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Spore dispersal of a resupinate ectomycorrhizal fungus, *Tomentella sublilacina*, via soil food webs

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Abstract: Patterns of fungal spore dispersal affect gene flow, population structure and fungal community structure. Many Basidiomycota produce resupinate (crust-like) basidiocarps buried in the soil. Although spores are actively discharged, they often do not appear to be well positioned for aerial dispersal. We investigated the potential spore dispersal mechanisms of one exemplar of this growth form, *Tomentella sublilacina*. It is a widespread ectomycorrhizal fungus that sporulates in the soil organic horizon, can establish from the spore bank shortly after disturbance, but also can be a dominant species in mature forest stands. We investigated whether its spores could be dispersed via spore-based food webs. We examined external surfaces, gut contents and feces from arthropod fungivores (mites, springtails, millipedes, beetles, fly larvae) and arthropod and vertebrate predators (centipedes, salamanders) from on and around *T. sublilacina* sporocarps. Spore densities were high in the guts of many individuals from all fungivore groups. Centipede gut contents, centipede feces and salamander feces contained undigested invertebrate exoskeletons and many apparently intact spores. DAPI staining of spores from feces of fungivores indicated that 7–73% of spores contained intact nuclei, whereas spores from predators had lower percentages of intact nuclei. The spiny spores often were lodged on invertebrate exoskeletons. To test the viability of spores that had passed through invertebrate guts we used fecal droppings of the millipede *Harpaphe haydeniana* to successfully inoculate seedlings of *Pinus muricata* (Bishop pine). These results indicate the potential for *T. sublilacina* spore dispersal via invertebrates and their predators in soil food webs and might help to explain the widespread distribution of this species. It is likely that this is a general mechanism of dispersal for fungi producing resupinate sporocarps, indicating a need to develop a fuller understanding of the linkages of soil food webs and spore dispersal.

Key words: beetles, centipedes, Chilopoda, Coleoptera, Collembola, ectozoochory, endozoochory, fungivory, invertebrates, millipedes, Myriapoda, oribatid mites, salamanders, sporivory, springtails

INTRODUCTION

Fungi are key regulators of ecosystem processes via their roles as pathogens, saprotrophs and mutualists. Our understanding of the processes that structure communities of one group of mutualists, the ectomycorrhizal fungi, is poorly developed (Bruns 1995), yet such understanding is critical to determining the role of ectomycorrhizae in ecosystems. Given the functional diversity of these communities, factors that affect community structure in turn could lead to changes in ecosystem function. One such factor is mode of spore dispersal.

Many fungi have obvious adaptations for specific spore dispersal modes. Although the majority of epigeous fungi appear to be wind dispersed, well documented examples exist for specialized dispersal relationships between insects and epigeous fungi, including Phallales, rusts and smuts (Ingold 1971, Malloch and Blackwell 1992, Roy 1994), and fungi dispersed by bark beetles (Malloch and Blackwell 1992). Studies have demonstrated a more general potential of invertebrates to disperse epigeous fungi (e.g. Malloch and Blackwell 1992, Franzolin et al 1999).

Fungal species that fruit hypogeously (below ground) include both microfungi and macrofungi with a broad range of ecological roles. Hypogeous fungi have fewer opportunities than epigeous fungi for effective abiotic dispersal. Therefore we would expect that biotic dispersal mechanisms would play a larger role for these fungi. Indeed fungivorous mammals are an important dispersal agent for many hypogeous truffle-like ectomycorrhizal fungi (Johnson 1996) and arbuscular mycorrhizal (AM) fungi that form sporocarps (e.g. Maser et al 1978, Warner et al 1987, Janos and Sahley 1995).

Many hypogeous fungi have undetermined means of dispersal. Various authors have noted the presence

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of spores of soil fungi in the digestive tracts of invertebrates, indicating that invertebrates might be important agents of spore dispersal for these fungi (Visser 1985 and references therein, Malloch and Blackwell 1992 and references therein, Chen et al 1996). Visser (1985) noted that most studies found evidence for dispersal of microfungi but not for ectomycorrhizal fungi. Most studies used media that select for fast growing microfungi during fungal isolation and so would not have detected the presence of viable mycorrhizal fungi, which typically grow slowly and do not compete well in mixed cultures. AM fungal spores can remain viable after passing through digestive tracts of earthworms (McIlveen and Cole 1976), sowbugs, and crickets (Rabatin and Stinner 1985), so we suggest that spores from hypogeous ectomycorrhizal fungi also may be viable after gut passage.

Some resupinate (i.e. thin, crust-like) fungi produce small sporocarps that essentially are buried in the litter, soil or substrate. Although spores may be actively discharged, aerial dispersal is likely limited. We have been investigating the life history strategy of a resupinate ectomycorrhizal fungus, *Tomentella sublilacina* (Ellis & Holw.) Wakef. This fungus can be a dominant or subdominant ectomycorrhizal species in mature forest stands (Gardes and Bruns 1996a, Horton and Bruns 1998, Taylor and Bruns 1999). It also establishes from the spore bank in bioassays and after stand-replacing fires (Taylor and Bruns 1999, Baar et al 1999). Resupinate basidiocarps develop on the underside of logs embedded in leaf litter or in the litter itself. This provides limited opportunities for wind dispersal, and the basidiocarps do not appear to be consumed by small mammals, yet this species has a worldwide distribution, including recently deglaciated circumpolar regions (Kõljalg 1995). Its ability to dominate ectomycorrhizal root communities and to survive in spore banks after disturbance explains how it can persist in a single location, but it does not answer the question: How are the spores of this fungus dispersed?

Two likely possibilities are dispersal by being eaten (endozoochory) by invertebrates and dispersal by adhesion to external surfaces of soil organisms (ectozoochory). In a study of competition among ectomycorrhizal fungi (Lilleskov and Bruns 2003), we noticed high levels of invertebrate grazing on the hymenial surface of many sporocarps of *T. sublilacina*. Any sporocarp in the soil or litter is exposed to large populations of fungivorous invertebrates, including Oribatida (oribatid mites), Collembola (springtails), Diptera (flies), Coleoptera (beetles), Diplopoda (millipedes). These fungivores in turn are exposed to a broad range of invertebrate and vertebrate predators such as Chilopoda (centipedes), salamanders, small mammals and birds. All these groups vary in both digestive physiology and mobility, potentially affecting both survival and dispersal distance of ingested spores. *T. sublilacina* spores are thick-walled, which presumably could aid in survival in digestive systems. Are these invertebrates likely dispersal agents of *T. sublilacina* spores? We also wondered whether these spores were likely to be dispersed via other trophic levels (i.e. via predators on the fungivorous invertebrates). We wanted to know specifically whether spores remain viable as they move through soil food webs.

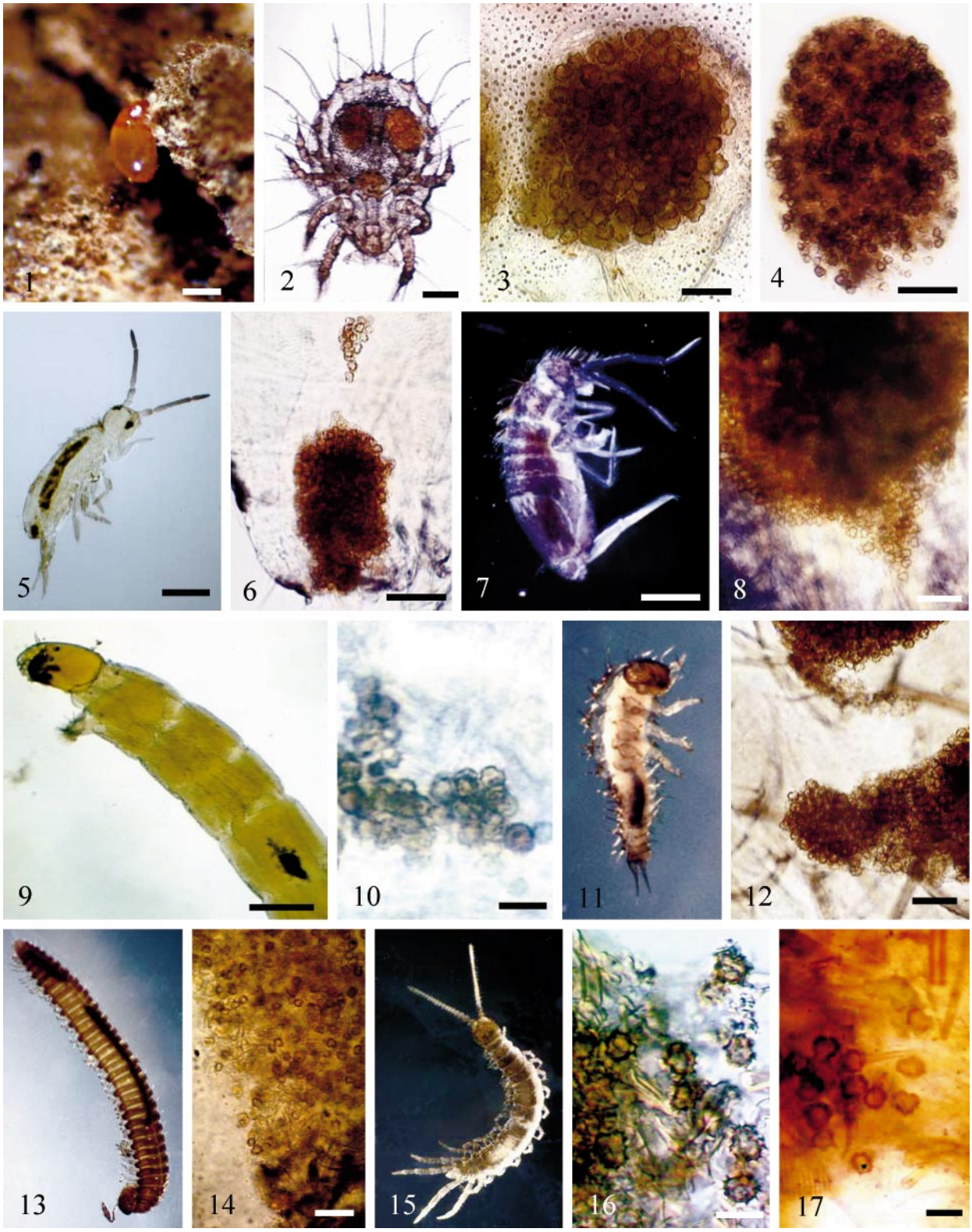
We also investigated whether these spiny spores could be dispersed by ectozoochory. Given the large populations of invertebrates attracted to the spores, a portion of these spores would be likely to adhere to external surfaces of these invertebrates. This potential avenue for invertebrate dispersal of spores has been demonstrated for a variety of fungi (Malloch and Blackwell 1992) but not for ectomycorrhizal fungi.

METHODS

We collected sporocarps of *T. sublilacina* and associated invertebrates at Salt Point State Park, on the Northern California coast (38°34′31″N, 123°18′43 ″W). Sporocarps were collected in a mature Bishop pine (*Pinus muricata* D. Don) forest from the underside of partially decomposed logs embedded in a thick (>10 cm) organic horizon, and in the surrounding partially decomposed pine needle litter. Collections were made at various times throughout the year.

Invertebrate and feces collection.—Invertebrates were collected from basidiocarps with two methods. Surfaces of sporocarps were examined and invertebrates collected directly from the surface. This method worked well for oribatid mites and some fly larvae. A more complete sample of invertebrates was collected by placing *T. sublilacina*-colonized bark and leaf litter in Berlese funnels over an ethanol trap or over a vial lined with moistened filter paper. Fecal material was collected from soil-collected sporivores and predators by placing them in sealed Petri dishes lined with moist filter paper. Fecal material from salamanders was collected by placing salamanders collected near *T. sublilacina* sporocarps in a plastic container for several hours, after which they were released and feces were collected and examined.

To generate large quantities of fecal material for tests of inoculum potential, we collected an individual of the millipede *Harpaphe haydeniana* from the sampling site and enclosed it with pieces of *T. sublilacina*-colonized bark in a large Petri plate lined with moistened filter paper. Pieces of bark covered with sporocarps were cut into ca 5 × 10 mm pieces, partially dried to eliminate the possibility of abiotic spore dispersal and arrayed face up on the paper. Sporocarps arrayed this way retained spores until eaten. All sporocarp fragments were consumed by the millipede. Fecal material deposited on the surface of the filter paper several



FIGS. 1–17. Mature oribatid mite on the surface of a *Tomentella sublilacina* sporocarp. 2. Whole immature oribatid with *T.sublilacina* spore-laden gut contents. 3. Close-up of *T. sublilacina* spores in oribatid gut contents. 4. Oribatid fecal pellet containing *T. sublilacina* spores. 5. Cleared collembola showing gut contents. 6. Close-up of hindgut of collembola from FIG. 5, showing *T. sublilacina* spores. 7. Cleared entomobryid collembola, showing gut contents. 8. Close-up of hind-gut of collembola from FIG. 7, showing pure *T. sublilacina* spores. 9. Cleared dipteran larva with spores in gut. 10. Close-up of *T. sublilacina* spores in gut of dipteran larva from FIG. 9. 11. Cleared beetle larva, showing gut contents. 12. Close-up

centimeters from the nearest sporocarp was collected, fecal material spore content was quantified, and staining reaction of these spores was compared with that of spores from ungrazed sporocarps.

Microscopic examination.—Invertebrates and fecal material were examined with light microscopy for presence of intact *Tomentella sublilicina* spores. The latter are identified easily by their distinctive shape, color and ornamentation. For examination of spore condition we used epifluorescence microscopy and the nuclear stain DAPI (4′,6-diamidino-2-phenylindole) as a vital stain. DAPI stains double stranded DNA, so intact nuclei are clearly visible. Initial trials with FDA (fluorescein diacetate) as an assay of metabolic activity indicated high variability in assay results, even in fresh sporocarps, presumably because of spore dormancy or low permeability. The unreliability of FDA and consistent staining with DAPI were noted by Miller et al (1993) with *Suillus* and *Rhizopogon* spores. We therefore chose DAPI as our primary indicator of intact, potentially viable spores.

DAPI staining was carried out by placing spores in an eppendorf tube with 40 μL of deionized H_2O and 20 μL of 10 g/l DAPI in 0.1M phosphate-buffered saline. The thick-walled spores had low permeability to DAPI. To improve staining we treated the spores by heating them at 90 C for 1 min in a heat block and returned them to room temperature until examined. Stained spores were examined with a Zeiss Axiophot epifluorescence microscope (Carl Zeiss MicroImaging Inc., Thornwood, New York) equipped with a 5 MPix QImaging Micropublisher low-light, cooled CCD color digital camera (QImaging, Burnaby, British Columbia, Canada). Slides were scanned systematically until at least 50 spores were examined or the entire slide was viewed. The number of spores exhibiting positive and negative staining reactions was recorded. Spores from intact sporocarps were stained similarly as controls.

We also examined the external surfaces of oribatid mites for spores with an Electroscan E3 environmental scanning electron microscope, or ESEM (FEI, Oregon) at the University of California at Berkeley Electron Microscope Laboratory. ESEM permits examination of living, unprepared specimens in ambient atmosphere.

Seedling inoculation.—We tested spores from the millipede *H. haydeniana* for their inoculum potential. The spores were applied to three chambers with steamed and leached peat, and three with unsteamed peat in flat 20 × 20 × 1 cm clear acrylic chambers with pine seedlings germinated under sterile conditions. Spores were applied in a liquid suspension prepared by filtration of spore slurries through 50 μm Nytex nylon mesh cloth (Tetko Inc., Briarcliff Manor, New York). Spore concentration in the filtrate was estimated at 28 000 ml^{-1} by examining several 5 μL aliquots under a light microscope. We applied approximately 200 000 spores per chamber (7.2 mL) as a fine mist with a hand-atomizing pump. As 28% of spores were found to have intact nuclei, this resulted in approximately 58 000 potentially live spores per chamber. Three unsteamed peat chambers were watered with distilled H_2O only as controls. After spore addition the chamber edges were sealed with adhesive tape. Seedlings were grown 276 d in a growth chamber (Enconair model GC8–2H-SP, Winnipeg, Canada) at ~350 μmol m^{-2} s^{-1}, and 16h at 18 C light and 8 h at 16 C dark period with deionized water added as needed. Colonization of roots by *T. sublilacina* was determined by examining roots at approximately monthly intervals and confirmed by polymerase chain reaction and restriction fragment length polymorphism analysis (PCR-RFLP) of the internal transcribed spacer (ITS) region of ribosomal DNA, with fungal specific primers ITS 1F and ITS 4 (Gardes and Bruns 1996b).

RESULTS

A high diversity of invertebrates was found to feed on the spores of *T. sublilacina*. These regularly included oribatid mites, springtails, fly larvae, beetle larvae and adults, and millipedes. Density of oribatid mites was high on the surface of the sporocarps where they consistently were observed consuming spores (FIG. 1). Examination of their gut contents and fecal material consistently revealed high spore content (FIGS. 2–4). Beetles, fly larvae and beetle larvae also were observed feeding on the surface of the sporocarps and had high concentrations of spores in their gut contents (FIGS. 5–12). Long, broad trails on the surface of sporocarps, indicative of feeding by larger arthropods such as millipedes, also were present. Examination of gut contents of millipedes from Berlese funnel collections revealed a diverse diet, including a significant proportion of *T. sublilacina* spores (FIGS. 13, 14).

In addition to their presence in fungivores, spores were found in digestive tracts and fecal material of predators. Centipede gut contents and fecal material revealed readily recognizable *T. sublilacina* spores associated with partially digested arthropods (FIGS. 15, 16). Salamander feces consistently contained recognizable *T. sublilacina* spores associated with invertebrate remains (FIG. 17). Spores were found in the digestive tract of a pselaphid beetle (FIGS. 18, 19).

DAPI staining of spores (FIG. 20) revealed that a percentage of *T. sublilacina* spores retained intact nuclei after passage through the digestive tracts of orib-

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of *T. sublilacina* spores in hind-gut of beetle larva from FIG. 11. 13. Cleared millipede. 14. *T. sublilacina* spores and hyphae in gut contents of millipede from FIG. 13. 15. Cleared centipede. 16. Close-up of *T. sublilacina* spores with partially digested invertebrates in gut of centipede. 17. Close-up of *T. sublilacina* spores in feces of salamander.

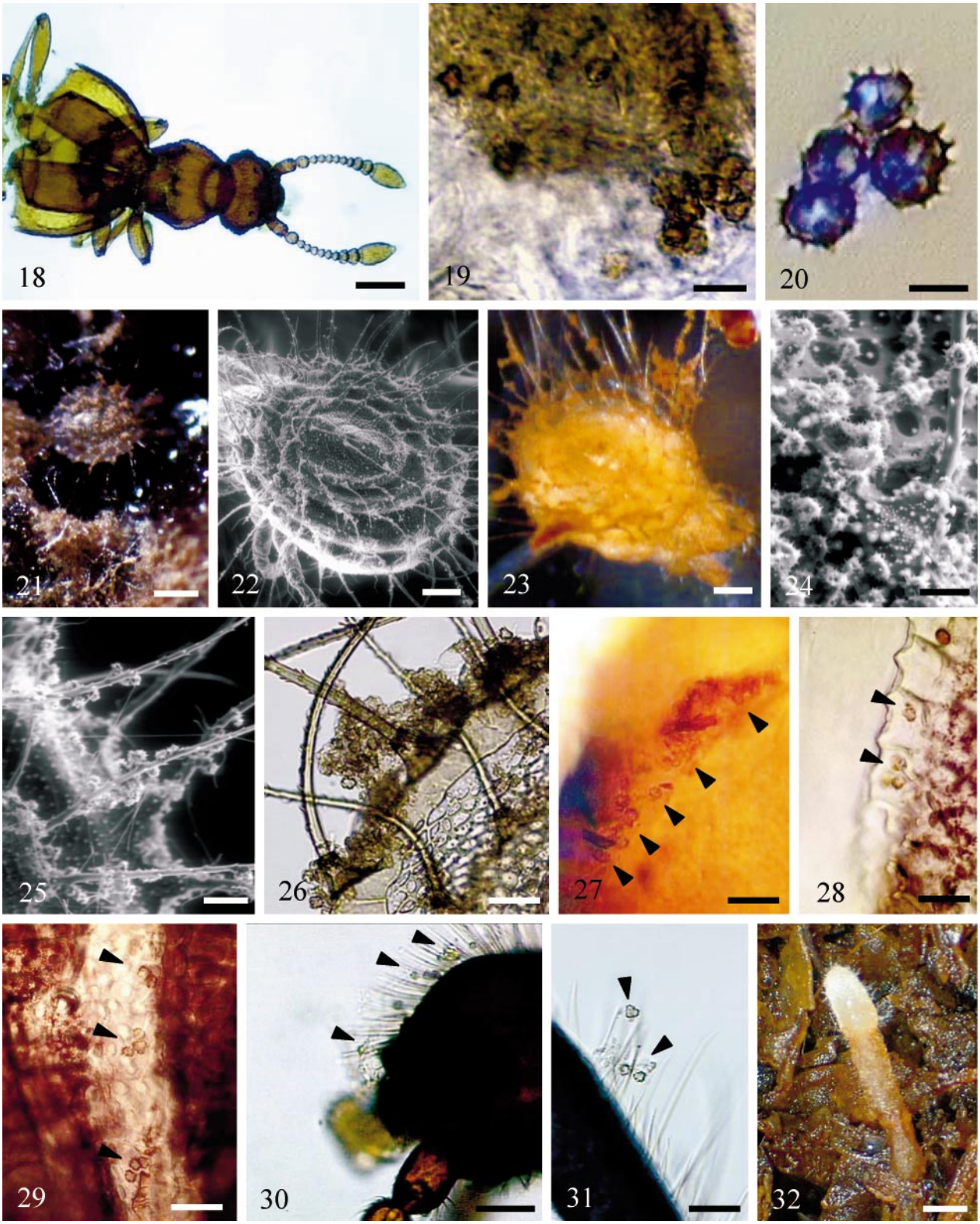

FIG. 18. Predatory pselaphid beetle. 19. *T. sublilacina* spores in gut contents of pselaphid beetle from FIG. 18. 20. *T. sublilacina* spores exhibiting positive DAPI staining reaction. Intact nuclei are indicated by concentrated area of blue staining within spore. 21. Immature oribatid mite feeding on surface of *T. sublilacina* sporocarp, showing dorsal surface coated with spores. 22. ESEM of immature oribatid mite, showing spores adhering to surface. 23. Immature oribatid mite submerged in water, showing strong adherence to dorsal surface by *T. sublilacina* spores. 24–25. ESEM of dorsal surface of mite from FIG. 22, showing spores adhering to notogaster and setae. 26. Close-up of immature oribatid mite in water, showing strong

atid mites, springtails, beetles, millipedes, centipedes and salamanders (TABLE I). The percentage of spores with intact nuclei from uneaten sporocarps were 82–94%. Of these initially intact spores, the percentage with intact nuclei after passage through fungivore digestive tracts was 7–73%. The corresponding percentage for intact spore nuclei in predator feces was lower, 0–20%.

Spiny *T. sublilacina* spores were found adhering to exoskeletons of a wide range of invertebrates, including oribatid mites (FIGS. 21–27), millipedes (FIGS. 28, 29), pselaphid beetles (FIG. 30) and springtails (FIG. 31). Scanning electron micrograph images of live mites revealed large numbers of spores adhered to their exoskeletons (FIGS. 22, 24, 25). The spores adhered so strongly they were not removed when mites were submerged in water (FIGS. 23, 26, 27).

Inoculation of Bishop pine seedlings with the fecal material of the millipede *Harpaphe haydeniana* resulted in successful inoculation of Bishop pine seedlings (FIG. 32). Based on morphological examination and PCR-RFLP of the ITS region, four of six seedlings (two each in steamed and unsteamed peat), were colonized by *T. sublilacina*. No control seedlings were colonized. First date of observed colonization was 121–276 d after inoculation.

DISCUSSION

This study demonstrates the potential of soil invertebrates to disperse viable inoculum of resupinate ectomycorrhizal fungi, both via endozoochory and ectozoochory. At the very least, this is a good mechanism for locally diffusing spores from a point source, such as a small sporocarp, out into a broader area. It seems likely that many basidiomycete and ascomycete fungi with resupinate sporocarps could be dispersed by invertebrates and their predators.

T. sublilacina spores clearly are dispersed on external surfaces of invertebrates and vertebrates. The spiny spores adhere well to external surfaces of invertebrates such as mites. Given that these thick-walled spores appear to maintain viability in the spore bank for at least several months and through stand-replacing fire (Baar et al 1999, Taylor and Bruns 1999), and apparently have delayed germination as seen in the present study, this mode of transport should be effective even if spores adhere to dispersal agents for an extended time.

Although we do not have any evidence of the distance over which the spores are transported, dispersal over tens of meters by this mechanism is possible. Oribatid mites, one of the least mobile of the groups found commonly on sporocarps, have the potential to disperse spores longer distances than might be expected. Berthet (1964) (cited in Behan and Hill 1978) estimated linear distance of <20.5 cm/d for an oribatid mite, although much lower rates (≤ 20 cm/wk) have been reported for both mites and edaphic springtails (Ojala and Huhta 2001).

Other invertebrates, such as millipedes, centipedes and beetles, have the potential for much longer distance dispersal. Reports of millipede movement rates vary from 1.2 m/h^{-1} (Bellairs et al 1983 as reported in Hopkins and Read 1992) to 34 cm/min^{-1} (Mukhopadhyaya and Saha 1984). Conservatively assuming a digestive tract residence time of 1 h and speed of 2 cm/min^{-1}, a millipede could transport spores 1.2 meters. With a digestive tract residence time of 8 h and a speed of 15 cm/min^{-1} a transport distance of 72 m is possible. Centipedes can travel much faster than millipedes, the fastest traveling at <50 cm s^{-1} (Barth and Broshears 1982). At even one-tenth of this speed, a centipede could travel 30 m in 10 min. Beetles vary greatly in flying ability, so spore dispersal potential will vary greatly among species but could be quite high. For example, pselaphid beetles often are captured in flight traps (Chandler 1987) and were found in the present study to have spores in their gut and adhering to their exoskeletons.

It is interesting that beetles associated with rotting wood are found more often in flight traps than species associated with litter, perhaps because the patchiness of the former necessitates longer-distance dispersal (Chandler 1987). Because *T. sublilacina* commonly is found sporulating on rotting wood, this behavior might aid spore dispersal. Many fungivorous beetles are caught in flight traps, presumably because

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adhesion of *T. sublilacina* spores to setae. 27. Close-up of anterior edge of the notogaster of a mature oribatid mite in water, showing the strong adhesion of *T. sublilacina* spores (arrows).. 28–29. Close-up of the exterior surface of a millipede, showing *T. sublilacina* spores (arrows) lodged between segments. 30. Close-up of head of pselaphid beetle in FIG. 18, showing *T. sublilacina* spores adhering to setae (arrows). 31. Close-up of antenna of entomobryid collembola, showing *T. sublilacina* spores adhering to setae (arrows). 32. Ectomycorrhiza of Bishop pine colonized by *T. sublilacina* after inoculation with spores from fecal deposits of *Harpaphe haydeniana*.

Bars FIGS. 1, 18, 21 = 250 μm; 2, 22, 23 = 100 μm; 3, 24 = 15 μm; 4, 6, 14, 30 = 50 μm; 5, 7, 32 = 500 μm; 8, 12, 25–29, 31 = 25 μm; 9 = 200 μm; 10, 16–17, 19 = 10 μm; 20 = 5 μm.

TABLE I. Persistence of intact nuclei in *Tomentella sublilacina* after passage through the digestive tract or various fungivores or predators

Feces source	Spores with intact nuclei (% of control)*	*N* examined
Fungivores		
Mites (Acari, Oribatida, Cepheidae, *Sphodrocepheus* cf. *tridactylus* Woolley & Higgins, 1963)	37	51
Fly larvae (Insecta, Diptera)	73	78
Beetle (Insecta, Coleoptera, Polyphaga)	46	49
Springtail a (Insecta, Collembola, Entomobryidae)	8	73
Springtail b (Insecta, Collembola, Entomobryidae)	7	67
Millipede (Diplopoda, *Harpaphe haydeniana*)	34	49
Predators		
Small centipede (Chilopoda)	0	43
Large centipede (Chilopoda)	20	6
Pacific Newt (Caudata, Salmandridae, *Taricha* sp.)	2	61
California Slender Salamander (Caudata, Plethodontidae, *Batrachoseps attenuatus*)	1	99

* = (Percent fecal material-derived spores with intact nuclei)/(percent sporocarp-derived spores with intact nuclei) × 100.

of the ephemeral nature of their food resources (Newton 1984, Wheeler and Hoebeke 1984).

Linkages between below ground and above ground food webs (Johnston 2000) could lead to even longer-distance transport of spores (e.g. consumption of millipedes by birds) (Malloch and Blackwell 1992). In the present study spore viability decreased to low levels after passage through two trophic levels. This is consistent with results of other studies showing reduced viability in spores passing through invertebrate digestive tracts (Malloch and Blackwell 1992). However, even low-level viability in predator digestive tracts could result in rare longer-distance dispersal, particularly if the number of spores involved were large. Furthermore, activity of predators in the area of sporocarps, as for sporivores, likely would lead to ectozoochory. Salamanders, mice and shrews feed on insects, and often use logs—the primary substrate for sporocarp production—for corridors or shelter. Thus stimulation of populations of palatable sporivores in the vicinity of sporocarps likely would attract predators to the sporocarps and increase opportunities for ectozoochory by highly motile predators. In addition, for invertebrates consumed by predators, spores adhering to external surfaces of prey would have to survive only through one digestive tract, increasing their chances of survival.

We have not quantified the relative importance of aerial vs animal dispersal in *T. sublilacina*. However several observations suggest that animal dispersal is common for this fungus. These include: the high levels of invertebrate grazing observed, high diversity of invertebrates involved, possibility of both ecto- and endozoochoric dispersal, inferred viability from DAPI staining and demonstrated viability from mycorrhizal inoculation. The nonspecialized nature of this dispersal seems particularly well suited to fungi such as *T. sublilacina*, which make small ephemeral sporocarps and seem to have a broad geographic, environmental and host range (Kõljalg 1995). *Tomentella* species are quantitatively important taxa in many ectomycorrhizal communities (Gardes and Bruns 1996a, Horton and Bruns 1998, Taylor and Bruns 1999). It seems likely that many other taxa of resupinate fungi that produce small ephemeral sporocarps in similar habitats also would be dispersed through high levels of invertebrate mycophagy.

The present study is the first to demonstrate the potential for invertebrates to affect spore dispersal of resupinate ectomycorrhizal fungi. Although the mechanisms discussed above remain to be tested as a significant component of dispersal, they point to the need for understanding the biotic linkages driving fungal community structure. Any factor that disrupts these food webs, such as the introduction or loss of ecosystem engineers like earthworms (Bohlen et al 2004), could alter patterns of gene flow, fungal population and community structure, which in turn could influence forest ecosystem function. Greater understanding of the role of invertebrate sporivores and their predators in structuring populations and communities of soil fungi will enhance our ability to manage and conserve the biodiversity and function of such communities.

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