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Carbon cycling through plant and fungal herbarium specimens tracks the Suess effect over more than a century of environmental change

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ABSTRACT

Although the anthropogenic decline in atmospheric carbon stable isotope ratios ($\delta^{13}C$) over the last 150 years (termed the Suess effect) is well-studied, how different terrestrial trophic levels and modes reflect this decline remains unresolved. To evaluate the Suess effect as an opportunistic tracer of terrestrial forest carbon cycling, this study analyzed the $\delta^{13}C$ in herbarium specimens collected in Minnesota, USA from 1877 to 2019. Our results suggest that both broadleaf trees and ectomycorrhizal fungi relied on recent photosynthate to produce leaves and sporocarps, while saprotrophic fungi on average used carbon fixed from the atmosphere 32–55 years ago for sporocarp construction. The $\delta^{13}C$ values of saprotrophic fungal collections were also sensitive to the age of their plant carbon substrate, with sporocarps of twig specialists tracking changes in atmospheric $\delta^{13}C$ more closely than saprotrophs growing on logs. Collectively, this study indicates that natural history collections can quantitatively track carbon cycling among plants and fungi over time.

1. Introduction

Anthropogenic carbon emissions have progressively labeled the atmosphere with isotopically light carbon (^{12}C) over the past two centuries. This is primarily due to the burning of fossil fuels, which are ^{13}C-depleted and thus impart a greater light carbon signature on the atmosphere (Keeling, 1979). From 1877 to 2019, atmospheric $\delta^{13}C$ (the ratio of ^{13}C–^{12}C compared to the ratio in the reference standard) dropped by approximately 1.9‰ (Keeling, 1979; Belmecheri and Lavergne, 2020). This overall trend is actually best described by a piecewise linear function, characterized by a gradual decline from approximately 1850 until 1957, and a steeper decline thereafter (Belmecheri and Lavergne, 2020). These differing rates of decline coincide closely with global carbon dioxide emissions, which increased five-fold from 1957 to 2022 (Andrew and Peters, 2023).

The anthropogenic change in atmospheric $\delta^{13}C$, termed the Suess effect, serves as an opportunistic label that can be tracked over time through isotopic analysis of natural history collections. For example, studies of marine organisms (corals, reef fishes) have shown consistent changes in tissue $\delta^{13}C$ that closely tracked the incorporation of progressively lighter C (more ^{12}C) in recent decades (Swart et al., 2010; Sabadel et al., 2020). While this effect is relatively widely recognized in marine ecosystems, how it manifests in terrestrial systems is less well documented (Hobbie et al., 2020). Testing whether the Suess effect manifests across different trophic levels and trophic modes is particularly important, as it will reflect the rate at which carbon moves into and through terrestrial ecosystems.

Fungi, as heterotrophs, have diverse trophic modes that affect how and when they assimilate photosynthetically-derived carbon. Ectomycorrhizal fungi are functionally obligate symbionts of plants and are characterized by their dependence on recent photosynthate (Högberg et al., 2010; Smith and Read, 2010; Hobbie et al., 2021), while saprotrophic fungi assimilate carbon from dead organic matter of variable ages (Hobbie et al., 2002, 2016, 2020; Newsham et al., 2018). These aspects of their ecology should affect their temporal $\delta^{13}C$ trends: ectomycorrhizal fungi should closely track the isotopic composition of photosynthate, while saprotrophic fungal $\delta^{13}C$ should mirror the composition of their substrate (e.g. leaf litter, logs, twigs).

Based on differing rates of decline in atmospheric $\delta^{13}C$ over the past 150 years, the isotopic composition of leaves produced by broadleaf trees, which incorporate recent photosynthate and stored carbon (Gaudinski et al., 2009; Muhr et al., 2016), should decline more steeply after 1957. Accordingly, ectomycorrhizal fungal $\delta^{13}C$, relying predominantly on photosynthate, should also decline more steeply after 1957.

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The point at which saprotrophic fungal δ^{13}C declines more steeply should reflect the average age of their substrate, providing a novel estimate of the age of fungal-available carbon in organic matter. For example, the overall decline in δ^{13}C should be less among saprotrophic fungi growing on older substrates (i.e., logs) than newer substrates (i.e., twigs), reflecting the slower decline in atmospheric δ^{13}C before 1957.

To evaluate these predictions, we analyzed the isotopic composition of 561 plant and fungal samples collected in Minnesota, USA between 1877 and 2019. First, we fit mixed linear models with appropriate random effects to evaluate whether δ^{13}C declined more quickly in plants and ectomycorrhizal fungi than in saprotrophic fungi. We then fit piecewise linear models to plant and fungal δ^{13}C and compared breakpoint values for recent photosynthate relative to saprotrophic fungi to estimate the average age of saprotrophic fungal carbon. Finally, we used a mixed linear model to assess whether δ^{13}C trends of saprotrophic fungi growing on twigs had a steeper negative slope than those growing on logs. Collectively, these analyses allow for quantitative estimates of the movement of carbon from the atmosphere through various forest trophic pools.

2. Materials and methods

2.1. Sample selection

Plant ($n = 286$) and fungal ($n = 275$) specimens collected in Minnesota from 1877 to 2019 were selected from the Bell Herbarium at the University of Minnesota. Plant collections represent eight common genera of woody plants (*Acer, Betula, Fraxinus, Juglans, Populus, Prunus, Tilia*, and *Ulmus*). The 109 ectomycorrhizal fungal specimens represent three common genera (*Amanita, Laccaria,* and *Scleroderma*). Of the 166 saprotrophic fungal collections, six genera are represented (*Cerioporus, Lycoperdon, Marasmius, Neofavolus, Phellinus,* and *Trichaptum*). Saprotrophic fungi specific to logs include *Trichaptum biforme*, *Phellinus gilvus*, and *Lycoperdon pyriforme*. Twig specialists include *Neofavolus alveolaris* and *Cerioporus leptocephalus* (Bessette et al., 1997; Kuo and Methven, 2014). Habitat descriptions of collections were referenced to confirm substrate specificity. Further information about sampling is available in Table 1.

2.2. Elemental and isotopic analysis

Air-dried foliar and sporocarp tissues were ground and packed at a mass of 1.2 ± 0.05 mg to the nearest 0.001 mg. Due to a multi-stage process of data generation, samples were analyzed at three different facilities. Samples were analyzed via an Elementar Vario Pyrocube (Hanau, Germany) interfaced to an Isoprime 100 isotope ratio mass spectrometer (Cheadle, UK) at the University of Minnesota, an Elementar Vario EL Cube interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California-Davis Stable Isotope Facility, or an Elementar Cube elemental analyzer interfaced to a GV Instruments Isoprime isotope ratio mass spectrometer (Manchester, UK) at Boston University Stable Isotope Laboratory. Samples at all facilities were run with internal control standards to ensure comparable data quality and comparisons of ^{15}N from a subset of the same specimens revealed no effect of facility on the obtained values (Michaud et al., 2023).

Table 1
Genus-level summary of collections analyzed in this study with reference to their ecological group (Sap: saprotrophic fungus, Ecto = ectomycorrhizal fungus, Plant = broadleaf tree), genus, number of species sampled in each genus (Species), and number of collections (Count).

Group	Genus	Species	Count
Sap	*Cerioporus*	1	16
Sap	*Lycoperdon*	12	36
Sap	*Marasmius*	10	36
Sap	*Neofavolus*	1	20
Sap	*Phellinus*	1	23
Sap	*Trichaptum*	1	35
Ecto	*Amanita*	8	47
Ecto	*Laccaria*	8	37
Ecto	*Scleroderma*	8	25
Plant	*Acer*	3	51
Plant	*Betula*	4	51
Plant	*Fraxinus*	1	36
Plant	*Juglans*	2	23
Plant	*Populus*	2	36
Plant	*Prunus*	1	28
Plant	*Tilia*	1	34
Plant	*Ulmus*	2	27

2.3. Statistical analyses

All statistical analyses were performed in R (version 4.1.2, R Core Team, 2021). Historical estimates of atmospheric δ^{13}C were compiled from Belmecheri and Lavergne (2020). To assess differences in the slope of δ^{13}C over time among plants, ectomycorrhizal fungi, and saprotrophic fungi, a linear mixed model was constructed using the lme4 and lmerTest packages (Bates et al., 2015; Kuznetsova et al., 2017) with random effects accounting for location (collection county), taxonomy (genus), and seasonality (month collected). Random effects were then backwards selected using the Akaike information criterion (AIC, threshold = 2) with the "step" function (base package) preserving genus alone. Group (plant, ectomycorrhizal fungus, saprotrophic fungus), year, and their interaction were included as fixed effects.

To assess the potential for differing rates of δ^{13}C decline over time, we investigated whether there was a breakpoint in δ^{13}C, i.e. when the slope of δ^{13}C decline was estimated to change, for atmospheric δ^{13}C and for each group. To estimate the breakpoint for atmospheric δ^{13}C based on the data of Belmecheri and Lavergne (2020), we used the "segmented" function in the segmented package on a linear model fit with interpolated δ^{13}C as the response variable and year as the independent variable, indicating that year was the variable to segment. For each group, a segmented or piecewise linear model was fit by first fitting a mixed linear model (Bates et al., 2015; Kuznetsova et al., 2017) with month, genus, and county as random effects and year as a fixed effect, performing backwards AIC selection on random effects to fit more parsimonious models, and then regressing the partial residuals from the reduced mixed model related to year against year using "lm" (base backage). A piecewise linear model was then fit using the function "segmented" (segmented package) (Muggeo, 2008) to estimate the most probable year at which the slope of δ^{13}C changed. The "conf.interval" function was used to produce confidence intervals and standard errors around the estimated breakpoints for each group. This enabled testing the differences among δ^{13}C breakpoints in plants, ectomycorrhizal fungi, and saprotrophic fungi via z-tests.

A subset of saprotrophic fungi were also used to test whether substrate age was linked with carbon age. Specifically, we identified saprotrophic fungi specific to logs and trunks (*Lycoperdon pyriforme,* $n = 19$*, Phellinus gilvus,* $n = 23$*, Trichaptum biforme,* $n = 35$) versus those growing on small branches and twigs (*Cerioporus leptocephalus,* $n = 16$*; Neofavolus alverolaris,* $n = 20$). Substrate specificity was also verified via observational notes included in the record collections. Potential differences in temporal δ^{13}C trends were tested using a linear mixed effects model (Bates et al., 2015; Kuznetsova et al., 2017). To test for slope differences reflecting substrate age, the model included a fixed term representing time (year collected) with an interaction between substrate (log or twig) and year. Random effects accounting for differences in taxonomy (species), and location (county of collection) were backwards AIC selected, yielding species alone as a random effect.

3. Results

3.1. *Historical declines in atmospheric, plant, and fungal $\delta^{13}C$*

As noted above, atmospheric $\delta^{13}C$ declined by 1.9‰ from 1877 to 2019 (Belmecheri and Lavergne 2020). Mixed linear modeling estimated that over the same period foliar $\delta^{13}C$ declined 3.5‰ on average (−0.024 ± 0.002‰ yr^{-1}, $t = -12.108$, $p < 0.001$), from −25.8‰ (95% CI: −26.4‰ to −25.3‰) to −29.3‰ (−29.8‰ to −28.8‰). Ectomycorrhizal fungal $\delta^{13}C$ declined by 2.4‰ on average (−0.017 ± 0.004‰ yr^{-1}, $t = -4.776$, $p < 0.001$), from −22.7‰ (−23.6‰ to −21.9‰) to −25.6‰ (−26.3‰ to −24.8‰), while saprotrophic fungal $\delta^{13}C$ declined 1.1‰ on average (−0.008 ± 0.003‰ yr^{-1}, $t = -2.984$, $p = 0.003$), from −22.7 (−23.4‰ to −22.0‰) to −23.8‰ (−24.4‰ to −23.2‰). Overall, the model explained 75.6% of the variation in the data (marginal $r^2 = 0.698$, conditional $r^2 = 0.756$). These declines differed significantly across groups, with saprotrophic fungal $\delta^{13}C$ declining significantly less than in plants ($t = -4.914$, $p < 0.001$) and in ectomycorrhizal fungi ($t = -1.986$, $p = 0.048$) (Fig. 1). Additionally, ectomycorrhizal fungal $\delta^{13}C$ declined less than in plants, although this trend was marginally significant ($t = -1.907$, $p = 0.057$) (Table S1).

3.2. *Breakpoint differences between atmospheric, foliar, and fungal $\delta^{13}C$*

A significant breakpoint, or the most probable year in which the slope of $\delta^{13}C$ decline changed, was detected in atmospheric $\delta^{13}C$ between 1956 and 1957 ($r^2 = 0.99$, 95% CI: 1956.2–1957.5, $p < 0.001$), consistent with separating an early period of shallow $\delta^{13}C$ decline from a later steep decline (Fig. 2A). In plants, after accounting for variation arising from the month of the collection and plant genus, a breakpoint was detected in 1957 ($r^2 = 0.31$, 1932.0–1982.0, $p = 0.013$) (Fig. 2B). In saprotrophic fungi, a marginally significant breakpoint was estimated at 2001 ($r^2 = 0.09$, 1989.2–2012.9, $p = 0.087$), after accounting for non-independence arising from genus identity (Fig. 2D). The breakpoint in $\delta^{13}C$ in saprotrophic fungi was significantly later than for the atmosphere and plants ($z = -7.351$, $p < 0.001$; $z = -3.129$, $p < 0.001$), while the breakpoint in plants was comparable to that in the atmosphere ($z = -0.013$, $p = 0.494$) (Fig. 2). In ectomycorrhizal fungi, after accounting for the same sources of potential non-independence, no significant breakpoint was detected ($p = 0.652$, Fig. 2C). Comparing the earlier and later slopes of saprotrophic fungi, plants, and the atmosphere revealed no significant differences based on 95% confidence intervals (Fig. S1).

3.3. *Difference in $\delta^{13}C$ trend among twig and log rotters*

In log-rotting saprotrophic fungi, $\delta^{13}C$ did not decline significantly over time ($p = 0.139$). In twig-rotting saprotroph fungi, however, $\delta^{13}C$ declined 2.2‰ on average (−0.015 ± 0.004‰ yr^{-1}, $t = -3.862$, $p < 0.001$) from −22.8‰ in 1877 (−23.8‰ to −21.8‰) to −25.0‰ in 2019 (−25.9‰ to −24.1‰). Comparing these two groups, the slope of $\delta^{13}C$ among log saprotrophs was significantly different from that of twig saprotrophs ($t = 2.115$, $p = 0.037$, Fig. 3). This model explained 35.9% of the variation in $\delta^{13}C$ (marginal $r^2 = 0.207$, conditional $r^2 = 0.359$) (Table S2).

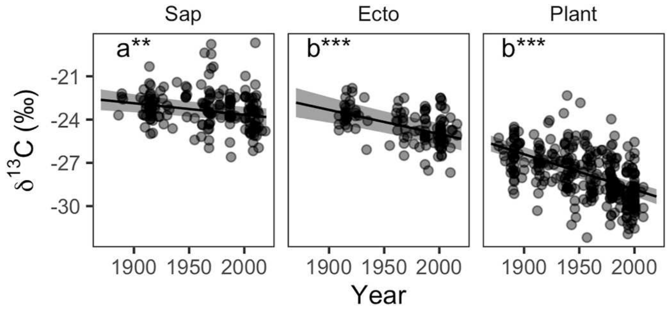

Fig. 1. Trends in tissue $\delta^{13}C$ among herbarium specimens, including saprotrophic (Sap) fungal sporocarps, ectomycorrhizal (Ecto) fungal sporocarps, and plant leaves over time. Letters denote significant slope differences, while the asterisks denote the significance of the trend (***: $p < 0.001$, **: $p < 0.01$).

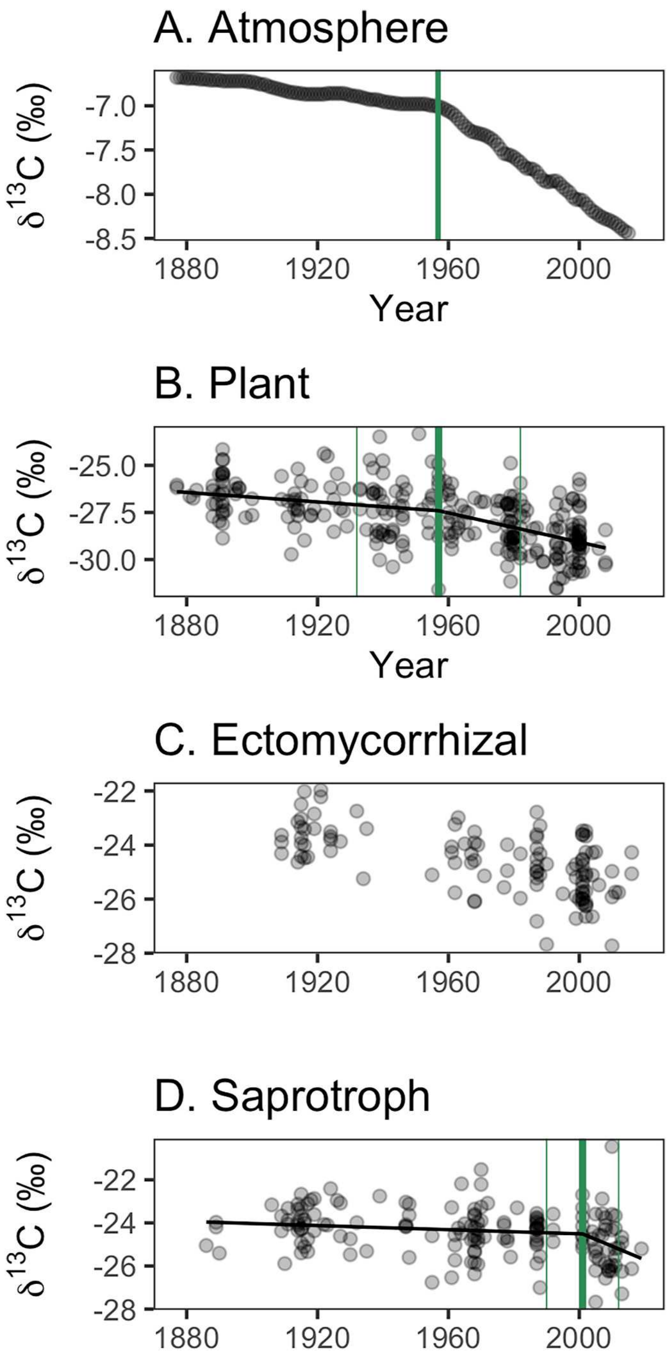

Fig. 2. Trends in tissue $\delta^{13}C$ over 14 decades. Differences in $\delta^{13}C$ breakpoint estimates are illustrated in green among (A) the atmosphere, (B) broadleaf trees, (C) ectomycorrhizal fungi, and (D) saprotrophic fungi (thick line = breakpoint estimate, thin lines = 95% confidence interval around estimate).

4. Discussion

In this study, we evaluated whether the Suess effect generated an opportunistic isotopic label in plant and fungal herbarium specimens that could track various aspects of terrestrial carbon cycling. Specifically, we compared 1) cumulative declines in $\delta^{13}C$ across broadleaf

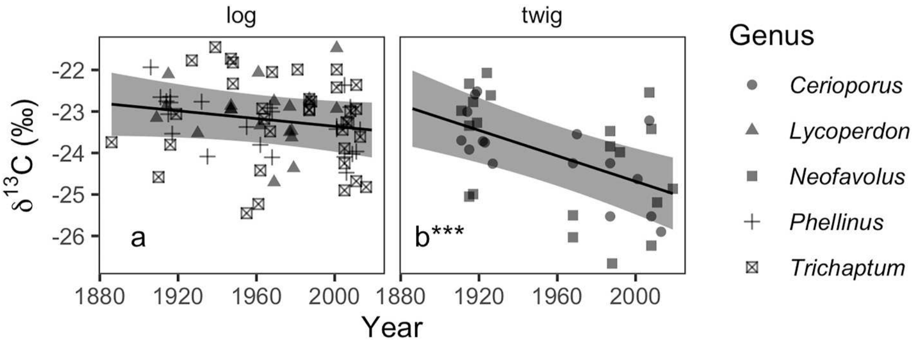

Fig. 3. Patterns in the δ^{13}C decline over time of twig-rotting and log-rotting saprotrophic fungi, with 95% confidence intervals around the mean line. Letters denote significant slope differences, while the asterisks denote the significance of the trend (***: $p < 0.001$). Point shapes correspond to fungal genus.

trees, ectomycorrhizal fungi, and saprotrophic fungi, 2) breakpoint estimates in δ^{13}C across the three groups, and 3) cumulative declines in δ^{13}C across saprotrophic fungi specializing on substrates of different ages (twigs versus logs). In line with our expectations, we found evidence that the Suess effect generated a strong isotopic signal in the carbon of both plant and fungal herbarium specimens. Our results indicated that leaves of broadleaved plants and ectomycorrhizal fungal sporocarps contained very recent carbon while sporocarps of saprotrophic fungi were built from carbon fixed 44 years prior to collection on average (i.e. saprotrophic fungal δ^{13}C breakpoint minus that of the atmosphere). Furthermore, among saprotrophs, δ^{13}C trends differed with substrate age, with twig-rotters reflecting the steep decline in atmospheric δ^{13}C since 1957 unlike log-rotters.

While the analysis of δ^{13}C breakpoints requires high sample size given data noisiness, our results suggest that this approach offers a novel method of estimating the age of fungal and plant carbon. Breakpoint analysis has been previously used with δ^{15}N values from herbarium specimens to approximate the onset of δ^{15}N decline in leaves (McLauchlan et al., 2010); this study extends its usage to natural abundance δ^{13}C, taking advantage of the piecewise decline in atmospheric δ^{13}C to estimate carbon age in both fungi and plants. The breakpoint detected in atmospheric δ^{13}C around 1957 was similar for plants, which is consistent with plant reliance on recent photosynthate to construct leaves (Gaudinski et al., 2009). In contrast, the 32–55 year delay in the breakpoint of saprotrophic fungi suggests a significant lag between when carbon is fixed from the atmosphere by plants and the production of fungal sporocarps resulting from its decomposition (Hobbie et al., 2016, 2020). We emphasize that the length of delay depends on the portion of the saprotrophic community sampled, which in our case was strongly biased towards wood-rotting fungi. Dendrochronological analysis reveals that wood δ^{13}C declines over time, supporting that wood δ^{13}C mirrors atmospheric δ^{13}C (Leavitt and Lara, 1994; Arneth et al., 2002; Robertson, et.al., 2004; Bassett et al., 2023), and passes that signature onto the fungi that decompose it.

The lack of a breakpoint among ectomycorrhizal fungi was surprising given the similar Suess effect trends between this fungal guild and plants. We suspect this absence may be due to differences in data composition; relative to plants, the ectomycorrhizal fungal samples were less numerous and absent between 1935 and 1955, the two decades prior to the δ^{13}C breakpoint that emerges in the atmosphere. The lack of a breakpoint may alternatively reflect differences in organic nitrogen (N) acquisition ability among ectomycorrhizal fungal species. In previous studies, ectomycorrhizal fungi varied considerably in their use of organic N, which contains carbon with higher δ^{13}C (Hobbie et al., 2013; Chen et al., 2016; Vaario et al., 2019). Incorporation of organic N may therefore obscure temporal trends when analyzed in aggregate, explaining why ectomycorrhizal fungal δ^{13}C does not directly match photosynthate or atmospheric δ^{13}C. This interpretation is bolstered somewhat by the marginally steeper decline in δ^{13}C among plants compared to ectomycorrhizal fungi that may reflect incorporation of older, ^{13}C- enriched carbon among some taxa. Alternatively, if any of the ectomycorrhizal fungi sampled were associated with trees not included in this study, then the δ^{13}C of those trees and the photosynthate passed to the ectomycorrhizal fungi could differ from the trees we measured. While this result may be due to the absence of ectomycorrhizal fungal observations during this temporal window, future work will need to investigate whether incorporation of soil-derived organic C into ectomycorrhizal fungal biomass could be significant enough to affect delta ^{13}C values.

Our comparison of twig-rotting fungi versus log-rotting fungi is also consistent with the time-dependent nature of saprotrophic fungal δ^{13}C. In line with the timing of plant tissue construction, the steeper decline in δ^{13}C over time among twig-rotters compared to log-rotters reflects that twig-rotters build sporocarps with more recently fixed carbon compared to log-rotters, thus indexing over more recent, steeper declines in atmospheric δ^{13}C. Logs contain many more years of carbon accumulation than twigs, leading us to hypothesize that log-rotting fungi would decline less in δ^{13}C than twig-rotting fungi. Their δ^{13}C did not decline at all. Given that this result emerged, we are confident that δ^{13}C in saprotrophic fungal collections is sensitive enough to track historical carbon cycling, opening a novel line of research. For example, differences in rates of organic matter decomposition could presumably be compared over geographic space using historical collections of the same fungal species. Additionally, this approach could be used with species-level collections of ectomycorrhizal fungi to assess differences in organic nitrogen use. The δ^{13}C of caps (high in protein) versus stipes (low in protein) of individual sporocarps could be compared over time, with a hypothesized greater ^{13}C enrichment of caps in more recent collections reflecting a greater ^{13}C enrichment of soil-derived organic N relative to recent photosynthate.

Collectively, our findings indicate that natural abundance δ^{13}C in preserved herbarium specimens is sensitive to the Suess effect, allowing us to track carbon age and cycling over historical timescales. Notably, our results highlight that broadleaf trees and ectomycorrhizal fungi build leaves and sporocarps with more recently fixed carbon than that in sporocarps of saprotrophic fungi. This finding, while not novel, demonstrates that the Suess effect can be used to track carbon cycling via longitudinal surveys of plant and fungal herbarium specimens. Given this demonstrated sensitivity, we encourage the use of natural history collections in conjunction with experimental studies to better understand terrestrial carbon cycling dynamics across different time scales.

Declaration of generative AI in scientific Writing

None declared.

Submission declaration

None declared.

Data availability

Data supporting the findings of this study are available at the Data Repository for the University of Minnesota (DRUM), https://doi.org/10.13020/DCC7-6R87.

CRediT authorship contribution statement

Talia Michaud: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Erik Hobbie:** Writing – review & editing, Writing – original draft, Validation, Conceptualization. **Peter Kennedy:** Writing – review & editing, Writing – original draft, Validation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2024.101372.

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