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Celia K. Boone

Diana Six
University of Montana - Missoula, diana.six@umontana.edu

Steven J. Krauth

Kenneth F. Raffa

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Assemblage of Hymenoptera arriving at logs colonized by *Ips pini* (Coleoptera: Curculionidae: Scolytinae) and its microbial symbionts in western Montana

Celia K. Boone

Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706, United
States of America

Diana L. Six

Department of Ecosystem and Conservation Sciences, University of Montana, Missoula,
Montana 59812, United States of America

Steven J. Krauth, Kenneth F. Raffa[1]

Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706, United
States of America

Abstract—Colonization of a tree by bark beetles and their symbionts creates a new habitat for a diverse assemblage of arthropods, including competing herbivores, xylophages, fungivores, saprophages, predators, and parasitoids. Understanding these assemblages is important for evaluating nontarget effects of various management tactics and for subsequently evaluating how changes in climate, the presence of invasive species, and altered forestry practices and land-use tenure may affect biodiversity. We characterized the assemblage of hymenopterans attracted to logs of ponderosa pine (*Pinus ponderosa* C. Lawson (Pinaceae)) colonized by the bark beetle *Ips pini* (Say) and its microbial symbionts. In one experiment, the composition and relative abundances of species arriving at hosts colonized by *I. pini*, and possible sources of attraction, were determined. Treatments consisted of a log containing *I. pini* with its natural complement of microorganisms, a log alone, and a blank control. A second experiment was carried out to determine whether or not Hymenoptera were attracted to microbial symbionts of *I. pini*. Treatments consisted of a blank control, a log alone, a log containing *I. pini* with its natural complement of microorganisms, either *Ophiostoma ips*, *Burkholderia* sp., or *Pichia scolyti*, and a log inoculated with a combination of these three microorganisms. Over 2 years, 5163 Hymenoptera were captured, of which over 98% were parasitoids. Braconidae, Platygastridae, Encyrtidae, Pteromalidae, and Ichneumonidae were the most abundant. Seven known species of bark beetle parasitoids (all Pteromalidae) were captured. However, parasitoids of Diptera, Lepidoptera, Hymenoptera, and non-wood-boring Coleoptera were also common. Nineteen species showed preferential attraction to host plants infested with *I. pini* and its complement of microorganisms, host plants inoculated with *I. pini* microbial symbionts, or host plants alone. Interestingly, many of these species were parasitoids of phytophagous, fungivorous, and saprophytic insects rather than of bark beetles themselves. These results suggest that a diverse assemblage of natural enemies that attack various feeding guilds within a common habitat exploit common olfactory cues.

Résumé—La colonisation d'un arbre par les scolytes et leurs symbiontes crée un nouvel habitat pour divers peuplements d'arthropodes, en particulier des herbivores compétiteurs, des xylophages, des mycétophages, des saprophages, des prédateurs et des parasitoïdes. Il est important de comprendre ces peuplements pour pouvoir évaluer les effets non ciblés des diverses tactiques de gestion et pour ensuite déterminer de quelle manière le changement climatique, la présence d' espèces envahissantes, ainsi que les changements dans les pratiques forestières et l'utilisation des terres, peuvent affecter la biodiversité. Nous décrivons le peuplement d'hyménoptères attirés par les troncs de pin ponderosa (*Pinus ponderosa* C. Lawson (Pinaceae)) colonisés par le scolyte du

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[1] Corresponding author (e-mail: raffa@entomology.wisc.edu).

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pin, *Ips pini* (Say) et ses symbiontes microbiens. Une première expérience cherchait à déterminer la composition et les abondances relatives des espèces qui se posaient sur les hôtes colonisés par *I. pini* et d'identifier les sources d'attraction. Les conditions expérimentales comprenaient un tronc habité par *I. pini* et son complément naturel de microorganismes, un tronc seul et un témoin à blanc. Une seconde expérience a été menée pour déterminer si les hyménoptères étaient attirés par les symbiontes microbiens d'*I. pini*. Les conditions expérimentales comprenaient un témoin à blanc, un tronc seul, un tronc avec *I. pini* et son complément naturel de microorganismes, soit *Ophiostoma ips*, *Burkholderia* sp. ou *Pichia scolyti*, et un tronc inoculé avec une combinaison de ces trois microorganismes. Sur deux années, nous avons capturé 5163 hyménoptères dont plus de 98 % étaient des parasitoïdes. Les plus abondants étaient les Braconidae, les Platygastridae, les Encyrtidae, les Pteromalidae et les Ichneumonidae. Nous avons capturé sept espèces connues pour être des parasitoïdes de scolytes (tous des Pteromalidae). Cependant, il y avait aussi en abondance des parasitoïdes de diptères, de lépidoptères, d'hyménoptères et de coléoptères non mineurs de bois. Dix-neuf espèces montraient une attraction préférentielle, par ordre, pour les plantes hôtes infestées par *I. pini* et son complément de microbes, puis les plantes hôtes inoculées des symbiontes microbiens d'*I. pini* et enfin les plantes hôtes seules. Remarquablement, plusieurs de ces espèces étaient des parasitoïdes des insectes phytophages, mycétophages et saprophytes, plutôt que des scolytes eux-mêmes. Ces résultats laissent croire que des regroupements divers d'ennemis naturels qui attaquent les différentes guildes alimentaires dans un même habitat utilisent des signaux olfactifs communs.

[Traduit par la Rédaction]

Introduction

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are important components of forest ecosystems and some are major disturbance agents that influence ecosystem processes such as nutrient cycling and biodiversity. During outbreaks of some species, millions of hectares of conifer forests are affected and significant economic losses incurred. Although some bark beetle species cause extensive tree mortality during outbreaks, their populations typically remain in a low-density, endemic state for decades between outbreaks. During these periods, bark beetles colonize stressed or recently killed trees.

A dead tree constitutes an important ecological unit that supports a diverse assemblage of species (Shelford 1913; Graham 1925). Sudden mortality of a tree due to bark beetle infestation provides the substrate and starting point for the formation of a new community (Stephen and Dahlsten 1976; Hanula *et al.* 2006). From the time of colonization, the chemical and physical characteristics of tree tissues change rapidly (Shelford 1913; Graham 1925; Lambert *et al.* 1980) and so habitat suitability subsequently varies over time for many distinct insect guilds (Grove 2002), including competing herbivores, xylophages, fungivores, saprophages, predators, and parasitoids (Aukema *et al.* 2004; Vanderwel *et al.* 2006). Characterizing these communities facilitates evaluation of nontarget effects of pest-management tactics and subsequently how changing conditions, such as altered climate, invasive species, forestry practices, and land-use patterns, may affect biodiversity (Majka and Selig 2006; Majka *et al.* 2007).

Location of host habitat by (and, ultimately, reproductive success of) parasitoids and predators of cryptic insects such as subcortical phytophages, including bark beetles, relies on their recognition of host-associated chemical cues (Turlings and Benrey 1998; De Moraes *et al.* 1998). Such cues may originate from the host insect (Kennedy 1984; Senger and Roitberg 1992; Raffa *et al.* 2007), from its food plant (Camors and Payne 1973; Shahjahan and Streams 1973; Hilker *et al.* 2002), or from microbial symbionts (Madden 1968; Spradberry 1974; Sullivan and Berisford 2004; Martinez *et al.* 2006; Adams and Six 2008; Boone *et al.* 2008). Bark beetles have complex associations with fungi and bacteria that they introduce into host trees in mycangia (structures of the adult integument specialized for transport of fungi) (Barras 1975; Six 2003), on their exoskeleton (Six and Paine 1998; Six 2003; Lim *et al.* 2005), or in oral secretions (Cardoza *et al.* 2006). These microorganisms are often highly consistent in their association with host beetles, and thus may provide a consistent signal for locating a host beetle.

Ophiostomatoid fungi are the main symbiotic microorganisms associated with bark beetles. They produce a variety of volatiles, including short-chain alcohols, esters, and terpenes, some of which are unique. Formation of these volatiles is frequently strain-dependent and influenced by culture conditions (Hanssen 1993). The presence of bark beetles and their associated microorganisms quantitatively and qualitatively alters the volatile emissions from trees in a pattern that varies across the different stages of beetle colonization and development (Pettersson and Boland 2003; Jost *et al.* 2008). When an attack is successful, the quantity of monoterpenes generally decreases with time after initial infestation and tree death (Raffa and Berryman 1983*a*, 1983*b*; Pettersson and Boland 2003). However, the concentrations of certain oxygenated monoterpenes and benzenoid compounds gradually increase during larval development. In many cases, mixtures of volatiles rather than individual compounds are most responsible for attracting parasitoids of bark beetles (Sullivan *et al.* 2000; Pettersson *et al.* 2001) and these mixtures may vary in composition over time.

Several surveys of arthropods have been conducted on live trees (Moran and Southwood 1982; Schowalter and Zhang 2005) and decomposing trees (Shelford 1913; Savely 1939; Howden and Vogt 1951; Hammond 1997; Vanderwel *et al.* 2006). However, relatively few surveys of parasites associated with trees infested with bark beetles have been conducted for specific bark beetle and host tree species (Dahlsten and Stephen 1974; Stephen and Dahlsten 1976; Riley and Goyer 1988; Aukema *et al.* 2004).

The pine engraver, *Ips pini* (Say), is an endemic, transcontinentally distributed bark beetle of North America associated with several pine species and some spruces (*Pinus* L. and *Picea* A. Dietr. (Pinaceae)). It is usually present in forests at low densities but can cause economic losses when changes in environmental conditions increase material suitable for brood development (Thomas 1961; Livingston 1979; Gara *et al.* 1999). Males select a host tree and produce aggregation pheromones that attract male and female conspecifics (Birch *et al.* 1980; Miller *et al.* 1989). A male constructs a nuptial chamber, where it mates with multiple females. The females construct ovipositional galleries radiating from the nuptial chamber. As they enter the tree and construct galleries, pine engravers introduce their symbiotic fungus, *Ophiostoma ips* (Rumbold) Nanfeldt (Klepzig *et al.* 1991; Furniss *et al.* 1995), which is carried on their exoskeleton. In the western United States of America, the pine engraver is typically bivoltine, with spring flights beginning in mid-April to early May and summer flights occurring in late June to mid-July (Livingston 1979). Our objective was to characterize the assemblage of hymenopterans responding to ponderosa pine (*Pinus ponderosa* C. Lawson) logs colonized by the pine engraver and its associated microorganisms.

Materials and methods

Study sites

All experiments were conducted at the University of Montana's Lubrecht Experimental Forest in Greenough, Montana (46°53.30′N, 113°26.00′W). Stands consisted of 70%–100% ponderosa pine. Other tree species (all Pinaceae) included Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and lesser components of western larch (*Larix occidentalis* Nutt.) and lodgepole pine (*Pinus contorta* Douglas *ex* Louden).

Experiment 1

Experiment 1 had two objectives: (1) to determine the identity and relative abundance of Hymenoptera arriving at trees colonized by *I. pini*; and (2) to assess for each species of Hymenoptera whether its arrival could be attributed to attraction to host trees or to host trees colonized by *I. pini* and its natural complement of microorganisms. This experiment was performed twice during 2002, once for each *I. pini* generation. The sampling periods were from 20 May to 15 July and from 17 July to 28 August. The three treatments consisted of (1) a log infested with *I. pini* and its natural complement of microorganisms, (2) a log alone, and (3) a blank control.

Sampling was conducted using a trap modified from Raffa and Dahlsten (1995) as described in Boone *et al.* (2008). Two healthy ponderosa pine trees approximately 15 cm diameter at 1.4 m height were felled and divided into 30 cm long logs. On the same day, the ends of the logs were sprayed with 10% sodium hypochlorite solution and sealed with paraffin wax. Treatment 1 was administered by introducing six male–female pairs into each of 12 logs 14–16 days after tree felling. The beetles were introduced by inserting one male and one female into a hole drilled in the phloem at one end of each log and covering the holes with a 2.5 cm by 2.5 cm piece of screen. The logs were wrapped with aluminum screening (1.5 mm mesh) to prevent entry by wild beetles.

Logs used for treatment 2 were treated in the same manner but no beetles were introduced into the logs. Treatment 3 (control) consisted of an empty aluminum screen of the same size and shape as that used in treatments 1 and 2.

Treatment logs and controls were placed on trap stands consisting of an aluminum conduit 2 m high by 1.3 cm in diameter. Two 15 cm lengths of copper wire (6 American wire gauge) inserted through holes 5 cm from the top provided support for treatment logs and blank controls. Each conduit was inserted into a 2.0 cm diameter support conduit in the ground. A sticky trap consisting of a piece of aluminum hardware cloth (3.0 mm mesh) 33 cm long by 31 cm wide coated with Tangle Trap was placed around each treatment log and blank control and secured to the copper-wire supports with wire (22 gauge) and 4 cm alligator clips.

Treatments were deployed in a randomized complete block design consisting of three sites with four blocks. Sites were established near areas with harvesting activities, logging slash, and detectable populations of *I. pini* and its natural enemies. The spacing was 10 m between treatments, 100 m between blocks, and at least 500 m between sites. Sticky traps were collected and replaced at 4-day intervals until adults emerged from the logs in treatment 1. Treatments were re-randomized at each collection period.

Insects were removed from sticky traps using a fine paint brush (size 0) dipped in 100% Citrisolv and stored in 15 mL vials in 100% Citrisolv. Taxonomic identifications were performed by the experts listed in the Acknowledgements. Individual parasitoids that could not be identified beyond family are designated “unknown” within that family. Voucher specimens were deposited at the Insect Research Collection in the Department of Entomology at the University of Wisconsin–Madison.

Experiment 2

Experiment 2 tested whether or not natural enemies are attracted to the predominant microbial symbionts of *I. pini* identified in Boone *et al.* (2008). It was conducted once for each generation in 2003, with sampling periods of 17 June – 3 August and 4–28 August. Five healthy trees were felled and prepared as described in experiment 1.

The treatments used during the first *I. pini* flight were (1) a blank control; (2) a log alone; (3) a log naturally infested with *I. pini* and its natural complement of microorganisms; (4) a log inoculated with *Ophiostoma ips* (Rumbold) Nannf., a symbiotic fungus; (5) a log inoculated with *Burkholderia* sp., a bacterium; (6) a log inoculated with *Pichia scolyti* (Phaff. & Yoney.) Kreger-van Rij, a yeast; and (7) a log with introduced adults of *I. pini* and its natural complement of microorganisms. The same treatments were tested in generation 2, except that treatment 7 was replaced with a log containing all three of the predominant microorganisms, *O. ips*, *Burkholderia* sp., and *P. scolyti* (six alternating inoculation points each). We had inadequate numbers of adults in generation 1 to artificially infest logs, so we used naturally infested trees containing L2–L3 larvae for treatment 3. No other species were observed in these logs. There were three sites with three blocks per site for generation 1 and three sites with four blocks per site for generation 2.

The microbial treatments were administered using actively growing (10 d) cultures on 2% malt extract agar. The bark was smoothed slightly with a drawshave and sprayed with 70% ethanol. Sixteen evenly spaced 0.6 cm diameter holes were then drilled through the bark and into the sapwood using a drill bit sterilized in 70% ethanol. A 0.6 cm diameter plug of agar containing the microbial culture was inserted into each hole using sterile forceps. The bark plug was then replaced and the hole sealed with inert silicone sealant. Treatment 2 (control) received equivalent agar plugs without microorganisms.

The treatments were evaluated according to four categories based on the potential attractant source: host plant plus *I. pini*, host plant plus microorganisms, host plant alone, or control. The proportion of Hymenoptera attracted to each category was calculated on the basis of the total number of treatments throughout the two experiments over both years (20 in total) and the number of individual treatments in each category (5, 7, 4, and 4, respectively). Parasitoid species with a sample size of at least 20 over 2 years were analyzed statistically. Counts for these parasitoids were aggregated across blocks within sites for each treatment and pooled across years prior to analysis. Each parasitoid genus or species was analyzed according to a randomized complete block design fitted with a Poisson regression using the Genmod procedure in SAS (SAS Institute Inc. 2003) followed by mean contrasts. The number of individual treatments in each category was used as a weight in the analyses. Some parasitoids were captured in only one year so analyses were confined to that year and the weight was adjusted accordingly. A Bonferroni adjustment was deemed too conservative for this large species list.

Results

A total of 5163 Hymenoptera representing 42 families and 159 genera were captured (Table 1). Over 98% were parasitoids, 1.0 % were phytophages, and less than 1.0% were predators. The most abundant families were Braconidae (18.6%), Platygastridae (14.3%), Encyrtidae (13.2%), Pteromalidae (11.9%), and Ichneumonidae (10.1%). Seven pteromalid species known to parasitize bark beetles represented 38.8% of this family and 4.9% of all Hymenoptera captured. Other parasitoid species known or suspected to parasitize bark beetles occurred in 7 genera in three other families and together comprised less than 1% of all Hymenoptera captured. Wasps reported to parasitize wood-borers or Curculionidae other than Scolytinae occurred in 17 genera in six families and comprised 1.9% of all Hymenoptera. Among other host types, parasitoids of Diptera were most common (8.5%), followed by parasitoids of Lepidoptera (7.7%), Hymenoptera (3.0%), and non-wood-boring Coleoptera (2.3%).

Of the individuals identified to species or genus, 32.0% consisted of a single specimen and 73.9% had 10 or fewer specimens (Fig. 1*a*). Within the 42 families identified, 42.9% had 10 or fewer specimens (Fig. 1*b*). When the taxa were categorized according to host type or guild, 64.3% had fewer than 5 specimens across all host types. Parasitoids of Scolytinae comprised only 7.7% of the total number of taxa captured, and 50.0% of those taxa had fewer than 5 specimens (Table 2).

In 2002, 2812 Hymenoptera were captured. Platygastridae was the most abundant family captured (20.4%), followed by Braconidae (18.7%), Encyrtidae (11.8%), Ichneumonidae (11.3%), and Pteromalidae (10.6%). The most common parasitoids were the pteromalids *Heydenia unica* Cook and Davis and *Rhopalicus pulchripennis* (Crawford), both of which exclusively attack bark beetles, and a generalist, *Dibrachys cavus* (Walker). These three species represented 16.4%, 14.6%, and 18.2% of all Pteromalidae and 1.7%, 1.6%, and 1.9% of all Hymenoptera, respectively. Their seasonal patterns and behavioral responses to potential sources of attraction are detailed in Boone *et al.* (2008). Parasitoids of Diptera were the most common wasps captured, comprising 13.8% of all Hymenoptera, followed by parasitoids of Lepidoptera (5.8%) and Coleoptera other than bark beetles (1.9%).

In 2003, 2351 Hymenoptera were captured. Braconidae was the most abundant family (18.7%), followed by Pteromalidae (15.4%), Encyrtidae (15.4%), Ichneumonidae (9.0%), and Platygastridae (8.5%). The most abundant bark beetle parasitoid was *H. unica*, which comprised 29.4% of all pteromalids captured. Parasitoids of Lepidoptera were the most abundant (8.1%), followed by those of other Coleoptera (2.6%) and Diptera (2.5%). Formicidae were captured on sticky traps in both years but were not counted.

Several genera of parasitoids showed preferential attraction to volatiles directly or indirectly associated with *I. pini* (Table 1). Six species were captured only in 2002 and so could not be included in tests for attraction to specific microorganisms. *Rhopalicus pulchripennis*, a parasitoid of Scolytinae, was more attracted to logs containing *I. pini* than to logs alone ($\chi^2 = 18.35$, $P < 0.0001$) or controls ($\chi^2 = 38.11$, $P < 0.0001$). A species of *Baryscapus* Förster (Eulophidae), a generalist and frequent hyperparasitoid, was more attracted to logs containing *I. pini* ($\chi^2 = 13.48$, $P = 0.0002$) than to controls ($\chi^2 = 5.28$, $P = 0.0216$). Parasitoids that were captured in both 2002 and 2003, or in 2003 only, also showed significant trends in attraction to odor sources. In addition to *H. unica*, four genera exhibited greater attraction to *I. pini*-infested logs than to other sources. A species of *Chelonus* Panzer (Braconidae), a parasitoid of Lepidoptera, was more attracted to *I. pini* than to microorganisms ($\chi^2 = 11.35$, $P = 0.0008$); a species of *Eurytoma* Illiger (Eurytomidae), a generalist, was more attracted to *I. pini* than to either microorganisms ($\chi^2 = 5.98$, $P = 0.0145$) or logs ($\chi^2 = 4.45$, $P = 0.0349$); a species of *Gelis* Thunberg (Ichneumonidae), a primary and hyperparasitoid on other Ichneumonoidea, was more attracted to *I. pini* than to microorganisms ($\chi^2 = 15.89$, $P < 0.0001$) or logs ($\chi^2 = 7.46$, $P = 0.0063$), and a species of *Platygaster* Latreille (Platygastridae), a parasitoid of gall-forming Diptera, was more attracted to *I. pini* than to controls ($\chi^2 = 26.89$, $P < 0.0001$). A species of *Sparasion* Latreille (Scelionidae), a parasitoid of grasshopper eggs, was more attracted to *I. pini* than to microorganisms ($\chi^2 = 57.80$, $P < 0.0001$). Two species were more attracted to microorganisms than to *I. pini*: *Laelius utilis*

Table 1. Hymenoptera collected from traps baited with *Ips pini* or its microbial symbionts and sorted into four categories: *Ips pini* (a ponderosa pine (*Pinus ponderosa*) log infested with *I. pini* and its natural complement of microorganisms), microorganisms (one log each inoculated with *Ophiostoma ips*, *Burkholderia* sp., or *Pichia scolyti*, or containing all of these three predominant microorganisms), host plant (log alone), and blank control (no log) at Lubrecht Experimental Forest, University of Montana, Greenough.

							Proportion in each treatment				
Family	Subfamily	Genus or species	Host^a	2002	2003	Total	*Ips pini*	Microorganisms	Host plant	Control	Treatment effect^b
Argidae		*Arge clavicornis* (Fabricius)	Phytophagous species (3, 5, 12)	0	1	1	0	0	0	1	i.d
	Total			0	1	1	0	0	0	1	
Aulacidae	Aulinae	*Pristaulacus rufitarsis* (Cresson)	Cerambycidae; Buprestidae (5)	3	0	3	0	0	0.33	0.67	i.d
	Unknown			0	5	5	0.2	0.8	0	0	i.d
	Total			3	5	8	0.125	0.5	0.125	0.25	
Bethylidae	Bethylinae	*Goniozus cellularis* (Say)	Curculionidae; Sylvanidae (1, 5)	5	3	8	0.13	0.37	0.25	0.25	i.d
	Cephalonominae	*Cephalonomia tarsalis* (Ashmead)	Microlepidoptera larvae (1, 5)	2	1	3	0.333	0.333	0	0.333	I.d
	Epyrinae	*Laelius utilis* Cockerell	Dermestidae (1, 5)	7	40	47	0.28	0.45	0.21	0.06	<0.0001*
		Sclerodermus macrogaster (Ashmead)	Cerambycidae eggs (1, 5)	0	1	1	1	0	0	0	i.d
	Pristocerinae	*Pseudisobrachium prolongatus* (Provancher)	Associated ants (1, 5)	1	0	1	1	0	0	0	i.d.
	Unknown			0	6	6	0.17	0.5	0.33	0	i.d
	Total			15	51	66	0.27	0.43	0.21	0.09	
Braconidae	Alysiinae	*Aphaereta* Förster	Sarcophagidae; Muscidae; Aulacigastridae; Calliphoridae (5, 13)	3	0	3	0	0	0	1	i.d
		Chorebus Haliday	Dryomyzidae; Ephydridae (5, 13)	11	0	11	0.18	0	0.09	0.73	i.d
		Dapsilarthra Förster	Syrphidae (5, 13)	1	0	1	0	0	1	0	i.d.
		Dinotrema Förster sp. *a*	Phoridae; Platypezidae (5, 13)	11	0	11	0.1	0	0.45	0.45	i.d.
		Dinotrema sp. *b*	Phoridae; Platypezidae (5, 13)	1	0	1	0	0	1	0	i.d.
	Aphidiinae	*Adialytus* Förster	Aphididae (5, 13)	1	0	1	0	0	0	1	i.d.
		Aphidius Nees	Aphididae (5, 13)	0	19	19	0.105	0.32	0.105	0.47	i.d.
		Aphidius sp. *a*	Aphididae (5, 13)	1	0	1	0	0	0	1	i.d.
		Aphidius sp. *b*	Aphididae (5, 13)	1	0	1	0	0	0	1	i.d.
		Aphidius sp. *c*	Aphididae (5, 13)	2	0	2	0	0	0	1	i.d.

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host[a]	2002	2003	Total	Proportion in each treatment: *Ips pini*	Microorganisms	Host plant	Control	Treatment effect[b]
		Aphidius sp. *d*	Aphididae (5, 13)	2	0	2	0.5	0	0	0.5	i.d.
		Aphidius sp. *e*	Aphididae (5, 13)	1	0	1	0	0	1	0	i.d.
		Aspilota Förster	Phoridae; Platypezidae (5, 13)	1	0	1	1	0	0	0	i.d.
		Lysiphlebus Förster	Aphididae (5, 13)	2	0	2	0	0	0.5	0.5	i.d.
		Pauesia Quilis sp. *a*	Lachnidae (5, 13)	1	0	1	0	0	1	0	i.d.
		Pauesia sp. *b*	Lachnidae (5, 13)	2	0	2	0	0	0	1	i.d.
		Trioxys Haliday	Aphididae (5, 13)	1	0	1	1	0	0	0	i.d.
		Xenostigmus bifasciatus (Ashmead)	Lachnidae (5, 13)	2	0	2	0	0	0	1	i.d.
	Blacinae	*Blacus* Nees sp. *a*	Coleoptera larvae (5, 13)	4	0	4	0.75	0	0.25	0	i.d.
		Blacus sp. *b*	Coleoptera larvae (5, 13)	20	0	20	0.1	0	0.3	0.6	i.d.
	Braconinae	*Atanycolus* Förster	Coleoptera, especially Buprestidae and Cerambycidae (5, 13)	1	0	1	0	0	1	0	i.d.
		Bracon Fabricius sp. *a*	Larvae of Lepidoptera, Coleoptera, and Diptera (5, 13)	2	0	2	0	0	0.5	0.5	i.d.
		Bracon sp. *b*	Larvae of Lepidoptera, Coleoptera, and Diptera (5, 13)	1	0	1	0	0	0	1	i.d.
		Bracon sp. *c*	Larvae of Lepidoptera, Coleoptera, and Diptera (5, 13)	3	0	3	0	0	0.67	0.33	i.d.
		Coeloides Wesmael sp. *a*	Larvae of Scolytidae, Curculionidae, and Buprestidae (5, 13)	1	0	1	1	0	0	0	i.d.
		Coeloides sp. *b*	Larvae of Scolytidae, Curculionidae, and Buprestidae (5, 13)	11	0	11	0.55	0	0.27	0.18	i.d.
		Habrobracon xanthonotus (Ashmead)	Concealed larvae of Coleoptera, Lepidoptera, Diptera, Hymenoptera, and grain moths (5, 13)	13	0	13	0.46	0	0.31	0.23	i.d.
	Cheloninae	*Ascogaster* Wesmael	Tortricidade; Geometridae; Pyralidae; Gelechiidae (5, 13)	1	7	8	0	0.75	0	0.25	i.d.
		Chelonus Panzer	Lepidoptera, 10 families (5, 13)	0	76	76	0.57	0.16	0.13	0.14	<0.0001*

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host[a]	2002	2003	Total	Proportion in each treatment				Treatment effect[b]
							Ips pini	Microorganisms	Host plant	Control	
		Chelonus (*Chelonus*) sp. *a* ♂	Lepidoptera, 10 families (5, 13)	1	0	1	0	0	1	0	i.d.
		Chelonus (*Chelonus*) sp. *a* ♀	Lepidoptera, 10 families (5, 13)	12	0	12	0.75	0	0.08	0.17	i.d.
		Chelonus (*Chelonus*) sp. *b*	Lepidoptera, 10 families (5, 13)	1	0	1	0	0	1	0	i.d.
		Chelonus (*Chelonus*) sp. *c*	Lepidoptera, 10 families (5, 13)	1	0	1	1	0	0	0	i.d.
		Chelonus (*Microchelonus*) sp. *a*	Lepidoptera, 10 families (5, 13)	1	0	1	0	0	0	1	i.d.
		Chelonus (*Microchelonus*) sp. *b*	Lepidoptera, 10 families (5, 13)	1	0	1	0	0	0	1	i.d.
		Chelonus absonus McComb	No recorded hosts (5, 13)	4	0	4	0.25	0	0.25	0.5	i.d
		Chelonus niger McComb	No recorded hosts (5, 13)	15	0	15	0.33	0	0.2	0.47	i.d.
		Phanerotoma Wesmael	Pyralidae; Gelechiidae; Tortricidae (5, 13)	1	1	2	0.5	0.5	0	0	i.d.
	Doryctinae	*Dendrosoter* Wesmael sp. *a*	Wood-boring Coleoptera, especially Scolytidae (5, 13)	1	0	1	0	0	1	0	i.d.
		Dendrosoter sp. *b*	Wood-boring Coleoptera, especially Scolytidae (5, 13)	16	0	16	0.75	0	0.19	0.06	i.d.
		Doryctes Haliday sp. *a*	Larvae of Buprestidae, Cerambycidae, and Scolytidae (5, 13)	4	0	4	0.25	0	0.25	0.5	i.d.
		Doryctes sp. *b*	Larvae of Buprestidae, Cerambycidae, and Scolytidae (5, 13)	3	0	3	0.333	0	0.333	0.333	i.d.
		Ecphylus Förster	Scolytidae; Bostrichidae; Lyctidae (5, 13)	2	0	2	0.5	0	0	0.5	i.d.
		Heterospilus Haliday sp. *a*	Wood-boring beetles; stem-boring sawflies and moths (5, 13)	8	0	8	0.625	0	0.25	0.125	i.d.
		Heterospilus sp. *b*	Wood-boring beetles; stem-boring sawflies and moths (5, 13)	2	0	2	0.5	0	0.5	0	i.d.
		Masonius Marsh	Biology unknown (5, 13)	2	0	2	1	0	0	0	i.d.
		Ontsira Cameron	Wood-boring beetle larvae; Tenebrionidae (5, 13)	1	0	1	0	0	1	0	i.d.

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host[a]	2002	2003	Total	Proportion in each treatment				Treatment effect[b]
							Ips pini	Microorganisms	Host plant	Control	
		Spathius Nees	Wood-boring beetle larvae (5, 13)	4	44	48	0.31	0.44	0.17	0.08	<0.0001*
	Euphorinae	*Cosmophorus* Ratzeburg	Adults of Scolytidae (5, 13)	2	0	2	0	0	0.5	0.5	i.d.
		Dinocampus coccinellae (Schrank)	Coccinellidae (5, 13)	25	0	25	0.16	0	0.84	0	i.d.
		Euphoriella Ashmead	Nymphs and adults of Psocoptera (5, 13)	16	0	16	0.19	0	0.31	0.5	i.d.
		Microctonus Wesmael	Curculionidae; Chrysomelidae; Carabidae (5, 13)	6	10	16	0.125	0.19	0.125	0.56	i.d.
	Helconinae	*Aliolus* Say	Cerambycidae; Curculionidae; Mordellidae (5, 13)	4	0	4	0.5	0	0.5	0	i.d.
		Eubazus Nees sp. *a*	Cerambycidae; Bruchidae; Curculionidae, especially Pissodes (5, 13)	2	0	2	0.5	0	0.5	0	i.d.
		Eubazus sp. *b*	Cerambycidae; Bruchidae; Curculionidae, especially Pissodes spp. (5, 13)	2	0	2	0.5	0	0	0.5	i.d.
		Triaspis Haliday	Larvae of Curculionidae and Bruchidae (5, 13)	24	0	24	0.54	0	0.38	0.08	0.0101*
		Urosigalphus rugosocorpus Gibson	Larvae of Curculionidae and Bruchidae (5, 13)	1	0	1	1	0	0	0	i.d.
	Horminae	*Hormius* Nees	Coleophoridae; Gelechiidae; Pyralidae; Tortricidae (5, 13)	1	0	1	1	0	0	0	i.d.
	Ichneutinae	*Ichneutes* Nees	Larvae of Tenthredinidae (5, 13)	1	0	1	1	0	0	0	i.d.
	Macrocentinae	*Macrocentrus crassipes* Muesebeck	Lepidoptera: Noctuidae (5, 13)	2	0	2	0	0	0.5	0.5	i.d.
	Meteorinae	*Meteorus* Haliday sp. *a*	Larvae of Coleoptera and Lepidoptera (5, 13)	1	0	1	0	0	1	0	i.d.
		Meteorus sp. *b*	Larvae of Coleoptera and Lepidoptera (5, 13)	1	0	1	0	0	1	0	i.d.
		Meteorus fumipennis Meusebeck	Larvae of Coleoptera and Lepidoptera (5, 13)	3	0	3	0.33	0	0.67	0	i.d.

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host[a]	2002	2003	Total	Proportion in each treatment				Treatment effect[b]
							Ips pini	Microorganisms	Host plant	Control	
		Meteorus politis (Provancher)	Larvae of Coleoptera and Lepidoptera (5, 13)	2	0	2	0.5	0	0.5	0	i.d.
		Meteorus versicolor (Wesmael)	Lymantridae (5, 13)	1	0	1	1	0	0	0	i.d.
	Microgastrinae	*Apanteles* Förster	Lepidoptera (5, 13)	0	45	45	0.16	0.42	0.11	0.31	<0.0001*
		Apanteles sp. *a*	Lepidoptera (5, 13)	13	0	13	0.38	0	0.08	0.54	i.d.
		Apanteles sp. *b*	Lepidoptera (5, 13)	5	0	5	0.2	0	0	0.8	i.d.
		Apanteles sp. *c*	Lepidoptera (5, 13)	2	0	2	0	0	0.5	0.5	i.d.
		Apanteles sp. *d*	Lepidoptera (5, 13)	1	0	1	0	0	0	1	i.d.
		Apanteles sp. *e*	Lepidoptera (5, 13)	2	0	2	0	0	0.5	0.5	i.d.
		Choeras Mason	Microlepidoptera (5, 13)	2	0	2	0	0	0	1	i.d.
		Cotesia Cameron sp. *a*	Macrolepidoptera (5, 13)	26	0	26	0.27	0	0.19	0.54	i.d.
		Cotesia sp. *b*	Macrolepidoptera (5, 13)	1	0	1	0	0	1	0	i.d.
		Iconella Mason	Microlepidoptera (5, 13)	1	0	1	1	0	0	0	i.d.
		Microgaster Latreille sp. *a*	Lepidoptera (5, 13)	4	0	4	0	0	0.25	0.75	i.d.
		Microgaster sp. *b*	Lepidoptera (5, 13)	1	0	1	0	0	0	1	i.d.
		Microplitis Förster	Macrolepidoptera (5, 13)	10	0	10	0.3	0	0.2	0.5	i.d.
	Miracinae	*Mirax* Haliday	Leaf-mining Lepidoptera (5, 13)	3	0	3	0	0	0.33	0.67	i.d.
	Neoneurinae	*Elasmosoma* Ruthe	Formicine ants (5, 13)	7	0	7	0	0	0.43	0.57	i.d.
		Neoneurus Haliday	Formicine ants (5, 13)	11	0	11	0.27	0	0.27	0.46	i.d.
	Opiinae	*Opius* Wesmael	Agromyzidae; Anthomyiidae; Chloropidae; Drosophilidae; Ephydridae; Lonchaeidae; Sarcophagidae; Tephritidae (5, 13)	4	0	4	0.25	0	0.25	0.5	i.d.
	Orgilinae	*Orgilus* Haliday	Larvae of Lepidoptera (5, 13)	46	0	46	0.37	0	0.3	0.33	
	Rogadinae	*Aleiodes* Wesmael	Macrolepidoptera (5, 13)	1	2	3	1	0	0	0	i.d.
		Aleiodes sp. *a*	Macrolepidoptera (5, 13)	8	0	8	0.125	0	0.625	0.25	i.d.
		Aleiodes sp. *b*	Macrolepidoptera (5, 13)	2	0	2	0.5	0	0.5	0	i.d.
	Unknown			91	235	326	0.25	0.3	0.2	0.25	i.d.
	Total			516	439	955	0.27	0.2	0.23	0.29	

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host^a	2002	2003	Total	Proportion in each treatment: *Ips pini*	Microorganisms	Host plant	Control	Treatment effect^b
Ceraphronidae		*Aphanognus* Thomson	Cecidomyiidae, hyperparasite on Hymenoptera (5)	0	1	1	1	0	0	0	i.d.
		Ceraphron Jurine	Diptera; Hymenoptera; Hemiptera (5)	2	0	2	0.5	0	0	0.5	i.d.
	Unknown			54	30	84	0.31	0.14	0.21	0.33	i.d.
	Total			56	31	87	0.32	0.14	0.21	0.33	
Chalcididae	Chalcidinae	*Brachymeria* Westwood	Lepidoptera; Diptera; Hymenoptera (2, 5)	0	1	1	0	0	0	1	i.d.
		Conura Spinola	Lepidoptera; Hymenoptera; Coleoptera; secondary parasites through Lepidoptera, Braconidae, and Ichneumonidae (2, 5)	1	2	3	0.33	0.67	0	0	i.d.
		Conura albifrons (Walsh)	Lepidoptera (5)	0	1	1	0	1	0	0	i.d.
		Trigonura Sichel	Curculionidae; Buprestidae; Scolytidae (2, 5)	0	1	1	0	0	0	1	i.d.
	Haltichellinae	*Hockeria* Walker	Pupae of Lepidoptera, Neuroptera, and Diprionidae (2, 5)	1	1	2	0	0	0.5	0.5	i.d.
		Haltichella Spinola	Lepidoptera (2, 5)	1	0	1	0	0	0	1	i.d.
	Unknown			5	1	6	0.17	0	0.17	0.66	i.d.
	Total			8	7	15	0.13	0.2	0.13	0.54	
Chrysididae	Amiseginae	*Amisega kahlii* (Ashmead)	Eggs of Phasmida (4, 5)	0	1	1	0	1	0	0	i.d.
	Chrysidinae	*Chrysis* Linnaeus	Vespidae; Megachilidae; Sphecidae; Anthophoridae (4, 5)	19	19	38	0.13	0.32	0.39	0.16	<0.0001*
		Omalus Panzer	Sphecidae (4, 5)	0	3	3	0.67	0	0	0.33	i.d.
	Cleptinae	*Cleptes aliena* Patton	Tenthredinidae (4, 5)	0	1	1	0	0	0	1	i.d.
	Unknown			13	2	15	0.33	0.13	0.2	0.33	i.d.
	Total			32	26	58	0.21	0.26	0.31	0.22	
Colletidae	Hylaeinae	*Hylaeus* Fabricius	Stem-nester (5, 7)	5	1	6	0.5	0	0.33	0.17	i.d.

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host^a	2002	2003	Total	Proportion in each treatment: *Ips pini*	Microorganisms	Host plant	Control	Treatment effect^b
	Unknown			0	1	1	0	0	0	1	i.d.
	Total			5	2	7	0.42	0	0.29	0.29	
Cynipidae	Unknown		Phytophagous species: gall-formers (5)	1	8	9	0	0.33	0.22	0.44	i.d.
	Total			1	8	9	0	0.33	0.22	0.44	
Diapriidae	Belytinae	*Acanosema* Kieffer	Diptera (5)	1	0	1	0	0	1	0	i.d.
		Aclista Förster	Diptera (5)	14	0	14	0.29	0	0.21	0.5	i.d.
		Acropiesta Förster	No host recorded (5)	2	0	2	0.5	0	0.5	0	i.d.
		Belyta Jurine	No host records for North American species (5)	3	0	3	0	0	0	1	i.d.
		Cinetus Jurine	Diptera (5)	14	0	14	0.14	0	0.29	0.57	i.d.
		Miota Förster	Host relationships unknown (5)	1	0	1	0	0	1	0	i.d.
		Opazon parvulum (Haliday)	Diptera (5)	56	0	56	0.31	0	0.21	0.48	i.d.
		Pantoclis Förster	Mycetophilidae; Sciaridae (5)	3	0	3	0	0	0.67	0.33	i.d.
		Zygota Förster	Mycetophilidae; Sciaridae (5)	9	0	9	0.22	0	0.11	0.67	i.d.
	Diapriinae	*Basalys* Westwood	Orthorrhapha; Cyclorrhapha; Anthomyiidae; Coleoptera Ant nests (5, 6)	12	0	12	0.42	0	0.33	0.25	i.d.
		Diapria Latreille	Syrphidae (5, 6)	1	8	9	0	0.67	0.22	0.11	i.d.
		Psilus Panzer	Anthomyiidae; Lonchaeidae; Tephritidae (5, 6, 9)	0	1	1	0	1	0	0	i.d.
		Trichopria Ashmead	Tephritidae; Tachinidae; Syrphidae; Ephydridae; Stratiomyidae; Calliphoridae; Sarcophagidae; Drosophilidae; Glossinidae; Tabanidae; Chloropidae; Agromyzidae; Sciomyzidae; Psephenidae (5, 6)	3	0	3	0.33	0	0.67	0	i.d.
	Unknown			4	52	56	0.11	0.39	0.21	0.29	i.d.
	Total			123	61	184	0.21	0.16	0.24	0.39	

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host^{a}	2002	2003	Total	Proportion in each treatment				Treatment effect^{b}
							Ips pini	Microorganisms	Host plant	Control	
Dryinidae	Anteoninae	*Anteon* Jurine	Nymphs of Homoptera (5)	0	12	12	0.08	0.25	0	0.67	i.d.
	Aphelopinae	*Aphelopus* Dalman	Nymphs of Homoptera (5)	0	7	7	0	0.57	0.14	0.29	i.d.
		Aphelopus albopictus Muesebeck	Nymphs of Homoptera (5)	8	0	8	0.25	0	0.25	0.5	i.d.
	Gonatopodinaea	*Tetradontochelys plesius* (Fenton)	Nymphs of Homoptera (10)	1	0	1	0	0	0	1	i.d.
	Unknown			0	6	6	0.17	0.33	0.17	0.33	i.d.
	Total			9	25	34	0.12	0.26	0.12	0.5	
Elasmidae		*Elasmus* Westwood	Lepidoptera; hyperparasites on Braconidae (5)	1	2	3	0.5	0.25	0.25	0	i.d.
	Unknown			1	0	1	0.333	0.333	0	0.333	i.d.
	Total			2	2	4	0.43	0.29	0.14	0.14	
Embolemidae	Unknown			1	1	2	0	0.5	0	0.5	i.d.
	Total			1	1	2	0	0.5	0	0.5	
Encyrtidae	Encyrtinae	*Copidosoma* Ratzeburg	Lepidoptera: Noctuidae, Papilionidae, and Tortricidae (5)	4	0	4	0.75	0	0	0.25	i.d.
		Encyrtus infida (Rossi)	Homoptera: Coccidae (5)	1	0	1	1	0	0	0	i.d.
	Unknown			308	363	671	0.36	0.25	0.21	0.18	i.d.
	Total			313	363	676	0.36	0.24	0.21	0.18	
Eucharitidae		*Pseudochalcura gibbosa* (Provancher)	Formicidae (2, 5)	0	23	23	0	0.61	0.17	0.22	<0.0001*
	Unknown			10	0	10	0.3	0	0.3	0.4	i.d.
	Total			10	23	33	0.09	0.42	0.21	0.27	
Eucoilidae	Unknown			6	7	13	0.31	0.31	0.15	0.23	i.d.
	Total			6	7	13	0.31	0.31	0.15	0.23	
Eulophidae	Entodontoniae	*Aprostocetus* Westwood	Diptera: larvae of Ceciomyiidae; ootheca of Blattidae; Anthophoridae; Megachilidae; Tephritidae (2, 5)	45	0	45	0.44	0	0.11	0.44	0.0024*

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host^{a}	2002	2003	Total	Proportion in each treatment: *Ips pini*	Proportion in each treatment: Microorganisms	Proportion in each treatment: Host plant	Proportion in each treatment: Control	Treatment effect^{b}
		Chrysocharis Förster	Leaf-mining Coleoptera, Lepidoptera, Diptera, and Hymenoptera (2, 5)	7	0	7	0.57	0	0.29	0.14	i.d.
		Closterocerus Westwood	Coleoptera; leaf-mining Diptera, Lepidoptera, and Hymenoptera (sawflies) (4, 5)	1	0	1	1	0	0	0	i.d.
		Entedon Dalman	Curculionidae (including Scolytinae); Bruchidae (2, 5)	2	0	2	0	0	1	0	i.d.
		Galeopsomyia Girault	Associated with galls; Cecidomyidae ; Cynipidae (2, 5)	0	2	2	0	1	0	0	i.d.
		Goetheana Girault	Thripidae (2)	2	0	2	0.5	0	0.5	0	i.d.
		Melittobia Westwood	Aculeata; Anthophoridae; Megachilidae; Torymidae (2, 5)	7	0	7	0.57	0	0.29	0.14	i.d.
		Pediobius Walker	Lepidoptera; Coleoptera; Diptera; Hymenoptera; spider eggs (2, 5)	3	3	6	0.5	0.17	0	0.33	i.d.
		Pediobius magniclavatus Peck	Unknown (11)	1	0	1	0	0	0	1	i.d.
		Tetrastichus Haliday	Coleoptera; Diptera; Lepidoptera; Hymenoptera (2, 5)	1	114	115	0.22	0.39	0.1	0.29	<0.0001*
	Euderinae	*Astichus* Förster	Coleoptera in bracket fungi (Ciidae, Tenebrionidae), emerged from cynipid gall (2, 5)	1	0	1	0	0	0	1	i.d.
		Euderus Haliday	Coleoptera; Hymenoptera; Lepidoptera (2, 5)	1	0	1	0	0	0.5	0.5	i.d.
	Eulophinae	Near *Comastichus* LaSalle	Spider egg sacs (2)	1	0	1	1	0	0	0	i.d.
		Dahlbominus fuscipennis (Zetterstedt)	Diprionidae (2, 5)	1	0	1	0	0	0	1	i.d.
		Euplectrus Westwood	Lepidoptera (2, 5)	3	2	5	0.2	0.2	0.2	0.4	i.d.
		Euplectrus platyhypenae Howard	Lepidoptera (2, 5)	1	0	1	0	0	0	1	i.d.

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host^a	2002	2003	Total	Proportion in each treatment				Treatment effect^b
							Ips pini	Microorganisms	Host plant	Control	
		Hyssopus Girault	Lepidoptera (2, 5)	5	15	20	0.25	0.5	0.25	0	<0.0001*
		Hyssopus rhyacioniae Gahan	Pyralidae (5)	3	0	3	0.5	0	0	0.5	i.d.
		Hyssopus sanninoideae (Girault)	Sessidae (5)	1	0	1	0.5	0	0.5	0	i.d.
		Pnigalio Schrank	Leaf-mining Coleoptera, Diptera, and Lepidoptera (2, 5)	1	0	1	0	0	1	0	i.d.
		Sympiesis Förster	Leaf-mining Lepidoptera (2, 5)	1	0	1	1	0	0	0	i.d.
	Tetrastichinae	*Baryscapus* Förster	Parasites or often hyperparasites of a wide range of hosts (2)	45	0	45	0.59	0	0.13	0.27	0.0008*
		Elachertus Spinola	Lepidoptera in concealed situations (2, 5)	2	0	2	0.5	0	0.5	0	i.d.
		Elachertus argissa (Walker)	Lepidoptera in concealed situations (2, 5)	1	0	1	0	0	0	1	i.d.
	Unknown			4	60	64	0.22	0.45	0.05	0.28	i.d.
	Total			140	196	336	0.32	0.26	0.13	0.29	
Eupelmidae	Calosotinae	*Calosota* Curtis	Stem-nesting wasps (2, 5)	1	0	1	0	0	0	1	i.d.
	Eupelminae	*Eupelmus vesicularis* (Retzius)	Larval or pupal stages of a wide variety of holometablous insects in concealed situations such as cocoons, galls, or other plant tissue (2, 5)	1	2	3	0.333	0	0.333	0.333	i.d.
	Unknown			7	14	21	0.14	0.14	0.38	0.34	i.d.
	Total			9	16	25	0.16	0.12	0.36	0.36	
Eurytomidae	Eurytominae	*Eurytoma* Illiger	Coleoptera; Diptera; Homoptera; Hymenoptera; Lepidoptera (2, 5)	7	17	24	0.42	0.25	0.25	0.08	< 0.0001*
		Eurytoma (male)	Coleoptera; Diptera; Homoptera; Hymenoptera; Lepidoptera (2, 5)	4	0	4	0.25	0	0.5	0.25	i.d.

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host^a	2002	2003	Total	Proportion in each treatment				Treatment effect^b
							Ips pini	Microorganisms	Host plant	Control	
		Eurytoma illinoisensis Girault	Harmolita sp. (Eurytomidae) (2, 5)	1	0	1	1	0	0	0	i.d.
		Eurytoma microneura Ratzeburg	No hosts recorded (5)	1	0	1	0	0	1	0	i.d.
		Eurytoma obtusiventris Gahan	Tephritidae (5)	1	0	1	0	0	0	1	i.d.
	Harmolitinae	*Tetramesa* Walker	Phytophagous species: gall-formers (2, 5)	0	3	3	0.333	0.333	0.333	0	i.d.
		Tetramesa bambusae Phillips	Phytophagous species: gall-formers (5)	4	0	4	0	0	0.5	0.5	i.d.
	Unknown			2	1	3	0.333	0.333	0	0.333	i.d.
	Total			20	21	41	0.34	0.2	0.29	0.17	
Figitidae	Unknown			1	1	2	0	0	0.5	0.5	i.d.
	Total			1	1	2	0	0	0.5	0.5	
Gasteruptidae	Gasteruptinae	*Gasteruption* Latreille	Solitary bees (Sphecidae) (5)	0	6	6	0.17	0.66	0.17	0	i.d.
	Total			0	6	6	0.17	0.66	0.17	0	
Halictidae	Halictinae	*Lasioglossum* (*Dialictus*) Curtis	Pollinator (5, 7)	1	1	2	0	0.5	0	0.5	i.d.
	Total			1	1	2	0	0.5	0	0.5	
Ichneumonidae	Cryptinae	*Gelis* Thunberg	Hyperparasitoid of Braconidae and Ichneumonidae; primary parasitoid of sawflies and Lepidoptera (5)	19	9	28	0.36	0.14	0.18	0.32	<0.0001*
	Ophioninae	*Ophion* Fabricius	Noctuidae; Scarabaeidae (5)	1	0	1	0	0	0	1	i.d.
	Pimplinae	*Itoplectus* Förster	Lepidoptera; Hymenoptera: Symphyta, Ichneumonoidea (5)	1	0	1	1	0	0	0	i.d.
		Pimpla Fabricius	Hymenoptera: Megachilidae and Vespidae (5)	2	0	2	1	0	0	0	i.d.
	Xoridinae	*Odontocolon* Cushman	Cerambycidae (5)	1	0	1	0	0	1	0	i.d.

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host[a]	2002	2003	Total	Proportion in each treatment: *Ips pini*	Microorganisms	Host plant	Control	Treatment effect[b]
	Unknown			283	203	486	0.28	0.19	0.25	0.28	i.d.
	Total			307	212	519	0.28	0.19	0.25	0.28	
Leucospidae		*Leucospis affinis* Say	Apiformes: solitary Vespidae, Sphecidae (2, 5)	0	1	1	0	1	0	0	i.d.
	Total			0	1	1	0	1	0	0	
Megachilidae	Megalinae	*Heriades* Spinola	Pollinator: polylectic, cavity-nester (8)	9	0	9	0.11	0	0.33	0.56	i.d.
		Osmia Panzer	Pollinator: polylectic, cavity-nester (8)	1	0	1	0	0	0	1	i.d.
	Unknown			0	6	6	0.17	0.5	0	0.33	i.d.
	Total			10	6	16	0.12	0.19	0.19	0.5	
Megaspilidae	Megaspilinae	*Dendrocerus* Ratzeburg	Hemiptera; Hymenoptera(5)	18	0	18	0.28	0	0.5	0.22	i.d.
	Unknown			29	36	65	0.25	0.23	0.18	0.34	i.d.
	Total			47	36	83	0.25	0.18	0.25	0.31	
Mutillidae	Unknown		Coleoptera; Diptera; Hymenoptera; Lepidoptera (5)	1	0	1	0	0	0	1	i.d.
	Total			1	0	1	0	0	0	1	
Mymaridae	Mymarinae	*Gonatocerus* Nees	Hemiptera (2, 5)	3	0	3	0.33	0	0.33	0.33	i.d.
	Unknown			12	4	16	0.06	0.125	0.19	0.625	i.d.
	Total			15	4	19	0.1	0.1	0.21	0.58	
Orussidae	Orussinae	*Orussus* Latreille	Wood-boring insects, especially Coleoptera (5)	0	1	1	1	0	0	0	i.d.
		Orussus terminalis (Newman)	Wood-boring insects, especially Coleoptera (5)	1	0	1	0	0	1	0	i.d.
		Orussus thoracicus Ashmead	Wood-boring insects, especially Coleoptera (5)	2	0	2	0.5	0	0.5	0	i.d.
	Unknown			3	1	4	0.25	0.25	0.5	0	i.d.
	Total			6	2	8	0.38	0.12	0.5	0	

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host^a	2002	2003	Total	Proportion in each treatment				Treatment effect^b
							Ips pini	Microorganisms	Host plant	Control	
Perilampidae	Perilampinae	*Perilampus* Latreille	Braconidae; Ichneumonidae; Chrysopidae; Tenthredinidae; Lepidoptera (2, 5)	0	2	2	0	1	0	0	i.d.
	Unknown			1	0	1	1	0	0	0	i.d.
	Total			1	2	3	0.33	0.67	0	0	
Platygastridae	Inostemminae	*Inostemma* Haliday	Gall-forming Cecidomyiidae and Cynipidae (5)	9	21	30	0.33	0.2	0.3	0.17	0.0004*
		Platygaster Latreille	Gall-forming Cecidomyiidae, Tephritidae, and Cynipidae (5)	207	25	232	0.4	0.03	0.27	0.29	<0.0001*
	Unknown			320	154	474	0.35	0.14	0.21	0.3	i.d.
	Total			536	200	736	0.37	0.11	0.24	0.29	
Pompilidae	Unknown		Araneae (5)	3	7	10	0.4	0.5	0	0.1	i.d.
	Total			3	7	10	0.4	0.5	0	0.1	
Proctotrupidae		*Proctotrupes* Latreille	Carabidae (5)	0	1	1	0	0	0	1	i.d.
	Unknown			3	20	23	0.22	0.26	0.13	0.39	i.d.
	Total			3	21	24	0.21	0.25	0.12	0.42	
Pteromalidae	Cleonyminae	*Heydenia unica* Cook and Davis	Scolytidae (2, 5)	46	107	153	0.52	0.36	0.11	0.01	<0.0001*
	Colotrechinae	*Colotrechnus* Thomson	Agromyzidae in flower heads; in Compositae flower heads (2, 5)	4	0	4	0.5	0	0	0.5	i.d.
	Eremerinae	*Roptrocerus xylophagorum* (Ratzeburg)	Scolytidae (2, 5)	4	5	9	0.67	0.11	0	0.22	i.d.
	Miscogasterinae	*Gastrancistrus* Westwood	Gall-forming Cecidomyiidae (2, 5)	18	0	18	0.39	0	0.33	0.28	i.d.
	Pteromalinae	*Callitula* Spinola	Agromyzidae; Cecidomyiidae (2, 5)	2	0	2	0.5	0	0	0.5	i.d.
		Cheiropachus Westwood	Wood-boring Coleoptera, especially Scolytidae; Curculionidae (2, 5)	6	0	6	0.33	0	0.33	0.33	i.d.

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host^{a}	2002	2003	Total	Proportion in each treatment				Treatment effect^{b}
							Ips pini	Microorganisms	Host plant	Control	
		Chlorocytus Graham	Insects in grass stems (2)	2	0	2	0.5	0	0	0.5	i.d.
		Choetospilisca tabida (Gahan)	Curculionidae: Cossinae (2, 5)	0	2	2	0	1	0	0	i.d.
		Cyclogastrella Bukovskij	Pupae of Tortricidae; Gelechiidae (2, 5)	15	0	15	0.13	0	0.33	0.53	i.d.
		Dibrachys cavus (Walker)	Generalist, mainly Lepidoptera (2, 5)	51	0	51	0.45	0	0.39	0.16	0.0154*
		Dinotiscus dendroctoni (Ashmead)	Scolytidae (2, 5)	9	0	9	0.56	0	0.11	0.33	i.d.
		Mesopolobus Westwood	Cynipidae; Lepidoptera; Coleoptera; Symphyta (2, 5)	25	1	26	0.5	0.04	0.38	0.08	0.0087*
		Metacolus fasciatus Girault	Scolytidae (2, 5)	0	13	13	0.23	0.54	0.23	0	i.d.
		Pandelus grisseli Boucek	Anobiidae (2)	0	1	1	1	0	0	0	i.d.
		Plutothrix Förster	Anobiidae; Cerambycidae; Ciidae; Tenebrionidae; Anthribidae; Trogossitidae (2, 5)	0	1	1	1	0	0	0	i.d.
		Pteromalus Swederus	Coleoptera and Lepidoptera and their hymenopterous parasites (2, 5)	2	2	4	0.25	0.25	0.25	0.25	i.d.
		Rhaphitelus maculatus Walker	Curculionidae, Scolytidae (2, 5)	5	10	15	0.47	0.13	0.2	0.2	i.d.
		Rhopalicus pulchripennis (Crawford)	Curculionidae; Scolytidae (2, 5)	41	1	42	0.79	0	0.19	0.02	<0.0001*
		Tomicobia Ashmead	Curculionidae; Scolytidae (2, 5)	3	0	3	1	0	0	0	i.d.
		Trichomalopsis Crawford	Coleoptera and Lepidoptera and their hymenopterous parasites (2)	1	0	1	0	0	0	1	i.d.
		Tritneptis Girault	Diprionidae; Lepidoptera (2, 5)	1	0	1	0	0	0	1	i.d.
		Zdenekiana squama Huggert	No host records (2)	6	0	6	0.17	0	0.66	0.17	i.d.
	Unknown			39	221	260	0.27	0.48	0.13	0.12	i.d.
	Total			280	364	644	0.41	0.29	0.18	0.12	

Table 1 (*continued*).

Family	Subfamily	Genus or species	Host^{a}	2002	2003	Total	Proportion in each treatment				Treatment effect^{b}
							Ips pini	Microorganisms	Host plant	Control	
Scelionidae	Scelioninae	*Gryon* Haliday	Eggs of Hemiptera, especially Coreidae (5)	2	5	7	0.43	0	0	0.57	i.d.
		Scelio Latreille	Grasshopper eggs (5)	0	5	5	0.4	0.4	0	0.2	i.d.
		Sparasion Latreille	Grasshopper eggs (5)	0	36	36	0.69	0.17	0.08	0.06	<0.0001*
	Telominae	*Telenomus* Haliday	Diptera; Hemiptera; Lepidoptera; Neuroptera (5)	41	10	51	0.22	0.14	0.29	0.35	<0.0001*
	Unknown			199	101	263	0.32	0.14	0.25	0.29	i.d.
	Total			242	157	399	0.35	0.14	0.23	0.28	
Signiphoridae	Unknown		Hemiptera: Coccidae; Aleyrodidae (2, 5, 14)	3	0	3	0.67	0	0.33	0	i.d.
	Total			3	0	3	0.67	0	0.33	0	
Sphecidae	Unknown		Arachnida (5)	29	16	45	0.22	0.16	0.38	0.24	i.d.
	Total			29	16	45	0.22	0.16	0.38	0.24	
Tenthredinidae	Unknown		Phytophagous species: leaf-feeder: leaf-miners, gall-former, or shoot-borer (5)	26	3	29	0.28	0	0.2	0.52	i.d.
	Total			26	3	29	0.28	0	0.2	0.52	
Tiphiidae	Unknown		Soil-dwelling Coleoptera and Hymenoptera (5)	1	0	1	0	0	0	1	i.d.
	Total			1	0	1	0	0	0	1	
Torymidae	Toryminae	*Monodontomerus dentipes* (Dalman)	Diptera; Hymenoptera; Lepidoptera (2, 5)	8	21	29	0.37	0.33	0.26	0.04	<0.0001*
		Zdenekius boucelei Grissell	Aculeata and their parasites on twigs (2)	2	0	2	1	0	0	0	i.d.
	Unknown			15	3	18	0.25	0.1	0.25	0.4	i.d.
	Total			25	24	49	0.35	0.22	0.24	0.18	
Vespidae	Eumeminae	*Ancistrocerus* Wesmael	Predator: larvae of Lepidoptera (5)	0	1	1	0	0	1	0	i.d.

Table 1 (*concluded*).

Family	Subfamily	Genus or species	Host[a]	2002	2003	Total	Proportion in each treatment				Treatment effect[b]
							Ips pini	Microorganisms	Host plant	Control	
		Stenodynerus Saussure	Predator: larvae of Coleoptera and Lepidoptera (5)	0	1	1	1	0	0	0	i.d.
	Unknown			5	1	6	0.67	0	0.33	0	i.d.
	Total			5	3	8	0.62	0	0.38	0	
Xyelidae	Unknown		Pollen feeders: *Pinus*, *Abies*, *Salix* (5)	1	0	1	0	0	1	0	i.d.
	Total			1	0	1	0	0	1	0	

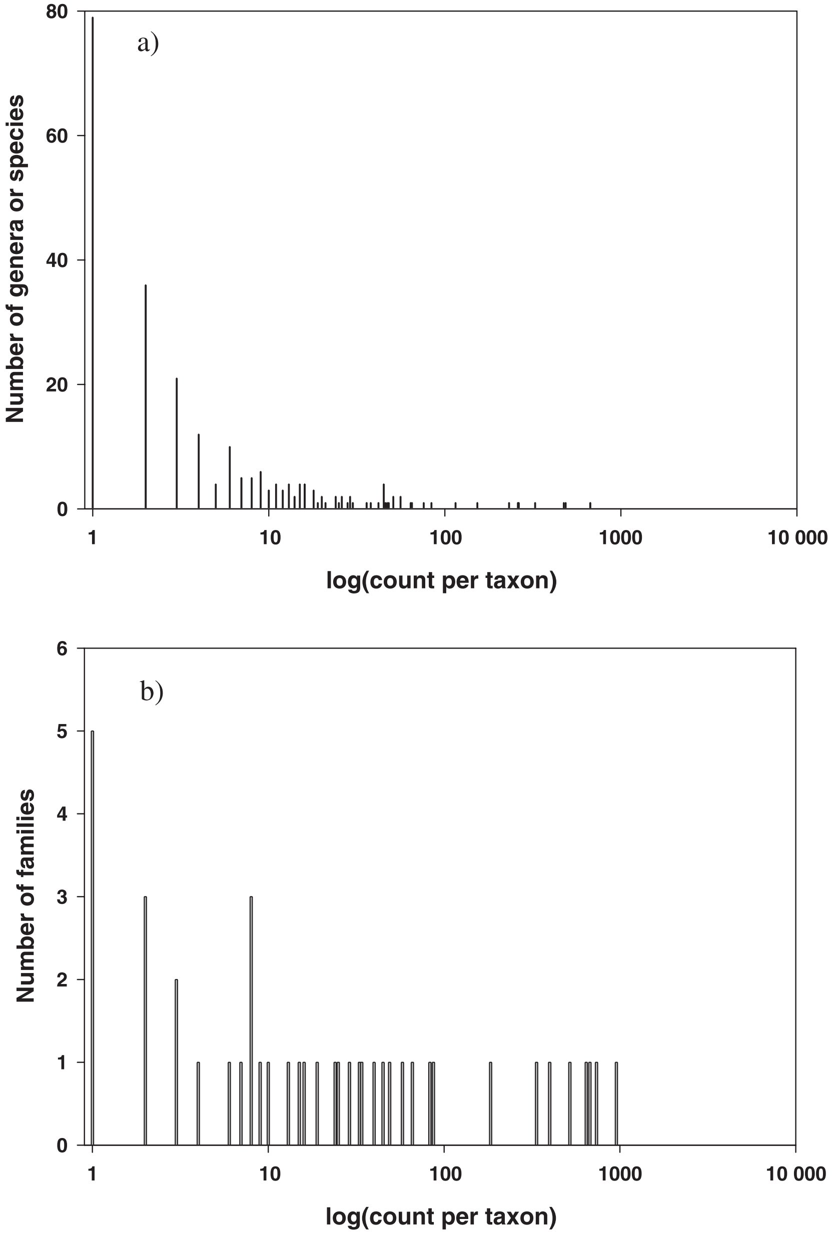
Note: If a species is not a parasitoid, the feeding guild is indicated. Treatments consisting of a log with *I. pini* and its natural complement of microorganisms, host plant, and blank control were used in 2002 and 2003; the remaining treatments consisting of microbial symbionts were used in 2003 only. Scolytidae has since been reclassified as Curculionidae: Scolytinae.

[a] Numbers in parentheses denote references: **1**, H.E. Evans. 1978. The Bethylidae of America north of Mexico. Memoirs of the American Entomological Institute No. 27. The American Entomological Institute. Ann Arbor, Michigan; **2**, G.A.P. Gibson, J.T. Huber, and J.B. Woolley. 1997. Annotated keys to the genera of Nearctic Chalcidoidea (Hymenoptera). Research Press, National Research Council of Canada, Ottawa, Ontario; **3**, H. Goulet. 1992. The genera and subgenera of the sawflies of Canada and Alaska. Hymenoptera: Symphyta. In The insects and arachnids of Canada. Part 20. Publication No. 1876, Agriculture Canada, Ottawa, Ontario; **4**, L.S. Kimsey and R.M. Bohart. 1990. The chrysidid wasps of the world. Oxford University Press, Oxford, New York and Toronto; **5**, K.V. Krombein, P.D. Hurd, D.R. Smith, and B.D. Burks. 1979. Catalogue of Hymenoptera in America north of Mexico. Smithsonian Institution Press, Washington, D.C.; **6**, I. Masner and J.L. Garcia. 2002. The genera of Diapriinae (Hymenoptera: Diapriidae) in the New World. Bulletin No. 268, American Museum of Natural History, New York; **7**, T.B. Mitchell. 1960. Bees of the eastern United States. Vol. I. Technical Bulletin No. 141, North Carolina Agricultural Experiment Station, with support from the National Science Foundation; **8**, T.B. Mitchell. 1962. Bees of the eastern United States. Vol. II. Technical Bulletin No. 152, North Carolina Agricultural Experiment Station, with support from the National Science Foundation; **9**, C.F.W. Musebeck. 1980. The Nearctic parasitic wasps of the genera *Psilus* Panzer and *Coptura* Say (Hymenoptera, Proctotrupoidea, Diapriidae). Technical Bulletin No. 1617, United States Department of Agriculture. pp. 1–71; **10**, M. Olmi. 1984. A revision of the Dryinidae (Hymneoptera). Memoirs of the American Entomological Institute No. 37. Part 2. pp. 947–1913; **11**, O. Peck. 1985. The taxonomy of the Nearctic species of *Pediobus* (Hymenoptera: Eulophidae), especially Canadian and Alaskan forms. The Canadian Entomologist, 117: 647–704; **12**, D.R. Smith. 1989. The sawfly genus *Arge* (Hymenoptera: Argidae), in the Western Hemisphere. Transactions of the American Entomological Society, 115: 83–205; **13**, R.A. Wharton, P.M. Marsh, and M.J. Sharkey. 1997. Manual of the New World genera of the family Braconidae (Hymenoptera). Special Publication of the International Society of Hymenopterists No. 1. Allen Press, Lawrence, Kansas; **14**, J.B. Woolley. 1990. Signiphoridae. *In* World crop pests. Vol. 4B. Armored scale insects: their biology, natural enemies and control. *Edited by* D. Rose. Elsevier, Amsterdam, the Netherlands. pp. 167–176.

[b] i.d., insufficient data for statistical analysis.

*Significant treatment effect at $P < 0.05$.

Fig. 1. Frequency distribution of Hymenoptera arriving at ponderosa pine (*Pinus ponderosa*) logs colonized by *Ips pini* and associated microorganisms in Montana during 2002 and 2003. (*a*) Genera or species. (*b*) Family. When two specimens from the same genus were given different morphotype identifications, they were counted as different species, not as a single genus.



Cockerell (Bethylidae), a parasitoid of Dermestidae (Coleoptera) ($\chi^2 = 10.94$, $P = 0.0009$), and a species of *Spathius* Nees (Braconidae), a parasitoid of wood-borer larvae ($\chi^2 = 5.81$, $P = 0.0160$). Two parasitoids showed greater attraction to microorganisms than to controls: *Pseudochalcura gibbosa* (Provancher) (Eucharitidae), a parasitoid of Formicidae ($\chi^2 = 81.05$, $P < 0.0001$), and a species of *Tetrastichus* Haliday (Eulophidae), a generalist ($\chi^2 = 5.61$, $P < 0.0179$). A species of *Hyssopus* Girault (Eulophidae), a parasitoid of Lepidoptera, was more attracted to microorganisms than to *I. pini* ($\chi^2 = 27.45$, $P < 0.0001$) or logs ($\chi^2 = 95.58$, $P < 0.0001$). A

Table 2. Frequency distribution of Hymenoptera arriving at ponderosa pine (*Pinus ponderosa*) logs colonized by *Ips pini* and associated microorganisms in Montana during 2002 and 2003, categorized by parasitoid host and feeding guild.

	Parasitoids (by host)										
Count per taxon*	Scolytinae†	Other Curculionidae‡	Other Coleoptera	Diptera	Lepidoptera	Hymenoptera	Hemiptera	Other	Generalist parasitoids§	Phytophages	Predators
1	3	1	10	4	12	6	8	2	17	3	2
2	2	3	1	2	4	2	5	1	10	1	
3	2		1	6	4	2	2		5	1	
4	1		2	2	1				3	1	
5					1			1	1		
6	1					1			1	1	
7						2	1	1	1		
8		1			2		1		1		
9	1	1		2						2	
10								1	1		
11	1			2		1					
12					1		1		1		
13	1								2		
14				2							
15	1				1						
16	1	1						1			
18				1					1		
19							1				
20			1		1						
23						1					
24		1							1		
25			1								
26									2		
28						1					
29									1	1	
30				1							
36								1			
38						1					
42	1										
45				1				1	2		

Table 2 (*concluded*).

	Parasitoids (by host)										
Count per taxon*	Scolytinae†	Other Curculionidae‡	Other Coleoptera	Diptera	Lepidoptera	Hymenoptera	Hemiptera	Other	Generalist parasitoids§	Phytophages	Predators
46					1						
47			1								
48			1								
51					1				1		
56				1							
76					1						
115									1		
153	1										
232				1							

Note: The number of taxa (species, genus, or family, as per Table 1, depending on the level of identification possible) is shown for each parasitoid host or feeding guild within columns. Two specimens from the same genus given different morphotype identifications were counted as different species, not as a single genus.

*Number of counts associated with each taxon within each category. For example, 2 species and 1 genus (3 taxa) of parasitic Hymenoptera that attack Scolytinae had counts of 1 each; 3 species and 0 genera (3 taxa) of parasitic Hymenoptera that attack other Curculionidae had counts of 2 each.

†Known parasitoids of Scolytinae were placed in the Scolytinae category in cases where both Scolytinae and other hosts are indicated.

‡Parasitoids of other Curculionidae were placed in that category in cases where both other Curculionidae and other hosts were indicated.

§Parasitoids with hosts in two or more orders were categorized as generalists.

species of *Inostemma* Haliday (Platygastridae), a parasitoid of gall-forming Diptera, and two generalist species, one each in the genera *Telenomus* Haliday (Scelionidae) and *Mesopolobus* Westwood (Pteromalidae), were attracted to *I. pini* and host-plant material equally. A species of *Chrysis* L. (Chrysididae), a parasitoid of sawflies (Hymenoptera: Symphyta), was attracted to microorganisms and host-plant material equally.

Two parasitoid genera obtained in this study represent new geographic records. The genus *Comastichus* LaSalle (Eulophidae) is known from Florida, Mexico, and Costa Rica but was previously unrecorded farther north (M. Gates, personal communication). The genus *Zdenekiana* Huggert (Pteromalidae) has been recorded in Canada (*Z. squama* Huggert) but there are no reports of this or other species of this genus elsewhere in North America. No specimen is available in the United States of America to confirm the assignment of our *Zdenekiana* prob. *squama* specimen to species (E. Grissell, personal communication).

Discussion

Colonization of ponderosa pine by the bark beetle *I. pini* is accompanied by the subsequent arrival of numerous species of Hymenoptera, particularly parasitoids. Many of these species were caught in low numbers, showed no attraction to cues associated with *I. pini*, and have no known association with bark beetles, so they were likely incidental captures. However, a diverse assemblage of 19 species showed a behavioral preference for either *I. pini* or its microbial associates within host trees. These species include known parasitoids of bark beetles as well as known parasitoids of other saprophytic or fungivorous insect groups that exploit the dead-tree habitat created or located by bark beetles.

Attraction to fungi is a widespread phenomenon in Coleoptera, Collembola, Diptera, Hymenoptera, and Lepidoptera and occurs in a diversity of habitats such as trees, soil, and decaying plants and food (Vet 1983; Bengtsson *et al.* 1988; Lin and Phelan 1991; Johansson *et al.* 2006). The first insects entering dead trees are usually phloem-feeding wood-borers, particularly Scolytinae (Graham 1925; Savely 1939; Vanderwel *et al.* 2006), which help to change the condition of the log and make it attractive to the large number of species that feed on fungi and decaying wood (Savely 1939). Natural enemies of these insects are also common in the early stages of decay (Savely 1939; Vanderwel *et al.* 2006). In this study, *I. pini* and its microbial associates may have been the initiating factor for attracting its parasitoids but parasitoids of phytophagous, fungivorous, or saprophytic Diptera and Lepidoptera were almost as common (Table 2). This suggests that natural enemies of insect herbivores that share a common resource may share common attractants.

The use of natural enemies for biological control is of interest in forest ecosystems because the utility of chemical pesticides is limited by environmental considerations, the marginal economic return of tree production, and the inaccessibility of subcortical insects (Dahlsten and Stephen 1974). In general, parasitoids kill more endophytic insect herbivores than do insect predators or pathogens (Hawkins *et al.* 1997). In this study, however, the diversity of bark beetle parasitoids was relatively high but the actual numbers arriving were relatively low. Instead, dipteran predators were more abundant than hymenopteran parasitoids (Boone *et al.* 2008) and their arrival coincided with the arrival of bark beetles (Vanderwel *et al.* 2006; Boone *et al.* 2008). Overall, dipteran predators appear to cause higher mortality among bark beetles than do parasitoids (Amman 1984), and coleopteran predators appear to be more important in influencing bark beetle populations (Amman 1984; Reeve 1997). Parasitoids are an important group for studying habitat viability, however. They are considered to be the most numerous and diverse of all insect groups (taxonomically and ecologically) (Gaston 1991), they are highly sensitive to environmental disturbances (Gibb and Hochuli 2002), and specialists are typically more sensitive to changes in the environment than their hosts (Kruess and Tscharntke 1994; Shaw and Hochberg 2001; Hilszczanski *et al.* 2005). Parasitoids of wood-inhabiting beetles are affected by forest successional stage, and characteristics of coarse woody debris and sustainable forest management that ensures adequate resources for these insects can aid in maintaining a healthy system (Hilszczanski *et al.* 2005; Vanderwel *et al.* 2006).

Baseline information about parasitoids associated with various feeding guilds is valuable for our understanding of how anthropogenic influences such as increased movement of wood, altered management and land-use practices that may influence the availablity of nectar sources for adult parasitoids (Matthews and Stephen

1999; VanLaerhoven *et al.* 2002), and increasing temperatures due to climate change affect species distribution. For example, increasing globalization has resulted in the disproportionately high introduction and establishment of wood-inhabiting beetles (Haack 2006). Baseline studies such as this can assist with evaluating the future impacts of new invasive species, assessing opportunities for their biological control, and interpreting evidence of potential species displacement.

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