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Differences in bark beetle (Coleoptera: Curculionidae) community composition within *Cecropia obtusifolia* (Cecropiaceae) petioles in two habitats in Monteverde, Costa Rica

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ABSTRACT

Cecropia obtusifolia trees shed leaves daily throughout the year, regularly dropping large, woody leaf petioles. These petioles serve as the perfect habitat for Scolytine bark beetles, which burrow in, lay their eggs, and feed on the moist, fibrous pith of the petiole (Wood 1983). *Cecropia* spp. are known to thrive in fragmented, edge habitats altered by human land use transformation (Bello et al. 1996) but success rates of associated fauna, including *Azteca* spp. ants, scale insects and Scolytine beetles, are less understood. This study examined the bark beetle community composition, morphospecies richness, and abundance inside *C. obtusifolia* petioles. It also investigated the rate of petiole colonization by Scolytine beetles, comparing two habitats: a *C. obtusifolia* population occurring in a forest tree fall light gap, and a population occurring along a neighborhood road. Both populations were located in Monteverde, Costa Rica. Fallen, dead petioles were collected and dissected from each habitat type, and all fauna found inside the woody petioles were removed, identified, and recorded. They were identified as either a Scolytine larva, one of five observed Scolytinae morphospecies, or a non-Scolytine organism. Differences between observed beetle communities in the two studied habitats were then compared. This revealed equal species richness and equal rates of petiole colonization for beetle communities at each site. The human disturbed habitat had greater Scolytinae abundance, while the forest light gap habitat had greater diversity due to higher evenness of morphospecies abundances. This is explained by the particularly high abundance of one morphospecies in disturbed habitat beetle communities. Overall, there were few evident differences between Scolytinae communities in the two examined habitats, indicating that observed Scolytinae populations are adaptable to human-caused habitat alterations and can disperse to fragmented *C. obtusifolia* trees. Their maintained survival and reproduction rates indicate that *C. obtusifolia* associated Scolytine beetles are poor indicators for biodiversity loss and impacts on species relationships that result from continued global deforestation and habitat degradation.

RESUMEN

Los árboles de la especie *Cecropia obtusifolia* diariamente a través del año, dejan caer largos y leñosos pecíolos de las hojas. Estos pecíolos sirven como hábitat perfecto para los escarabajos de la subfamilia Scolytine que habitan en la corteza de los árboles. Estos escarabajos hacen cuevas y ponen sus huevos en estas, además se alimentan de la madera del pecíolo (Wood 1983). *Cecropia* spp. se encuentra en hábitats alterados por los humanos como fragmentos o bordes de bosque (Bello et al. 1996), pero los grados de sucesión asociados a la fauna que viven dentro de esta especie como los presentados por las hormigas *Azteca* spp. y los escarabajos de la subfamilia Scolytinae, son menos conocidos. Este estudio examina la composición en la comunidad de escarabajos de la corteza en cuanto a número de morfoespecies y abundancia de individuos dentro de los pecíolos de la especie *C. obtusifolia*. También se investiga el rango de colonización de los escarabajos de la subfamilia Scolytinae comparando entre individuos encontrados en poblaciones en los claros de bosque y a la orilla de los caminos. Ambas poblaciones estuvieron localizadas en Monteverde, Costa Rica. Se recolectaron y se disectaron pecíolos caídos en el suelo en cada tipo de hábitat y luego se identificó la fauna encontrada adentro de la corteza de los pecíolos. La fauna encontrada fue identificada a nivel de morfoespecies los escarabajos adultos, larvas de estos escarabajos y los individuos no pertenecientes a esta subfamilia. Se encontraron diferencias entre las dos comunidades estudiadas. Estas revelan

similar riqueza de especies y rango de colonización entre comunidades. En el hábitat alterado se encontró mayor abundancia de individuos pero el sitio de los claros de bosque tiene una diversidad más alta, debido a la equidad encontrada entre en la abundancia de las morfoespecies. Esto se puede explicar a la alta abundancia de una morfoespecie en el hábitat alterado. Sobretudo, se encontraron pocas diferencias entre las dos comunidades, indicando que las poblaciones de scoltidos son adaptables a las alteraciones en el hábitat causadas por los humanos y se pueden dispersar a poblaciones fragmentadas de árboles de *C. obtusifolia*. La supervivencia y el grado de reproducción de estos escarabajos de la subfamilia Scolytinae indican que estos son indicadores pobres de la pérdida de biodiversidad y del impacto de la deforestación y la degradación del hábitat en la relaciones entre las especies.

INTRODUCTION

Tropical forest biomes have the highest biodiversity, most complex habitat specialization and highest rates of endemism across the globe. They harbor nearly 50% of described species, while covering less than seven percent of the earth's surface (Plotkin et al. 2000). These ecologically important and rich landscapes have been and are continuing to be transformed into a deforested mosaic of urbanization, cattle pastures, agricultural plots, monoculture plantations, logged forests and secondary growth with only scattered fragments of primary growth remaining (Nepstad et al. 1996). Rich tropical communities, due to their high rates of specialization and endemism, are particularly vulnerable to the impacts of fragmentation and habitat destruction. These impacts are often amplified for organisms reliant on close inter-species relationships (Sankaran 2001).

Cecropia trees are common pioneers of secondary growth forests and benefit from natural or human caused canopy disturbances. As a result, their populations increase along with deforestation rates (Bello et al. 1996). *Cecropia* interact closely with fauna such as *Azteca* ants and scale insects, as well as Scolytine bark beetles that use the large, woody petioles from the tree as their obligatory reproductive site (Wood 1983). *Cecropia* shed dead leaves year-round, and therefore are good hosts, despite low nutrient content and patchy community distribution (Wilkinson 2002). These beetles are entirely dependent upon *Cecropia*, while *Cecropia* neither benefit nor are compromised by the commensalist relationship (A. Masters, personal communication).

Adult male Scolytine beetles burrow through the cortex of the petiole (typically three to five days after the leaf has fallen) and leave a pheromone trail for a female to follow. Copulation takes place inside the burrowed tunnel, and the female subsequently carves a pocket in the petiole pith for egg deposition. Eggs hatch three to five days later, and pupation occurs within the petiole. Adult beetles then bore out through the cortex to reproduce in a new host petiole. The duration of this cycle is generally around 25 days (Wood 1983). Multiple Scolytinae species have evolved the same *Cecropia*-dependent reproduction patterns and can share petioles—up to four adult pairs can inhabit the same petiole. Different beetle species within one petiole often exhibit niche partitioning to reduce resource competition (Wilkinson 2002). Inbreeding is common due to the closed petiole ecosystem, in which the majority of the Scolytinae life cycle is spent, because siblings frequently mate before exiting their birth petiole (Beaver et al. 2001).

In this study, I assess differences in community composition and colonization rates of various Scolytinae morphospecies in petioles of *C. obtusifolia* in areas of high human disturbance versus natural primary forest light gaps. My objective was to determine how these bark beetles respond to habitat fragmentation.

Given that *Cecropia* shed leaves year round, beetle populations are not accustomed to dispersing far, and upon leaving the birth petiole, young adult beetles often choose petioles in very close proximity to use for mating and colonization (Jordal and Kirkendall 1998). For this

reason, despite host success, I expect that rates of colonization of Scolytinae beetles will be lower in highly disturbed human habitats due to their infrequent need for far dispersal and the resulting inability of the beetles to travel successfully between highly fragmented *C. obtusifolia* communities. Following the same logic, I anticipate lower species richness of beetles in petioles from human-altered habitats, but higher abundance of each present species due to increased availability of petiole material for oviposition and less resource competition between species.

MATERIALS AND METHODS

Study Sites

Two sites in Monteverde, Costa Rica were used for this study, each with a population of at least four mature *C. obtusifolia* trees that shed leaves daily. One site was located in the forest of the Bosque Eterno de los Niños, at the Bajo del Tigre entrance in a natural tree fall light gap. The other site was located along the roads in the Bajo del Tigre neighborhood, a once-forested habitat that was altered by humans. The two sites were within 50 meters in elevation of each other (1340 m – 1390 m) to control for potential variation in beetle colonization and composition caused by changes in elevation.

In each study site, four suitable trees in close proximity to each other were selected and recorded. From each tree, ten petioles of similar age, moisture content, color, length, and diameter were gathered from the ground or from vegetation up to three meters off the ground. Samples were immediately placed individually into large Ziploc plastic bags, which were sealed and labeled; 80 petioles were collected in total. According to Wood (1983), leaves that fell three to 15 days prior to collection are ideal for analyzing Scolytinae communities because the petioles during this time are in adequate condition to support these beetle populations. Ideal petioles are moist and fresh, moderately stiff to the touch and medium brown in color (Jordal and Kirkendall 1998)—these criteria were used in selecting petioles of approximately the same age.

Length from the petiole base to the base of the leaf blade was measured using a tape measure and was between 25 cm and 50 cm for each examined petiole. The diameter of each, measured with a caliper at the midpoint between petiole base and base of leaf blade, was between 0.6 cm and 1.2 cm for each petiole. These criteria control for potential variance in community dynamics within each petiole caused by varied age and size of leaf.

Within ten days of collection, each petiole was removed from its sealed bag and dissected using tweezers and scissors, by cutting down the center of the petiole along its length. Tweezers were used to peel back strips of bark along the petiole cortex, and the petiole was additionally cut into 0.5 cm long discs horizontally down the entire length of the petiole. All fauna present in the petiole or in the Ziploc bag were removed using tweezers and placed into labeled vials filled with 70% alcohol solution to maintain the insects until identification. Petioles that were not colonized by any Scolytinae were recorded as $S = 0$.

For each petiole, all fauna were removed one by one and identified to morphospecies of Scolytinae using a dissecting scope. Morphospecies was distinguished based on color, size, pubescence and elytra characteristics. Scolytine larvae present in the petioles were recorded; however morphospecies identities of observed larvae were not determined. Any non-Scolytinae insects found in the petioles, such as ants or spiders, were noted as well.

Morphospecies richness (S) and abundance of individuals in each morphospecies (N) were recorded per petiole. Shannon-Weiner's diversity index (H') and evenness (E) were

calculated comparing the two habitat types using the total beetle abundance and richness values from the examined 40 petioles from each site. A t-test was applied to the H' value to compare the habitat diversity differences per site. Margalef's index (S_{marg}) was calculated to compare the difference in sample size per site.

Sorenson's quantitative index was applied at the tree level to discern whether similarity values of the beetle composition at the two separate habitats differed from similarity values within the same habitat. This was used to account for compositional variance in beetle communities between trees at each site, using the mean calculated index value per comparison category (within forest habitat, within disturbed habitat and between the two distinct habitats). Colonization rates per site were calculated as percentage of petioles containing at least one Scolytine beetle, and compared between sites.

RESULTS

From both the human disturbed habitat site and the forest habitat site, 38 of the 40 examined petioles contained Scolytinae individuals so that each site showed an equal colonization rate of 95%. A total of 1042 beetles were found and identified as either Scolytine larvae or one of five observed morphospecies of adult beetle. All five morphospecies were observed in petioles from each habitat (Table 1). A total of 237 observed non-Scolytinae fauna were found between both sites.

TABLE 1. Abundance (N), Morphospecies Richness (S), Diversity (H') and Evenness (E) values of Scolytinae beetles found in total per habitat, excluding larvae.

	Forest Site	Disturbed Site
N	336	457
S	5	5
H'	1.40	1.24
E	0.87	0.77

Patterns of Compared Community Composition between Habitat Types

Abundance of total observed Scolytinae beetles was higher in the human-disturbed habitat (Table 1). There was a difference in diversity of Scolytine beetles found between the forest habitat ($H' = 1.40$) and the human disturbed habitat ($H' = 1.24$; Modified t-test, $t = 4.43$, $P < 0.05$).

In the petioles collected from the forest habitat site, 70 individuals of morphospecies one, 50 individuals of morphospecies two, five individuals of morphospecies three, 103 individuals of morphospecies four and 108 individuals of morphospecies five were found, along with 109 Scolytinae larvae and 158 non-Scolytinae individuals. In the petioles collected from the human disturbed habitat site, 100 individuals of morphospecies one, 33 individuals of morphospecies two, two individuals of morphospecies three, 104 individuals of morphospecies four and 218 individuals of morphospecies five were found, along with 139 Scolytine larvae and 79 non-

Scolytinae individuals. Distribution of the abundance of each morphospecies found per tree within each habitat is shown in Figure 1.

Morphospecies one, two, three and four showed no difference in occupancy between habitats (Figure 2a, 2b, 2c, 2d). Morphospecies five showed a higher incidence of occupancy in *C. obtusifolia* petioles of the human-disturbed habitat ($P = 0.0058$; Figure 2e). Scolytine larvae abundance per petiole was not different between sites (Figure 3). The non-Scolytinae fauna species found were more abundant in forest habitat *C. obtusifolia* petioles ($P = 0.0443$; Figure 4).

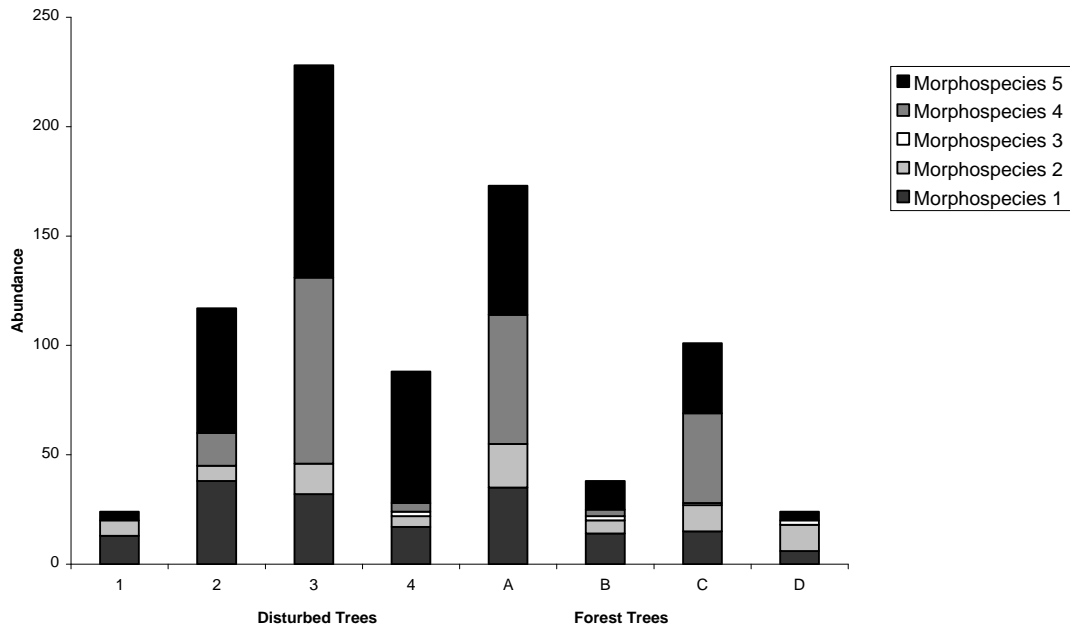
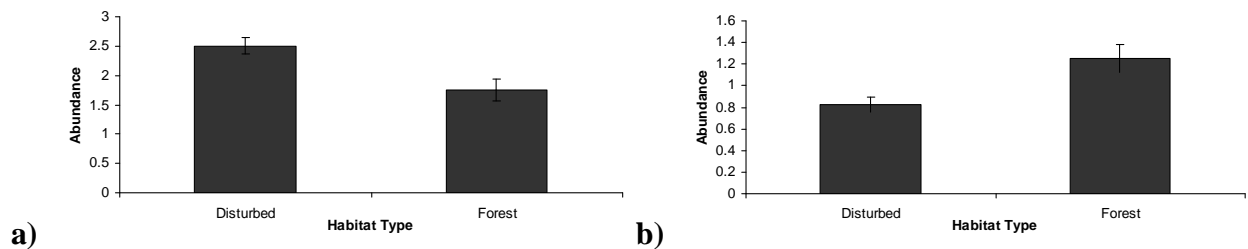


FIGURE 1. Scolytinae (Coleoptera) abundance of each of five morphospecies found per *C. obtusifolia* individual in both disturbed and forest habitats.



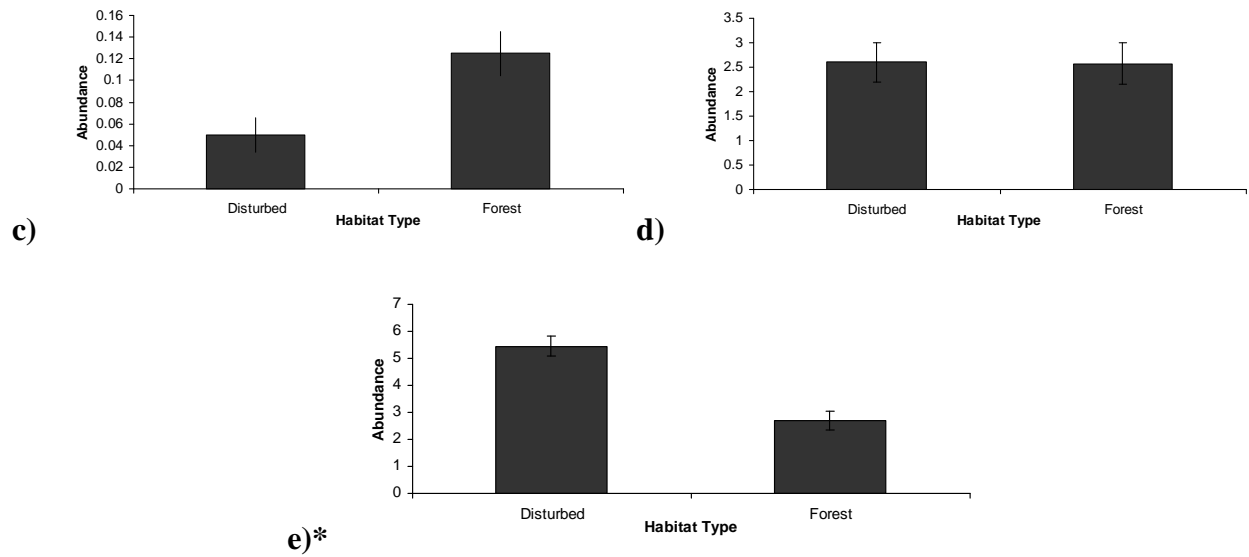


FIGURE 2. Average abundance of each morphospecies (Coleoptera: Scolytinae) per *C. obtusifolia* petiole in human disturbed versus forest habitats. **a)** Morphospecies one ($t = 0.990$, $df = 78$, $P = 0.325$, Std Error = 0.758) **b)** Morphospecies two ($t = -0.934$, $df = 78$, $P = 0.353$, Std Error = 0.455) **c)** Morphospecies three ($t = -0.924$, $df = 78$, $P = 0.358$, Std Error = 0.081) **d)** Morphospecies four ($t = 0.014$, $df = 78$, $P = 0.99$, Std Error = 1.844) **e)** Morphospecies five ($t = 2.838$, $df = 78$, $P = 0.0058$) *Indicates $p < 0.05$.

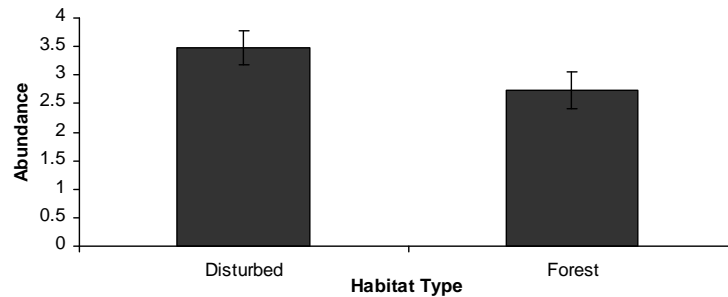


FIGURE 3. Average abundance of Scolytine (Coleoptera) larvae found per *C. obtusifolia* petiole in human disturbed versus forest habitats. ($t = 0.538$, $df = 78$, $P = 0.592$, Std Error = 1.393)

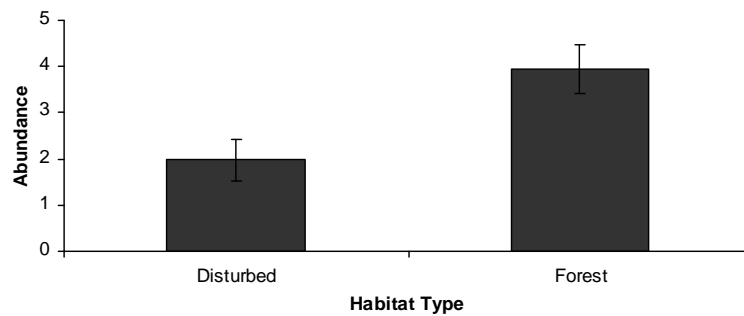


FIGURE 4. Average abundance of non-Scolytinae (Coleoptera) organisms found per *C. obtusifolia* petiole in human disturbed versus forest habitats. ($t = -2.045$, $df = 78$, $P = 0.0443$, Std Error = 1.668)

Similarity between individual *C. obtusifolia* trees within each separate habitat showed no difference from the similarity between the two overall habitats ($n = 8$; Table 2). Standard error values reveal high variability of beetle composition between individual trees of both habitats (Table 2).

TABLE 2. Sorenson's quantitative index of similarity calculated between every *Cecropia* individual combination within both habitats separately and between habitats. Recorded indices reflect mean index value of each tree combination index calculation per comparison category.

Comparison Localities	Sorenson's Quantitative Index	Standard Error
Within Disturbed Habitat	0.518	0.100
Within Forest Habitat	0.463	0.0756
Between Habitats	0.511	0.0549

DISCUSSION

The findings of this study show higher overall Scolytinae abundance in the habitat altered by humans than in the forest light gap, indicating the ability of bark beetles to successfully find host populations in patchy open areas, as well as in forest habitats. This is also implicated by the equal species richness between the two observed habitats with the same five morphospecies present, as well as the equal colonization rates of 95% that are evident at both sites. These trends oppose the previously hypothesized differences in both species richness and colonization ability

between habitats, demonstrating that the impacts of habitat fragmentation do not significantly alter either species richness of the associated beetles or their ability to occupy petioles.

One possible explanation for this adaptability relies on the fact that tropical bark beetle populations are known to thrive even with extremely low brood sizes and thus are resilient when their population densities are threatened (Jordal and Kirkendall 1998). Therefore, even if only a few beetles of each species arrive at *C. obtusifolia* trees in areas affected by human land use, their populations can survive to recover to normal densities in the new site. This is in part because mortality caused by predation and parasitism are low in the closed and protected petiole system (Jordal and Kirkendall 1998). Additionally, according to a study performed by Beaver et al. (2001), inbreeding insect populations such as bark beetles have more successful distribution to islands than outbreeding populations, because they are less challenged by mate location and have quicker generational turnover. Thus they have a higher rate of population size increase due to more highly female-biased populations. Such trends on island systems can be applied to this study in that human disturbance causes *Cecropia* populations along roadsides to be isolated and therefore act as habitat “islands.”

While colonization and richness between the two habitats did not differ and abundance of Scolytine beetles was greater in the disturbed habitat, data indicate a significant difference between the diversity of the two habitats, showing greater diversity in the forest habitat. Because species richness is identical between sites but diversity differs, the compositional difference between populations lies in the evenness of each morphospecies. These results agree with the study by Didham et al.(1998) that found no change in beetle community species richness as a result of tropical forest fragmentation, but did find differences in relative success rates of various beetle species showing differential adaptability between species. Nearly half of the observed Scolytine beetles in the human altered habitat were members of morphospecies five, while the forest habitat had a much more even distribution of morphospecies, with the most abundant morphospecies appearing less than one third of the time. It could be that morphospecies five thrives particularly where the landscape has been altered by humans. Ribera et al. (2001) demonstrate that beetles small in size and with high dispersal ability are most likely to do well in highly degraded habitats. This concurs with my study in that morphospecies five was distinguished in part by its particularly small size. The higher overall beetle abundance in the disturbed habitat may be a result of the particular success of morphospecies five, because each of the other four morphospecies maintained relatively similar population sizes between sites.

While abundance of Scolytinae was found to be greater in the human disturbed habitat, the abundance of non-Scolytine fauna was greater in the forest habitat. This may be due to the fact that forest light gap habitats are in much closer proximity to continuous forest than are areas highly impacted by humans, such as the roadside site examined in this study. The *C. obtusifolia* individuals in the disturbed habitat were isolated, and surrounded by little non-*Cecropia* vegetation. In the natural forest light gaps, however, *C. obtusifolia* individuals were in very close proximity to high quantities of forest vegetation. Under the assumption that non-Scolytinae fauna are not specialized to rely on *Cecropia* petioles, this trend can be explained by a decreased likelihood that non-Scolytine individuals could survive successfully in areas with very little plant diversity or abundance aside from *C. obtusifolia*. Additionally, this pattern may suggest that the increased presence of non-Scolytine beetles inside *C. obtusifolia* petioles in the forest habitat explains the lower abundance of Scolytine beetles in this habitat, possibly due to predation, parasitism or competition for resources. Further research focused on interactions between Scolytinae and non-Scolytinae would add insight to the patterns observed here.

Community similarity at the tree level reveals values that do not vary substantially between within-site tests and between-site tests. This indicates that there is nearly equivalent variability in beetle community composition from all *C. obtusifolia* individuals, despite which *C. obtusifolia* population the tree is from. This may suggest that microhabitat differences in *C. obtusifolia* trees impact beetle community composition as much as macrohabitat differences between the two sites. This overall similarity of beetle composition in petioles between trees and between habitats may be due to the fact that abiotic conditions of each site are similar in how they differ from abiotic conditions in continuous forest. Light gaps and human-impacted edge environments have increased light, decreased humidity and higher temperatures than continuous, closed canopy forest conditions (Williams-Linera 1990; Denslow et al. 1990). Scolytine beetles associated with *C. obtusifolia*, which are light gap pioneers, may be particularly adapted to such abiotic conditions. The maintenance of beetle reproductive rates and population densities at both sites may be explained by the similarity in environmental conditions of light gaps (natural canopy disturbance) and altered land-use habitats (disturbance caused by humans). In order to more thoroughly compare and contrast forest habitat *C. obtusifolia* associated beetle communities with human altered habitat communities, a greater sample size of trees per site would be useful. Increased sample size would be useful to discern whether between tree variance within one habitat is a common characteristic of these particular communities, or whether there are distinguishable habitat based differences in beetle community composition between sites.

As deforestation, habitat degradation and global climate change continue to destroy primary forest habitats, it is essential to identify and understand trends in biodiversity as they are impacted by these large-scale changes. While global biodiversity is declining rapidly in response to anthropogenic changes to the natural landscape (Sala et al. 2000), this study shows that Scolytinae species associated with *C. obtusifolia* can successfully adapt to such changes. For this reason, these beetles would serve as poor indicator species for the impacts of deforestation on biodiversity and species interactions.

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