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# Ecosystem engineers on plants: indirect facilitation of arthropod communities by leaf-rollers at different scales

CAMILA VIEIRA<sup>1</sup> AND GUSTAVO Q. ROMERO<sup>2,3</sup>

<sup>1</sup>*Pós-graduação em Ecologia, Universidade Estadual de Campinas (UNICAMP), CP 6109, CEP 13083-970, Campinas-SP, Brazil*

<sup>2</sup>*Departamento de Biologia Animal, IB, Universidade Estadual de Campinas (UNICAMP), CP 6109, CEP 13083-970, Campinas-SP, Brazil*

**Abstract.** Ecosystem engineering is a process by which organisms change the distribution of resources and create new habitats for other species via non-trophic interactions. Leaf-rolling caterpillars can act as ecosystem engineers because they provide shelter to secondary users. In this study, we report the influence of leaf-rolling caterpillars on speciose tropical arthropod communities along both spatial scales (leaf-level and plant-level effects) and temporal scales (dry and rainy seasons). We predict that rolled leaves can amplify arthropod diversity at both the leaf and plant levels and that this effect is stronger in dry seasons, when arthropods are prone to desiccation. Our results show that the abundance, richness, and biomass of arthropods within several guilds increased up to 22-fold in naturally and artificially created leaf shelters relative to unaltered leaves. These effects were observed at similar magnitudes at both the leaf and plant scales. Variation in the shelter architecture (funnel, cylinders) did not influence arthropod parameters, as diversity, abundance, or biomass, but rolled leaves had distinct species composition if compared with unaltered leaves. As expected, these arthropod parameters on the plants with rolled leaves were on average approximately twofold higher in the dry season. Empty leaf rolls and whole plants were rapidly recolonized by arthropods over time, implying a fast replacement of individuals; within 15-day intervals the rolls and plants reached a species saturation. This study is the first to examine the extended effects of engineering caterpillars as diversity amplifiers at different temporal and spatial scales. Because shelter-building caterpillars are ubiquitous organisms in tropical and temperate forests, they can be considered key structuring elements for arthropod communities on plants.

**Key words:** *arthropod diversity; arthropod functional groups; ecosystem engineers; herbivory; indirect facilitation; leaf-rolling caterpillars; leaf shelter; Lepidoptera; spatial and temporal scales; trophic cascade.*

## INTRODUCTION

Ecosystem engineers are organisms that directly or indirectly control resource availability to other individuals by physically changing biotic and abiotic components (Jones et al. 1994, 2010). These physical changes vary along environmental gradients (Crain and Bertness 2006, Badano et al. 2010), altering biogeochemical processes, resource availability, and nutrient cycling (Caraco et al. 2006, Gutiérrez and Jones 2006). Ecosystem engineering is a non-trophic interaction that may have a negative (i.e., inhibition) or positive (i.e., facilitation) ecological effect on other species (Martinsen et al. 2000, Stachowicz 2001, Marquis and Lill 2007; Lima et al. 2013). The positive interactions are pivotal structuring factors of ecological communities, as whole communities may disappear without a key facilitator (Stachowicz 2001, Fuller and Peckarsky 2011). The magnitude of facilitation of the engineer is influenced by several factors, such as the size of the habitat built,

environmental stress, and predation risk from secondary colonizers. These factors also vary according to the architectural complexity and the number of engineers found in nature (Gutiérrez et al. 2003). The engineering species may coexist with the benefiting species or be temporally or spatially separated from them (Jones et al. 1994, 2010, Stachowicz 2001).

Ecosystem engineering is a common process for the communities of species inhabiting land plants. Shelters are constructed by herbivores (e.g., galling, leaf-tiers, and miners [Crawford et al. 2007]; stem borers [Calderón-Cortés et al. 2011]) and other arthropod guilds (e.g., predators, parasites [Martinsen et al. 2000, Fukui 2001, Lill and Marquis 2003, Nakamura and Ohgushi 2003]). Many lepidopteran larvae are ecosystem engineers, building several types of leaf shelters on plants (e.g., cylindrical, funnel, web, and tent), and many arthropod species may secondarily colonize abandoned leaf shelters (Martinsen et al. 2000, Fukui 2001, Nakamura and Ohgushi 2003, Lill and Marquis 2007, Wang et al. 2012). Secondary colonizers may be classified into potential leaf-rollers (conspecifics or heterospecifics) or free-living species that do not build their own shelter (Fukui 2001). Leaf shelters can modify

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<sup>3</sup> Corresponding author. E-mail: gqromero@unicamp.br

the physical architecture of a plant, increasing habitat heterogeneity, and as a result, the biodiversity in ecosystems (Fukui 2001, Nakamura and Ohgushi 2003, Lill and Marquis 2007).

The effects of engineering caterpillars can arise at different spatial and temporal scales. Although several observational and experimental studies have shown that caterpillar shelters may affect the diversity of arthropods at the leaf level (i.e., inside rolled leaves [Cappuccino and Martin 1994, Martinsen et al. 2000, Nakamura and Ohgushi 2003, Lill and Marquis 2007, 2010, Marquis and Lill 2007, Ohgushi 2007]), only one study evaluated the plant-level effects of engineering caterpillars and did so only for specific guilds (i.e., herbivores; Lill and Marquis 2003). However, no studies have examined how diverse tropical communities respond to the impacts of engineering caterpillars at different spatial (i.e., leaf-level and plant-level effects) and temporal scales (i.e., dry and rainy seasons).

Because the dry season shows a pronounced negative effect on arthropod abundance in the tropics (e.g., Wolda 1988), we predict that the strength of the beneficial effects of engineering caterpillars on the invertebrate colonization of leaf shelters may also vary temporally and be intensified during the dry season; it is likely that these shelters represent microenvironments that protect arthropods from UV radiation and desiccation. In addition, we predict that the local effects of leaf-rolling engineers might extend to the whole plant community (i.e., plant-level effect), consistent with the principles of the extended phenotype (Dawkins 1982), because diversified arthropod communities sheltered inside the rolls, assembled mostly by small herbivores, detritivores, and predators, could support a different community of larger top consumers; if this is true, we expect a different species composition between leaf- and plant-level scales. Furthermore, abiotic factors such as temperature, humidity, air circulation, and solar ray incidence may vary depending on the shape and volume of the leaf shelter. Thus, we predict that the type of shelter built by leaf-rolling caterpillars could also influence secondary colonization by arthropods. Finally, we verified the consistency of our results by including the effects of engineers on several arthropod guilds (predators, herbivores, detritivores, parasites, parasitoids, omnivores).

In this study we used a combination of observational and experiment studies to test if (1) leaf shelters amplify arthropod diversity on plants, and if this effect is stronger during dry seasons, when arthropods are more prone to desiccation, (2) shelter shape (funnel and cylinders with different diameters) affects arthropod colonization and species composition, and (3) the engineering effects are leaf-level (within curled leaves, “leaf-level” hereafter) or whether they extend to the entire arthropod community on the whole plant (“plant-level” hereafter).

## MATERIALS AND METHODS

### *Study area and organisms*

This study was undertaken at the Biological Reserve of the Serra do Japi, in southeastern Brazil. The climate is seasonal; the driest periods range from June to September and the wet season occurs between December and March. The survey and experiments were conducted using *Croton floribundus* (Euphorbiaceae) shrubs, a key element from the Atlantic Rainforest. This plant species does not have extrafloral nectaries and occurs mainly at the forest edges. Three species of *Anaea* (Lepidoptera: Nymphalidae) have been associated with *Croton* (Queiroz 2002). The caterpillars in the *Anaea* genus usually roll leaves with secreted silk at the fourth instar stage and remain within the shelter up to the non-feeding fifth instar stage (Appendix A). Finally, when the caterpillar is ready to pupate, it leaves the leaf shelter and attaches to a substrate to complete the metamorphosis and become an adult (Queiroz 2002). These leaf shelters remain intact for up to 12 months, thus including all seasons (C. Vieira and G. Q. Romero, *personal observations*).

### *Surveys of expanded leaves and leaves rolled by caterpillars*

Prior to the experiments, we sampled the fauna on naturally rolled and expanded *C. floribundus* leaves. We sampled rolled and expanded leaves from 67 *C. floribundus* shrubs between 1 and 2.5 m height between August and October 2008 (a period of higher abundance of leaf shelters abandoned by *Anaea*). The randomly chosen shrubs were 2–50 m apart from each other along a track. For each plant, we collected a leaf rolled by a caterpillar and an intact leaf (expanded). The dry biomass of the rolled and expanded leaves did not differ ( $t = 0.360$ ,  $df = 127$ ,  $P = 0.711$ ). We carefully selected expanded leaves that showed little damage. The rolled and expanded leaves were inspected under a stereomicroscope, and all of the arthropods (except mites) were collected. All of the arthropods were identified to the family level and then sorted into morphospecies to evaluate the abundance, richness, and biomass of each taxonomic group, in addition to the guilds (e.g., predators, herbivores, parasites, parasitoids, detritivores, and omnivores) and species composition in the expanded and rolled leaves. We estimated the dry biomass of arthropods per leaf using standard linear equations from the literature for each arthropod family (Hódar 1996) or equations built using our own data.

### *Effects of temporal and spatial scales and shelter features: manipulating leaf rolling artificially*

To evaluate the effect of *Anaea* caterpillars on the arthropod colonization rate and arthropod species composition in shelters, we designed a field experiment in which we selected *C. floribundus* plants bearing at least 10 leaves each, along a transect; these plants were

1–2.5 m in height and 2–30 m apart from each other. The plants ( $n = 60$ ) were sequentially numbered according to the order of encounter and then randomly assigned to the following treatments: (1) expanded leaves (control;  $n = 15$ ), (2) rolled leaves forming a cylinder 0.5 cm in diameter ( $n = 15$ ), (3) rolled leaves forming a cylinder 1.5 cm in diameter ( $n = 15$ ), and (4) rolled leaves forming a funnel of 1.5 and 0.5 cm diameter ( $n = 15$ ). All three types of shelters are typically found in leaves of *C. floribundus* in the study area (G. Q. Romero and C. Vieira, *personal observations*). The leaves were manually rolled completely from the adaxial to the abaxial surface in a manner similar to some engineering *Anaea* larvae at the study site. The leaves were kept rolled with plastic paper clips to prevent oxidation. The control leaves were also marked with paper clips to control for any influence of the treatment. We randomly assigned 4–5 leaves from each plant to the different treatment groups (the number of leaves varied proportionally based on the number of leaves in the plant). We selected only young, expanded leaves without apparent damage for the randomization. Prior to the experiment, the leaves were cleaned with a brush to exclude all arthropods. This experiment was repeated in three different seasons between May and June 2008 (after rainfall season), August and October 2008 (dry season), and January and March 2009 (rainy season), using different sets of plants for each period.

To evaluate the effect of the engineers at the leaf-level scale, we carefully opened the artificially rolled leaves by removing the paper clips every 15 days, over 45 days, to survey for arthropods (i.e., three repeated measures within 45 days for each roll and plant). Then the same leaves were again carefully rolled to keep the original shape for the next 15-day survey; these leaves were not damaged with this procedure. To evaluate the effect of the engineer at the plant-level scale, we surveyed all of the arthropods on the stems and unrolled leaves of each experimental plant every 15 days; these surveys were performed simultaneously with the leaf-level surveys. However, we did not join data on arthropods from inside the leaf rolls with data on arthropods from the whole plant, thus allowing them to be treated separately. With this sampling design we have a colonization rate represented by mean abundance, richness, and biomass of arthropods at each 15 days; by averaging the data on these three fortnight censuses we minimize variations of colonization rate within the same roll or plant. A previous bioassay using the same system and protocol evidenced that arthropods can colonize the rolls within a 24-hour interval (C. Vieira and G. Q. Romero, *unpublished data*); thus a 15-day interval was enough for the colonization to occur. Overall, repeated-measures ANOVAs comparing the three fortnightly censuses of arthropod abundance, richness, and biomass within each leaf roll and whole plant did not differ (within-subject,  $P \geq 0.07$ ). This means that empty leaf rolls and whole plants were rapidly recolonized by arthropods

over time, but the arthropod community seems to reach saturation in <15 days.

The abundance, richness, and biomass were weighted by the total biomass of each experimental plant. The biomass of each experimental plant was estimated by nondestructive methods; first, we randomly selected 20 *C. floribundus* plants of varying sizes in the field. Then, the number of leaves was correlated to the dry mass of the entire plant. The linear regression model obtained was suitable for estimating the biomass of the experimental plants from their total numbers of leaves ( $R^2 = 0.93$ ,  $F_{1,13} = 177.60$ ,  $P < 0.001$ ).

At the leaf-level scale, we weighed the response variables per leaf (e.g., abundance per leaf), and at the plant-level scale we weighed the response variables per dry plant biomass (e.g., abundance per gram).

#### Statistical analysis

*Surveys.*—To test whether abundance, richness, and total biomass of arthropods belonging to several guilds are higher in leaves rolled by *Anaea* larvae than expanded leaves, we used mixed-models multivariate analysis of covariance (MANCOVA) through Wilks' lambda  $F$  statistics, with varying guilds as dependent variables. The number of leaves per plant was the covariate, treatment (two levels) was a fixed factor, and block was a random factor. We used a multivariate analyses approach to minimize Type I error and to achieve independence of data when comparing many guilds. Each guild was compared separately by linear mixed-effect models (LME), using variance components and restricted maximum likelihood (REML) approaches; in this model leaf structure (i.e., expanded or rolled by larvae) was a fixed effect, and individual plant was the random factor. To compare the species composition of the expanded and rolled leaves (naturally and artificially), we used an analysis of similarity (ANOSIM) through the PRIMER 5.0 program (Plymouth Marine Labs, Plymouth, UK).

*Manipulative experiment.*—We averaged the data from three censuses every two weeks over 45 days in each seasonal period for comparisons; this procedure allowed us to minimize variations within each leaf roll or whole plant, and to estimate the arthropod colonization rate upon leaves and whole plants. In addition, the response variables were compared among treatments (four levels) and seasonal periods (three levels) using mixed-models multivariate analysis of covariance (MANCOVA), with seasonal period as a random factor. To test if the strength of the engineering effect is stronger in dry seasons, we used contrast analyses for multivariate analyses of variance (Wilks' lambda  $F$ ) for pairwise comparisons among different seasonal periods. Univariate  $F$  tests were also used to test if richness, abundance, and biomass of each arthropod guild separately are higher in rolled leaves than expanded leaves. For these univariate analyses, if necessary, the treatments were compared using a post hoc Fisher LSD

test. We inspected the data graphically (e.g., Box M, q-q plots), and when necessary, prior to the analyses the data were square-root transformed to achieve normality and homoscedasticity. We performed sample-based and individual-based rarefaction curves (Gotelli and Colwell 2001) for each treatment at both leaf-level and plant-level scales, in different seasonal periods, to estimate richness and to measure sampling efforts among different treatments on each plant.

To compare the species composition among treatments within each season we performed analyses of similarity (ANOSIM). Nonmetric multidimensional scaling analyses (NMDS) were performed to visualize similarities or dissimilarities among our four treatments. To compare the species composition between seasons and the leaf-level vs. plant-level fauna, we used similarity indices based on incidence (Koleff et al. 2003). We calculate the index and variances with a bootstrap ( $n = 200$  iterations) using the SPADE program (Chao and Shen 2005). The index ( $\beta_{sim}$ ) ranges from 0 (dissimilar communities with no species shared) to 1 (identical communities), representing high rate of species turnover (high beta diversity) and low turnover rate (low beta diversity), respectively.

## RESULTS

### *Surveys of expanded leaves and leaves rolled by caterpillars*

Sixty percent of the *C. floribundus* plants inspected had leaf shelters built by *Anaea* larvae. The arthropods found in the surveys ( $n = 393$ ) belonged to 10 orders (see Appendices B and C). The average abundance, richness, and biomass of the arthropods on the leaves rolled by larvae was 6, 5, and 8 times higher, respectively, than these measures on expanded leaves (MANCOVA, all  $P < 0.001$ ; Fig. 1; Appendix C). The rolled leaves also exhibited a higher abundance and richness of predatory, herbivorous, and detritivorous arthropods; parasites, parasitoids, and omnivores were only present on rolled leaves (Fig. 1; Appendix C). The species composition differed between the rolled and expanded *C. floribundus* leaves (ANOSIM, global  $R = 0.068$ ,  $P = 0.001$ ).

### *Effects of temporal and spatial scales and shelter features: manipulating leaf rolling artificially*

**Leaf- and plant-level effects.**—Overall, we found 16 arthropod orders inhabiting the interior of artificially rolled leaves or plants that had their leaves rolled during the experiments. Treatment effects were manifested as differences in abundance, richness, and biomass, both at the leaf and plant level (MANCOVAs, all  $P \leq 0.001$ ; Fig. 2; Appendices E–I).

At the leaf level, the species richness in rolled leaves in the after rainfall, dry, and rainy seasons were 3, 9, and 5 times higher than that in expanded leaves, respectively (Fig. 2; see Appendix D for statistics). Our sample-based rarefaction curves showed that this increase in species richness in rolled leaves is related to the increase in

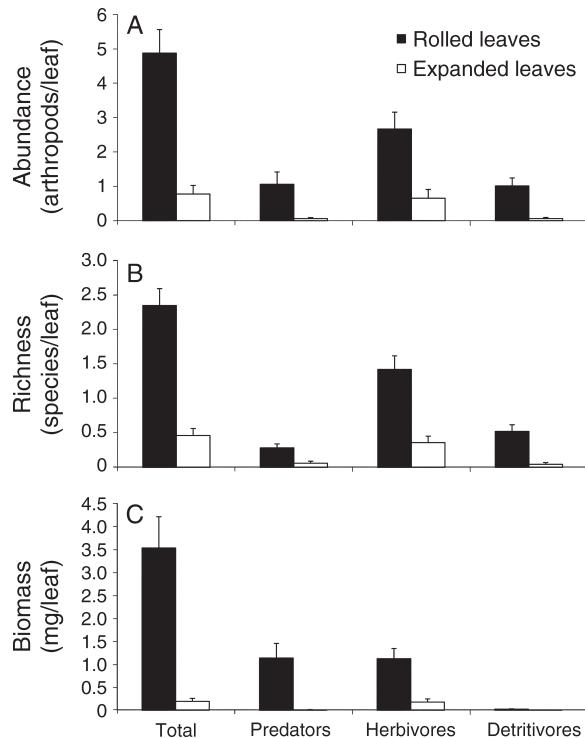


FIG. 1. (A) Abundance, (B) richness, and (C) total biomass of predator, herbivore, and detritivore guilds on expanded and rolled *Croton floribundus* leaves. Error bars represent  $\pm$ SE. Values for rolled leaves and expanded leaves were significantly different for every parameter in every guild ( $P < 0.05$ ; ANCOVA).

number of individuals sampled (see Appendix I). In fact, the abundance of arthropods inside shelters in the after rainfall, dry, and rainy seasons were 3, 9, and 6 times higher than that in expanded leaves, respectively (Appendices D and E). Arthropod biomass inside the rolled leaves in the after rainfall, dry, and rainy seasons were 5, 22, and 10 times higher than that in expanded leaves, respectively (Appendices D and F). The abundance, richness, and biomass of predators, herbivores, and detritivores per rolled leaf unit were also distinct from artificially rolled leaves and expanded leaves (see data in Appendices E–G, and Appendix H for univariate  $F$  statistics); the abundance, richness, and biomass of parasites, parasitoids, and omnivores varied in each treatment (Appendices E–H). In general, the abundance, richness, and arthropod biomass did not differ between the three different types of leaf shelters (Fig. 2; Appendices E–H). The seasons influenced the abundance, richness, and total biomass of arthropods at the leaf and plant level (Fig. 2; see Appendix D for analyses of contrast); the dry season exhibited the highest abundance (three times) and highest biomass (two times) of arthropods in rolled leaves compared to expanded leaves. A very similar pattern obtained for leaf level was also observed at plant level (Fig. 2; Appendices D–I).

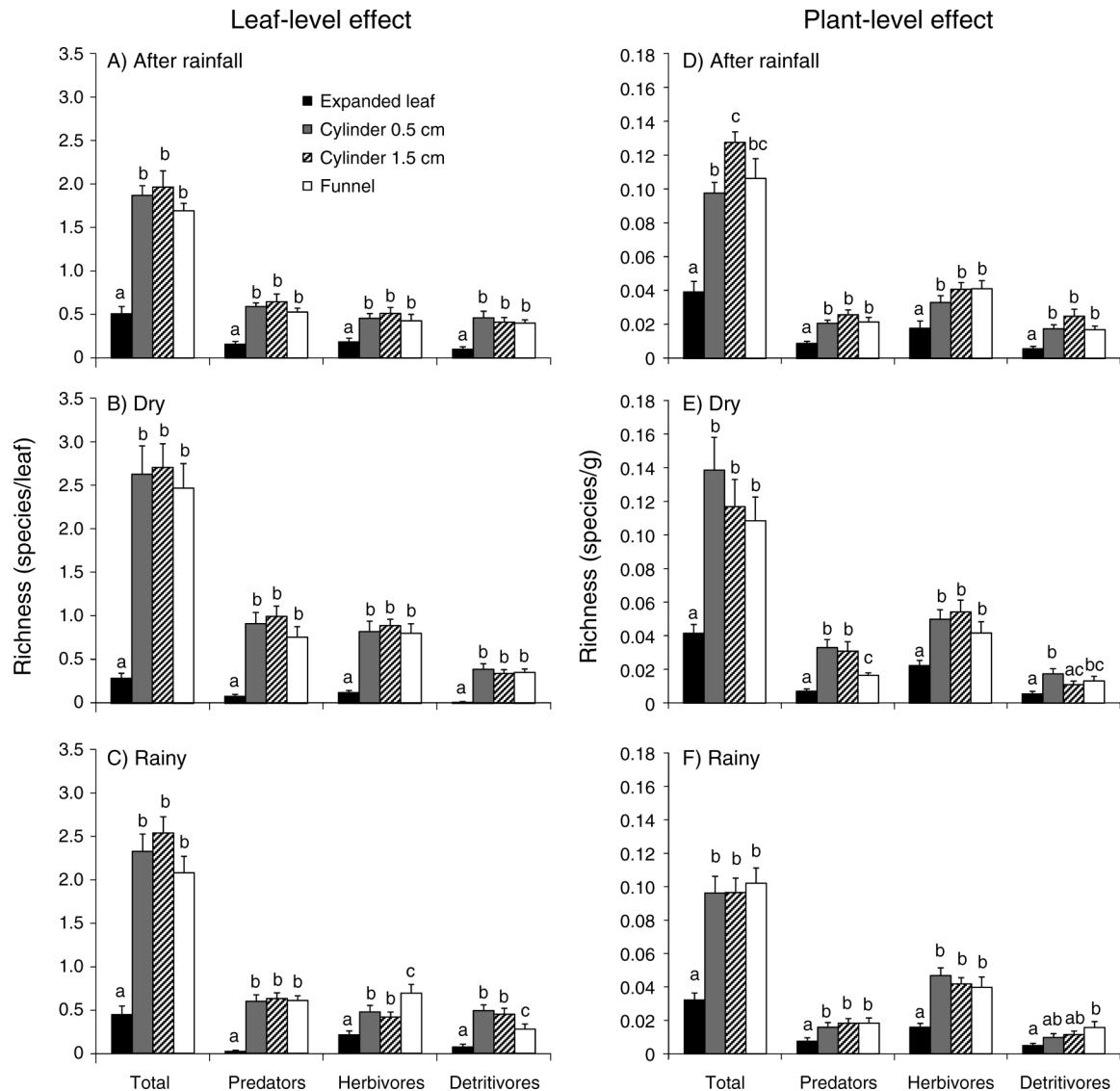


FIG. 2. Total richness of arthropod guilds (predator, herbivore, detritivore) at the leaf and plant level during each season: (A, D) after rainfall, (B, E) dry, and (C, F) rainy. Error bars represent  $\pm$ SE. Different lowercase letters indicate significant differences ( $P < 0.05$ ; ANCOVA/Fisher's LSD post hoc test;  $\alpha = 0.05$ ).

*Species composition: spatial and temporal variations.*— The species composition differed between the treatments at both the leaf-level and plant-level scales (Fig. 3; Appendix J); overall, this difference occurred between unaltered leaves (control) and those rolled, but the community was similar among the treatments in which the leaves were rolled (see Fig. 3 and Appendices J and K). The species composition at the leaf level and plant level exhibited high similarity, i.e., the arthropod communities inside leaf shelters are similar to the plant community as a whole ( $\beta_{sim}$ , after rainfall =  $0.801 \pm 0.021$ , mean  $\pm$  SE; dry period =  $0.830 \pm 0.032$ ; rainy =  $0.801 \pm 0.022$ ). The arthropod species composition throughout the seasons was also similar ( $\beta_{sim}$ , leaf-level comparison, after rainfall vs. dry period =  $0.550 \pm$

$0.020$ ; after rainfall vs. rainy =  $0.500 \pm 0.021$ ; dry vs. rainy period =  $0.510 \pm 0.020$ ; plant-level comparison, after rainfall vs. dry period =  $0.621 \pm 0.020$ ; after rainfall vs. rainy =  $0.601 \pm 0.022$ ; dry season vs. rainy =  $0.573 \pm 0.022$ ).

## DISCUSSION

Our results clearly demonstrate the positive indirect effect of engineering caterpillars as important amplifiers of arthropod diversity on tropical plants. This effect is caused by a biotic element that facilitates the occurrence of arthropods not only at the leaf level but also at the level of the entire plant (plant-level effect). The effect of caterpillars on arthropod communities varied seasonally; a higher arthropod richness occurred on plants with

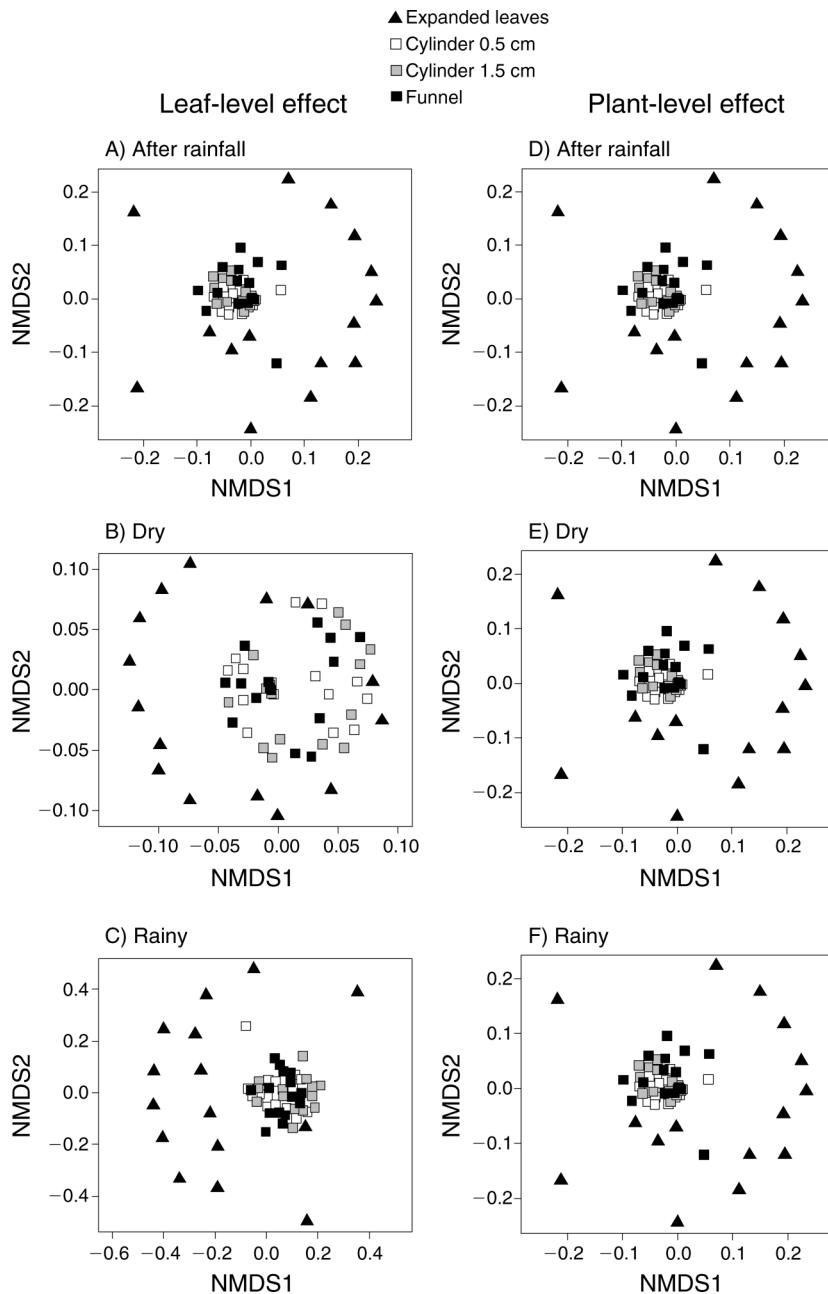


FIG. 3. Graphics of nonmetric multidimensional scaling (NMDS) showing variation in species composition among four treatments, at the leaf and plant level, in three seasonal periods. The stress value was calculated for each graph: (A) stress value = 0.242; (B) stress value = 0.288; (C) stress value = 0.273; (D) stress value = 0.311; (E) stress value = 0.300; (F) stress value = 0.307.

leaf shelters in the dry season. In addition, empty leaf rolls and whole plants were rapidly recolonized by arthropods over time, implying a fast replacement of individuals, and that within 15-day intervals the rolls and plants reached a species saturation. Although observational and experimental studies have reported that leaf-rolling caterpillars increase the arthropod diversity at the local scale (Cappuccino and Martin 1994, Martinsen et al. 2000, Lill and Marquis 2003,

2007, Nakamura and Ohgushi 2003, Ohgushi 2007) and may additionally increase the regional herbivore diversity (Lill and Marquis 2003), this is the first study to show the impact of the engineering caterpillar on diverse arthropod communities, including several guilds on different spatial (leaf and plant effects) and temporal scales (different seasons).

Rolled leaves increased the parameters abundance, richness, and biomass of several arthropod guilds (i.e.,

predators, herbivores, detritivores, omnivores) on plants. However, these parameters overall did not differ between the different types of shelter architecture (funnel and cylinder with different sizes). This finding indicates that the tenant arthropods do not choose specific types of shelter architecture, but rather choose the shelter itself. These results contrast with those found by Wang et al. (2012), who reported a strong variation of inquiline composition and diversity depending on the type of leaflet. As observed in our study, leaf shelters may offer many benefits to their occupants, often serving as a shelter from desiccation or as nesting, and foraging and breeding sites (e.g., Nakamura and Ohgushi 2003), regardless of architecture. In general, leaf shelters also seem to be secondarily colonized by several species of lepidopteran larvae (Fukui 2001). In our study, we observed several Charaxinae larvae occupying shelters, many of which belonged to leaf-rolling species present on *Croton floribundus*. Lepidopteran caterpillars seem to benefit from these leaf shelters because they save time and energy investments in the construction of leaf shelters by occupying preexisting ones (see Fukui 2001). Furthermore, such caterpillars would be exposed to predation for less time. Indeed, shelter building involves high energy costs for Lepidoptera, as the silk is secreted many times to prevent degradation over time and the shelter structure often needs regular maintenance (Ruggiero and Merchant 1986, Fitzgerald et al. 1991). Furthermore, rolled leaves can be a good food resource for larvae as secondary occupants because they have less phenolic compounds and less stiffness when compared to expanded leaves (Fukui et al. 2002).

The magnitude of the engineering effect on arthropod abundance and biomass was higher in the dry season than in the rainy and after rainfall periods at both the leaf- and plant-level scales. These results could be related to differences in the composition of the inquiline species in different seasons. However, similarity analyses indicated that the species composition was similar between seasons (>50% similarity). Therefore, the same species seem to be acting differently in different seasons. For example, some species could be migrating to the interior of the shelters more frequently in dry periods to minimize desiccation. In contrast, Romero and Vasconcelos-Neto (2003) demonstrated a decrease in the abundance of vegetation-dwelling arthropods (without leaf shelters) in the same area in the dry season. Additionally, studies by Wolda (1988) in tropical forests also showed a decrease in the insect abundance and biomass in the dry season. Wolda (1988) questions the fate of arthropods in extreme conditions (dry) in these forests. Our work suggests that some of the arthropods that “disappear” during dry periods may be in shelters such as leaves rolled by engineering larvae. Leaf shelters may protect organisms against desiccation (Fukui 2001), attracting arthropods in particular during periods of low rainfall. Studies support the ideas that insects often

suffer high mortality in immature life stages and factors such as dehydration can affect population dynamics (Cornell and Hawkins 1995). Thus, our study suggests that leaf shelters can function as favorable refuges against drought, although we cannot generalize these results to other dry seasons because of absence of replication (i.e., only one dry season).

The leaf effect engineering extended to the whole plant (plant-level effect). Arthropods sheltered inside the rolls could represent assemblages of prey that attract a different assemblage of predatory arthropods to these plants. It is supposed that plant structures (e.g., leaf domatia) that shelter prey (phytophages) can attract predators and stabilize predator-prey oscillations (Romero and Benson 2004). However, this hypothesis is not supported by the fact that leaf rolls shared a large amount of species with the whole plant (>80% in similarity for all periods). One alternative hypothesis to explain the extent of the engineer effect at the plant scale would be that arthropods are primarily attracted to plant shelters (i.e., modified leaves), and the dense population inside these shelters forces arthropods to colonize other plant parts that have not been modified. Marquis and Lill (2007) proposed this hypothesis for guilds of herbivores (i.e., lepidopteran larvae) on host plants (oaks). In our study, this can be evidenced by the fact that species richness has reached saturation inside leaf rolls in <15 days (see *Materials and methods*), thus limiting space for late colonizers. Another alternative hypothesis is that these arthropods leave the shelter to forage on the host plant and return to rolled leaves later; this was already evidenced for herbivores (e.g., Lill and Marquis 2007). Further studies on arthropod behaviors and population dynamics between plant and shelter could be a suitable topic for future research.

This is the first experimental study to demonstrate the effect of engineering caterpillars on diverse arthropod communities at both spatial (leaf level and plant level) and temporal scales (dry to wet season). According to Jones et al. (1994) and Hastings et al. (2007), the impact of the biotic interaction of the engineer depends on the spatial and temporal scales of their actions, as well as on the engineer activity time, population density, spatial distribution, and number of species affected by their changes. Here we showed that engineering caterpillars changed species composition, and their effects extended to a large spatial scale (local and regional), equivalent to the beaver engineering effects, for example. Additionally, caterpillar-abandoned leaf shelters are common in natural forests (Cappuccino and Martin 1994), have a wide spatial distribution, and may remain in nature for a large time scale, thus indirectly influencing the community of conspecific and heterospecific species for up to a year (C. Vieira and G. Q. Romero, *personal observations*). The numerous species of leaf-rolling caterpillars represent a large portion of the Lepidoptera fauna in forests. For example, 60% of the caterpillars in Costa Rican forests build shelters (Janzen 1988). Because these

caterpillars are ubiquitous organisms in both temperate and tropical regions and can act as facilitators of other species, they can be considered key elements in structuring arthropod communities on plants.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

Photos from the study system and experimental design ([Ecological Archives E094-137-A1](#)).

##### Appendix B

The fauna, climate, and natural history of the system ([Ecological Archives E094-137-A2](#)).

##### Appendix C

Data on surveys of arthropods from several guilds ([Ecological Archives E094-137-A3](#)).

##### Appendix D

Results of MANCOVAs ([Ecological Archives E094-137-A4](#)).

##### Appendix E

Data on abundance of arthropods from varying guilds collected during the experiments ([Ecological Archives E094-137-A5](#)).

##### Appendix F

Data on biomass of arthropods from varying guilds collected during the experiments ([Ecological Archives E094-137-A6](#)).

##### Appendix G

Data on richness of arthropods belonging to the guilds' parasitoids, parasites, and omnivores collected during the experiments ([Ecological Archives E094-137-A7](#)).

##### Appendix H

Univariate analyses of covariance (ANCOVA) ([Ecological Archives E094-137-A8](#)).

##### Appendix I

Sample-based and individual-based rarefaction curves ([Ecological Archives E094-137-A9](#)).

##### Appendix J

Analysis of similarity (ANOSIM) and similarity percentage (SIMPER) comparing species composition among treatments ([Ecological Archives E094-137-A10](#)).

##### Appendix K

Nonmetric multidimensional scaling (NMDS) with stable solution from random starts, axis scaling, and species scores ([Ecological Archives E094-137-A11](#)).