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Herbivorous mites as ecological engineers: indirect effects on arthropods inhabiting papaya foliage

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Abstract We examined the potential of a leaf roller to indirectly influence a community of arthropods. Two mite species are the key herbivores on papaya leaves in Hawaii: a spider mite, *Tetranychus cinnabarinus* Boisduval, and an eriophyid mite, *Calacarus flagelliseta*, which induces upward curling of the leaf margin at the end of the summer when populations reach high densities. A survey and three manipulative field experiments demonstrated that (1) leaf rolls induce a consistent shift in the spatial distribution of spider mites and their predators, the coccinellid *Stethorus siphonulus* Kapur, the predatory mites *Phytoseiulus* spp., and the tangle-web building spider *Nesticodes rufipes* Lucas; (2) the overall abundance of spiders increases on leaves with rolls; (3) the specialist predators *Stethorus* and *Phytoseiulus* inhabit the rolls in response to their spider mite prey; and (4) the spider inhabits the rolls in response to the architecture of the roll itself. This study shows the importance of indirect effects in structuring a terrestrial community of herbivores.

Keywords Herbivory · Leaf rolling · Plant architecture · Spider

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Introduction

Ecologists are increasingly appreciating the importance of indirect interactions in structuring animal communities (Strauss 1991; Wootton 1994; Polis and Winemiller 1996; Janssen et al. 1998). For arthropod communities in particular, indirect interactions can be mediated by shelters created by one species and subsequently used by another species (Damman 1993).

Shelter building through leaf rolling, folding, or tying is a common behavior among several arthropod taxa, including caterpillars (Lepidoptera), sawflies (Hymenoptera: Pamphiliidae), weevils (Coleoptera: Attelabidae), and herbivorous mites in the superfamily Eriophyoidea (Acari) (Frost 1959; Keifer et al. 1982; Castagnoli 1996; Westphal and Manson 1996). By protecting residents from natural enemies, providing a suitable microenvironment for development, or reducing effects of plant defenses, leaf shelters may have strong impacts on the survivorship, abundance, distribution, and diversity of other plant-dwelling arthropods (reviewed in Fukui 2001). For example, leaf rolling by early-season lepidopterans facilitates later colonization and survival by late-season lepidopterans (Cappuccino 1993). Leaf rolls made by lepidopteran larva on cottonwood trees enhance arthropod abundance sevenfold and biodiversity fourfold (Martinsen et al. 2000). Leaf rollers exemplify "bioengineers" or "physical ecosystem engineers," organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic and abiotic materials (Jones et al. 1997).

Here we report a study in which a herbivorous mite modifies the architecture of its host plant, papaya, by inducing leaf rolls. We conducted a survey and three manipulative field experiments to address the following questions: (1) Do leaf rolls modify the spatial distribution of foliar arthropods in the community? (2) Do leaf rolls change the population densities of arthropods in the community? (3) Do predators colonize leaf rolls in response to the architecture of the rolled leaf itself or in response to spider mite prey?

Materials and methods

Study system

Papaya (*Carica papaya* L., Caricaceae) is a short-lived perennial crop, native to Central America (Storey 1976). Papaya trees in commercial orchards typically consist of a single erect stem with a terminal crown of about 25–30 large leaves. The midrib of mature leaves reaches 35–40 cm in length, and the total leaf area averages approximately 1,000 cm^2. Leaves are held on long petioles (45–70 cm in length) that extend horizontally from the trunk. New leaves are produced year-round, emerging from the growing point at the tip of the trunk. They are palmately lobed and usually possess seven major fingers, each of which is subdivided into 3–8 minor fingers, for a total of 40–50 fingers per leaf (Fig. 1). The life span of a papaya leaf varies from 75 to 125 days in a pesticide-free orchard (V. Fournier, unpublished data).

The community of arthropods inhabiting papaya foliage in Hawaii includes two key herbivorous mites: the host-specific eriophyid mite, *Calacarus flagelliseta* Fletchmann, DeMoraes, and Barbosa (Acari: Eriophyidae), and the polyphagous carmine spider mite, *Tetranychus cinnabarinus* Boisduval (Acari: Tetranychidae). The most common predators in the system are the predatory mites *Phytoseiulus macropilis* Banks and *P. persimilis* Athias-Henriot (Acari: Phytoseiidae), the beetle *Stethorus siphonulus* Kapur (Coleoptera: Coccinellidae), and the tangle-web building spider *Nesticodes rufipes* Lucas (Araneae: Theridiidae) (Esguerra and Haramoto 1980; Rosenheim et al., unpublished data). The phytoseiid mites and the coccinellid are specialist consumers of spider mites (Prasad 1973; Raros and Haramoto 1974), whereas the spider *Nesticodes*, which spins a sparse and hardly discernable web at the junction of leaf veins, is a generalist that preys upon a wide variety of arthropods (Barreto et al. 1987; Cushing and LeBeck 1994; Fox 1998), including the carmine spider mite (Esguerra and Haramoto 1980), *Stethorus*, and *Phytoseiulus* spp. (Rosenheim et al., unpublished data) (Fig. 2). No natural enemies of the eriophyid mite are known to occur in Hawaii (V. Fournier, personal observation).

The eriophyid *Calacarus* can colonize both the surfaces of papaya leaves and the fruits (*C. citrifolii* in Jeppson et al. 1975; Fletchmann et al. 2001), but it prefers the lower (abaxial) surface of leaves (V. Fournier, unpublished data). These herbivorous mites tend to shift to the upper (adaxial) leaf surface when densities on the lower surface become high (>10,000 adults/leaf). When moving from the lower to the upper surface of the leaf, the mites first infest the upper leaf margin and induce the edge to curl upward. Curling may occur on some or all of the fingers of a leaf, with a heavily infested leaf supporting from 25 to 45 rolled leaf segments. When leaf rolling is very severe, the rolls may form complete tubes. Rolls are about 10 cm in length and 2 cm in diameter. Usually, only the leaves located in the middle and lowest parts of the canopy crown are affected by rolling (V. Fournier, personal observation). *Calacarus* infests papaya all year long, but leaf rolling is mostly observed in the late summer, when population densities peak (V. Fournier, unpublished data).

When papaya leaves are unrolled, the spider mite and its predators usually inhabit the lower leaf surfaces (Esguerra and Haramoto 1980). However, when the leaves are rolled by *Calacarus* mites, preliminary observations suggested that members of the arthropod community may colonize the upper surfaces of leaves within the leaf rolls and coexist there with the leaf edgeroller mites.

Experimental site

Our research was conducted at the University of Hawaii Poamoho Experimental Station on Oahu, Hawaii, during the summers of 2001 and 2002. Trees used in this study were from pesticide-free papaya plots (Solo variety, cv. X77). They were 8 months old and approximately 1.75 m tall in 2001 and 20 months old and 3.5 m tall in 2002.

Survey

We measured arthropod distribution and abundance on papaya leaves with and without rolls. We censused insects, mites, and arachnids on 13–16 August 2001, when the density of the leaf edgeroller mite population peaked and leaves began to roll. We surveyed 50 mid-crown leaves, 25 with rolls and 25 without rolls,

Fig. 1 *Carica papaya* leaf and a leaf roll. Papaya leaves are palmately lobed and usually possess seven major fingers, each of which is subdivided into three to eight minor fingers. When densities of *Calacarus flagelliseta* peak and trigger the edge of the leaves to curl upward, each one of the minor fingers can roll and form a complete tube

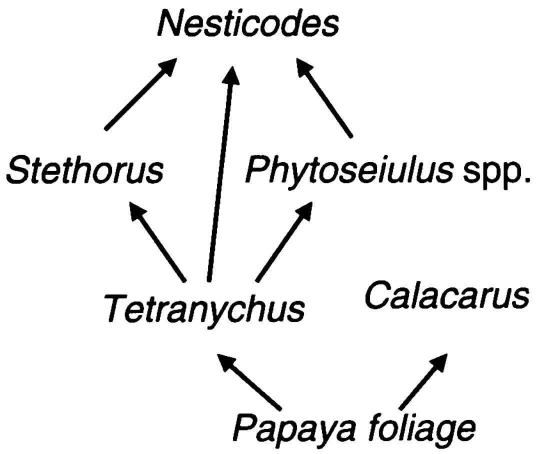

Fig. 2 Simplified food web of the key herbivores and predators occurring on papaya leaves

distributed over several trees. We sampled both rolled and unrolled leaves located on the same tree.

We counted individuals of the following arthropods: (1) the herbivores: the eriophyid mite *Calacarus* (all motile instars, subsampling technique described below) and the carmine spider mite *Tetranychus* (adult females); and (2) the predators: the predatory mites *Phytoseiulus* spp. (adult females), the beetle *Stethorus* (all stages, including eggs), the tangle-web building spider *Nesticodes* (motile instars), and other spiders, including primarily jumping spiders (Araneae: Salticidae) (motile instars). Arthropod densities were assessed on upper and lower leaf surfaces. Eriophyid mite populations can be very large (up to 100,000 mites/leaf; J. A. Rosenheim, unpublished data). Thus, we subsampled individuals using a 2.5×2.5 cm grid (collapsible magnifier, Bioquip Products Inc., Garneda, Calif., USA) as a subsample unit. We randomly selected four subsamples on each side of the leaf and counted all motile instars of *Calacarus*. We also recorded the number of fingers that were rolled on each sampled leaf.

Our survey was performed when some but not all of the mid-crown leaves of the orchard were rolled. There are two potential problems associated with this non-manipulative approach. First, despite our attempts to choose equivalent leaves in the mid-crown canopy, rolled leaves are likely to be older than unrolled leaves because leaves take some time to roll. Second, high densities of *Calacarus* mites cause the rolled leaves to senesce quickly (V. Fournier, unpublished data). Each of these factors may influence arthropod densities in addition to the rolled versus unrolled state. We circumvented problems with such confounding variables by conducting experiments in which we created artificial papaya leaf rolls.

Manipulative experiment: spatial distribution and abundance

We repeated this experiment twice in different papaya fields: 3–18 July 2001 (experiment 1a), and 16 July–9 August 2001 (experiment 1b). We chose to conduct the manipulative experiments just prior to the onset of natural leaf rolling so that we could observe an arthropod fauna similar to that observed under natural leaf rolling. We made artificial rolls using either rubber bands (experiment 1a; 12PCI, Continental Western Corporation, San Leandro, Calif., USA) or wire rings (experiment 1b; Steelwire galvanized, 28 gauge, Elco, Textron Logistics Co., Rockford, Ill., USA). Preliminary tests indicated that rubber bands and wires were not dislodged by the wind and did not damage the leaves. The experimental unit was a single leaf. Ten and 15 fingers were rolled per leaf in experiment 1a and experiment 1b, respectively. We also controlled for a possible effect of rubber bands and wire rings by fitting leaf fingers with rubber bands or wires without forming rolls. Leaves were randomly assigned to one of three treatments: (1) no rolls (unmanipulated control); (2) presence of wires or rubber bands but no rolls (wire/rubber band control); or (3) artificial rolls. Identical numbers of rubber bands or wire rings were used in treatments 2 and 3.

Experiment 1a comprised 30 replicates of each treatment (total of 90 leaves) distributed over 22 trees. Experiment 1b comprised 51 replicates of each treatment (total of 153 leaves) over 37 trees. All experimental leaves were located at the mid-crown height of the trees to standardize leaf age and reduce the effect of leaf senescence. Experiments ran until the experimental leaves started showing signs of senescence and/or natural rolling. Experiment 1a ran for 15 days, and experiment 1b ran for 26 days (at 30 °C the carmine spider mite requires 6–7 days to develop from egg to adult [Hazan et al. 1973]). Arthropod densities on upper and lower leaf surfaces were estimated weekly using the non-destructive sampling procedures described above. Artificial rolls were sampled by gently removing the rubber bands/wire rings, counting the arthropods, and then carefully replacing the roll; this produced minimal disturbance to the resident arthropods. Missing rubber bands or wire rings were replaced once a week.

Manipulative experiment: mechanisms behind the predator responses

We conducted a second manipulative experiment (experiment 2) from 2–11 July 2002 to determine whether the predators *Phytoseiulus*, *Stethorus*, and *Nesticodes* colonize rolls in response to the presence of spider mite prey within rolls or in response to the roll architecture. We set up 15 replicates of each of the following treatments: (1) no rolls, no spider mites on the upper leaf surface; (2) artificial rolls, spider mites on the upper leaf surface (i.e., in the rolls); and (3) artificial rolls, no spider mites in the rolls. Thus the experiment was an incomplete 2×2 factorial design in which the treatment "no rolls, spider mites on the upper leaf surface" was missing because spider mites are difficult to maintain on the upper leaf surface when rolls are absent. For treatments 2 and 3, 10 fingers per leaf were rolled using wire rings. In treatments 1 and 3, spider mites were removed from the upper surface daily by using a paintbrush. Densities of *Nesticodes*, *Stethorus*, and *Phytoseiulus* on upper leaf surfaces were recorded every morning, and all spiders were subsequently removed to prevent predation on *Stethorus*.

Statistical analysis

Data from the survey and experiments 1a and 1b did not meet the assumption of normality and homogeneity of variance. We therefore used non-parametric Wilcoxon rank-sum tests to compare arthropod densities on rolled versus unrolled leaves (JMP 2000). In experiments 1a and 1b, we tested for main effects of leaf rolling on the density of arthropods by summing across all samples taken from the end of the first week until the end of the experiments.

For experiment 2 we evaluated the effects of leaf rolls and spider mites on the mean density of *Stethorus*, *Phytoseiulus*, and *Nesticodes* over the course of the experiment using a two-way ANOVA (JMP 2000) with rolls and spider mites as the main effects. For *Stethorus*, the statistical analysis was performed on the mean density of eggs, larvae, and pupae combined. We excluded adult coccinellids because they can be very mobile (J.A. Rosenheim et al., unpublished) and were commonly found on upper leaf surfaces in all treatments during the course of this experiment ($F_{2,45}$=0.65, P=0.53).

Results

Survey

On average, rolled leaves (*n*=25) had 60% of their fingers rolled (range: 22–100%), whereas unrolled leaves (*n*=25) had 4.4% of their fingers rolled. The high incidence of leaf rolling across the field prevented us from finding leaves with none of their fingers rolled; therefore, we will use the terminology "lightly rolled" leaves versus "heavily rolled" leaves. Heavily rolled leaves had significantly higher densities of *Calacarus* on their upper surface (X^2=10.4, *df*=1, *P*=0.001, *n*=10; Fig. 3A) and significantly lower densities of *Calacarus* on their lower surface compared to lightly rolled leaves (X^2=16.3, *df*=1, *P*=0.0001; *n*=10; Fig. 3A).

Heavily rolled leaves had significantly higher densities of spider mites on their upper surface (X^2=11.3, *df*=1, *P*=0.0008; *n*=25; Fig. 3B) and significantly lower densities of spider mites on their lower surface compared to lightly rolled leaves (X^2=7.7, *df*=1, *P*=0.005; *n*=25; Fig. 3B). Heavily rolled leaves had higher densities of the beetle *Stethorus* on their upper surface (X^2=3.7, *df*=1, *P*=0.054; *n*=25), whereas similar densities of the beetle occurred on the lower surfaces of heavily and lightly rolled leaves (Fig. 3C).

Nesticodes dominated the spider community (99% of all sampled individuals [*n*=277]). *Nesticodes* were almost completely absent from the upper surface of lightly rolled leaves but achieved high densities on the upper surface of heavily rolled leaves (X^2=21.8, *df*=1, *P*=0.0001, *n*=25; Fig. 3D). *Nesticodes* densities on the lower surfaces of heavily rolled and lightly rolled leaves did not differ, and thus, total *Nesticodes* density (upper + lower leaf surfaces) increased substantially on heavily rolled leaves (X^2=7.7, *df*=1, *P*=0.006, *n*=25; Fig. 3D).

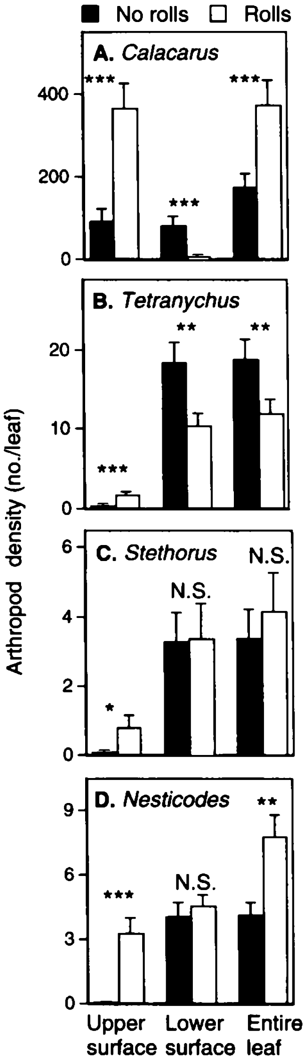

Fig. 3A–C Survey of heavily rolled (rolls) versus lightly rolled leaves (no rolls). Shown are the mean densities (+1SE) of arthropods on the upper leaf surface, lower leaf surface, and both leaf surfaces (entire leaf) of **A** *Calacarus flagelliseta* (motile instars); **B** *Tetranychus cinnabarinus* (adults); **C** *Stethorus siphonulus* (all instars combined); and **D** *Nesticodes rufipes* (motile instars). The symbols above the error bars report the results of pairwise contrasts performed with Wilcoxon rank-sum tests, where * $P<0.05$, ** $P<0.01$, *** $P<0.001$, and *n.s.* not significant at α=0.05

Manipulative experiment: spatial distribution and abundance

Experiment 1a

Attaching rubber bands to leaves without producing artificial rolls had no significant effects on the arthropod densities on either leaf surface (Fig. 4A, C, E).

The initial density of spider mites was approximately 10 adults per leaf for all treatments, none of them located on the upper leaf surface. A substantial population of spider mites became established on the upper leaf surface of artificially rolled leaves (X^2=33.28, *df*=1, *P*=0.0001; Fig. 4A). Leaf rolling did not have a significant influence on spider mite densities on the lower leaf surface, and the increase in the total mite population (upper + lower leaf surfaces combined) was not statistically significant (Fig. 4A). The predatory beetle *Stethorus* responded to the leaf rolling treatment with increased density on the upper leaf surface (X^2=5.35, *df*=1, *P*=0.02; Fig. 4C), but there was no increase in its overall abundance (upper + lower leaf surfaces) (Fig. 4C). The other specialist predator of spider mites, *Phytoseiulus*, responded similarly to leaf rolling, with increased density on the upper leaf surface (X^2=3.0, *df*=1, *P*=0.08).

The spider community was dominated by *Nesticodes*, which constituted 97.3% of all sampled individuals (*n*=665) and initially built all of its webs on the lower leaf surface. *Nesticodes* responded strongly to the leaf rolling treatment, colonizing the upper leaf surface and nearly doubling their total population density per leaf (upper leaf surface: X^2=36.75, *df*=1, *P*=0.0001; entire leaf: X^2=19.76, *df*=1, *P*=0.0001; Fig. 4E).

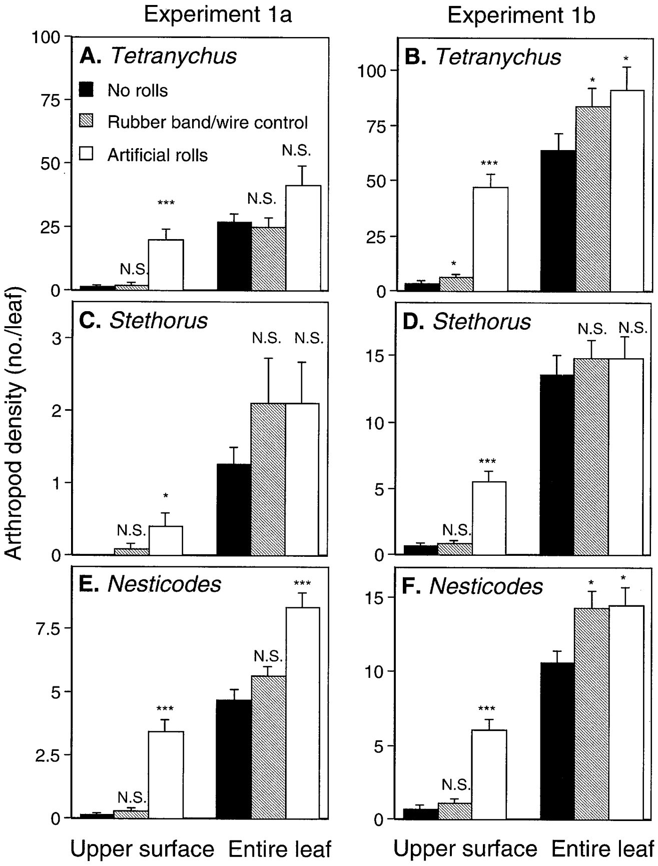

Fig. 4A–F Influence of artificial leaf rolls on the summation of mean densities (±1SE) across 3–18 July (experiment 1a) and 16 July–9 August 2001 (experiment 1b) of **A**, **B** *Tetranychus cinnabarinus* (adults), **C**, **D** *Stethorus siphonulus* (all instars combined), and **E**, **F** *Nesticodes rufipes* (motile instars) on the upper leaf surface and the entire leaf (upper + lower leaf surfaces). Treatments included (1) no rolls, *solid bars*; (2) no rolls but presence of rubber bands or wires (rubber bands/wires control), *hatched bars*; and (3) artificial rolls, *open bars*. Each treatment was replicated 30 times in experiment 1a and 51 times in experiment 1b. The symbols above the error bars report the results of pairwise contrasts performed with Wilcoxon rank-sum tests (treatments 2 and 3 were compared to the control [1]); * $P<0.05$, *** $P<0.001$, and *n.s.* not significant at $\alpha=0.05$

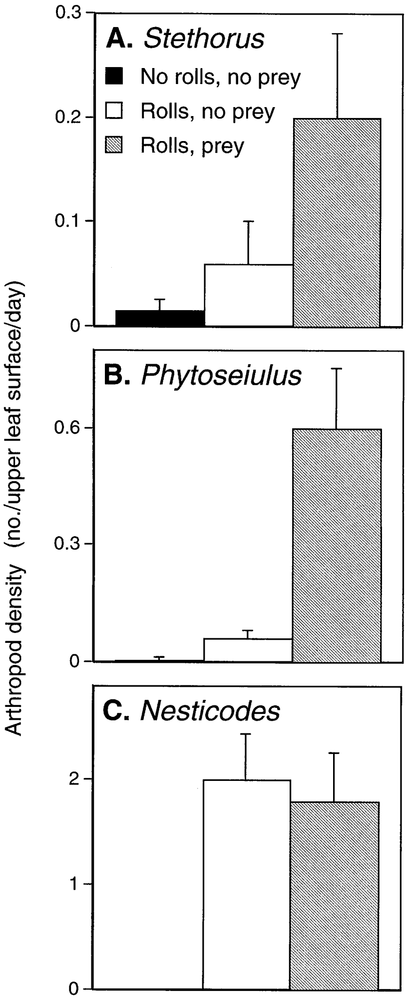

Fig. 5A–C Mechanisms behind predator responses to leaf rolls: do the predators colonize rolls in response to their spider mite prey or in response to the roll architecture? Shown are daily mean densities (+1SE) of **A** *Stethorus siphonulus* (eggs, larvae, and pupae), **B** *Phytoseiulus* spp. (adults), and **C** *Nesticodes rufipes* (all motile instars) on the upper surface of (1) unmanipulated leaves (no rolls, no prey; *solid bars*), (2) artificially rolled leaves with no spider mites in the rolls (rolls, no prey; *open bars*), and (3) artificially rolled leaves with spider mites in the rolls (rolls, prey; *hatched bars*). Each treatment was replicated 15 times

Experiment 1b

We established the same three treatments as in experiment 1a, with the exception that artificial rolls were created using wires. We preferred wires to rubber bands because we could produce artificial rolls that more closely mimicked the *Calacarus*-produced rolls. We found, however, that the wires did have a positive, direct effect on spider mite and spider densities (Figs. 4B, F). Direct effects of the wires on arthropod abundance on the upper surface of leaves were modest in magnitude (Fig. 4B); thus, we expect that most of the effects of the artificial leaf rolls can be attributed to leaf architecture rather than the presence of wires. However, the magnitude of the wire effect was larger at the level of the entire leaf (Figs. 4B, F), because the wires increased spider mite and spider densities on the lower surface of leaves (data not shown). We do not know why the wires produced this positive effect on the lower surface of unrolled leaves (with wires) and not on the lower surface of artificially rolled leaves. Despite the direct effect of wires, the results obtained in experiment 1b were congruent with those obtained in experiment 1a (Fig. 4).

For all treatments, initial densities of spider mites were 10 adult females per leaf, and, with the exception of one individual found on the upper surface, all spider mites were located on the lower leaf surface. A substantial population of spider mites became established on the upper leaf surface of artificially rolled leaves ($X^2=52.78$, $df=1$, $P=0.0001$; Fig. 4B), generating an increase in the total population of spider mites on rolled leaves ($X^2=3.78$, *df*=1, *P*=0.05; Fig. 4B). Artificially rolled leaves had significantly higher densities of the predatory beetle *Stethorus* on their upper leaf surface compared to unrolled leaves (X^2=32.4, *df*=1, *P*=0.0001; Fig. 4D), but this increase did not translate into higher densities at the level of entire leaf (upper + lower leaf surfaces; Fig. 4D).

Once again, the spider community was dominated by *Nesticodes*, which constituted 96.8% of all sampled individuals (*n*=2,382). At the beginning of the experiment, 99.5% of the spiders were recorded on lower leaf surfaces. As in experiment 1a, *Nesticodes*' response to the leaf-rolling treatment was strong: spiders colonized the upper leaf surfaces (i.e., artificial rolls) (X^2=52.07, *df*=1, *P*=0.0001; Fig. 4F), and the total population density (upper + lower leaf surfaces) increased significantly (X^2=5.02, *df*=1, *P*=0.02; Fig. 4F).

Mechanisms behind the predator responses

The two specialist predators appeared to move into leaf rolls in response to the presence of their spider mite prey (*Stethorus*: spider mite effect: $F_{1,45}$=3.17, *P*=0.08; roll effect: $F_{1,45}$=0.35, *P*=0.56; Fig. 5A; *Phytoseiulus* spp.: spider mite effect: $F_{1,45}$=17.96, *P*=0.0001; roll effect: $F_{1,45}$=0.17, *P*=0.68; Fig. 5B). The small and non-significant increases in the densities of *Stethorus* and *Phytoseiulus* on rolled leaves from which we attempted to remove spider mites were likely in response to the spider mites that colonized the leaf rolls between the daily removals. In contrast, the spider *Nesticodes* moved into leaf rolls in response to the roll architecture, with no additional response to the presence of spider mite prey (spider mite effect: $F_{1,45}$=0.15, *P*=0.7; roll effect: $F_{1,45}$=14.92, *P*=0.0004; Fig. 5C).

Discussion

The eriophyid mite *Calacarus* causes community-level indirect effects mediated through its production of leaf rolls. Both our survey and manipulative experiments showed that leaf rolls altered the spatial distribution of spider mites and their specialist predators, *Phytoseiulus* spp. and *Stethorus*, and enhanced the total abundance of the tangle-web spider *Nesticodes*. Moreover, our study demonstrated that shifts in arthropod community structure can take place over a very short period of time (i.e., within 15–26 days). Finally, both specialist predators appeared to colonize rolls in response to the presence of their spider mite prey, whereas the tangle-web spider seemed to inhabit rolls in response to the architecture of the roll itself.

In this study we did not attempt to study the direct interactions between *Calacarus* and its papaya host plant. We do not know, for example, whether leaf rolling is actively initiated by *Calacarus* or whether it is simply a plant response to feeding damage generated by the mite. Furthermore, we do not know if the rolls provide benefits to *Calacarus*. The leaf rolls do shield *Calacarus* mites from direct exposure to sun and desiccation. This may be important, given that *Calacarus* prefers to inhabit the shaded lower surfaces of papaya leaves and never builds to high populations on the upper surfaces of the leaves until rolls appear (V. Fournier, unpublished data).

Use of leaf rolls by spider mites

We demonstrated that leaf rolling consistently led to spider mites rapidly colonizing the upper leaf surface to inhabit the rolls, whereas unrolled papaya leaves rarely harbored spider mites on their upper surface. Moreover, overall densities of spider mites tended to be higher on rolled leaves than on unrolled leaves, suggesting that such leaves may offer some advantages over unrolled leaves. We discuss two non-exclusive hypotheses to address why spider mites move into leaf rolls.

First, spider mites may colonize leaf rolls because these structures produce a microenvironment that is similar to their normal habitat, the lower leaf surface. Like spider mites residing on the lower leaf surface, individuals inhabiting leaf rolls achieve protection from direct exposure to sunlight, rain, and wind. These climatic factors can be harmful to spider mites in the genus *Tetranychus* (Putman 1970; Tulisalo 1974; Barcelo 1981). Moreover, preliminary measurements suggest that leaf rolls might offer an even more suitable microenvironment for spider mites than is provided by the lower surface of leaves, because temperatures inside leaf rolls are slightly higher than on the lower leaf surface (inside rolls: 34.26±0.27 °C; outside rolls on upper surface: 33.96±0.45 °C; lower surface: 32.94±0.28 °C; *n*=5; *F*=4.05, *df*=2, *P*=0.045; measured during the daytime). Spider mites develop more rapidly with increasing temperature until an upper threshold is reached (Hazan et al. 1973; Holtzer et al. 1988; Roy et al. 2002). Finally, leaf roll curvature also provides suitable attachment points for spider mite webbing.

Second, spider mites may move into leaf rolls to escape specialist predators. The idea that leaf rolls may act as a refuge from predation is supported by some studies (Heads and Lawton 1985; Damman 1987; Altegrim 1992; Eubanks et al. 1997). Our study was not designed to assess the risk of predation experienced by spider mites on rolled versus unrolled leaves. However, other work conducted in this system suggests the possibility that the colonization of leaf rolls by *Nesticodes* may protect spider mites in rolls from predation by *Stethorus*. *Nesticodes* are predators of *Stethorus* and can disrupt the ability of *Stethorus* to suppress spider mite populations (J.A. Rosenheim et al., unpublished; Rosenheim and Corbett 2003). Additional work is necessary to evaluate the hypothesis that spider mites experience reduced risk of predation in rolled leaves.

Use of leaf rolls by specialist predators

We found that both specialist predators of the carmine spider mite, *Phytoseiulus* and *Stethorus*, moved into the rolls in response to their prey rather than in quest of a shelter. A similar question was addressed by Martinsen et al. (2000), who examined arthropod abundance and diversity in leaf rolls on cottonwood inhabited by larvae of the leaf roller *Anacampsis niveopulvella* (Chambers) (Lepidoptera: Gelechiidae). They found that experimental rolls supported a similar number of taxa and an even greater abundance of arthropods than natural rolls. They argued that the presence of arthropods in leaf rolls was motivated by the protection they provided rather than the food (lepidopteran larvae) they contained. However, a more detailed analysis revealed that while the abundance of herbivores was higher in artificial rolls than in natural rolls, the abundance of predators was actually lower in artificial rolls, suggesting that some predators may be attracted by food rather than shelter.

Use of leaf rolls by spiders

Our study showed a strong positive response of *Nesticodes* to leaf rolling: leaf rolling not only modified the spatial distribution of *Nesticodes* but also enhanced its total abundance. We also demonstrated that spiders colonize leaf rolls in response to the roll architecture.

Both prey availability and the physical structure of the habitat can influence spider population densities (Wise 1993). Spiders can display numerical responses through either aggregation or reproduction (Olive 1982; Rypstra 1985; Wise 1993), and vegetation structure has been shown to influence species composition, abundance, and habitat selection by spiders (Robinson 1981; Rypstra 1983, 1986; Greenstone 1984; Gunnarson 1990; Wise 1993; Halaj et al. 1998, 2000; Rypstra et al. 1999; McNett and Rypstra 2000; Sunderland and Samu 2000). Most of these studies suggest that the more complex the vegetation structure, the more diverse and/or abundant the arachnid fauna. McNett and Rypstra (2000) showed that the primary factor in the selection of a new habitat by the orb weaver *Argiope trifasciata* Forskal (Araneae: Araneidae) was the structure of the vegetation rather than prey availability. More complex habitats may attract prey or provide shade, protection from the wind, spaces for retreats, or attachment sites for the snares of web weavers (Wise 1993).

Unexpectedly, the wire rings we used to make artificial rolls on papaya leaves significantly increased *Nesticodes* densities, probably by providing additional web-site attachment points. In contrast, the rubber bands did not generate a direct effect. Therefore, it is likely that we overestimated the effects of leaf rolls on *Nesticodes* in experiment 1b. The remaining community members showed consistent responses to artificial rolls made with either rubber bands or wires.

Knowledge of the source of spiders inhabiting the rolls would contribute to understanding microhabitat selection by *Nesticodes* and the mechanisms leading to an increase in its total abundance. *Nesticodes* that colonized experimental rolls may have come from populations found on (1) the lower surface of rolled leaves, (2) unrolled leaves from the same tree, (3) unrolled leaves from other papaya trees, or (4) other plant species in the habitat. *Nesticodes* is common in many agricultural systems on Oahu, Hawaii (Hooks and Johnson 2002). Leaf rolling might simply redistribute spiders at the level of the papaya field, or might actually generate an increase in the total population density of *Nesticodes*. In the latter case, leaf rolling might have consequences for herbivory imposed on papaya. Larger *Nesticodes* populations might increase spider mite densities, as *Nesticodes* can disrupt the natural control of spider mites by preying upon *Stethorus* (J.A. Rosenheim et al., unpublished; Rosenheim and Corbett 2003).

Herbivorous mites as ecological engineers

Jones et al. (1994) have suggested that the impact of an ecological engineer depends upon the spatial and temporal scale of its actions. They listed several factors likely to scale the impact of engineering: (1) the lifetime per capita activity of individual organisms; (2) the density of the engineering population; (3) the spatial distribution, both locally and regionally, of the population; (4) the length of time the population has been present at the site; (5) the durability of the engineered construct in the absence of the original engineer; (6) the number and types of resource flows that are modulated by the constructs; and (7) the number of other species dependent upon these flows. The herbivorous mite *Calacarus* does reach large population densities on papaya leaves (100,000 mites/leaf; J.A. Rosenheim, unpublished data) and is generally distributed relatively uniformly in papaya fields, producing field-wide leaf rolling (V. Fournier, unpublished data). However, the physical engineering by *Calacarus* gives rise to structures that persist for only approximately 4–6 months per year in papaya. Furthermore, although leaf rolling seems to modulate resource flows by increasing spider abundance, *Nesticodes* is not dependent upon these flows to colonize papaya leaves. Therefore, with regard to Jones et al.'s (1994) criteria, the ecological and evolutionary consequences of engineering by the eriophyid mite in the papaya agroecosystem may be relatively modest. Nevertheless, leaf rolling, although transient, may have large, direct short-term effects on spider mites and *Nesticodes* as well as indirect effects on *Stethorus* and *Phytoseiulus*. In years when spider mite outbreaks occur, indirect effects may also extend to the performance of the host plant. Thus, *Calacarus*, by producing leaf rolls, may have important indirect effects on this plant-herbivore-natural enemy community.

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