

A. TITLE PAGE**Bird's nest ferns promote resource sharing by centipedes.**Josie W. Phillips¹, Arthur Y. C. Chung², Gregory D. Edgecombe³ and M. D. FarnonEllwood^{1, 4}

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B. ABSTRACT

Bird's nest ferns (*Asplenium* spp.) support large numbers of invertebrates, including centipedes. As top invertebrate predators, centipedes drive ecosystem function, for example by regulating decomposer populations, but we know little of their ecology in forest canopies. We provide the first detailed observations of the diversity and structure of the centipede communities of bird's nest ferns, revealing the importance of these epiphytes as nurseries for centipedes. We collected 305 centipedes equating to ~11,300 mg of centipede biomass from 44 bird's nest ferns (22 of which were from the high canopy, and 22 from the low canopy) in primary tropical rainforest in Sabah, Malaysian Borneo. Most abundant were the Scolopendromorpha ($n = 227$ individuals), followed by the Geophilomorpha ($n = 59$), Lithobiomorpha ($n = 14$), and Scutigleromorpha ($n = 5$). Although we observed very little overlap in species between the forest strata, scolopendromorph centipedes dominated throughout the canopy. Null model analysis revealed no significant competitive interactions;

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on the contrary, we observed centipedes sharing nest sites within the ferns on three of the ten occasions that we found nests. All nests belonged to centipedes of the family Scolopendridae, which are typically aggressive, and usually show negative spatial association. This study reveals a diverse community of canopy centipedes, providing further evidence of the importance of bird's nest ferns to a wide range of animals, many of which use the ferns at critical life stages. Future conservation strategies should regard these ubiquitous epiphytes as umbrella species and protect them accordingly in landscape management decisions.

C. KEYWORDS

Key words: Borneo; Chilopoda; resource sharing; predation; competition; ecosystem function, *Asplenium* epiphytes; forest canopies

D. TEXT

CENTIPEDES (MYRIAPODA: CHILOPODA) PREDATE A WIDE RANGE OF FUNCTIONALLY IMPORTANT ANIMALS, from springtails and earthworms (Gao *et al.* 2017) to many kinds of larval and adult insects, including cockroaches (Molinari *et al.* 2005) and beetles (Juen & Traugott 2007). In the case of large Scolopendridae, prey includes vertebrates such as bats (Srbek-Araujo *et al.* 2012) and geckos (Pike *et al.* 2010) (see Lewis 1981 for a comprehensive review of observations in the field and in captivity). Predators exert direct control on functionally important animals such as detritivores and fungivores (Lawrence & Wise 2000, Zhao *et al.* 2013), and as top invertebrate predators in many ecosystems (Klarner *et al.* 2017), centipedes affect the structure of soil faunal communities worldwide. Despite the fact that centipedes represent a functionally significant component of the ground soil fauna (Kalisz & Powell 2000, Nordberg *et al.* 2018), they have received far less attention than other soil organisms. Although ground soil food webs have been studied in detail (de Ruiter *et al.* 1995, Wardle 2002, Wurst *et al.* 2018), very little attention has been directed upwards to the trophic structure of suspended soils such as those associated with canopy epiphytes. While

the centipedes of ground soils are poorly understood, the ecology and behaviour of centipedes living in rainforest canopies is virtually unknown.

Trophic interactions between soil invertebrates are typically determined from animals collected from the ‘ground zone’ (0-6 inches above the ground) (Elton 1973), and this two-dimensional view of the world is represented by the way in which arthropod abundance, even within tropical rainforest canopies, is expressed per m² (Basset 2001). However, our entomological perspective is improving with an increasing number of studies focussing on the vertical distribution of arthropods within forest canopies (Basset *et al.* 1992, Ellwood *et al.* 2002, Basset *et al.* 2003, Ellwood *et al.* 2009, Basset *et al.* 2015). Recent studies have begun to consider how organisms and their associated functions ‘spillover’ from forests into degraded habitats (Foster *et al.* 2011, Blitzer *et al.* 2012, Lucey & Hill 2012, Edwards *et al.* 2014), but few studies consider whether a functional cascade occurs as the composition of entire ecological assemblages changes in different forest strata. This is surprising, not least because species adapted to withstand climatic extremes in the high canopy (Dial *et al.* 2006) may be more tolerant of habitat degradation and climate change (Foster *et al.* 2011). An improved understanding of the assembly rules governing canopy communities could offer unique insights into the effects of disturbance and climate change on invertebrate communities.

Several studies have recorded centipedes from within the canopies of temperate forests, including the trunks (Frund 1987) and crowns (Gruppe *et al.* 2008) of trees. One study recorded completely different species of centipede between the ground, tree trunks and canopy (Gruppe *et al.* 2008). However, the canopies of Southeast Asia’s lowland tropical rainforest frequently exceed heights of 50m (Ellwood & Foster 2001). One study, of the animal communities of epiphytic bird’s nest ferns (*Asplenium nidus*) in the high canopy of these forests, found large numbers of centipedes (a mean of 126 ± 60 per fern, in large

(~200kg) mature ferns) (Ellwood *et al.* 2002). Centipedes accounted for 12% of the total invertebrate biomass of the ferns, and 5% of the total biomass of the host tree crowns (Ellwood & Foster 2004). In terms of abundance, these results from Sabah, Malaysia, approximate to the numbers of centipedes found in Sumatra, where a density of *ca* 109 centipedes per m² were recorded in forest ground soils (Klarner *et al.* 2017). In terms of their species richness, abundance and biomass, centipedes are likely to be fundamental to the functioning of the ecosystem, but none of the above studies elucidated the community structure, or the role of centipedes in the canopy environment. We investigated the biology of rainforest centipedes using bird's nest ferns as natural microcosms to pinpoint the precise three-dimensional distribution of species. We asked the following questions: (1) What is the abundance of centipedes in bird's nest ferns? (2) How much biomass do these centipedes contribute to the rainforest canopy? (3) How similar is the species diversity of centipedes in the high and low canopy? (4) How are these species assembled into communities? (5) Why do centipedes use bird's nest ferns?

METHODS

STUDY SITE

We worked in primary tropical rainforest in the Danum Valley Conservation Area (DVCA) in Sabah, Malaysian Borneo (4° 58' N, 117° 48' E; *ca* 100 masl) in April 2018. DVCA covers approximately 43,000 ha and is classified as lowland evergreen dipterocarp forest (Marsh & Greer 1992). We inserted climbing lines into the highest branches (Ellwood & Foster 2001) and accessed the high canopy using Double Rope Technique (DRT) (Maher 2006). The low canopy (Moffett 1993, 2000) was accessed using a ladder or DRT. Annual average rainfall at the Danum Valley Field Centre is 2822 mm, with a mean annual temperature of 26.7°C and a

mean annual relative humidity of 94.5% at 0800 h and 72% at 1400 h (Walsh & Newbery 1999).

FERN SAMPLING AND CENTIPEDE IDENTIFICATION

We collected 44 ferns with leaf rosette diameters of 30–60 cm (as per Ellwood *et al.* (2002)) from the forest canopy. Of these ferns, 22 came from the high canopy (~40 m) and 22 came from the low canopy (~4 m). All ferns were of similar size (fresh weights ~4 kg) and hosted by *Parashorea tomentella* trees (Sym.) Meijer (Dipterocarpaceae). We plucked the ferns from their attachment points and placed them into heavy duty, transparent plastic bags. Clear bags gave advance warning of centipedes emerging from the ferns. The bags were sealed and lowered from the trees using a pulley system. At the field centre, ferns were removed from their bags, dissected and sorted by hand. All centipedes were placed into 75% ethanol solution. Hand sorting allowed all centipede nests to be recorded. A brood nest was confirmed by the presence of an adult centipede protecting a clutch of eggs or young juveniles. The remains of the fern soil core (Ellwood *et al.* 2002, Turner & Foster 2009) were placed in Winkler bags (Besuchet *et al.* 1987) for four days. Fern soils were checked upon removal from the Winkler bags to ensure that any remaining animals were collected. All specimens were transferred to clean ethanol solution and stored at -20°C before being exported to the UK in Whirlpac™ bags. Identifications were performed using the primary taxonomic literature and relevant keys (Lewis 2010a, b).

ESTIMATIONS OF BIOMASS

Individual body mass (dry mass) was determined using body size-weight regressions (Richardson *et al.* 2000). Body length was measured from the tip of head to the end of the last trunk segment, excluding the posterior legs. Measurements were taken to the nearest 0.1mm using callipers or a calibrated graticule under the microscope. Power law models were used to establish size – weight relationships of the form $y = a(x)^b$, with y the dry weight (mg), x the

body length and b the regression coefficient (Richardson *et al.* 2000). Total biomass was calculated as the dry weight of all individual centipedes expressed in milligrams.

MICROCLIMATE MEASUREMENTS

We deployed two Squirrel SQ2040 data loggers, one into the high canopy and one into the low canopy, with each taking simultaneous recordings of fern soil and ambient air temperatures 1 m away from the fern. At each height, an air temperature probe was suspended under a protective solar shield and a soil temperature sensor was inserted to a depth of approximately 5 cm into the soil of a bird's nest fern. Temperatures were recorded every 60 seconds between 1000 h and 1900 h in order to provide a snapshot of the extent to which bird's nest fern soils buffer microclimate relative to temperatures in the surrounding canopy.

STATISTICAL ANALYSIS

We used Mann Whitney U Tests to determine whether centipede abundance differed between high and low canopy ferns. We also tested whether individual and total biomass differed between high and low canopy ferns. Abundance and biomass data were \log_{10} transformed prior to analysis. The diversity and evenness of centipede species in each fern was quantified using Species richness (S), Shannon's Diversity Index (H), Simpson's Diversity Index (D) and Pielou's Evenness Index (J'). We used Mann Whitney U Tests to determine whether any of these measures of diversity and evenness differed between high and low canopy ferns. To quantify the extent to which centipede species assemblages differed between the forest strata we used non-metric multidimensional scaling (nMDS) ordinations, similarity percentage analysis (SIMPER), and hierarchical clustering analysis based on Bray-Curtis similarity (PRIMER-e 2017). This also allowed us to test for variability in between-group species composition (i.e. β -diversity) (Anderson *et al.* 2006, Barnes & Ellwood 2012). To determine whether community composition was structured by interspecific competition, we used

EcoSim (Gotelli & Entsminger 2004) to perform *C*-Score analysis (Stone & Roberts 1990). The *C*-Score is a measure of the amount of mutual exclusion between species in a matrix consisting of all of the co-occurrences of each species across each fern. For each analysis, EcoSim simulates 10,000 random matrices and then uses the *C*-Score to test for differences between the simulated and observed communities. When a community is structured by competition, the *C*-Score of the observed community should be greater than the *C*-Score of randomly simulated communities (Gotelli 2000). We used EcoSim's default randomization algorithm which maintains fixed sums for row (species) and column (fern) totals, so that each of the randomised matrices had the same number of samples as the original matrix (Connor & Simberloff 1979). This algorithm has a low chance of falsely rejecting the null hypothesis (Type I error), but provides good power for detecting non-random patterns (Gotelli 2000). Finally, to reveal the importance of bird's nest ferns as microclimate refugia in the forest canopy, we used a One-Way ANOVA to determine whether daytime temperatures differed between the fern soils and the ambient conditions of the surrounding canopy.

RESULTS

We collected 305 centipedes in total (Table 1). In the high canopy, all but one of the ferns contained centipedes, giving a total of 185 centipedes from 21 ferns. In the low canopy, 120 centipedes were recorded from 16 ferns. Six ferns in the low canopy did not contain any centipedes. The mean number of centipedes per fern was 8.4 ± 2.9 in the high canopy and 5.5 ± 1.6 in the low canopy. This gave an overall mean of 6.9 ± 1.6 centipedes per fern across ferns from both heights. Across all ferns, 84% (37/44) contained centipedes, as well as other invertebrates. Though seven ferns across the forest strata did not contain centipedes, they still contained insects and other arthropods. Although the number of centipedes per fern was higher in the high canopy, the difference was not significant ($U = 191.5$, $p = 0.232$).

We collected a total centipede biomass of 11,300 mg, which equated to 256.8 ± 51.3 mg per fern. Given that there are *ca* 50 bird's nest ferns per hectare in Danum Valley (Ellwood *et al.* 2002), we essentially collected one hectare of canopy's worth of centipede biomass ($256.8 \text{ mg} \times 50 \text{ ferns} = 12,840 \text{ mg}$ per hectare). The bulk of the total centipede biomass recorded was concentrated in the high canopy (70.4 % High = 7952 mg, 29.6% Low = 3346 mg; Fig. 1). While the number of centipedes per fern did not differ significantly, biomass contribution did differ significantly between the high and the low canopy. Centipedes in the high canopy were larger (mean length $17.5 \pm 1.3 \text{ mm}$) than those in the low canopy (mean length $11.4 \pm 0.6 \text{ mm}$), and therefore contributed significantly more biomass per individual (High = $49 \pm 10.8 \text{ mg}$, Low = $22.5 \pm 1.7 \text{ mg}$, $U = 170.5$, $p = 0.036$). In fact, the mean biomass per fern in the high canopy was more than double that of ferns in the low canopy (High = $362 \pm 88 \text{ mg}$, Low = $148 \pm 43.3 \text{ mg}$, $U = 131.0$, $p = 0.009$). The greatest contribution to total biomass came from centipedes of the family Scolopendridae, which made up 75% (5936 mg) of the total biomass in the high canopy, and 31% (1050 mg) of the total biomass in the low canopy (Fig. 1). In the high canopy, a further 18% (1444 mg) of the total biomass was contributed by the Mecistocephalidae. The greatest contribution to biomass in the low canopy (39%; 1317 mg) came from the Cryptopidae. Cryptopidae and Scolopendridae are both families of the order Scolopendromorpha. Scolopendromorpha dominated the ferns both in terms of abundance and biomass, of which the total contribution was 8326 mg (74% of the total biomass recorded).

Centipedes recorded in this study belonged to four Orders [Scolopendromorpha ($n = 227$), Geophilomorpha ($n = 59$), Lithobiomorpha ($n = 14$) and Scutigleromorpha ($n = 5$)] and 13 species across 8 families (Table 1). Centipedes ranged in body length from 2.6 mm to 119.9 mm ($15.1 \pm 0.8 \text{ mm}$) corresponding to a range of individual biomasses between 4.1 mg and 311 mg (mean individual biomass $36.7 \pm 2.2 \text{ mg}$). *Scolopendra subspinipes* (Leach,

1815) were the largest centipedes we recorded, reaching up to 119.9 mm in body length, while *Lamyctes* sp. (Meinert, 1868) were the smallest, with one adult specimen recorded from the high canopy being only 2.6 mm in length. Although centipedes in the high canopy were larger, centipede species diversity and evenness did not differ significantly between the high and the low canopy. We observed no significant differences in Species Richness (S) ($U = 213.5, p = 0.165$), Shannon's Diversity Index (H) ($U = 217.5, p = 0.13$), Simpson's Diversity Index (D) ($U = 220.5, p = 0.108$) or Pielou's Evenness Index (J') ($U = 204.5, p = 0.267$). Some species were rare and occurred in a few ferns only; the abundance of species in each of the ferns is given in Table S1. Although species diversity and community structure were consistent within and between the two heights, community composition was quite distinct between the forest strata. Despite a small degree of overlap, SIMPER analysis revealed an average dissimilarity of 86% between ferns in the high and low canopy. This dissimilarity was driven largely by variation in the abundance of the scolopendromorphs *Cryptops* spp. (which dominated the low canopy), *Otostigmus angusticeps*, *Scolopendra subspinipes*, and the geophilomorph *Mecistocephalus* spp. (which were abundant in the high canopy). These four species accounted for 29%, 18%, 8% and 19% of the total observed differences, respectively. nMDS ordinations based on Bray-Curtis similarities confirmed the near complete vertical stratification of centipede communities between the forest strata (Fig. 2).

Though the centipede communities were vertically stratified, C -score analysis did not reveal significant levels of mutual exclusion ($C_{\text{obs}} = 16.62, C_{\text{sim}} = 16.59, p = 0.44$). We separated the centipedes into high and low canopy communities. Again the C -scores were not significant in terms of species co-occurrence. Moreover, in the low canopy the observed C -score was lower than that of simulated random communities ($C_{\text{obs}} = 3.97, C_{\text{sim}} = 7.91, p = 0.38$), suggesting species aggregation rather than segregation (Ellwood *et al.* 2016). In the high canopy, the observed C -score was higher than that of the random simulations,

suggesting species segregation, although this result was not significant ($C_{\text{obs}} = 8.05$, $C_{\text{sim}} = 7.81$, $p = 0.085$).

We found 10 active centipede nests in seven ferns (Table 1). All nests consisted of an adult female curled protectively around a clutch of eggs or a cluster of young juveniles (Siriwut *et al.* 2014). Several ferns supported more than one nest, all of which were collected from the high canopy. Two centipede nests were recorded from ferns in the low canopy (Table 1). Regardless of the biological reasons for choosing where to nest, ambient physical conditions in the forest high canopy are harsher than in the low canopy (Foster *et al.* 2011). However, mean daytime temperatures inside bird's nest ferns were significantly lower than those of the surrounding canopy at both heights (One Way ANOVA $F = 15.39$, $df = 3$, $p < 0.001$; Fig. 3). In the high canopy, mean daytime temperatures in the fern soil ($26.3 \pm 0.2^\circ\text{C}$) were 3°C cooler than ambient air temperature ($29.3 \pm 0.4^\circ\text{C}$). Remarkably, the difference between ambient air and fern soil temperature in the high canopy was three times greater than the 1°C difference between ambient air temperatures in the high ($29.3 \pm 0.4^\circ\text{C}$) and low ($28.4 \pm 0.4^\circ\text{C}$) canopy. At 1500 h, differences between fern soil and ambient air temperatures in the high canopy were as high as 6°C (Fig. 3). Even in the low canopy, mean fern soil temperature ($26.8 \pm 0.2^\circ\text{C}$) was 1.6°C cooler than ambient air temperature ($28.4 \pm 0.5^\circ\text{C}$). Generally, as ambient air temperatures increased, fern soils became cooler, leaving a difference of just 0.5°C in mean temperature between the high and low canopy ferns. This difference was not significant (Tukey HSD $p = 0.756$).

DISCUSSION

Centipedes have been understudied in tropical ecosystems compared with other invertebrate groups, despite their functional significance as top predators. Our results are in line with previous studies that have reported high abundances (Ellwood *et al.* 2002) and biomasses

(Ellwood & Foster 2004) of centipedes in bird's nest ferns. Karasawa *et al.* (2008) reported two species of centipede, *Mecistocephalus takakuwai* and *Ityphilus cf. tenuicollis* (both Geophilomorpha) amongst the invertebrate communities of bird's nest ferns in a Japanese subtropical forest. By using these epiphytic ferns as discrete, highly focussed sampling units, we have been able to provide a detailed account of the abundance, diversity and community structure of centipedes in two different strata of a forest canopy. Moreover, in revealing the widespread complementary usage (i.e. coexistence and resource sharing) of the ferns by centipedes, we can add these ecologically important animals to the growing list of organisms that rely on the unique resources provided by bird's nest ferns. The ferns are renowned as intensely concentrated pockets of biodiversity, and concentrations of prey attract the attention of predators. Predation pressures could therefore be much higher in canopy soils than in ground soil communities. Future studies can compare the predator-prey ratios of bird's nest ferns in different habitats, as presumably such ratios will yield important insights into the functioning of a range of natural and modified ecosystems.

A study of centipedes from Sumatran rainforest floor recorded a mean biomass of 31.62 mg / m² (Klarner *et al.* 2017). Klarner *et al.* (2017) sampled centipedes from 1 m x 1 m quadrats and the top 5cm of soil, meaning that their values for abundance and biomass represented 0.05 m³ of habitat. In our study, each bird's nest fern had a soil core diameter of *ca* 15 cm, which would have equated to an approximate soil volume of 0.014 m³ per fern. Thus, from three and a half times less soil by volume (0.014 m³ versus 0.05m³), our mean centipede biomass per fern was an order of magnitude greater than that recorded by Klarner *et al.* (2017) from the forest floor (256.76 mg versus 31.62 mg). Our study has revealed that centipede biomass is more highly concentrated in the suspended soils of bird's nest ferns than in ground soils, although this is perhaps unsurprising given the limited availability of soil in the forest canopy.

Biomass is a traditional measure of the functional significance (Schneider & Brose 2013) of individual animals, but we also focussed on species diversity and community composition. In our study, the Scolopendromorpha were responsible for partitioning the high and low canopy, despite accounting for 74% of all the centipedes we recorded, and dominating at both heights. Though we did not detect competition to be the driving force structuring the species assemblages, we did observe a fairly distinct vertical stratification in species composition between the high and low canopy. In the low canopy, *Cryptops* spp. were abundant, and contributed a significant amount of the biomass, yet they were almost absent from the high canopy. *Cryptops* spp. were the smallest scolopendromorph centipedes to be collected in this study (Table 1), and we found that centipedes from the high canopy were significantly larger than those in the low canopy. Though the low canopy is likely to be a worthwhile foraging extension of the forest floor for smaller centipedes, the high canopy may be a frontier too far removed from the subterranean existence to which many centipedes are adapted. *Cryptops* and geophilomorph centipedes are blind (lacking ocelli), and rely on a highly developed sense of touch when hunting. In contrast, Scutigleromorpha have compound eyes, and *Otostigmus* and *Scolopendra* have ocelli, which means that these centipedes are equipped to hunt in both free spaces and in shallow soils (Lewis 1981). Centipedes with compound eyes or ocelli may encounter the ferns whilst foraging throughout the canopy, whereas blind centipedes may be more likely to reside permanently in bird's nest ferns and in other suspended soils such as those of staghorn ferns (*Platycerium* spp.). Body size could also limit canopy access if it is more energetically expensive for smaller centipedes to climb into the canopy, and perhaps desiccation risks are higher. Smaller species may also be at greater risk of predation in the high canopy. In contrast, *Otostigmus* and *Scolopendra* are large, aggressive and highly mobile centipedes (Guizze *et al.* 2016), and it is therefore logical that these centipedes would dominate the high canopy.

Centipedes are not social animals; they are typically aggressive predators, and thus we would have expected them to show negative spatial associations with each other, in the same way that some large predatory ants exclude one another from bird's nest ferns (Ellwood *et al.* 2016). Yet we observed the opposite of what we expected, in that centipedes were coexisting within the ferns. While unexpected, these low levels of competition echo the remarkably low levels of competition observed between other invertebrates in bird's nest ferns, such as arthropod decomposers (Ellwood *et al.* 2009) and ant communities (Fayle *et al.* 2015, Ellwood *et al.* 2016). These previous studies concluded that competition must be less important in the harsh physical conditions of the high canopy (Ellwood *et al.* 2009, Ellwood *et al.* 2016). However, we should continue to look at other biological explanations, such as resource partitioning, complementarity or predation pressure. Until now, no study has considered the potential impacts of the highest trophic levels on the structure of invertebrate communities in the bird's nest fern microcosm. Given that centipedes are generalist predators, their possibly indiscriminate feeding behaviour may account for the diminished strength of interspecific competition, and the apparent importance of 'neutral' processes in structuring the arthropod communities of bird's nest ferns (Ellwood *et al.* 2009, Fayle *et al.* 2015, Ellwood *et al.* 2016). Unfortunately, trophic guild structure within centipede communities has not yet been defined, although guild structure is not always sufficient to explain species interactions (Ellwood *et al.* 2016).

According to classical ecology, e.g. Diamond (1975), communities are shaped by interspecific competition for shared resources. While attention remains fixed on the differences between species, very few empirical studies address the 'stabilising' mechanisms of species diversity (Chesson 2000). Stabilising and equalising mechanisms essentially govern how rare species increase, and common species decrease in abundance (Chesson 2000). Unlike equalising mechanisms, which govern interspecific interactions such as

321 competition, stabilising mechanisms increase the relative importance of intraspecific
322 interactions such as resource partitioning and frequency dependent predation. Resource
323 partitioning and species complementarity would explain why our *C*-scores did not detect any
324 significant competitive interactions between centipedes in any of the ferns. Complementary
325 resource use is known to lead to fewer antagonistic interactions (Ashton *et al.* 2010) and this
326 would also explain the consistently high invertebrate diversity found in bird's nest ferns
327 (Ellwood *et al.* 2002, Ellwood & Foster 2004), as well as the remarkably high levels of
328 stochasticity within the invertebrate communities (Ellwood *et al.* 2009). While interspecific
329 competition may be the dominant force structuring communities in diffuse systems such as
330 the wider canopy, the invertebrate communities of concentrated systems such as bird's nest
331 ferns may be structured more forcefully by predation (Menge & Sutherland 1976).

332 Bird's nest ferns are an important foraging resource for centipedes, providing a
333 plethora of prey throughout the canopy (Ellwood *et al.* 2002, Ellwood & Foster 2004). The
334 ferns, with their self-contained ecological communities, therefore provide an opportunity to
335 study the interactions between predators and prey. For example, centipedes are opportunistic
336 (Edgecombe & Giribet 2007, Chiacchio *et al.* 2017), and although predator foraging is said to
337 be less efficient in complex environments (Menge & Sutherland 1976), centipedes alternate
338 foraging strategies according to prey abundance (Scharf *et al.* 2011). When abundance is
339 high, centipedes sit and wait (Guizze *et al.* 2016), whereas when abundance is low, they
340 actively forage or ambush prey (Formanowicz Jr & Bradley 1987). However, this would
341 bring centipedes into contact with predators such as skinks and geckos, which also use the
342 ferns (Donald *et al.* 2017). Previous research has shown negative spatial associations between
343 these groups (Hickerson *et al.* 2004), resulting from competition or intra-guild predation
344 (Hickerson *et al.* 2012, Hickerson *et al.* 2018). The bird's nest ferns microcosm is ideally

345 suited for empirical studies of how trophically equivalent groups partition themselves within
346 the canopy.

347 Centipedes are able climbers (Remington 1950, Molinari *et al.* 2005, Lindley *et al.*
348 2017); their strength is such that large Scolopendridae can seize bats while suspending
349 themselves from cave ceilings (Molinari *et al.* 2005). However, centipedes are highly
350 vulnerable to desiccation because they lack a discrete epicuticular layer (Cloudsley-
351 Thompson & Crawford 1970). Like caves, bird's nest ferns provide moist, dark
352 environments, a stark contrast to the characteristic extremes in temperature and humidity of
353 the wider canopy environment (Luskin & Potts 2011, Hardwick *et al.* 2015). The air
354 surrounding these ferns is consistently cooler and moister than ambient conditions in the
355 canopy (Turner & Foster 2006, Freiberg & Turton 2007, Scheffers *et al.* 2013, Scheffers *et*
356 *al.* 2014), and the ferns provide opportunities for environmentally sensitive animals to evade
357 extreme physical conditions in the canopy environment. Scheffers *et al.* (2014) drew this
358 conclusion when they investigated the use of bird's nest ferns by frogs in Philippine montane
359 rainforest. Centipedes will also benefit from the buffering capabilities of these ferns. We
360 performed a simple comparison of two ferns, one in the high canopy and one in the low
361 canopy, to show that bird's nest ferns buffer ambient temperature variations. Both ferns
362 became cooler as ambient temperatures increased (Fig. 3). Interestingly, the high canopy fern
363 remained consistently cooler than the low canopy fern. Given that bird's nest ferns in the
364 upper reaches of the canopy can be as cool as or even cooler than those in the low canopy,
365 their importance to environmentally sensitive animals may be even greater than previously
366 thought (Turner & Foster 2006, Scheffers *et al.* 2013, Scheffers *et al.* 2014). During the
367 hottest part of the day, fern soils were 5°C and 6°C cooler than ambient temperatures in the
368 low and high canopy respectively. To put this into perspective, these temperature differences
369 are comparable to those between rainforests and oil palm plantations (Foster *et al.* 2011,

Hardwick *et al.* 2015). Although we only recorded microclimatic conditions over a short timescale, and with a single fern at each height, our results are consistent with those of other studies highlighting the buffering capabilities of bird's nest ferns (Turner & Foster 2006, Scheffers *et al.* 2014). It is striking that these ferns could shield their inhabitants by almost 6°C during the hottest part of the day, underlining the importance of these ubiquitous epiphytes for canopy animals, particularly those that are susceptible to extreme physical conditions.

Centipedes provide parental care (Tallamy 2001, Bonato & Minelli 2002, Edgecombe & Giribet 2007, Trumbo 2012, Siriwt *et al.* 2014) and brooding females, which are particularly vulnerable during this life stage (Lewis 1981, Machado 2000), will benefit from the climate buffering abilities of the ferns. This coupled with the abundance of prey items would make the ferns ideal nurseries for juvenile centipedes. Although the reproductive and brooding behaviours of scolopendromorph centipedes are documented (Brunhuber 1970, Mitić *et al.* 2012, Cupul-Magaña *et al.* 2018), until now there have been no reports of centipedes nesting in the canopy. Moreover, there have been no recorded instances of Scolopendromorpha sharing nest sites, which we observed on three occasions. Our study provides compelling evidence for resource sharing by these apparently aggressive centipedes.

CONCLUSION

This is the first detailed account of centipedes in tropical forest canopies, and the first focussed study of an exclusive group of predators within the bird's nest fern microcosm. We have revealed the importance of the ferns as a resource and refuge for centipedes, enabling them to hunt, take shelter and nest throughout the canopy. Further, we have revealed that estimates of centipede abundance and biomass in rainforest ecosystems need significant revision upwards to account for their prevalence in above ground strata. Our results have

extended the functional importance of bird's nest ferns, from maintaining biodiversity to increasing predation pressure throughout the canopy. Moving forward, these microcosms will enable us to quantify the relative importance of frequency dependent predation, and the way in which environmental disturbance affects this stabilising mechanism in space and time, for example in natural habitats under different levels of disturbance, and in human modified landscapes such as agricultural plantations. We have shown that these ferns facilitate the spillover of functionally significant groups between forest strata; an intriguing question is whether the ferns can facilitate spillover between natural and disturbed habitats. The availability of these ferns could underpin the resilience of invertebrate communities to habitat disturbance and climate change. Bird's nest ferns should be classified as umbrella species because prioritising these epiphytes in conservation decisions will indirectly protect the many species that rely on them. Certainly, the potential for bird's nest ferns to facilitate ecological restoration warrants further research.

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F. DATA AVAILABILITY STATEMENT

Data available from the UWE Data Repository (<http://researchdata.uwe.ac.uk/475>). Voucher specimens are retained at UWE Bristol and can be made available upon request.

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- 619

H. TABLES

TABLE 1: List of centipede species or morphospecies, including full taxonomic name and authority, family affiliation, number collected from low and high canopy, mean individual biomass (\pm standard error), number, size, development stage of nests and location in the canopy.

Species or Morphospecies	Family	<i>n</i> collected		Mean individual biomass (mg) (\pm SE)	<i>n</i> , size and development stage of nests (location in canopy)
		low	high		
<i>Ballophilus</i> sp. Cook, 1896	Ballophilidae	1	0	81.8	n / a
<i>Cryptops</i> sp. or spp. Leach, 1815	Cryptopidae	68	2	19.1 (\pm 0.95)	n / a
<i>Lamycles</i> sp. Meinert, 1868	Henicopidae	4	7	13.6 (\pm 3.8)	n / a
Undetermined Lithobiidae	Lithobiidae	2	1	25.2 (\pm 3.2)	n / a
<i>Mecistocephalus</i> cf. <i>punctifrons</i> Newport, 1843	Mecistocephalidae	14	34	35.0 (\pm 1.6)	n / a
<i>Mecistocephalus</i> sp. Newport, 1843	Mecistocephalidae	2	6	52.0 (\pm 3.5)	n / a
<i>Otostigmus</i> <i>angusticeps</i> Pocock, 1898	Scolopendridae	1	121	37.2 (\pm 2.5)	six nests, 18 and 27 eggs, 18, 22, 23 and 24 hatchlings respectively (all high)

<i>Otostigmus</i> sp. 1	Scolopendridae	0	2	94.2 (\pm 8.0)	n / a
<i>Otostigmus</i> sp. 2	Scolopendridae	18	0	33.0 (\pm 5.3)	one nest, 17 hatchlings (low)
undetermined Schendylidae	Schendylidae	0	2	81.6 (\pm 23.8)	n / a
<i>Scolopendra</i> <i>subspinipes</i> Leach, 1815	Scolopendridae	10	5	111.2 (\pm 28.9)	three nests, 26 and 32 eggs (both high), nine hatchlings (low) respectively
undetermined Scutigera	Scutigera	0	2	41.7 (\pm 23.7)	n / a
undetermined Thereuoneminae	Scutigera	0	3	22.0 (\pm 9.8)	n / a
Total		120	185		

I. FIGURE LEGENDS

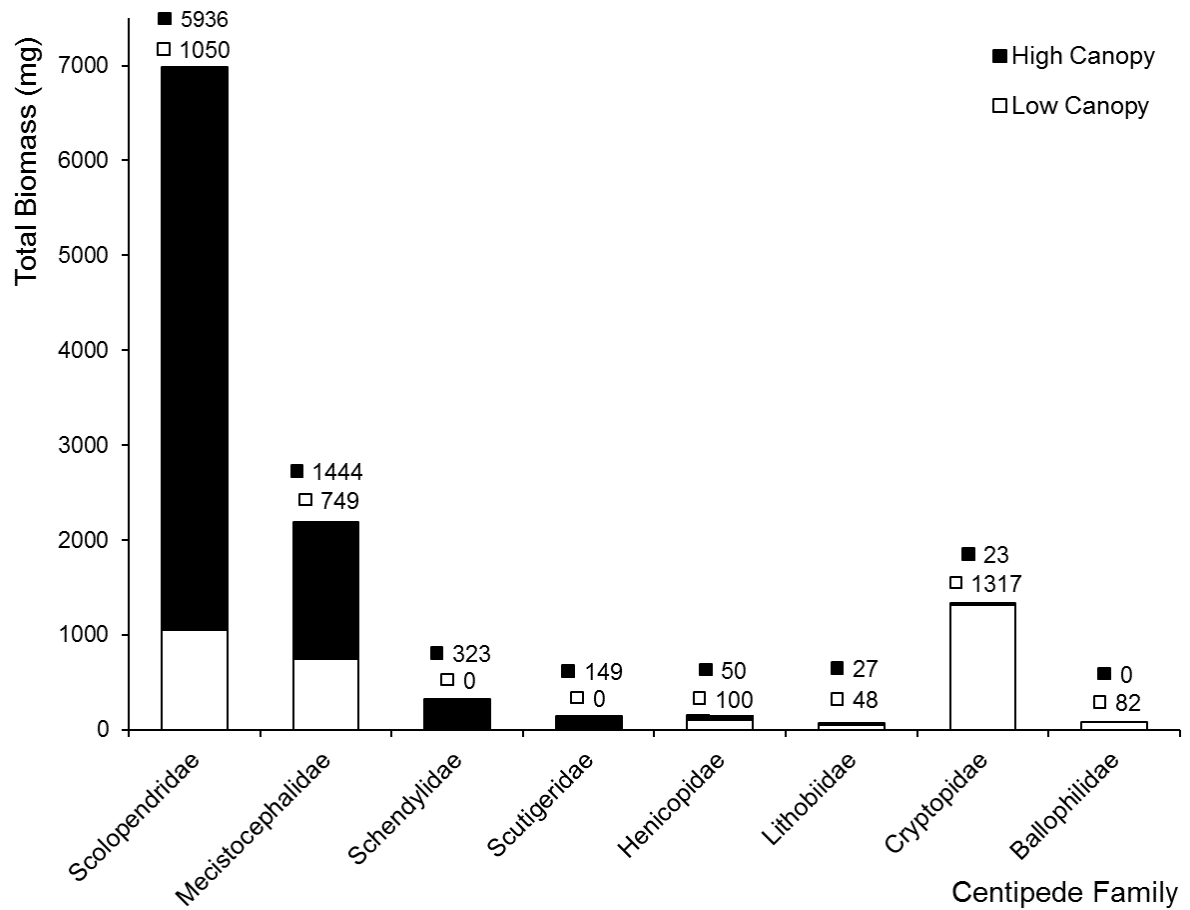
FIGURE 1. The proportional contribution of different centipede families to total biomass in bird's nest ferns in the high canopy (total centipede biomass 7952 mg) and the low canopy (total centipede biomass 3346 mg).

FIGURE 2. Non-metric multi-dimensional scaling (nMDS) of the species assembly of centipedes from bird's nest ferns in the high and low canopy of a tropical forest.

FIGURE 3. Daytime temperature variations between ambient conditions (1 m away from each fern) and inside the soil core of a bird's nest fern in both high and low canopy environments between 1000 h and 1900 h.

J. FIGURES

FIGURE 1



657 FIGURE 2

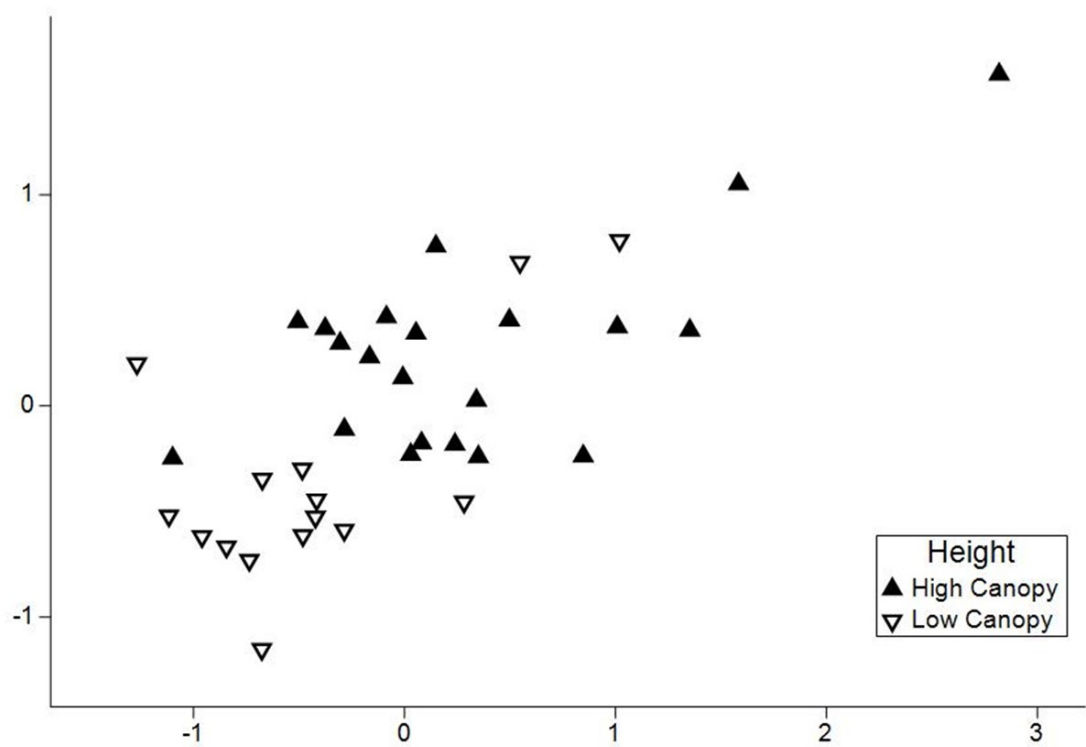


FIGURE 3

