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Cannibalism has its limits in soil food webs

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ABSTRACT

Cannibalism imperfectly recycles resources back to the same species and so decreases trophic transfer efficiency in food webs. As such, viable populations have some limit on how much of their diet can come from cannibalism. We applied a Lotka-Volterra model to derive a theoretical maximum for the proportion of the diet coming from cannibalism. This proportion is set by the food conversion efficiency for both cannibalism and alternative prey. We apply the result to sixteen published soil food web models and find that cannibalism cannot exceed 20% of the diet of most organisms, which includes eating conspecifics that were already dead. However, predators can show a strong (>80%) preference for cannibalism because encountering conspecifics is rare. Cannibalism increased carbon and nitrogen mineralization in fifteen soil food webs and had non-monotonic effects in the remaining one. Our estimates map a physiological parameter (conversion efficiency) to an ecological one (cannibalism) to help to improve model fit and to help soil ecologists identify taxa where cannibalism may be most important.

1. Introduction

Robust estimates of cannibalism, as well as the related process of cannibalistic necrophagy (eating dead conspecifics), are important because they impact trophic transfer efficiency and so change our calculations of nutrient flow through food webs (Polis 1981). Cannibalism also affects stable isotopic signatures (Hobson & Welch 1995; Koltz & Wright 2020) often used to infer trophic positions. Previous cannibalism research has focused on trophic cascades (Polis 1991), stability (Claessen et al. 2004), and nutrition (Wise 2006). While these remain important, a growing interest in predicting the flow of carbon and other nutrients through food webs makes estimates of self-feeding of renewed importance (Andrés et al. 2016; Koltz et al. 2018; Schmitz et al. 2018).

An estimate of maximum cannibalism rate could be especially useful for soil food webs to reduce model uncertainty and direct empirical research. The reason is that soil organisms are prone to the practice and their life history is difficult to observe in the opaque soil matrix (Digel et al. 2014). Where they are known, cannibalism rates for soil organisms vary based on alternative prey availability, conspecific density, and life-stage (Berndt et al. 2003; Wise 2006; Lima 2016; Koltz & Wright 2020). Despite the documented effect of cannibalism on trophic transfer efficiency, most soil food web models do not explicitly include cannibalism in their calculations (but see Koltz et al. 2018). Better measures of the effect of cannibalism on the transfer of elements, such as carbon and nitrogen, across trophic levels would help to improve our predictions of their cycling and loss rates from the soil (Allison et al. 2010; Buchkowski & Lindo 2021).

Cannibalistic necrophagy and coprophagy (eating your own species faeces) are common in soil food webs and can be included with cannibalism in food web models based on nutrient biomass (De Ruiter et al. 1993; Nalepa et al. 2001; Moore & de Ruiter 2012; Jahnes et al. 2019). The role and importance of ‘cannibalism’ empirically and in food web models will change depending on whether it is restricted to predatory cannibalism or expanded to include necrophagy and coprophagy. In models tracking abundance, necrophagy and coprophagy are different from predatory cannibalism when the latter causes new deaths in the population (Polis 1981). However, necrophagy, coprophagy, and true cannibalism are analogous in models where populations are tracked as a stock of nutrients because they all recycle nutrients back into the same node. High rates of necrophagy or coprophagy interact with the efficiency with which organisms convert food into more biomass (i.e., conversion efficiency) in food web models. Necrophagy and coprophagy could thereby create a bias if the model allocation of these processes does not correspond with the empirical situation.

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We compiled data on sixteen food webs from literature (Table 1). In each food web, we determined the location of cannibalistic necrophagy and coprophagy by (1) food web structure and (2) the parameterization of assimilation efficiency and natural death rates (Figure 1). Our interpretation of the models is that necrophagy should be included in cannibalism but coprophagy should not. Coprophagy is accounted for separately because (1) coprophagous trophic species are often allowed to consume the detritus pool into which their faeces are added and (2) conversion efficiency parameters are measured using standard techniques that deduct faeces from assimilated material (e.g., Chamberlain et al. 2004; Ott et al. 2012). Conversely, most predators known to be necrophagous are not consuming detritus pools and so any necrophagy must be either deducted from natural death rates or assumed to be zero (Tosi & Sartini 1983; Berndt et al. 2003).

We use population viability to place an upper limit on the dietary proportion of cannibalism and the preference for eating conspecifics. This upper limit is not a predictor of true cannibalism rate nor is it a reason for a cannibal to turn down a good meal (Schausberger & Croft 2000; Getto et al. 2005; Wise 2006; Guill & Paulau 2015; Lightfoot et al. 2019). Instead, considerations of population viability can be used to calculate a maximum cannibalism rate because the species which persist are not eating themselves to extinction.

There are several ecological reasons why population viability does not actually predict cannibalism rate. Many taxa do not have the mouthpart morphology to consume conspecifics (Richardson et al. 2010), while others have a spatial or temporal separation of adults and juveniles (Hobson & Welch 1995; Wise 2006), defensive mechanisms (Wise 2006), nutrient requirements (Wise 2006), or size differences (Polis 1981; Martel & Flynn 2008) that make cannibalism less likely or restrict it to certain individuals. However, maximum rates of cannibalism derived from a food web analysis can help guide food web modelling efforts and identify the species where the practice is likely to be most common.

We calculate the theoretical limit on cannibalism in food webs and evaluate its relevance to ecological interactions and elemental cycling. We accomplish our goal by (1) calculating the maximum proportion of cannibalism in the diet of trophic species using a Lotka-Volterra model, (2) applying these results to soil food web models, (3) evaluating whether the maximum proportions are reasonable given the data on cannibalism in soil systems, and (4) predicting the effect of cannibalism on carbon and nitrogen mineralization. We found that cannibalism is limited by food conversion efficiency and that it tends to increase carbon and nitrogen mineralization in most, but not all, soil food webs.

Table 1
The sources for the soil food web models and isotope data used in our analyses.

Reference	Ecosystem	Number of food webs	Treatments/ Gradient	Location
Andrés et al. (2016)	Shortgrass Steppe	6	Grazing	Colorado, USA
Holtkamp et al. (2011)	Old field and Heathland	4	Old-field succession	Veluwe, Netherlands
Hunt et al. 1987	Shortgrass Steppe	1	NA	Colorado, USA
Koltz et al. (2018)	Moist acidic tundra	1	NA	Alaska, USA
de Ruiter et al. (1994)	Lovinkhoeve Experimental Farm	4	Conventional versus integrated management and soil depth	Marknesse, Netherlands
Oelbermann and Scheu (2010)	Forest and meadow	*	Transition between forest and meadow	Hessen, Germany
Jassey et al. (2013)	Peatland	*	NA	Jura Mountains, France
Mieczan et al. (2015)	Peatland	*	Seasonal differences	Polesie Lubelskie, Poland

*Sources for the isotope data.

2. Material and Methods

2.1. Model definition

We studied cannibalism in Lotka-Volterra food web models. The general model takes the following form (Figure 1A):

$$\frac{dX_i}{dt} = a_i p_i \sum_{j \neq i} F_{ij} - D_i - \sum_{j \neq i} F_{ji} - (1 - \hat{a}_i \hat{p}_i) F_{ii} \tag{1}$$

where X_i is the trophic species biomass typically indexed in carbon. F_{ij} is the rate of the focal species i eating species j, while F_{ji} is species j eating focal species i. Assimilation efficiency, production efficiency, and death rate are denoted a_i, p_i, and D_i, respectively. F_{ii} is the rate of cannibalism with $\hat{a}_i$ and $\hat{p}_i$ being the assimilation and production efficiency for cannibalistic feeding. It is likely that $\hat{a}_i \hat{p}_i$ will be larger than $a_i p_i$ for detritivores and herbivores and closer to $a_i p_i$ for carnivores (Polis 1981; Zimmer 2002; Jahnes et al. 2019). Consumption (F_{ij}) can take any functional form, typically based on predator and prey biomass whereas death rate (D_i) is often a first or second order function of biomass.

Notice that the population level model focuses on the role of cannibalism in resource use and does not include important deterrents such as the evolutionary costs of eating your kin (Getto et al. 2005; Wise 2006; Lightfoot et al. 2019) or incentives such as the lifeboat mechanism (i.e., eating conspecifics to survive hard times) and reduced competition (Polis 1981; Getto et al. 2005). Using these equations to model cannibalism assumes that it occurs because conspecifics are viable prey options and defines cannibalism based on the assumptions used to determine feeding rates F_{ij} (Stevens 2009; Koltz et al. 2018). Soil food web models often assume feeding rates are based on mass action (i.e., Type I functional response) with preferences set by relative biomass or some user-defined correction (Moore & de Ruiter 2012; Andrés et al. 2016).

We incorporate cannibalism into soil food web models by deriving its rate (F_{ii}) simultaneously with all other predation (Figure 1A; Koltz et al. 2018). Soil food web models often assume equilibrium biomass (X_i^*) and calculate consumption rate for each species $\left\{\sum_j^N F_{1j}, \sum_j^N F_{2j}, \ldots, \sum_j^N F_{Nj}\right\}$ using the system of equations defined by the N species $\left\{\frac{dX_1}{dt}, \frac{dX_2}{dt}, \ldots \frac{dX_N}{dt}\right\}$ (Moore & de Ruiter 2012). We assume that total predation rate, which we shorthand as F_{iT} (Eqn 2a), is distributed among the prey species using their relative abundance (X_j^*; Moore & de Ruiter 2012) modified by feeding preferences, w_{ij} (Eqn 2). So, we set the following definitions and constraints:

$$\text{Total Predation rate}: F_{iT} := \sum_j F_{ij} \tag{2a}$$

$$\text{Total prey biomass}: X_{iT} := \sum_j w_{ij} X_j^* \tag{2b}$$

$$\text{Preference weights sum to 1}: \sum_j w_{ij} = 1 \tag{2c}$$

$$\text{Diet proportions}: \frac{F_{ij}}{F_{iT}} = \frac{w_{ij} X_j^*}{X_{iT}} \tag{2d}$$

Assuming equilibrium $\left(\frac{dX_i}{dt} = 0\right)$ and using Eqn 2d to relate cannibalism and total consumption, we can calculate the rate of cannibalism from Eqn 1 as:

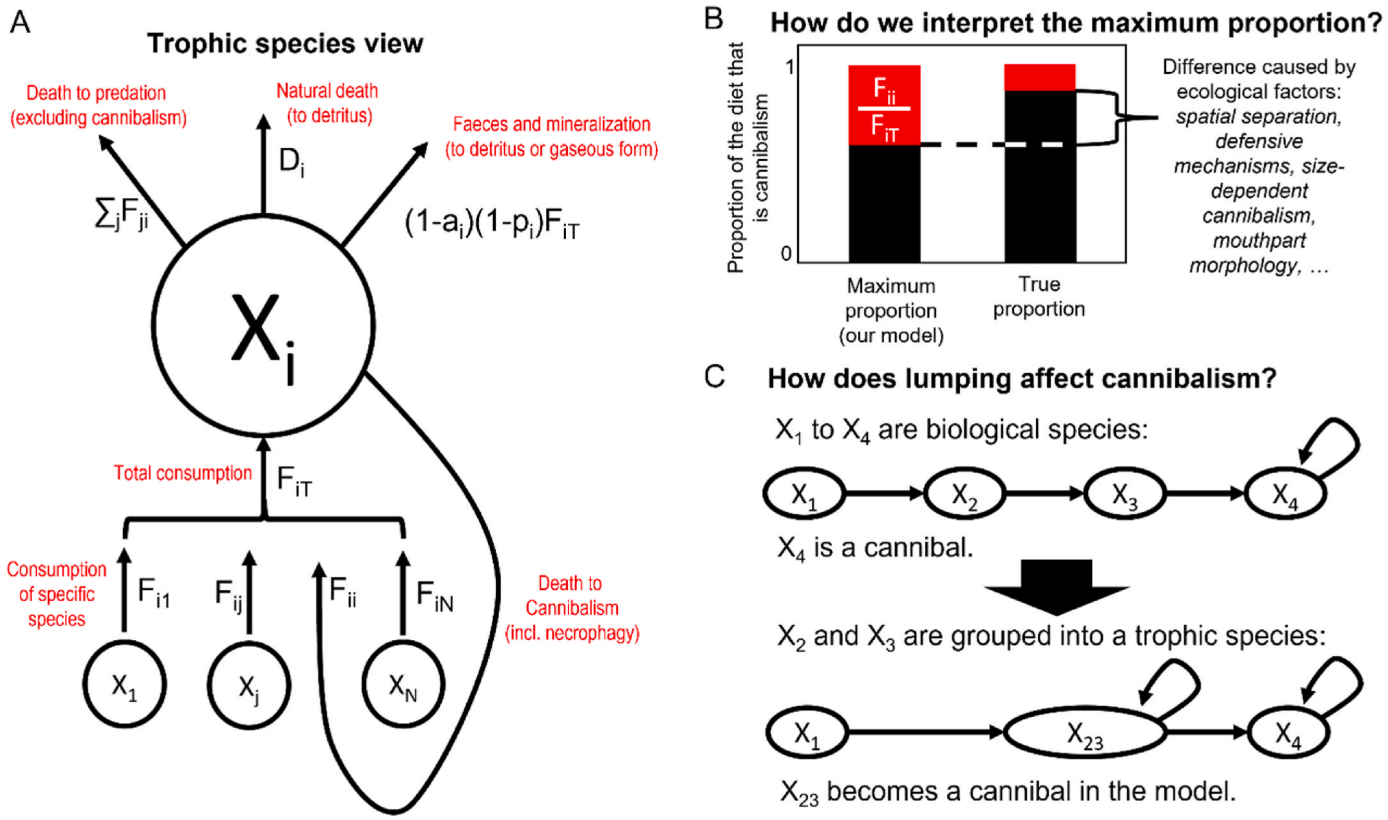

Figure 1. Three concepts important to interpreting the Lotka-Volterra models used in our analysis. (A) The trophic species model used in soil food web analyses and to estimate maximum cannibalism rate. The focal trophic species X_i consumes carbon and nitrogen from several sources (i.e., $\{1, 2, \ldots, N\}$) and loses them to predators, death, and physiological inefficiency. If we assume that the group must maintain a non-negative carbon or nitrogen budget, the maximum rate of cannibalism is set by the physiological efficiency. F_{ij} is the feeding of i on j, F_{iT} is the total feeding of i, a_i is the assimilation efficiency, p_i is the production efficiency, and D_i is the natural death rate. Natural death rate D_i excludes carbon in dead bodies that are consumed by conspecifics because necrophagy is included in cannibalism F_{ii} (B) The difference between the maximum proportion of the diet that is cannibalism and the true proportion. (C) A diagram showing how the lumping of biological species into trophic species influences our definition of who is cannibalistic and what portion of the diet is considered cannibalism in our calculations.

$$F_{ii} = \frac{D_i + \sum_{j \neq i} F_{ji}}{a_i p_i \left(\frac{X_{iT}}{w_{ii} X_i^*} - 1\right) - 1 + \widehat{a}_i \widehat{p}_i} \tag{3}$$

Cannibalism rate in units of carbon is determined by all the model parameters: death rates, predation rates, conversion efficiency, and prey availability. This result is consistent with a carbon budget view of each trophic species (Figure 1A).

The maximum proportion of cannibalism in the diet is only affected by the conversion efficiencies (Eqn 3; Figure 1B). Cannibalism rate can be positive at equilibrium only when the denominator of equation (3) is positive. The denominator of equation (3) incorporates information on the cannibalism rate $\left(\frac{X_{iT}}{w_{ii} X_i^*}\right)^{-1}$, which we define as the proportion of the diet that comes from cannibalism (Wise 2006). Given that $\frac{X_{iT}}{w_{ii} X_i^*} = \frac{F_{iT}}{F_{ii}}$ from (2d), the condition for cannibalism at equilibrium from equation (3) is:

$$\frac{F_{ii}}{F_{iT}} < \frac{a_i p_i}{1 - \widehat{a}_i \widehat{p}_i + a_i p_i} \tag{4}$$

The maximum possible proportion of cannibalism in the diet $\left(\frac{F_{ii}}{F_{iT}}\right)$ is set by the conversion efficiency of cannibalism $(\widehat{a}_i \widehat{p}_i)$ when it is less than perfect or different from the conversion efficiency for other prey ($a_i p_i$; Figure 2). The maximum proportion of cannibalism in the diet is 1 if the conversion efficiency of cannibalism is 1 (Eqn 4). When we assume that cannibalism and non-cannibalism have the same conversion efficiency (i.e., $a_i = \widehat{a}_i = \check{a}_i$ and $p_i = \widehat{p}_i = \check{p}_i$), the condition simplifies to:

$$\frac{F_{ii}}{F_{iT}} < \check{a}_i \check{p}_i \tag{5}$$

2.2. Model analysis

We calculated maximum cannibalism rate using conversion efficiencies (Appendix Table A1). We take these conversion efficiency parameters from the soil food web literature (Table 1), which often reuses them when modelling different systems (De Ruiter *et al. 1993*; Holtkamp et al. 2011; Moore & de Ruiter 2012; Andrés et al. 2016; Koltz et al. 2018; Buchkowski & Lindo 2021). So, we will find that the maximum proportion of cannibalism in diet of soil organisms is the same for most models (Table 2; Eqn 5).

We calculated the maximum preference for cannibalism (w_{ii}) with data on prey abundance and feeding preference information. We do this by decomposing $\frac{F_{ii}}{F_{iT}}$ back into $\frac{w_{ii} X_i^*}{X_{iT}}$, so that $w_{ii} < \frac{\check{a}_i \check{p}_i X_{iT}}{X_i^*}$. The maximum preference for cannibalism is useful for food web models but can be difficult to interpret because the value for 'no preference' changes with the number of diet items. So, we report Jacob's index of food selection (Eqn 6; Jacobs 1974) wherein a value of -1 indicates maximum avoidance, 0 indicates no preference, and 1 indicates maximum preference.

$$\text{Jacob's index}: \quad \mathrm{JI} = \frac{\frac{F_{ii}}{F_{iT}} - \frac{X_i^*}{\sum_j X_j^*}}{\frac{F_{ii}}{F_{iT}} + \frac{X_i^*}{\sum_j X_j^*} - 2\left(\frac{F_{ii}}{F_{iT}}\right)\left(\frac{X_i^*}{\sum_j X_j^*}\right)} \tag{6}$$

We calculated maximum cannibalism rate and Jacob's index for

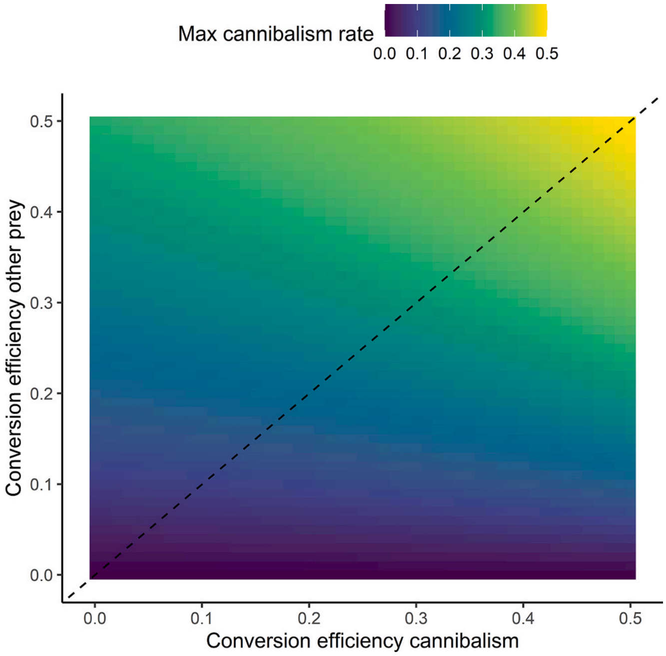

Figure 2. The maximum proportion of the diet that can be cannibalism $\left(\frac{F_{ii}}{F_{iT}}\right)$ across gradients of conversion efficiency (assimilation times production efficiency; $a_i p_i$) of conspecifics (x-axis) and all other prey (y-axis). The maximum proportions are calculated from equation (4) and the dashed line shows the behavior of equation (5) when we assume the conversion efficiency is constant for all prey.

sixteen published soil food web models (Table 1). We found these models by searching the literature for soil food web models and included all those available in the published literature for which we could find complete data. We excluded models that did not report conversion efficiency and turnover parameters (e.g., Hendrix et al. 1986), since our analysis required them. We used the same predator-prey relationships and model parameters as the original publications as well as their definitions of feeding type (e.g., herbivores, omnivores, etc.).

2.3. Comparison with isotope data

We compared our estimate of maximum cannibalism to an estimate using ^{15}N data from three publications (Table 1). We used ^{15}N data reported for three predatory invertebrate groups in forest litter and a microbial community in a peatland along with ^{15}N data on their potential prey (Oelbermann & Scheu 2010; Jassey et al. 2013; Mieczan et al. 2015). We calculated the maximum rate of cannibalism using linear programming to maximize the fraction of cannibalism in the diet while ensuring that the measured ^{15}N content of the predator was enriched 3.4‰ higher than the mixture of ^{15}N content from the diet (Oelbermann & Scheu 2010).

2.4. The effects of cannibalism on nutrient cycling

We estimated carbon and nitrogen mineralization from all sixteen of our focal soil food webs from 0 to 99% of the maximum cannibalism rate (Table 2; note Eqn 4 is $>$ not $\geq$ so 100% is undefined by equation [3]). We applied the same proportion of maximum cannibalism rate to each node in the food web except for phytophagous nematodes, plants, and organic matter—the former not having any cannibalism because they do not have the mouthpart morphology for predation (Richardson et al. 2010). We allowed bacterivorous and fungivorous nematodes to be cannibals in these models because of reports that they can switch to predatory morphs under resource scarcity (Renahan & Sommer 2021).

Table 2
The maximum proportions of each trophic species' diet that can come from cannibalism and Jacob' index of feeding preference. Cannibalism is defined as feeding on your own TROPHIC SPECIES. Ranges are provided when there are differences across webs. Calculations were made using sixteen published food webs with some additional grouping of trophic species after the calculations to make the table a reasonable size (Hunt et al. 1987; de Ruiter et al. 1994; Holtkamp et al. 2011; Andrés et al. 2016; Koltz et al. 2018). N is the number of estimates, with numbers over 16 occurring when multiple trophic species from the same web occur in the same group. Jacob's index ranges from avoidance (-1) to preference (1) with no preference being 0.

Trophic Species	Feeding Type	N	Maximum Cannibalism (Proportion of dietary carbon)	Jacob's Index [-1,1]
Amoebae	Microbivore	16	0.38	0.94 to 1
Bact. Nematodes	Microbivore	16	0.22	0.84 to 1
Bacteria	Detritivore	16	0.3	0.62 to 1
Beetles	Carnivore	1	0.2	0.69
Ciliates	Microbivore	7	0.38	1
Collembola	Microbivore	17	0.18	0.59 to 1
Earthworms	Detritivore	4	0.09‡	1
Enchytraeids	Microbivore	9	0.1 to 0.11†‡	1
Flagellates	Microbivore	16	0.22 to 0.38*	0.98 to 1
Fung. Nematodes	Microbivore	16	0.14	0.9 to 1
Fungi	Detritivore	16	0.3	0.91 to 1
Mites	Microbivore	40	0.18	0.77 to 1
Nem. Mites	Carnivore	16	0.18 to 0.32*	0.35 to 1
Omn. Nematodes	Carnivore	12	0.22	0.84 to 0.99
Phyto. Nematodes	Herbivore	16	0.092‡	0.83 to 1
Pred. Collembola	Carnivore	8	0.18	0.73 to 1
Pred. Diplurans	Carnivore	6	0.31	0.7 to 0.87
Pred. Mites	Carnivore	16	0.21	0.31 to 0.92
Pred. Nematodes	Carnivore	16	0.18	-0.15 to 1
Proturans	Carnivore	6	0.18	1
Rotifers	Carnivore	1	0.22	1
Spiders	Carnivore	5	0.21	0.29 to 0.98
Symphyla	Carnivore	6	0.13	1
Tardigrades	Microbivore	1	0.22	1

* Koltz *et al.* (2018) reports different conversion efficiencies for these groups. † de Ruiter *et al.* (1994) reports a different conversion efficiency for this group. ‡A likely case where $a_i p_i \neq \hat{a}_i \hat{p}_i$.

For one food web reported by Koltz et al. (2018), we combined trophic species feeding on each other in a second analysis. The combined trophic species had the average parameters of the individual trophic species weighted by their relative biomass (Buchkowski & Lindo 2021).

3. Results

3.1. Conceptual results

Our analytical results suggest that: (1) the dietary contribution of cannibalism can be higher in species that have higher conversion efficiencies (Figure 2) and (2) cannibalism preference can be stronger when resources are scarce and conspecifics are common. Our analysis separates these two components of cannibalism—actual diet and prey preference—making the restrictions on them distinct.

The maximum dietary contribution of cannibalism is defined in equations (4) and (5). It implies that soil microbial taxa such as ciliates, amoebae, flagellates, or nematodes could maintain a high level of cannibalism because of their relatively high conversion efficiencies (e.g., Hunt et al. 1987). The estimate of maximum cannibalism preference comes from the decomposition of $\frac{F_{ii}}{F_{iT}}$ into $\frac{w_{ii}X_i^*}{X_{iT}}$. It implies that taxa living with a low density of conspecifics relative to their prey, such as microbivores, can exhibit a high theoretical preference for cannibalism. The reason cannibalism preference can be so high is that encountering conspecifics is rare enough that it is difficult for them to exceed the maximum cannibalism rate even if they have a high preference for cannibalism. Conversely, organisms living at a similar density to their prey, such as spiders, must have more restricted preferences to have cannibalism rates below the theoretical maximum that we calculated.

3.2. *Quantifying cannibalism rates*

The maximum rate of cannibalism was similar across the sixteen food webs because they use the same conversion efficiency parameters. Cannibalistic preference varied more because of the differences in the ratio of available prey to conspecific biomass across ecosystems (Table 2). We presented these data as a range from min to max for each taxonomic group (Table 2; full data provided in the associated R code).

The maximum proportion of cannibalism in the diet calculated by equation (5) was often around 0.20 across the trophic species in these soil food webs. Single celled predators (e.g., Amoebae) stand out with high conversion efficiency and therefore a high maximum cannibalism rate. Intermediate maximum cannibalism rates occurred for many predatory species including spiders, mites, and beetles. The lowest values were the herbivores and detritivores (Table 2) because of their low assimilation efficiencies.

The maximum preference for cannibalism as measured by Jacob's index was large for most species because their prey was often far more abundant than them (Table 2). The only case where cannibalism had to be less preferred than other prey sources (i.e., Jacob's index < 0) was for predatory nematodes in the young field studied by Holtkamp et al. (2011). Predatory nematodes were highly abundant in this field relative to their prey, which explains the negative index.

3.3. *Comparison with isotope data*

The ^{15}N analyses were often not as effective at constraining cannibalism rate than the theoretical analysis proposed here. The three aggregate invertebrate predator groups proposed by Oelbermann and Scheu (2010) produced estimates of maximum cannibalism rate at 0.44, 0.60, and 0.63 for groups of spiders and beetles identified in the original manuscript (Oelbermann & Scheu 2010). Comparable estimates from our theoretical analyses were 0.2 and 0.21 (Table 2). The protist *Hyalosphenia papilio* had a maximum cannibalism rate of 0.38 when we calculated it using the ^{15}N data (Jassey et al. 2013), which is identical to the prediction made here (Table 2). The same protist had a maximum cannibalism rate between 0.43 and 0.60 when using ^{15}N data collected in different seasons (Mieczan et al. 2015). Isotope data on rotifers across seasons produced maximum cannibalism rate estimates from 0 in the spring, 0.37 in the summer, and 0.23 in the fall (Mieczan et al. 2015), which spans the estimate made here of 0.22 (Table 1). To combine our theoretical and ^{15}N analyses, we could select the lower estimate of the two as the best estimate of the maximum cannibalism rate, which according to these data would often be the one produced by our theoretical approach.

3.4. *The effects of cannibalism on nutrient cycling*

Cannibalism increased carbon and nitrogen mineralization relative

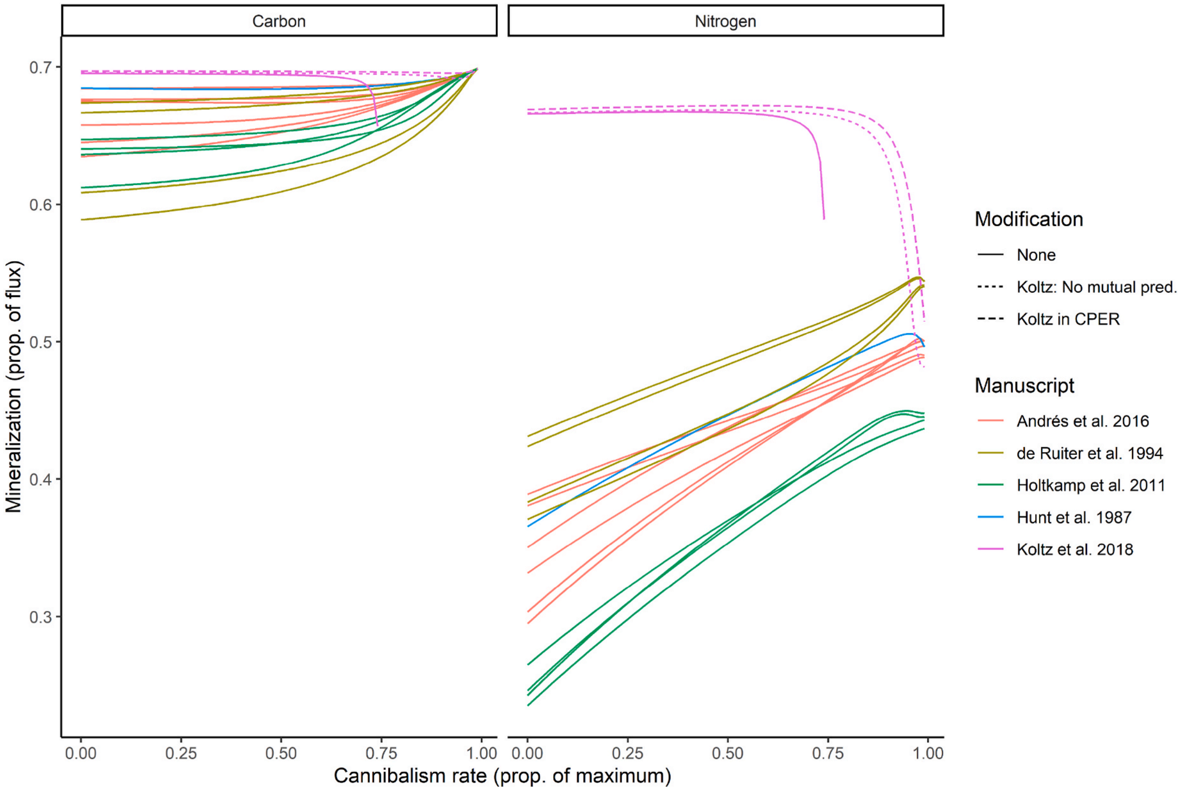

Figure 3. The efficiency of carbon and nitrogen cycling in published soil food webs along a gradient of cannibalism from 0 to 99% of the maximum rate (Table 2) for all nodes except phytophagous nematodes, plants parts, and organic matter. A larger value on the y-axis indicates more mineralization per unit of element cycling in the web (i.e., the web is less efficient). Cannibalism makes most of the soil food webs less efficient. It makes the Koltz web untenable over 0.74 because of mutual feeders (Koltz: No mutual feeders) and reduces nitrogen loss because of the non-monotonic biomass pyramid (Koltz in CPER). Holtkamp et al. (2011) present webs for Young to Heathland field types (N=4), Andrés et al. (2016) have three sites with grazed and ungrazed plots (N = 6), and de Ruiter et al. (1994) have conventional and integrated management sites at two depths (N = 4). The effect of removing mutual predation and placing the Koltz et al. (2018) biomass data into the CPER (Hunt et al. 1987) are differentiated by line type.

to the internal flux for the food webs in four of the five published studies (15 of 16 webs; Figure 3). Cannibalism increased nitrogen mineralization more than carbon mineralization and had the largest effect at the highest rates of cannibalism. Cannibalism also caused carbon mineralization to converge on a value approximately 70% of the total system flux (Figure 3). Cannibalism increased nitrogen mineralization far more dramatically, with a small drop near the maximum in some cases and it did not converge on a fixed proportion of nitrogen flux (Figure 3).

Cannibalism had a negative and non-monotonic effect on mineralization in the only Arctic food web (Koltz et al. 2018) in our data set. Two features of this system explain its unique behavior. Versions of the food web with more than 74% of the maximum cannibalism rate were not feasible because mutual feeding between top predators such as spiders and beetles prevented positive solutions. The web became feasible at higher cannibalism rates when we lumped these nodes (Figure 3: short dashes). The negative effect of cannibalism on nitrogen mineralization in the arctic food web was caused by the atypical biomass pyramid. The site had high arthropod biomass but relatively low nematode biomass producing a staggered biomass pyramid. This biomass pyramid is responsible for the decrease in nitrogen mineralization because we observed the same negative trend when we placed the biomasses and parameters from the arctic system into the soil food web model structure for a field in Colorado (Koltz et al. 2018; Hunt et al. 1987; Figure 3: long dashes).

4. Discussion

Food web models often handle the diversity of soil systems by lumping together similar organisms and their shared feeding relationships, physiological properties, and life histories (Moore & de Ruiter 2012). Such methods can use existing data to predict key life history traits, like cannibalism, and can help soil ecologists answer recent calls to document the functional importance of soil communities (AO, ITPS, GSBI, SCBD, and EC 2020). We use a general ecological model to derive a theoretical limit for cannibalism and demonstrate the potential importance of cannibalism across sixteen soil food webs in a manner that standardizes cannibalism rate based on an organism's capacity to persist while eating conspecifics. Our work contributes to the growing body of literature on soil food web model structural uncertainty and parameterization (e.g., Buchkowski & Lindo 2021).

4.1. Model interpretation

Using trophic species and general food web parameters influences our interpretation of maximum cannibalism rate and maximum cannibalism preference. The definition of cannibalism in our analysis is broad because it includes any consumption of the same trophic species (Figure 1C). Cannibalism is often estimated in field studies of soil food webs based on intraguild predation, so this model assumption matches much of our empirical data (Bilgrami et al. 1986; Koltz & Wright 2020; Parimuchová et al. 2021).

Lumping individual species together can produce aggregation effects that influence our calculations (Figure 1C). Lumping influences our calculations because $mean(a_1 \times p_1, a_2 \times p_2) \neq mean((a_1, a_2) \times mean(p_1, p_2)$ (i.e., Jensen's inequality). These considerations are relevant to our results because the properties of assimilation and production efficiency are not always measured on trophic species. Instead, they can be measured on individuals or laboratory populations (Chamberlain et al. 2004). We would expect similar lumping errors to occur in both our theoretical calculations and ^{15}N calculations. These errors should be minor if trophic species are created by grouping biological species with similar conversion efficiencies (Buchkowski & Lindo 2021).

In fact, lumping trophic species together in the Hunt et al. (1987) food web had little effect on maximum cannibalism rate and cannibalism's effect on nutrient mineralization (Appendix Figure A1). However, it did alter maximum cannibalism preference, because lumping changes the relative abundance of conspecifics and prey most dramatically.

4.2. Conceptual results

Our mathematical analysis predicts that species with higher conversion efficiency have the highest capacity for cannibalism. This prediction is difficult to evaluate in soil food webs because measurements of cannibalism are scarce. Certainly, cannibalism is relatively common in ciliates where engulfment of prey makes feeding efficient (Polis 1981) and when adults feed on eggs, juvenile animals, or larvae where we might expect assimilation to be more efficient (Figure 1B; Getto et al. 2005; Polis 1981). But it is also common in groups with less efficient feeding (Devi 1964; Koltz & Wright 2020). So, our theoretical result calls for empirical validation.

Estimates of cannibalism rate are rare for soil biota and typically report the percentage of individuals who cannibalize. This makes cannibalism rate as a proportion of the diet difficult to estimate. For example, less than 5% of ciliates appear to be cannibals in cultures, 44% of mites and 25% of beetles in a cave ecosystem have conspecific DNA in their guts, and 20% of monarch nematodes had conspecifics in their guts (Bilgrami et al. 1986; Devi 1964; Parimuchová et al. 2021; Polis 1981). Within a single taxa like nematodes, some species appear to be enthusiastic cannibals (Bilgrami et al. 1986; Devi 1964), while others refuse conspecifics even without alternative prey (Nelmes 1974). So, the limits placed on cannibalism by our analyses are useful as initial estimates for a process that has little empirical data to constrain it.

Our theoretical analysis predicted that cannibalism rate should be high when food is scarce and conspecifics are abundant. This result is well documented (Jassey et al. 2013; Mayntz & Toft 2006; Polis 1981; Wise 2006). Our analysis also predicts that a species preference for cannibalism must be low relative to other prey where encounters between conspecifics are common. A low preference for cannibalism is essential in these situations to keep the overall cannibalism rate below the maximum. Mathematically, w_{ii} can easily cause the term $\left(\frac{X_{iT}}{w_{ii}X_i^*} - 1\right)$ to be negative when X_i^* is large (Eqn 3). In other words, we expect ecological or evolutionary controls preventing cannibalism, which manifest as a weak preference for cannibalism, to be important when conspecifics are abundant, prey are scarce, and physiological efficiency is low (Jassey et al. 2013; Polis 1981; Wise 2006).

4.3. Ecological interpretation of the quantitative results

Soil organisms are generally thought to be opportunistic cannibals, which implies that the maximum rates of cannibalism may be reached rarely or sporadically. For example, protists have cannibalistic morphs that typically make up 2-3% of the population. So, cannibalism probably accounts for no more than 10% of feeding on average even if we assume that these large cannibals eat more (Jassey et al. 2013; Martel & Flynn 2008; Polis 1981). For comparison, the maximum rate we calculate from our mathematical method and using ^{15}N mixing is ~40%. Cannibalism appears to be limited to larger, stronger, or more developed individuals in many species, so considering ecological aspects after physiological constraints would explain the gap between these estimates and further limit maximum cannibalism rates (Berndt et al. 2003; Le Clec'h et al. 2013; Polis 1981).

Interestingly, our theoretical limit on cannibalism preference is strongest among the predatory species that have the mouthpart morphology best suited to it, such as spiders, predatory mites, and beetles (Berndt et al. 2003; Polis 1981; Wise 2006; Table 2). The reason is that these species are much closer in abundance to their prey and are more likely to encounter conspecifics in a well-mixed system. So, wolf spiders can only show a preference of 0.116 for cannibalism in the Arctic because wolf spiders are abundant (2.163 $mg_C\ m^{-2}$) relative to their prey (Koltz et al. 2018). Alternatively, crab spiders can show a maximum preference of 0.863 for cannibalism to achieve the same diet proportion of 0.21 because of their lower density (0.049 $mg_C\ m^{-2}$). The difference in maximum preference between these spiders may be even larger than their biomass suggests because roaming wolf spiders are more likely to encounter each other than sit-and-wait crab spiders (Smith & Schmitz 2016; Wise 2006).

Besides predators, we found that organisms eating plants and detritus have a low propensity for cannibalism (Table 2) if we assume that their conversion efficiency as cannibals remains low. This demonstrates a weakness of the naïve assumption that assimilation efficiency is constant across all food sources (Eqn 5). For example, herbivores probably have higher conversion efficiency as cannibals than when eating plant tissue. We can relax this assumption using data on the conversion efficiency of cannibalism relative to other food (Figure 1; Eqn 4). Food-specific conversion efficiency parameters are scarce for soil organisms, so one strategy might be to calculate the potential difference from first principles using our understanding of metabolic efficiency of different food types (Chamberlain et al. 2004; Taipale et al. 2014).

4.4. *Ecological consequences of cannibalism in food webs*

Our findings demonstrate that uncertainty in the rates of cannibalism in soil food web models could introduce up to a 10% and 30% error in carbon and nitrogen mineralization relative to their total flux, respectively (Figure 3). Indeed, carbon mineralization across all sixteen food webs converged towards 70% of the system flux as cannibalism increased (Figure 3). Since cannibalism does not influence individual node efficiency (i.e., a and p remain constant), the convergence must be explained by shifting resource flows. In fact, the convergence occurs because the reduced trophic transfer efficiency caused by cannibalism necessitates greater resource consumption at the higher trophic levels and pulls more carbon through the microbial biomass at the base of the soil food web at equilibrium. In other words, cannibals compete with their predators and cause more consumptive pressure at their own trophic level, which passes down the web and makes each population grow faster as they are pushed further from their carrying capacity. As this happens, microbial carbon cycling grows in relative importance so the overall carbon use efficiency of the web (i.e., 100-70 = 30%) approaches the microbial carbon use efficiency (i.e., 30%). Essentially, high levels of cannibalism cause the carbon use efficiency of soil food webs to converge on that of microorganisms by increasing total fluxes through basal pools (Figure 3).

Cannibalism increased nitrogen mineralization across fifteen of sixteen food webs more than it did carbon mineralization. Nitrogen mineralization increased more than carbon mineralization because it is affected by both reduced trophic transfer efficiency and by cannibals consuming higher nitrogen diets that yield more nitrogen waste (Polis 1981; Wise 2006). The different effect sizes of cannibalism on carbon and nitrogen suggest that it may alter the stoichiometry of soil food webs.

4.5. *Caveats*

Important assumptions in our analysis are (1) equilibrium conditions, (2) a well-mixed system, and (3) the assumption that conversion efficiency is consistent across food types. The first assumption means our estimates are suitable for populations over multiple generations and do not capture short term peaks or valleys in cannibalism, such as during reproduction (Polis 1981; Wise 2006). The second assumption of a well-mixed system affects our calculations of maximum preference for cannibalism and does not influence the maximum cannibalism rate (Eqns 4 & 5). The third assumption of a constant conversion efficiency across different food items is common in soil food web models (Moore & de Ruiter 2012) and can be relaxed if data on food-specific conversion are available (c.f., Eqns 4 & 5). These data would increase the maximum rate of cannibalism for herbivores and detritivores for which the conversion efficiency for cannibalism is likely higher than for other resources (Figure 2: look above the dashed line).

Defining cannibalism at the trophic species level matches our taxonomic resolution but does not necessarily match ecological processes. For example, predatory and omnivorous tardigrades consume herbivorous tardigrades (Bryndová et al. 2020). This would be considered cannibalism in soil food web models because tardigrades are assigned to a single node (e.g., Koltz et al. 2018; Figure 1C). However, many of the deterrents against cannibalism, such as kin recognition (Lightfoot et al. 2019), would not apply in this case. The risk of attacking conspecifics that can fight back might also not apply for broadly defined trophic species like tardigrades, where herbivorous species may not be as dangerous to predators (Bryndová et al. 2020; Wise 2006). Interpreting the gap between the maximum possible rate of cannibalism and the true cannibalism rate of trophic species requires a careful parsing of the different mechanisms limiting intraspecific feeding and intrageneric feeding.

Our estimates of cannibalism in units of C or N also obscure variation between individuals. Cannibalistic morphs often account for most cannibalism in a population (Polis 1981). We did not explore individual differences or the importance of cannibalism in stage structured populations but recognize their potential importance for soil organisms, especially for species with different diet breaths across ontogeny (e.g., mesostigmatid mites; Berndt et al. 2003; Getto et al. 2005; Polis 1981). A value of our analysis is that it can be reapplied to more detailed species data when they are available.

5. Conclusions

The estimates of maximum cannibalism rate presented here have two uses. First, they provide a means of reducing the parameter space that we need to search during our sensitivity analyses of food web models (Topping et al. 2015). Getting these parameters right is especially important for soil food web models because their hierarchical structure means that the rates of cannibalism affect our estimates of feeding rates at all the lower trophic levels. Second, the estimates can also be used by soil ecologists to identify species for which cannibalism may be important and so should be further studied.

Soil ecologists can test our estimates of cannibalism rates by comparing empirical data on cannibalism to data on physiological efficiency using equations (4) and (5) along with individual-specific DNA methods, gut content analysis, or behavioral observations (Berndt et al. 2003; Dahl et al. 2018; Jassey et al. 2013). Equation (4) maps physiological rates to cannibalism, so that any differences between this predicted maximum and the true maximum rates we measure can be interpreted using the mechanisms not included in our model assumptions. Finally, our model could be evaluated in other ecosystems for which data on the conversion efficiency of (trophic) species are available (e.g., Rand & Stewart 1998).

Statement of Authorship

RWB wrote the code and drafted the manuscript. ZL, JB, and VJ compiled literature on cannibalism rates and provided expert feedback on the maximum cannibalism rates for each taxon. All authors made substantial revisions to the manuscript.

Data accessibility

All the code necessary to recreate our analyses are available on GitHub, https://github.com/robertwbuchkowski/cannibalism, with a permanent DOI at 10.6084/m9.figshare.20292435. All data were taken from published papers and are repeated in the repository for convenience with the appropriate citations.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2022.108773.

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