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Patterns in the occurrence of saprophytic fungi carried by arthropods caught in traps baited with rotted wood and dung

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Abstract: Fungi from approximately 1700 individual arthropods that had been captured in traps set in aspen-dominated woodland in western Canada and baited with coyote dung, moose dung, white-rotted wood, brown-rotted wood and fiberglass were isolated in pure culture and identified. These data were analysed with principal components analysis (PCA) to determine whether different types of substrate attracted specific arthropods and whether these animals carried unique assemblages of fungi with known proclivities for the new habitat. Mycobiotic agar was used to restrict the numbers of fungi isolated and resulted in the recovery of 1687 isolates representing 65 species across 12 orders. Isolates of cosmopolitan fungal taxa such as species of *Cladosporium*, *Penicillium*, and *Beauveria* were the most numerous. Taxa with predilections for specific substrates, such as *Myxotrichum* and *Cryptendoxyla* that are known inhabitants of cellulose-rich materials (i.e. rotted wood), and various representatives of the keratinophilic Onygenales were recovered from arthropods attracted respectively to baits rich in cellulose and keratin. When traps were analysed according to the identity and numbers of arthropods captured, there was considerable overlap among clusters representing specific bait types, with traps baited with coyote dung being the most divergent partly because they captured significantly more arthropods than those baited with moose dung or rotted wood. When bait type was examined according to the identity and numbers of fungi on trapped arthropods the degree of overlap was also high although a few trends could be discerned. In particular traps baited with brown-rotted wood and coyote dung diverged slightly indicating that arthropods visiting these bait types were carrying somewhat different suites of fungi.

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INTRODUCTION

The numbers and diversity of arthropods associated with decaying wood and dung suggest that these animals would carry on the surface of their bodies not only a wide range of ubiquitous saprobic fungi but also specific groups of more specialized taxa associated with the breakdown of these materials. There are few data available supporting this hypothesis although it is well known that mycangial arthropods (e.g. wood wasps and bark beetles) are involved in the transfer of specific fungi from substrate to substrate (Slippers et al 2000, Levieux et al 1989) and that others carry specific plant pathogenic fungi from one host to another (e.g. *Ophiostoma ulmi* carried by bark beetles in Dutch elm disease, agents of blue stain, etc.) (Harrington 1993, Jacobs and Wingfield 2001). Some investigators have isolated and identified fungi on the bodies of specific types of arthropods, including springtails from soils (Visser et al 1987, Christen 1975), mites (Renker et al 2005), wasps (Gambino and Thomas 1988), beetles (Haberkern et al 2002) and termites (Zoberi and Grace 1990) from wood and show that arthropods, removed or emerging from a given sample, are carrying propagules of the fungi involved in the decomposition of the main constituents of that sample (Talbot 1952). It is not known whether these saprobic fungi are effectively transmitted to new substrates or if their transmission to appropriate new substrates by arthropod carriers is anything more than a purely random process.

To test the hypothesis that arthropod taxa carry unique sets of saprobic fungi to different substrates, we set up a series of traps, baited with either decaying wood or dung, in relatively undisturbed woodland. Trapped arthropods and adhering, filamentous fungi that were isolated in pure culture were both identified. Using principal components analyses of the resulting taxonomic and numerical data, we searched for patterns in the relationship, first between arthropod taxa and bait type and second between the fungal taxa being carried on the body surface of these animals and the bait to which they had been attracted.

MATERIALS AND METHODS

Arthropods were collected May—Aug 2002 and 2003 with baited traps set in a southern boreal mixed wood forest dominated by *Populus tremuloides* Michx. and located 100 km east of Edmonton, Alberta. Traps consisted of 5 L plastic pails with a pair of holes, 2.2 cm diam, cut approximately 11 cm from the bottom and on opposite sides. The neck of the top 10 cm portion of a plastic 2 L plastic pop bottle was fitted into each hole and fastened in place to form a funnel that opened into the pail. The interior surface of the lid and the top third of the interior walls of each pail were coated with Fluon™ (AGC Chemicals Americas Inc., Bayonne, New Jersey) to prevent arthropods from crawling out of the trap.

Forty traps were prepared; 10 each were baited with moose (herbivore) dung, coyote (carnivore) dung, white-rotted wood or brown-rotted wood, all previously collected as fresh samples from the study site and kept frozen until needed. Three additional traps were baited with moistened fiberglass. Each bait sample was placed in the bottom half of a plastic Petri plate that formed the floor of a 9 × 9 × 9 cm cage constructed of 1 mm diameter bailing wire. To prevent trapped arthropods from coming into contact with the bait, and picking up fungi developing on it, the cage was covered with nylon fabric (mesh size 0.3–0.5 mm) and suspended from a hook on the inside of the lid of the pail.

Traps were placed on the ground and fastened with wire to nearby trees. Nine groups of traps were placed approximately 100 m apart along a 1 km trail. Each group consisted of 4–7 traps positioned 4–5 m from its neighbor. Baits were remoistened with sterile water 2 wk later and replaced with fresh material monthly. Captured arthropods were removed once a week and placed in sterile, 64 mL plastic vials for transport to the laboratory.

Arthropods were stored at 4 C until examined individually under a dissecting microscope, within 24–36 h of collection, for evidence of attachment of fungal propagules. Using sterile insect forceps (Bioquip Products Inc., Rancho Dominguez, California), arthropods either were rolled or, if small or delicate, flipped end-over-end across the surface of a single Petri plate of Mycobiotic™ agar (35.6 g Mycobiotic agar (BD, Oakville, Ontario) and 1 L dH_2O). This medium contains 0.05 g/L chloramphenicol to suppress bacterial growth and 0.5 g/L cycloheximide, a fungal inhibitor that slows or prevents the growth of common aggressive species and allows detection of slower growing taxa. Arthropod specimens were identified, at least to order, and those that did not disintegrate during streaking were stored in 70% ethanol-5% glycerine solution and deposited in the Strickland Insect Collection at the University of Alberta. Fungal vouchers were deposited as permanent slides in the University of Alberta Cryptogamic Herbarium (ALTA) or as living cultures in the University of Alberta Microfungus Collection and Herbarium (UAMH).

Plates were incubated 4–6 mo at room temperature and under ambient light and examined regularly for fungal growth. Colonies from primary isolation plates were transferred to cornmeal agar (CMA, 17g Acumedia™ cornmeal media (Neogen Corp., Lansing, Michigan) and 1 L dH_2O incubated under ambient light at room temperature, and identified with morphological criteria.

Data from both years of collection were combined and principal components analyses were conducted with PC-ORD 4.0 (MJM software design, Gleneden Beach, Oregon) with the variance/covariance (centered) option selected for the cross product matrix. The first analysis compared bait types with the number and identity of arthropod orders caught in each trap as variables (note that ants, Hymenoptera: Formicidae, and all unidentified arthropods each were treated as a separate order). The second analysis compared bait types using the number and identity of fungal species isolated from arthropods retrieved from each trap as variables. From the resulting point swarms, the pair of orthogonal axes accounting for the maximum linear variation was determined. The effect of trap location on arthropods recovered and fungi isolated (i.e. among the nine groups) was determined by PCA to be negligible and is not considered further.

RESULTS

Over the 2 y period 1696 arthropods were captured and most were identified at least to order (TABLE I). Direct observation with a dissecting microscope of the scant amounts of debris adhering to their surface was insufficient to distinguish and identify fungal propagules, but 1687 isolates of filamentous fungi representing at least 65 species were recovered as pure cultures from streaks made with 1068 arthropod specimens (TABLE II). Fungal taxa were scored once per primary isolation plate regardless of the number of colonies that had formed. Yeasts and bacteria were discarded. The majority (81.7%) of isolates was represented by species of *Cladosporium, Beauveria, Penicillium* and *Verticillium*. Species of *Acremonium, Geomyces, Leptographium* and *Paecilomyces* made up an additional 10.1%, and 35 species in 23 other genera made up the remaining 8.2% (TABLE II). Most fungi were Hyphomycetes with ascomycetous affinities. Eight of these formed ascomata and were identified with a teleomorph name. The Zygomycota was represented by five species. Filamentous basidiomycetes were not isolated. There was a linear relationship between numbers of arthropods captured per taxon and numbers of fungal isolates recovered ($R^2 = 0.9593$, $P < 0.0001$) (FIG. 1) and a logarithmic relationship between number of arthropods captured per taxon and number of fungal species recovered ($R^2 = 0.923$, $P < 0.0001$) (FIG. 2).

The average number of arthropods caught was lowest in May and highest in July although exceptions occurred with beetles, and butterflies and moths, whose numbers peaked in June, and harvestermen, whose numbers peaked in August. On average over

TABLE I. Total numbers of arthropods per taxon (i.e. 12 orders, with the Formicidae and unknowns each treated as a separate order) captured in traps baited with five different materials

	Coyote dung	Moose dung	Brown-rotted wood	White-rotted wood	Fiberglass	Total
Acari (Mites)	55	29	35	50	15	184
Araneae (Spiders)	78	67	92	94	38	369
Coleoptera (Beetles)	79	20	44	20	11	174
Collembola (Springtails)	9	0	16	15	2	42
Diptera (Flies)	171	138	82	83	23	497
Hemiptera (Bugs)	32	35	24	13	7	111
Hymenoptera (Bees and Wasps)	10	4	12	11	3	40
Hymenoptera: Formicidae (Ants)	79	50	43	11	11	194
Lepidoptera (Butterflies and Moths)	19	7	10	5	4	45
Neuroptera (Lacewings)	1	0	1	3	0	5
Opilione (Harvestermen)	1	5	3	1	0	10
Pscoptera (Booklice)	2	1	3	3	0	9
Trichoptera (Caddisflies)	1	0	1	1	0	3
Unknown	5	1	4	2	1	13
	542	357	370	312	115	1696

the sampling period, traps baited with moose dung, brown-rotted wood, white-rotted wood and fiberglass attracted 31–37 arthropods per trap and coyote dung 54 arthropods per trap. The coyote dung, brown-rotted wood and white-rotted wood attracted representatives from all 13 orders of arthropods recorded. Traps baited with moose dung and fiberglass each attracted arthropods representing 10 and 9 orders respectively (TABLE I).

Traps baited with coyote dung attracted arthropods that yielded 476 fungal isolates representing 45 species in eight orders; nine fungal taxa were unique to this group. Arthropods from traps baited with brown-rotted wood yielded 392 fungal isolates representing 38 species in eight orders. Three of these species were unique. Traps baited with white-rotted wood attracted arthropods that yielded 361 fungal isolates representing 34 species in six orders. Three species in this group were unique to traps with this bait type. From traps baited with moose dung, arthropods yielded 352 fungal isolates representing 39 species in eight orders; five of these species were unique. The traps baited with fiberglass yielded 106 fungal isolates representing 25 species in six orders. Only one species was unique to the fiberglass baited traps (TABLE III).

An examination of the broken-stick eigenvalues obtained from the first PCA (bait type vs. number and type of arthropod) showed that the first four axes were significant, accounting for 88.9% of total variation, with axis 1 (representing number of captures of each taxon) accounting for 46.4% of the variation, and axis 2 (representing the taxonomic richness of the captured arthropods) representing 19%. Axes 3 and 4 were significant at 12.8% and 10.6% but were not considered further. Plotting data along the first two axes resulted in the majority of points representing traps baited with coyote dung and moose dung positioned to the left of the origin and points representing traps baited with both types of decayed wood mostly to the right (FIG. 3). Traps baited with white-rotted wood fell closely together to form a cluster lying below the origin of axis 2. One trap baited with coyote dung appeared as an outlier to the left of the main cluster; it had the most flies, mites and caddis flies for this bait type. One trap baited with moose dung also was positioned far to the left and had a much higher number of beetles than other traps with this bait (FIG. 3).

An examination of the broken-stick eigenvalues obtained from the second PCA analysis (i.e. bait type vs. number and identity of fungal isolates) showed that the first five axes were significant and accounted for 80.6% of variation, with axis 1 (representing the number of isolates of each species) accounting for 44.8% of the variation, and axis 2 (representing the taxonomic richness of the isolated species) accounting for 15.6%. Axes 3, 4 and 5 were significant but accounted for only 9.7%, 6.1% and 4.2% of total variation respectively and were not considered further. Plotting data along the first two axes resulted in points representing all but one trap baited with each of coyote dung, moose dung, brown-rotted wood, and white-rotted wood positioned in a loose central cluster around the origin (FIG. 4). Seven of the traps baited with coyote dung were to the right of the origin while the majority of traps baited with moose dung (7 of 10) and white-rotted wood (7 of 10) were to the left

TABLE II. Identity and numbers of fungi isolated from each arthropod taxon over the 2 y trapping period

	Acari	Araneae	Coleoptera	Collembola	Diptera	Hemiptera	Hymenoptera	Hymenoptera: Formicidae	Lepidoptera	Neuroptera	Opilione	Pscoptera	Trichoptera	Unknown	total
Absidia corymbifera	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Absidia glauca	4	0	2	0	2	0	3	5	0	0	0	0	0	0	16
Acremonium butyri	0	1	0	1	4	0	0	0	0	0	0	0	0	0	6
Acremonium fusidioides	1	3	0	0	5	0	0	1	0	0	0	0	0	0	10
Acremonium kiliense	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2
Acremonium longisporum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Acremonium strictum	2	8	0	0	11	2	0	0	1	0	0	0	0	0	24
Arthroderma curreyi	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Arthroderma sp. I	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3
Auxarthron compactum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Auxarthron conjugatum	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
Alternaria alternata	3	0	4	0	5	0	0	3	2	0	0	0	0	0	17
Aphanocladium aranearum	0	0	0	0	5	0	0	0	0	0	0	0	0	0	5
Aspergillus candidus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Aspergillus fumigatus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Beauveria bassiana	47	120	47	8	103	19	10	45	22	2	5	1	0	0	429
Ceratocystis sp. I	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Chalara fusidioides	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Chalara sp. I	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Cladosporium cladosporioides	35	93	34	3	136	33	11	41	20	2	3	2	1	1	415
Cladosporium sphaerospermum	19	28	6	1	38	6	6	9	2	1	1	0	0	1	118
Cladosporium herbarum	1	0	0	0	1	0	0	1	0	0	0	0	0	0	3
Cladosporium orchidis	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2
Conidiobolus coronatus	0	1	0	0	2	0	0	0	0	0	0	0	0	0	3
Cryptendoxyla hypophloia	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2
Chrysosporium merdarium	0	0	1	0	1	1	0	0	0	0	0	0	0	0	3
Eupenicillium brefeldianum	1	2	1	0	5	1	1	3	1	0	0	0	0	0	15
Fusarium cf. *solani*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Geomyces pannorus	2	4	7	1	10	2	0	11	2	1	0	0	0	0	40
Gliocladium cf. *penicillioides*	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2
Hormiactis candida	0	2	0	1	0	0	0	1	0	0	0	0	0	1	5
Leptographium piriforme	3	3	5	1	4	2	0	7	2	0	0	1	1	0	29
Mucor hiemalis	0	2	1	0	12	1	0	1	0	0	0	0	1	0	18
Myxotrichum deflexum	0	1	0	0	0	0	0	1	0	0	0	0	0	0	2
Oidiodendron griseum	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2
Oidiodendron maius	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Oidiodendron periconioides	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Oidiodendron state of *Myxotrichum arcticum*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Paecilomyces farinosus	7	4	1	0	7	2	0	2	3	1	0	0	0	0	27
Paecilomyces fumosoroseus	2	0	0	0	1	1	0	1	0	0	0	0	0	0	5
Paecilomyces marquandii	7	6	1	0	6	1	1	2	2	0	0	0	0	1	27
Penicillium cf. *brevicompactum*	9	12	7	1	23	3	0	6	4	0	0	0	1	1	67
Penicillium cf. *frequetans*	0	0	1	0	0	0	1	0	0	0	0	0	0	0	2
Penicillium cf. *griseofulvum*	1	1	0	0	1	0	0	1	0	0	0	0	0	0	4
Penicillium cf. *implicatum*	1	1	0	1	3	0	0	2	0	0	0	0	0	0	8
Penicillium cf. *inflatum*	0	1	0	0	0	0	0	1	0	0	0	0	0	0	2
Penicillium cf. *janthinellum*	0	1	0	0	3	0	1	1	1	0	0	0	0	0	7
Penicillium raistrickii	1	1	4	0	1	0	0	0	0	0	0	0	0	0	7
Penicillium restrictum	0	1	0	0	3	0	0	0	0	0	0	0	0	0	4
Penicillium cf. *rubrum*	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2

TABLE II. Continued

	Acari	Araneae	Coleoptera	Collembola	Diptera	Hemiptera	Hymenoptera	Hymenoptera: Formicidae	Lepidoptera	Neuroptera	Opilione	Pscoptera	Trichoptera	Unknown	total
Penicillium cf. *steckii*	10	23	11	3	35	6	5	5	2	0	0	0	0	0	100
Penicillium sp. I	5	3	0	0	3	0	1	0	0	1	0	0	0	0	13
Penicillium sp. II	5	11	6	0	10	1	0	8	1	0	0	0	0	1	43
Phialophora americana	1	0	1	0	4	1	1	2	1	0	0	0	0	0	11
Polyscytalum pustulans	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Ramichloridium schulzeri	1	2	0	0	0	1	0	1	0	0	0	0	0	0	5
Rhizopus stolonifer	1	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Sagenomella diversispora	1	0	0	0	1	0	0	1	0	0	0	0	0	0	3
Scopulariopsis brevicaulis	0	3	0	0	0	1	0	1	0	0	0	0	0	0	5
Veronaea carlinae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Veronaea indica	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Veronaea parvispora	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Verticillium lamellicola	6	12	1	0	24	1	1	4	4	0	0	0	0	0	53
Verticillium lecanii	12	12	3	3	25	4	1	7	3	1	1	0	0	0	72
Verticillium psalliotae	4	4	0	4	8	1	3	3	0	0	0	0	0	0	27
Total isolates	193	369	152	33	510	94	46	181	76	9	10	4	4	6	1687
Total species	28	33	25	15	41	25	14	33	20	7	4	3	4	6	

(FIG. 4). Eight of 10 traps baited with brown-rotted wood formed a tight cluster just below axis 2 with a majority of these traps located to the left of the origin. Among traps baited with coyote dung the most distant outlier in the lower right hand quadrant had exceptionally high numbers of isolates of species of *Beauveria, Penicillium*, and *Verticillium*. The outlier among traps baited with moose dung had the highest number of fungal isolates for this bait as well as the highest number of isolates of *Beauveria bassiana, Cladosporium cladosporioides*, and *Verticillium lamellicola*. It also yielded the only isolates of *Scopulariopsis brevicaulis* and *V. psalliotae* for this bait type. The outlier for the traps baited with brown-rotted wood had the most isolates of species of *Cladosporium* in addition to the only isolates of species of *Cryptendoxyla, Oidiodendron* and *Rhizopus* recovered from traps with this bait type. The outlier for the traps baited with white-rotted wood had the highest number of isolates of *Hormiactis candida, Penicillium* cf. *steckii* and *Verticillium lamellicola* as well as the only isolates of *Mucor heimalis* and *P.* cf. *griseofulvum* for this bait type. The three traps baited with moistened fiberglass were close to the origin in both analyses (FIGS. 3–4).

DISCUSSION

The objective of this study was to test the hypothesis that arthropods associated with different types of decaying wood and dung carry and potentially deliver specific groups of saprophytic fungi that are associated with the breakdown of these materials. This hypothesis would be supported by finding fungal taxa with known predilections for cellulose and lignocellulose on arthropods caught in traps baited with decayed wood and moose dung, and fungal taxa with predilections for keratin on the arthropods caught in traps baited with coyote dung. Although each of the baits had a preponderance of the native forms of these complex macromolecules, they also contained many other substances that could affect the types of arthropods lured into the traps. In addition the unavoidable isolation of ubiquitous fungal taxa from trapped arthropods ostensibly created some level of ''background noise'' that reduced the resolution of the analyses. Nevertheless several patterns emerged from our observations and analyses that provide some support, albeit weak, for the initial hypothesis.

We were unable to recognize fungal propagules on the surface of the captured arthropods but the isolation data show that a diverse range of viable fungi was being transported into the traps. The trapped microfauna are thus dispersal agents for the species of fungi they were carrying (Dowd 1998). The linear relationship between the number of fungal isolates recovered and the numbers of arthropods collected and the logarithmic relationship between fungal species and arthropods recovered indicate that

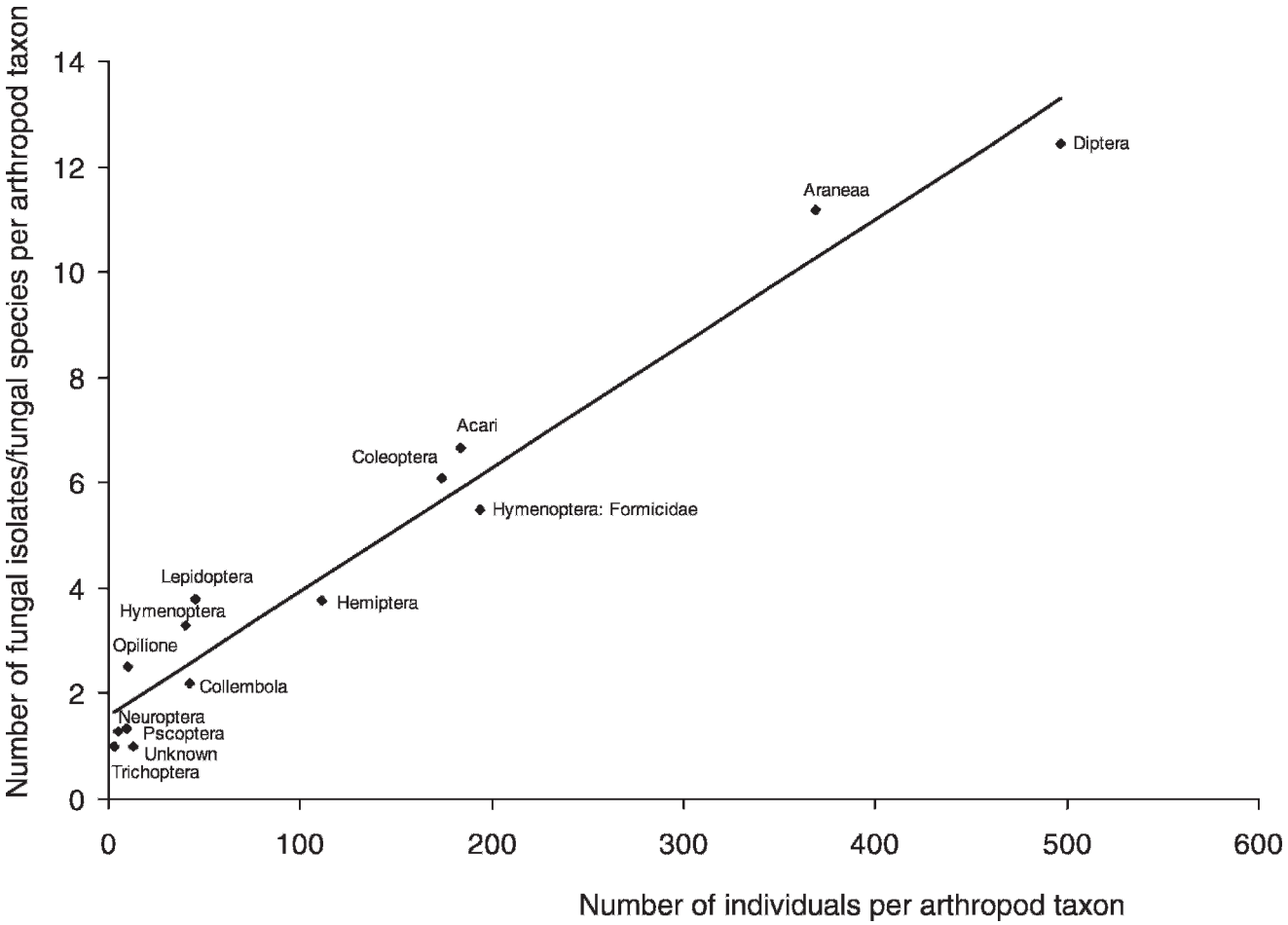

FIG. 1. Number of fungal isolates (corrected for number of species) per arthropod taxon.

continued trapping and isolating with our culturing protocol would be expected to yield greater numbers of isolates but diminishing numbers of new fungal species (FIGS. 1–2).

As anticipated most fungi isolated were ubiquitous taxa; 81.7% were species of *Beauveria, Verticillium, Cladosporium* and *Penicillium*, all versatile saprobes and prolific spore producers. The entomopathogen *Beauveria bassiana* represented one-quarter of all isolates and was frequent on mites, beetles, flies and ants and was particularly abundant on spiders. Species of *Verticillium* (*V. lamellicola, V. lecanii* and *V. psalliotae*) were most abundant on flies and spiders and, like *B. bassiana*, were evenly distributed across bait types. The abundant recovery of entomopathogenic species across multiple taxa and from presumably healthy specimens suggests that these fungi are common components of the surface mycota of these animals and are not restricted to specimens exhibiting obvious signs of mycosis.

Species of *Cladosporium* and *Penicillium* together accounted for 47% of all isolates. *Cladosporium cladosporioides* was the most common, representing 77% of isolates in the genus. Its distribution was similar to *B. bassiana*, being most common on mites, spiders, beetles, flies, ants and bugs. These observations are similar to reports concerning the prevalence of *C. cladosporioides* on arthropods (Visser et al 1987, Pherson and Beattie 1979, Senna Nunes Sales et al 2002, Zoberi and Grace 1990, Martin et al 1987, Reddersen 1995). Species of *Penicillium* comprised 17% of all isolates and, although abundant on arthropods attracted to all bait types, almost half of all isolates came from flies and spiders, the two most abundant arthropod groups recovered. *Penicillium* cf. *steckii* was the most common, representing 35% of isolates in this genus. *Penicillium* species are a common component of the mycoflora isolated from arthropods (Visser et al 1987, Pherson and Beattie 1979, Senna Nunes Sales et al 2002, Zoberi and Grace 1990, Martin et al 1987, Gambino and Thomas 1988). *Cladosporium* and *Penicillium* are also among the most common fungi isolated during surveys of airborne fungi (Airaudi and Marchisio 1996, Marchisio et al 1993, Calvo et al 1982).

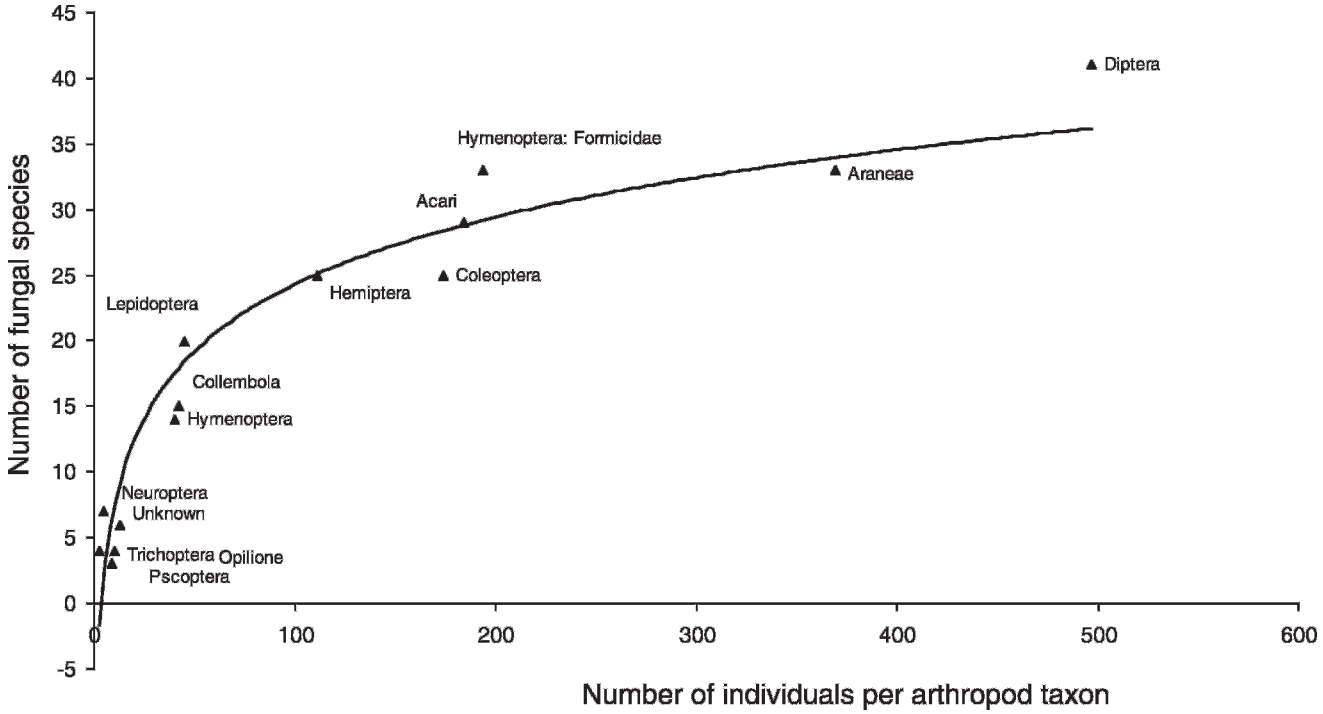

FIG. 2. Number of fungal species recovered from each arthropod taxon.

Some ubiquitous hyphomycete taxa (i.e. *Alternaria, Fusarium, Gliocladium* and *Scopulariopsis*) and zygomycete taxa (i.e. *Absidia corymbifera, A. glauca, Mucor hiemalis* and *Rhizopus stolonifer*) were recovered in remarkably small numbers. These 62 isolates (4% of total) were fewer than expected considering their usual high frequencies in soil and among airborne spores (Keller and Bidochka 1998, Franca and Caretta 1984). Some intolerance to cycloheximide might partly explain this observation for some taxa, such as species of *Mucor* and *Rhizopus*, but *Scopulariopsis, Alternaria* and *Fusarium* are cycloheximide resistant and also common components of the airborne mycoflora (Franca and Caretta 1984, Airudi and Marchisio 1996, Marchisio et al 1993, Calvo et al 1982). These fungi all are common saprobes on decaying herbaceous plant materials (Loiveke et al 2004, Ioos et al 2004) and might have been excluded partially by arthropods that are associated with or attracted to rotted wood and dung. Higher frequencies for these taxa might have been obtained if a set of traps had been baited with decaying herbaceous plant material.

In contrast to these records were less frequently isolated taxa with more specific habitat preferences that are uncommon in surveys of airborne fungi (Airudi and Marchisio 1996, Marchisio et al 1993, Calvo et al 1982) and have a presumed reliance on animals for dispersal. These include isolates in the Onygenales (species of *Auxarthron, Arthroderma* and *Chrysosporium*) and Myxotrichaceae (species of *Geomyces, Oidiodendron* and *Myxotrichum*), *Cryptendoxyla hypophloia, Leptographium piriforme, Conidiobolus coronatus* and species of *Chalara*.

The gymnothecial ascomata produced by many of the Arthrodermataceae, Onygenaceae (Onygenales) and Myxotrichaceae (Leotiales, incertae sedis) have a mesh-like peridial wall (reticuloperidium) that in vitro lets the setae of insects pass through the spaces between peridial hyphae, causing the ascospores to cling to the body of the arthropod (Greif and Currah 2003). Many of these taxa also produce dry, cylindrical arthroconidia which may adhere electrostatically to arthropod carriers. Gymnothecial fungi were obtained from 3.4% of the arthropods. The Arthrodermataceae has been reported previously from captured insects (Diptera) (Pinetti et al 1974, Gip and Svenson 1968), but these reports of the Onygenaceae and Myxotrichaceae from living arthropods are unique. Gymnothecial taxa tend to be poor competitors (Pugh 1963) and presumably rely primarily on direct substrate-to-substrate transfer to establish new colonies. The recovery here of 11 different gymnothecial species suggests their shared suite of reproductive characteristics is playing some role in their dispersal by arthropods. A similar targeted dispersal mechanism has been suggested for species of *Arthroderma, Ctenomyces* and their anamorphs (Onygenales) asso-

TABLE III. Number of isolates per fungal species from arthropods associated with each of five types of bait

Fungi	Bait type: Coyote dung	Moose dung	Brown-rotted wood	White-rotted wood	Fibreglass	Total
Absidia corymbifera (Cohn) Sacc. & Trotter	1	0	0	0	0	1
Absidia glauca Hagem	2	4	5	5	0	16
Acremonium butyri (J.F.H. Beyma) W. Gams	0	1	3	1	1	6
Acremonium fusidioides (Nicot) W. Gams	3	3	4	0	0	10
Acremonium kiliense Grütz	1	0	0	1	0	2
Acremonium longisporum (Preuss) W. Gams	1	0	0	0	0	1
Acremonium strictum W. Gams	6	7	4	5	2	24
Arthroderma curreyi Berk.	1	0	0	0	0	1
Arthroderma sp. I	2	0	0	0	1	3
Auxarthron compactum G.F. Orr & Plunkett	0	0	1	0	0	1
Auxarthron conjugatum (Kuehn) G.F. Orr & Kuehn	0	1	1	0	0	2
Alternaria alternata (Fr.) Keissl.	3	5	4	4	1	17
Aphanocladium aranearum (Petch) W. Gams	3	2	0	0	0	5
Aspergillus candidus Link	0	1	0	0	0	1
Aspergillus fumigatus Fresen.	0	0	0	1	0	1
Beauveria bassiana (Bals.-Criv.) Vuill.	124	95	102	83	25	429
Ceratocystis sp. I	1	0	0	0	0	1
Chalara fusidioides (Corda) Rabenh.	1	0	0	0	0	1
Chalara sp. I	0	2	0	0	0	2
Cladosporium cladosporioides (Fresen.) G.A. de Vries	119	96	84	89	27	415
Cladosporium sphaerospermum Penz.	35	20	27	30	6	118
Cladosporium herbarum (Pers.) Link	3	0	0	0	0	3
Cladosporium orchidis E.A. Ellis & M.B. Ellis	0	1	1	0	0	2
Conidiobolus coronatus (Costantin) A. Batko	2	1	0	0	0	3
Cryptendoxyla hypophloia Malloch & Cain	0	0	1	1	0	2
Chrysosporium merdarium (Ehrenb.) J.W. Carmich.	3	0	0	0	0	3
Eupenicillium brefeldianum (B.O. Dodge) Stolk & D.B.	3	6	3	3	0	15
Fusarium solani (Mart.) Sacc.	0	0	1	0	0	1
Geomyces pannorus (Link) Sigler & J.W. Carmichael	11	8	10	6	5	40
Gliocladium cf. *penicillioides* Corda	0	0	0	2	0	2
Hormiactis candida Höhn.	2	0	0	3	0	5
Leptographium piriforme	22	1	2	2	2	29
Mucor hiemalis Wehmer	8	3	3	2	2	18
Myxotrichum deflexum Berk.	1	0	0	0	1	2
Oidiodendron griseum Robak	1	0	1	0	0	2
Oidiodendron maius G.L. Barron	0	0	0	1	0	1
Oidiodendron periconioides Morrall	0	0	1	0	0	1
Oidiodendron state of *Myxotrichum arcticum* Udagawa, Uchiv. & Kamiva	0	1	0	0	0	1
Paecilomyces farinosus (Holmsk.) A.H.S. Br. & G. Sm.	10	6	7	2	2	27
Paecilomyces fumosoroseus (Wize) A.H.S. Br. & G. Sm.	1	0	0	2	2	5
Paecilomyces marquandii (Massee) S. Hughes	9	2	3	7	6	27
Penicillium cf. *brevicompactum* Dierckx	17	12	19	17	2	67
Penicillium cf. *frequetans* Westling	0	0	1	1	0	2
Penicillium cf. *griseofulvum* Dierckx	1	1	0	1	1	4
Penicillium cf. *implicatum* Biourge	0	1	5	2	0	8
Penicillium cf. *inflatum* Stolk & Malla	2	0	0	0	0	2
Penicillium cf. *janthinellum* Biourge	0	2	4	1	0	7
Penicillium raistrickii G. Sm.	3	1	1	2	0	7
Penicillium restrictum J.C. Gilman & E.V. Abbott	1	1	1	0	1	4
Penicillium cf. *rubrum* Sopp	1	0	0	0	1	2
Penicillium cf. *steckii* K.M. Zalessky	15	13	35	35	2	100
Penicillium sp. I	2	3	1	7	0	13
Penicillium sp. II	9	11	8	11	4	43

TABLE III. Continued

Fungi	Bait type: Coyote dung	Moose dung	Brown-rotted wood	White-rotted wood	Fibreglass	Total
Phialophora americana (Nannf.) S. Hughes	2	2	5	2	0	11
Polyscytalum pustulans (M.N. Owen & Wakef.) M.B. Ellis	1	0	0	0	0	1
Ramichloridium schulzeri (Sacc.) de Hoog	1	2	1	0	1	5
Rhizopus stolonifer (Ehrenb.) Vuill.	0	0	1	1	0	2
Sagenomella diversispora (J.F.H. Beyma) W. Gams	1	1	1	0	0	3
Scopulariopsis brevicaulis (Sacc.) Bainier	2	2	1	0	0	5
Veronaea carlinae M.B. Ellis	0	0	0	0	1	1
Veronaea indica (Subram.) M.B. Ellis	0	1	0	0	0	1
Veronaea parvispora M.B. Ellis	0	1	0	0	0	1
Verticillium lamellicola (F.E.V. Sm.) W. Gams	14	11	14	11	3	53
Verticillium lecanii (Zimm.) Viégas	16	20	16	15	5	72
Verticillium psalliotae Treschew	9	1	10	5	2	27
total	476	352	392	361	106	1687

ciated with birds and bird nests (Pugh 1965, Pugh and Evans 1970).

A majority of representatives of the Onygenaceae and Arthrodermataceae, both groups with known proclivities for keratin-rich substrates (Currah 1985), was isolated from arthropods attracted to the coyote dung, while species in the Myxotrichaceae, a group known primarily from cellulose-rich substrates, were isolated mostly from arthropods attracted to baits with ostensibly higher levels of cellulose (moose dung, brown- and white-rotted wood). Of 47 isolates representing the Myxotrichaceae, 60.7% were isolated from visitors to traps containing moose dung, brown-rotted wood and white-rotted wood. Three isolates from the Arthrodermataceae were collected from traps baited with coyote dung and the fourth was collected from a round fungus beetle (Coleoptera: Leodidae: *Catops* sp.) from a fiberglass-baited trap. Species of *Catops* are known to visit habitats rich in keratin, such as animal dung, the soil around animal burrows and owl pellets (Peck and Cook 2002, Peck 2001).

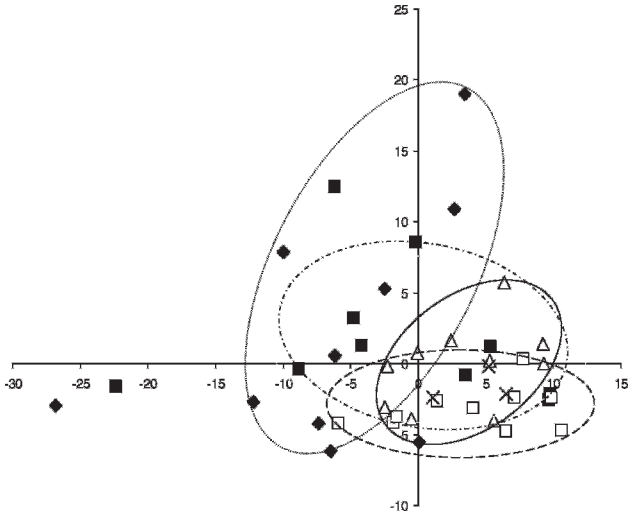

FIG. 3. Scatter-plot of the PCA of 43 baited traps using number and identity of captured arthropods. Traps were baited with either coyote dung (♦ ·····), moose dung (■ -·-·-·-), brown-rotted wood (△——), white-rotted wood (□——) or fiberglass (X). Lines demarcate cluster swarms to aid in viewing and do not indicate per cent similarity.

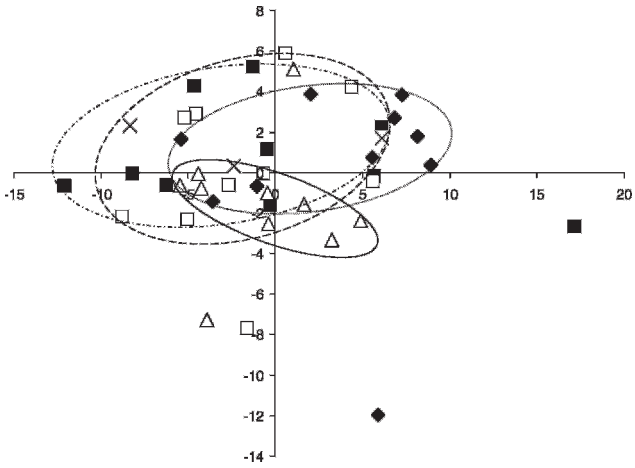

FIG. 4. Scatter-plot of the PCA of 43 baited traps with number and identity of fungi isolated from arthropods. Traps were baited with either coyote dung (♦ ·····), moose dung (■ -·-·-·-), brown-rotted wood (△——), white-rotted wood (□——) or fiberglass (X). Lines demarcate cluster swarms to aid in viewing and do not indicate per cent similarity.

Leptographium piriforme exhibited the most specific pattern of occurrence with 22 of 29 isolates coming from arthropods attracted to traps containing coyote dung. This species was most abundant on ants with seven individuals yielding this fungus, followed by beetles (five isolates) (TABLE II). These isolates represent a species similar to *L. crassivaginatum* M.J. Wingf. (Griffin 1968, Jacobs and Wingfield 2001, Greif et al 2006) but show marked differences in the morphology of the conidia and conidiogenous cells. Other species in *Leptographium* have well known associations with arthropods and many are common and well known pathogens of timber species (Jacobs and Wingfield 2001). *L. crassivaginatum* has been reported from *Populus tremuloides* (Griffin 1968) and *Leptographium piriforme* also might be a pathogen on this species, but its presence on arthropods associated with dung suggests a coprophilous phase in its life history.

Two isolates of *Cryptendoxyla hypophloia,* a cleistothecial ascomycete with a presumed affinity for woody substrates and arthropod dispersal agents (Malloch and Cain 1970, Greif et al 2004) came from a beetle and a springtail, both of which had been captured in traps baited with decayed wood. This fungus forms cephalothecoid ascomata that open and close with alternating dry and wet conditions and also produces an unnamed *Chalara* anamorph that produces cylindrical conidia in sticky clumps. *Chalara* anamorphs also have been linked to ophiostomatoid species that are mainly vectored by beetles (Malloch and Blackwell 1993, Seifert et al 1993). Although here *Leptographium piriforme* was from a wide variety of arthropods (see above) the single unidentified isolate of *Ceratocystis* was from an ant; and *Chalara fusidioides* and *Chalara* sp. I came respectively from a mite and spider.

Conidiobolus coronatus was obtained from two flies and a spider captured in traps baited with coyote and moose dung respectively. This fungus, reported previously as a saprophyte and also a pathogen of arthropods (Chandler et al 2000) and mammals (Rippon 1974), has been recorded from mites in Germany (Renker et al 2005), springtails in the US and Denmark (Christen 1975, Dromph et al 2001), although it is more common in warmer climates. Other species in the genus also have been isolated from mites (Chandler et al 2000, Balazy et al 1987).

The PCA of bait types according to the suites of arthropod taxa trapped reveals considerable overlap among clusters, but some trends can be discerned. Clusters comprising traps baited with both types of decayed wood (i.e., cellulose and ligno-cellulose-rich materials) show considerable overlap and tend to be distinct from the traps baited with coyote dung (keratin-rich material). The cluster comprising traps baited with moose dung overlaps in part with the cluster baited with coyote dung and with both white- and brown-rotted wood (FIG. 3). This position could be coincidental or might reflect the obvious high levels of lignocellulosic debris in the moose dung which also contains materials of animal origin, such as hair from grooming. As a result it ostensibly would attract arthropods seeking both lignocellulosic and fecal materials. A subsequent examination of the raw data after performing the principal components analyses indicated that axis 1 represents the number of arthropods (or fungal isolates in the second PCA, FIG. 4) and axis 2 taxonomic richness. Traps baited with coyote dung captured not only the most arthropods compared to other baits but also more ants, flies, beetles and butterflies on average than traps baited with moose dung and decayed wood. Traps baited with decayed wood yielded more spiders and springtails than traps baited with either type of dung. Specific suites of volatile compounds arising from each of these materials (e.g. Honda et al 1988) might have been signals indicating the availability of a direct food source, protective habitat for adults or eggs/offspring or a suitable hunting ground for prey (Daly et al 1998) and might account for these differences in arthropod richness.

The second PCA (using the number and identity of fungal isolates as variables) yielded clusters with an overall greater degree of overlap than in the first PCA (FIG. 3) but was somewhat similar in that the cluster based on traps baited with coyote dung diverged from the others (FIG. 4). The number of fungal species and isolates thereof from arthropods captured in traps baited with coyote dung differed from traps baited with other materials and account in part for the divergent position of this cluster; more arthropods were associated with the traps baited with coyote dung and as a result a greater number of fungi were isolated. The taxonomic diversity of fungi associated with the arthropods also differed from other bait types and included species with known proclivities for keratin rich substrates (i.e. taxa in the Onygenales).

Traps baited with brown-rotted wood formed a tight cluster, below the first axis, that also diverged somewhat from clusters comprising traps baited with moose dung and white-rotted wood. Difference in cluster shape, size and position between these bait types also can be attributed to species richness and abundance. Arthropods captured in traps baited with brown-rotted wood yielded more isolates than arthropods attracted to moose dung and white-rotted wood. Species in common between traps baited with brown-rotted wood and with moose dung were generally

more abundant in the former (TABLE III). In addition more species of fungi were associated with traps baited with brown-rotted as opposed to white-rotted wood. Clusters based on traps baited with moose dung and with white-rotted wood almost completely overlapped. This overlap can be attributed to the similarity in number of fungal isolates and species richness between these two bait types.

The three fiberglass traps were spread out along axis 1 in the first and second PCA (FIGS. 3–4) and were located within the clusters of two or more of the other bait types, indicating that neither arthropod nor fungal richness differed substantially from the organic baits. These data also show that the arthropods were carrying fungi into the traps rather than picking up propagules from the bait samples once inside.

The differences in position among cluster swarms, among bait types in both statistical analyses, indicate that there is some detectable variation in the suites of fungi being dispersed by different taxonomic groups of arthropods attracted to particular substrates, but the great degree of overlap suggests that most fungal saprobes are generalists rather than associates of specific substrates. The lack of resolution among clusters also might be a consequence of the experimental design. Our trapping protocol was designed to capture arthropods attracted to different types of substrate, and while results from the first PCA (FIG. 3) indicate that it was at least partially effective the structure of the traps would tend to eliminate crawling species (e.g. centipedes and millipedes) and larger taxa such as dragonflies. Trap modifications such as the provision of ground-level access points and/or larger openings might lead to the capture of a broader spectrum of arthropods. In addition some arthropods might have entered the traps in search of shelter or in the pursuit of prey rather than being drawn in by the bait. A greater volume of bait per trap might create a stronger attractant for specific arthropods; this might result in an improvement in the cluster resolution in statistical analyses.

The amount of overlap among clusters in the second PCA (FIG. 4) suggests that fungal species richness was similar across bait types, and this might have resulted from our choice of isolation medium. For example the use of cycloheximide eliminated basidiomycetes from the suite of fungi recovered. The use of more types of isolation media, including those containing different restrictive agents, such as Benomyl, which discourages the growth of most fungi other than basidiomycetes, and molecular techniques (Renker et al 2005) would be expected to contribute to the creation of a more robust dataset and a potential improvement in cluster resolution in the principal components analysis.

Studies have found a variety of habitat-specific fungi associated with the arthropods collected directly from decaying logs (Lilleskov and Bruns 2005, Talbot, 1952), wheat fields (Christen 1975) and leaf litter (Lilleskov and Bruns 2005, Renken et al 2005, Visser et al 1987, Pherson and Beattie 1979), and arthropod visitation has been shown to affect species diversity in dung (Lussenhop et al 1980). To obtain a clearer picture of the role arthropods play in the dispersal of saprobic fungi, data of this sort require complementary investigations concerning which fungal species arrive at new habitats in viable condition. More data of this type will elucidate patterns among substrates, fungal saprobes and their arthropod carriers and will contribute to our understanding of the dynamics of fungal communities and their broader importance to biodiversity and landscape ecology.

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