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Effect of forest succession and microenvironmental variables on the abundance of two wandering spider species (Araneae: Ctenidae) in a montane tropical forest

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Abstract. This study assessed the effects of forest succession and microenvironmental variables on the abundance of ctenid spiders in a montane tropical forest in Costa Rica. We surveyed 20 plots (5 × 5 m) in both primary and secondary forest for a total of 40 samples measuring the following variables: leaf litter depth, canopy density, slope, number of trees above 3 m and average stem diameter of trees exceeding 3 m in height. A total of 150 adult and subadult specimens belonging to five species were observed. The most abundant species were *Spinoctenus escalerete* Hazzi et al., 2018 which has not previously been recorded in Central America and *Kiekie griswoldi* Polotow & Brescovit, 2018. The larger species, *K. griswoldi* was significantly more abundant in primary than in secondary forest. Conversely, *S. escalerete* was more abundant in the secondary forest. A generalized linear model indicated that the most important variable influencing ctenids abundance was leaf litter depth. Whereas the abundance of *K. griswoldi* was positively related with leaf litter depth, the abundance of *S. escalerete* was negatively related to litter depth. Thus, forest succession and leaf litter are important factors that influence the abundance of floor ctenid community and may allow the coexistence of co-occurring species.

Keywords: Ctenid community, leaf litter, predators, vegetation

The family Ctenidae includes medium to large (5–50 mm) wandering spiders that usually inhabit the forest floor and low vegetation, although a few species are arboreal. To date, 519 species in 48 genera have been recorded in this family, most of them distributed in the tropics (World Spider Catalog 2019). Their large size and predominant abundance in most tropical forests suggest that ctenids play an important role in tropical ecosystems as top generalist predators of invertebrates and small vertebrates (Folt & Lapinski 2017). It is common to find several species of this family co-occurring in the same habitats and microhabitats, suggesting that interspecific competition is strong (Gasnier et al. 2009; Torres-Sanchez & Gasnier 2010; Pétillon et al. 2018). Furthermore, intra-guild predation and cannibalism seem to be common in co-occurring ctenids, where larger individuals prey on smaller ones (Hazzi et al. 2018). Some of these species are restricted to forests and their population densities decrease significantly when forested habitats suffer fragmentation and disturbance (Jocqué et al. 2005; Rego et al. 2005, 2007; Mestre & Gasnier 2008). These attributes make ctenids promising ecological models to understand species interactions and habitat disturbance effects (Gasnier & Höfer 2001; Gasnier et al. 2002; Torres-Sanchez & Gasnier 2010; Lapinski & Tschapka 2013; Portela et al. 2013; Hazzi et al. 2018; Pétillon et al. 2018).

Tropical forests harbor more than 80% of the world's terrestrial biodiversity (Brown 2014), and in these systems, soil arthropods may constitute three-quarters of the total animal biomass (Wilson 1990). In the face of widespread anthropogenic changes, understanding how and which environmental factors affect forest floor arthropod abundance is crucial for maintaining tropical biodiversity (Silveira et al. 2010). A large number of studies have shown that leaf litter availability is one of the most important variables affecting floor-dwelling arthropods, including spiders, as litter offers resources such as shelter, food and stable microclimatic conditions (Uetz 1979; Bultman & Uetz 1982, 1984; Stevenson & Dindal 1982; Silveira et al. 2010; Cala-Riquelme & Colombo 2011; Lira et al. 2014; Dionisio-da-Silva et al. 2018). In addition, the density of wandering spiders can be influenced by abiotic factors such as soil type (Gasnier & Höfer 2001; Portela et al. 2013) and degree of forest perturbance (Rego et al. 2005, 2007); and by biotic factors such as the presence of army ants (Vieira & Höfer 1998), and likely by interspecific competition and intraguild predation (Rego et al. 2005; Torres-Sánchez & Gasnier 2010).

To date, all ecological studies of ctenids have been conducted in lowland tropical rain forests where the diversity of Ctenidae is usually greater than at higher elevations, and there has been no work on assessing ecological interactions and effects of forest perturbance in montane ecosystems. This study assesses the effects of forest succession and microenvironmental variables on the abundance of wandering spiders in a montane tropical forest. We address the following questions: (1) How do forest succession and microenvironmental variables affect the abundance of ctenid spiders? (2) Do ctenid spider species that occupy the same microhabitat (leaf litter of forest floor) have similar responses on abundance to forest succession and microenvironmental conditions?

METHODS

The study was conducted from June to July 2018 in the Las Cruces Biological Station, San Vito, Coto Brus, Puntarenas, Costa Rica (8°47.7′N, 82°57.32′W, 1200m); (see Organization for Tropical Studies, Las Cruces Research Station, online at https://tropicalstudies.org). The site is characterized by annual precipitation of 3500–4000 mm, a temperature range of 13°C to 26°C, and the presence of two seasons: the dry season from December through March, and rainy from April through November. This area is classified as a tropical premontane rainforest (Holdridge et al. 1971) and it has ca. 200 and 50 hectares of primary and secondary forest (10–25 years of recovering), respectively. Both forest types are adjacent to each other; see supplementary Fig. S1 (online at http://dx.doi.org/10.1636/JoA-S-19-070.s1)

The primary forest is characterized by irregular ground with trees 30–35 m tall with a variety of epiphyte communities on branches and trunks. Among the most representative plant families are Melastomataceae, especially the genus *Miconia*, including the endemic species *Miconia povedae*; Lauraceae genera such as *Licania*, *Nectandra*, and *Aiouea*; and Fabaceae genera including *Quercus* (Kriebel & Oviedo-Brenes 2013). In secondary forest, it is common to find clearings, trees and shrubs of smaller size, and introduced species such as the shrubs *Razisea spicata* (Acanthaceae), *Quararibea aurantiocalyx* (Malvaceae), and *Heliconia latispatha* (Heliconiaceae) and tree species like *Garcinia intermedia* (Clusiaceae), *Pseudolmedia spuria* (Moraceae) and *Tapirira mexicana* (Anacardiaceae), which are common in the restoration forests of the area (Cole et al. 2011; Ley-López et al. 2016).

To estimate ctenid abundance in the primary and secondary forest, we surveyed 20 plots (5 × 5 m) in each habitat for a total of 40 unit samples. Plots were placed arbitrarily, separated by a minimum of 30 m from each other, and more than 30 m from the edge of the forest. From the 40 plots, we selected twenty (10 in primary and 10 in secondary forest) and took measurements for the following variables: leaf litter depth, canopy density, slope, number of trees above 3 m and diameter stem average of those trees. To estimate leaf litter depth, canopy density and slope in each plot, we took measurements at each of the plot's corners and center, to calculate an average for the plot. Leaf litter depth, canopy density, and slope were measured with a ruler, spherical densiometer, and inclinometer, respectively. Some of these variables are well known to influence the abundance of floor dwelling arthropods and may also represent unique features of the two forests types (Rego et al. 2005, 2007). Ctenid spiders were counted and collected (preserved in 95% ethanol) in each plot at night with headlamps and located by the reflection of the light in their eyes' tapetum. Because diurnal rainfall can affect the nocturnal activity of wandering spiders (Queiroz & Gasnier 2017), we avoided sampling during nights when strong rains occurred the previous day. We spent 30 min/person in each plot searching for spiders from the floor level up to 2 m high, and all surveys were conducted between 20:00 and 24:00 hrs.

Ctenids were collected and identified to species using the taxonomic revisions of Hazzi et al. (2018) and Polotow & Brescovit (2018). This analysis only considered adult and subadult specimens (penultimate instar) because it was not possible to reliably assign younger specimens to species. All statistical analyses were conducted in R (R Core Team 2019). To evaluate the influence of the five microenvironmental variables (leaf litter depth, slope, canopy cover, number of trees above 3 m and stem average of those trees) and forest type (primary vs secondary) on the abundance in each of the ctenid species, we used Generalized Linear Models (GLMs) with a Poisson distribution or a Negative Binomial distribution when data presented overdispersion. Given the low sample size and the high number of predictor variables, we preferred to analyze the effects of forest type (primary vs secondary) and the five microenvironmental variables separately. Firstly, because approximately ten samples per variable are recommended for adequate inference (Zuur & Ieno 2016); and secondly, we think that these five variables characterize the succession process of the forests in a continuous way. The microenvironmental variables presented low collinearity (Pearson correlation < 0.45). Model selection with the continuous variables was carried out with a full model including all variables and interactions. Then, we used best subset approaches (Zhang 2016) with the package "bestglm" and Akaike information criteria (AIC) (Mcleod & Xu 2010), to select the best model. The amount of variance explained by the model and each of the predictor variables (when other variables are held constant) was estimated with an adjusted R-squared and partial R-squared, respectively. Adjusted R-squared are suitable for GLMs with nonlinear responses (Cameron & Windmeijer 1997) and were calculated using the function *rsq.kl* in the package "rsq" (Zhang 2016).

RESULTS

A total of 150 adult and subadult specimens were found across five species. The two most abundant species were *Spinoctenus escalerete* Hazzi et al., 2018 ($n = 96$), which has not previously been recorded in Central America, and *Kiekie griswoldi* Polotow & Brescovit, 2018 ($n = 49$). We recorded three additional species with much lower abundances, which were excluded from our analyses: *Kiekie montanensis* Polotow & Brescovit, 2018 ($n = 3$), *Phoneutria boliviensis* (F.O.Pickard-Cambridge, 1897) ($n = 1$) and *Phymatoctenus* sp. ($n = 1$). More than 95% of both *S. escalerete* and *K. griswoldi* were found on the leaf litter, indicating that these two species are specific ground-dwelling spiders and share the same microhabitat. The remaining individuals were found on low vegetation.

As a whole, the family Ctenidae did not show a difference in abundance between primary and secondary forest (Negative Binomial GLM, $Z = -1.40$, $P = 0.16$, Fig. 1). However, when the abundance of the two most common species were assessed separately, contrasting patterns were found. While *K. griswoldi* (the larger species) was more abundant in primary than secondary forest (Negative Bionomial GLM, $Z = -3.47$, $P < 0.001$, Fig. 1), *S. escalerete* was more abundant in secondary than in primary forest (GLM, $Z = 5.31$, $P < 0.001$, Fig. 1). Nevertheless, *S. escalerete* and *K. griswoldi* were seen in similar abundance in primary forest, indicating that both species co-occur at the same numbers in this habitat.

Among all assessed models with different combinations of predictor variables, leaf litter depth + slope, and leaf litter depth were selected as the best models for explaining the abundance of *K. griswoldi* and *S. escalerete*, respectively. Leaf litter depth was the most important variable regarding the abundance of both ctenid species, explaining 50% of the variation in the abundance for *K. griswoldi* (GLM, $z = 0.65$, $P < 0.01$) and 20% for *S. escalerete* (GLM, $z = -0.26$, $P = 0.03$). As with the abundance of these two species in primary and secondary forests, these two species had opposite responses to

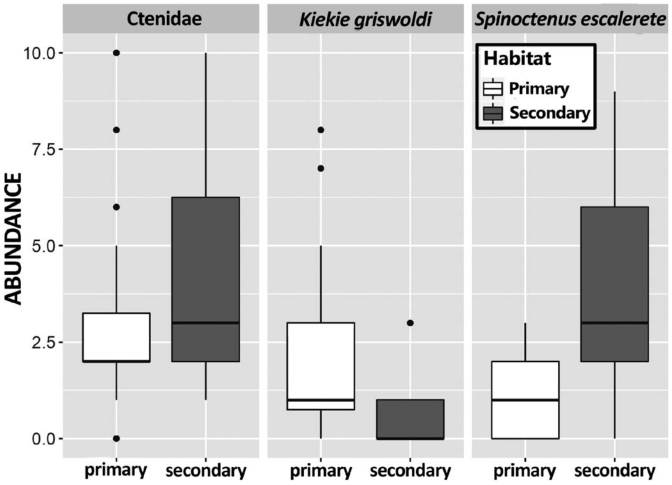

Figure 1.—Box plots of the abundance per 25 m^2 of ctenid spiders in primary and secondary forest.

leaf litter depth. While *K. griswoldi* abundance was affected positively by leaf litter depth (Fig. 2A), *S. escalerete* was affected negatively (Fig. 2B). In addition, slope explains 16% of the abundance of *K. griswoldi*, positively affecting the abundance of this species. However, this effect was of marginal significance (GLM, z = 0.04, $P = 0.08$).

DISCUSSION

Although studies of ctenid ecology in montane tropical habitats are lacking, the available tropical studies generally suggest that ctenids are negatively affected by disturbance. Jocqué et al. (2005) showed that the densities of Ctenidae in a lowland African rain forest significantly decrease in disturbed habitats. Similarly, Rego et al. (2005) found that small patches of isolated Amazonian forest presented lower abundances of ctenid spiders compared to larger areas of continuous forest. While we had anticipated a similar pattern of higher ctenid abundances in less perturbed habitats, we found that the abundance of the family did not differ between primary and secondary forests. However, when assessed individually, the two most abundant species found in these forests show strong responses to forest disturbance. Although we have found that forest perturbance has clear species-specific effects on ctenid abundance, assessing the family as a whole causes this effect to disappear.

To our knowledge, only few studies have assessed species-specific impacts of disturbance on ctenid abundance. Rego et al. (2007) assessed the effects of forest fragmentation in four sympatric Amazonian species of *Ctenus* and found that two species (*C. amphora* Mello-Leitão, 1930 and *C. villasboasi* Mello-Leitão, 1949) presented lower abundances in fragmented forest than in continuous forest. The remaining species (*C. manauara* Höfer, Brescovit & Gasnier, 1994 and *C. crulsi* Mello-Leitão, 1930) did not differ in abundance between these two kinds of forests. Moreover, Lapinski & Tschapka (2013) found forest perturbation may increase the abundance of some wandering spiders as *P. boliviensis* and *Cupiennius getazi* Simon, 1891. Therefore, with *S. escalerete,* our study also presents evidence that forest perturbation may result in an increase of the abundance of some ctenid species. However, it is important to highlight that the secondary forest surveyed in this study has been intact and recovering for around 10–25 years. Thus, the higher abundance of this species in secondary forest is not necessarily due to forest degradation, but most likely due to perturbation processes that create succession habitats that subsequently recover.

Leaf litter is a crucial factor that affects diversity and abundance of floor dwelling arthropods because it offers shelter, stable microclimatic conditions, and protection against predators (Bultman & Uetz 1982; Barrientos 2012). The GLM regressions indicate that leaf litter depth was the most important variable explaining 50% and 20% of the abundance for *K. griswoldi* and *Spinoctenus escalerete*, respectively, supporting the findings of previous studies on the importance of this variable on the abundance of forest floor arachnids (Bultman & Uetz 1982; Cala-Riquelme & Colombo 2011; Lira et al. 2014). Moreover, these two species presented different

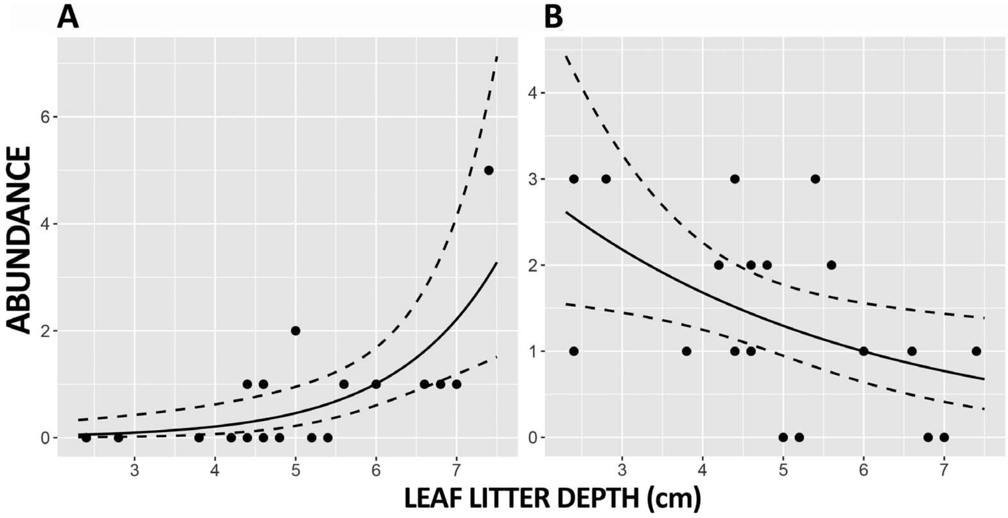

Figure 2.—Poisson regression of leaf litter depth predicting ctenid abundance: (A) *Kiekie griswoldi*; (B) *Spinoctenus escalerete*. Dashed lines indicate standard errors for the fitted values.

responses to leaf litter depth. Because greater depth in the litter layer could offer more suitable refuges to larger species, this factor may explain the positive relationship of the abundance of the larger size species (*K. griswoldi*) with leaf litter depth. On other hand, the abundance of the smaller species *Spinoctenus escalerete* was negatively related with leaf litter depth. However, although we see a steady negative relationship (Fig. 2B), it is important to highlight that this species is exclusive to floor of forests habitats, and its population will always need a cover of leaf litter to survive.

Natural history observations of ctenids and close relatives commonly find different species of the same guild (cursorial floor-dwelling spiders) co-occurring in the same habitats and microhabitats, indicating some degree of interspecific competition to the same resource (Gasnier et al. 2009; Hazzi 2014; Hazzi et al. 2018). Many ecological studies have been carried out in order to understand the ecological basis of these coexistences. For instance, in the Amazonia region, three species of *Phoneutria* (*P. boliviensis*, *P. fera* Perty, 1833 and *P. reidyi* (F. O. Pickard-Cambridge, 1897)) occur sympatrically. According to Torres-Sanchez & Gasnier (2010), *P. boliviensis* seems to be restricted to inundation forests while the two larger species (*P. fera* and *P. reidyi*) appear to be abundant in non-flooded forests ('terra firme'). In the case of these two species, *P. fera* prefers the ground surface of the forest (leaf litter) as microhabitat and *P. reidyi* shows preference for lower vegetation, especially acaulescent palms. Furthermore, these species have different reproductive seasons (Torres-Sanchez & Gasnier 2010). In the case of two sympatric species of *Ctenus*, *C. crulsi* shows a marked preference for clay soils compared to *C. amphora*, and the latter species is more abundant on sandy soils (Gasnier et al. 2009; Portela et al. 2013). The preference of *Kiekie griswoldi* in primary forest and deeper layers of leaf litter may promote habitat segregation between the two focal species of our study, and lead *S. escalerete* to be more abundant in secondary forest than in primary.

Because most species of ctenids living in the leaf litter are generalist predators (Gasnier et al. 2009), intraguild predation and cannibalism in co-occurring species may be an additional factor in promoting habitat differentiation between sympatric species (Wagner & Wise 1996; Samu et al. 1999; Balfour et al. 2003; Buddle et al. 2003; Portela et al. 2013). Field observations indicate that it is relatively common in ctenids to find larger individuals preying on smaller ones of different species or even the same species (Gasnier et al. 2009; Hazzi et al. 2018). Furthermore, lab and field experiments on close relatives of ctenids, wolf spiders (Lycosidae), have shown that cannibalism and intraguild predation are important factors that regulate their densities (Wagner & Wise 1996), and this is strongly influenced by size differences (Rypstra & Samu 2005). In the case of the two dominant species in Las Cruces, we observed an event of intraguild predation where an adult female of *K. griswoldi* was eating an adult male of *S. escalerete* in the primary forest (Fig. 3). The female was recorded eating the male on a leaf 40 cm above the ground and he was already wrapped in silk. Hazzi (2014) studied the prey wrapping behavior of *P. boliviensis* and other ctenids (Hazzi, unpublish data); after they catch the prey on the forest floor, they will always wrap and eat the prey above the ground. Therefore, we think that the female of *K. griswoldi* hunted the male of *S. escalerete* on the ground where they usually live and then, she climbed to the leaves of the plant where she wrapped and started eating the prey. This natural history observation could suggest that predation on *S. escalerete* by the larger species *K. griswoldi* may be an additional factor explaining the higher abundance of *S. escalerete* in secondary forest, where larger adults of *K. griswoldi* are almost absent.

Figure 3.—Adult female of *Kiekie griswoldi* feeding on an adult male of *Spinoctenus escalerete* on a leaf 40 cm above the ground. Wrapping silk on the male and silk lines fixed on the leaf are visible.

In conclusion, our study shows a clear habitat and microhabitat segregation between two sympatric species in a montane tropical forest, where the smaller species (*S. escalerete*) is more abundant in secondary forest and the larger species (*K. griswoldi*) is more abundant in primary forest. Furthermore, these differences can be partially explained by the depth of leaf litter in these environments, because the abundance of dominant species in primary forest has a positive relationship with leaf litter depth, while the abundance dominant species in secondary forest has a negative response. The opposing responses of the abundances of these two species to forest succession and leaf litter depth may reduce interspecific competition and intraguild predation, allowing these two species to coexist. Thus, forest succession is an important factor influencing the abundance of the forest floor spider community and allowing the coexistence of species of the same family. Because this work was conducted in only one area of primary and secondary forest, our results are preliminary and future studies should include more areas to support or refute these findings.

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SUPPLEMENTARY MATERIALS

Figure S1, Map of Las Cruces Biological Station, online at http://dx.doi.org/10.1636/JoA-S-19-070.s1

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