

Diversity and Host Use of Mites (Acari: Mesostigmata, Oribatida) Phoretic on Bark Beetles (Coleoptera: Scolytinae): Global Generalists, Local Specialists?

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ABSTRACT Mites (Arachnida: Acari) are one of the most diverse groups of organisms associated with bark beetles (Curculionidae: Scolytinae), but their taxonomy and ecology are poorly understood, including in Canada. Here we address this by describing the diversity, species composition, and host associations of mesostigmatic and oribatid mites collected from scolytines across four sites in eastern Ontario, Canada, in 2008 and 2009. Using Lindgren funnel traps baited with α -pinene, ethanol lures, or *Ips pini* (Say) pheromone lures, a total of 5,635 bark beetles (30 species) were collected, and 16.4% of these beetles had at least one mite. From these beetles, a total of 2,424 mites representing 33 species from seven families were collected. The majority of mite species had a narrow host range from one (33.3%) or two (36.4%) host species, and fewer species had a host range of three or more hosts (30.3%). This study represents the first broad investigation of the acarofauna of scolytines in Canada, and we expand upon the known (worldwide) host records of described mite species by 19%, and uncover 12 new species. Half (7) of the 14 most common mites collected in this study showed a marked preference for a single host species, which contradicts the hypothesis that nonparasitic mites are typically not host specific, at least locally. Moreover, host records from the literature and those of this study together suggest that at a global scale, bark beetle mites have a broad host range, while at a local scale many species are host specific.

KEY WORDS host specificity, species composition, Mesostigmata, Oribatida, bark beetle

The subcortical niche of dead, dying, and living trees provide a habitat for a broad assemblage of wood-burrowing beetles (Cerambycidae, Buprestidae, Curculionidae: Scolytinae) and a suite of organisms that exploit these beetles or their galleries. This symbiotic community is dominated by mites, nematodes, and fungi. True bark beetles, Scolytinae, feed and reproduce in the cambium or xylem tissue of many tree species across the globe (Wood 1982). Many scolytine species feed on dead or dying trees, and these species likely serve a beneficial role in forest ecosystems as nutrient recyclers. However, some species of the genera *Ips*, *Dendroctonus*, and *Scolytus* cause extensive economic losses in North America (Wood 1982). For example, *Dendroctonus rufipennis* (Kirby) kills ≈ 0.55 billion board feet of spruce timber per year, and *Dendroctonus ponderosae* Hopkins, is responsible for an estimated timber loss of 1.5 billion board feet per year (Wood 1982). Over 5,800 described species of scolytines are known worldwide, and there are ≈ 525 spe-

cies and subspecies in Canada and the continental United States (Rabaglia 2002).

Mites represent the largest group of arthropods associated with bark beetles, and their association is ancient and diverse. One of the oldest records of mites associated with insects are tortoise mites (Mesostigmata: Uropodina) attached to bark beetles in 20–40 million year old amber (Poinar 1982). In total, 97 species of mites from 65 genera and 40 families were collected under the bark and from the galleries of bark beetle infested pine trees (Moser and Roton 1971); however, some of the mites collected by Moser and Roton (1971) may be primarily dead wood or bark inhabitants and not truly associated with bark beetles. Some scolytine species of temperate forests are associated with an assemblage of 15–20 mite species (Lindquist 1969); however, the acarofauna of most bark beetle species are poorly understood taxonomically and ecologically.

Mites dwelling in bark beetle galleries are generally phoretic, in that they hitch a ride on dispersing beetles to new coarse woody debris. These mites include fungivores, predators of insects and nematodes, omnivores, and parasites and parasitoids of scolytines (Lindquist 1970). The symbiotic relationship between mites and their hosts may vary from beneficial to detrimental across and even within mite species

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(Hirschmann and Rühm 1955; Kinn 1967, 1980, 1984; Moser 1975). Overall, the nature of symbiosis and the impact that most mite species have on their bark beetle hosts are largely unknown. Generally, predatory and omnivorous (nonparasitic) mite species are not considered to be host-specific, but rather they tend to be habitat-specific, and are reported from a broad range of coexistent host taxa that share similar habitats (Lindquist 1970, Moser 1995). Indeed, many bark beetle mites are found on a broad range of hosts (Moser and Roton 1971), which suggests that these mites are not specific. However, since most surveys provide little data beyond the observed host association, it is unclear how strong the actual relationship is between these mites and their hosts.

The mites associated with several species of scolytines have been surveyed in other countries, but usually these surveys focus on economically important species, such as *Ips typographus* (L.) in Germany and Sweden (Moser and Bogenschutz 1984, Moser et al. 1989), *Dendroctonus frontalis* Zimmermann, in Louisiana, Central America, and Mexico (Moser and Roton 1971, Moser et al. 1974), *D. ponderosae* in Alberta (Canada; Mori et al. 2011), *Scolytus multistriatus* (Marsham) and *Scolytus pygmaeus* (F.) in Austria (Moser et al. 2005). In this study we attempted to address the scarcity of data in Canada, by describing the diversity, prevalence, and host range of two major groups of mites (Mesostigmata, Oribatida) associated with bark beetles collected across six sites in eastern Ontario, using baited Lindgren funnel traps. In addition, using our findings on host range of bark beetle mites, as well as published host records, we explored the hypothesis that nonparasitic mites can be host specific, at least at a local scale.

Materials and Methods

Study Sites and Sampling Design. Bark beetles were sampled in four study sites in eastern Ontario from mid-April to late August in 2008. Two sites were in the mixed wood ecozone, one near Charleston Lake (S1) (44.500, -76.072) and the other near Frontenac Provincial Park (PP) (S2) (44.447, -76.577). The other two sites were in the boreal shield ecozone, in Algonquin PP: Algonquin site 1 (N1) (45.902, -77.605) and Algonquin site 2 (N2) (45.895, -78.071). Sites S1 and S2 were in isolated stands of white pine, along the Frontenac axis, surrounded by deciduous forests. Sites N1 and N2 were in large contiguous stands of white and red pines. In each site, five Lindgren 12-unit funnel dry traps (Synergy Semiochemicals Corp., Burnaby, British Columbia) with four 1 cm³ pest strips (Ortho Home Defense Max; to kill beetles and mites) and baited with lures, were placed at least 16 m apart; collection cups were ≈80 cm off the ground and at least 2 m from any host trees (distance from trees, trap height, and distance between traps based upon Miller and Duerr 2008). From mid-April to mid-May, three traps were baited with ipsdienol (100 mg released at ≈400 μg/d) and lanerione (4 mg) to attract *I. pini* adults, and the other two traps were baited with

α-pinene and 95% ethanol (released at 2 g/d and 400 mg/d, respectively) lures (Synergy Semiochemicals) to attract beetles seeking dead or dying coarse woody debris. At mid-May, trap lures were changed so that in each site there were four traps baited with α-pinene and 95% ethanol lures, and one trap baited with ipsdienol and lanerione lures, for the remainder of the 2008 sampling period. Traps were emptied approximately every 2 wk, trap lures were replaced every 8 wk, insecticide strips were replaced during each visit to maintain effectiveness, and any mites detached from their host were discarded with the preservative. The diversity and abundance of mites may have been underestimated by ignoring the detached mites; however, without knowledge of the host association the loose mites would provide misleading data. Each beetle specimen captured was placed individually into a 1.5 ml microfuge tube with 95% ethanol.

From mid-April to early August 2009, sampling was repeated in Algonquin PP (N1, N2) because of the high abundance and diversity of bark beetles obtained in these sites in 2008, and sampling was also conducted in two new sites in deciduous stands to broaden the diversity of scolytines and mites collected: one near Carbine road (S3) outside of Pakenham (45.330, -76.371), and another on Highway 132 (S4) near Dacre (45.369, -76.988). Sites S3 and S4 were in mixed wood forest dominated by deciduous trees. Four Lindgren traps with propylene glycol insecticide were placed in each study site following the same protocol. Traps were baited with α-pinene (α-pinene is an attractant for conifer-feeding scolytines) and 95% ethanol lures in sites N1 and N2, and baited with 95% ethanol lures in sites S3 and S4. Traps were visited and specimens were collected following the same protocol as in 2008.

Identifications and Mite Associations. Scolytines were identified to species using a dissecting microscope and keys from Bright (1976) and Wood (1982), and tribes were based on Alonso-Zarazaga and Lyal (2009). The presence, abundance, and attachment location of mesostigmatic and oribatid mites (hereafter mites) was recorded; other mites (Prostigmata, Astigmata) were not retained or studied. Mesostigmatic and oribatid mites were selected because they are abundant and conspicuous mites that firmly attach to their host. Prevalence was defined as the percentage of beetles with mites of a given species. Intensity was defined as the number of mites of a given species, carried per beetle with mites (beetles without mites excluded). All mesostigmatic and oribatid mites were removed from the host, cleared in 85% lactic acid for 1–24 h depending on the degree of opacity, slide-mounted in a polyvinyl alcohol medium and cured on a slide warmer at ≈40°C for 3–4 d. Slide-mounted specimens were examined using a compound microscope (Leica DM 5500B or Nikon 80I) and identified to species or morphospecies using taxonomically informative morphological characters based on species descriptions from the literature (Hirschmann 1960, 1972, 1989; Hirschmann and Zirngiebl-Nicol 1961; Hurlbutt 1967; Hirschmann and Wicniewski 1982,

Table 1. Total abundance of scolytine species collected across four sites in eastern Ontario in 2008 and 2009 (° mites present)

Tribe	Beetle species	2008 sites ^a				2009 sites ^a			
		N1	N2	S1	S2	N1	N2	S3	S4
Corthylini	<i>Corthylus punctatissimus</i> ^b	—	—	1	1	—	—	—	1
	<i>Gnathotrichus materiarius</i>	135°	26	8°	14°	19°	39°	—	—
	<i>G. materiarius</i> ^c	2	2	—	—	—	—	—	—
	<i>Monarthrum mali</i> ^b	—	—	—	—	—	1	—	—
	<i>Pityophthorus</i> sp.	15	28	2	2	3	5	—	3
	<i>Pityophthorus</i> sp. ^c	—	4	3	3	—	—	—	—
Crypturgini	<i>Crypturgus pusillus</i>	2	—	—	—	—	—	—	—
	Dryocoetini	<i>Dryocoetes affaber</i>	9	—	—	7	5°	1	—
<i>D. affaber</i> ^c		1	—	—	—	—	—	—	—
<i>D. autographus</i>		22°	—	—	—	11°	—	1	—
<i>Lymantor decipiens</i> ^b		—	—	—	—	—	1	—	—
<i>L. decipiens</i> ^{b,c}		—	—	1	40	—	—	—	—
Hylastini		<i>Hylastes opacus</i>	154°	221°	10	11	17	388	—
	<i>H. opacus</i> ^c	1	3	4	—	—	—	—	—
	<i>H. porculus</i>	603°	42°	14°	67	291°	104°	2	1
	<i>H. porculus</i> ^c	—	1	—	—	—	—	—	—
	<i>Hylurgops pinifex</i>	26°	11°	1	1	3°	6°	—	—
	<i>H. pinifex</i> ^c	1	—	—	—	—	—	—	—
Hylesinini	<i>Hylesinus aculeatus</i> ^b	—	—	1	—	—	—	3	15°
	<i>H. aculeatus</i> ^{b,c}	—	—	1°	—	—	—	—	—
Hylurgini	<i>Dendroctonus rufipennis</i>	2	—	—	—	—	—	—	—
	<i>D. valens</i>	102°	93°	1	3	12°	194°	—	—
	<i>D. valens</i> ^c	—	2	1	—	—	—	—	—
	<i>Hylurgopinus rufipes</i> ^b	—	—	—	—	—	—	—	4
	<i>Tomicus piniperda</i>	—	—	—	—	—	1	—	—
Ipini	<i>Ips grandicollis</i>	80°	93°	16°	23	30°	83°	—	—
	<i>I. grandicollis</i> ^c	—	2	—	—	—	—	—	—
	<i>I. perroti</i> ^c	—	1	—	—	—	—	—	—
	<i>I. pini</i>	9°	5°	—	6	2°	7°	—	—
	<i>I. pini</i> ^c	170°	504°	511°	230°	—	—	—	—
	<i>Orthotomicus caelatus</i>	142°	36°	12°	10°	15°	83°	—	—
	<i>O. caelatus</i> ^c	1	—	—	—	—	—	—	—
	<i>Pityogenes hopkinsi</i>	6	25	1	—	1	14°	—	3
	<i>P. hopkinsi</i> ^c	4	14	2	1	—	—	—	—
	<i>P. plagiatus</i>	—	6	—	—	1	1	—	—
	<i>P. plagiatus</i> ^c	1	6	—	—	—	—	—	—
	<i>Pityogenes</i> sp.	—	1	—	—	—	—	—	—
	<i>Pityokteines sparsus</i>	1	3	1	—	—	1°	—	2°
	<i>P. sparsus</i> ^c	—	3	—	—	—	—	—	—
Polygraphini	<i>Polygraphus rufipennis</i>	18	8°	—	1	11°	1°	2°	1
	<i>P. rufipennis</i> ^c	—	1	—	—	—	—	—	—
Xyleborini	<i>Xyleborus dispar</i> ^b	—	—	—	—	—	—	14	60
	<i>X. sayi</i> ^b	3°	2	19	24	—	—	39	31
Xyloterini	<i>Trypodendron lineatum</i>	232°	—	2	—	21	4	—	6
	<i>T. lineatum</i> ^c	9	—	1	—	—	—	—	—
	<i>T. retusum</i> ^b	—	—	—	—	2°	2	—	—
	<i>Xyloterinus politus</i> ^b	1	—	—	—	2	3	6	6
	<i>X. politus</i> ^{b,c}	7	—	90°	1	—	—	—	—
	Total no. individuals	1,562	600	89	170	446	939	67	133
	no. individuals ^c	197	543	614	275	—	—	—	—
Total no. species	19	15	14	13	17	20	7	12	
no. species ^c	10	12	9	5	—	—	—	—	

^a N1, Algonquin park 1; N2, Algonquin park 2; S1, Charleston lake; S2, Frontenac; S3, Pakenham; S4, Dacre.

^b Scolytine species associated with deciduous host species, all other species are associated with coniferous hosts (Wood 1982).

^c Traps baited with *Ips pini* pheromone lures.

1986, 1987, 1989; Wunderle et al. 1990). Voucher specimens are deposited in the Canadian National Collection of Insects, Arachnids and Nematodes, in Ottawa, Canada.

Results

Traps with General Lures. In total, 4,006 bark beetles from 29 species, 21 genera and 10 tribes were collected in traps with general lures (α -pinene, ethanol, or both), across four sites in 2008 and 2009 (Table

1). Beetle abundance was higher in 2008 than in 2009 (2,421 and 1,585 beetles, respectively), but species richness was higher in 2009 than in 2008 (26 and 23 species, respectively), possibly because two distinct forest types were sampled in 2009 (Table 1). Beetles were collected almost exclusively in the spring; in 2008, 96% of all beetles were collected from mid-April to mid-June, and in 2009, 98% from mid-April to late June. *Hylastes porculus* Erichson (25–30% of all beetle individuals), *H. opacus* Erichson (16–26%), and *Dendroctonus valens* LeConte (8–13%) were the three

Table 2. Prevalence (%) (total abundance) of mites associated with scolytines collected across four sites in eastern Ontario in 2008 and 2009

Mite family ^a	Mite species	<i>Gnathotrichus materius</i>	<i>Dryocoetes affaber</i>	<i>D. autographus</i>	<i>Hylastes opacus</i>	<i>H. porculus</i>	<i>Hylurgops pinifex</i>	<i>Hylesinus aculeatus</i> ^b	<i>Hylesinus aculeatus</i> ^{b,c}	<i>Dendroctonus valens</i>	<i>Ips grandicollis</i>
AMR	<i>Epicriopsis</i> n.sp.	0.4(1)	—	—	—	0.1 (1)	2.1 (1)	—	—	1 (4)	0.3 (1)
DCM	<i>Dendrolaelaps hexaspinosus</i>	0.4 (1)	—	—	0.4 (3)	0.5 (6)	8.3 (7)	—	—	4.9 (26)	3.1 (11)
	<i>D. louisianae</i>	—	—	—	—	—	—	—	—	—	0.9 (3)
	<i>D. n.sp. 1</i>	—	—	—	0.1 (1)	0.1 (1)	—	—	—	18.3 (156)	—
	<i>D. n.sp. 2</i>	—	—	—	—	0.4 (8)	22.9 (20)	—	—	—	—
	<i>D. n.sp. 3</i>	—	—	—	—	—	—	—	—	—	—
	<i>D. n.sp. 4</i>	—	—	—	—	—	—	—	—	0.2 (1)	—
	<i>D. neodisetus</i>	—	—	—	—	—	—	—	—	0.2 (1)	—
	<i>D. quadrisetosimilis</i>	—	—	—	—	—	—	—	—	—	—
	<i>D. quadrisetus</i>	—	—	—	—	—	—	—	—	—	1.2 (4)
	<i>D. quadritorus</i>	—	—	—	0.1 (1)	0.3 (3)	—	—	—	1.2 (5)	0.3 (1)
	<i>Longoseius cumiculus</i>	—	—	—	—	0.1 (1)	—	—	—	—	—
MAC	<i>Macrocheles</i> n.sp.	—	—	—	—	0.3 (3)	—	—	—	0.5 (2)	—
MLC	<i>Proctolaelaps fiseri</i>	—	—	—	—	1.4 (20)	—	—	—	—	—
	<i>P. hystrix</i>	—	—	—	0.1 (1)	—	—	—	—	1 (5)	—
	<i>P. n.sp. 1</i>	—	—	—	—	0.2 (6)	—	—	—	0.2 (1)	—
	<i>P. n.sp. 2</i>	—	—	—	—	2.3 (60)	—	—	—	—	—
	<i>P. n.sp. 4</i>	—	—	—	—	—	—	—	—	—	—
TRM	<i>Trichouropoda australis</i>	—	—	—	—	—	—	—	—	0.2 (1)	1.5 (7)
	<i>T. bipilis</i>	—	—	—	—	—	—	10.5 (3)	100 (1)	—	—
	<i>T. fallax</i>	—	—	—	—	—	6.3 (4)	—	—	—	—
	<i>T. hirsuta</i>	—	—	—	—	0.4 (10)	2.1 (3)	—	—	2 (10)	0.9 (4)
	<i>T. lamellosa</i>	—	—	—	—	0.2 (2)	—	—	—	0.7 (3)	0.6 (3)
	<i>T. moseri</i>	—	—	—	—	—	—	—	—	—	—
	<i>T. n.sp. 3</i>	—	—	—	—	—	—	—	—	—	—
	<i>T. n.sp. 12</i>	—	—	—	0.1 (1)	0.1 (1)	—	—	—	—	—
	<i>T. parisiensis</i>	4.1 (15)	—	—	—	—	—	—	—	—	—
URO	<i>Uroobovella americana</i>	—	—	—	—	0.4 (5)	—	—	—	8.9 (151)	—
	<i>U. dryocoetes</i>	—	—	17.6 (6)	—	1.6 (35)	—	—	—	0.5 (2)	0.3 (1)
	<i>U. orri</i>	—	4.5 (1)	—	—	—	—	—	—	—	0.6 (4)
	<i>U. vinicolora</i>	—	—	—	—	—	—	—	—	0.5 (2)	—
ORB	<i>Paraleius leontonycha</i>	0.4 (1)	—	—	—	0.5 (7)	—	—	—	0.7 (3)	0.9 (3)
	<i>P. n.sp.</i>	—	—	—	—	5.2 (100)	—	—	—	10.1 (76)	—
Total	Beetle abundance	241	22	34	801	1,124	48	19	1	405	325
	no. mite species (33)	4	1	1	5	17	5	1	1	17	11
	Mite abundance (2,424)	18	1	6	7	269	35	3	1	449	42
	Mite prevalence (%)	5.4	4.5	17.6	0.9	12.4	37.5	10.5	100	38.0	9.5

most abundant species across all sites in 2008 and 2009, respectively (Table 1). The majority of beetle individuals were collected from Algonquin PP in 2008 (89%) and 2009 (87%), and species diversity was also highest in Algonquin in both years (Table 1).

Across all sites and both years, 12% of the 4,006 beetles examined had at least one mesostigmatic or oribatid mite (hereafter mites), and of the 29 host species examined, only 17 species (13 genera and nine tribes) had mites (Table 1). Overall prevalence was higher in 2009 than in 2008 (13.5 and 10%, respectively). Nine bark beetle species (242 individuals) that feed on deciduous hosts were collected (Table 1), three of which had mites with an overall prevalence of 2.8% (0.8–25%). In total, 19 conifer-feeding bark beetle species (3,706 individuals) were collected (Table 1), 14 of which had mites with an overall prevalence of 12.4% (0.4–38%); more than four times higher than on bark beetles from deciduous hosts. The host associations of one species, *Pityophthorus* sp., are unknown because members of this genus may feed on deciduous or coniferous trees (Wood 1982). *D. valens* and *H. porculus*, two of the three most abundant beetle species, exhibited the highest mite abundance (43.8 and 26.2% of all mites collected, respectively) and mite

diversity (both with 17 species) (Table 2). *Ips grandicollis* (Eichhoff), the fourth most abundant beetle, also showed a high-mite diversity (11 species) despite a relatively lower mite abundance and prevalence (Table 2). *D. valens*, *Hylurgops pinifex* Wood & Bright, and *I. pini* had the highest mite prevalence (35–38%; Table 2).

In total, 1,025 mites representing 33 species, eight genera and seven families (six of Mesostigmata, one of Oribatida), were collected across all sites and both years (Table 2). Site N1 in 2008, was the most species rich site, with 26 mite species from seven genera and seven families (Supp. Table 1 [available online only]). Sites outside of Algonquin PP were poor: in 2008 sites S1 and S2 had only six and two species, respectively, and in 2009 sites S3 and S4 also had only one and two species, respectively (Supp. Table 1 [available online only]). The Digamasellidae was the most abundant and diverse family, with 11 species (two genera) and 39% (395 mites) of all mite individuals collected (Table 2). Also abundant and diverse were the Urodinychidae (241 mites, four species), Trematuridae (88 mites, nine species), and Melicharidae (94 mites, five species) (Table 2). Oribatulidae (194 mites, two spe-

Table 2. Continued

<i>I. pini</i>	<i>I. pini</i> ^c	<i>Orthotomicus caelatus</i>	<i>Pityogenes hopkinsi</i>	<i>Pityokteines sparsus</i>	<i>Polygraphus rufipennis</i>	<i>Xyleborus sayi</i> ^b	<i>Trypodendron lineatum</i>	<i>T. retusum</i> ^b	<i>Xyloterinus politus</i> ^{b,c}	Total mite abundance	No. of host species ^d
—	—	—	—	—	—	—	—	—	—	8	5
—	—	0.3 (1)	—	—	—	—	—	—	—	55	7
—	—	—	—	—	—	—	—	—	—	3	1
—	—	—	—	—	—	—	—	—	—	158	3
—	—	—	—	—	—	—	—	—	—	28	2
—	0.1 (1)	—	—	—	—	—	0.4 (1)	—	—	2	2
—	—	—	—	—	—	—	—	—	—	1	1
—	—	—	—	—	—	—	—	—	—	1	1
—	—	18.1 (112)	4 (3)	—	—	—	—	—	—	115	2
17.2 (18)	30.2 (1,302)	—	—	—	—	—	—	—	—	1,324	2
—	—	—	—	—	—	—	—	—	—	10	4
—	—	—	—	—	—	—	—	—	—	1	1
—	—	—	—	—	—	—	—	—	—	5	2
—	—	—	—	—	—	—	—	—	—	20	1
—	—	—	—	—	—	—	—	—	—	6	2
—	—	—	—	—	—	—	—	—	—	7	2
—	—	—	—	—	—	—	—	—	—	60	1
—	—	0.3 (1)	—	—	—	—	—	—	—	1	1
17.2 (14)	4 (86)	—	—	—	—	—	—	—	1 (1)	109	4
—	—	—	—	—	—	—	—	—	—	4	1
—	—	—	—	—	—	—	—	—	—	4	1
0.1 (2)	—	—	—	—	—	—	—	—	—	29	5
—	—	—	—	—	—	0.8 (1)	—	—	—	9	4
—	—	—	—	12.5 (1)	2.4 (1)	—	—	—	—	2	2
—	—	—	6 (3)	—	—	—	—	—	—	3	1
—	—	—	—	—	—	—	—	—	—	2	2
—	—	—	—	—	—	—	—	—	—	2	2
—	—	—	—	—	—	—	—	25 (1)	—	16	2
—	—	—	—	—	—	—	—	—	—	156	2
—	—	—	—	—	—	—	—	—	—	44	4
—	—	4.4 (21)	—	12.5 (2)	7.1 (11)	—	—	—	—	39	5
—	—	—	—	—	—	—	—	—	—	2	1
—	0.4 (6)	1.3 (4)	—	—	—	—	—	—	—	24	6
—	—	—	—	—	—	—	—	—	—	176	2
29	1415	298	50	8	42	118	265	4	98		
2	5	5	2	2	2	1	1	1	1		
32	1397	139	6	3	12	1	1	1	1		
34.5	32.7	22.1	10	25	9.5	0.8	0.4	25	1		

^a AMR, Ameroseiidae; DGM, Digamasellidae; MAC, Macrochelidae; MLC, Melicharidae; TRM, Trematuridae; URO, Urodynychidae; ORB, Oribatulidae.

^b Scolytine species associated with deciduous host species, all other species are associated with coniferous hosts (Wood 1982).

^c Traps baited with *Ips pini* pheromone lures.

^d Species with abundance ≥ 20 in bold.

cies) and Macrochelidae (5 mites, one species) were the least diverse (Table 2).

Typically, only one mite individual, occasionally two, were collected per beetle (58 and 19% of all beetles with mites, respectively); more rarely, 3 (7%), 4 (7%), or 5–11 mites (9%) were found on an individual beetle. Most bark beetle individuals with mites were associated with only one mite species (84%); fewer had two (12%) or three species (3%), and the maximum was four species collected from a single *D. valens* specimen. *D. valens* reached an exceptionally high number of mites, with 24, 27, and a maximum of 29 mites per host, and a single individual had as much as four species of mites.

From traps with general lures, the mites with the highest prevalence on a given beetle species were *Dendrolaelaps* n.sp. 2 (22.9% prevalence on *Hylurgops pinifex*), *Dendrolaelaps* n.sp. 1 (18.3% on *D. valens*), *D. quadrisetosimilis* Hirschmann (18.1% on *Orthotomicus caelatus* (Eichhoff)), and *Uroobovella dryocoetes* (Vitzthum) (17.6% on *Dryocoetes autographus* (Rat-

zeburg)) (excluding the instances with <5 beetles collected) (Table 2). Also from traps with general lures, the most frequently collected mite species were *Paraleius* n.sp. (Oribatulidae) (17.2% of all mites collected), *Dendrolaelaps* n.sp. 1 (15.4%), *Uroobovella americana* Hirschmann (15.2%), and *D. quadrisetosimilis* (11.2%) (Table 2). *Uroobovella orri* Hirschmann was collected from five host species (three tribes), and it was relatively common on two of these hosts, *Orthotomicus caelatus* and *Polygraphus rufipennis* (Kirby) (Table 2). It should be noted that the specimens from *O. caelatus* may not be *U. orri*, but instead they may represent a cryptic species, *Uroobovella* n.sp. 6 (sensu Knee et al. 2012b), which is primarily detectable by molecular methods.

Most mite species showed minimal variation in total abundance, prevalence or mean intensity across sites or years, with the exception of a few species. *Dendrolaelaps* n.sp. 1 showed an approximately threefold increase (8.6–29.4%) in prevalence on *D. valens* from 2008 to 2009 in site N2, as well as an eightfold increase

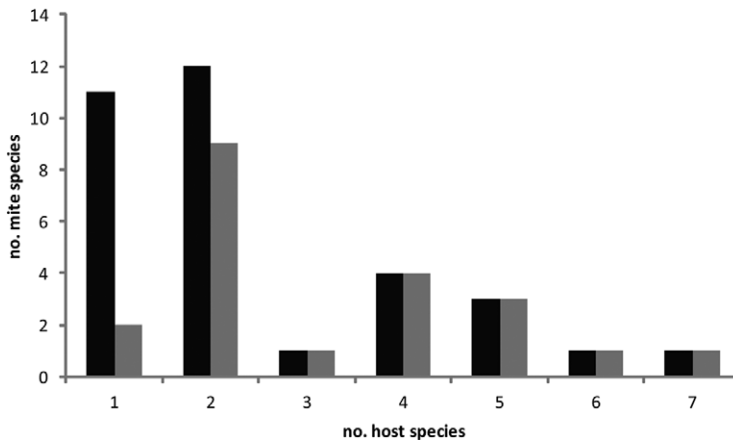


Fig. 1. Distribution of the breadth of host range of mites collected from bark beetles sampled across four sites in eastern Ontario, for all 33 mite species collected (black), and only for the 21 species with an abundance ≥ 5 (gray).

in total abundance from 2008 to 2009 (Supp. Table 1 [available online only]). *Paraleius* n.sp. associated with *D. valens* showed more than a fourfold increase (4.3–18.6%) in prevalence, and a 14 times increase in abundance in site N2 from 2008 to 2009 (Supp. Table 1 [available online only]). The prevalence of *Dendrolaelaps quadrisetosimilis* increased from 8.3 to 20.5% in site N2 from 2008 to 2009 (Supp. Table 1 [available online only]). In contrast, the prevalence of *D. quadrisetosimilis* on *O. caelatus* dropped from 20.4 to 6.7%, and its abundance dropped from 68 to 2, in site N1 from 2008 to 2009 (Supp. Table 1 [available online only]).

***I. pini* Pheromone Traps.** In total, 1,629 bark beetles from 19 species, 15 genera, and 8 tribes, were collected in traps baited with *I. pini* pheromone lures, across four sites in 2008 (Table 1). *I. pini* represented 86.9% of all beetles collected in these pheromone lure traps. From a total of 19 beetle species collected, only three species had mites (Table 1). In total, 1,399 mites representing six species, three genera, and three families, were collected (Supp. Table 1 [available online only]). Five of the six mite species collected were found on *I. pini*, which had an overall mite prevalence of 32.7% (Supp. Table 1 [available online only]).

Dendrolaelaps quadrisetus (sensu Hirschmann 1960) and *Trichouropoda australis* Hirschmann, were collected from *I. pini* in all four sites in 2008 (Supp. Table 1 [available online only]). *D. quadrisetus* had the highest prevalence (20–33.5%), abundance (93% of all individuals), and mean intensity (3.2/beetle), whereas *T. australis* had the second highest prevalence (3–4.7%), abundance (6%), and mean intensity (1.9/beetle) (Supp. Table 1 [available online only]).

Combined across traps with general lures and those with *I. pini* pheromone lures, a total of 5,635 bark beetles from 30 species were collected, and 16.4% of these hosts had at least one mite. In total, 2,424 mites from 33 species, including 12 new species, were collected from both trapping methods.

Host Range and Variation With Published Host Records. Mite species were found on an average of 2.5 ± 1.7 (SD) beetle species (pooled data from general and pheromone specific traps). Most mite species had a narrow host range, occurring on one (33.3%) or two (36.4%) host species; much fewer species had a broader host range occurring on three (3%), four (12.1%), five (9.1%), or six (3%) host species; *Dendrolaelaps hexaspinosus* Hirschmann, was found on seven host species (Fig. 1). After removing mite species with an overall abundance < 5 , the average number of host species per mite species increased to 3.2 ± 1.7 ; also, there were still slightly more mites with one or two hosts (52.4%) than those with three or more host species (47.6%), but only two species (9.5%) had a single host (Fig. 1). Beyond the species level, there was no apparent specificity of mite taxa toward particular beetle taxa: each mite family and most genera were found on at least two tribes and two genera (Table 2).

We assessed the degree of host specificity of relatively common mites (those with an abundance ≥ 20) by considering, first the number of host species exploited, and second, the prevalence and abundance on a given host species. Among the 14 mite species with an abundance ≥ 20 , eight appeared to be more or less host specific, and six had a broad host range (Table 2). Of the eight 'host-specific' species, seven were collected from one or two hosts, and six of these species showed a strong preference for a single host species, being much more prevalent and abundant on that host (*Dendrolaelaps* n.sp. 2, *D. quadrisetosimilis*, *D. quadrisetus*, *Proctolaelaps fiseri* Samsinák, *P.* n.sp. 2, *U. americana*). *Paraleius* n.sp. exhibited a strong preference for two host species, *H. porculus* and *D. valens*, which both live in the stumps and roots of dead or dying conifers (Wood 1982). *Dendrolaelaps* n.sp. 1 was found on three hosts, but this mite was almost exclusively collected from *D. valens*, and rarely (one instance each) from its two other hosts (Table 2). The six remaining species were found on 4–7 hosts, and

these species did not exhibit any clear host preference, with the exception of *T. australis* (Table 2). *T. australis* was collected from four hosts, and did show a preference for *I. pini* (even when excluding data from *I. pini* pheromone traps); however, this mite is not a strict host specialist, not even locally, and has been found frequently on *I. grandicollis* and rarely on *Ips perturbatus* (Eichhoff) in Ontario and Quebec (Knee et al. 2012b).

The host records for the 21 described species collected in this study increased considerably, from 186 records to 221 (19% increase; Table 3). Combined across the literature and this study, the described species were found on an average of 10.5 ± 6.6 beetle species, with a maximum of 26 hosts for *D. quadrisetus* (Table 3). Most (60%) of the host associations observed in this study represent new records. Novel host records were reported for 17 of the 21 described species collected (Table 3). More importantly, there was little overlap in bark beetle hosts between this study and the literature for many of the most common species (e.g., *D. quadrisetus*, *D. quadrisetosimilis*, *T. australis*, and *U. americana* each with only 0–2 host species shared; Table 3).

The host range breadth of several mite species collected in this study differed from that of published host records (Table 3). *Dendrolaelaps neodisetus* Hurlbutt, *D. quadrisetosimilis*, and *D. quadrisetus*, were each collected from few host species (one or two) in this study, suggesting that these mites are relatively host specific; however, according to published host records these mites are host generalists (Table 3). In contrast, *D. quadritorus* Robillard, appeared to be more generalized in this study (four host spp. in three genera) than in the literature (only two *Ips* spp. from Louisiana). *Proctolaelaps fiseri* and *P. hystrix* (Vitzthum) both appeared to be host specific in this study, while in the literature these two species are apparent host generalists (Table 3). Similarly, *T. fallax* (Vitzthum) and *U. americana* were collected from one to two host species in this study, whereas published records suggest that these two species are host generalists (each seven host spp. in three genera).

Phoretic Attachment Location. The attachment location of mites indicates that different groups of mites attach to different locations on host beetles. Mites from the Order Mesostigmata, excluding Uropodoidea, were collected almost exclusively from under the elytra of their hosts, with 97.2% of mites under the elytra, 0.5% on the dorsal surface of the elytra, 1% on the ventral thorax or abdomen, 0.8% on the legs, and 0.5% on the head or pronotum of their hosts. However, the usage of a liquid insect preservative may have biased the attachment location of some mesostigmatic mites (excluding uropodoids) by dislodging mites that were not under the elytra. Uropodoids (Trematuridae, Urodinychidae) were most often found glued with their anal pedicel to ventral surfaces of their hosts: 55% on the ventral thorax or abdomen, and 9% on the legs. Uropodoids were also found on dorsal surfaces of their hosts: 20% on the elytral declivity, 7% on the elytra (excluding

the declivity), and 9% on the head or pronotum. Oribatids were also typically located on ventral surfaces of their hosts, with 86% on the ventral prothorax, 12% on the ventral meso- or metathorax, and 2% on the elytral declivity.

Discussion

A rich assemblage of mites was found on bark beetles in Ontario, with 33 species and 7 families of mites collected from 18 host species from only six sites. Considering that two major groups of Acari (Prostigmata, Astigmata) were not studied here, our findings represent only a fraction of the scolytine-associated mites in the region. The prevalence of mites varied substantially among hosts. For instance, *D. valens*, *I. pini*, *O. caelatus*, and *H. pinifex*, frequently carried mites (22–38% of beetles), whereas other host species, such as *Hylastes opacus*, *Xyleborus saji* (Hopkins), and *Trypodendron lineatum* (Olivier), were virtually devoid of mites (0.4–0.9%). This apparent rarity of mites is probably not due to a lack of sampling, since some of the relatively mite-free beetle species were fairly common (e.g., *H. opacus* and *T. lineatum*). Therefore, ecological factors such as beetle microhabitat, behavior or phenology, may favor certain host associations.

Studies on scolytine-associated mites often ignored potential associations with other families of wood-boring beetles. Overall, mites associated with scolytines are infrequently collected from other families of wood-boring beetles, with the exception of a few species (Kinn and Linit 1989). In this study, four species, *D. neodisetus*, *L. cucicularius* Chant, *T. hirsuta* Hirschmann, and *T. lamellosa* Hirschmann, are not scolytine specialists but are actually primarily associated with cerambycids (Chant 1961, Kinn 1987, Kinn and Linit 1989, Moser and Roton 1971).

Host Specificity, Locally, and Globally. The majority of mites (23 of 33 spp.) were collected from only one or two host species, with the remainder associated with 3–7 hosts. This seemingly high host specificity is in part because of the low abundance of some mites. Indeed, the removal of mite species with fewer than five individuals collected dropped the number of mites with a narrow host range (1–2 hosts) from 23 to 11 species, with only two remaining mite species being monospecific. Nevertheless, our data suggests that several of these 11 species may have a preference for a single host, or two, at least at a local scale.

The mites collected in this study represent a mixed assemblage of predators, fungivores, omnivores, and scavengers (Kinn 1967, 1982, 1987; Moser 1975). Since these mites are not parasitic (therefore not closely associated with their host physiology) and are presumably primarily associated with bark beetles for phoretic dispersal to new subcortical habitats (Lindquist 1970), there may be little selection for host specificity, and any bark beetle species encountered could serve as a potential phoretic carrier. To some extent, the findings of this study contradict this hypothesis. Among the 14 most commonly collected mite species, six species appear to

Table 3. Comparing observed host records (this study) with published records (publ.) for the 21 described mite species collected from scolytines and other families of wood-boring beetles across four sites in eastern Ontario (the no. of + indicates the no. of shared host spp.)

Mite species	No. host spp./genera		Published host species (spp. shared with present study)	Regions ^b	References
	This study	Publ.			
<i>Dendrolaelaps hexaspinosus</i>	7/6	6/6	<i>Cryphalus piceae</i> , <i>Dryocoetes autographus</i> , <i>Hylurgops palliatus</i> , <i>Hylurgus ligniperda</i> , <i>Pityogenes quadridentis</i> , <i>Tomicus piniperda</i>	Austria, Poland, Ukraine	Hirschmann and Wiczeniewski 1982
<i>D. louisianae</i>	1	1	CUR ^c ; <i>Hylobius pales</i>	LA	Hirschmann and Wiczeniewski 1982
<i>D. neodisetus</i>	1	15 ⁺ /7	<i>Dendroctonus brevicornis</i> , <i>D. frontalis</i> , <i>D. simplex</i> , <i>D. terebrans</i> , <i>D. valens</i> , <i>Ips avulsus</i> , <i>I. grandicollis</i> , <i>I. pini</i> ; CER: <i>Monochamus carolinensis</i> , <i>M. scutellatus</i> , <i>M. titillator</i> , <i>Neacanthosinus obsoletus</i> ; BUP: <i>Buprestis lineata</i> ; CUR: <i>Hylobius pales</i> ; TRO: <i>Tennochila virescens</i>	AB, ON, AZ, CA, MS, LA, TX; Honduras	Hirschmann and Wiczeniewski 1982; Hofstetter 1967; Kinn and Limit 1989; Knee et al. 2012a; McGraw and Farris 1969; Moser and Roton 1971
<i>D. quadrisetosinilis</i>	2/2	5/4	<i>Dryocoetes autographus</i> , <i>Ips avulsus</i> , <i>I. calligraphus</i> , <i>Pityokteines minutus</i> , <i>Tomicus piniperda</i>	AB; LA; Poland, Germany	Hirschmann and Wiczeniewski 1982; Hurlbutt 1967; Moser and Roton 1971
<i>D. quadrisetus</i>	2/1	26 ⁺ /7	<i>Dendroctonus adjunctus</i> , <i>D. brevicornis</i> , <i>D. frontalis</i> , <i>D. pseudotsugae</i> , <i>D. rufipennis</i> , <i>D. terebrans</i> , <i>D. valens</i> , <i>Dryocoetes confusus</i> , <i>Hylastes cunicularius</i> , <i>H. opacatus</i> , <i>H. palliatus</i> , <i>Ips avulsus</i> , <i>I. calligraphus</i> , <i>I. confusus</i> , <i>I. grandicollis</i> , <i>I. latidens</i> , <i>I. pini</i> , <i>I. plastographus</i> , <i>I. ponderosa</i> , <i>I. sexdentatus</i> , <i>Phloeosinus punctatus</i> , <i>P. sequoiae</i> , <i>Pityokteines curvidens</i> , <i>P. spinidens</i> , <i>P. vorontzovi</i> , <i>Tomicus piniperda</i>	AK, AZ, CA, ID, NC, PA, VA; Croatia, France, Germany, Switzerland	Cardoza et al. 2008; Hirschmann 1960; Hirschmann and Wiczeniewski 1982; Hofstetter 2008; Hurlbutt 1967; Kinn 1967; Leveux et al. 1989; McGraw and Farris 1969; Moser and Bogenschütz 1984; Pernek et al. 2008
<i>D. quadritonus</i>	4/3	2 ⁺ /1	<i>Ips avulsus</i> , <i>I. grandicollis</i>	LA	Robillard 1971
<i>Longosetus cuniculus</i>	1	11/5	<i>Dendroctonus approximatus</i> , <i>D. frontalis</i> , <i>Ips avulsus</i> , <i>I. calligraphus</i> , <i>I. grandicollis</i> ; CER: <i>Monochamus carolinensis</i> , <i>M. notatus</i> , <i>M. scutellatus</i> , <i>M. titillator</i> , <i>Neacanthosinus obsoletus</i> ; CLR: <i>Thanasimus dubius</i>	AZ, LA, ME, MS, NC, TX, VA	Chant 1961; Hofstetter 2008; Hurlbutt 1967; Kinn 1987; McGraw and Farris 1969; Moser and Roton 1971; Soper and Olsen 1963
<i>Proctolaelaps fiseri</i>	1	10/8	<i>Dendroctonus valens</i> , <i>Dryocoetes</i> sp., <i>Erioporus</i> sp., <i>Gnathotrichus materiarius</i> , <i>Hylurgops</i> sp., <i>Ips avulsus</i> , <i>I. calligraphus</i> , <i>I. typographus</i> , <i>Pityokteines</i> sp., <i>Tomicus</i> sp.	AZ, GA, LA; Germany	Hirschmann and Rühm 1953; Hofstetter 2008; Lindquist and Hunter 1965; Moser and Roton 1971; Westerboer 1963
<i>P. hystrix</i>	2/2	8 ⁺ /4	<i>Dendroctonus frontalis</i> , <i>D. micans</i> , <i>D. terebrans</i> , <i>D. valens</i> , <i>Dryocoetes autographus</i> , <i>Hylastes ater</i> , <i>Ips calligraphus</i> , <i>I. pini</i>	AZ, CA, LA; Austria, Poland	Hunter 1965; Moser and Roton 1971
<i>Trichouropoda australis</i>	4/3	17 ⁺ /3	<i>Dendroctonus brevicornis</i> , <i>D. frontalis</i> , <i>D. ponderosae</i> , <i>D. simplex</i> , <i>D. terebrans</i> , <i>Ips avulsus</i> , <i>I. bonansai</i> , <i>I. calligraphus</i> , <i>I. confusus</i> , <i>I. cribricollis</i> , <i>I. grandicollis</i> , <i>I. hunteri</i> , <i>I. lecontei</i> , <i>I. perturbatus</i> , <i>I. pilifrons</i> , <i>I. pini</i> ; CER: <i>Neacanthosinus obsoletus</i>	NS, ON, QC; AZ, FL, LA, MS, NM, NY, RI, TX; Mexico	Hofstetter 2008; Kinn and Limit 1989; Knee et al. 2012b; Moser and Roton 1971
<i>T. bipilis</i>	1	1	<i>Scolytus pygmaeus</i>	Austria	Hirschmann and Wiczeniewski 1989
<i>T. fallax</i>	1	7 ⁺ /3	<i>Dendroctonus adjunctus</i> , <i>Hylastes ater</i> , <i>H. cunicularius</i> , <i>H. interstitialis</i> , <i>H. ruber</i> , <i>Hylurgops pinifex</i> , <i>H. rugipennis pinifex</i>	BC, NS; LA, UT; Siberia; Belgium	Hirschmann and Wiczeniewski 1989; Hofstetter 2008; Knee et al. 2012b

Table 3. Continued

Mite species	No. host spp./genera		Published host species (spp. shared with present study)	Regions ^b	References
	This study	Publ.			
<i>T. hirsuta</i>	5/4	17 ⁺⁺⁺ /9	<i>Dendroctonus approximatus</i> , <i>D. brevicornis</i> , <i>D. frontalis</i> , <i>D. valens</i> ^o , <i>Dryocoetes affaber</i> , <i>Gnathotrichus materiarius</i> , <i>Ips aculus</i> , <i>I. calligraphus</i> , <i>I. grandicollis</i> ^o , <i>I. pini</i> ^o , <i>Polygraphus rufipennis</i> , <i>Trypodendron scabricollis</i> ; CER: <i>Monochamus carolinensis</i> , <i>M. scutellator</i> , <i>M. titillator</i> ; Neacanthosinus <i>obsolletus</i> , <i>Xyloterus sagittatus</i>	AB, ON, QC, NS; AZ, LA, MS, TX	Hirschmann and Wicniewski 1986; Hofstetter 2008; Kinn and Linit 1989; Knee et al. 2012a, b; Moser and Roton 1971
<i>T. lamellosa</i>	4/4	11 ⁺ /6	<i>Dendroctonus ponderosae</i> , <i>D. pseudotsugae</i> , <i>Dryocoetes confusus</i> ; <i>Ips aculus</i> , <i>I. calligraphus</i> , <i>I. grandicollis</i> ^o ; CER: <i>Monochamus carolinensis</i> , <i>M. scutellator</i> , <i>M. titillator</i> ; Neacanthosinus <i>obsolletus</i> , <i>Xyloterus sagittatus</i>	AB, ON; AZ, LA, MS	Hofstetter 2008; Kinn 1987; Kinn and Linit 1989; Knee et al. 2012a, b; Moser and Roton 1971
<i>T. moseri</i>	2/2	2 ⁺ /2	<i>Dendroctonus simplex</i> , <i>Polygraphus rufipennis</i> ^o	AB, QC	Hirschmann 1972; Knee et al. 2012b
<i>T. parisiانا</i>	2/2	4 ⁺ /3	<i>Gnathotrichus materiarius</i> ^o , <i>Ips sexdentatus</i> , <i>I. typographus</i> , <i>Xyleborinus saxesenii</i>	BC, QC, NS; MI; France	Hirschmann and Wicniewski 1987; Knee et al. 2012b
<i>Urobovella americana</i>	2/2	7 ⁺ /3	<i>Dendroctonus pseudotsugae</i> , <i>D. terebrans</i> , <i>D. valens</i> ^o , <i>Gnathotrichus materiarius</i> , <i>Ips aculus</i> , <i>I. calligraphus</i> , <i>I. grandicollis</i>	QC; AZ, LA, OH, PA, WI	Hofstetter 2008; Knee et al. 2012b; Moser and Roton 1971
<i>U. dryocoetes</i>	4/4	7 ⁺⁺⁺ /5	<i>Dendroctonus valens</i> ^o , <i>Dryocoetes affaber</i> , <i>D. autographus</i> ^o , <i>Hylastes cunicularius</i> , <i>H. porcalus</i> ^o , <i>Ips sexdentatus</i> , <i>Polygraphus rufipennis</i>	NB, NS, QC; Austria	Hirschmann 1989; Knee et al. 2012b
<i>U. orri</i>	5/5	18 ⁺⁺⁺⁺ /6	<i>Dendroctonus brevicornis</i> , <i>D. frontalis</i> , <i>D. obsesus</i> , <i>D. pseudotsugae</i> , <i>D. rufipennis</i> , <i>D. valens</i> , <i>Dryocoetes affaber</i> ^o , <i>D. confusus</i> , <i>Gnathotrichus materiarius</i> , <i>Ips aculus</i> , <i>I. calligraphus</i> , <i>I. emarginatus</i> , <i>I. grandicollis</i> ^o , <i>I. pini</i> , <i>I. plastographus</i> , <i>Pityokteines curvidens</i> , <i>P. sparsus</i> ^o , <i>Polygraphus rufipennis</i> ^o	AB, ON, NS, QC; AZ, CA, LA, MS, TX; Croatia	Hofstetter 2008; Knee et al. 2012b; Moser and Roton 1971
<i>U. vinicolora</i>	1	3 ⁺ /3	<i>Dendroctonus valens</i> ^o , <i>Hylurgops</i> sp., <i>Ips typographus</i>	CA; Germany, Mexico	Knee et al. 2012b; Moser and Bogenschütz 1984
<i>Paralates teontonycha</i>	6/5	8/4	<i>Dendroctonus frontalis</i> , <i>Dryocoetes affaber</i> , <i>D. confusus</i> , <i>Hylastes nigrinus</i> , <i>H. salebrosus</i> , <i>Pityokteines curvidens</i> , <i>P. spinidens</i> , <i>P. vorontzovi</i>	AK, AZ, LA, OR; Austria, Croatia	Hofstetter 2008; Norton 1980; Pernek et al. 2008, 2012

^a BUP, Buprestidae; CER, Cerambycidae; CLR, Cleridae; CUR, Curculionidae; TRO, Trogossitidae.

^b Provinces and states of Canada and the United States follow accepted abbreviations.

have a broad host range (≥ 4 hosts, from ≥ 3 genera), with no sign of host preferences, whereas eight species showed a marked preference for one or two hosts. Moreover, four of the five most common species (*Dendrolaelaps* n.sp. 1, *D. quadrisetus*, *D. quadrisetosimilis*, and *U. americana*) were primarily associated with a single host species. The other most common species, *Paraleius* n.sp., was exclusively collected from two unrelated hosts that occupy similar habitats (Wood 1982). If these results represent actual host preferences, then there has been some form of selection for host specificity.

In contrast, when published host records are taken into consideration, strict host specificity appears to be rare. The combined host records from this study and the literature indicate that the majority of the 21 described species collected here have a broad host range (up to 26 host spp.); with the most host-specific mites (four species) having two to three hosts representing two to three genera. According to published host records, all of described species that were relatively common (10 spp. with at least 20 individuals collected) in this study have a broad host range. Unfortunately, most published surveys do not provide prevalence or abundance data, making it almost impossible to discriminate between strong and loose or accidental host associations.

The host records from the literature and the findings of this study together suggest that at a global scale bark beetle-associated mites have a broad host range, while at a local scale many species tend to be host specific. For instance, *P. fiseri* was reported from 10 different host species from eight genera, in southeastern United States and Germany. In Ontario, we found *P. fiseri* only on one host species, *H. porculus*. Similarly, *D. quadrisetus* was found on 26 scolytine species from seven genera across United States and Europe; whereas in Ontario, we collected it primarily on *I. pini*, and rarely from the congeneric *I. grandicollis*. At a local scale, many of these mites appear to be primarily associated with a single bark beetle species, despite the availability of many other hosts. Therefore, non-parasitic mite species may be host specific and not, or at least not only, habitat specific. Host specificity to one group of phoretic carrier (e.g., to a family or genus of insects) is common in mite taxa associated with patchy habitats (e.g., carrion, dung, fungal fruiting bodies; O'Connor 1982, Krantz 1998), but there are few well studied cases that show high host specificity. For example in Mesostigmata, species complexes of *Poecilochirus* (Parasitidae) and *Uroobovella* (Urod-nychidae) appear to prefer one species or a few species of *Nicrophorus* (Silphidae) beetles (Brown and Wilson 1992, Knee et al. 2012c). Between geographic regions populations may be differentially constrained by variation in local host availability, and by local adaptation to biotic or abiotic factors (Poulin 2007). This variation through space could explain why a given symbiont may be a host specialist at a local scale and a generalist at a global scale (Krasnov et al. 2004, 2011;

Šimková et al. 2006), as suggested here for several mite species phoretic on bark beetles.

Challenges of Host Specificity Studies. The host range differences between this study and the literature is significant: 60% of the mite-host associations recorded for described species in this study are novel, and 88% of previously published associations for described species were not found in this study. The absence of overlapping records between this study and the literature is in part because of most published records being from Europe and southern United States, where the bark beetle fauna differs considerably from that of Ontario, as well as because of variation in sampling techniques across studies. This also shows the dearth of sampling in Canada and most regions of United States. Indeed, most scolytine species have not been studied for mites, and those that have been were typically done so locally. Therefore, current host records represent the tip of the iceberg. The lack of such baseline data on host associations obfuscates any analyses of host specificity.

The observed discrepancies in host range breadth may not only reflect natural geographic variation in host preferences, but also some of the challenges inherent to the study of host specificity. Clear and stable species concepts, as well as accurate taxonomic identifications are the buttresses of any biodiversity or ecological study, but particularly to studies focusing on host associations. Parasite and symbiont identifications have historically been exclusively based on morphological characters. However, the latter may alone be insufficient for delineating species boundaries in groups that include cryptic species (Poulin and Keeney 2007), which are distinguished by no or subtle morphological differences. It is possible that the observed differences in host range breadth of bark beetle mites are a result of unrecognized cryptic diversity, in which putatively widespread generalists (e.g., *D. quadrisetus*) represent complexes of cryptic species with relatively narrow host preferences. For example, morphological and molecular analyses revealed that a single generalist uropodoid species, *Uroobovella nova* (Oudemans), associated with silphid beetles, is actually a complex of cryptic species with varying degrees of host specificity (Knee et al. 2012c).

Poorly understood taxonomy can easily lead to inaccurate species level identifications by both experts and nonexperts. For example, several publications on *Mucroseius* (Melicharidae), a genus of mites associated with cerambycid beetles, contained several incorrectly identified species, which were uncovered by Lindquist and Wu (1991). In addition, before the revision of the genus *Dermanyssus* (Dermanyssidae), many researchers misidentified various *Dermanyssus* species as *D. gallinae* (De Geer) (Moss 1978). Species identifications in biodiversity studies are frequently performed by nonspecialists, sometimes with minimal support from taxonomic experts, inevitably leading to occasional erroneous identifications. Even so, there are instances where specialists, with decades of expe-

rience on a particular group have difficulty correctly diagnosing specimens to species (Packer et al. 2009). Naturally, incorrect identifications are much more likely in taxa for which there are few or no dichotomous keys or reliable species descriptions, as seen in many groups of symbiotic taxa (Kijewska et al. 2002, Locke et al. 2010). Interpreting host specificity across studies can be severely hampered by these sometimes rampant misidentifications.

Changes in species concepts through time, or among authors, can further obscure host specificity estimates. For instance, *D. quadrisetus* and *D. quadrisetosimilis* are currently considered distinct species, but historically *D. quadrisetosimilis* was synonymized under *D. quadrisetus* (McGraw and Farrier 1969). Unfortunately, fluctuations and disagreements in species concepts are present in virtually all groups of arthropods. Hopefully, more refined systematic tools, such as improved microscopy techniques, and the use of currently available and novel molecular markers, will bring relative stability to species concepts.

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