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Research article

Structure of Phoretic Mite Assemblages Across Subcortical Beetle Species at a Regional Scale

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Abstract

Mites associated with subcortical beetles feed and reproduce within habitats transformed by tree-killing herbivores. Mites lack the ability to independently disperse among these habitats, and thus have evolved characteristics that facilitate using insects as transport between resources. Studies on associations between mites and beetles have historically been beetle-centric, where an assemblage of mite species is characterized on a single beetle species. However, available evidence suggests there may be substantial overlap among mite species on various species of beetles utilizing similar host trees. We assessed the mite communities of multiple beetle species attracted to baited funnel traps in *Pinus* stands in southern Wisconsin, northern Arizona, and northern Georgia to better characterize mite dispersal and the formation of mite–beetle phoretic associations at multiple scales. We identified approximately 21 mite species totaling 10,575 individuals on 36 beetle species totaling 983 beetles. Of the mites collected, 97% were represented by eight species. Many species of mites were common across beetle species, likely owing to these beetles' common association with trees in the genus *Pinus*. Most mite species were found on at least three beetle species. *Histiostoma* spp., *Iponemus confusus* Lindquist, *Histiogaster arborsignis* Woodring and *Trichouropoda australis* Hirschmann were each found on at least seven species of beetles. While beetles had largely similar mite membership, the abundances of individual mite species were highly variable among beetle species within each sampling region. Phoretic mite communities also varied within beetle species between regions, notably for *Ips pini* (Say) and *Ips grandicollis* (Eichhoff).

Key words: commensalism, *Dendroctonus, Ips*, phoresy, *Pinus*

Numerous organisms exploit the subcortical environment transformed by colonization by bark beetles, including tree death, fragmentation by tunneling, and gallery enrichment by frass deposition (Hofstetter et al. 2015). Mites (Acari) readily feed and reproduce within tree phloem, and have a diverse array of life history characteristics and resource requirements (Hofstetter and Moser 2014). These life histories include nematode predators such as *Dendrolaelaps quadrisetus* (Berlese; Kinn 1984), egg parasitoids of beetles such as *Iponemus confusus* (Lindquist; Lindquist 1969b), generalist bacterial filter feeders such as *Histiostoma varia* Stone and Simpson (O'Connor 1984), and fungivores such as *Tarsonemus ips* Lindquist (Moser and Roton 1971) and *Histiogaster arborsignis* Woodring (Cardoza et al. 2008). Mites range from relatively specialized feeders to broad feeding generalists that include scavengers and facultative predatory or fungal feeders. Some mites have been implicated as predators of bark beetles, including those in the genus *Dendrolaelaps* and *Proctolaelaps* (Lindquist 1969a, Moser 1975, Lindquist et al. 2009); however, influences of mites on beetle reproductive success are largely unknown. Interactions between beetles and mites are likely driven by multiple factors, including habitat availability, micro climate (Hofstetter et al. 2007), fungal populations (Lombardero et al. 2003), and natural enemy prevalence. The high variation in phoretic mite morphologies and life histories is likely related to the large number of ecological niches available within the beetle-generated habitat.

While beetle-associated mites can be highly successful at utilizing available resources within the subcortical environment, dispersal poses a significant challenge. Mites are limited in their ability to colonize new resources owing to their small size, poor motility, and narrow range of tolerated environmental conditions (Mitchell 1970). Recently killed trees are patchy, ephemeral, and dictated in abundance and distribution by bark beetle populations, which themselves are quite variable, across the landscape. In response to these pressures, many mites have evolved mechanisms that facilitate

transport and dispersal between resource islands (Farish and Axtell 1971, Hofstetter and Moser 2014). These adaptations include behavioral specializations in attachment location (Pfammatter 2015) and morphological structures that facilitate attachment to specific host structures (Hofstetter and Moser 2014). Some examples of behavioral modifications include selective alignment of *D. quadrisetus* underneath elytra of host beetles (Moser and Bogenschuütz 1984, Pernek et al. 2007), and attachment of *I. confusus* inside the relatively disturbance-free elytral declivity (Lindquist 1969b). Examples of morphological adaptations include a series of suckers on the anal plate of *Histiostoma* spp. (Binns 1982), haustoria stalks on *Trichouropoda australis* Hirschmann (Faasch 1967, Binns 1982), and modified claw-like forelegs *Elattoma* sp. (Binns 1982).

Patterns of phoretic mite associations with bark beetles have most often been studied from the perspective of single host beetle species. Examples of bark beetle species that have been examined for phoretic mites include the pine engraver (Pfammatter et al. 2013), European elm bark beetle (Moser et al. 2005), European spruce beetle (Takov et al. 2010), fir bark beetle (Pernek et al. 2007), spruce beetle (Cardoza et al. 2008), and southern pine beetle, *Dendroctonus frontalis* Zimmermann (Moser and Roton 1971, Moser et al. 1974). Hofstetter et al. (2015) lists 270 phoretic mite species associated with bark beetles and associated phloem insects such as predators and woodborers. These studies have provided invaluable insight into our understanding of paired beetle–mite associations, but we have less understanding of the mite communities associated with these beetles and groups of beetles at local and regional scales. One influence on our lack of understanding may be attributed to the fact that mites are often driven by bottom-up ecological processes and so may be more likely to be habitat- than vector-specific (Moser 1995). That is, they may exploit the diverse array of subcortical beetles and host tree habitats across different regions with variable levels of behavioral specificity.

The processes that influence the patterns of phoretic associations observed between entire communities of beetles and mites remain largely unknown. Given that mites have the potential to impact bark beetles and the community structure of beetle-generated habitat (Lombardero et al. 2003, Hofstetter et al. 2006), it is important to investigate the structure of these phoretic associations, and how they differ within and among beetle species within and among regions across landscapes.

Conservatively, North America has over 475 species of bark and ambrosia beetles (Wood 1982) and numerous other subcortical beetle species. Many, including all the native North American irruptive species, are associated with conifers and use aggregation pheromones to mass-attack trees (Coulson 1979, Wood 1982). Conifer-associated bark beetles have varying behaviors, strategies, and mechanisms for colonizing host trees (Lindgren and Raffa 2013, Vega and Hofstetter 2015), and thereby transforming an inhospitable subcortical environment into one suitable for brood production. This transformed environment is also suitable for co-habitation by a large diversity of organisms such as nematodes, fungi, bacteria, and other arthropods, in addition to phoretic mites (Hofstetter et al. 2015). We know little about community characteristics such as fidelity, redundancy, and substitutability of mites within these systems, both within their tree host and on their host carrier beetles.

The purpose of this research is to quantify the extent to which phoretic mite communities vary among potential bark beetle vectors within and among regions. This information will provide insight into the extent to which these symbioses are driven by factors unique to each interspecific relationship, local abiotic and tree-species factors, and general features of the bark beetle-generated habitat.

Materials and Methods

We characterized the phoretic mite communities of pine-associated bark beetles in Wisconsin, Arizona, and Georgia. We compared mite communities among beetle species within and across regions, and evaluated whether the feeding breadth of mite species influences the relative degree of overlap in the communities.

Beetle Sampling

Beetles were trapped live at three mixed pine stands (sites) in each of the three sample regions (southern Wisconsin, northern Arizona, and northern Georgia) in 2013. Sites consisted primarily of *Pinus resinosa* Ait. plantation with sparse *Pinus strobus* L., and various *Quercus* and *Acer* species in Wisconsin; ponderosa pine with sparse *Quercus gambelii* Nutt. and locust in Arizona; and planted *Pinus taeda* L. with hardwood components including *Liquidambar*, *Liriodendron tulipfera* L., and various *Quercus* species in Georgia. Beetles were also sampled in *P. resinosa* sites near Arkdale and Mazomanie, Wisconsin, in 2011 (Table 1), with emphasis on beetles known to be associated with *Ips*-colonized trees, such as *Dendroctonus valens* LeConte, *Monochamus* spp., *Platysoma* spp., and *Thanasimus dubius* (F.).

Each of the three multiple-funnel traps (Lindgren 1983) at each site were baited with one of three lures deemed to be most attractive to the predominant bark beetle species in each region. In Arizona, $50^{+}/50^{-}$ α-pinene and EtOH ultra-high release lures, Ipsdienol $3^{+}/97^{-}$ 40-mg bubble caps, or western pine beetle lure (exo-brevicomin, frontalin, and myrcene) were used, and in Georgia and Wisconsin, $50^{+}/50^{-}$ α-pinene and EtOH ultra-high release lures, Ipsdienol $50^{+}/50^{-}$ 40-mg and 4-mg bubble caps, or Ipsenol $50^{+}/50^{-}$ 40-mg bubble caps were used. All lures were purchased from Contech Enterprises Inc. (BC, Canada). Traps were suspended from a wire between two trees or from a metal pole 1.5 m above the ground. All beetles were collected live from dry collection cups during eight-hour trapping sessions in which fresh lures were cut open to release high volumes of attractants. Collection cups were partially filled with Kimwipes (Kimberly-Clark, Irving, TX) to protect trapped beetles from predators. Live trapping allows for the analysis of phoretic mite communities on a per beetle basis while minimizing the disturbances associated with host insect death (Pfammatter et al. 2013).

Beetles were sampled on four occasions, 25–27 June, 9–10 July, 25–27 July, and 6–8 August at each site. Collected beetles were placed in individual gel capsules that were placed on ice immediately and frozen within the same day. Beetle identifications were confirmed using a combination of the following resources: Yanega (1996), Arango and Young (2012), Lingafelter (2007), Wood (1982), Dorshorst and Young (2009), Arnett and Thomas (2000),

Table 1. Collection sites of bark beetles sampled for phoretic mites in Wisconsin, Arizona, and Georgia

Year	Region	County	GPS coordinates	Major tree type
2011	Wisconsin	Dane	43.210150, −89.792150	*P. resinosa*
2011[a]	Wisconsin	Adams	NA	*P. resinosa*
2013	Wisconsin	Sauk	43.180194, −90.155444	*P. resinosa*
2013	Wisconsin	Waushara	44.259528, −89.314000	*P. resinosa*
2013	Wisconsin	Walworth	42.832414, −88.610179	*P. resinosa*
2013	Georgia	Jackson	34.123996, −83.796720	*P. taeda*
2013	Georgia	Greensboro	33.738522, −83.271386	*P. taeda*
2013	Georgia	Jasper	33.275289, −83.738976	*P. taeda*
2013	Arizona	Coconino	35.16865, −111.77169	*P. ponderosa*
2013	Arizona	Coconino	35.26780, −111.80611	*P. ponderosa*
2013	Arizona	Coconino	35.24715, −111. 63531	*P. ponderosa*

[a]*Dendroctonus valens* were excavated from recently cut *P. resinosa* stumps approximately 5 km north northeast of Arkdale, WI.

and Arnett et al. (2010). Additionally, *De. valens* were excavated from newly cut *P. resinosa* tree stumps in 2011. These were handled identically to the other beetle samples.

Phoretic Mite Sampling

Mites were removed from each beetle using a size no. 1 insect pin affixed to a Pasteur pipette and mounted on a 75 by 25-mm glass microscope slide (Corning Glass Works, Corning, NY) with specimen clearing fluid (#6373A, Bioquip, Rancho Dominguez, CA). Microscope slides with mites were placed in a drying oven at 80°C for a minimum of 24 h in conjunction with clearing fluid to allow for rapid lipid digestion of mite internal organs. After lipid digestion, only chitinous products remained, facilitating identification based on mite exoskeleton morphology. Phoretic mites from beetles in all regions were counted and identified, and representative samples were confirmed by J.C. Moser.

Statistical Analyses

All data were analyzed using R statistical software v3.0.2 (R Core Team 2014). Rarefaction curves were generated to determine the effectiveness of sampling intensity (Heck et al. 1975) in each region. Rarefaction curves were generated using code from Chao et al. (2014), where q = 0, 0.5, 1, and 2 (described in the next section).

The diversities of phoretic mite communities from beetle species with at least 35 representative specimens from each capture region were compared using the rarefied "Hill numbers" procedure, as described by Chao et al. (2014). Hill numbers, expressed as q values, provide a method for unifying community diversity indexes (Hill 1973). Hill's equations (at any value for q) generate a value for effective species richness that is interpretable as species richness at q = 0, the exponential Shannon's index at q = 1, and the inverse Simpson's index at q = 2 (Hill 1973). We present Hill numbers for q = 0, 1, and 2 rarefied over total number of beetles for each region. We also present a rarefied Hill index at q = 0.5, which weights the integration of species evenness toward the least common species in the community (Chao et al. 2014). Calculations of rarefied Hill numbers and rarefaction curves were performed for species groupings as defined in Table 2. We hereafter refer to expected species richness at q values of 0, 0.5, 1, and 2 by superscript annotation (i.e., expected species richness^{0}, richness$^{0.5}$, etc.).

Phoretic mite communities on individual beetles were visualized using nonmetric multidimensional scaling (NMS; function: nmds, package: ecodist, 150 runs, random start configuration; Shepard 1962, Kruskal 1964) and labeled by region and beetle species. Analysis of similarities (ANOSIM; function: anosim, package: vegan, 999 permutations) was used to test for significance of separation for both region and beetle species. Significant ($P < 0.05$) correlation vectors (Jongman et al. 1995; function: vf, package: ecodist) of mite species were overlaid on the NMS visualization. Ordination (NMS, ANOSIM, and vector correlations) analyses were performed on additively aggregated (function: aggregate, constraints: beetle species, and collection region), square root transformed, Wisconsin double-standardized (function: wisconsin; Bray and Curtis 1957) phoretic mite community abundance data resembled to a Bray–Curtis dissimilarity matrix (function: distance, package: ecodist). Unidentified beetles, beetles with less than 10 representative individuals, and beetles species not co-occurring with at least one phoretic mite species were removed from the ordination.

We individually assessed regional variation in the community of relatively abundant phoretic mites on *Ips pini* and *Ips grandicollis* with a series of generalized linear models fit with a Poisson distribution, as residual plots from Poisson models demonstrated a better fit than linear models on untransformed data. Post hoc Tukey tests were performed to compare individual mite abundances between regions in a pairwise manner. Mite species occurring fewer than 10 times on *Ips* spp. were removed from model consideration.

We calculated Pearson correlations and associated *P*-values for pairs of phoretic mite species on beetle species with at least 35 representative individuals in a region. Resultant matrices were visualized (function: corrplot, package: "corrplot") with nonsignificant correlation values marked with an "X". Mite species that occurred less than 10 times across the group of beetles selected for this analyses were removed from analysis.

Results

We sampled 983 individual beetles, representing 36 species from nine families (Table 2). Sixteen of these 36 beetle species carried at least one phoretic mite. All of the beetle species on which no phoretic mites were observed were captured in relatively low numbers. Species that carried mites averaged just under five mite species per host beetle. Overall, we found approximately 21 mite species totaling 10,575 individuals. The eight most abundant phoretic mite species represented 97% of all mites (based on 2013 data owing to alternative collection methods in 2011 as described in Methods). Owing to taxonomic challenges, we were unable to identify mites on six individual beetles in 2013, and we found approximately seven unidentified phoretic mite species, mostly in association with *T. dubius*, on beetles in 2011. Rarefaction of the phoretic mite communities on pooled beetle samples indicated adequate sampling effort (Fig. 1). Expected mite species richness for Wisconsin, Arizona, and Georgia were similar, although estimates of the effective species richness from samples in Georgia may be slightly lower than the other two regions (Fig. 1). Projections indicate a potential for higher species richness for phoretic mite communities on beetles in Arizona, given a stronger sampling effort (Fig. 1).

The prevalence and abundance of various mite species on each beetle species × region × year combination are presented in Table 2. The average proportion for each of the identified phoretic mite species on beetle species that carried mites (pooled by region and year) is presented in a network map in Figure 2. Across all beetle species, we found more *Elattoma* sp. (6,561) than any other species of mite. We also obtained high numbers of *I. confusus* (1,923), *Histiostoma* spp. (659), *Histiogaster* spp. (296), *Tr. australis* (268), *Tarsonemus* spp. (258), and *D. quadrisetus* (238). All other phoretic mite species were represented by less than 125 individuals each. *Histiostoma* spp. had the widest breadth of phoretic association, occurring on 12 beetle species (Table 2). *I. confusus* and *H. arborsignis* were found on nine, *Tarsonemus* spp. and *Elattoma* sp. were found on seven, and *D. quadrisetus* and *Proctolaelaps* sp. were each found on six beetle species (Table 2). *Mexecheles virginiensis* (Baker) and *Schwiebia* sp. had the narrowest breadth of host beetle species association, only being found on one and two beetle species, respectively (Table 2).

Phoretic mite community assemblages varied among sampling regions (3D NMS Stress = 0.094, $r^2 = 0.927$; ANOSIM $R = 0.191$, $P = 0.053$; Fig. 3). Samples from each region visually appear moderately clustered with some points, such as *Pachylobius picivorus* (Germar) from Georgia falling outside of the clustering. This pattern appears to be owing to the strong significance of beetle species in predicting phoretic mite community dissimilarity (ANOSIM $R = 0.643$, $P = 0.01$; NMS Stress = 0.188, $r^2 = 0.819$; Fig. 3). NMS

Table 2. Beetle and phoretic mites obtained in Wisconsin (WI), Arizona (AZ), and Georgia (GA) in 2011 and 2013

Region	Beetle family	Beetle species	Total beetles (mites)	Total mite species	*Iponemus confusus* Lindquist	*Dendrolaelaps neodisetus* (Hurlburt)	*D. quadrisetus* (Berlese)	*Ereynetes propescutulis* Hunter	*Paracarophaenax* sp.	*Tarsonemus* spp[a]	*Elattoma* sp.	*Histiogaster arborsignis* Woodring	*Histiostoma* spp[b]	*Histiostoma anops*	*Trichouropoda australis* Hirschmann	*Proctolaelaps*sp.	Unidentified
GA	Cerambycidae	Monochamus spp[c]	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI		Monochamus scutellatus (LeConte)	2 (20)	2	0	0	0	0	0	0	0	0	0	0	0.5 (20)	0	0
WI[c]		Rhagium inquisitor L.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI		*Xylotrechus* sp.	1 (200)	5	0	0	0	1 (1)	0	0	0	1 (92)	0	0	0	0	1 (107)
GA	Cleridae	*Enoclerus ichneumoneus* (F.)	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI		*Enoclerus nigrifrons* (Say)	4 (1)	2	0	0	0	0	0	0	0	0.25 (1)	0	0	0	0	0
WI[d]		*Thanasimus dubius*[e] (F.)	21 (91)	14	0.1 (2)	0.14 (3)	0	0.05 (1)	0	0.05 (1)	0	0.57 (3.08)	0.24 (1.8)	0.05 (6)	0.5 (1)		0.5 (6)
GA		*Thanasimus dubius* (F.)	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI		*Thanasimus dubius* (F.)	17 (131)	4	0	0	0	0	0	0	0	0.29 (21)	0.29 (2.8)	0	0.18 (4)	0	0
GA	Colydiinae	*Lasconotus* sp.	3 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
GA		*Cossonus* sp.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI	Curculionidae	*Anthonomus* sp. Germar	1 (2)	3	1 (1)	0	0	0	0	0	0	1 (1)	0	0	0	0	0
AZ		*Dendroctonus brevicomis*[f] LeConte	137 (152)	10	0.01 (1)	0	0	0	0.04 (3.6)	0.22 (3.07)	0.05 (2.86)	0	0	0	0.03 (1.5)	0	0.01 (1)
AZ		*Dendroctonus frontalis* Zimmermann	36 (48)	6	0.06 (4.5)	0	0	0	0.03 (1)	0.19 (2)	0.17 (3.33)	0	0	0	0	0.03 (1)	0
AZ		*Dendroctonus* sp.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
AZ		*Dendroctonus valens* LeConte	1 (15)	2	0	0	0	0	0	0	0	0	0	1 (15)	0	0	0
GA		*Dendroctonus valens* LeConte	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI[d]		*Dendroctonus valens* LeConte	55 (118)	6	0.02 (2)	0	0	0	0	0	0	0.02 (1)	0.35 (4.42)	0	0.04 (3.5)	0.09 (4.4)	0
WI		*Dendroctonus valens* LeConte	1 (2)	3	0	0	1(1)	0	0	0	0	0	0	0	1 (1)	0	0
GA		*Dryocoetes autographus* (Ratzeburg)	3 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Wi[d]		*Dryopthorus americanus* Bedel	5 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
GA		*Dryopthorus americanus* Bedel	4 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI		*Dryopthorus americanus* Bedel	2 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
GA		*Gnathotrichus materarius* Bedel	2 (3)	2	0	0	0.5 (2)	0	0	0	0	0	0	0	0	0	0
AZ		*Hylastes porculus* Erichson	1 (1)	2	0	0	0	0	0	0	1 (1)	0	0	0	0	0	0
GA		*Hylastes porculus* Erichson	47 (16)	6	0	0	0	0	0	0.02 (2)	0	0.04 (1)	0.04 (1)	0	0	0	0.02 (1)
WI[c]		*Hylastes porculus* Erichson	3 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
GA		*Hylobius* sp.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
GA		*Ips avulsus* (Eichhoff)	239 (2886)	9	0.23 (2.57)	0.02 (1)	0	0	0	0.16 (2.03)	0.6 (17.78)	0 (1)	0.02 (4.5)	0	0.13 (1.44)	0 (1)	0
AZ		*Ips calligraphus* (Germar)	11 (194)	5	0.45 (17.8)	0.18 (3)	0.18 (3)	0	0	0	0.55 (16)	0	0	0	0.09 (2)	0	0
GA		*Ips calligraphus* (Germar)	1 (36)	3	0	0	0	0	0	0	1 (35)	0	1 (1)	0	0	0	0
GA		*Ips grandicollis* (Eichhoff)	35 (407)	7	0.29 (2.2)	0	0	0	0	0.06 (2.5)	0.26 (20.44)	0.03 (1)	0.37 (12.92)	0	0.17 (4.5)	0	0
WI		*Ips grandicollis* (Eichhoff)	10 (189)	6	0.8 (4.12)	0	0.2 (3.5)	0	0	0.1 (1)	0	0	0.5 (21.4)	0	0.1 (40)	0	0
AZ		*Ips pini* (Say)	222 (4688)	14	0.44 (14.05)	0.02 (1.75)	0.23 (3.56)	0.07 (1.75)	0.01 (1.33)	0.08 (2.44)	0.65 (19.91)	0.02 (10.8)	0.05 (1.83)	0	0.21 (2.07)	0.01 (1)	0 (1)
GA		*Ips pini* (Say)	51 (901)	11	0.33 (4.76)	0	0	0.02 (4)	0	0.14 (2.86)	0.76 (19.95)	0.02 (1)	0.02 (1)	0	0.08 (1)	0.02 (1)	0.04 (1)
WI		*Ips pini* (Say)	20 (203)	7	0.3 (27)	0	0.25 (3.4)	0	0	0	0	0	0.25 (3)	0	0.25 (1.2)	0	0.1 (1.5)
AZ		*Orthotomicus caelatus* (Eichhoff)	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
GA		*Pachylobius picivorus* (Germar)	15 (215)	5	0	0	0.07 (4)	0	0	0	0	0	0.07 (1)	0.2 (53.67)	0	0.07 (49)	0
GA		*Pityopthorus* sp.	2 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI		*Rhyncolus* sp.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
GA		*Xylosandrus* sp.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI	Elateridae	*Ampedus* sp.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI		*Melanotus* sp.	1 (7)	2	0	0	0	0	0	0	0	0	1 (7)	0	0	0	0
WI[d]		*Platysoma cylindrical* (Paykull)	4 (7)	2	0	0	0	0	0	0	0	0	1 (1.75)	0	0	0	0
WI[d]	Tenebrionidae	*Corticeus parallelus* (Melsheimer)	5 (41)	6	0.4 (1.5)	0	0.2 (16)	0	0	0	0	0	0.8 (5)	0	0.2 (1)	0.2 (1)	0
WI		*Corticeus parallelus* (Melsheimer)	1 (1)	2	0	0	0	0	0	0	0	0	1 (1)	0	0	0	0
GA		*Hymenorus* sp.	3 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
WI		*Hymenorus* sp.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
GA		*Isomira* sp.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
AZ	Trogossitidae	*Temnochila* sp.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
GA	Zopheridae	*Lasconotus* sp.	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
GA		*Namunaria*	1 (0)	0	–	–	–	–	–	–	–	–	–	–	–	–	–
		Total beetle species carrying	–	–	9	3	6	3	3	7	7	9	12	3	9	6	5

Beetles of the same species are grouped by region. Cells represent the proportion of beetles carrying phoretic mites followed (in parentheses) by the average number of phoretic mites on beetles carrying mites.

[a]The majority of *Tarsonemus* spp. were *Tarsonemus ips* Lindquist; *Tarsonemus fusarii* Coorman were identified in a few samples. Small structural features make conclusive differentiation difficult, so we pool them to genus here.

[b]Most of the *Histiostoma* spp. obtained were *Histiostoma varia* Woodring and Moser, but small structural features make it difficult to confirm that all are *Hi. varia*.

[c]*Monochamus titallator* (F.) and *Monochamus carolinensis* Oliver are morphologically indistinguishable in this region.

[d]Samples were collected in 2011. All samples not marked [d] were collected in 2013.

[e]*Thanasimus dubius* from Wisconsin in 2011 carried 0.14 (1.33) *Schwiebia* sp.

[f]*Dendroctonus brevicomis* from Arizona carried 0.04 (1.2) *Mexecheles virginiensis* and 0.1 (3) *Schwiebia* sp.

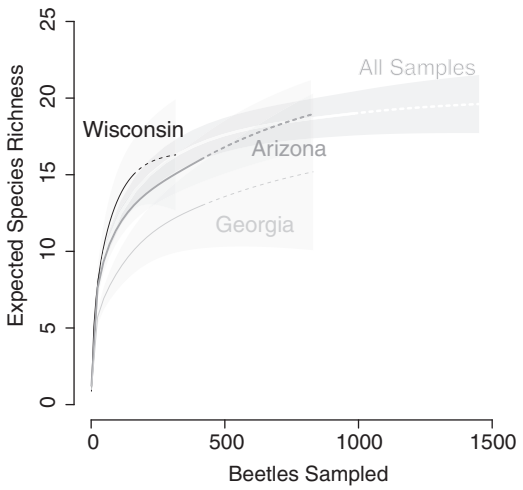

Fig. 1. Rarefaction curves for phoretic mite communities on bark beetles: All samples (thick, white), Wisconsin (thin, black), Arizona (thick, black), and Georgia (thin, gray) in 2013. Solid lines represent data from actual samples; dotted lines predict the Hill-rarefaction curves to twice the original sample size. Shaded bands around each curve represent 95% confidence intervals.

visualization indicates clustering of the phoretic mite communities on samples from *Ips* spp. from all three sample regions (Fig. 3A). Beetles in the genus *Ips* varied in their associations with *D. quadrisetus*, *I. confusus*, or *Elattoma* sp. depending on beetle species and sampling region (Fig. 3A). *Dendroctonus brevicomis* LeConte and *De. frontalis* from Arizona had very similar phoretic mite communities, where both were characterized by a high abundance of *Ta. ips* (Fig. 3A). The phoretic mite community on the predator *T. dubius* ordinated opposite that of *Ips* spp. and *Dendroctonus* spp., and were highly associated with *H. arborsignis* and the collective presence of unidentified mite species.

T. dubius in Wisconsin and *Hylastes porculus* Erichson in Georgia, respectively, had the highest and lowest expected phoretic mite species richness^0 of any beetle species (Fig. 4A). Expected species richness^0 approaches asymptotes for *Ip. pini* in Arizona and *Hy. porculus* in Georgia (Fig. 4A). Projections for *T. dubius* in Arizona, *Ip. pini* in Georgia, *De. frontalis* in Arizona, *De. brevicomis* in Arizona, and *De. valens* in Wisconsin indicate the potential for increased species richness^0 given increased sample effort (Fig. 4A). *T. dubius* in Wisconsin, followed by *Ip. pini* in Arizona, had the highest effective species richness$^{0.5}$ of any species × region combination (Fig. 4B), while *De. frontalis* in Arizona, *Hy. porculus* in Georgia, *De. valens* in Wisconsin, and *Ips avulsus* Eichoff in Georgia had the lowest expected species richness$^{0.5}$ values (Fig. 4B). Dramatic increases in the relative effective species richness^2 for *Ip. grandicollis* in Georgia and *Hy. porculus* in Georgia were observed relative to indices less heavily weighted toward common species (i.e., species richness^0; Fig. 4D). Effective species richness^2 for *T. dubius* in Wisconsin remained highest, but projections for samples > 100 exceed effective species richness^2 for all other species × region combinations (Fig. 4D). Data for the beetle community at effective species richness^1 (Fig. 4C) can be described as intermediate between effective species richness^0 and richness^2 where trends described as emergent at values of q = 2 begin to diverge from the q = 0.5 values.

I. confusus occurred on *Ips* spp. more often than on any other beetle genus (Fig. 5A). *H. arborsignis* occurred in relatively low incidence on *Ip. pini* in Wisconsin and Arizona, *Ip. grandicollis* in Georgia, *Ip. avulsus* in Georgia, *Hy. porculus* in Georgia, and *De. valens* in Wisconsin, but on over 40% of *T. dubius* in Wisconsin (Fig. 4B). *Ta. ips* occurred relatively frequently on many species (Fig. 5C). *Elattoma* sp. occurred on *Ip. pini* in Arizona and Georgia but not in Wisconsin, and on *Ip. grandicollis* from Wisconsin and Georgia but not Arizona (Fig. 5D). *Elattoma* sp. occurred on approximately 20% of *De. frontalis* and *De. brevicomis* (Fig. 5D). *Histiostoma* spp. occurred on over 20% of *De. valens*, *Ip. pini*, and *T. dubius* in Wisconsin, and *Ip. grandicollis* in Georgia and Wisconsin (Fig. 5E). *Tr. australis* occurred on approximately 10% of beetles *Ip. avulsus* in Georgia, *Ips calligraphus* in Arizona and Wisconsin, *Ip. pini* in Arizona, and *T. dubius* in Wisconsin, and on 15–25% of *Ip. grandicollis* in Georgia, *Ip. pini* in Georgia, and *Ip. pini* in Wisconsin (Fig. 5F). *D. quadrisetus* occurred on approximately 20% of *Ip. calligraphus* in Arizona and Wisconsin and *Ip. pini* in Georgia and Wisconsin (Fig. 5G). *Proctolaelaps* sp. occurred on fewer than 10% on *De. valens* in Wisconsin and *Pa. picivorus* in Georgia and on less than 5% on *De. frontalis* in Arizona, *Ip. avulsus* in Georgia, and *Ip. pini* in Georgia and Arizona (Fig. 5H).

Models for regional phoretic mite variation within *Ip. pini* showed significant differences in incidence rates for *I. confusus*, *H. arborsignis*, *Ta. ips*, *Elattoma* sp., *Histiostoma* spp., *Tr. Australis*, and *D. quadrisetus* (Table 3). Regional phoretic mite variation models for *Ip. grandicollis* showed significant differences for *I. confusus*, *Elattoma* sp., *Histiostoma* spp., *Tr. australis*, and *D. quadrisetus* (Table 3).

Figure 6 presents an overview of the pairwise associations between mite species on *Ip. grandicollis* (left) and *Ip. pini* (right) beetles in Arizona (top), Georgia (middle), and Wisconsin (bottom). Paired species *Ta. ips*:*Elattoma* sp., *Ta. ips*:*Tr. australis*, *Elattoma* sp.:*D. quadrisetus*, *H. arborsignis*:*Paracarophaenax* sp., and *Tr. australis*:*D. quadrisetus* were found in positive association on *Ip. pini* in Arizona (Fig. 6B). *I. confusus*:*Ta. ips*:*Elattoma* sp. and *I. confusus*:*Elattoma* sp. were found in positive association on *Ip. pini* in Georgia (Fig. 6D). *Ip. pini* in Wisconsin carried fewer phoretic mite species than other *Ips* spp. (Table 2). We found no significant inter-mite associations on *Ip. pini* in Wisconsin (Fig. 6F). *Histiostoma* spp.:*Ta. ips* and *Tr. australis*:*D. quadrisetus* were found in strong positive correlations on *Ip. grandicollis* in Wisconsin (Fig. 6E), but not in Arizona or Georgia. *I. confusus* was found in positive association with *Ta. ips* and *Elattoma* sp. on *Ip. grandicollis* in Georgia (Fig. 6C), but not in Arizona or Wisconsin. *Ip. calligraphus* in Arizona had no phoretic mite species in significant constant association with one another (Fig. 6A). *I. confusus*, *Ta. ips* and *Elattoma* sp. showed a strong positive association on *Ip. avulsus* in Georgia (Fig. 6J). For all pairwise comparisons, no combination of mite species was found to be significantly negatively associated with one another (Fig. 6). *De. brevicomis*, *Hy. porculus*, *Pa. picivorus*, and *T. dubius* had no mite species that showed any degree of association with each other (Fig. 6G, I, K, and L).

Discussion

We characterized the phoretic mite communities of 36 beetle species across three geographic regions in the United States. While we found differences in the community composition of phoretic mites associated with individual beetle species and collection regions, our study also demonstrates substantial overlap in phoretic mite community membership on bark beetle species. We found most phoretic mites in association with at least 3 and ranging up to 12 species beetle species. Even those mite species that we observed on few host beetle species, such as *M. virginiensis* and *Schwiebia* sp.,

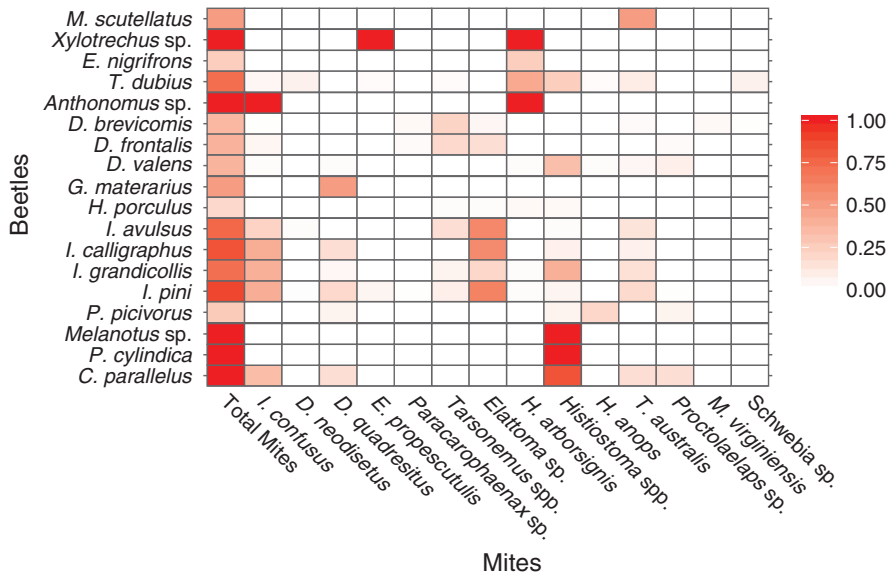

Fig. 2. Network representation of the average proportion of phoretic mite species on beetle species that carried phoretic mites. A darker color indicates a higher average proportion of association. Beetles species were pooled between regions and years. Unidentified mites were removed from this representation.

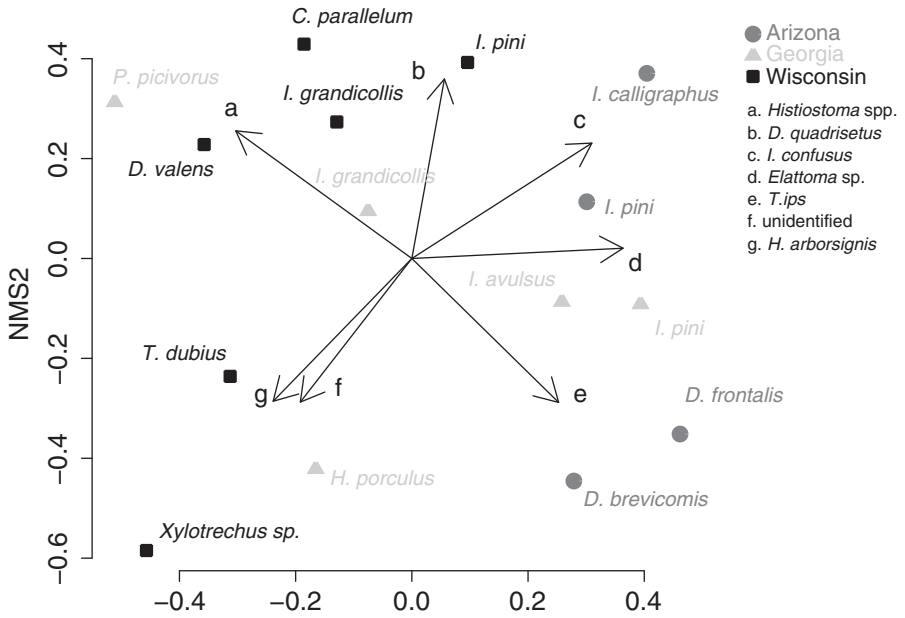

Fig. 3. Nonmetric multidimensional scaling (NMS) visualization of similarities among phoretic mite communities on subcortical beetle species captured in Wisconsin (squares), Arizona (circles), and Georgia (triangles) in 2013 (NMS Stress = 0.188, $r^2 = 0.819$). Wisconsin double-standardized and Bray–Curtis resembled data (aggregated by beetle species collected at each regions) were ordinated and labeled by collection region and beetle species. Phoretic mite communities from different beetle species (ANOSIM $R = 0.643$, $P = 0.01$) and collection regions (ANOSIM $R = 0.191$, $P = 0.053$) were significantly different. Significant ($P < 0.05$) mite species correlations are overlaid.

have been previously found on pine-associated beetles (Pfammatter et al. 2013, Hofstetter et al. 2015). This overlap is almost surely underestimated in our study, because all of the beetle species represented by at least five individuals yielded mites. These undersampled beetle species would likely carry mites from a similar membership pool.

Overall, phoretic associations between beetles and mites were relatively diffuse (i.e., not strong and consistent patterns of association) within and among beetle species and sampling regions. This may be owing to the fact that many mite species associated with bark beetles are generalist in nature found to occur in many environments. For example, *H. arborsignis* is ubiquitous across subcortical habitats (Moser 1995) and has been found in association with Hymenoptera and Diptera in addition to Coleoptera (O'Connor 1990). However, even mite species such as *I. confusus*, which we would predict to have more specialist mite–carrier relationship owing to its specificity of feeding on bark beetle eggs, was found on nine beetle species. One species, *T. dubius* accounted for the highest number of morphologically different and taxonomically unidentifiable mite species. These morphologically different mite species may

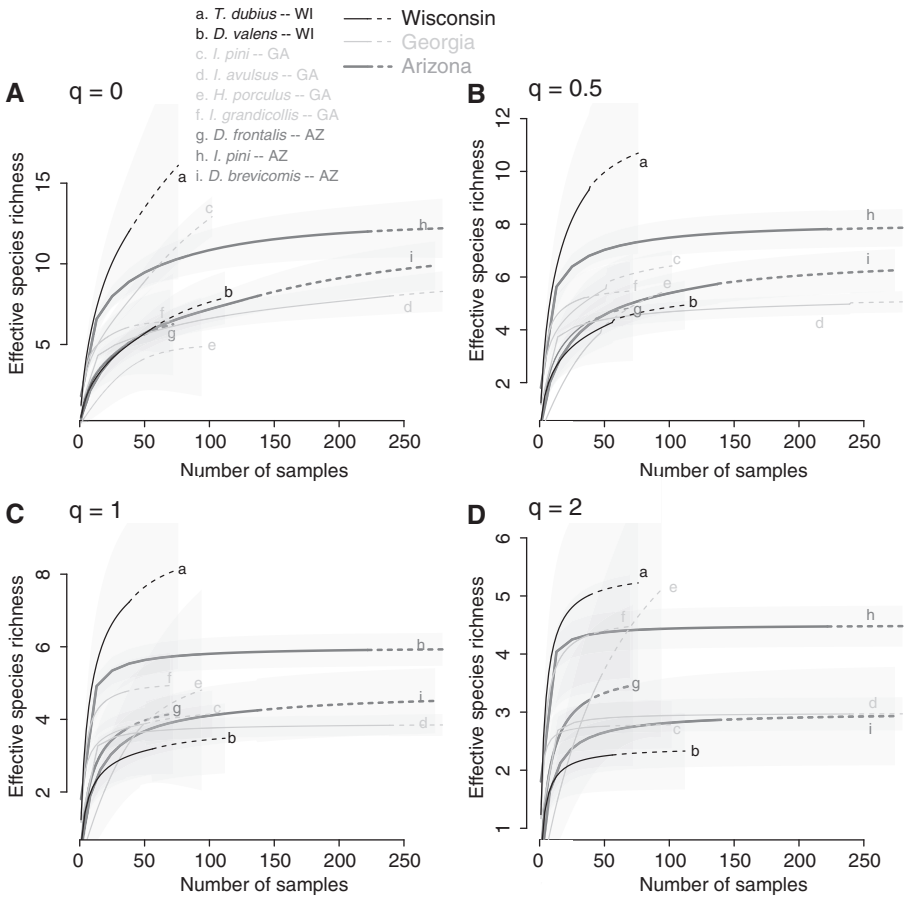

Fig. 4. Rarefied curves for Hill numbers for phoretic mite communities of *De. brevicomis, De. frontalis,* and *Ip. pini* in Arizona; and *Hy. porculus, Ip. avulsus, Ip. grandicollis,* and *Ip. pini* in Georgia; A) q = 0, B) q = 0.5, C) q = 1, and D) q = 2. Beetles not represented by at least 35 specimens were removed from rarefied Hill indices. Solid lines represent data from actual samples; dotted lines predict the hill-rarefaction curves to twice the original sample size. Shaded bands around each curve represent 95% confidence intervals.

indicate a different (and potentially more specific) relationship with some mites than the other beetles in the study. In general, we found little evidence for close pairwise relationships between specific beetle and mite species. In addition, it is difficult to ascribe regional patterns of beetle–mite associations to account for the variability in these associations. This may be because while regional variation exists, it is strongly confounded by the variability in the dominant tree species between the regions.

We also considered that positive or negative correlations between pairs of co-transporting mite species might be influential in structuring patterns of beetle–mite phoretic relationships. That is, competition and synergy between two species both in the phoretic and within-tree life stages could account for variation that we see among beetle species and regions. We were surprised to find little evidence of strongly positive and almost no evidence for negative associations among phoretic mite species co-occurrences during phoretic transport. This indicates that mites are likely tree habitat specialized and that most patterns of phoretic mite–beetle associations are likely driven by within-tree factors including nematode (Lindquist 1969b) and fungal abundance. Alternatively, beetles may be so readily available that mites can move freely between them prior to tree departure and thus competition between mites may be low. The processes that drive the within-tree success of mites, and thus the likelihood of these mites dispersing and acting as pioneers in new habitat, are largely unknown.

Mite–bark beetles associations appear to show both differences and similarities with other well-described mite–host relationships, such as that of *Macrocheles saceri* Costa, which stays in constant association with one or very few species of dung beetles (Niogret and Lumaret 2009). Other, more generalist *Macrocheles* mites associated with dung beetles are less selective of their carrier hosts, appearing in association with many beetle species—these mites species are more selective of habitat quality than phoretic host (Niogret and Lumaret 2009). Most mites in our system may be more aptly described as habitat specialists, requiring the environment tunneled by bark beetles rather than a specific mite–carrier relationships or food source. Thus, most mites are likely more generalist than specialist in their phoretic preferences. Niogret and Lumaret (2009) described a positive relationship between ephemeral resource longevity and phoretic mite–carrier specificity in dung beetle systems. Degrading beetle-attacked trees may provide suitable food and shelter resources for more than 5 yr (personal observation), which may be an important contributor to the patterns of diffuse mite–carrier relationships we see in our system. The relatively high variability in patterns of mite–bark beetle relationships is consistent with strong effects of bottom-up ecological processes related to resource quality and abiotic environmental conditions. Variability in patterns that drive individual tree resource quality may contribute to the lack of strong associations at the site, beetle species, or regional levels. Results of this landscape-scale study are consistent with the

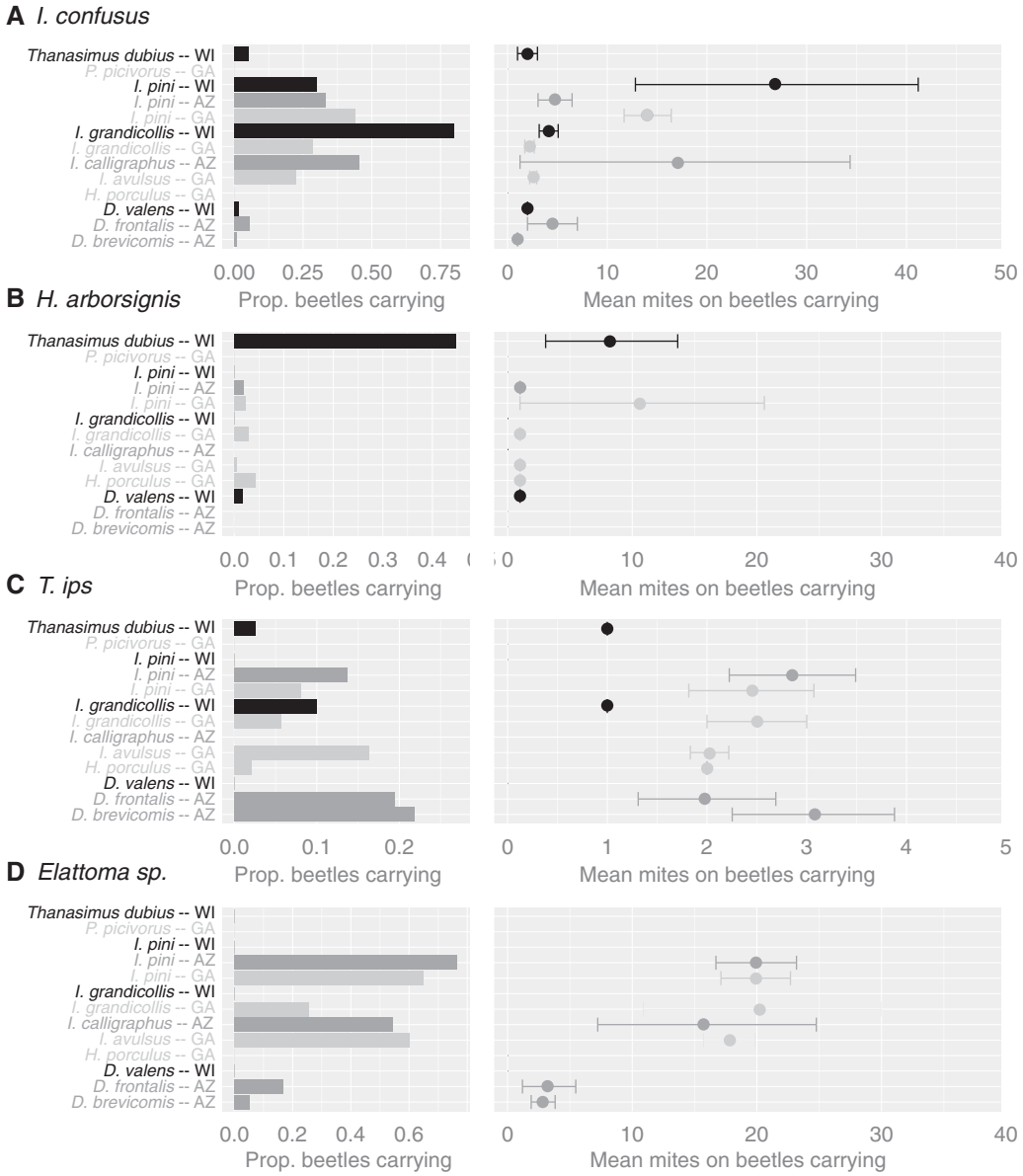

Fig. 5. Proportions of *T. dubius* (WI), *Pa. picivorus* (GA), *Ip. pini* (WI, AZ, GA), *Ip. grandicollis* (WI, GA), *Ip. calligraphus* (AZ), *Ip. avulsus* (GA), *Hy. porculus* (GA), *De. valens* (WI), *De. frontalis* (AZ), and *De. brevicomis* (AZ)) carrying phoretic mites, and mean number of mites on mite-carrying beetles A) *I. confusus*, B) *H. arborsignis*, C) *Ta. ips*, D) *Elattoma* sp., E) *Histiostoma* spp., F) *Tr. australis*, G) *D. quadrisetus*, and H) *Proctolaelaps* sp. Beetle species represented by fewer than 10 samples and mite species found fewer than 40 times are not presented.

variation in phoretic mite communities previously studied on *Ip. pini* among red pine sites across Wisconsin (Pfammatter et al. 2013).

The limited species richness of phoretic mite communities likely reflects the specificity of the recently dead pine habitat shared among the sampled beetle species. We might expect to encounter additional phoretic mites within a region on subcortical beetles associated with distantly related trees. For example, mite communities associated with the elm-colonizing *Scolytus multistriatus* (Marsham) are somewhat different than those obtained in our study, including species from the genera *Chelacheles* and *Pseudotarsonemoides* (Moser et al. 2005). Even across these widely separated plant genera, however, there are overlapping species such as *Elattoma* sp., *Proctolaelaps* spp., and *Trichouropoda*. Crossover of these species might occur in mixed hardwood–conifer forests. Mites such as *Proctolaelaps* spp. move quite rapidly within trees while in their tree-associated stage (personal observation) and could possibly travel between trees that have fallen over one another. Some species such as *Hi. varia* are also found commonly across many beetle and habitat groups (Woodring and Moser 1970, Houck and O'Connor 1991), and may move unassisted across the forest floor. We found *Hi. varia* at a rate of 1 mite per liter of soil in 5% of duff samples in healthy red pine sites (Pfammatter 2015). It is possible that *Hi. varia* feeds and reproduces in these leaf litter habitats in addition to dispersing. We found no evidence of any of the other mites phoretically associated with beetles outside of degrading tree or host beetle environments.

At least two factors hinder our understanding of phoretic mite–bark beetle systems and delineate needs for future studies. First, interactions between phoretic mites and bark beetles are most easily studied during the phoretic stage. Studies within tree habitat have

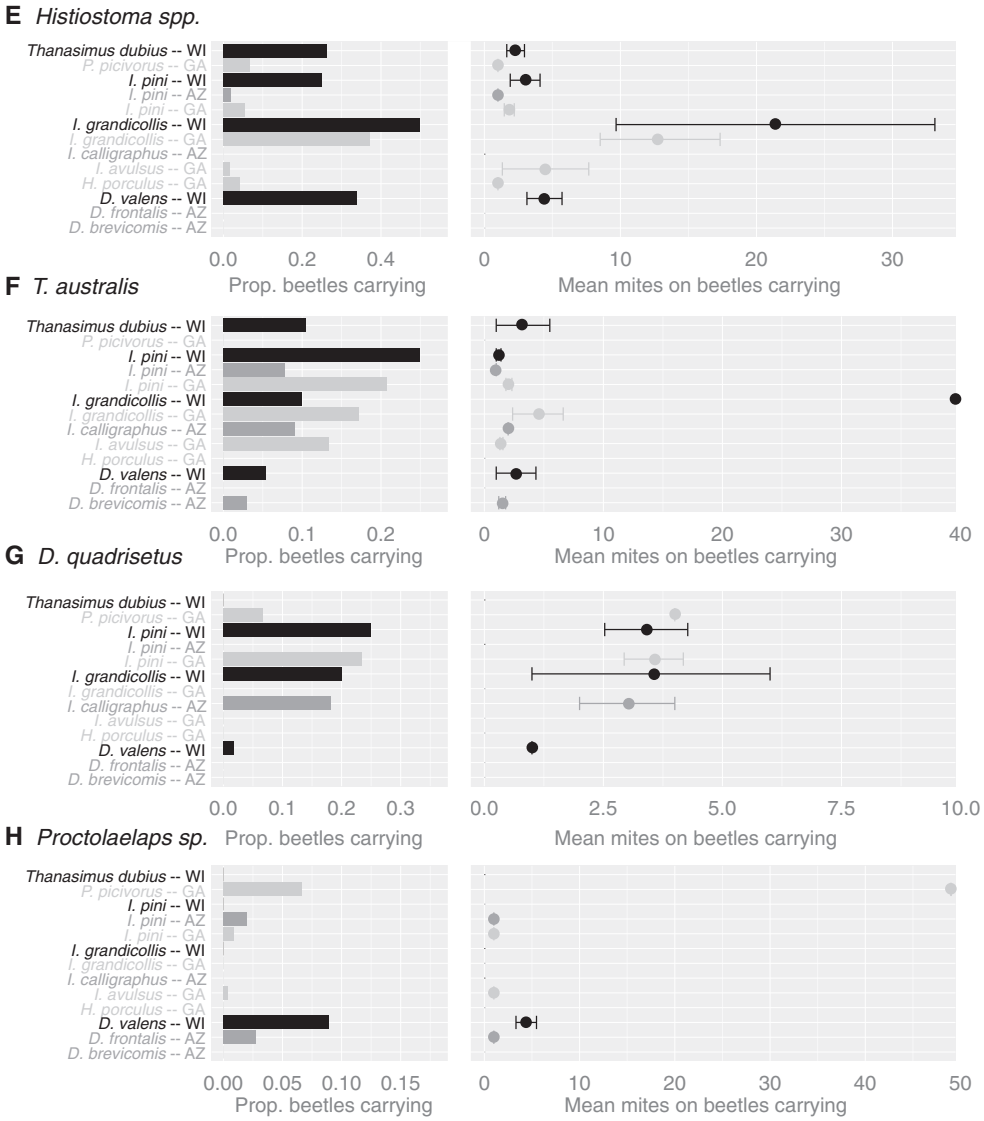

Fig. 5. Continued

Table 3. Poisson model estimates, *P* values for regional comparisons of the abundances of individual mites species on *Ip. pini* and *Ip. Grandicollis*, and pairwise post hoc Tukey test *P* values for models of mite abundances on *Ip. pini*

Beetle species	Mite species	Model estimates (mean mites per beetle)			*P* values			
		AZ	GA	WI	Overall	GA – AZ	WI – AZ	WI – GA
Ips pini	*Iponemus confusus*	6.20	1.59	8.1	<0.001	<0.001	0.004	<0.001
	Histiogaster arborsignis	0.24	0.02	0	<0.001	0.025	1	1
	Tarsonemus ips	0.20	0.39	0	0.001	0.023	1	1
	Elattoma sp.	12.91	15.26	0	<0.001	<0.001	0.994	0.994
	Histiostoma spp.	0.10	0.02	0.75	<0.001	0.233	<0.001	0.001
	Ereynetes propescutulis	0.13	0.08	0	0.067	0.608	1	1
	Trichouropoda australis	0.43	0.08	0.3	<0.001	0.003	0.665	0.089
	Dendrolaelaps quadrisetus	0.83	0	0.85	<0.001	0.999	0.996	0.999
Ips grandicollis	*Iponemus confusus*	–	0.63	3.3	–	–	–	<0.001
	Elattoma sp.	–	5.36	0	–	–	–	<0.001
	Histiostoma spp.	–	4.8	10.7	–	–	–	<0.001
	Trichouropoda australis	–	0.77	4.00	–	–	–	<0.001
	Dendrolaelaps quadrisetus	–	0	0.7	–	–	–	<0.001

Mite species occurring fewer than 10 times on *Ips* spp. were removed from model consideration.

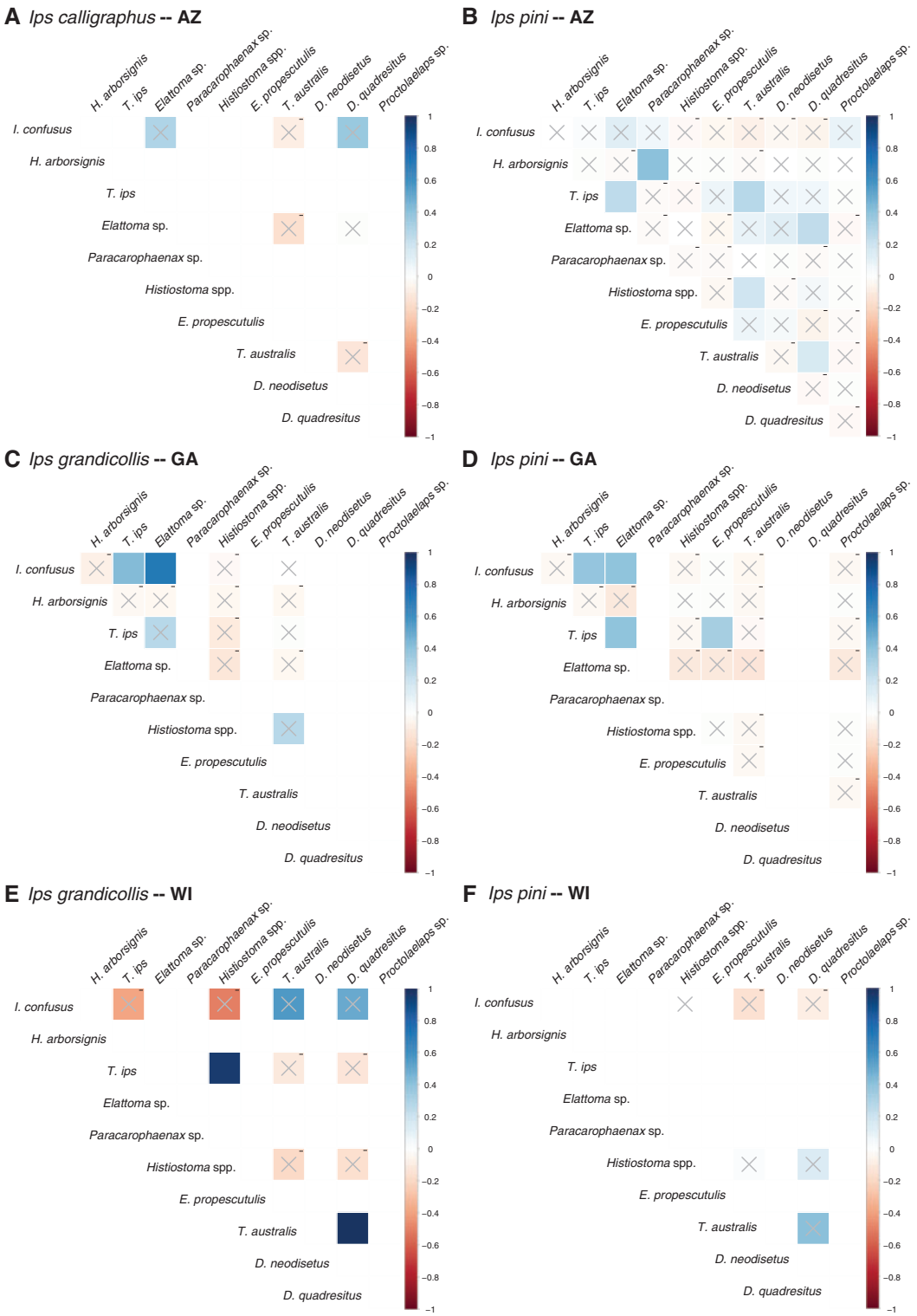

Fig. 6. Colorimetric visualizations of Pearson correlations for paired mite species phoretic on A) *Ip. calligraphus* – AZ, B) *Ip. pini* – AZ, C) *Ip. grandicollis* – GA, D) *Ip. pini* – GA, E) *Ip. grandicollis* – WI, F) *Ip. pini* – WI, G) *De. brevicomis* – AZ, H) *De. frontalis* – AZ, I) *Hy. porculus* – GA, J) *Ip. avulsus* – GA, K) *Pa. picivorus* – GA, and L) *T. dubius* – WI. Correlations closer to 1 or negative 1 are indicated by the darker saturation of blue (positive) or red (negative). Negative associations are also indicated by a negative sign in the upper right corner of each negatively correlated matrix cell. Insignificant correlations are marked with an X.

provided new insight into the formation of patterns of phoretic mite–bark beetle associations (Aflitto et al. 2014), but more work is necessary to aid in further elucidating of these relationships. Second, some species identifications of mites are extremely difficult owing to the relatively understudied nature of this group's taxonomy. A recent study involving molecular analysis of mites phoretically associated with *Nicrophorus* burying beetles found that *Uroobovella nova* (Oudemans) includes at least five morphologically cryptic

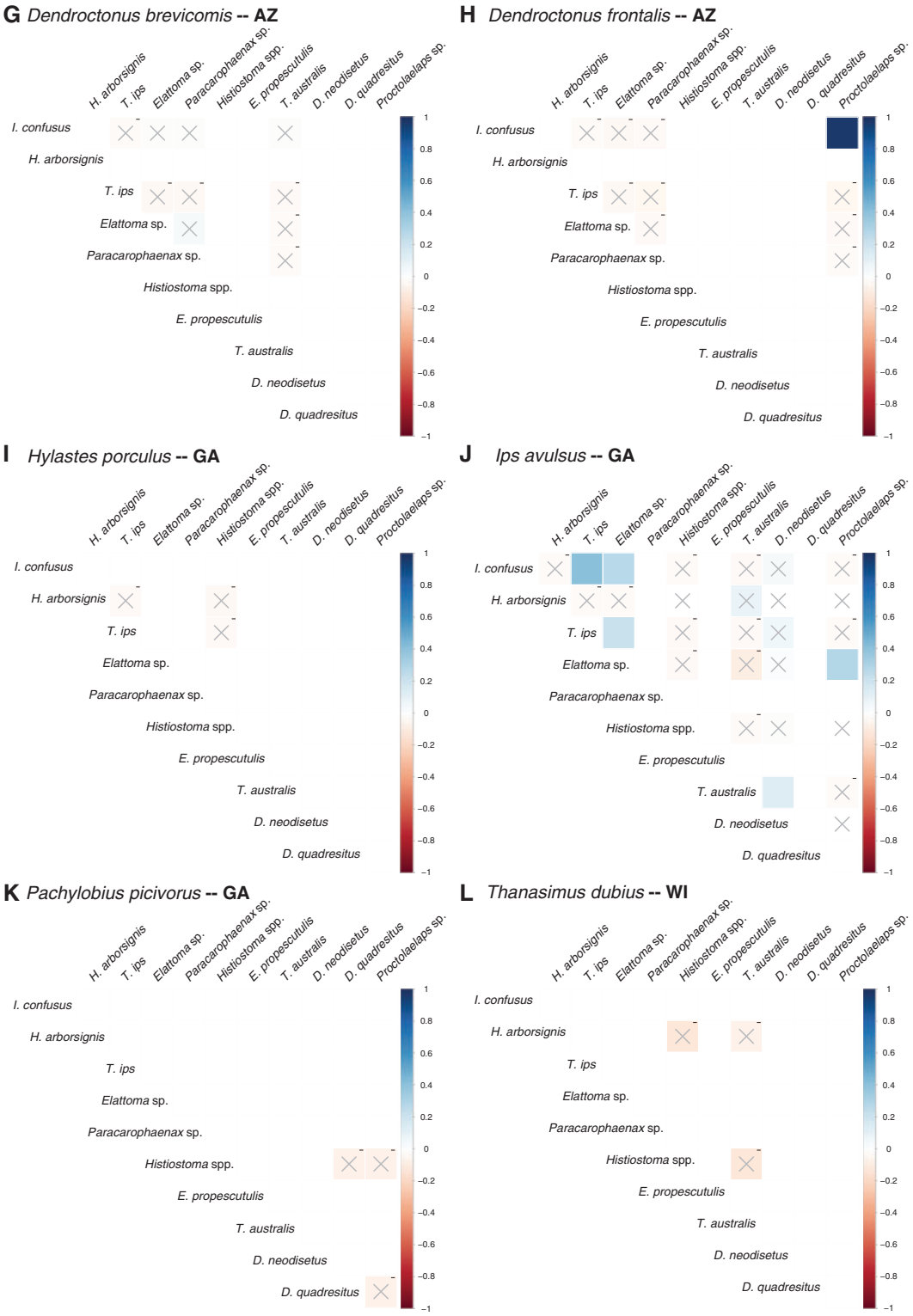

Fig. 6. Continued

species (Knee et al. 2012). Further development of molecular identification methods applicable to rapid identification of individual mites could greatly facilitate ecologically oriented studies.

Overall, our findings suggest that highly specific paired relationships may be relatively uncommon between bark beetle and phoretic mites in pine systems. Perhaps the high diversity of bark beetle species, subcortical habitat, and associated insects within these study locations contribute to the lack of strong and specific mite–beetle associations. Most of these mites are likely habitat specific rather than beetle specific. As a result, mites likely maximize reproduction and development within trees for as long as favorable breeding conditions persist (Binns 1982), and proceed to attach nonspecifically to

a broad range of departing beetle species across a relatively long timescale of beetle–tree interactions.

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John Moser not only coauthored this paper but also provided the foundation on which it was built through his decades of groundbreaking work on phoretic mites. He passed the day after its acceptance. Kurt Steele (Oconee NF, USFS) and William Lott (D.B. Warnell School of Forestry and Natural Resources, UGA) helped select sites in Georgia. Nicholas Aflitto (Northern Arizona University); Courtney Brissey and Kris Smoot (D.B. Warnell School of Forestry and Natural Resources, UGA); and Nichole Boyea, Lukas Brown, Stephanie Jagemann, Kareem Malas, and Thomas Olson (University of Wisconsin–Madison) assisted with field operations, sample preparation, and beetle identification. Claudio Gratton, Tony Ives, John Orrock, and Dan Mahr (University of Wisconsin-Madison) provided helpful reviews. This work was supported by McIntire-Stennis WIS01430 and the University of Wisconsin–Madison College of Agricultural and Life Sciences. Comments by three anonymous reviewers improved our manuscript.

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