conducted to evaluate the vegetation, surface litter accumulation and soil parameters in BM and NB forest

communities in the same three study sites (Wijewickrama et al., 2020; Wijewickrama et al., 2022). Information from this study was used to investigate potential relationships between litter-dwelling arthropods and relevant vegetation, litter and soil variables.

At the time of collecting litter samples to quantify litter-dwelling arthropods, soil samples (up to a depth of 10 cm) were also collected to analyse pH in soil: distilled water in 1:2.5 ratio with a pH meter (Model: HM-20S; Brand: TOA DKK) and gravimetric soil moisture content (Anderson & Ingram, 1993). Plant individuals >2 m in height were sampled along the same transects along which arthropods were sampled. Along each transect, 100 m² quadrats were laid at regular intervals of 0, 20, 40, 60, 80 and 100 m totaling 36 quadrats per study site. All plant individuals were counted and identified to species levels. Completely and/or partially dead individuals were also recorded. In each quadrat, the number of culms was recorded. Surface litter samples were collected using 1 m² guadrats and air-dried before taking weight measurements. The vegetation survey was carried out during the period from January to April, 2017 (Wijewickrama et al., 2020). Vegetation characteristics such as plant density and richness (per 100 sq. m), culm density (number of culms per 100 sq. m), mortality (partially/completely dead trees/shrubs per 100 sg. m) and surface litter biomass (dry biomass Kg per sq. m) were used to investigate associations with litter-dwelling arthropods.

Data analysis

The collected data were summarised using descriptive statistics. Correlations among environmental variables (litter mass, soil moisture, soil pH, culm density, plant abundance, plant richness and tree mortality), arthropod abundance and order richness with respect to the forest types (BM/NB) were assessed using the Spearman correlation coefficients. Fisher's Exact test was conducted to test for associations between the arthropod orders and forest type. A multivariate two-sample Hotelling's-T² test was used to compare the significant difference in the means of environmental variables between the two forest types followed by the univariate 95% Bonferroni confidence interval for each variable. To identify the percentage contribution of each order to the observed value of the Bray-Curtis dissimilarity, the similarity percentage (SIMPER) was calculated. General Linear Mixed-Effects models were fitted to test for effects of the environmental variables, study site, and forest type on arthropod abundance and order richness. The sites (GAL/MOR/ MAR) and distances (0, 20, 40, 60, 80 and 100 m) from the edge were considered as random effects while the forest type (BM/NB) was a fixed effect. The covariates of the model were the environmental variables considered in the study (soil pH, soil moisture, litter mass, plant abundance, plant richness, tree mortality and culm density). A Principal Component Analysis (PCA) was performed to identify the existence of significant groupings among the observations with respect to the study site and the forest type. The statistical analyses were carried out using the R statistical software (R Core Team, 2020) along with the relevant libraries such as ggplot2



FIGURE 1 (a) Mean abundance (mean number of individuals per sq. m) and (b) mean order richness (mean number of orders per sq. m) of litter-dwelling arthropods between bamboo (BM, shown in grey) and non-bamboo (NB, shown in white) forests across study sites, Galboda (GAL), Moragolla (MOR) and Maragomuwa (MAR), in Central Province of Sri Lanka (n = 54). The mean order richness of arthropods in BM forests is significantly higher than that of NB forest in GAL site, as indicated by*

(Wickham, 2016), Ime4 (Bates et al., 2015) and Hotelling (Curran & Hersh, 2021) at 0.05 significance level. To test that the arthropods were sampled to completion, accumulation curves (number of orders) were plotted against area and abundance using the software Past 4.0 (Hammer et al., 2001).

RESULTS

Abundance and richness of litter-dwelling arthropods

A total of 1982 individuals of litter-dwelling arthropods belonging to 18 orders were recorded in the study. Of 18 orders, 10 (\approx 56%) were recorded across all forest types (BM/NB) and study sites (GAL/MOR/ MAR). The order accumulation curves (drawn with the number of orders against the area and the abundance) reached a plateau more rapidly in NB forests than in BM indicating a relatively more homogeneous nature of the litter-dwelling arthropod community in non-bamboo forests (Figure S1). A multivariate analysis followed by Hotelling's- T² test revealed a significant difference between means of the Simpson 1-D index, Shannon H index and evenness between the two forest types (Hotelling's-T² = 10.736, df₁ = 3, df₂ = 105, p < 0.001). Univariate analysis of each variable indicated that the mean Shannon H index was higher in BM forests (1.74 ± 0.100) than that of NB (1.50 ± 0.471), while the evenness for BM (0.93 ± 0.222) was lower than that of NB (1.06 ± 0.208) forests.

The mean arthropod abundance and order richness were higher in the bamboo (BM) forests compared to non-bamboo (NB) (Figure 1). The mean order richness for BM was 1.78 orders higher than that of NB while the mean abundance for BM was 15.26 (individuals per trap) higher than that of NB. The results revealed that the fixed effect forest type was significant (F = 18.84, df = 1, p < 0.001) while the variance component of the random effects was not significantly different. Among the covariates of the model, the only significant covariate was surface litter biomass (F = 5.13, df = 1, p = 0.026). A similar model for arthropod abundance indicated that the fixed effect (forest type) was significant (F = 22.00, df = 1, p < 0.001) and the variance component of the random effects were not significantly different from zero. Among the covariates of the model, none of them were significant. The mean abundance or the order richness of litter-dwelling arthropods showed no consistent variation from the forest edge towards the forest interior (Figure S2).

The SIMPER analysis was performed to identify arthropod orders and their relative contribution (as a %) to the potential dissimilarity between BM and NB forests. Accordingly, three orders collectively contributed towards the total dissimilarity between BM and NB forest communities at GAL (57.0%) and MOR (54.1%), while four orders contributed to 54.8% dissimilarity at MAR (Table 1). Of all 18 orders, Blattodea (representing cockroaches and litter-dwelling termites) played the most prominent role in discriminating arthropod assemblages between BM and NB forest communities in all three study sites. In addition, Hymenoptera and Diptera also contributed to differences in litter-dwelling arthropod assemblages between BM and NB forests (Table 1). Further analysis was carried out using Fisher's Exact test to see whether there were any associations between the arthropod orders to either BM or NB forests. Diptera, Lepidoptera, Orthoptera Ecological Entomology

Site	Order	Contribution %	Cumulative %	Mean abundance BM	Mean abundance NB
Galboda	Blattodea	26.6	26.6	13.3	0.4
	Orthoptera	15.6	42.3	4.5	0.1
	Diptera	14.8	57.1	4.1	0.1
	Araneae	14.6	71.6	3.9	3.3
Moragolla	Araneae	23.5	23.5	7.8	1.8
	Hymenoptera	18.0	41.5	7.3	3.0
	Blattodea	12.6	54.1	5.2	1.1
	Diptera	10.5	64.5	4.5	2.2
	Hemiptera	7.8	72.3	2.1	1.5
	Neuroptera	5.0	77.3	0.2	1.4
	Acari	4.4	81.7	0.1	1.3
Maragomuwa	Blattodea	16.3	16.3	1.3	2.1
	Hymenoptera	15.9	32.2	2.9	1.7
	Coleoptera	13.3	45.5	2.9	1.9
	Diptera	9.3	54.8	1.3	0.2
	Metastigmata	8.7	63.5	1.4	0.9
	Orthoptera	6.9	70.5	1.0	0.4
	Araneae	6.7	77.1	0.6	0.8
	Hemiptera	4.5	81.7	0.5	0.3

Note: The orders in bold letters collectively contribute approximately 50% of the total dissimilarity between BM and NB forest communities.

and Psocoptera were more likely to be observed in BM forests than that of NB (with Odds Ratios of 9.52, 5.85, 7.58 and 9.80, respectively at Fisher's Exact $p \le 0.001$ for each).

Environmental variables in BM and NB forests

A multivariate two-sample test (Hotelling's-T² test) revealed a significant difference between means of environmental parameters in BM and NB forests (Hotelling's-T² = 27.931; df₁ = 7, df₂ = 101, p < 0.0001). According to 95% Bonferroni confidence intervals, means of all parameters except soil moisture significantly differed between BM and NB forest communities. Soil pH and abundance of dead tree/ shrub individuals were significantly higher in BM, while litter biomass, abundance and richness of the above-ground vegetation were higher in NB forests (Figure S3).

Arthropod assemblage versus environmental variables

According to the Spearman correlation analysis, environmental variables such as surface litter biomass, and abundance and richness of aboveground vegetation were significantly and positively correlated with both order richness and abundance of litter-dwelling arthropods in NB forests (Table 2), while no similar correlations were observed in BM forests with any of the environmental variables tested.

The PCA biplot showed a clear partitioning of BM and NB forest communities (Figure 2). In general, our results highlight the complex interplay of environmental variables (soil, litter and vegetation) governing the litter-dwelling arthropod abundance and richness across the three study sites. According to the PCA, the key environmental variables including culm density, tree mortality and soil pH were relatively more decisive environmental variables for the clear separation of litter-dwelling arthropod community of BM forests from NB.

DISCUSSION

The effects of bamboo spread on litter-dwelling arthropods

Our results show that the abundance and order richness of litterdwelling arthropods was higher in bamboo than in non-bamboo forests across all three study sites (Figure 1), indicating a potential facilitative role of the *B. bambos* spread on litter-dwelling arthropods. Previous studies observed a strong correlation between litterdwelling arthropod communities and specific features of the extant vegetation (Basset et al., 2012; Lynggaard et al., 2020; Zhang et al., 2016). Vegetation features such as tree density and canopy

TABLE 2 The Spearman's correlation coefficients of abundance and order richness of litter-dwelling arthropods and environmental parameters (soil pH, soil moisture, litter biomass, richness and abundance of the vegetation and tree mortality) in BM and NB forests, separately

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	Arthropod order ric	nness	Arthropod abundance	
	BM	NB	BM	NB
pН	-0.034	-0.172	0.068	-0.031
Moisture	-0.123	-0.174	-0.198	-0.217
Litter	0.167	0.376**	0.237	0.272*
Plant Abundance	0.115	0.311*	0.011	0.204
Plant richness	0.143	0.399**	0.146	0.289*
Tree mortality	0.059	0.174	-0.135	0.021

Note: The level of significance indicated by p-value *< 0.05; **< 0.01.



FIGURE 2 Biplot of the principal component analysis (PCA) on abundance and richness of litter-dwelling arthropods and environmental variables (soil, litter and vegetation) showing the projection of the data set in the PC1 × PC2 planes (31.56% and 17.97% of the total variance, respectively). The two principal components (PC1 and PC2) showed a clear partitioning of arthropod communities in bamboo (BM) and non-bamboo (NB) forest communities

gaps are known to modify forest floor characteristics such as soil moisture, shade and the amount of litter, and in turn influencing soildwelling faunal communities (Cerda et al., 2015; Higgins et al., 2017; Jacobs et al., 2018; Perry et al., 2018; Swengel & Swengel, 2007). The creation of canopy gaps seems to have a stronger impact on ground-dwelling arthropods than other disturbances to the understory vegetation (Perry et al., 2018). A vegetation survey carried out concurrently at the same study sites noted that the *B. bambos* spread has inflicted some structural and compositional modifications to these forest communities (Wijewickrama et al., 2020). The linear correlation analysis showed a positive association between the above-ground vegetation and litter-dwelling arthropod assemblages in non-bamboo forests, further endorsing the vital role of the extant vegetation on litter-dwelling soil fauna perhaps through shared feed-back (Donoso et al., 2013; Jacobs et al., 2018; O'Brien et al., 2017). The lack of similar associations in bamboo forests may be caused by the heterogeneous nature of the vegetation and its accompanying microclimatic conditions following the *B. bambos* spread, masking the potential impacts. The higher prevalence of dead woody material on the forest floor and the patchy nature of the bamboo spread have

transformed these native forests into highly heterogeneous habitats that may favour litter-dwelling arthropods. Previous studies noted that coarse woody debris (branches >10 cm in diameter) are known to increase the habitat complexity whilst providing food and a hospitable habitat for the litter-dwelling fauna (McElhinny et al., 2005; Tews et al., 2004).

Associations between environmental variables and litter-dwelling arthropods

The overriding effect of physical attributes of the habitat on shaping arthropod diversity and abundance has been highlighted previously (Southwood et al., 1979). Despite differences in environmental variables (such as pH. litter biomass and tree mortality) between BM and NB forests (Figure S2), no distinct associations were observed between litter-dwelling arthropods and environmental variables in BM forests (Table 2) suggesting the intricate nature of factors influencing arthropod assemblages. However, the PCA biplot shows a notable contribution of tree mortality and culm density that lead to a clear separation of litter-dwelling arthropod assemblages of BM and NB forests. The high prevalence of dead trees and shrubs in bamboo forests has created more frequent canopy openings, allowing more sunlight to reach the forest interior, thus creating a denser and richer ground vegetation compared to non-bamboo forests (Wijewickrama et al., 2022). Accordingly, the bamboo spread has the potential to modify the microclimate of the forest floor (Araujo, 2008; Griscom et al., 2013; Rother et al., 2016) by increasing the soil temperature and diminishing the soil moisture (Collins et al., 1985; Fahey & Puettmann, 2007; Gray et al., 2002; Ishizuka et al., 2002; Perry & Herms, 2016). These modifications may create more diverse and suitable niches for arthropods (Perry et al., 2021), thus increasing their abundance and richness.

Community structure of litter-dwelling arthropods

Our results show that litter-dwelling arthropod orders such as Blattodea, Orthoptera, Diptera, Araneae, Coleoptera, Lepidotera and Hymenoptera contributed notably to dissimilarities observed between arthropod assemblages of BM and NB forests. Some arthropod orders were either more abundant or exclusively linked to BM forests, indicating their preferences for micro-habitat conditions under the bamboo canopy over that of non-bamboo forests. Previous studies noted that the composition of litter-dwelling spiders (Araneae) can be shaped by the thickness of the surface litter than their nutritional and structural characteristics (Anderson, 1978; Bultman & Uetz, 1982). Although NB forests had a higher litter biomass than BM forests (Wijewickrama et al., 2022), the field observations confirmed that BM forests have a thicker surface litter layer than NB forests, further supporting the pivotal role of bamboo litter (leaf and culm) in shaping litter-dwelling arthropod assemblages. In neo-tropical ecosystems, dead bamboo culms provide important

nesting sites for ants (Arruda et al., 2015; Cobb et al., 2006; Davidson et al., 2006; Fagundes et al., 2011; Leite et al., 2013; Powell, 2008). Furthermore, falling bamboo leaves and other woody debris also seem to provide suitable nesting sites for arthropod colonies (Silveira et al., 2010). The recalcitrant nature of bamboo leaf litter (Liu et al., 2021) appears to provide a better substrate for breeding and nesting of soil fauna than broadleaved litter that is easily compostable (O'Brien et al., 2017).

The overall results suggest that the increased abundance and order richness of litter-dwelling arthropods in BM forests is possibly due to a combination of factors that make the forest floor more habitable for litter-dwelling arthropods following the bamboo spread. Perhaps due to the sensitive nature of fluctuating micro-environmental parameters (Levings & Windsor, 1984) and high habitat heterogeneity. our results revealed no distinct link between the abundance and order richness of litter-dwelling arthropods and the tested environmental variables. The findings also reiterate the intricate nature of factors (altered micro-climatic conditions in the forest floor and availability of litter and woody debris) responsible for the prevalence of litterdwelling arthropods and their composition. The use of arthropod orders instead of identifying them into genus/species levels is one of the main limitations of this study. Further studies to explore the impacts on litter-dwelling arthropods driven by various modifications to extant vegetation may help implicating their potential role as bioindicators of tropical forests.

CONCLUSION

The study concludes that the presence of *B. bambos* has increased the abundance, order richness and diversity of litter-dwelling arthropods possibly through bamboo-driven microclimatic modifications on the forest floor. High prevalence of plant debris in bamboo forests seems to provide a more hospitable habitat for litter-dwelling arthropods. The study also provides evidence to suggest compositional shifts of arthropod assemblages following the spread of *B. bambos*. Further studies are warranted in order to investigate species-level preferences of litter-dwelling arthropods and their seasonality following the population expansion of the native bamboo, *B. bambos*.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1 Accumulation curves of arthropod orders drawn against (i) abundance and (ii) area in bamboo-(solid line) and non-bamboo (dotted line) forest communities in study sites at Galboda (GAL), Moragolla (MOR) and Maragomuwa (MAR) in the Central Province of Sri Lanka. In GAL and MOR sites, the accumulation curves differ in shape, while at MAR curves display almost similar shapes.

Figure S2: Interval plot of arthropod abundance and order richness (95% CI for the mean) with distance from the edge of the forest (0 m) towards the forest interior (20, 40, 60 80 and 100 m).

Figure S3: Interval plot showing the 95% Bonferroni confidence interval for the mean difference between the BM and NB treatment for each environmental variable (litter, moisture, soil pH, plant abundance, plant richness and tree mortality), Arthropod abundance and Richness. The zero-reference line (dashed red colour) that falls outside the interval indicates a significant difference

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