Cannibalism has its limits in soil food webs

Robert W.Buchkowski, Janna M.Barel, Vincent E.J.Jassey, Zoë Lindo

Cannibalism has its limits in food webs

Robert W. Buchkowski[1,3*], Janna M. Barel[2], Vincent E.J. Jassey[2], and Zoë Lindo[1]

1. Department of Biology, Western University, London, Ontario, Canada
2. Laboratoire Ecologie Fonctionelle et Environnement, Université de Toulouse, CNRS, Toulouse, France
3. Atlantic Forestry Centre, Natural Resources Canada, Fredericton, New Brunswick, Canada

*Correspondence: robert.buchkowski@gmail.com; 1151 Richmond Street, London, ON, N6A 5B7, 519-850-2542

Abstract

Cannibalism imperfectly recycles resources back to the same species and so decreases trophic transfer efficiency in food webs. So, viable populations have some limit on how much of their diet can come from cannibalism. We apply 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.

Keywords: necrophagy; food web models; mites; mineralization; protists; spiders

a supprimé: limit for the

a supprimé: that can come

a supprimé: 40

a supprimé: when added to

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). 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 for reducing model uncertainty and directing 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 food web models will change depending on whether it is restricted to

a supprimé: techniques because it affects isotopic

a supprimé:

a supprimé: because the

a supprimé: have been studied

a supprimé: known

a supprimé: this

a supprimé: (eating dead conspecifics)

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 would thereby create a bias if the model allocation of these processes does not correspond with the empirical situation.

We study sixteen soil food web models, which were all that we could find in the literature (Table 1). In these models, the location of cannibalistic necrophagy and coprophagy is determined 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 coprophagous trophic species are often allowed to consume the detritus pool into which its faeces are added and 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. Population viability is not a good 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), so it is not a predictor of true cannibalism rate. Instead, it is one way to set a theoretical upper limit on cannibalism and the preference for eating conspecifics. The reason is that species which persist are not eating themselves to extinction.

a supprimé: are

a supprimé: very

a supprimé: because neither

a supprimé: can be

a supprimé: conversion

a supprimé: and

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), nutritive 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.

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):

$$\frac{dX_i}{dt} = a_i p_i \sum_{j \neq i} F_{ij} - D_i - \sum_{j \neq i} F_{ji} - (1 - a_i p_i) F_{ii} \quad (1)$$

where X_i is the trophic species biomass typically indexed in carbon. F_{ij} is the rate that the focal species *i* eats species *j*. F_{ji} is the rate that species *j* eats focal species *i*. a_i, p_i, and D_i are the assimilation efficiency, production efficiency, and death rate, respectively. F_{ii} is the rate of cannibalism with a_i and

a supprimé: predict where

a supprimé: and

a supprimé: are the rates of consumption by the focal species (*i*) and the rates that species is eaten, respectively

p_i being the assimilation and production efficiency for cannibalistic feeding. It is likely that $a_i p_i$ will be (1) larger than $a_i p_i$ for detritivores and herbivores and (2) 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 $\{\sum_j^N F_{1j}, \sum_j^N F_{2j}, \dots, \sum_j^N F_{Nj}\}$ using the system of equations defined by the *N* species $\left\{\frac{dX_1}{dt}, \frac{dX_2}{dt}, \dots \frac{dX_N}{dt}\right\}$ (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:

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

a supprimé: only

a supprimé: above

a supprimé: solve the system of equations at

a supprimé:

a supprimé: ,

a déplacé (et inséré) [1]

a supprimé: , by

a supprimé: ing

a supprimé: of each as the unknowns

a supprimé: predation rates

a déplacé vers le haut [1]: consumption rate of each as the unknowns $\{\sum_j^N F_{1j}, \sum_j^N F_{2j}, \dots, \sum_j^N F_{Nj}\}$

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

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

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

144 Assuming equilibrium $\left(\frac{dX_i}{dt} = 0\right)$ and using the relation in Eqn 2d to relate cannibalism and total

145 consumption, we can calculate the rate of cannibalism from Eqn 1 as:

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

146 Cannibalism rate in units of carbon is determined by all the model parameters: death rates, predation

147 rates, conversion efficiency, and prey availability. This result is consistent with a carbon budget view of

148 each trophic species (Figure 1A).

149 The maximum proportion of cannibalism in the diet is only affected by the conversion efficiencies (Eqn

150 3; Figure 1B). Cannibalism rate can be positive at equilibrium only when the denominator of equation (3)

151 is positive. The denominator of equation (3) incorporates information on the cannibalism rate $\left(\frac{X_{iT}}{w_{ii} X_i^*}\right)^{-1}$,

152 which we define as the proportion of the diet that comes from cannibalism (Wise 2006). Given that

153 $\frac{X_{iT}}{w_{ii} X_i^*} = \frac{F_{iT}}{F_{ii}}$ from (2d), the condition for cannibalism at equilibrium from equation (3) is:

$$\frac{a_i p_i}{1 - a_i p_i + a_i p_i} > \frac{F_{ii}}{F_{iT}} \tag{4}$$

154 The maximum possible proportion of cannibalism in the diet $\left(\frac{F_{ii}}{F_{iT}}\right)$ is set by the conversion efficiency of

155 cannibalism $(a_i p_i)$ when it is less than perfect or different from the conversion efficiency for other prey

156 $(a_i p_i$; 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., $a_i = \alpha_i = \alpha_i$ and $p_i = p_i = p_i$), the condition simplifies to:

$$\alpha_i p_i > \frac{F_{ii}}{F_{iT}} \tag{5}$$

2.2 Model analysis

We calculated maximum cannibalism rate using conversion efficiencies. 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 $w_{ii} < \frac{\alpha_i p_i X_{iT}}{X_i^*}$. 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.

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

We calculated maximum cannibalism rate and Jacob's index for 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 papers 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 maximized 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).

a supprimé: a

a supprimé: that

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 being excluded 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). 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).

a supprimé: because

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 preference for cannibalism. The reason cannibalism rates 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

a supprimé: estimate

a supprimé: because

a supprimé: so

a supprimé: with more

a supprimé: comparable

a supprimé: mostly identical

a supprimé: Trophic species that stand out with high maximum cannibalism proportions are single

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 be the one produced by our theoretical approach.

3.4 The effects of cannibalism on nutrient cycling

a supprimé: worse

a supprimé: the

a supprimé: on source of

a supprimé: , but

a mis en forme : Exposant

Cannibalism increased carbon and nitrogen mineralization relative to the internal flux for the food webs in four of 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 in our data set (Koltz *et al.* 2018). 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 of mutual feeding between top predators such as spiders and beetles produced no 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).

a supprimé: In the only arctic food web that we found,

a supprimé: c

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). So, any methods that utilize existing data to predict key life history traits, like cannibalism, 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 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 interpret 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 errors to occur in both our theoretical calculations and ^{15}N calculations. If biological species are grouped into trophic species when conversion efficiencies are similar, then these errors should be minor (Buchkowski & Lindo, 2021).

In fact, lumping trophic species together for the Hunt et al. (1987) food web had little effect on maximum cannibalism rate and its effect on nutrient mineralization (Appendix 1). It did alter maximum

a mis en forme : Exposant

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 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

a supprimé: it

a supprimé: result

a supprimé: is most

a supprimé: common

a supprimé: common

a supprimé:

a supprimé: Our

a supprimé: model

a supprimé: that the

a supprimé: can be very high when the density of the cannibalistic species (X_c) is low

a supprimé: its prey

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

a supprimé: because

a supprimé: be very large before the term

a supprimé: becomes

a supprimé: too negative

a supprimé: and its negative impacts on population persistence remain low when conspecifics are unlikely to encounter each other …

a supprimé: are larger than conspecifics and these

a supprimé: bigger individuals

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 their 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 grows faster as they are pushed further from their carrying capacity. As this happens, microbial carbon cycling grows in relative importance so

a supprimé: as

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 viable for persisting populations over the long-term 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

a supprimé: We built our model with more generality by allowing conversion efficiency to be different for cannibalism than for other food types (Eqn 4) but found the empirical measurements were not available to carry out the analysis (Eqn 5). This assumption reduced

a supprimé: cases

a supprimé: where

a supprimé: higher

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.

4.6 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

a supprimé: ces

a supprimé: If we think of individual nodes as submodules, the limits of cannibalism represent the range of parameters wherein we get reasonable submodule behavior (Lorscheid & Meyer, 2016). …

a supprimé: These

a supprimé: tested by

a supprimé: studying the feeding habitats of soil organisms

a supprimé: cannibalism rates

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 for other ecosystems for which data on the conversion efficiency of (trophic) species are available (e.g., Rand & Stewart, 1998).

5 Acknowledgements

Robert Buchkowski was supported by a postdoctoral fellowship grant from the Natural Science and Engineering Research Council of Canada. Janna Barel was supported by MIXOPEAT, a project funded by the French National Research Agency (grant number ANR-17-CE01-0007 to VEJJ). The authors thank André Franco, Diana Wall, and Dorota Porazinska for their input on nematode cannibalism.

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.

Declaration of competing interests

The authors declare no competing interests.

Data accessibility

All the code necessary to recreate our analyses are available on GitHub, https://github.com/robertwbuchkowski/cannibalism, with a permanent link to be created upon publication. All data were taken from published papers and are repeated in the repository for convenience with the appropriate citations.

References

Allison, S.D., Wallenstein, M.D. & Bradford, M.A. 2010. Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience.*, 3, 336–340.

Andrés, P., Moore, Simpson, R.T., Selby, G., Cotrufo, F., Denef, K., *et al.* 2016. Soil food web stability in response to grazing in a semi-arid prairie: The importance of soil textural heterogeneity. *Soil Biology Biochemistry*, 97, 131–143.

AO, ITPS, GSBI, SCBD, and EC. 2020. *State of knowledge of soil biodiversity - Status, challenges and potentialities*. FAO, Rome.

Berndt, O., Meyhöfer, R. & Poehling, H.-M. 2003. Propensity towards cannibalism among *Hypoaspis aculeifer* and *H. miles* , two soil-dwelling predatory mite species. *Experimental and Applied Acarology*, 31, 1–14.

Bilgrami, A.L., Ahmad, I. & Shamim Jairajpuri, M. 1986. A study of the intestinal contents of some mononchs. *Revue de nématologie*, 9, 191–194.

Bryndová, M., Stec, D., Schill, R.O., Michalczyk, Ł. & Devetter, M. 2020. Dietary preferences and diet effects on life-history traits of tardigrades. *Zoological Journal of the Linnean Society*, 188, 865–877.

Buchkowski, R.W. & Lindo, Z. (2021). Stoichiometric and structural uncertainty in soil food web models. *Functional Ecology*, 35, 288–300.

Chamberlain, P.M., Bull, I.D., Black, H.I.J., Ineson, P. & Evershed, R.P. 2004. Lipid content and carbon assimilation in Collembola: implications for the use of compound-specific carbon isotope analysis in animal dietary studies. *Oecologia*, 139, 325–335.

Claessen, D., de Roos, A.M. & Persson, L. 2004. Population dynamic theory of size–dependent cannibalism. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271, 333–340.

502 Dahl, K.A., Portnoy, D.S., Hogan, J.D., Johnson, J.E., Gold, J.R. & Patterson, W.F. 2018. Genotyping
503 confirms significant cannibalism in northern Gulf of Mexico invasive red lionfish, Pterois volitans.
504 *Biological Invasions*, 20, 3513–3526.
505 De Ruiter, P.C., Van Veen, J.A., Moore, J.C., Brussaard, L. & Hunt, H.W. 1993. Calculation of nitrogen
506 mineralization in soil food webs. *Plant and Soil*, 157, 263–273.
507 Devi, R.V. 1964. Cannibalism in *Frontonia leucas* Ehr. *The Journal of Protozoology*, 11, 304–307.
508 Digel, C., Curtsdotter, A., Riede, J., Klarner, B. & Brose, U. 2014. Unravelling the complex structure of
509 forest soil food webs: higher omnivory and more trophic levels. *Oikos*, 123, 1157-1172.
510 Getto, Ph., Diekmann, O. & de Roos, A.M. 2005. On the (dis) advantages of cannibalism. *Journal of*
511 *Mathematical Biology*, 51, 695–712.
512 Guill, C. & Paulau, P. 2015. Prohibition rules for three-node substructures in ordered food webs with
513 cannibalistic species. *Israel Journal of Ecology and Evolution*, 61, 69–76.
514 Hendrix, P.F., Parmelee, R.W., Crossley, D.A., Coleman, D.C., Odum, E.P. & Groffman, P.M. 1986. Detritus
515 food webs in conventional and no-tillage agroecosystems. *Bioscience*, 36, 374–380.
516 Hobson, K.A. & Welch, H.E. 1995. Cannibalism and trophic structure in a high Arctic lake: insights from
517 stable-isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 1195–1201.
518 Holtkamp, R., van der Wal, A., Kardol, P., van der Putten, W.H., de Ruiter, P.C. & Dekker, S.C. 2011.
519 Modelling C and N mineralisation in soil food webs during secondary succession on ex-arable
520 land. *Soil Biology and Biochemistry*, 43, 251–260.
521 Hunt, H.W., Coleman, D.C., Ingham, E.R., Ingham, R.E., Elliott, E.T., Moore, J.C., *et al.* 1987s. The detrial
522 food web in a shortgrass prairie. *Biology and Fertility of Soils*, 3, 57–68.
523 Jacobs, J. 1974. Quantitative measurement of food selection: A modification of the forage ratio and
524 Ivlev's electivity index. *Oecologia*, 14, 413–417.

525 Jahnes, B.C., Herrmann, M. & Sabree, Z.L. 2019. Conspecific coprophagy stimulates normal development
526 in a germ-free model invertebrate. *PeerJ*, 7, e6914.
527 Jassey, V.E.J., Meyer, C., Dupuy, C., Bernard, N., Mitchell, E.A.D., Toussaint, M.-L., *et al.* 2013. To What
528 Extent Do Food Preferences Explain the Trophic Position of Heterotrophic and Mixotrophic
529 Microbial Consumers in a Sphagnum Peatland? *Microbial Ecology*, 66, 571–580.
530 Koltz, A.M., Asmus, A., Gough, L., Pressler, Y. & Moore, J.C. 2018. The detritus-based microbial-
531 invertebrate food web contributes disproportionately to carbon and nitrogen cycling in the
532 Arctic. *Polar Biology*, 41, 1531–1545.
533 Koltz, A.M. & Wright, J.P. 2020. Impacts of female body size on cannibalism and juvenile abundance in a
534 dominant arctic spider. *Journal of Animal Ecology*, 89, 1788–1798.
535 Le Clec'h, W., Chevalier, F.D., Genty, L., Bertaux, J., Bouchon, D. & Sicard, M. 2013. Cannibalism and
536 Predation as Paths for Horizontal Passage of Wolbachia between Terrestrial Isopods. *PLoS ONE*,
537 8, e60232.
538 Lightfoot, J.W., Wilecki, M., Rödelsperger, C., Moreno, E., Susoy, V., Witte, H., *et al.* 2019. Small peptide–
539 mediated self-recognition prevents cannibalism in predatory nematodes. *Science*, 364, 86–89.
540 Lima, T.D.N. 2016. Cannibalism among *Myrmeleon brasiliensis* larvae (Návas, 1914) (Neuroptera,
541 Myrmeleontidae). *Acta Scientiarum. Biological Sciences*, 38, 447.
542 Lorscheid, I. & Meyer, M. 2016. Divide and conquer: Configuring submodels for valid and efficient
543 analyses of complex simulation models. *Ecological Modelling*, 326, 152–161.
544 Martel, C.M. & Flynn, K.J. 2008. Morphological controls on cannibalism in a planktonic marine
545 phagotroph. *Protist*, 159, 41–51.
546 Mayntz, D. & Toft, S. 2006. Nutritional value of cannibalism and the role of starvation and nutrient
547 imbalance for cannibalistic tendencies in a generalist predator. *Journal of Animal Ecology*, 75,
548 288–297.

549 Mieczan, T., Michał, N., Adamczuk, M. & Bielańska-Grajner, I. 2015. Stable isotope analyses revealed
550 high seasonal dynamics in the food web structure of a peatbog: Food preferences of microbial
551 consumers in wetland. *International Review of Hydrobiology*, 100, 141–150.
552 Moore, J.C. & de Ruiter, P. C. 2012. *Energetic Food Webs: An Analysis of Real and Model Ecosystems*.
553 Oxford University Press, Oxford.
554 Nalepa, C.A., Bignell, D.E. & Bandi, C. 2001. Detritivory, coprophagy, and the evolution of digestive
555 mutualisms in Dictyoptera. *Insectes Sociaux*, 48, 194–201.
556 Nelmes, A.J. 1974. Evaluation of the feeding behaviour of *Prionchulus punctatus* (Cobb), a nematode
557 predator. *Journal of Animal Ecology*, 43, 553.
558 Oelbermann, K. & Scheu, S. 2010. Trophic guilds of generalist feeders in soil animal communities as
559 indicated by stable isotope analysis (15N/14N). *Bulletin of Entomological Research*, 100, 511–
560 520.
561 Ott, D., Rall, B.C. & Brose, U. (2012). Climate change effects on macrofaunal litter decomposition: the
562 interplay of temperature, body masses and stoichiometry. *Philosophical Transactions of the*
563 *Royal Society B-Biological Sciences*, 367, 3025–3032.
564 Parimuchová, A., Dušátková, L.P., Kováč, Ľ., Macháčková, T., Slabý, O. & Pekár, S. 2021. The food web in
565 a subterranean ecosystem is driven by intraguild predation. *Scientific Reports*, 11, 4994.
566 Polis, G.A. 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and*
567 *Systematics*, 12, 225–251.
568 Polis, G.A. 1991. Complex trophic interactions in deserts: An empirical critique of food-web theory. *The*
569 *American Naturalist*, 138, 123–155.
570 Rand, P.S. & Stewart, D.J. 1998. Prey fish exploitation, salmonine production, and pelagic food web
571 efficiency in Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 318–327.

572 Renahan, T. & Sommer, R.J. 2021. Nematode interactions on beetle hosts indicate a role of mouth-form
573 plasticity in resource competition. *Frontiers in Ecology Evolution*, 9, 752695.
574 Richardson, M.L., Mitchell, R.F., Reagel, P.F. & Hanks, L.M. (2010). Causes and consequences of
575 cannibalism in noncarnivorous insects. *Annual Review of Entomology*, 55, 39–53.
576 de Ruiter, P.C., Bloem, J., Bouwman, L.A., Didden, W.A.M., Hoenderboom, G.H.J., Lebbink, G., *et al.*
577 (1994). Simulation of dynamics in nitrogen mineralisation in the belowground food webs of two
578 arable farming systems. *Agriculture, Ecosystems & Environment*, 51, 199–208.
579 Schausberger, P. & Croft, B.A. 2000. Nutritional benefits of intraguild predation and cannibalism among
580 generalist and specialist phytoseiid mites. *Ecological Entomology*, 25, 473–480.
581 Schmitz, O.J., Wilmers, C.C., Leroux, S.J., Doughty, C.E., Atwood, T.B., Galetti, M., *et al.* 2018. Animals
582 and the zoogeochemistry of the carbon cycle. *Science*, 362, eaar3213.
583 Smith, J.R. & Schmitz, O.J. 2016. Cascading ecological effects of landscape moderated arthropod
584 diversity. *Oikos*, 125, 1261–1272.
585 Stevens, M.H.H. 2009. *A primer of ecology with R*. Use R! Springer, New York.
586 Taipale, S.J., Brett, M.T., Hahn, M.W., Martin-Creuzburg, D., Yeung, S., Hiltunen, M., *et al.* 2014. Differing
587 *Daphnia magna* assimilation efficiencies for terrestrial, bacterial, and algal carbon and fatty
588 acids. *Ecology*, 95, 563–576.
589 Topping, C.J., Alrøe, H.F., Farrell, K.N. & Grimm, V. 2015. Per aspera ad astra: Through complex
590 population modeling to predictive theory. *The American Naturalist*, 186, 669–674.
591 Tosi, L. & Sartini, M. 1983. Interactions between social and feeding behaviour in *Sinella coeca*
592 (Collembola). *Bolletino di zoologia*, 50, 189–195.
593 Wise, D.H. 2006. Cannibalism, food limitation, intraspecific competition, and the regulations of spider
594 populations. *Annual Review of Entomology*, 51, 441–465.

595 Zimmer, M. 2002. Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological
596 approach. *Biological Reviews*, 77, 455–493.

597 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

598 *Sources for the isotope data.

599 Table 2: The maximum proportions of each trophic species' diet that can come from cannibalism and
600 Jacob' index of feeding preference. Cannibalism is defined as feeding on your own TROPHIC SPECIES.
601 Ranges are provided when there are differences across webs. Calculations were made using sixteen
602 published food webs with some additional grouping of trophic species after the calculations to make the
603 table a reasonable size (Hunt et al. 1987; de Ruiter et al. 1994; Holtkamp et al. 2011; Andrés et al. 2016;
604 Koltz et al. 2018). N is the number of estimates, with numbers over 16 occurring when multiple trophic
605 species from the same web occur in the same group. Jacob's index ranges from avoidance (-1) to
606 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

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

a supprimé: to 0.3

610 Figure Captions:

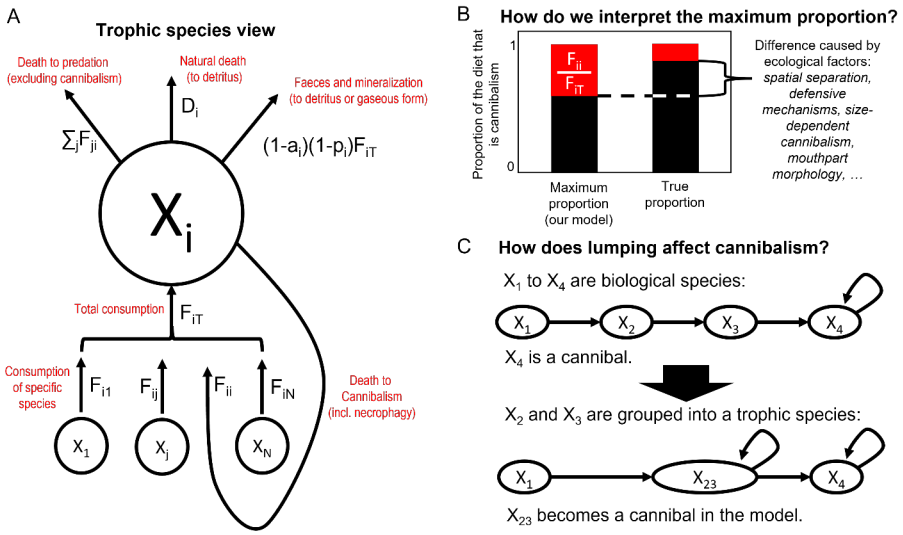
611 Figure 1: Three concepts important to interpreting the Lotka-Volterra models used in our analysis. (A)
612 The trophic species model used in soil food web analyses and to estimate maximum cannibalism rate.
613 The focal trophic species X_i consumes carbon and nitrogen from several sources (i.e.,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

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

627 Figure 3: The efficiency of carbon and nitrogen cycling in published soil food webs along a gradient of
628 cannibalism from 0 to 99% of the maximum rate (Table 2) for all nodes except phytophagous
629 nematodes, plants parts, and organic matter. A larger value on the y-axis indicates more mineralization
630 per unit of element cycling in the web (i.e., the web is less efficient). Cannibalism makes most of the soil
631 food webs less efficient. It makes the Koltz web untenable over 0.74 because of mutual feeders (Koltz:
632 No mutual feeders) and reduces nitrogen loss because of the non-monotonic biomass pyramid (Koltz in

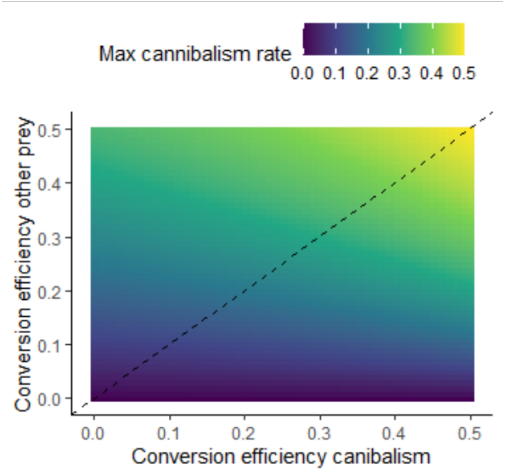
CPER). Holtkamp et al. (2011) present webs for Young to Heathland field types (N=4), Andrés et al. (2016) have three sites with grazed and ungrazed plots (N = 6), and de Ruiter et al. (1994) have conventional and integrated management sites at two depths (N = 4). The effect of removing mutual predation and placing the Koltz et al. (2018) biomass data into the CPER (Hunt et al. 1987) are differentiated by line type.

638 **Figure 1**

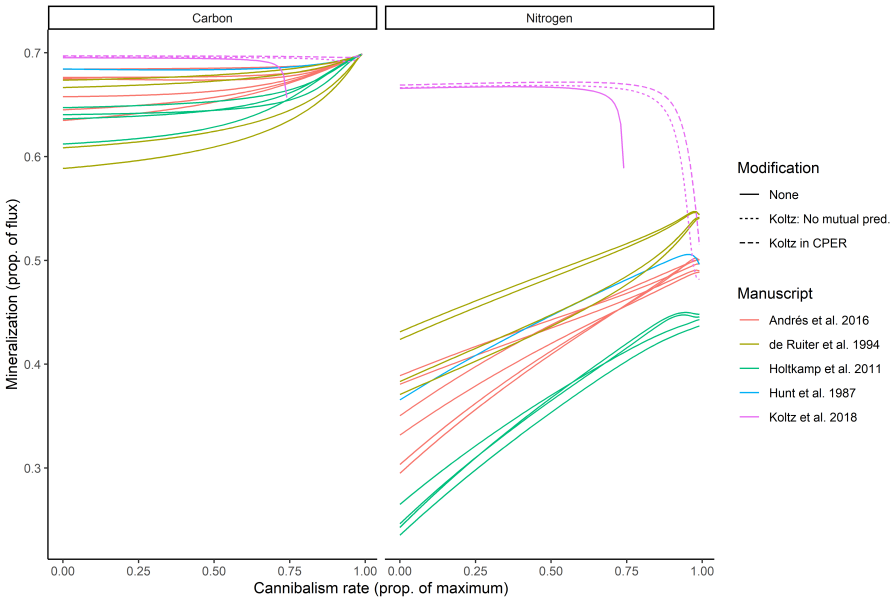


639

Figure 2


Max cannibalism rate
0.0 0.1 0.2 0.3 0.4 0.5
Conversion efficiency other prey
0.0
0.1
0.2
0.3
0.4
0.5
Conversion efficiency canibalism

642 **Figure 3**



643