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ARTICLE

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The coupling of green and brown food webs regulates trophic position in a montane mammal guild

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Abstract

Food web ecology has revolutionized our understanding of ecological processes, but the drivers of food web properties like trophic position (TP) and food chain length are notoriously enigmatic. In terrestrial ecosystems, above- and belowground systems were historically compartmentalized into "green" and "brown" food webs, but the coupling of these systems by animal consumers is increasingly recognized, with potential consequences for trophic structure. We used stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) of individual amino acids to trace the flow of essential biomolecules and jointly measure multichannel feeding, food web coupling, and TP in a guild of small mammals. We then tested the hypothesis that brown energy fluxes to aboveground consumers increase terrestrial food chain length via cryptic trophic transfers during microbial decomposition. We found that the average small mammal consumer acquired nearly 70% of their essential amino acids (69.0% ± 7.6%) from brown food webs, leading to significant increases in TP across species and functional groups. Fungi were the primary conduit of brown energy to aboveground consumers, providing nearly half the amino acid budget for small mammals on average (44.3% ± 12.0%). These findings illustrate the tightly coupled nature of green and brown food webs and show that microbially mediated energy flow ultimately regulates food web structure in aboveground consumers. Consequently, we propose that the integration of green and brown energy channels is a cryptic driver of food chain length in terrestrial ecosystems.

KEYWORDS
compound-specific stable isotope analysis, multichannelling, *Peromyscus maniculatus*, Rocky Mountains, *Sorex cinereus*, *Sorex monticola*, stable isotope fingerprinting, trophic level

INTRODUCTION

Despite nearly a century of research, identifying the drivers of trophic structure and energy flow remains one of the most elusive problems in ecology (Elton, 1927; Lindeman, 1942; Post & Takimoto, 2007; Pringle & Hutchinson, 2020). Natural food webs contain countless reticulate connections between consumers and resources that link energy channels and dictate trophic structure at multiple scales (Polis, 1991; Polis &

Strong, 1996). Historically, food webs were classified as either "green" grazer chains stemming from primary producers or "brown" detrital chains with decomposers fueled by detritus (Figure 1; Hutchinson, 1959; Polis & Strong, 1996); however, the interdependence of green and brown food webs is increasingly recognized (Steffan & Dharampal, 2019; Wolkovich et al., 2014). Indeed, brown food webs are inherently donor controlled (Hairston et al., 1960), and up to 90% of green primary production escapes herbivory and is decomposed within brown webs that regulate nutrient cycling, resource availability, and biodiversity (Cebrián, 1999; Moore et al., 2004). Animal consumers likewise link green and brown energy channels through multichannel feeding that governs the stability of ecosystem processes (Wolkovich et al., 2014; Zou et al., 2016). Collectively, this coupling of green and brown food webs is critical to trophic structure and ecosystem function, but while

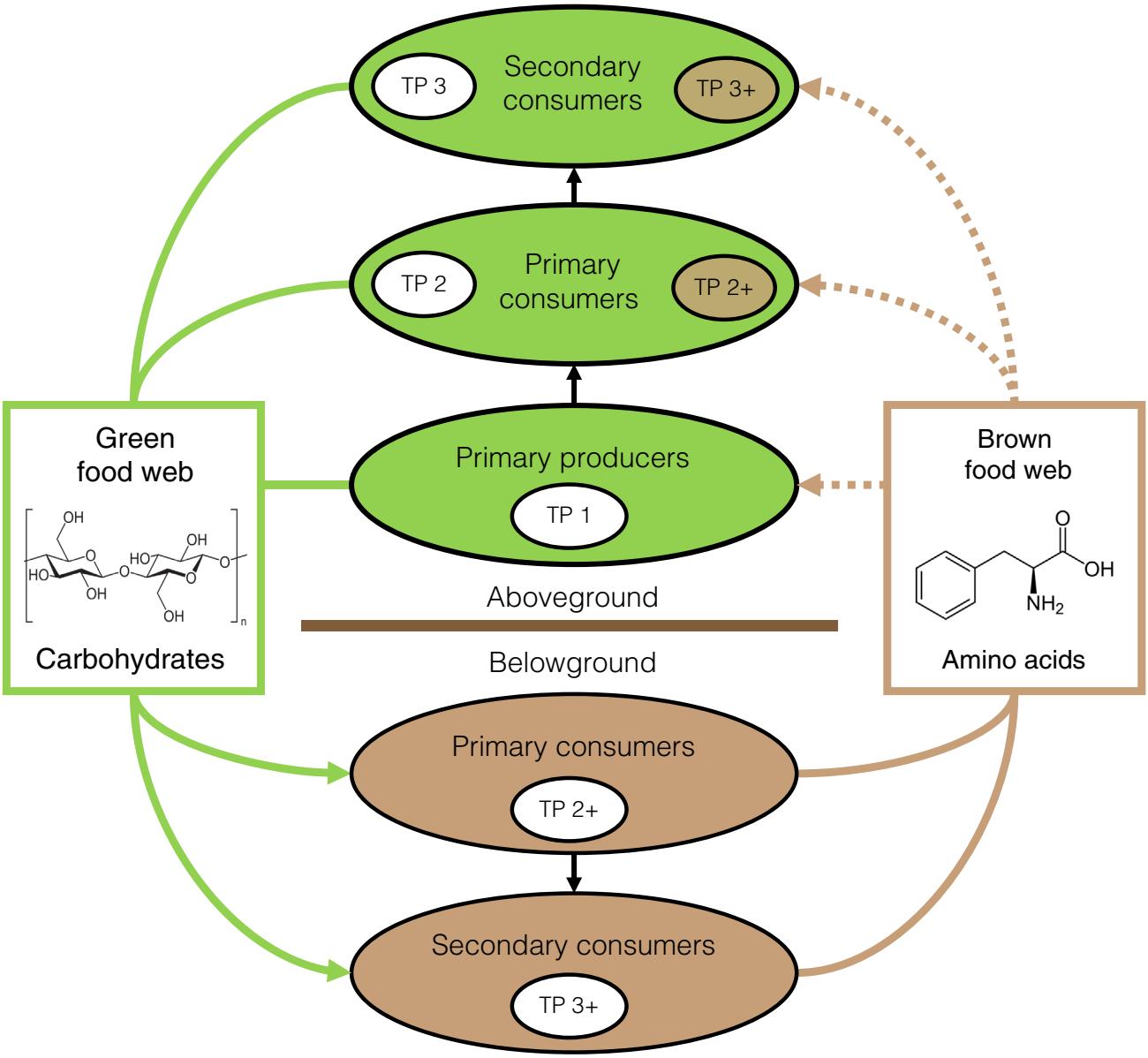

FIGURE 1 Conceptual model of green–brown food web coupling and the impact on trophic structure. Residual energy from green, aboveground webs—primarily in the form of structural carbohydrates like cellulose—is concentrated in brown, belowground webs (solid green lines), where it is decomposed and transformed into useable biomolecules like amino acids. The reciprocal flow of this brown energy to green, aboveground food webs is uncertain (dashed brown lines), and this unquantified energy flux has the potential to alter consumer trophic position (TP) and food chain length. Large ovals represent classical trophic levels in aboveground (green) and belowground (brown) food webs. Small white ovals represent assumed TPs, and small brown ovals represent hypothesized increases in TP due to brown energy integration.

the flow of green energy to brown food webs is well established, the reciprocal flow of brown energy to "aboveground" consumers is unclear (Figure 1).

Trophic levels and food chain length are the most enigmatic and controversial aspects of trophic structure. Considerable debate has surrounded ecologists' ability to measure trophic levels (Oksanen, 1991), and numerous hypotheses have been proposed to explain variation in food chain length across ecosystems (Post & Takimoto, 2007). For example, classic theories like the trophic-dynamic concept suggest primary production limits food chain length via energy constraints (Hutchinson, 1959; Lindeman, 1942), but emergent hypotheses have identified ecosystem size and disturbance as additional drivers (Post & Takimoto, 2007). In terrestrial ecosystems, the mechanisms governing food web structure remain uncertain as contemporary studies have reported contrasting empirical support for all three hypotheses (Takimoto et al., 2008; Young et al., 2013).

The coupling of green and brown food webs can drive trophic structure and may account for the unexplained variation in terrestrial food chain length (Figure 1; Moore et al., 2004). Detritus is a significant reserve of energy in terrestrial systems, but the availability of this resource to animal consumers is mediated by both primary production and heterotrophic microorganisms (Cebrián, 1999; Hättenschwiler et al., 2005). In particular, bacterial and fungal decomposers convert residual green energy (e.g., leaf litter) into accessible brown energy by transforming recalcitrant plant matter like cellulose and lignin into digestible biomolecules like fatty acids and amino acids (Allison, 2006; Steffan & Dharampal, 2019). Animal detritivores, in turn, rely heavily on this liberated brown energy via direct microbivory and the consumption of soil organic matter (Digel et al., 2014; Pollierer et al., 2007; Potapov et al., 2019). Likewise, ectomycorrhizal fungi combine carbon (e.g., sugars) from plants with scavenged organic and inorganic nitrogen from humus to create fruiting bodies that are directly consumed by animals (Johnson, 1996; Lindahl & Tunlid, 2015). These conversions of green to brown energy and its subsequent consumption by animal consumers represent important but often overlooked trophic links that can regulate energy flow and food web structure (Polis & Strong, 1996; Steffan et al., 2017). Indeed, recent evidence suggests that these microbial conversions of recalcitrant energy are trophic analogs of classic predator–prey interactions and may represent cryptic trophic levels in terrestrial food webs (Ruess & Müller-Navarra, 2019; Steffan et al., 2015, 2017).

Food web ecology has historically been limited by an inability to accurately measure food web linkages and consumer trophic position (TP) (Oksanen, 1991; Polis, 1991). Recently, compound-specific stable isotope analysis has emerged as a promising tool to quantify food web properties (Pollierer et al., 2019). Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis of individual amino acids is particularly powerful because it can jointly trace both basal carbon sources (i.e., green vs. brown energy) and consumer TP at the individual level (Pollierer et al., 2019; Potapov et al., 2019). Essential amino acids (EAAs) are ideal biomarkers to trace the flow of green and brown energy because EAAs can only be synthesized by bacteria, fungi, and photoautotrophs (e.g., plants), each via unique biosynthetic pathways that impart distinct $\delta^{13}C$ patterns across EAAs (Besser et al., 2022). These multivariate patterns, or "fingerprints," are distinct between green (i.e., plant) and brown (i.e., bacterial and fungal) protein sources (Larsen et al., 2009). Because animals cannot synthesize EAAs de novo, they must assimilate these molecules from their diets, and EAA $\delta^{13}C$ fingerprints can then be used to quantify the use of green and brown food webs by consumers (Manlick & Newsome, 2022). Similarly, patterns in amino acid $\delta^{15}N$ values can be used to quantify consumer TP. Nitrogen isotopes have long been used to estimate TP due to the bioaccumulation of "heavy" nitrogen (^{15}N) as it passes through food chains (Post, 2002). This ^{15}N accumulation is the result of deamination and transamination during the metabolic processing of amino acids, leading to higher $\delta^{15}N$ values in consumer tissues relative to their diets. However, the degree of processing varies by amino acid such that "trophic" amino acids (e.g., glutamic acid [Glu]) increase with each trophic transfer, whereas "source" amino acids (e.g., phenylalanine [Phe]) remain largely unchanged (O'Connell, 2017). Isotopic differences between trophic and source amino acids (i.e., $\delta^{15}N_{Glu}$–$\delta^{15}N_{Phe}$) can thus be used to estimate consumer TP and food chain length (Steffan et al., 2015). Given that animals are limited by essential biomolecules like amino acids and that these constitute the vast majority of nitrogen and approximately half the carbon in animals, tracing amino acids provides a reliable proxy for energy flow and trophic structure in natural food webs (Larsen et al., 2013; Manlick & Newsome, 2022; Steffan et al., 2015).

Here, we use stable isotope analysis of individual amino acids to jointly measure multichannel feeding, food web coupling, and TP in consumers. We then test the hypothesis that decomposition of terrestrial organic matter in brown food webs increases food chain length via cryptic trophic transfers (Figure 1). Using a montane small-mammal community as a model, we first measured the $\delta^{13}C$ fingerprints of consumers and three potential energy channels (plants, fungi, bacteria). We then used Bayesian isotopic mixing models to estimate the proportional assimilation of green and brown energy by consumers from different functional groups (e.g., omnivore vs. insectivore; Manlick & Newsome, 2022). Lastly, we calculated TP for individual consumers via amino acid

$\delta^{15}N$ analysis, and we used multiple linear regression to test the relationship between brown energy assimilation and TP. We expected that all individuals would exhibit multichannel feeding, and we predicted that TP would increase significantly with the proportion of brown energy (e.g., bacteria, fungi) assimilated by individual consumers (Figure 1).

METHODS

Study site and sample collection

We quantified food web coupling and trophic structure in small mammals from the Santa Fe National Forest (NM, USA) at the southern extent of the Rocky Mountains (35°48′58.1″ N, 105°40′47.5″ W). At approximately 2500 m elevation, the system was characterized by mixed conifer forests with high snowpack, seasonal precipitation, and Alfisol soils with a cryic temperature regime (Appendix S1: Section S1). We opportunistically sampled plants and fungal fruiting bodies to characterize green and brown energy sources, and we sampled soil from xeric and mesic habitats to culture bacteria and fungi (Data File S1 in Manlick, 2022). We sampled three small mammal consumers: deer mice (*Peromyscus maniculatus*), masked shrews (*Sorex cinereus*), and montane shrews (*Sorex monticola*). Deer mice are primary consumers and generalist omnivores that directly consume both green and brown energy sources (e.g., vegetation, fungi) but also channel brown energy through the consumption of arthropod detritivores (Wolff et al., 1985). Both shrew species are insectivorous tertiary (or higher) consumers that rely heavily on detrital channels (Smith & Belk, 1996; Whitaker, 2004). We sampled muscle from each species for isotopic analysis, with tissues acquired from the University of New Mexico Museum of Southwestern Biology (UNM-MSB, Albuquerque, NM). All animals were collected by UNM-MSB in September 2019 (Data File S2 in Manlick, 2022), and tissues were immediately preserved in liquid nitrogen for long-term storage at −190°C. All sampling adhered to ethical guidelines outlined by the American Society of Mammalogists (Sikes, 2016), and specimen preservation was consistent with open-data policies (Colella et al., 2021).

Stable isotope analysis

We analyzed skeletal muscle (quadriceps femoris) from 10 individuals of each species ($N = 30$). Muscle tissue has an isotopic incorporation rate of ~90 days for small mammals (Miller et al., 2008), so our analyses represent trophic dynamics in summer (~June–September), when primary production and decomposition is highest. We measured amino acid $\delta^{13}C$ values for all consumers ($N = 30$) and sources ($N = 36$) to quantify energy channels and multichannel feeding, and we measured amino acid $\delta^{15}N$ values in all consumers ($N = 30$) and a subset of sources ($N_{plant} = 6$, $N_{fungi} = 4$, $N_{bacteria} = 4$) to estimate TP (Appendix S1: Section S1). Consumer and resource tissues were hydrolyzed and then derivatized to *N*-trifluoroacetic acid isopropyl esters for analysis via gas chromatography combustion isotope ratio mass spectrometry (GC-C-IRMS) following established protocols (Silfer et al., 1991; Appendix S1). All samples were analyzed in duplicate and bracketed by an internal reference material that was used to correct measured $\delta^{13}C$ values following O'Brien et al. (2002; Appendix S1: Table S1) and $\delta^{15}N$ following Whiteman et al. (2021). In total, we measured $\delta^{13}C$ and $\delta^{15}N$ values of 14 amino acids for each sample (Data File S1 in Manlick, 2022) and report isotope data in δ-notation as parts per mil (‰) relative to the international standards Vienna Pee Dee Belemnite and atmospheric nitrogen for $\delta^{13}C$ and $\delta^{15}N$, respectively. We conducted 22 GC-C-IRMS runs with 88 reference injections ($\bar{x} = 4.0$/run) for $\delta^{13}C$ and 18 runs with 91 reference injections ($\bar{x} = 5.1$/run) for $\delta^{15}N$. Analytical precision varied by amino acid (Appendix S1: Tables S1 and S2)—mean within-run standard deviation of reference material was ≤0.6‰ ($\bar{x} = 0.4$‰) for the six EAAs used in $\delta^{13}C$ fingerprinting and ≤0.4‰ ($\bar{x} = 0.3$‰) for the trophic and source amino acids measured for $\delta^{15}N$. All analyses were conducted at the UNM Center for Stable Isotopes (Albuquerque, NM).

EAA fingerprinting

To quantify multichannel feeding, we used $\delta^{13}C$ values from six EAAs: isoleucine (Ile), leucine (Leu), lysine (Lys), phenylalanine (Phe), threonine (Thr), and valine (Val). We combined measured values with published EAA $\delta^{13}C$ data (Larsen et al., 2009; Appendix S1) and characterized $\delta^{13}C$ fingerprints for sources using linear discriminant analysis (LDA), which maximizes separation of groups in multivariate space and can distinguish green from brown energy channels (Larsen et al., 2009; Manlick & Newsome, 2022). We trained the LDA using EAA $\delta^{13}C$ values of the three source groups, used leave-one-out cross-validation to assess classification accuracy, and then used the model to predict group membership for animal consumers. All analyses were completed in the R package mass version 7.3-54 (Ripley et al., 2013). Finally, we tested for differences in energy channeling between consumer species using a perMANOVA with 10,000 permutations of the

predicted first and second linear discriminant coordinates (hereafter, "LDA coordinates") in the R package vegan version 2.5-7 (Oksanen et al., 2013).

To quantify the proportional assimilation of energy channels by consumers, we used Bayesian mixing models in the R package simmr version 0.4.5 (Parnell & Inger, 2016). Following Manlick and Newsome (2022), we parameterized source and consumer mixtures using LDA coordinates from $\delta^{13}C$ fingerprinting and ran two separate models: (1) animals grouped by species to estimate proportional use of energy channels at the species level and (2) animals grouped by individual to estimate proportions for each consumer (Appendix S1: Section S1). To corroborate estimates from mixing models, we also quantified energy channeling with an independent LDA bootstrap using 10,000 iterations of our LDA model with random sampling of energy sources (Fox et al., 2019; Manlick & Newsome, 2022). Here, each iteration varied the source distribution to which consumers were classified, thereby providing a distribution of possible consumer classifications, which we used to estimate the mean contributions of EAAs to consumers.

Trophic position

We estimated TP for each consumer using $\delta^{15}N$ measurements from a trophic (Glu) and source (Phe) amino acid. We estimated TP following Equation (1) (Chikaraishi et al., 2009):

$$TP = \frac{\left(\delta^{15}N_{Glu} - \delta^{15}N_{Phe} - \beta\right)}{TDF_{Glu-Phe}} + \lambda, \quad (1)$$

where $\delta^{15}N_{Glu}$ and $\delta^{15}N_{Phe}$ represent the trophic and source $\delta^{15}N$ values per consumer, β represents the difference between $\delta^{15}N_{Glu}$ and $\delta^{15}N_{Phe}$ in primary producers, $TDF_{Glu-Phe}$ represents the difference in trophic discrimination between tissue and diet for glutamic acid and phenylalanine in consumer tissues (i.e., $\Delta_{Glu} - \Delta_{Phe}$), and λ represents the basal trophic level (here, 1). We measured $\delta^{15}N_{Glu}$ and $\delta^{15}N_{Phe}$ for consumers directly, and we estimated β using a subset of primary producers from our system ($N = 6$; $\beta = -7.9 \pm 4.5$). Because trophic discrimination is often dictated by dietary protein content, we used a mean (±SD) trophic discrimination factor (TDF) of 4.6‰ (±0.3), or the average $TDF_{Glu-Phe}$ observed in mice held on diets ranging from 5% to 37% in protein content (Whiteman et al., 2021). We also estimated TP for a subset of fungal fruiting bodies with unknown TP ($N = 4$) and a subset of bacterial cultures with a known TP of 2 ($N = 4$). We calculated TP as explained earlier but used a $TDF_{Glu-Phe}$ of 7.3‰ (±1.2) and 6.7‰ (±0.3) for fungi and bacteria, respectively (Steffan et al., 2015). For all consumers, fungi, and bacterial cultures, we also estimated mean TP and propagated error using a Monte Carlo simulation (100,000 iterations) in the R package propagate version 1.0-6 (Spiess, 2018).

Statistical analysis

To test the effect of food web coupling on TP, we regressed individual TP estimates as a function of species and the proportion of brown energy assimilated per consumer defined as the additive proportion of bacterial and fungal energy using mean proportions from mixing models and LDA bootstrapping. We used analysis of covariance (ANCOVA) to first test the interactive effect of species and brown energy assimilation on TP (i.e., differences in slopes and intercepts; $p_{boot} = 0.64$, $p_{mixing} = 0.81$) but removed the insignificant interaction to create a more parsimonious additive model. We then split brown energy assimilation into its constituents, resulting in an additive model with species, proportion of bacteria, and proportion of fungi. We used ordinary least squares regression (OLS) in the R stats package version 4.2.0 (R Core Team, 2022), and we confirmed that model assumptions were met using the R package performance version 0.9.1 (Lüdecke et al., 2021).

RESULTS

We characterized EAA $\delta^{13}C$ fingerprints for bacterial, fungal, and plant sources with classification accuracies of 100%, 85.7%, and 95.0%, respectively (Figure 2A). We observed significant multivariate differences in EAA $\delta^{13}C$ values and LDA coordinates between both sources ($p < 0.001$) and consumer species ($p < 0.01$). Consumers classified almost exclusively as fungi (≥80% for all species, 27/30 total), and species-level mixing models estimated mean proportional fungal contributions of 0.47 (95% credible interval [CI] = 0.30–0.64) for *P. maniculatus*, 0.38 (CI = 0.24–0.52) for *S. cinereus*, and 0.61 (CI = 0.46–0.77) for *S. monticola* (Data File S3 in Manlick, 2022). Plants were the second largest energy channel for both *P. maniculatus* ($\bar{x}_{plant} = 0.37$, CI = 0.20–0.52) and *S. monticola* ($\bar{x}_{plant} = 0.22$, CI = 0.08–0.37), while bacteria were the second largest energy channel for *S. cinereus* ($\bar{x}_{bacteria} = 0.33$, CI = 0.24–0.42; Figure 2B). Individual-level mixing models revealed considerable variation in energy channeling (Figure 3; Data File S4 in Manlick, 2022), but all

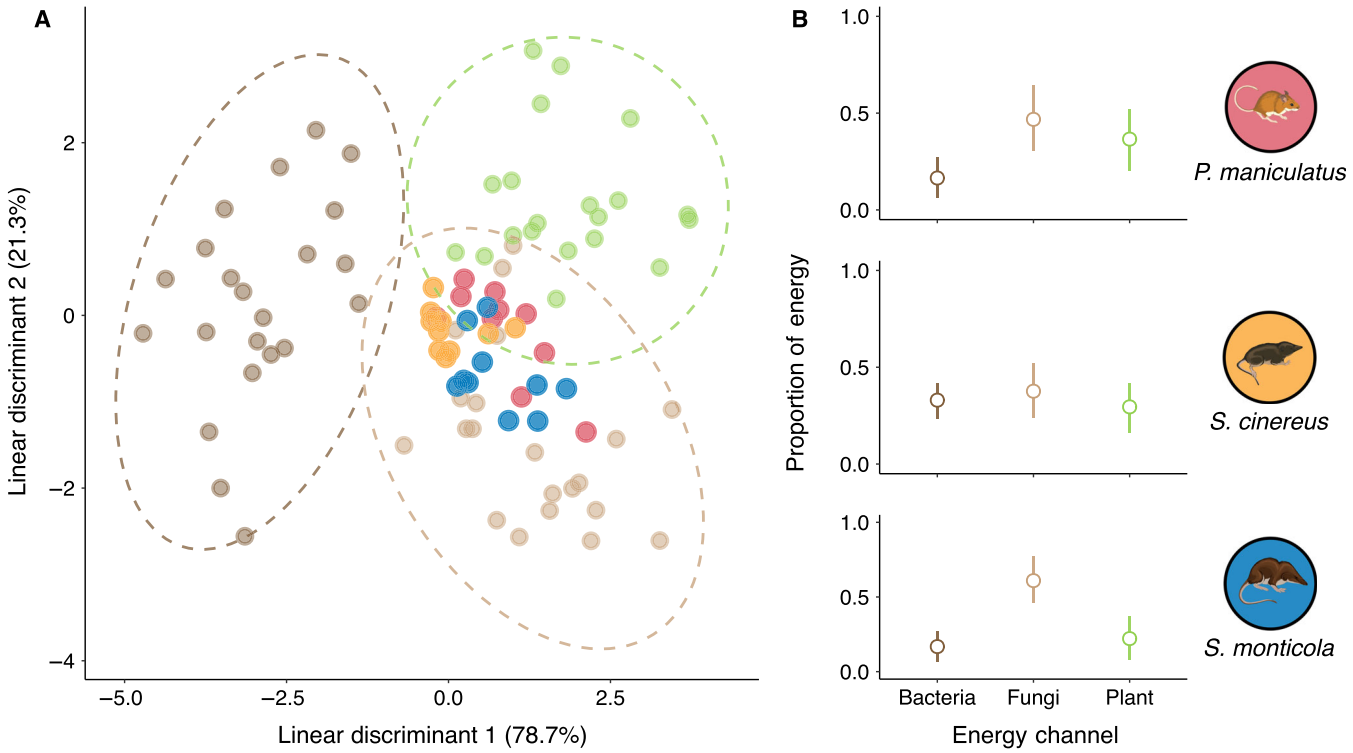

FIGURE 2 Linear discriminant analysis (LDA) of $\delta^{13}C$ values in six essential amino acids (EAAs) from energy channels (transparent) and consumers (solid; A), and proportional estimates of energy channel use by consumer species (B). Energy channels included plants (green), fungi (light brown), and bacteria (dark brown). Consumers included deer mice (*Peromyscus maniculatus*; red), masked shrews (*Sorex cinereus*; yellow), and montane shrews (*Sorex monticola*; blue). (A) Standard ellipse areas (95%) for energy channels are represented by dashed lines, and the percentage of variation described by each linear discriminant is in parentheses. (B) Median estimated proportions are denoted by empty circles, and vertical lines represent 95% credible intervals.

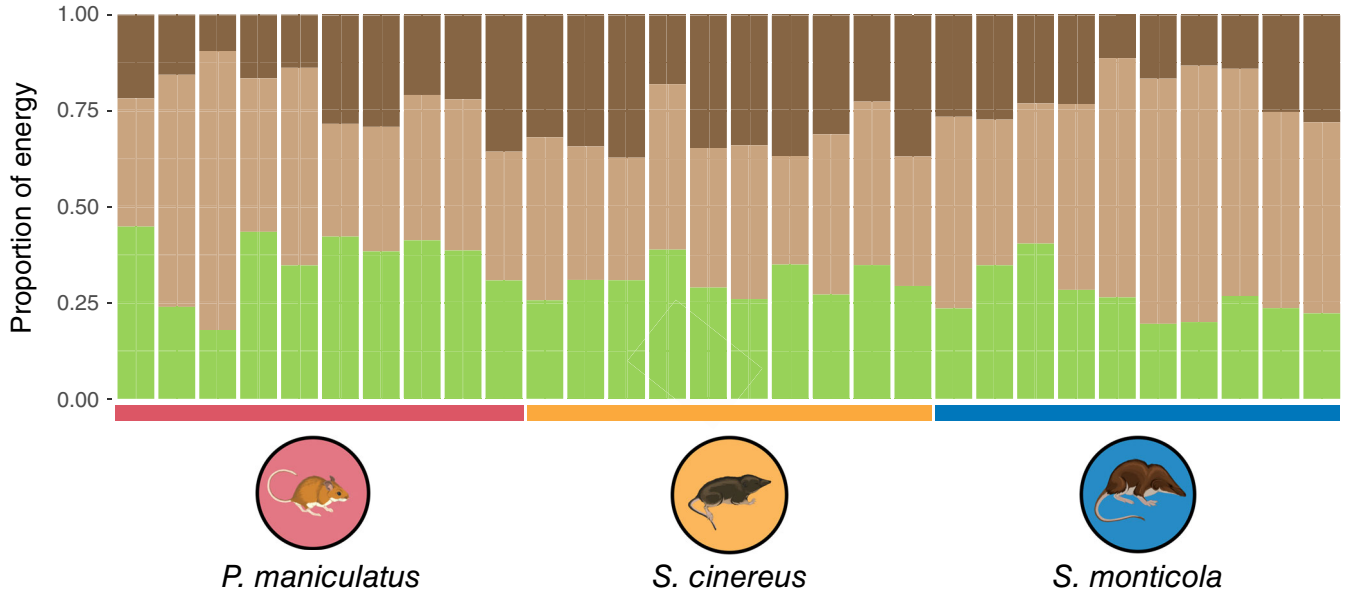

FIGURE 3 Proportional contributions of plant (green), fungal (light brown), and bacterial (dark brown) energy to individual deer mice (*Peromyscus maniculatus*; red), masked shrews (*Sorex cinereus*; yellow), and montane shrews (*Sorex monticola*; blue). Proportions represent mean contributions estimated from Bayesian isotopic mixing models.

individuals assimilated over half their energy from brown channels, while species-level estimates exceeded 0.60 for all species (Figure 4A). LDA bootstrapping corroborated these results, with an average brown energy contribution of 0.80 (±0.22) per individual (Appendix S1: Table S3).

TP estimates showed predictable patterns among consumers, with *P. maniculatus* at the lowest TP (3.0 ± 1.0) followed by *S. monticola* (3.8 ± 1.0) and *S. cinereus* (3.9 ± 1.0). Individual estimates ranged from 2.6 to 4.2 for all consumers (Figure 4B, Appendix S1: Table S4). Likewise, fungal samples ranged across multiple trophic levels (2.0–4.0, $\bar{x} = 2.9 \pm 1.3$), while bacterial cultures expectedly averaged 2.3 (±1.0). Regression models revealed a significant effect of both species ($F_{3,26} = 92.7$, $p < 0.001$) and brown energy assimilation ($F_{3,26} = 7.17$, $p = 0.013$, adjusted $R^2 = 0.87$) on TP (Figure 4B), indicating that average TP varied by species but increased significantly with brown energy assimilation for all consumers. Parsing brown energy into constituent components revealed that species ($F_{4,25} = 89.3$, $p < 0.001$) and fungal energy ($F_{4,25} = 6.9$, $p = 0.012$; adjusted $R^2 = 0.86$) had significant effects on TP, whereas bacterial energy did not ($F_{4,25} = 0.1$, $p = 0.81$). Bootstrapped LDA estimates yielded nearly identical results, again revealing significant effects of both species ($F_{3,26} = 90.95$, $p < 0.001$) and brown energy assimilation ($F_{3,26} = 6.54$, $p = 0.020$, adjusted $R^2 = 0.86$) on TP (Appendix S1: Figure S1).

DISCUSSION

Green and brown food webs are frequently linked by animals, but the extent of this multichannelling and its consequences for trophic structure are often unclear (Wolkovich et al., 2014). Consistent with theoretical food web models (Rooney et al., 2006), we found that small mammals were heavily subsidized by brown energy channels (i.e., bacteria, fungi) and that the assimilation of brown energy regulated TP across species and functional groups (Figure 4). These results demonstrate that brown energy assimilation is a significant driver of TP, and we propose that the coupling of green and brown food webs is a cryptic driver of food chain length in terrestrial ecosystems. Here, we outline the potential mechanisms regulating this process, explore the consequences of food web coupling by mammalian consumers, and outline future steps needed to resolve food web complexity.

Two proximate mechanisms drive TP and food chain length: (1) the insertion or deletion of consumers in a food chain and (2) changes in the degree of trophic omnivory (here defined as feeding at multiple trophic levels; Post & Takimoto, 2007). We found that the assimilation of brown energy by aboveground consumers leads to higher TPs, and we posit that this increases food chain length via both the insertion and omnivory mechanisms. First, the decomposition of autotrophic biomass by

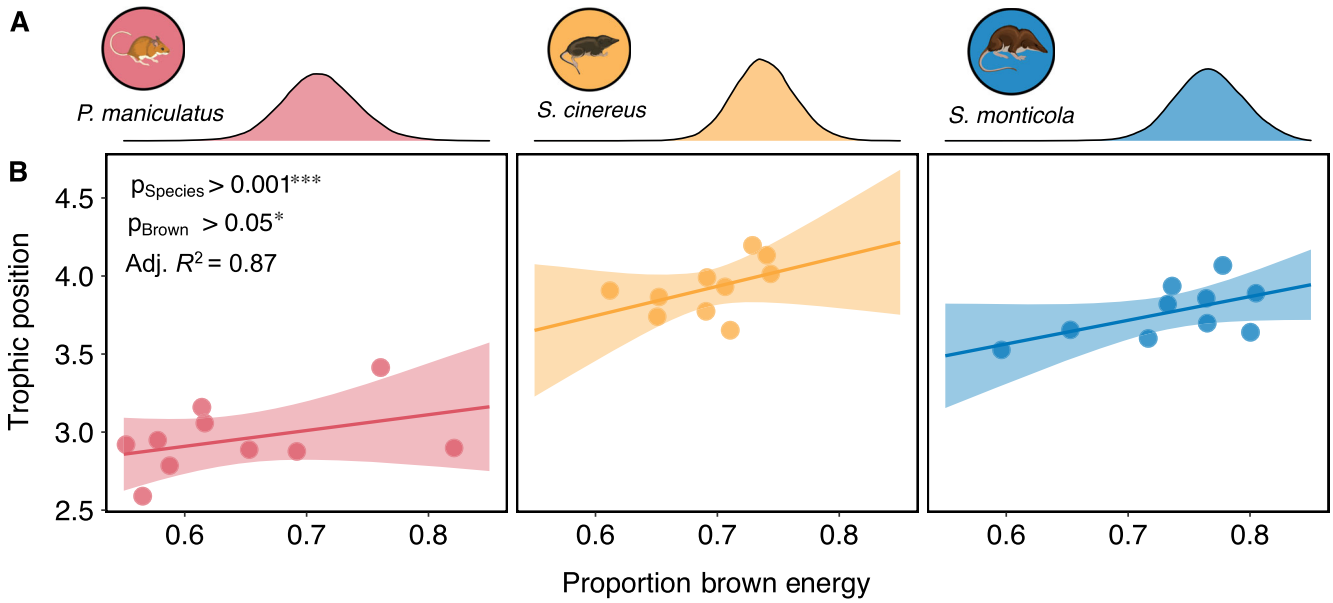

FIGURE 4 Relationship between proportion of assimilated brown energy and trophic position (TP) for deer mice (*Peromyscus maniculatus*; red), masked shrews (*Sorex cinereus*; yellow), and montane shrews (*Sorex monticola*; blue). (A) Posterior distributions represent the combined contributions of bacterial and fungal energy estimated at the species level, while (B) points represent the combined mean contributions of bacterial and fungal energy for individuals. All proportions were estimated using Bayesian isotopic mixing models, and colored ribbons represent 95% confidence intervals from multiple linear regression. Both species and proportion of brown energy had significant effects on TP (B).

bacteria and fungi represents the insertion of a heterotrophic consumer guild that directly extends food chains (Cummins, 1974; Steffan et al., 2015, 2017). Termed the "external rumen hypothesis," many animals rely on microbial heterotrophs to transform recalcitrant plant material into usable biomolecules due to the low nutritional quality and transfer efficiency of detritus (Cummins, 1974; Hairston & Hairston, 1993; Swift et al., 1979). Given the ubiquity of detritus and multichannel feeding (Hagen et al., 2012; Wolkovich, 2016), we suspect that microbial insertions into food chains are likely universal in terrestrial food webs. We also found that fungi occupied several trophic levels (2.0–4.0, Appendix S1: Table S4), indicating that microbial insertions could occur at multiple points in the trophic chain (Pollierer et al., 2020; Steffan et al., 2015). Second, omnivory can extend food chains, and we found that all small mammal species were feeding across trophic levels, with TPs ranging from 2.6 to 4.2 as a function of brown energy assimilation. Similar patterns have been reported in squirrels (Pauli et al., 2019), bees (Steffan et al., 2019), and earthworms (Potapov et al., 2019), all exhibiting higher TPs due to omnivory, microbivory, or mycophagy. As prey for many predators, this widespread variance in TP within and among species due to omnivory can propagate through food webs leading to food chain extensions (Post & Takimoto, 2007; Sprules & Bowerman, 1988). Indeed, detrital webs are typified by longer food chains due to omnivory (Digel et al., 2014; Moore et al., 2004; Rooney & McCann, 2012), and here we show that detrital energy is ultimately linked to aboveground consumers, leading to elevated TPs in purported green web consumers as well (Figure 1).

Ecologists often segregate above- and belowground food webs into green and brown energy channels, but our results join a growing body of empirical evidence illustrating that these channels are coupled by aboveground consumers (Haraguchi et al., 2013; Hyodo et al., 2015; Pauli et al., 2019; Perkins et al., 2017). On average, we found that nearly 70% of energy assimilated by small mammals was derived from detrital channels, indicating that belowground food webs were a critical source of energy for vertebrate consumers. This is likely because the energy retained in brown food webs greatly exceeds that of green webs (Cebrián & Duarte, 1995), with microflora like bacteria and fungi constituting the majority of assimilable energy in an ecosystem (Hairston & Hairston, 1993; Pokarzhevskii et al., 2003). Detrital accumulation combined with gradual rates of decomposition provide a consistent "slow" energy channel that may enhance secondary production and support abundant terrestrial consumer populations (Hagen et al., 2012; Rooney & McCann, 2012). The mechanisms driving this pattern, however, remain underexplored. For example, detritus and microbial subsidies can augment individual survival (Dharampal et al., 2019), alter consumer densities (Halaj & Wise, 2002), and regulate competitive interactions (Wardle & Yeates, 1993), but these processes have not been substantively tested beyond soil food webs. The significance and ubiquity of multichannelling is now recognized as a fundamental property of soil food webs (Wolkovich, 2016), but the importance of microbially mediated energy flow remains largely "sanitized" from broader food web theory (Steffan & Dharampal, 2019). Our results unequivocally show that microbially mediated energy structures aboveground food webs, but further research on the population-, community-, and ecosystem-level consequences of this food web coupling is needed.

We found that small mammals were mainly supported by fungal energy (Figure 3), indicating that fungal decomposers were the primary conduit of brown energy to aboveground consumers in our forest ecosystem. This is consistent with previous findings that fungi are the dominant decomposers in temperate forests characterized by high volumes of recalcitrant plant biomass (e.g., cellulose, lignin; Hättenschwiler et al., 2005). Fungal networks are also resilient to drought (De Vries et al., 2012), and our study coincided with a historic period of aridification in the American Southwest (Williams et al., 2022). These results suggest that slow, fungal energy channels may become increasingly important to sustain secondary production and terrestrial food web stability under future climate warming and aridification. Indeed, both theoretical and empirical studies indicate that the incorporation of slow energy channels can stabilize ecosystems, especially when energy flow is distributed across slow (brown) and fast (green) channels, as we observed (Figure 3; Moore et al., 2004; Rooney & McCann, 2012). Our data, however, represent only the summer diets of small mammals, and it is likely that seasonal fluctuations in resource availability and decomposition rates alter multichannel feeding. Human-induced global change is similarly predicted to alter food web connections (Bartley et al., 2019) as well as the availability of green versus brown energy (Thakur, 2020). Continued research is therefore needed to assess the causes and consequences of spatiotemporal variation in food web coupling.

The processes mediating brown energy assimilation by small mammals are currently unclear, but two discrete pathways likely drove the observed flux of fungal energy to mammalian consumers. First, fungi channel energy directly from detritus to soil invertebrates like collembola, earthworms, and spiders (Pollierer et al., 2012; Potapov et al., 2019), all of which constitute

key prey for mice and shrews (Whitaker, 2004; Wolff et al., 1985). This pathway would correspond to a microbial insertion at trophic level two with fungi as the primary detritivore, and it maps directly to the mean TPs of *S. cinereus* ($\bar{x} = 3.8$) and *S. monticola* ($\bar{x} = 3.9$). These estimates are consistent with previous findings that shrews occupy TPs >3 (Baltensperger et al., 2015), indicating that shrews are apex or near-apex predators in soil food webs. Given their high densities, elevated metabolic rates, and generalist foraging, shrews likely exert strong top-down effects on soil food webs and directly couple above- and belowground systems, but these functional roles have been largely unexplored (Whitaker, 2004). Second, small mammals can directly channel brown energy via mycophagy, and many rodents, including deer mice, directly consume fungal fruiting bodies, often from ectomycorrhizal symbionts (Pyare & Longland, 2001; Stephens et al., 2021; Stephens & Rowe, 2020). In our study, *P. maniculatus* had the lowest mean TP ($\bar{x} = 3.0$) but assimilated almost 50% fungal energy. This suggests that deer mice directly consume primary decomposers or ectomycorrhizal symbionts at trophic level two (Pollierer et al., 2020), likely conferring important ecological functions like spore dispersal that promote forest resilience (Stephens & Rowe, 2020). Our data do not enable us to directly identify the entry point of brown energy into the food web, but doing so will be an important future step because the location of multichannel linkages would illuminate these functional roles and is predicted to impact food web stability (Wollrab et al., 2012). Future studies should consider pairing isotope techniques with direct estimates of diet from DNA metabarcoding of feces or stomach contents to jointly estimate proportional energy channeling, functional roles, and the foraging patterns governing energy linkages.

Ecologists often struggle to quantify energy flow and trophic structure, but stable isotope analysis of individual amino acids has emerged as a powerful tool to characterize food webs with unprecedented resolution (Manlick & Newsome, 2022; Pollierer et al., 2019; Steffan et al., 2015). Nevertheless, some uncertainties surrounding this emerging technique could have affected our results. First, we identified energy channels using $\delta^{13}C$ EAA fingerprints for bacteria, fungi, and plants, but the separation of these sources in isotopic space was not perfect. Although plant and bacterial sources were identifiable with ≥95% accuracy, fungal characterization lagged at 86%, thereby inflating the error associated with proportional estimates. Ecologically, this likely reflects the fact that our sampled fungi are mixotrophs that can directly acquire EAAs from external sources like plants, and the amino acid composition of substrates can dictate fungal fingerprints (Arsenault et al., 2022). Three fungal samples in our data set overlapped with plant fingerprints (Figure 2), all ectomycorrhizal symbionts (*Boletus*, *Lactarius*, and *Russula* spp.), and $\delta^{15}N$ data for two of these samples yielded estimated TPs of 2.0 and 2.2. This suggests that fungal symbionts draw amino acids from hosts, leading to elevated TPs similar to primary consumers and decomposers (Pollierer et al., 2020), or that ectomycorrhizal fungi uptake amino acids from humus that have already undergone metabolic processing during microbial decomposition. Methodologically, this EAA exchange could hinder the accuracy of energy channeling estimates from isotope-based approaches but represents real variation present in natural systems. Like the bacteria used in our study, most $\delta^{13}C$ fingerprints used to estimate multichannelling to date are derived from cultured sources where all EAAs are synthesized de novo, thereby producing perfect separation among sources in multivariate space (Larsen et al., 2009). More data are needed from wild sources to characterize EAA exchange among sources and how this affects estimates of multichannelling by consumers. Second, we traced EAAs as a proxy for energy flow, but these biomolecules make up only ~30%–40% of proteinaceous tissues (Hobbie, 2017; Wolf et al., 2015). The primary constituent of proteins are non-essential amino acids that can either be directly assimilated from dietary protein or synthesized de novo using other macromolecules like carbohydrates (Newsome et al., 2014). Controlled feeding experiments on small mammals, however, show that >50% of all amino acids are directly assimilated into consumer tissues, particularly in high-TP consumers like the omnivores and insectivores we analyzed (Hobbie, 2017; Jim et al., 2006). Further, recent feeding experiments showed that $\delta^{13}C$ fingerprinting accurately quantified both the source and proportion of crude protein in consumer diets (Manlick & Newsome, 2022), collectively indicating that our estimates of EAA assimilation are representative of energy flow and dietary protein assimilation in this system. Lastly, known variation in β values could have affected our estimates of TP. We report sizable error around TP estimates, but this was almost entirely driven by the large variation in measured β values, which inflated SDs during error propagation (Appendix S1: Table S4). Nevertheless, this error is real and likely due to bimodalities in β values for woody ($\bar{\beta} = -10.5$) and herbaceous ($\bar{\beta} = -2.7$) C_3 plants caused by the production of secondary compounds and structural biomolecules like lignin (Ramirez et al., 2021). Given the broad co-occurrence of woody and herbaceous vegetation, the observed error in TP estimates may be unavoidable in C_3-based forest ecosystems until linkages between energy channels are more proximately identified. Despite these intricacies, amino acid isotope analysis remains the best tool ecologists have

to map and *quantify* multichannel linkages in wild systems (Manlick & Newsome, 2022; Steffan et al., 2017), a key step in disentangling food web complexity and informing models of ecosystem stability (Rooney et al., 2006; Wolkovich et al., 2014).

CONCLUSIONS

Collectively, this study shows that food web coupling and multichannel energy linkages shape terrestrial food webs, including food chain length. This introduces an important alternative hypothesis to existing food web theory, that brown energy assimilation is a cryptic driver of food chain length. We also show that brown energy, particularly in the form of fungi, permeates aboveground food webs, constituting nearly 70% of the total energy flux to putative green web consumers like small mammals. Given the ubiquity of detritus and the pervasive nature of multichannel feeding (Polis & Strong, 1996; Wolkovich et al., 2014), we echo recent calls to desegregate green and brown food webs (Steffan & Dharampal, 2019) and urge food web ecologists to reconsider historical paradigms that emphasized the role of microbially mediated energy flow across ecosystem boundaries (Lindeman, 1942; Minshall, 1967).

AUTHOR CONTRIBUTIONS

All authors conceived of the study. Philip J. Manlick and Joseph A. Cook collected the data, Philip J. Manlick and Seth D. Newsome conducted laboratory analyses, and Philip J. Manlick conducted all statistical analyses and wrote the first draft of the manuscript. All authors contributed to revisions.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and code (Manlick, 2022) are available in Figshare at https://doi.org/10.6084/m9.figshare.20520567.v2. Specimen metadata was downloaded from Arctos (https://arctos.database.museum/) by searching for the "Arctos_ID" given in "supporting data file S1" in Manlick (2022) as the identifier. Previously published data sets used in this research include Larsen et al. (2009).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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