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Isotopic evidence indicates saprotrophy in post-fire *Morchella* in Oregon and Alaska

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Abstract: We assessed the nutritional strategy of true morels (genus *Morchella*) collected in 2003 and 2004 in Oregon and Alaska, 1 or 2 y after forest fires. We hypothesized that the patterns of stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) in the sporocarps would match those of saprotrophic fungi and that radiocarbon ($\Delta^{14}C$) analyses would indicate that *Morchella* was assimilating old carbon not current-year photosynthate. We compared radiocarbon and stable isotopes in *Morchella* with values from concurrently collected foliage, the ectomycorrhizal *Geopyxis carbonaria* (Alb. & Schwein.) Sacc., the saprotrophic *Plicaria endocarpoides* (Berk.) Rifai, and with literature to determine isotopic values for ectomycorrhizal or saprotrophic fungi. *Geopyxis, Plicaria* and *Morchella*, respectively, were 3‰, 5‰ and 6‰ higher in ^{13}C than foliage and 5‰, 7‰ and 7‰ higher in ^{15}N. High ^{15}N enrichment in *Morchella* indicated that recent litter was not the primary source for *Morchella* nitrogen, and similar ^{13}C and ^{15}N enrichments to *Plicaria* suggest that *Morchella* assimilates its carbon and nitrogen from the same source pool as this saprotrophic fungus. From radiocarbon analyses *Morchella* averaged 11 $\pm$ 6 y old (n = 19), *Plicaria* averaged 17 $\pm$ 5 y old (n = 3), foliage averaged 1 $\pm$ 2 y old (n = 8) and *Geopyxis* (n = 1) resembled foliage in $\Delta^{14}C$. We conclude that morels fruiting in post-fire environments in our study assimilated old carbon and were saprotrophic.

Key words: carbon sources, ectomycorrhizal, life history, post-fire, saprotrophy

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Introduction

Morchella is a genus of highly desired edible fungi, several species of which fruit in post-fire habitats in western North America (Kuo et al. 2012, Masaphy and Zabari 2013, Du et al. 2015). The genus is generally considered saprotrophic (Brock 1951, Robbins and Hervey 1959, Dahlstrom et al. 2000), although some evidence suggests ectomycorrhizal status with species of Pinaceae (Buscot and Kottke 1990, Buscot 1993, Dahlstrom et al. 2000) and with the terrestrial orchid *Gymnadenia conopsea* (Stark et al. 2009). Researchers have assessed ectomycorrhizal status with various techniques, such as inoculation and pure culture synthesis studies, root tip colonization and molecular techniques (Hansen et al. 2013). Because the carbon and nitrogen sources of saprotrophic and ectomycorrhizal fungi often differ (Lindahl et al. 2007; Hobbie et al. 2014a, 2014b), another tool uses natural isotopic tracers to distinguish between these two functional groups. Stable isotope measurements use small differences in ratios of $^{13}C:^{12}C$ and $^{15}N:^{14}N$ (expressed as $\delta^{13}C$ and $\delta^{15}N$ values) among different sources as markers for those sources (Hobbie et al. 2001, Wilson et al. 2007). They also can be used as markers of differences between saprotrophic and ectomycorrhizal fungi in how they process nitrogen and carbon within fungi once assimilated (Hobbie et al. 2005, 2012).

Composition of sporocarps can affect stable isotopes, in that the $\delta^{13}C$ and $\delta^{15}N$ values of protein, carbohydrates and chitin differ. Because these compound classes also differ in elemental composition, %N and %C commonly co-vary with $\delta^{13}C$ and $\delta^{15}N$ values (Hobbie et al. 2012). Accordingly, variability in elemental composition should be accounted for when different fungi are compared to assess life-history strategy, so that isotopic values essentially can be normalized to a standard composition. In addition, climate (Kohn 2010) may influence $\delta^{13}C$ of photosynthate, so if possible these potential influences also should be considered.

Thermonuclear explosions in the 1950s and 1960s doubled background radiocarbon (^{14}C) in the atmosphere. Because this bomb spike of ^{14}C has declined over time because the $^{14}CO_2$ was taken up by terrestrial plants, phytoplankton or the oceans, radiocarbon measurements (expressed as $\Delta^{14}C$) can provide a short-term dating tool for carbon age. Accordingly we can determine from $\Delta^{14}C$ measurements on sporocarps whether fungi are assimilating current-year photosynthate or older carbon (Hobbie et al. 2002).

TABLE I. Locations for site collections of post-fire fungi and foliage

Site No.	Month/year collected	State	Fire name	Lat (N)	Long (W)	Elev (m)	MAT (C)	MAP (mm)	Foliar $\Delta^{14}C$ sample
1	5/2003	OR	Biscuit	42.54	123.99	469	11.3	1913	*Node*
2	5/2003	OR	Biscuit	42.50	124.09	611	10.9	2079	*Psme*
3	5/2004	OR	B & B	44.57	121.69	1085	8.0	1291	*Abgr*
4	5/2004	OR	B & B	44.57	121.73	1357	6.9	1526	*Abgr*
5	6/2003	OR	Eyerly	44.63	121.56	1224	6.9	1500	—
6	4/2003	OR	Paul Dunn	44.72	123.31	121	12.0	1509	*Arme, Abgr*
7	6/2003	AK	Tanana	65.04	149.09	95	−1.7	352	*Pigl*
8	6/2003	AK	Chena	65.04	146.09	609	−4.9	357	*Pigl*
9	6/2003	AK	Livengood	64.39	148.17	177	−3.5	352	*Pigl*

Abbreviations: OR = Oregon; AK = Alaska; Lat = latitude; Long = longitude; Elev = elevation; MAT = mean annual temperature; MAP = mean annual precipitation. Dominant vegetation at sites: (1 and 2) *Pseudotsuga menziesii* (*Psme*), *Notholithocarpus densiflorus* (*Node*); (3 and 4) *Pseudotsuga menziesii, Pinus ponderosa, Abies grandis* (*Abgr*); (5) *Abies concolor, Pseudotsuga menziesii*; (6) clear-cut *Pseudotsuga menziesii*, edge of burned slash pile, *Arbutus menziesii* (*Arme*); (7) *Picea glauca* (*Pigl*), *Populus tremuloides, Betula papyrifera*; (8) *Picea glauca, Populus tremuloides, Betula papyrifera*; (9) *Picea mariana, P. glauca*. Adiabatic lapse rate used to calculate MAT for site 9 using temperature data from Fairbanks weather station WBAN: 26411. Foliage at each site analyzed for radiocarbon is also indicated.

In this study we investigated the ectomycorrhizal status of post-fire fungi collected in 2003 and 2004 in Oregon and Alaska. We hypothesized that the profile of stable isotopes in morels from post-fire habitats would match those of saprotrophic fungi and radiocarbon analyses would indicate that *Morchella* is assimilating older carbon and not current-year photosynthate. Comparisons of radiocarbon and stable isotopes with concurrently collected foliage from the burn areas and with literature values were used to determine likely isotopic values for ectomycorrhizal versus saprotrophic fungi. Multiple regression analyses will test the influence of climatic variables (mean annual temperature and precipitation), carbon concentrations, nitrogen concentrations, carbon : nitrogen ratios, and taxa on sporocarp $\delta^{13}C$ and $\delta^{15}N$ values.

MATERIALS AND METHODS

Collections and sample locations.—Numerous wildfires occurred throughout Oregon and Alaska in the early 2000s, and collections of post-fire Pezizales were obtained from several locations to encompass a broad geographic distribution and diverse habitats. Sporocarps and foliage of dominant trees were collected from burned areas 1–2 y after wildfires (TABLE I). Taxon, habit and substrate were recorded (TABLE II). Collections were identified to the lowest taxonomic level possible using macroscopic characters on fresh specimens. Collections were dried in portable dehydrators at about 35–40 C for 12–24 h. Collections were further described after microscopy (TABLE II). Voucher specimens are deposited at the Oregon State University Herbarium under accession numbers OSC 153584–153612.

Isotopic methods.—Stable isotope ratios were measured at the Macko laboratory at the University of Virginia. Acetanilide and pine needles were used as internal standards for elemental concentrations and isotopic ratios. Stable isotope ratios are reported as

$$\delta^{13}C = \left(R_{sample}/R_{standard} - 1\right) \times 1000\,(‰) \qquad (1)$$

where R is the $^{13}C : {}^{12}C$ ratio of either the sample or the reference standard (Vienna-PeeDee Belemnite). Nitrogen isotope ratios ($\delta^{15}N$) are similarly determined but with atmospheric nitrogen as the standard.

The ^{14}C abundances were measured in 2005 by accelerator mass spectrometry at the Woods Hole Oceanographic Institution radiocarbon laboratory to a measurement error of 4.8‰ for foliage and 5.6‰ for fungi (standard deviation). Results are reported as $\Delta^{14}C$, with

$$\Delta^{14}C = \left(pM \times e^{-\lambda(ts-1950)} - 1\right) \times 1000\,(‰) \qquad (2)$$

where t_s is the year of sampling, $\lambda = 1/8267\ yr^{-1}$ and pM (%Modern) is

$$pM = \left(A_{sample}/A_{standard}\right) \times (1/0.7459) \times \left(\left[1 + \delta^{13}C_{standard}\right]/\left[1 + \delta^{13}C_{sample}\right]\right)^2 \qquad (3)$$

A is the ^{14}C activity of sample or standard, and $\delta^{13}C_{standard}$ that of the new oxalic acid (NBS SRM 4990C). These equations allow ^{14}C measurements to be reported independently of isotopic fractionation by normalizing results to a $\delta^{13}C$ value of −25‰. The squared term, $([1 + \delta^{13}C_{standard}]/[1 + \delta^{13}C_{sample}])^2$, accounts from fractionation against ^{14}C being roughly twice that of ^{13}C. Data from Hua et al. (2013) on the $\Delta^{14}C$ of atmospheric CO_2 1950–2010 were

TABLE II. Fungal samples collected and analyzed for $\delta^{13}C$ and $\delta^{15}N$

Site	Herbarium OSC No.	Collection No.	Taxon	Habit	Substrate	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
1	153584	JES 8023 (R)	*Morchella*	Scattered	Soil	−19.95	7.61
2	153585	JES 8042 (R)	*Plicaria*	Scattered	Soil	−22.67	2.76
2	153586	JES 8057 (R)	*Morchella*	Solitary	Soil	−22.16	5.45
3	153587	JES 8087	*Geopyxis*	Clustered	Soil	−25.47	1.53
3	153588	JES 8088 (R)	*Plicaria*	Clustered	Soil	−22.79	6.85
3	153591	JES 8093 (R)	*Plicaria*	Clustered	Soil	−25.32	4.22
3	153592	JES 8094 (R)	*Geopyxis*	Clustered	Soil	−25.45	3.72
4	153589	JES 8089	*Morchella*	Scattered	Soil	−19.23	7.90
4	153590	JES 8090	*Morchella*	Scattered	Soil	−20.56	6.78
4	153593	JES 8095	*Morchella*	Scattered	Soil	−23.19	4.98
4	153594	JES 8096 (R)	*Morchella*	Solitary	Soil	−21.65	5.78
4	153595	JES 8097 (R)	*Morchella*	Scattered	Soil	−21.70	5.54
4	153596	JES 8098 (R)	*Morchella*	Scattered	Soil	−20.97	8.39
5	153602	NSW 9043	*Morchella*	Solitary	Soil	−23.06	4.55
5	153603	NSW 9045 (R)	*Morchella*	Scattered	Soil	−22.82	3.10
5	153604	NSW 9052 (R)	*Morchella*	Solitary	Soil	−22.60	5.04
5	153605	NSW 9059 (R)	*Morchella*	Gregarious	Soil	NA	NA
6	153597	NSW 8992	*Morchella*	Sol/sca	S/ch fd	−22.48	4.48
6	153598	NSW 8994	*Morchella*	Sol/sca	S/ch fd	−22.24	4.30
6	153599	NSW 8996 (R)	*Morchella*	Sol/sca	S/ch fd	−22.91	3.43
6	153600	NSW 8998 (R)	*Morchella*	Sol/sca	Soil	−26.29	3.04
6	153601	NSW 9000 (R)	*Morchella*	Sol/sca	Soil	−22.23	4.97
7	153611	NSW 9085 (R)	*Morchella*	Scattered	Soil	−22.57	1.07
8	153606	NSW 9065 (R)	*Morchella*	Solitary	Soil	−23.46	1.48
9	153612	AKFL 3 (R)	*Morchella*	Scattered	Soil	−22.16	6.49
9	153607	NSW 9069	*Morchella*	Sca/gre	Soil	−22.18	2.12
9	153608	NSW 9071	*Morchella*	Sca/gre	Soil	−23.61	1.44
9	153609	NSW 9072 (R)	*Morchella*	Gregarious	Soil	−23.04	5.99
9	153610	NSW 9075 (R)	*Morchella*	Solitary	Soil	−23.12	1.92

Note: Site numbers, herbarium numbers and collection numbers are provided as are taxon, habit and substrate. Herbarium numbers are OSC 153584-153612. An R next to the collection number indicates that it was analyzed for radiocarbon. Habit: sol/sca = solitary to scattered, sca/gre = scattered to gregarious; substrate: s/ch fd = soil/charred forest debris. Taxon: *Plicaria* = *Plicaria endocarpoides*; *Geopyxis* = *Geopyxis carbonaria*.

used to compare average $\Delta^{14}C$ of atmospheric CO_2 for each year with measured $\Delta^{14}C$ values in sporocarps. To estimate sample age, sample $\Delta^{14}C$ was compared against the Hua et al. database of $\Delta^{14}C$ measurements, with the simplifying assumption that all sample C was derived from a single year (Gaudinksi et al. 2001).

Estimating local climate.—Average annual temperature and precipitation during the year of collection was determined with the Daymet single-pixel extraction tool using the latitude and longitude of sample sites (daymet.ornl.gov). The single-pixel extraction tool supports only latitude and longitude within the contiguous USA, so Alaskan sites Tanana and Livengood used data from the National Climate Data Center (www.ncdc.noaa.gov), specifically a weather station in Fairbanks (WBAN: 26411). We assumed that annual temperature at Tanana (site 7) did not change from the nearby weather station, however, an adiabatic lapse rate of 1.0 C per 100 m was applied to Livengood (site 9) due to its higher elevation. A separate weather station located at Chena Hot Springs (Alaska) was used for Chena (site 8).

Statistical analyses.—The statistical package JMP (SAS Institute, Middleton, Massachusetts) was used for all analyses. If only two groups were compared, *t*-tests were used. If more than two groups were compared, ANOVA with a post hoc Tukey test was used. To assess the factors influencing $\delta^{13}C$ and $\delta^{15}N$ in fungi, we used stepwise multiple regression models that included these factors: the natural log of annual

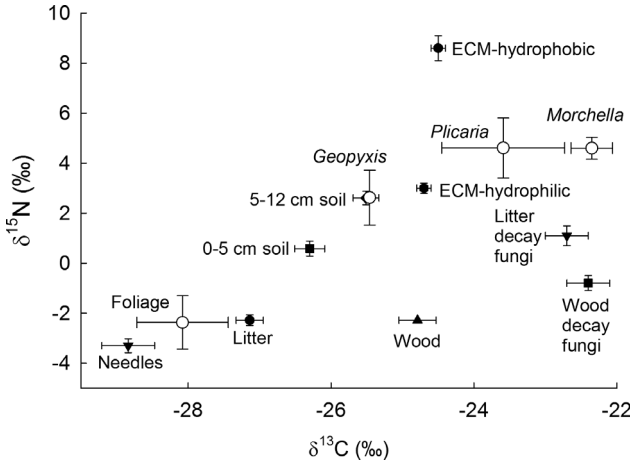

FIG. 1. $\delta^{13}C$ and $\delta^{15}N$ of foliage, *Geopyxis*, *Plicaria* and *Morchella*, ± SE, by clear symbols. *Geopyxis* SE is only 0.01‰, so not visible. Solid symbols are average values from a survey of Oregon sporocarps, needles, litter, wood and soil (data from Hobbie et al. 2012). Sporocarps are classified by functional category into litter decay, wood decay, ectomycorrhizal (ECM) with hydrophilic ectomycorrhizae and ECM with hydrophobic ectomycorrhizae.

precipitation, annual temperature, %N, %C, C/N and taxa. Location was set as a random factor. Significance was set at an α of 0.05. Data are reported as means ± standard errors.

RESULTS

Comparisons of radiocarbon and stable isotope values with concurrently collected specimens of *Plicaria*, *Geopyxis* and foliage and with literature values were used to determine likely isotopic values for ectomycorrhizal versus saprotrophic fungi. Relative to foliage the ectomycorrhizal *Geopyxis*, saprotrophic *Plicaria* and *Morchella* were 3‰, 5‰ and 6‰ higher in ^{13}C and 5‰, 7‰, and 7‰ higher in ^{15}N. These values are plotted together with those of needles, litter, soil, litter-decay fungi, wood-decay fungi and ectomycorrhizal fungi from an extensive fungal survey in Oregon (Hobbie et al. 2012) (FIG. 1). In Tukey tests foliage was significantly lower in both $\delta^{13}C$ and $\delta^{15}N$ than the three fungal taxa, *Morchella* was significantly higher in $\delta^{13}C$ than *Geopyxis* but not significantly different from *Plicaria*, while the three fungal taxa did not differ significantly in $\delta^{15}N$. In contrast, in a multiple regression model for $\delta^{15}N$ that included precipitation, taxa and the interaction of nitrogen concentration and taxa as fixed effects and location as a random effect the $\delta^{15}N$ was significantly affected by taxa ($P = 0.0146$) and the overall model explained 55% of variance (TABLE III). Location accounted for 48% of variance in random effects. In this regression model *Morchella* was 5.5‰ and 0.5‰ higher in ^{15}N than *Geopyxis* and *Plicaria*, respectively. $\delta^{15}N$ and $\delta^{13}C$ values for samples are provided (TABLE II).

In a multiple regression model for $\delta^{13}C$ that included precipitation, taxa and the interaction of nitrogen concentration and taxa as fixed effects and location as a random effect, $\delta^{13}C$ was significantly affected by taxa ($P = 0.0088$) and the overall model explained 72% of variance (TABLE III). Location accounted for 51% of variance in random effects. In this regression model *Morchella* was 3‰ and 0.7‰ higher in ^{13}C than *Geopyxis* and *Plicaria*, respectively.

Radiocarbon ($\Delta^{14}C$) in atmospheric CO_2 1974–2006 (FIG. 2a) illustrates the steady decline in the bomb spike ^{14}C over that period and its potential as a short-term dating tool. Here (FIG. 2b) foliage (eight samples from five different species) was similar to atmospheric CO_2 in $\Delta^{14}C$ whereas *Morchella* (n = 19) was consistently higher in $\Delta^{14}C$ than atmospheric CO_2. *Morchella* and foliage (n = 8) differed in $\Delta^{14}C$ by 62.9 ± 11.4‰ (*t*-test, df = 26, $P < 0.0001$), with foliage similar to

TABLE III. Regression model of $\delta^{15}N$ and $\delta^{13}C$ as selected based on highest adjusted r^2

Term	$\delta^{15}N$ model value ± SE	Prob > |t|	$\delta^{13}C$ model value ± SE	Prob > |t|
Intercept	0.45 ± 1.75	0.8037	−35.20 ± 4.47	<0.0001
MAP (m)	1.82 ± 1.15	0.1545	3.46 ± 1.76	0.0687
Taxa	—	**0.0146**	—	**0.0088**
Geopyxis	−3.54 ± 1.36	0.0176	−2.73 ± 1.05	0.0179
Morchella	2.01 ± 0.71	0.0102	1.71 ± 0.50	0.003
Plicaria	1.52	—	1.02	—
Taxa × %N	—	0.2412	—	0.1620
Geopyxis × %N	−3.10 ± 2.23	0.1814	−2.88 ± 1.46	0.0646
Morchella × %N	0.85 ± 0.60	0.1713	0.28 ± 0.51	0.5918
Plicaria × %N	2.24	—	2.60	—

Note: Fixed variables are %N, mean annual precipitation (MAP, in m), taxa and the interaction of taxa and %N. Location was a random effect. Adjusted r^2 for the $\delta^{15}N$ model was 0.551 and for the $\delta^{13}C$ model was 0.715, n = 28.

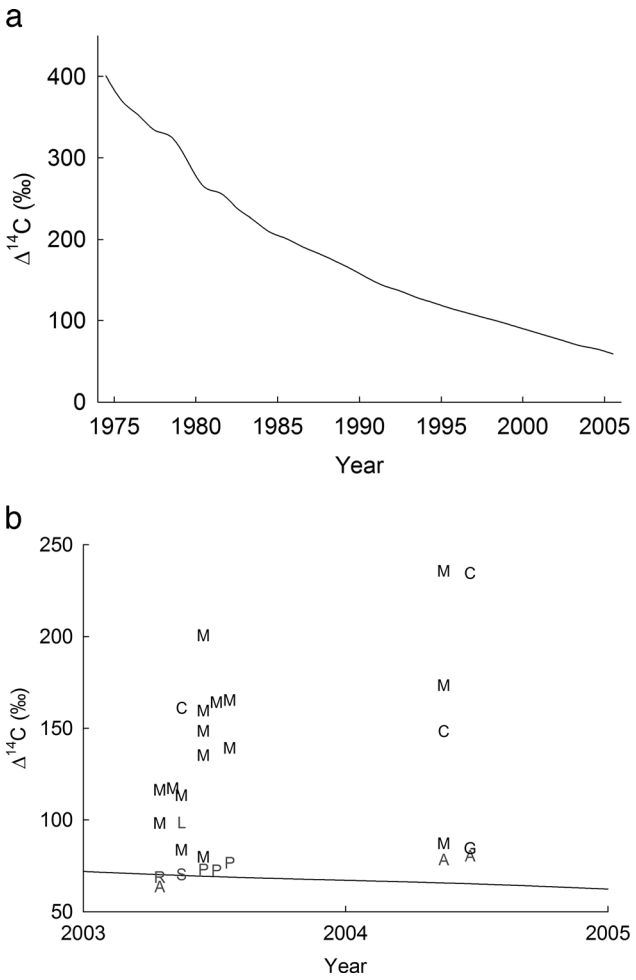

FIG. 2. a. Atmospheric $\Delta^{14}C$ curve for carbon dioxide 1974-2006. Data from Hua et al. (2013). b. $\Delta^{14}C$ of fungi and foliage post-fire by year of collection. Fungi are designated with black M (*Morchella*), C (*Plicaria*) or G (*Geopyxis*); foliage designated with gray A (*Abies*), R (*Arbutus*), L (*Lithocarpus*), P (*Picea*), and S (*Pseudotsuga*). Line for $\Delta^{14}C$ of atmospheric CO_2 is illustrated. So that all symbols could be individually distinguished, x-axis locations were increased slightly for four symbols for *Morchella*, two symbols each for *Plicaria* and *Picea*, and one symbol each for *Geopyxis* and *Abies*.

atmospheric CO_2 in $\Delta^{14}C$ and *Morchella* consistently higher in $\Delta^{14}C$ (FIG. 2b). Carbon in *Morchella* averaged 11 $\pm$ 6 y old, *Plicaria* averaged 17 $\pm$ 5 y old (n = 3) and foliage averaged 1 $\pm$ 2 y old. *Geopyxis* (n = 1) resembled foliage in $\Delta^{14}C$.

DISCUSSION

Morchella is a large genus with an estimated 65 phylogenetically distinct species worldwide, some of which appear endemic to North America based on recent phylogenetic investigation (O'Donnell et al. 2011, Richard et al. 2014, Du et al. 2015). Morels occur in diverse habitats and some species within the "black morel" elata clade commonly fruit after fire (Kuo et al. 2012, Masaphy and Zabari 2013). In an investigation of ectomycorrhizal root tips after a low severity fire Fujimura et al. (2005) observed *Morchella* sporocarps but found no Pinaceae root tips colonized by *Morchella* at their site. Furthermore, stable isotope measurements have suggested that some species of *Morchella* are saprotrophic (Harrington et al. 1999, Hobbie et al. 2001). In contrast, two species of *Morchella* from forests not recently burned formed ectomycorrhizal structures (mantles and Hartig nets) with four species of Pinaceae, specifically *Larix occidentalis* Nutt., *Pinus contorta* Loudon, *Pinus ponderosa* Douglas ex C. Laws. and *Pseudotsuga menziesii* (Mirb.) Franco (Dahlstrom et al. 2000). Both the esculenta and the elata clades contain species from diverse habitats including hardwood and coniferous forests with ectomycorrhizal hosts as well as environments without ectomycorrhizal trees, such as older apple orchards, gardens and woodchips (Kuo et al. 2012).

The role of fungi in ecosystem processes includes nutrient acquisition and cycling; however, the precise ecological functions of many fungal species after fire remain undetermined (Claridge et al. 2009). *Morchella*, *Plicaria* and *Geopyxis* belong to three families within Pezizales, a large and heterogeneous order of Pezizomycetes known from a broad range of habitats, including recently burned sites (Fujimura et al. 2005, Hansen et al. 2013). Within the family Morchellaceae morels are well-known post-fire fungi and typically fruit 1–2 y after forest fires (Pilz et al. 2007, Greene et al. 2010). Most species of Pyronemataceae have been considered saprotrophic (Hansen et al. 2013). However, within this family, which includes *Geopyxis*, ectomycorrhizal taxa may have evolved multiple times from saprotrophic ancestors (Hansen et al. 2013). Furthermore, Tedersoo et al. (2006) describe ectomycorrhiza-forming taxa within multiple families of Pezizales.

Isotopic patterns between fungi and potential nitrogen and carbon sources can provide insight into resource partitioning. In a prior Oregon study litter was only 1‰ higher in $\delta^{15}N$ than needles of dominant trees (-2.3 ± 0.9‰ vs. -3.3 ± 1.3‰) (Hobbie et al. 2012) and in other reports sporocarps of litter decay fungi were 3–5‰ enriched in ^{15}N relative to litter and foliage (Hobbie et al. 2005, 2014b). High ^{15}N enrichment in *Morchella* suggested that recent litter was not the primary source for *Morchella* nitrogen, which also is indicated by greater *Morchella* fruiting after extensive duff removal through fire (Winder and Keefer 2008) and abundant *Morchella* fruiting after intensive fire and ground disturbance by machinery (Masaphy and Zabari 2013). Similar ^{13}C and ^{15}N

enrichments of *Morchella* to *Plicaria* suggest that *Morchella* may assimilate its carbon and nitrogen from the same source as this saprotrophic fungus. Literature values for $\delta^{13}C$ for saprotrophic fungi were similar to those here for *Plicaria* and *Morchella*, with Mayor et al. (2009) reporting site averages of −23.0‰ and −25.5‰ for saprotrophic fungi and ectomycorrhizal fungi, respectively, in a worldwide compilation. Worldwide averages of $\delta^{15}N$ for saprotrophic fungi (−0.3‰) were lower than those reported here, suggesting either that *Morchella* may rely on other nitrogen sources than most saprotrophic fungi or that the fire-dominated systems where *Morchella* occurs in western North America have higher $\delta^{15}N$ signatures in general (e.g. in plants, fungi, soils) than previously studied systems. By removing surficial, ^{15}N-depleted litter layers, fire will increase $\delta^{15}N$ of the remaining soil and plants growing post-fire (Boeckx et al. 2005). However, we lack sufficient information about other saprotrophic fungi from these same locations to warrant further speculation. Even higher $\delta^{15}N$ values in saprotrophic fungi than those given here have been reported from two studies, one on the saprotrophic *Amanita thiersii* from Midwestern lawns (Wolfe et al. 2012) and the other on *Hygrocybe* from grasslands (Gareth et al. 2012).

Morchella ascocarps in our study were enriched by 5‰ in ^{13}C relative to foliage. This is similar to the ^{13}C enrichment of 4.8‰ of litter decay fungi relative to *Pseudotsuga menziesii* foliage observed in samples from the Oregon Coast Range (Hobbie et al. 2001), and contrasts with ^{13}C enrichments of 6.3‰ and 2.4‰ of wood decay fungi and ectomycorrhizal fungi, respectively, from the same study. In a second Oregon study (FIG. 1) caps of wood-decay fungi, litter decay fungi and ectomycorrhizal fungi averaged 6‰, 6‰ and 4‰ enriched in ^{13}C relative to needles (Hobbie et al. 2012).

Two other post-fire fungi were collected and analyzed for stable isotopes. *Geopyxis carbonaria* has been reported as ectomycorrhizal with *Picea abies* (L.) Karst. in Norway (Vrålstad et al. 1998) and presumably was ectomycorrhizal with conifers in this study, although we did not confirm this through detailed analyses of root materials. Its mean $\delta^{13}C$ value was lower by 3‰ than *Morchella* at −25.5‰ and was similar to the mean value of −25‰ of ectomycorrhizal fungi in an extensive survey of Oregon sporocarps that suggested ectomycorrhizal status. Saprotrophic fungi in that same survey averaged −23‰. The other fungal species analyzed, *Plicaria endocarpoides*, has been reported as saprotrophic (Warcup 1990, Motiejūnaitė et al. 2014). One $\delta^{13}C$ value resembled *Geopyxis* and one resembled *Morchella*, so based on stable isotopes alone we cannot assign it to one or the other life-history strategy. In the multiple regression analysis (TABLE III), the $\delta^{13}C$ coefficient for *Plicaria* was about 2‰ higher than that for *Geopyxis*, suggesting saprotrophic status for *Plicaria*. Its $\delta^{15}N$ resembled that of *Morchella*, although we lack sufficient information on $\delta^{15}N$ patterns in post-fire fungi to make this a useful marker. $\delta^{13}C$ did not correlate significantly with climatic parameters, although comprehensive literature compilations have illustrated how temperature and precipitation influence plant $\delta^{13}C$ over large spatial scales, with higher temperatures and less precipitation associated with higher $\delta^{13}C$ values (Kohn 2010). Because fungi ultimately rely on plant photosynthate for their carbon, fungal $\delta^{13}C$ likewise should correlate with climatic parameters. The lack of correlation may therefore reflect the rather restricted climatic space of our Alaskan and Oregon sites (TABLE I) relative to the climatic space occupied in the Kohn (2010) compilation.

Although we could have assumed various distributions of radiocarbon age, such as assuming that carbon over a 10 y period contributed equally to sporocarp carbon, for simplicity we assumed that all carbon derived from a single year, as estimated from radiocarbon values, because we had no specific basis for assuming any particular age distribution. In their life cycle *Morchella* spp. form vegetative resting structures (sclerotia) that can overwinter (Volk and Leonard 1990) and that are important for future sporocarp formation (Kanwal and Reddy 2012). However, we did not find evidence in the literature for multiyear persistence of these sclerotia and thus think that our radiocarbon age estimates are a reasonable proxy for the age of the assimilated carbon.

Radiocarbon measures the age of carbon since fixation from CO_2, and appears more definitive than stable isotopes for assessing ectomycorrhizal or saprotrophic status in fungi. In a prior radiocarbon study in an Oregon *Pseudotsuga menziesii* stand, carbon of the ectomycorrhizal taxa *Amanita*, *Cantharellus*, *Gomphidius* and *Tuber* had an estimated age of 0–2 y, whereas individual samples of three saprotrophic taxa were 11 y (*Lepiota*), 18 y (*Hypholoma*) and 50+ y (*Pleurocybella*), respectively (Hobbie et al. 2002). Here *Morchella* carbon was 2–22 y old and averaged 11 y old. Based on the radiocarbon measures (FIG. 2) we conclude that *Morchella* in these post-fire environments is saprotrophic. Although *Morchella* appears capable of assimilating carbon of a wide range of ages, we cannot deduce whether it can use carbon of different qualities and degradability, in that our approach is necessarily restricted to *Morchella* that have produced sporocarps. Despite this fact radiocarbon appears to be a powerful tool for assessing fungal carbon sources for taxa of uncertain life history.

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