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Conservation of ectomycorrhizal fungi: exploring the linkages between functional and taxonomic responses to anthropogenic N deposition

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ABSTRACT

Anthropogenic nitrogen (N) deposition alters ectomycorrhizal fungal communities, but the effect on functional diversity is not clear. In this review we explore whether fungi that respond differently to N deposition also differ in functional traits, including organic N use, hydrophobicity and exploration type (extent and pattern of extraradical hyphae). *Cortinarius*, *Tricholoma*, *Piloderma*, and *Suillus* had the strongest evidence of consistent negative effects of N deposition. *Cortinarius*, *Tricholoma* and *Piloderma* display consistent protein use and produce medium-distance fringe exploration types with hydrophobic mycorrhizas and rhizomorphs. Genera that produce long-distance exploration types (mostly Boletales) and contact short-distance exploration types (e.g., Russulaceae, Thelephoraceae, some athelioid genera) vary in sensitivity to N deposition. Members of Bankeraceae have declined in Europe but their enzymatic activity and belowground occurrence are largely unknown. Bankeraceae produce a distinct hydrophobic mat exploration type that may also be important in N acquisition under conditions of low N availability.

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Introduction

Conservation biologists have traditionally focused on conservation of species diversity but have more recently addressed how to conserve other aspects of diversity, including functional diversity (Walker 1992; Schwartz *et al.* 2000; Rosenfeld 2002). While the need for conserving species diversity is clear, the need for conserving functional diversity depends on the functional redundancy of species in ecosystems. Debate centers on

whether species are functionally redundant, and on how much diversity is necessary to maintain ecosystem function. One school of thought is that functional redundancy of species is high, and therefore arguments for retaining diversity to retain function are weak (Schwartz *et al.* 2000). Another viewpoint is that investigations of functional redundancy typically look at only one or a few traits rather than multidimensional niche space, and therefore underestimate the effect of species diversity on function and overestimate functional redundancy

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(Rosenfeld 2002). Here we address a special case in which one strong environmental filter (anthropogenic atmospheric nitrogen deposition) is leading to the regional to sub-continental decline in a suite of putatively functionally related taxa specialized in N mobilization under strongly N limiting conditions. We ask about the likely consequences for forest ecosystems if these functionally related species are eliminated from large regions. We hypothesize that one functional axis, the ability to mine nitrogen from organic nitrogen pools, will be dramatically truncated by loss of this pool of species. Whether the loss of these species will affect other functions such as uptake of other nutrients, water uptake, and pathogen resistance depends on whether other traits are correlated with the trait under strong negative environmental filtration.

Ectomycorrhizal fungi (EMF) are a diverse group of symbionts that colonize the roots of many trees, including all species of Pinaceae, Fagaceae, Betulaceae, Salicaceae and many species of Myrtaceae, Fabaceae (e.g., Caesalpinioideae) and Ericaceae (e.g., Arbutoideae, Monotropodieae, Pyroloideae). There are about 6 000 species of EMF that have been classified to date. This is a conservative estimate because many morphological species concepts are proving to be species complexes, many species in North America have been given European names but in fact are unique species, many areas of the tropics and the Asian continent have not been thoroughly surveyed, and some species fruit rarely or cryptically. Identifying species of concern has been hampered by the sporadic occurrence of the sexual fruit bodies (sporocarps) of the fungi, the cryptic nature and the lack of morphological characters of the vegetative state, and the difficulty in culturing most species for lab work. Although DNA-based molecular tools have provided us with new insights about uncharacterized diversity, we cannot use this information by itself to name new species.

Recent advances in molecular tools have both confirmed the existence of many species not yet characterized by taxonomists, and provided researchers with the ability to identify the fungi from ectomycorrhizal root tips and mycelium. As a result we are gaining critical ecological knowledge of this important group of fungi (Horton & Bruns 2001; Lilleskov & Bruns 2001). Here we review evidence that some EMF are being threatened by nitrogen pollution and explore their suite of functional traits.

Anthropogenic inorganic N pollution in terrestrial systems is a major ecological crisis (Vitousek *et al.* 1997). Some EMF compete directly with other soil microbes for organic nitrogen (Schimel & Bennett 2004; Hobbie & Hobbie 2008), aided by direct access to carbon from their hosts. When plants are supplied with inorganic forms of N the number of ectomycorrhizal root tips declines (Meyer 1988; Treseder 2004), presumably because plant carbon allocation belowground is reduced. Atmospheric N deposition is believed to have led to the reduction of ectomycorrhizal root tips and species richness in European forests (reviewed in Meyer 1988). Arnolds (1991) reported a reduction in EMF species richness in Europe based on sporocarp records over the last century and made the case that nitrogen deposition was causal in this decline. He highlighted the following genera as declining synchronously over this region: *Phellodon*, *Hydnellum*, *Suillus*, *Tricholoma* and *Cortinarius*. This is an interesting group of EMF in that they all produce large amounts of extraradical hyphae to explore for nutrients in soils and these hyphae are connected via

hydrophobic rhizomorphs (long-distance transport structures) to hydrophobic ectomycorrhizas (Agerer 2001). Hobbie & Agerer (2010) hypothesized that these fungi have strong capabilities to acquire organic N, which may explain the functional shift away from these taxa under high N availability; we will return to this theme below. First we review recent studies investigating the impact of N deposition on EMF communities based on sporocarp and belowground samples of root tips and soil hyphae.

Responses to nitrogen deposition

Ectomycorrhizal community response to nitrogen

We combined the literature from previous reviews of ectomycorrhizal fungal community response to nitrogen deposition (Wallenda & Kottke 1998; Lilleskov 2005) with information from more recent studies. These studies can be broken down into studies of sporocarps (i.e., mushrooms and related reproductive structures), and more recent studies of EMF belowground as either ectomycorrhizas or extraradical hyphae. Each provides unique and valuable information. Sporocarp studies provide information about changes in reproductive output, and for some taxa sporocarps appear to be a good indicator of belowground abundance, whereas for other taxa sporocarp and belowground abundances are poorly correlated (Lilleskov *et al.* 2002a). Studies of belowground abundance are a more direct measure of the vegetative response of fungi to N deposition. To evaluate support for the Arnolds (1991) contention that N deposition was a major contributor to mycorrhizal decline, we compare the longitudinal trends of sporocarp decline described by him with the above- and below-ground ectomycorrhizal fungal community response to N deposition gradients and fertilization experiments.

Responses based on changes in sporocarp production

Studies examining sporocarp production have generally found that ectomycorrhizal fungal communities respond to relatively short-term (<5 yr) fertilization with declines in diversity and changes in species dominance (Table 1), suggesting that dispersal could be altered quite rapidly by N deposition. Studies have yet to directly address the conservation biology implications of reduced spore production. Because continued persistence requires that new establishment balances mortality, these declines, independent of any impact on the vegetative mycelium, could ultimately reduce or eliminate certain taxa. Recent population genetic studies have demonstrated that the genets of many mycorrhizal fungi can be quite small (<0.5 m²) and that the turnover of individuals within populations can be quite rapid (Gherbi *et al.* 1999; Redecker *et al.* 2001; Bergemann & Miller 2002; Dunham *et al.* 2003; Gryta *et al.* 2006). Thus taxonomic declines could be driven solely by reduced reproductive output. These declines are likely to be more severe in large regions affected by N deposition than in small-scale fertilization experiments, simply because spore dispersal limitation will be greater in the former.

Table 1 – Summary of generic responses to elevated N, decline in Europe over time, and selected functional traits (exploration types, hydrophobicity, protein use). Taxa are organized by hydrophobicity and exploration type

Genus	Response to elevated N (support) ^a	Citations on response to elevated N ^b		European sporocarp decline ^c	Exploration type ^d	Hydrophobicity ^d	Protein use ^e
		Positive	Negative				
<i>Hygrophorus</i>	Mixed	17		--	Cont/short	hi	nd
<i>Lactarius</i>	Mostly tolerant	1,3,5,6,7,9,10,12, 17,18,19,25	8,17,21,22	-	Cont/short/med	hi	Variable (40,43)
<i>Tomentella</i>	Mixed	19	19	nd	Cont/short/med	hi	nd
<i>Clavulina</i>	Tolerant?		16	nd	Short (31)	hi?	nd
<i>Craterellus</i>	Tolerant	10,13,18		nd	Short	hi	nd
<i>Elaphomyces</i>	Tolerant?		27	nd	Short	hi	No (37)
<i>Inocybe</i>	Mixed	8	16,22	--	Short	hi	nd
<i>Pseudotomentella</i>	Sensitive?		27	nd	Short	hi	nd
<i>Tylospora</i>	Mostly tolerant	12,15,22	11,16,19	nd	Short	hi	Variable (36,42)
<i>Cenococcum</i>	Weakly sensitive		22,23	nd	Short (- med)	hi	Variable (33,34,42,43)
<i>Russula</i>	Mixed	20,24,27	3,19	--	Med-smooth/short	hi	Yes (42)
<i>Laccaria</i>	Mostly tolerant	8,17,26	10,13,16,17,18,23,26,27	0	Med-smooth	hi	No-poor (35,41,43)
<i>Thelephora</i>	Tolerant	27	8	nd	Med-smooth	hi	Variable (35)
<i>Cantharellus</i>	nd	na		--	Med-smooth	hi	Variable (44)
<i>Gomphidius</i>	nd	na		--	Med-smooth	hi	nd
<i>Hebeloma</i>	Mixed	4	17	-	Short (32)	hi (30), ho	Yes (37,40,45,46)
<i>Amanita</i>	Mixed	3	16	--	Med-smooth (32)/long	ho	nd
<i>Boletus</i>	Sensitive?		24	--	Long	ho	Variable (33,35,38,39,42)
<i>Paxillus</i>	Tolerant	1,2,5,6,19	10,17	0	Long	ho	nd
<i>Scleroderma</i>	nd			0	Long	ho	nd
<i>Suillus</i>	Sensitive		3,6,12	---	Long	ho	Yes ^f (33,35,38,40)
<i>Tylopilus</i>	Tolerant?	26		nd	Long	ho	Yes (40)
<i>Xerocomus</i>	Mixed	4,7,26	17	-	Long	ho	nd
<i>Amphinema</i>	Sensitive?		19	nd	Med-fringe	ho	nd
<i>Cortinarius</i>	Sensitive		6,8,10,12,13,15,17,18,19,22,26	---	Med-fringe	ho	Yes (42,43)
<i>Hydnium</i>	nd			---	Med-fringe	ho	nd
<i>Piroloma</i>	Sensitive	21	12,19,26,27	nd	Med-fringe (32)	ho	Yes (35,38)
<i>Tricholoma</i>	Sensitive		4,17,19	---	Med-fringe	ho	Yes (43)
<i>Bankera</i>	nd	na		---	Med-mat	ho	nd
<i>Boletopsis</i>	nd	na		---	Med-mat	ho	nd
<i>Hydnellum</i>	nd	na		---	Med-mat	ho	nd
<i>Phellodon</i>	nd	na		---	Med-mat	ho	nd
<i>Sarcodon</i>	nd	na		---	Med-mat	ho	nd

a "Support" indicates strength of literature support for categorization, based on citations in the adjacent columns: l = low, m = medium, h = high, na = not applicable.

b Numbers indicate citation numbers from following list: 1 – Hora 1959; 2 – Laiho 1970; 3 – Menge & Grand 1978; 4 – Ritter & Tolle 1978; 5 – Salo 1979; 6 – Wåsterlund 1982; 7 – Rühling & Tyler 1991; 8 – Termorshuizen 1993; 9 – Wiklund et al. 1995; 10 – Brandrud et al. 1995; 11 – Kårén & Nylund 1997; 12 – Kårén 1997; 13 – Brandrud & Timmermann 1998; 14 – Jonsson et al. 2000; 15 – Taylor et al. 2000; 16 – Peter et al. 2001; 17 – Lilleskov et al. 2001; 18 – Strengbom et al. 2002a; 19 – Lilleskov et al. 2002a; 20 – Avis et al. 2003; 21 – Frey et al. 2004; 22 – Carfrae et al. 2006; 23 – Parrent & Vilgalys 2007; 24 – Avis et al. 2008; 25 – Wright et al. 2009; 26 – Parrent et al. unpublished; 27 – Cox et al. 2010. A study may be cited under different response categories if species within the genus differed in their response.

c Based on Arnolds 1991 and references therein: 0 = increase or no decline, + = slight decline, ++ = moderate decline, +++ = strong decline, nd = no data, either because sporocarps are absent or cryptic, or because response was not reported.

d Exploration types and hydrophobicity (ho) or hydrophilicity (hi) references and exploration types are from Agerer 2001 or 2006 unless indicated by numbers referring to following references: 30 – Unestam & Sun 1995; 31 – Rineau & Garbaye 2009; 32 – Agerer & Rambold 2004–2010; for exploration types, cont = contact, short = short-distance, long = long-distance; med = medium-distance; for sub-types, smooth = smooth subtype, fringe = fringe subtype, mat = mat subtype

e Growth on protein from the following citations: 33 – Abuzinadah & Read 1986; 34 – El Badaoui & Botton 1989; 35 – Finlay et al. 1992; 36 – Ryan & Alexander 1992; 37 – Turnbull et al. 1995; 38 – Bending & Read 1996; 39 – Keller 1996; 40 – Dickie et al. 1998; 41 – Yamanaka 1999; 42 – Taylor et al. 2000; 43 – Lilleskov et al. 2002b; 44 – Rangel-Castro et al. 2002; 45 – Sawyer et al. 2003a; 46 – Sawyer et al. 2003b; studies that recorded protease activity but not growth on protein, or that did not have controls, were not included.

f All but one isolate of Dickie et al. 1998. That isolate grew poorly overall.

Responses based on changes in root tips and soil hyphae

Until relatively recently there was little information on the belowground response of ectomycorrhizal fungal communities to N deposition. With the advent of both advanced morphological keys for EMF (Agerer 1987–2002), and advanced molecular techniques for fungal identification (Horton & Bruns 2001), our understanding of the belowground responses of EMF to nitrogen inputs has expanded rapidly. Studies over deposition gradients, natural fertility gradients and fertilization experiments have provided new insights into the belowground fungal community response. These studies have generally found that short-term belowground responses to increased N availability are more subtle than sporocarp responses, typically resulting in small changes in relative frequency or abundance rather than major community shifts (e.g., Kårén & Nylund 1997; Peter et al. 2001). By contrast, response to long-term elevated N inputs can be quite dramatic, leading to a major shift in dominant fungi and reduced belowground diversity (e.g., Kårén 1997; Taylor et al. 2000; Lilleskov et al. 2002a; Cox et al. 2010). The lag in a belowground response could be caused by greater cumulative dose effects or greater belowground community inertia. Cumulative dose does not seem sufficient to explain the slow community response, because short-term fertilization experiments with high doses have generally found minimal belowground responses. Community inertia could be mediated by priority effects on root tips (e.g., Lilleskov & Bruns 2003) that minimize the loss of access to host carbon, perhaps by prioritizing resource allocation from reproduction to vegetative persistence on tips. Alternatively, reduced sporocarp production could be reducing inoculum input, with consequent declines in new genet establishment for affected taxa leading to species replacement by less affected taxa as genets die.

Taxon-level responses

Taxon-level responses are suggested if taxa respond similarly across studies. The numerous factors influencing the community and the differing response trajectories of individual taxa make this a challenging task. One important factor influencing response is the nitrogen saturation status of the studied system. In many cases the nitrogen dose applied during the study is only a small fraction of the nitrogen deposited on the site during the previous decades. Species abundance assorts independently over space and time, responding to increasing N inputs with monotonic or unimodal relationships. Therefore, some variation in both the initial community and the sign of response to experimental N inputs probably results from where on the nitrogen saturation curve the site is at the time the experiment was begun. For example, the study site of Peter et al. (2001) was reported to have deposition of 17.5 kg N ha⁻¹ yr⁻¹, at least 10 times pre-industrial N deposition rates. Using some simple assumptions, we estimate that the site had received approximately 1 000 kg ha⁻¹ of N deposition in the 100 yr before the study. This level of deposition is likely to have significantly altered the site and associated ectomycorrhizal fungal community before the experimental addition of 300 kg N ha⁻¹ over 2 yr. Not surprisingly, even in their control plots they reported low frequency of *Cortinarius*, no *Piloderma* and no *Tricholoma* either fruiting or on roots. This contrasts

with the studies of Kårén (1997) and Lilleskov et al. (2002a) where background deposition over the same period was $\sim 1\text{--}2\text{ kg N ha}^{-1}\text{ yr}^{-1}$, resulting in $\sim 100\text{ kg N ha}^{-1}$ over the last century, a small fraction of the deposition at the high N sites. In these plots *Cortinarius*, *Piloderma* and *Tricholoma* colonized over 30 % of root tips. Given these issues, not all plots will provide much data on the most nitrogen-sensitive taxa.

Analyses of EMF community compositional and structural responses to elevated N indicate patterns that are variable at the family level, and ranging from broadly consistent to variable at the genus and species level (Table 1). At the family level there is little evidence of a conservative response to elevated N. Within the Cortinariaceae, the evidence suggests a range of sensitivity to N, with *Cortinarius* more sensitive than *Inocybe* and *Hebeloma*. In the Boletaceae, *Suillus* appears to be more sensitive than *Xerocomus*. Within the Atheliaceae (sensu Larsson 2007), *Piloderma* is more sensitive than *Tylospora*. Similarly, in the Russulaceae, *Russula* appears to be more sensitive than *Lactarius* (but see below regarding infrageneric variability in response). Given the consistent intrafamilial variation in response to N we hypothesize that diversification within these families may be linked to fundamental nutritional or physiological shifts.

Genera that fairly consistently exhibit a moderately supported to very well supported negative response to elevated N include *Cortinarius*, *Suillus*, *Tricholoma* and *Piloderma*. Genera exhibiting a largely positive relationship with N availability include *Thelephora*, *Laccaria* and *Lactarius*. Some genera exhibit a clearly mixed response to N deposition, with the best example being *Russula*. This genus contains taxa with relatively strong positive (e.g., *Russula ochroleuca*) and negative (e.g., *Russula paludosa*) responses to elevated N inputs.

The data for most species are rarely as strong as those for genera, simply because of the patchy occurrence of species across multiple studies. This is especially true in declining, species-rich genera like *Cortinarius*. Certain widespread species, such as *Paxillus involutus*, stand out as responding positively to N across multiple studies. Some species exhibit an apparently variable response to N deposition, e.g., *Lactarius rufus*. It is likely that intraspecific variability is due to a variety of causes, including variation in stage of N saturation among studies noted above, interaction with other nutrient limitations and environmental variables, intraspecific physiological variation (Cairney 1999), and cryptic species (i.e., species complexes within a single morphological species concept). Teasing apart the relative importance of these causes of variation will require a combination of genetic and ecological studies that specifically address these alternative mechanisms.

Comparison of N effects on EMF communities with European decline in sporocarp production

Europeans have been tracking sporocarp diversity and production for many decades, and in the latter part of the 20th century observed declines in many genera and species of fungi. In his excellent compilation of the data on European sporocarp decline, Arnolds (1991) argued convincingly that a dominant cause of sporocarp decline in Europe was the extremely high levels of N deposition experienced there. How do the findings of experimental fertilization and N availability gradient studies compare with those of long-term trends of

declining sporocarp production in nitrogen-polluted regions of Europe?

In general the concordance between the two is quite high. Genera Arnolds (1991) described as declining most steeply in Europe include hydroid fungi, *Tricholoma*, *Suillus*, *Cantharellus* and *Cortinarius*. Of those, we have strong evidence for decline in response to N fertilization for *Tricholoma*, *Suillus* and *Cortinarius*. The data are sparse for *Cantharellus*. *Cantharellus cibarius*, the species of *Cantharellus* showing the most widespread decline, has declined more in areas with higher air pollution. While N pollution was not explicitly tested, N deposition is correlated with SO_2 concentrations, which showed a strong negative relationship with *C. cibarius* abundance (Jansen & van Dobben 1987). For certain genera specified by Arnolds as declining we have little experimental or gradient-based data regarding their response to elevated N. These include the hydroid fungi (*Bankera*, *Hydnellum*, *Phellodon*, *Sarcodon*, *Boletopsis*) and *Boletus sensu stricto*. We hypothesize that the sensitivity of these taxa to elevated N parallels the pattern of decline seen over time in Europe.

Genera Arnolds (1991) described as declining in species richness, but less steeply include *Lactarius*, *Russula*, *Inocybe*, *Amanita* and *Boletus (sensu lato, which includes Xerocomus)*. These genera generally correspond to those with mixed positive and negative or predominantly positive responses to elevated N availability. Species within these genera which declined in fruiting over time, such as *Russula paludosa*, also declined over deposition gradients. For species he recognized as relatively persistent (e.g., *Lactarius theiogalus (=tabidus)*) we find relative tolerance of elevated N.

The species-poor genera *Laccaria* and *Paxillus* did not decline according to Arnolds (1991). These genera also tolerate elevated N in fertilization experiments.

In sum, the parallels between patterns of decline over time and data from N fertilization and gradient studies lend strong support to the hypothesis that N deposition is a major contributor to the decline observed across Europe in a broad array of ectomycorrhizal species.

Functional response to N deposition

This section is by necessity speculative. Most of what follows should be considered as hypotheses requiring further testing rather than established fact. Data on functional responses of many taxa are sparse to non-existent (Table 1). It is our hope that identifying these gaps and hypothesizing functional consequences of N deposition will stimulate efforts to test our hypotheses and fill the information gaps.

Functional aspects of the ectomycorrhizal symbiosis have been relatively neglected compared to the tremendous explosion of information on fungal community composition brought on by molecular techniques of the last 20 yr. EMF functionality is necessarily linked to how fungi interact with the soil environment. To understand whether response to nitrogen deposition is linked with specific functional traits, we must relate function with taxonomic groups of known response to N. We derived data from the literature about hydrophobicity, exploration type sensu Agerer (2001), and protein use. We focus on these traits because of their likely relevance to organic

N resource capture and because sufficient data exist to begin to make some generalizations (Table 1).

Protein use and N deposition

Taxa that grow with proteins as a sole N source generally, but not universally, decline in response to fertilization and N deposition, although we are missing information on many taxa (Table 1). Ectomycorrhizal species with a high capacity to use complex organic nitrogen sources decreased in abundance in ecosystems exposed to nitrogen additions along a nitrogen gradient in Europe (Taylor et al. 2000). Along a nitrogen deposition gradient in Alaska, 70 % of root tips were ectomycorrhizal with the ability to grow on protein at low nitrogen deposition vs. only 7 % at the highest nitrogen deposition (Lilleskov et al. 2002b).

Exploration types, protein use, and N deposition

Agerer (2001) developed the concept of exploration types to describe and organize the diversity of anatomical features seen

in fungal mycelium of ectomycorrhizal fungi. These exploration types are characterized by: the distance that hyphae extend from host root tips; the presence or absence and morphology of rhizomorphs; the overall branching pattern of the mycelial network emanating from a root tip; the presence or absence of hydrophobicity in different regions of the vegetative mycelium; and a number of other features (Fig 1).

This system provides a framework for discussing anatomical features that influence fungal exploration of the soil, and in our case it facilitates examination of the consequences of N deposition for soil exploration. The most striking pattern is the dramatic decline in taxa in the medium-distance fringe category of exploration types in response to N deposition. Genera with this exploration type (*Tricholoma*, *Cortinarius*, *Piloderma*; Agerer 2001, 2006; www.deemy.de) all had a consistently negative response to N deposition. This hydrophobic exploration subtype typically involves a dense proliferation of hyphae into loose, relatively undifferentiated rhizomorphs that ramify with high hyphal density around patches of organic matter, often in organic horizons.



Fig 1 – Exploration types representing different foraging strategies in ectomycorrhizal fungi (modified from Agerer 2001; Hobbie & Agerer 2010). These characteristics provide clues about how the fungi explore for, acquire and translocate soil nutrients. Large open circles represent root tips in cross section. Five exploration types are highlighted: L ho = long distance with hydrophobic EM rhizomorphs formed by some *Amanita*, *Boletus*, *Paxillus*, *Rhizopogon*, *Suillus*; S hi = short-distance with hydrophilic EM and no rhizomorphs, formed by *Cenococcum*, *Inocybe*, *Tylospora*; C hi = contact with hydrophilic EM and no rhizomorphs, formed by some *Lactarius*, *Russula*, some *Tomentella*, *Tuber*; M_s hi = medium-distance smooth with hydrophilic EM and rhizomorphs formed by some *Amanita*, *Lactarius*, some *Tomentella*, *Tricholoma*, some *Tuber*; M_{f,m} ho = medium-distance fringe or mat with hydrophobic EM and rhizomorphs formed by *Amphinema*, *Cortinarius*, *Piloderma*, *Tricholoma* (all four genera M_f), *Ramaria*, *Bankeraceae* (both M_m). The images on the right show representative ectomycorrhizal root tips for (top to bottom) contact, short-distance, medium-distance fringe, and long-distance exploration types. Genera in the M_{f,m} ho group are most negatively affected by anthropogenic N deposition, perhaps a function of their specialization on foraging for organic N sources. Additional information about known enzymatic activity for different taxa is in Table 1.

Representatives of these taxa that have been tested exhibit significant growth on protein (Table 1), suggesting that this exploration type is well-adapted morphologically to explore for organic N under N-limited conditions.

Given the decline in Europe of the Bankeraceae (*Bankera*, *Hydnellum*, *Phellodon*, *Sarcodon*) noted above, it is striking that these are members of the similar hydrophobic, medium-distance mat-forming subtype, likely indicating a functional similarity of these two groups. However, relatively little physiological work has been done with this group. We hypothesize extensive capacity for organic N use in this group, based on their morphological similarity to the medium fringe exploration type, their decline in N polluted regions, indications of proteolytic ability (Lee 1986; Lee et al. 1989; Nygren 2008), as well as extensive enzymatic capabilities reported for taxonomically unrelated but morphologically similar mat-forming ECM Gomphales in the Pacific Northwest, USA (Griffiths et al. 1991). However, for neither group is there specific information about organic N uptake.

By contrast, most genera with mixed or positive responses to N deposition (e.g., *Russula*, *Lactarius*, *Laccaria*, *Tylospora*, *Thelephora*, *Tomentella*) have hydrophilic exploration types that include contact, short-distance, and medium-distance smooth types (Table 1). These exploration types involve a lower investment in transport mycelium, and hence would be generally expected to be of lower carbon cost to their hosts than the more intensely rhizomorphic taxa. Thus, under conditions of low belowground C allocation this group is likely to be favored. This group also includes many taxa with limited protein use in pure culture.

These patterns suggest two main ectomycorrhizal strategies for growth and nitrogen acquisition, one focusing on uptake of labile nitrogen forms such as amino acids, ammonium, and nitrate, and one focusing on insoluble, complex organic resources. This second strategy might be enhanced by hydrophobic rhizomorphs to prevent leakage of solutes during medium- to long-distance transport. Such medium- to long-distance exploration types are unlikely to rely on labile substrates under conditions of low nutrient availability, as such substrates are too scarce (e.g., free amino acids) to make the exploratory investment worthwhile. Their clumped hyphal organization also creates overlapping depletion zones, which would be an inefficient strategy for uptake of diffusible inorganic and monomeric organic N. Therefore, we hypothesize that this strategy also requires hydrolytic capabilities to facilitate access to insoluble substances such as proteins. This does not imply that protein use is only present in this exploration type, i.e., some EMF with hydrophilic shorter-distance exploration types can access proteins, e.g., *C. cibarius* (Rangel-Castro et al. 2002). However, there is at present no evidence that any of the medium-distance fringe fungi lack ability to depolymerize and grow on proteins.

Interestingly, sensitivity to added N within the hydrophobic long-distance exploration types (mostly Boletales) is quite variable, with taxa such as *Suillus* declining strongly, taxa such as *Xerocomus* and perhaps *Tylophilus* varying in their response among different studies, and taxa such as *P. involutus* showing little response or increasing in response to N. This suggests that allocation to extensive exploration types that likely involves significant C demand is not strictly limited to N-sensitive taxa

(elsewhere labeled as 'nitrophobic', meaning fungi that decline with anthropogenic N deposition; Lilleskov et al. 2001, 2002a). There are a couple of possible explanations for this. First, it is possible that these taxa specialize on distinct organic resources, i.e., organic N for the N-sensitive taxa and organic P for the N-tolerant taxa (elsewhere labeled as 'nitrophilic', meaning fungi that increase with anthropogenic N deposition; Lilleskov et al. 2001, 2002a). Carbon allocation belowground tends to be high under both strongly N-limited and strongly P-limited conditions (Ericsson 1995). Although most long-distance exploration types appear adapted to explore for organic N, a subset of taxa may be adapted to high efficiency of mining organic P resources. This hypothesis would suggest that these taxa would have dramatically different enzymatic capabilities and effects on host N vs. P uptake. Associated with this would be mechanisms that limit the carbon expended in uptake of nitrogen (Wallander 1995). Consistent with this, *P. involutus* provides hosts with less N relative to P than N-sensitive long-distance explorers like *Suillus* spp. (Högberg et al. 1999); its growth is less inhibited by N availability than that of N-sensitive taxa (Arnebrant 1994), its respiration rate increases less than other hydrophobic taxa such as *Rhizopogon* after N addition in pine cultures (Bidartondo et al. 2001), and it has higher acid phosphatase activity than other species (Pacheco et al. 1991). If this hypothesis is true, we would expect these taxa to do poorly under conditions of high overall fertility, and perform well under conditions of strong N or P limitation, depending on the species. Alternatively, the exploration type could also be unrelated to organic resource capture, and be more associated with other traits, such as adaptation for drought and efficient water transport, elevated sink strength for host C, bridging of separated resources such as deep roots and surface resources, or rapid production of sporocarps (Lilleskov et al. 2009). These hypotheses await diagnostic experimental tests.

What are the functional consequences of this reorganization of fungal communities? At present we do not know, but it clearly depends on the answer to a number of subsidiary questions. First, does the overall reduction in hydrophobic types, especially the medium-distance types that are so prevalent in N-limited high latitude forests, truly represent the loss of a functional group? If so, is the primary function of this group organic N acquisition? Are there other traits associated with these hydrophobic medium-distance exploration types that, if lost, might have functional consequences for tree hosts or ecosystem processes? Are any species or genera in these groups eliminated from large regions, or is their local abundance simply greatly reduced? How rapidly will this functional group recover and recolonize affected areas after N deposition declines, and is this primarily dependent on change in soil properties, or is recolonization limited by dispersal?

The last two questions have relevance to both conservation of taxa and conservation of function. Although the answers are far from certain, some information is available. Regarding the reduction or elimination of taxa, nitrogen pollution is highly patchy regionally, and there is nothing to suggest that entire genera are distributed in such a regionally restricted fashion, so complete elimination of genera globally is highly unlikely. In general, most species are considered to have fairly wide ranges, with relatively little evidence for strong regional endemism (Arnolds 2007), but more intensive and extensive

belowground molecular analyses are needed to test this (Lilleskov & Parrent 2007). Cryptic species could well have more restricted ranges, but existence of endemism at the level of cryptic species would be more likely to have implications for the conservation of species than for the conservation of function. Although regional elimination of some taxa in areas, such as the Netherlands, that have experienced the highest N deposition is possible, even there sporocarp records suggest that residual populations exist for some of the most critically affected taxa such as *Sarcodon imbricatus* (Arnolds 2007).

Functional elimination of taxa from high deposition areas is quite possible, however. Long-term high deposition combined with other factors has led to inclusion in Red Lists of thousands of fungal species on regional lists across Europe, and hundreds of species of concern for the entire region, about a third of which are EMF (Arnolds 2007). Regional extinctions have been reported, e.g. for many hydroid fungi associated with conifers in the Netherlands (Arnolds 2010). Combined with our data on belowground responses of many of these taxa, this suggests that abundance of these taxa could be reduced enough to make them functionally absent within entire high deposition regions.

There is sparse information on the ability of these functional communities to recover after cessation of N inputs. While data examining recovery of communities belowground are lacking, sporocarp fruiting can be depressed for decades after fertilization, even when N is applied at the plot level (Strengbom et al. 2001). This is not surprising, given that soil effects of high levels of fertilization can persist for many years, suggesting that recovery of these functional groups affected by N deposition might be slow. Further, dispersal limitations may reduce the ability for a species to recolonize a location rapidly. Consistent with this notion, in the Netherlands signs of recovery of stipitate hydroid populations following reduction of nitrogen inputs are limited to roadside verges planted with angiosperms, where oligotrophic conditions have been maintained by management practices (Arnolds 2010). No recovery has been seen in natural broadleaf forests or in association with conifers.

For ectomycorrhizal fungal communities to recover, N deposition will have to be reduced significantly in many parts of the world. Different empirical critical loads for N deposition effects on ectomycorrhizal fungal communities have been proposed. Wallenda & Kottke (1998) suggested that a load of 20–30 kg was too high for sensitive taxa. Bobbink et al. (2002) proposed a critical load of 10–20 kg N ha⁻¹ yr⁻¹, and Pardo et al. (in press) proposed a critical load of 5–10 kg N ha⁻¹ yr⁻¹ for many ecosystem types. The decline in the proposed critical load threshold reflects the growing body of literature that even modest long-term N deposition can significantly affect ectomycorrhizal fungal communities (Pardo et al. in press).

In conclusion, ectomycorrhizal fungal communities respond strongly to N deposition, with certain genera and species declining steeply in response to elevated N availability. These genera have a relatively conserved vegetative extraradical mycelial anatomy of medium-distance hydrophobic exploration types that, for taxa tested so far, generally have strong growth on protein in pure culture. The extent and reversibility of these community changes are poorly known and need further investigation before the implications for fungal conservation biology and ecosystem function can be determined.

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