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ARTHROPOD COMMUNITY STRUCTURE ON BARK OF KOA (ACACIA KOA) AND 'ŌHI'A (METROSIDEROS POLYMORPHA) AT HAKALAU FOREST NATIONAL WILDLIFE REFUGE, HAWAI'I ISLAND, HAWAI'I

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ABSTRACT

The arthropod community associated with tree bark contains a wide variety of taxa but is poorly described, particularly in Hawai'i. Our overall goals were to evaluate the abundance of arthropods available to foraging birds and how variation in bark substrates may contribute to arthropod distributions in native forests. Our study aimed to identify this fauna on the dominant canopy-forming trees koa (Acacia koa) and 'ōhi'a (Metrosideros polymorpha) within wet montane forest at Hakalau Forest National Wildlife Refuge, Hawai'i Island. At two sites roughly similar in elevation and habitat structure, we deployed three trap types designed to intercept arthropods moving along bark within tree canopies; a bole trap based on a pre-existing design and two traps specially designed for this study. Bole traps were placed on koa and 'ōhi'a while branch traps were established on large and small branches of 'ōhi'a. In total, 15 arthropod orders were identified, with Collembola most abundant (number/trap-day) generally followed by Isopoda and Araneae. Differences in abundance were found in some instances, but overall, few differences were detected between tree species or sites. Relative abundances of arthropod groups were also generally similar between trees and sites and among different parts of 'ōhi'a. These results indicate that bark-dwelling arthropod communities are similar on koa and 'ōhi'a, and birds should not develop strong preferences for gleaning arthropods from the bark of either species of tree based on prey availability.

INTRODUCTION

The arthropod fauna found on and within tree bark is comprised of a diverse assemblage of taxa represented by several functional guilds. Bark characteristics vary among tree species, providing a range of habitats for obligate bark dwellers, a thoroughfare for those moving between the forest floor and the canopy, and a cryptic substrate for hiding when not active (Hanula and Franzreb 1998, Halaj *et al.* 2009). The abundance and diversity of the bark fauna is influenced by several factors, including microclimate associated with bark structure (Nicolai 1986, Horn and Hanula 2002), food availability (Horvath *et al.* 2005), and the composition of the arthropod community living within adjacent forest floor and canopy foliage habitats (Hanula and Franzreb 1998). Arthropods living on bark play a key role in forest food web dynamics and are often important prey for birds (e.g., Jackson 1979, Hooper and Lennartz 1981, Mariani and Manuwal 1990), including Hawaiian forest birds (Banko and Banko 2009), and reptiles (Vitt *et al.* 1981). Despite its importance in forest ecosystems, the arthropod fauna found on bark substrates is relatively poorly known.

A variety of techniques have been used to study bark arthropod communities. Methods designed to assess entire communities most commonly utilize interception traps to capture arthropods moving up or down the boles of trees (Moeed and Meads 1983, Hanula and Franzreb 1998) or along branches (Koponen *et al.* 1997, Pinzon and Spence 2008). In contrast, flight traps placed on tree boles have been used to identify the subset of the fauna that accesses bark via the air (Hanula and Franzreb 1998). Spiders have been the focus of several studies, and surveys for these arthropods often employ artificial substrates such as bubble wrap or corrugated cardboard placed directly over bark to exploit sheltering and overwintering behaviors (Horton *et al.* 2001, Boyd and Reeves 2003, Horvath *et al.* 2005, Isaia *et al.* 2006, Hodge *et al.* 2007). Overall, these techniques are effective at estimating relative abundances of

arthropods on or among trees. To estimate arthropod densities, Horn and Hanula (2002) used knock-down insecticides applied to tree trunks to collect arthropods from known quantities of bark.

Bark arthropod communities are among the most poorly studied faunas in Hawai'i. While taxon-specific studies occasionally target arthropods on bark surfaces (Gillespie 1991, Liebherr and Zimmerman 2000), none, to our knowledge, have attempted to describe or quantify the entire arthropod community found on this substrate for any tree species. Several studies have identified arthropod communities associated with Hawaiian trees, but those efforts primarily focused on arthropods more closely associated with foliage. For example, Gruner (2007) fogged the canopy of 'ōhi'a (*Metrosideros polymorpha*) and Gagne (1979) fogged the canopies of koa (*Acacia koa*) and 'ōhi'a using pyrethrum to dislodge and collect arthropods associated with these trees, but the technique did not allow arthropods from bark and foliage substrates to be differentiated.

This study was designed to further our understanding of the arthropod fauna associated with tree bark surfaces of koa and 'ōhi'a, the dominant canopy-forming trees within wet montane habitats in Hawai'i. The bark arthropod fauna within Hawaiian montane forests is particularly important because it represents most of the prey base for several specialized insectivorous birds, including three species federally listed as endangered, the 'akiapōlā'au (*Hemignathus munroi*), Hawai'i creeper (*Oreomystis mana*), and kiwikiu (*Pseudonestor xanthophrys*). To assess this fauna, we sampled the bole of both koa and 'ōhi'a, but we additionally sampled microhabitats associated with different parts of 'ōhi'a tree branches, including larger diameter sections close to the base of the branch and smaller diameter sections towards the outer canopy. To conduct this study, we developed two novel trap types and used one trap that had been developed previously for use in conifer forests of the mainland U.S. (Hanula and Franzreb 1998, Halaj *et al.* 2009).

METHODS

Study Sites

The study took place within upper elevations of the Pua 'Ākala and Maulua sections of Hakalau Forest National Wildlife Refuge (hereafter Hakalau), Hawai'i Island, Hawai'i (Figure 1). The canopy of this wet montane forest is dominated by old-growth 'ōhi'a and koa but contains other species including 'ōlapa (*Cheirodendron tryginum*), kōlea (*Myrsine lessertiana*), and kawā'u (*Ilex anomala*). Mean annual rainfall at the study sites is about 2400 mm (Giambelluca *et al.* 2013) although amounts can vary greatly within and among years. Historically, both study areas have been impacted by cattle and feral pigs that reduced the diversity and biomass of native understory plants, but habitats are now largely free of these ungulates and are in the process of recovery. The study sites support some of the highest densities of native forest birds on the island (Scott *et al.* 1986, Gorresen *et al.* 2009, Camp *et al.* 2010), including the 'akiapōlā'au and Hawai'i creeper, species that forage extensively on bark surfaces of 'ōhi'a, koa, and other trees.

Bark Trapping Methods

Three types of traps were used in this study: bole traps, large branch traps, and small branch traps. All traps are unidirectional and work by intercepting arthropods that move along the bark surface, but each differed by design and was placed on different parts of the tree. Bole traps were placed on the main trunk and collected arthropods moving up the tree. In contrast,

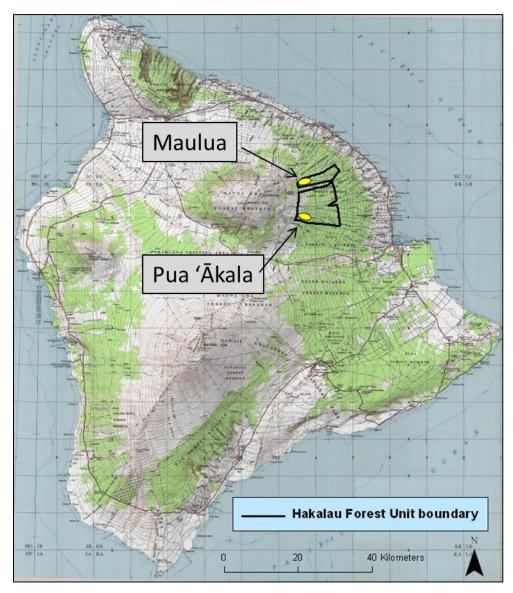


Figure 1. Hakalau Unit of Hakalau Forest National Wildlife Refuge, Hawai'i Island, Hawai'i. The yellow ovals within the unit indicate the locations of the study areas within the Maulua and Pua 'Ākala sections of the refuge.

branch traps were placed on horizontal or near-horizontal branches; large branch traps were placed near the trunk and collected arthropods moving outward, away from the bole, while small branch traps were placed closer to the outer canopy and trapped arthropods more closely associated with foliage. Large and small branch traps faced opposite directions because we wanted to assess the greater number of arthropods expected to be associated with trunks and foliage rather than found on the middle of branches. Bole traps were based on the design of Hanula and New (1996) and the two branch traps were developed and implemented for the first time in this study. Details of the traps are provided below. Bole traps were placed on koa and 'ōhi'a while branch traps were placed only on 'ōhi'a.

Bole traps

Bole traps consist of a modified inverted metal funnel firmly attached to the trunk of the tree, a collection head mounted at the top of the funnel, and a mesh fence radiating down and outwards from the bottom of the funnel that acts to guide arthropods moving up the tree into the trap (Figure 2). The funnel was modified by having a triangular section cut out (12 cm on each side) and the sides along the opening bent outward about 1 cm to allow the funnel to be set tightly against the bark of the tree. The diameters of the top and bottom of the funnel were approximately 2.5 and 18 cm, respectively. The funnel was attached to the tree by three wires stapled to the bark: one at each bottom side and one at the top. Sand embedded in flat black paint was applied to the inside of the funnel to provide a rough surface onto which arthropods could better climb. The collection head consisted of a re-sealable 14 x 14 x 5 cm plastic sandwich container into which 3.5 cm holes were cut in the bottom to allow mounting onto the neck of the funnel and arthropods to drop into a 120 ml collection cup attached to the bottom of the container. The sandwich container was mounted to the funnel using silicone caulk, and the lid of the collection cup was secured to the bottom of the sandwich container using two screws allowing easy removal of the cup. The mesh fence was comprised of aluminum window screen cut into strips approximately 120 x 25 cm. Each section of fence was attached to the inside of the funnel with silicone caulk and then stapled (using 3/8 inch staples) tightly to the bark along a route roughly following the angle of the funnel to form an opening approximately 100 cm wide. Prior to attachment, a 2.5 cm fold was made along the mesh to facilitate stapling to the tree. Because most trees onto which traps were mounted were large, this opening completely encircled the tree on only a few occasions. Clothes pins were used to help secure the outer edge of the mesh fence to the edge of the funnel. Silicone caulk was used to seal gaps between the mesh or funnel and the bark of the tree. The mesh fence was a modification of the trap designed by Hanula and New (1996), who used a horizontal band of metal flashing coated with slippery fluon as a barrier to movement of arthropods up the tree. The high levels of rain experienced at our sites rendered the flashing and fluon barrier method ineffective.

At each site, traps were placed on 15 koa and 15 'ōhi'a. The exact placement of traps was influenced by tree shape and our ability to locate branches to support a climbing rope. Because guide fences encompassed most of the bole of the tree, any differences in orientation to the sun were considered minor. Traps were set up in 2008 on the following dates: 16-18 June (20 traps); 8-9 July (35 traps); and 8 August (5 traps). Once established, all traps ran continuously until 5-7 November 2008. Traps were checked and samples removed at 21-33 day intervals throughout the study. The mean number of days each trap ran was 106 ± 2.3 and 133.3 ± 2.0 at Maulua and Pua 'Ākala, respectively.

Large branch traps

Large branch traps were comprised of two opposite-facing funnels constructed of aluminum window mesh joined at their widest points and modified to encircle a branch (Figure 3). Diameters of the large and small ends of each funnel were approximately 25 and 2 cm, respectively. The top funnel supported a 15 cm diameter blue plastic funnel (Custom Accessories, Inc., Niles, IL) onto which a 120 ml plastic collection cup was attached by cutting a 2.5 cm hole in the bottom of the cup and securing it to the neck of the funnel using silicone caulk. The plastic funnel allowed the collection cup to be removed without disassembling the trap from the branch; it was loosely attached to the mesh funnel by two 15 cm sections of wire. The narrow portion of the bottom funnel was inserted into a 2.5 cm hole in the downward-facing lid of a 120 ml collection cup. The lid was secured to the funnel using silicone caulk. Prior to mounting on the branch, two semi-circles were cut into each funnel: a larger (approximately

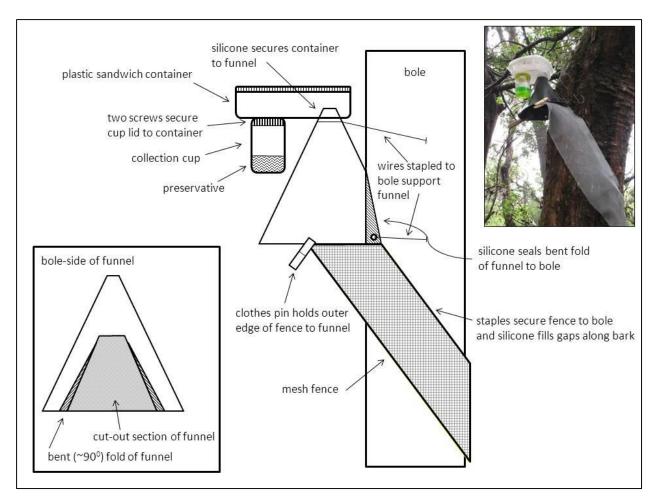


Figure 2. Schematic view of a bole trap. The inset at the bottom left shows the funnel as it faces the tree bole and illustrates the area removed. The inset at the top right shows the trap placed on an 'ōhi'a. Bole traps were placed on koa and 'ōhi'a.

20 cm wide) cut on the front (bole-facing) and a smaller (approximately 10 cm wide) cut on the back (foliage-facing). The front opening allowed arthropods to enter the trap while the back tightly encircled the branch; staples and silicone caulk helped seal the back of the trap. The two halves of the trap were assembled around the branch and secured together using staples. The trap was stabilized with a 25 cm piece of wire linking the back of the top funnel to the branch.

At each site, 10 traps were placed on branches of 'ōhi'a. Traps were established and opened in 2008 on 8 August (8 traps), 27–28 August (10 traps), and 9–10 September (2 traps), and ran continuously through 6 or 7 November 2008. The mean number of days of trapping was 68.0 ± 1.7 and 85.6 ± 2.4 at Maulua and Pua 'Ākala, respectively. Traps were checked and samples removed at 12-42 day intervals.

Small branch traps

The small branch trap was similar in design and function to the large branch trap except that 15 cm diameter blue plastic funnels, rather than mesh, were used to form the top and bottom of the trap (Figure 4). The top half of the trap consisted of two identical funnels, one inserted

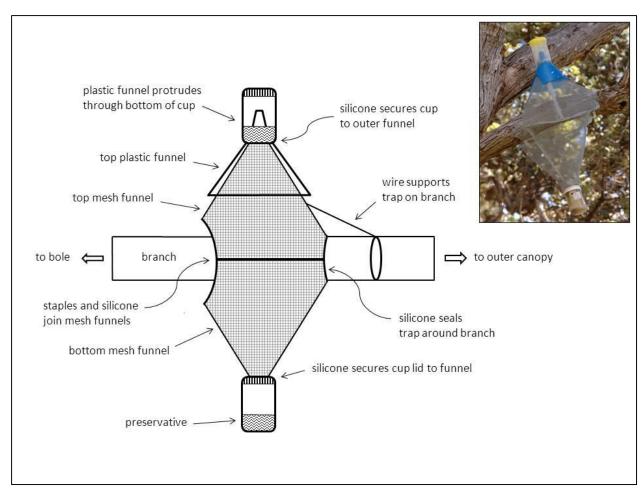


Figure 3. Schematic view of a large branch trap. The inset at the top right shows the trap placed on an 'ōhi'a branch. Large branch traps were only placed on 'ōhi'a.

onto the other. The inner funnel was lined with sand-embedded flat black paint while the outer funnel supported an upward-facing 120 ml plastic collection cup lid that had a 2.5 cm center hole cut out to allow silicone-mounting onto the neck of the funnel. The second, top-most funnel was necessary to allow the collection cup to be removed without disassembling the trap from the branch. The bottom half of the trap secured a downward-facing lid and cup identical to that used in the top portion of the trap. Prior to mounting on the branch, front (foliage-facing) and back (bole-facing) semi-circles of 10 and 4 cm, respectively, were cut into each funnel. Silicone caulk was used to seal the back of the trap around the branch. The two halves of the trap were assembled around the branch and secured together using duct tape. To help support the trap, a 25 cm length of wire was extended from a hole in the back of the trap and wrapped around the branch. To remove specimens, duct tape securing the two top funnels together was removed and the outer funnel inverted to allow the collection cup to be unscrewed from the lid without spilling the sample.

A total of 16 traps were placed in 'ōhi'a trees: 7 at Pua 'Ākala and 9 at Maulua. Fourteen traps were established and opened on 10 September 2008, and two traps were established and opened on 7 October 2008. All traps ran continuously through 5, 6, or 7 November 2008. The

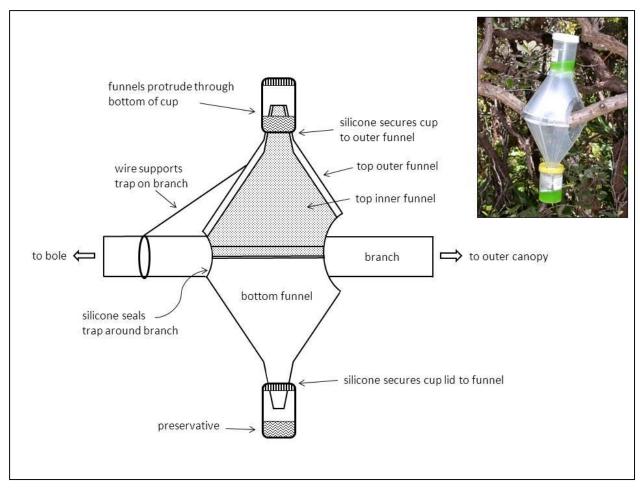


Figure 4. Schematic view of a small branch trap. The inset at the top right shows the trap placed on an 'ōhi'a branch. Small branch traps were only placed on 'ōhi'a. Funnels comprising the small branch trap in the photo are clear but those used in the study were blue.

mean number of days each trap ran was 54.1 ± 3.1 and 52.4 ± 3.9 at Maulua and Pua 'Ākala, respectively. Traps were checked and samples removed at 27-29 day intervals.

Because we wanted to sample arthropods where birds forage most heavily, all traps were placed within the canopy of trees. Tree canopies were accessed using single-rope techniques (Perry 1978, Laman 1995). Trees were chosen from a subset of all mature, relatively straight-boled trees (generally >100-cm circumference at mid-canopy) that were safe for climbing. Approximately 40% of all branch traps were placed in the same tree that supported a bole trap (50% of large horizontal traps and 31% of all small horizontal traps). In trees with both trap types, branch traps were generally placed on branches lower in the tree than the bole trap to reduce interference between traps.

For all traps, the height (m) at the top of the trap and the circumference of the bole or branch at the base of the trap were measured (cm). Equal parts propylene glycol and water were used as a preservative in all traps.

Arthropod identification

All arthropods were identified to the order level, although Araneae, Homoptera, Hemiptera, Coleoptera, and Hymenoptera were further identified to the family level because they are considered important food for birds (U.S. Geological Survey unpublished data). Throughout this report we use the older classification scheme that recognizes Homoptera as a distinct order rather than the recently adopted, and potentially less familiar, scheme that sinks Homoptera into the suborders Auchenorrhyncha and Sternorrhynca. Lepidoptera are also important prey, but poor preservation of adults in the fluid preservative and difficulty identifying larvae to the family level precluded further identification. Larval and adult Lepidoptera were differentiated because their behavior potentially resulted in differential use of bark surfaces.

Data analysis

To account for differences in the number of days that each trap ran, the arthropod abundance for each trap was standardized by dividing the total number of arthropods collected by the total number of days each trap sampled the fauna.

For most taxa, distributions of abundance did not conform to the assumptions of parametric analyses, so non-parametric Mann-Whitney U-tests were used to compare capture rates among sites, tree species, and parts of trees. Because we had no *a priori* expectation as to how the arthropod community would be constructed, we applied a Bonferroni adjustment to the conventional significance level of $\alpha=0.05$ when testing multiple arthropod taxa for differences in abundance between sites, tree species, and parts of trees. Since 13 taxa were compared, we recognized significant differences at $\alpha \leq 0.004$. While this approach may be viewed as conservative, it maintains the family-wise error rate and helps protect against making Type 1 errors. All values presented are means \pm SEM.

While behavioral differences among arthropod taxa led us to expect varying numbers of individuals within top and bottom portions of horizontal traps, the two portions were pooled for analysis because our interest was in obtaining values for the entire trap rather than comparing how each part of the trap performed individually. The traps used in this study intercept arthropods moving along bark surfaces, rather than sampling areas of known volume, thus they more effectively measure arthropod activity (number/day) than density (number/area). Because the volume of area effectively sampled by each trap type varied considerably, and the relative efficiency of each trap was unknown, we limited our comparisons among trap types to relative abundances of taxa composing the fauna.

RESULTS

Bole Traps on Koa and 'Ōhi'a

No significant differences were detected in the height of the traps or the circumference of the trees at the traps between Maulua and Pua 'Ākala for either koa (t-test, P = 0.40 and 0.73, respectively) or 'ōhi'a (t-test, P = 0.44 and 0.31, respectively; Table 1). With the two sites combined, no difference existed in trap height between tree types although the difference was only marginally non-significant, being slightly greater on koa than on 'ōhi'a (mean = 10.1 ± 0.46 m and 8.9 ± 0.34 m, respectively; t-test, P = 0.054). Similarly, tree circumference at the traps was not significantly different between tree types with sites combined (172.7 ± 10.9 cm and 152.5 ± 7.6 cm in koa and 'ōhi'a, respectively; t-test, P = 0.133).

Table 1. Mean (± SEM) height of traps and circumference of boles and branches at traps on

'ōhi'a and koa at Pua 'Ākala and Maulua study sites.

			Bole tra	эр)		Large branch trap			Small branch trap		
			Ht	Circ			Ht	Circ		Ht	Circ	
Tree	Site	n	(m)	(cm)		n	(m)	(cm)	n	(m)	(cm)	
`Ōhi`a	Pua `Ākala	15	8.7	144.6		10	8.1	32.7	9	7.0	11.9	
			(0.5)	(10.1)			(0.6)	(2.1)		(8.0)	(0.8)	
	Maulua	15	9.2	160.4		10	9.6	31.7	7	7.9	9.1	
			(0.5)	(11.4)			(0.6)	(1.6)		(0.8)	(0.6)	
Koa	Pua `Ākala	15	10.5	168.6								
			(0.7)	(11.3)								
	Maulua	15	9.7	176.4								
			(0.6)	(18.4)								

Overall, 35,067 arthropods were collected in bole traps placed in koa and 'ōhi'a over 7,192 trap-days. Based on standardized trapping efforts (number/trap-day), Collembola were most abundant (71.1% of the total), followed by Isopoda (19.0%), Araneae (5.8%), Homoptera (0.9%), Hymenoptera (0.8%), and adult Lepidoptera (0.7%).

Arthropod abundance was generally similar between Maulua and Pua 'Ākala, with the fauna dominated by Collembola and Isopoda in both 'ōhi'a and koa (Table 2), although Collembola abundance was nearly 15 times higher in 'ōhi'a than in koa at Pua 'Ākala (9.77 \pm 3.67 vs. 0.662 \pm 0.207 individuals/trap-day). This large difference was primarily due to four samples at Pua 'Ākala containing >20 individuals/trap-day. Mean abundances for most taxa were similar between sites for both tree species, although significant differences were found in several instances. Coleoptera were more abundant at Maulua in both koa and 'ōhi'a (P = 0.002 and <0.001, respectively); Homoptera were more abundant at Pua 'Ākala in koa (P = 0.002); and Isopoda were more abundant at Maulua in koa (P < 0.001). Similarly, mean arthropod abundance (all taxa) on koa and 'ōhi'a was indistinguishable when Maulua and Pua 'Ākala data were combined (Figure 5).

Large Branch Traps on 'Ōhi'a

No significant differences were detected between Pua 'Ākala and Maulua study sites in the height of traps or the circumference of the branches at the traps placed in 'ōhi'a (Table 1; t-tests, P = 0.112 and 0.710, respectively).

Overall, 3,707 arthropods were collected in large branch traps placed on 'ōhi'a over 1,536 trap-days. Collembola dominated the samples (59.9% of the total) followed by Isopoda (11.2%), Araneae (6.4%), Acari (5.3%), Diptera (4.6%), Psocoptera (4.5%), Hymenoptera (2.5%), and Homoptera (2.0%). A difference in abundance between study sites was found only for Diptera, which were significantly greater at Pua 'Ākala than at Maulua (P = 0.002; Table 3). Isopoda were 7.4 times more abundant at Maulua than at Pua 'Ākala, but the difference was marginally non-significant (P = 0.005).

Small Branch Traps on 'Ōhi'a

No significant difference in the height of traps was detected between Pua ' \bar{A} kala and Maulua (Table 1; t-test, P = 0.428) but branch circumference at the traps was significantly greater at

Table 2. Mean (\pm SEM) abundance (number/trap-day) of arthropods collected in bole traps on 'ōhi'a and koa at Maulua and Pua 'Ākala during 2008. Comparisons that were significantly different at the adjusted level of $\alpha = 0.004$ are indicated in bold.

	<u>`</u> Ōhi`a			Koa			
Taxon	Maulua	Pua 'Ākala	Р	Maulua	Pua `Ākala	Р	
Acari	0.031 (0.008)	0.012 (0.004)	0.049	0.011 (0.006)	0.009 (0.002)	0.283	
Araneae	0.302 (0.029)	0.252 (0.014)	0.290	0.284 (0.026)	0.238 (0.022)	0.221	
Coleoptera	0.015 (0.005)	0.001 (0.001)	< 0.001	0.014 (0.004)	0.001 (0.001)	0.002	
Collembola	1.428 (0.519)	9.773 (3.670)	0.191	1.381 (0.464)	0.662 (0.207)	0.221	
Diptera	0.014 (0.004)	0.013 (0.004)	0.949	0.011 (0.005)	0.014 (0.004)	0.456	
Hemiptera	0.029 (0.005)	0.023 (0.005)	0.289	0.021 (0.007)	0.024 (0.008)	0.816	
Homoptera	0.015 (0.007)	0.057 (0.010)	0.002	0.030 (0.012)	0.061 (0.023)	0.252	
Hymenoptera	0.081 (0.028)	0.015 (0.004)	0.057	0.031 (0.008)	0.021 (0.007)	0.187	
Isopoda	1.841 (0.638)	0.235 (0.090)	0.021	1.369 (0.595)	0.097 (0.038)	0.001	
Lepidoptera (adult)	0.025 (0.008)	0.033 (0.010)	0.545	0.027 (0.007)	0.038 (0.009)	0.405	
Lepidoptera (larvae)	0.006 (0.003)	0.007 (0.002)	0.725	0.015 (0.007)	0.024 (0.012)	0.949	
Psocoptera	0.012 (0.004)	0.005 (0.002)	0.060	0.007 (0.002)	0.003 (0.001)	0.030	
other ¹	0.010 (0.004)	0.014 (0.005)	0.739	0.008 (0.007)	0.007 (0.004)	0.202	

¹ Includes Diplopoda, Neuroptera, and Thysanoptera

Pua 'Ākala than at Maulua (Table 1; t-test, P = 0.012). In total, 5,895 arthropods were collected in small bark traps over 854 trap-days. Collembola were most abundant (66.1% of the fauna) followed by Acari (7.0%), Araneae (6.8%), Homoptera (5.4%), Isopoda (5.0%), adult Lepidoptera (2.5%), Psocoptera (2.2%), and Diptera (1.4%).

A difference in arthropod abundance between Maulua and Pua 'Ākala was found only for Collembola (P = 0.004) which was 3.5 times more common at Maulua (Table 4). Large differences were found for Isopoda and adult Lepidoptera (34.2 and 16.8 times more abundant at Maulua), but they were marginally non-significant (P = 0.017 and 0.007) due to high within-site variability among samples and low statistical power. For Isopoda, 3 of 9 traps at Maulua collected 46% of the total and 7 of all 16 small branch traps contained no individuals.

Relative Abundance of Arthropods on Koa and 'Ōhi'a

Order level determinations

In general, relative abundances of arthropod orders were similar on bark of koa and 'ōhi'a, with Collembola being dominant, ranging from 78.7% of all arthropods on 'ōhi'a boles to 46.3% on koa boles (Figure 6). Isopoda and Araneae ranked second and third in

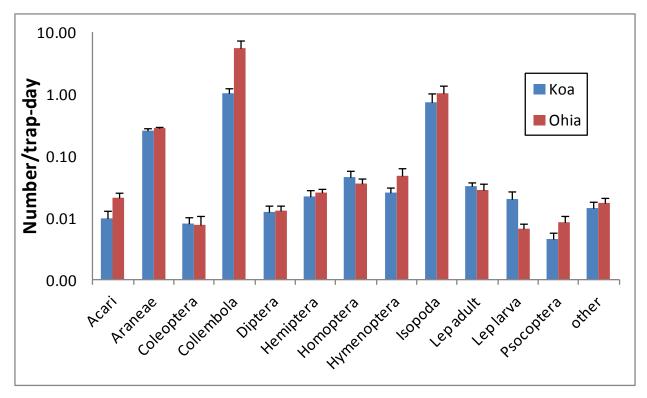


Figure 5. Mean (\pm SEM) abundance (number/trap-day) of arthropods collected in bole traps on koa and 'ōhi'a in 2008. Data for Maulua and Pua 'Ākala were combined for each tree species. No significant difference in abundance was found between tree species for any arthropod group at the adjusted level of a=0.004. Note the log scale of the y-axis.

Table 3. Mean (\pm SEM) abundance (number/trap-day) of arthropods collected in large branch traps set on 'ōhi'a at Maulua and Pua 'Ākala in 2008. Samples from the top and bottom parts of each trap were combined. Comparisons that were significantly different at the adjusted level of $\alpha = 0.004$ are indicated in bold.

Taxon	Maulua	Pua 'Ākala	<i>P</i> value
Acari	0.182 (0.069)	0.206 (0.041)	0.257
Araneae	0.239 (0.030)	0.232 (0.031)	0.940
Coleoptera	0.016 (0.006)	0.009 (0.003)	0.389
Collembola	0.974 (0.232)	3.414 (1.381)	0.406
Diptera	0.102 (0.023)	0.238 (0.030)	0.002
Hemiptera	0.043 (0.017)	0.049 (0.012)	0.404
Homoptera	0.042 (0.014)	0.101 (0.039)	0.211
Hymenoptera	0.097 (0.018)	0.085 (0.012)	0.791
Isopoda	0.723 (0.314)	0.098 (0.025)	0.005
Lepidoptera (adult)	0.029 (0.009)	0.035 (0.007)	0.403
Lepidoptera (larvae)	0.012 (0.003)	0.010 (0.005)	0.474
Psocoptera	0.135 (0.020)	0.197 (0.023)	0.034
other ¹	0.019 (0.011)	0.036 (0.019)	0.381

¹ Includes Chilopoda, Diplopoda, Neuroptera, and Thysanoptera

Table 4. Mean (\pm SEM) abundance (number/trap-day) of arthropods collected in small branch traps set on 'ōhi'a at Maulua and Pua 'Ākala over the course of the study. Samples from the top and bottom parts of the traps were combined. Comparisons that were significantly different at the adjusted level of $\alpha = 0.004$ are indicated in bold.

Taxon	Maulua	Pua 'Ākala	Р
Acari	0.199 (0.063)	0.058 (0.010)	0.030
Araneae	0.176 (0.026)	0.082 (0.023)	0.030
Coleoptera	0.006 (0.004)	0.007 (0.005)	0.781
Collembola	1.899 (0.456)	0.543 (0.095)	0.004
Diptera	0.033 (0.008)	0.020 (0.008)	0.518
Hemiptera	0.019 (0.007)	0.008 (0.004)	0.504
Homoptera	0.176 (0.068)	0.015 (0.005)	0.037
Hymenoptera	0.029 (0.007)	0.003 (0.003)	0.011
Isopoda	0.171 (0.096)	0.005 (0.003)	0.017
Lepidoptera (adult)	0.084 (0.027)	0.005 (0.003)	0.007
Lepidoptera (larvae)	0.044 (0.020)	0.005 (0.003)	0.187
Psocoptera	0.045 (0.008)	0.040 (0.008)	1.000
other ¹	0.012 (0.008)	0.003 (0.003)	0.161

¹ Includes Chilopoda, Diplopoda, Neuroptera, and Thysanoptera

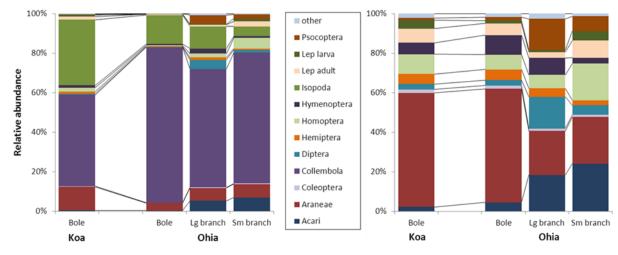


Figure 6. Relative abundance (%) of arthropod orders collected in traps set on bark surfaces of koa and 'ōhi'a. Data from Pua 'Ākala and Maulua study sites were combined. The graph on the left includes all taxa while the graph on the right includes all taxa except the numerically dominant orders Collembola and Isopoda.

abundance, respectively. Isopoda composed 11.2% of all arthropods collected on large 'ōhi'a branches and 33.2% on koa boles. Araneae composed 6.4% of the sample on large 'ōhi'a branches and 11.8% on koa boles. On small 'ōhi'a branches, Acari (7.0%), Araneae (6.8%), and Homoptera (5.4%) were all slightly more numerous than Isopoda (5.0%). For all bark locations, no other arthropod order composed >5% of the total collected.

Family level determinations

For Araneae, Philodromidae were most common on all bark substrates, ranging from 74.6% of all Araneae on large 'ōhi'a branches to 31.0% on small 'ōhi'a branches (Figure 7). Theridiidae ranked second in abundance on koa boles (24.5%), 'ōhi'a boles (20.2%), and large 'ōhi'a branches (13.0%). Small 'ōhi'a branches differed from other substrates in the relatively greater proportions of Linyphiidae (29.6%) and Tetragnathidae (18.6%). Salticidae and Thomisidae were rarely collected anywhere.

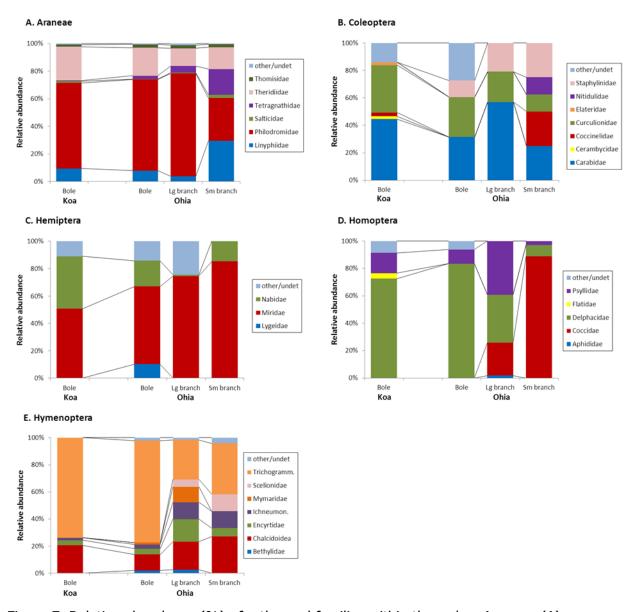


Figure 7. Relative abundance (%) of arthropod families within the orders Araneae (A), Coleoptera (B), Hemiptera (C), Homoptera (D), and Hymenoptera (E) on bark surfaces of koa and 'ōhi'a. Data from Pua 'Ākala and Maulua were combined.

Seven Coleoptera families were identified on bark, with Carabidae ranking first in abundance on boles and large branches (31.5% on 'ōhi'a boles, 56.9% on large 'ōhi'a branches) and Curculionidae ranking second (34.6% on koa boles, 22.2% on large 'ōhi'a branches; Figure 7). On small 'ōhi'a branches, the abundance of Carabidae, Coccinelidae, and Staphylinidae was 25% each, followed by Curculionidae and Nitidulidae at 12.5% each.

Miridae were the dominant Hemiptera on all bark surfaces (ranging from 85.2% on small 'ōhi'a branches to 50.6% on koa boles; Figure 7). Nabidae ranked second in abundance on koa boles (38.3%), 'ōhi'a boles (18.8%), and small 'ōhi'a branches (14.8%), while other or undetermined taxa (primarily early instar nymphs) were the second most common hemipteran on large 'ōhi'a branches (24.5%). A relatively small number of Lygeidae were also recorded on koa boles.

The relative abundance of the five families of Homoptera that we identified varied considerably among bark locations. Delphacidae was dominant on boles of koa (72.5%) and 'ōhi'a (83.6%); Psyllidae and Delphacidae were both relatively common on large 'ōhi'a branches (39.2% and 35.1%, respectively); and Coccidae was most common on small 'ōhi'a branches (88.9%; Figure 7).

Six families and one superfamily of Hymenoptera were identified from the traps (Figure 7). Trichogrammidae was the most common group collected on all bark surfaces, but it was considerably more abundant on koa boles (73.8%) and 'ōhi'a boles (75.1%) than on large 'ōhi'a branches (29.2%) or small 'ōhi'a branches (37.5%). The superfamily Chalcidoidea composed >20% of the hymenopteran fauna on all substrates except 'ōhi'a boles, where it made up 11.8%. Other abundant taxa included Encyrtidae (16.6% on large 'ōhi'a branches), Ichneumonidae (12.5% on large and small 'ōhi'a branches), and Scelionidae (12.5% on small 'ōhi'a branches).

DISCUSSION

We found that the arthropod fauna found on the bark of koa and 'ōhi'a within wet montane forest at Hakalau Forest National Wildlife Refuge consisted of at least 15 orders, was numerically dominated by relatively few taxa, and overlapped considerably in composition at the order and family levels within and among tree species. While our study represents only a brief snapshot of this diverse community, it nonetheless contributes to the scant knowledge of this ecologically important group of arthropods in Hawai'i. Others in Hawai'i have collected arthropods associated with bark during generalized tree sampling (Gagne 1979, Gruner 2007), but to our knowledge, ours is the first study specifically targeting the entire bark community.

Regardless of study site, tree species, or location within 'ōhi'a, Collembola were the dominant arthropod group collected, generally followed by Isopoda and Araneae. Collembola are tiny, wingless, and among the most abundant arthropods in forest ecosystems; as primary consumers of fungi, bacteria, algae, and decomposing vegetation, they are important contributors to litter decomposition and nutrient cycling (Rusek 1998). In our samples, a single species of Collembola within the family Entomobryidae was the most abundant taxon encountered. Entomobryidae are generally most abundant in soil and litter but several species have been found in the canopy of 'ōhi'a (Gagne 1979, Gruner 2004). Our results are not without precedence, however, as Collembola have been found to be the most numerous arthropod collected in interception traps set on tree boles in New Zealand lowland forest (Moeed and Meads 1983) and on Douglas-fir (*Pseudotsuga menziesii*) in Oregon and

Washington (Halaj *et al.* 2009). Relatively low numbers of Collembola in 'ōhi'a foliage (Fretz 2002, U.S. Geological Survey unpublished data) indicate that they are residing on bark rather than just transiting between the ground and foliage, as suggested by Halaj *et al.* (2009) in forests of the western U.S.

Isopods are also generally considered inhabitants of soil and litter, but they are commonly found on and under tree bark. The dominant (and perhaps only) isopod collected in our study was the non-native woodlouse, *Porcellio scaber*, a widespread tramp species that feeds on decomposing bark and other plant material that often collects in bark crevices (Zimmer *et al.* 2003). While it is possible that this species was simply using the bark of koa and 'ōhi'a for refuge during inactive periods, it is likely that it was feeding within the bark matrix. This species is also abundant in forest floor litter on the study sites, particularly near the bases of trees.

The six families of Araneae we identified vary considerably in size and life-history, but the dominant Philodromidae (primarily *Pagiopalus atomarius*) are relatively large-bodied, mostly arboreal hunting spiders that are considerably more common on bark than in foliage (U.S. Geological Survey unpublished data) on our study sites. Their preference for bark substrates likely explains their relative scarcity on small branches. Small branches are where we most often collected Linyphiidae, Tetragnathidae, and Theridiidae, which are typically associated with foliage (see also Fretz 2002). Due to the relatively large size of philodromid spiders, conversion of numerical abundance to biomass based on body length (Gruner 2003) would have resulted in a higher representation of Araneae overall, and Philodromidae in particular, in the arthropod community on koa and 'ōhi'a.

The highly similar distribution and abundance of arthropods on the boles of koa and 'ōhi'a indicate little ecological differentiation of this community on these dominant forest species. This is surprising since arthropod communities often reflect microhabitat differences associated with bark structure. The structure of bark differs significantly on mature koa and 'ōhi'a; the bark of 'ōhi'a is generally flakey and often peels away in strips whereas koa bark is rough and deeply fissured. Variation in microhabitats associated with bark structure can influence the abundance of arthropods, including Collembola and Isopoda, under environmental conditions of desiccation and thermal stress (Nicolai 1986, Prinzing 2005). However, protection from desiccation and thermal extremes may be less important in montane habitats at Hakalau compared to seasonally drier and colder conditions found at higher elevations and latitudes. The structural variability of bark can also provide an assortment of microhabitats in which arthropods can hide or hunt. Hanula et al. (2000) found arthropod abundance and biomass to be positively correlated with bark thickness, and speculated that deep furrows associated with thick bark were particularly important to nocturnally active arthropods as it allowed refuge from diurnally active predators such as birds. Additionally, the ability of bark to retain moisture may influence the growth of fungi and algae, affecting the availability of food resources for arthropods such as Collembola (Prinzing and Woas 2003). Our results are similar to those of Horn and Hanula (2002) and Nicolai (1986), who found that different tree species in the same habitat supported similar communities of bark arthropods, which suggests that habitat may be a more important driver of faunal composition than bark structure.

The strong similarity of the arthropod community between Maulua and Pua 'Ākala is likely explained by proximity and habitat structure. The two sites are only about 9 km apart, are similar in plant species composition and canopy height (VanderWerf 1999) and appear to share similar ungulate-driven disturbance histories. Perhaps the strongest between-site difference was

found for Isopoda, which was significantly more abundant at Maulua on koa boles and showed a strong but marginally non-significant trend toward higher abundance on the bole and large and small branches of 'ōhi'a. At Maulua, overall cover of non-native grasses (primarily kikuyu grass, *Cenchrus clandestinus*) is greater than at Pua 'Ākala (Hess *et al.* 2010), which may offer more favorable habitat for isopods and provide a source for the population inhabiting tree bark. On koa and 'ōhi'a boles, Coleoptera, dominated by Carabidae and Curculionidae, were also more abundant at Maulua than at Pua 'Ākala with only 4 of 50 total Coleoptera trapped at the latter site. The reason for this difference is unclear.

Despite the proximity of the two sites, bird surveys at Hakalau have yielded greater numbers of insectivorous species, including the bark-feeding Hawai'i creeper and 'akiapōlā'au, at Pua 'Ākala, which is comprised of open-canopy and closed-canopy forest habitat, compared to Maulua, which is comprised only of open-canopy forest habitat (Camp et al. 2010). Although we did not measure bark surface area, we assume that greater tree density at Pua 'Ākala affords more bark substrate to birds foraging there, given the similarities between the two sites in canopy height, species composition, and trunk diameter (Fretz 2002). Fretz (2002) concluded that the insectivorous Hawai'i 'ākepa (Loxops coccineus coccineus) was more abundant at Pua 'Ākala in part because of greater canopy cover compared to Maulua and not because arthropod abundance within the canopy foliage was different. Similarly, we found few differences in arthropod abundance within trees between these two sites, suggesting that greater tree density at Pua 'Ākala contributes to the greater abundance of insectivorous birds there. In particular, Lepidoptera larvae and Araneae, the primary prey for these birds (U.S. Geological Survey unpublished data), did not differ between sites. Although Coleoptera were more abundant on boles of koa and 'ōhi'a at Maulua than they were at Pua 'Ākala, Cerambycidae, the larvae of which are commonly consumed by 'akiapōlā'au, composed only 2.1% of all Coleoptera on koa and were not collected on 'ōhi'a. Alternative trapping methods, trapping at other times of the year, or surveys targeting cerambycid larvae that live under bark, may have yielded different results. Nevertheless, we conclude that differences in the arthropod community living on the bark of the dominant tree species across Hakalau are slight and not likely to influence the distributions of insectivorous birds.

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