Species traits and community properties explain species extinction effects on detritus-based food webs

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Abstract

Effects of species extinction, and particularly of changing functional composition, on nutrient cycling in soil communities are still not well understood. Models simulating community dynamics overcome the technical challenges of conducting species removal experiments in the field. However, to date, available soil food web models do not adequately represent the organic matter processing chain which is key for soil dynamics. Here, we present a new model of soil food web dynamics accounting for allometric scaling of metabolic rate and ontogeny of organic matter along with explicit representation of nitrogen and carbon flows. We use this model to determine which traits are best predictors of species effects on community productivity, and on nutrient cycling. To do so, we removed 161 tropho-species (group of functionally identical species) one at a time from 48 forest soil food webs, and simulated their dynamics until equilibrium. We assessed tropho-species removal effects as the relative changes between the biomass of each component (consumers, detritus, producers, microbes and nitrogen) before, and after the removal. Simulations revealed that combinations of traits determine species effects. The smallest species with a low C:N ratio are the most competitive ones, but carnivores of various body masses presenting the highest connectivity and resource similarity could be key stone species in the regulation of competitive forces. Despite this, most removals had low effects and none of the removals changed the amount of available inorganic nitrogen. These results suggest a high resistance of soil food webs to species extinction, resulting from high species redundancy and the adaptability of the microbial community. We also highlight for the first time that food web structure and soil fertility can drastically change species effects in an unpreventable way. Moreover, the exclusion of detritus and stoichiometric constraints in past studies lead to underestimations of indirect effects and retroactions. While additional work is needed to incorporate complementarity between detritivores, it is essential to take into account these mechanisms in models in order to improve the understanding of soil food web functioning.
Introduction

Soil communities are largely under-documented despite their importance in the provision of several ecosystem services [Bardgett and Wardle 2010]. Soil food webs are based on detritus and then have a distinct functioning relative to other types of food webs [Moore et al. 2004, Digel et al. 2014]. This particularity added to the wide diversity of life forms within soil community lead to important feed-backs, and make difficult the study of relationships between soil food web structure and functioning. Theoretical studies and mesocosm experiments investigated the role of several taxonomic groups in the process of litter decomposition, but so far, we do not know which species characteristics best predict the way it affects this process. Functional traits can reveal generalities across ecosystems [McGill et al. 2006, Violle et al. 2007, Cardinale et al. 2012], and provide a common currency to reduce the tremendous diversity of soil food webs. Therefore, it is legitimate to ask if the trait based approach could be used to better understand how changes in community structure could alter ecosystem functions [Wardle 2006, Bardgett and Wardle 2010].

A species effect on ecosystem functions, such as productivity or nutrient cycling, can be direct, caused by a particular characteristic involved in a specific function. For example, a grazer can efficiently regulate bacteria biomass, and the vertical movement of earthworms distributes organic matter in the soil profile. Species effects on ecosystem functions can also be indirect via trophic regulation that propagates throughout the network of interactions [Montoya et al. 2009]. A species effect on other species biomass can cascade from the bottom to the top of the food chain, such as the plant composition of a community that can affect the abundance and the composition of herbivores, detritivores, predators and parasitoids [Hawes et al. 2003, Bohan et al. 2005]. Alternatively, looking from the top to the bottom, Schmitz 2003, 2009 showed how predator functional type, mostly determined by hunting strategy, influences herbivores behavior, plant composition, and consequently nutrient cycling. Indirect effects can also be observed between species due to apparent
or exploitative competition for a shared consumer or resource, respectively. For instance, Montoya et al. [2009] showed that predators increased the equilibrium biomass of their prey within soil web models instead of decreasing it for 40% of predator-prey interactions. Indirect effects in food webs although being often counter-intuitive, are common and can have significant effects on population dynamics. Consequently, several authors [Raffaelli et al., 2002, Werner and Peacor, 2003, Tylianakis et al., 2008, Brose and Hillebrand, 2016] have suggested that a multi-trophic assessment of community dynamics is required to understand processes involved in community assembly and ecosystem functioning.

Models of community dynamics are powerful tools to investigate theoretically how species can directly and indirectly affect each other, and how they could affect the ecosystem functioning [Duffy et al., 2007, Gravel et al., 2016]. Numerous models of soil community dynamics have been built. For instance, Hunt et al. [1987], Hunt and Wall [2002] and de Ruiter et al. [1993] used models to explore the role of different taxonomic groups in the mineralization process. These models provided some insight on soil functioning, but they lacked precision and reproducibility. Alternatively, Yodzis P. and Innes S. [1992] and Brose et al. [2006] developed Allometric Trophic Network (ATN) models which are based on allometric relationships [Peters, 1983, Brown et al., 2004], and represent energy flows within food webs. ATN models gain in generality building on the universal scaling of metabolic rates with body mass, but they loose realism for soils by neglecting key aspects of soil community dynamics such as stoichiometry [Daufresne and Loreau, 2001], ontogenetic decomposition process [Moore et al., 2004] and slow-fast channels [Rooney et al., 2008]. Stoichiometric constraints improve the representation of consumer-resource dynamics [Elser et al., 2000], and provide a more rigorous treatment of biochemical processes by accounting for nutrient imbalances [Woodward and Hildrew, 2002, Elser and Urabe, 1999]. The progressive modification of organic matter C:N is also a key feature of the organic matter processing chain in soil food webs but is rarely included in models of community dynamics [Moore et al., 2004]. A model incorporating those aspects of soil dynamics may improve the investigation
of species contributions to nutrient cycling, and may provide some insight on general rules
determining species extinction effects in soil food webs.

To our knowledge, the ability to determine species effects on soil ecosystem functions
from functional traits has never been investigated in a multi-trophic context. The objective
of our study is to assess whether we could explain species effects on the food web from its
traits and trophic position. We developed a model of soil community dynamics in which
carbon and nitrogen flows are determined by stoichiometric constraints, and metabolic rates
are calculated from species body mass. We considered the topology of 48 forest soil food
webs previously documented in Germany along with the functional traits of 878 species,
that comprise them, gathered in tropho-species. We performed numerical experiments in
which we removed each tropho-species one at a time, and then ran the model until equilib-
rium. We computed the effect of these removals on the biomass of consumers, producers,
microbes, detritus, and on inorganic nitrogen to assess species effects. Per population, and
per capita effects of tropho-species were modeled as a function of its functional and trophic
attributes. We expected that body mass, C:N ratio of a tropho-species, and its mean
functional distance from other species would determine its effect on other species, and on
nitrogen mineralization.

Methods

We ran numerical experiments using an empirically-derived model that simulates community
dynamics of diverse soil food webs with changing species composition.

Dynamics

The model consists of five components: producers (P), detritus (D), inorganic nitrogen
(N), microbes (bacteria and fungi - M) and consumers (E). Biomass flows are divided into
carbon and nitrogen flows (Figure 1). We present below the equations we employed to
describe carbon biomass variation over time, and inorganic nitrogen dynamic. All variables are expressed in mass per unit area. Estimated parameters are presented in table 1.

![Diagram of flows and components considered in the model. Carbon flows are represented in green, nitrogen in red, and both in blue. Dotted arrows represent litter loss, respiration and leaching; dashed arrows represent excretion and plain arrows represent consumption or absorption.]

**Producers** assimilate inorganic nitrogen and carbon dioxide, and lose biomass by leaf senescence and consumption. We considered that producers were not limited by light, water or CO$_2$. Producer growth is described using a Monod equation [Monod, 1949] following [Tilman, 1982] and [Daufréne and Hedin, 2005], and is thus nitrogen limited. The model represents both the biomass of underground and aerial parts. Producer biomass production and loss are thus described as:

$$\frac{dP}{dt} = r_p P_p \frac{N}{K_p + N} - (l_p P_p) - \sum_{i=consumers} S_{pi},$$  \hspace{1cm} (1)$$

where $r_p$ is the asymptotic growth rate of producer species $p$, $P_p$ is producer $p$ biomass in units of carbon, $N$ is the inorganic nitrogen available in the soil, $K_p$ is the half saturation constant for nitrogen of producer $p$, $l_p$ is the litter loss rate of producer $p$ and $S_{pi}$ is the biomass of $p$ consumed by consumer $i$. 
| Component      | Parameter | Value                          | Details                                                                 | Source                  |
|---------------|-----------|--------------------------------|------------------------------------------------------------------------|-------------------------|
| Producers     | \( r_p \) | 5, 50, 64, 96                  | Producers with the lowest C:N                                            |                         |
|               | \( K_p \) | 1, 2, 10, 30                   | are more performant in nitrogen rich soil, and vice versa.              |                         |
|               | \( l_p \) | 0, 0.5, 0.4, 0.2               | Producers with the higher growth rate lose more leaves                  |                         |
| Microbes      | \( r_m \) | 668, 512, 256, 1536, 1024, 512 | Microbes with the lowest C:N are more performant when detritus are rich in N, and vice versa. |                         |
|               | \( K_m \) | 300, 125, 25, 125, 300, 25     |                                                                         |                         |
|               | \( g_m \) | 0.01, 0.01, 0.01, 0.1, 0.1     | Fungi have lower turn rates over than bacteria                          | Strickland and Rousk 2010 |
| Consumers     | \( y_i \) | 8                              | Determined for invertebrates                                            | Brose et al. 2006       |
|               | \( B_0 \) | 0.5                            | Uniform relative consumption rate                                       | Brose et al. 2006       |
|               | \( h \)  | 2                              | Functional response III                                                 | Brose et al. 2006       |
|               | \( e_i \) | 0.85, 0.65                     | For animal resource and others, respectively                           | Brose et al. 2006       |
|               | \( x_i \) | 0.314                          | Determined for invertebrates                                            | Brose et al. 2006       |
|               | \( c \)  | -                              | For bodymass \(< 1.10^{-5}\), \(< 1.10^{-5}\) and \(> 1.10^{-7}\), \(> 1.10^{-10}\), respectively | DeLong et al. 2015      |
| Detritus      | \( L \)  | 30                             | Random                                                                  |                         |
| Nitrogen      | \( T \)  | 0.1                            | Random                                                                  |                         |
|               | \( h \)  | 0.1 or 0.5                     | Random                                                                  |                         |

**Table 1:** Estimated parameters used in the model.
**Microbes** consume only detritus. Microbial growth follows a modified Monod equation [Holmberg, 1982, Blagodatsky and Richter 1998, Moorhead and Sinsabaugh 2006], and lose carbon by respiration and predation:

\[
\frac{dM_m}{dt} = r_m M_m \sum_{d=\text{detritus}} \frac{f_{md} D_d}{K_m + \sum_{d=\text{detritus}} f_{md} D_d} - (g_m M_m) - \sum_{i=\text{consumers}} S_{mi},
\]  

(2)

where \(r_m\) is microbe \(m\) asymptotic growth rate, \(M_m\) is microbe \(m\) biomass in units of carbon, \(f_{md}\) is microbe \(m\) preference for detritus \(d\), \(D_d\) is the biomass of detritus \(d\), \(K_m\) is microbe \(m\) half saturation constant for detritus, \(g_m\) is microbe \(m\) respiration rate, and \(S_{mi}\) is the biomass of microbe \(m\) consumed by consumer \(i\). The model considers stoichiometry of C and N explicitly assuming a fixed homeostasis of microbes, as in Daufresne and Loreau [2001]. Microbes absorb inorganic nitrogen if carbon is in excess in the consumed detritus, or excrete carbon when soil nitrogen availability is too low, while they excrete nitrogen when it is in excess [McLaren et al., 1996]. We considered carbon excretion as humus (pure carbon) while excreted nitrogen goes directly into the inorganic nitrogen pool.

**Consumers** feed on detritus, producers, microbes or on other consumers. Consumption rates are calculated following the work of Yodzis P. and Innes S. [1992] and Brose et al. [2006]. As suggested by de Ruiter et al. [1993], consumers convert into their own biomass only a part of the biomass they consume according to their assimilation efficiency \(e_j\), which depends on type of food consumed (animal or non-animal), while the rest is excreted and respired. Consumers dynamics are represented by:
\[
\frac{dE_i}{dt} = E_i y_i z_i \sum_{j=\text{prey}} e_j \left( \frac{f_{ij} R_j}{B_0^h + \sum_{w=\text{prey}} f_{iw} R_w} \right) - (E_i z_i) - \sum_{j=\text{consumers}} S_{ij},
\]

where \(E_i\) is biomass of consumer \(i\), \(y_i\) is the maximum consumption rate relative to metabolic rate of \(i\), \(f_{ij}\) is species \(i\) preference for species \(j\), \(R_j\) is the biomass of resource \(j\), \(B_0\) is the half-saturation density, \(h\) is the Hill exponent, \(S_{ij}\) is the biomass of \(i\) consumed by consumer \(j\). \(z_i\) is the mass specific metabolic rate of consumer \(i\) calculated as:

\[
z_i = x_i E_i^c,
\]

where \(x_i\) is the allometric constant of consumer \(i\), \(c\) is an allometric exponent assessed according to Reuman et al. [2009]. Total carbon and nitrogen assimilated and lost are calculated. Surplus of carbon or nitrogen are excreted into the detritus pool to maintain homeostasis.

**Detritus** inputs come from leaf loss and from microbes and consumers excretions, while losses come from consumption by microbes and consumers, and leaching:

\[
\frac{dD_d}{dt} = \sum_{i=\text{consumers}} H_i + \sum_{p=\text{producers}} H_p + \sum_{m=\text{microbes}} H_m - \sum_{i=\text{consumers}} S_{di} - g_d D_d.
\]

where \(D_d\) is the biomass of detritus \(d\), \(H_i\), \(H_p\) and \(H_m\) are the inputs from consumer \(i\), producers \(p\) and microbes \(m\), respectively, \(S_{di}\) is the consumption of detritus \(d\) by species \(i\), and \(g_d\) is the leaching rate of detritus \(d\). Detritus are divided into five different pools according to their quality as advised by Moore et al. [2004]. Detritus quality is defined by
their C:N ratio: $1 < C : N < 10$, $10 < C : N < 20$, $20 < C : N < 35$, $35 < C : N < 50$, No N (humus). The C:N ratio of the input is calculated to know which pool will be filled. At the end of each time step the new C:N ratio of detritus is updated to keep mass balance. We suppose a constant tree leaf input with a C:N ratio of 26, corresponding to the mean C:N ratio of detritus in temperate forest litter [Gloaguen and Touffet, 1982].

**Inorganic nitrogen** is lost by leaching and producer and microbial absorption, and is replenished by atmospheric deposition, as well as excretion from consumer and microbes:

\[
\frac{dN}{dt} = \sum_{i=\text{consumers}} X_i + \sum_{m=\text{microbes}} X_m - \sum_{p=\text{producers}} A_p - \sum_{m=\text{microbes}} A_m + T - h.N, \tag{6}
\]

where $X_i$ is nitrogen excreted by consumer $i$, $X_m$ is nitrogen excreted by microbe $m$, $A_p$ is nitrogen absorbed by producer $p$, $A_m$ is nitrogen absorbed by microbe $m$, $T$ is the amount of atmospheric deposition and $h$ is the leaching rate of nitrogen.

The model was written in C++ and the numerical integration performed with the Runge Kutta Fehlberg 78 method [Fehlberg, 1969], using the package 'odeint' [Ahnert et al., 2011].

**Data**

We used 48 forest soil food webs documented by [Digel et al., 2014] to define the network structure, along with species body mass to parameterize the model. These food webs were inventoried in beech and coniferous forests in Germany. Interactions were detected using a combination of methods ranging from molecular gut content analyses to cafeteria experiments (details in [Digel et al., 2014]). The smallest species and those at low trophic levels, were not identified to the species levels (e.g. nematodes). Detritus, producers and microbes
were divided into five, four and six groups, respectively. Microbes were further divided into three bacteria and three fungi. The various groups have variable C:N ratios. Growth rates of producers and microbes increase inversely with their C:N ratio [Garnier et al., 2004]. Producers and microbes with a low C:N ratio are more efficient in N rich systems, and species with high C:N are more efficient in N poor systems. C:N ratio of fungi and bacteria were documented from Mouginot et al. [2014], and C:N ratio of producers were documented from the TOPIC database (Traits of Plants in Canada, [Aubin et al. 2012]). Metabolic rates of consumers were estimated using their body masses originally measured by Digel et al. [2014], following the negative-quarter power law relationship with body mass Peters [1983], and DeLong et al. [2010]. The C:N ratios of consumers were assessed according to Hunt et al. [1987] and Crotty et al. [2014]. Producers and detritus with smaller C:N ratios were preferentially consumed, in comparison to ones with higher C:N ratios.

We simulated community dynamics of the food webs with various tropho-species removals to test their effects on the food web. Tropho-species were composed of one to 94 functionally identical consumer species, for a total of 161 tropho-species. Each food web was then comprised of 46 to 71 consumer tropho-species. Traits considered were body mass, soil vertical position, mobility, toughness, use of poison to hunt, use of web, and diet (table 2). We added species order (taxonomic rank) as a proxy of latent traits that are not measurable or which are the result of several traits (i.e. behavior, chemical defenses) [Rohr et al. 2010, Mouquet et al. 2012]. Because of the high intra-specific variability in body mass, species were categorized into 10 body mass classes. Tropho-species were then comprised of species belonging to the same order, body mass class, and having identical trait values. We considered that pairs of tropho-species interacting with each other in at least one food web also interacted with each other in all food webs where they co-occurred.
| Trait                  | Type       | Description                                                                 | Documentation |
|-----------------------|------------|------------------------------------------------------------------------------|---------------|
| Observed Prey capture strategy | Boolean    | Web builder or not                                                           | Literature    |
| Poison                | Boolean    | Use of poison to kill prey or not                                             | Literature    |
| Body mass             | Continuous | Logarithm of the mass of an individual (in grams)                             | Measurement, literature* |
| Mobility              | Categorical| 1: immobile, 2: crawling (no legs), 3: short legs, 4: long legs, 5: jumping, 6: flight | Literature    |
| Toughness             | Categorical| 0: soft (no chitin, or few lignin), 0.5: hard, 1: has a shell (or is a seed) | Literature    |
| Latent Feeding guild  | Boolean    | Carnivore: 1/0, detritivore: 1/0, microbivore: 1/0, herbivore: 1/0            | Literature    |
| Taxonomy              | Continuous | Scores on the 2 PCoA axes                                                    | Literature    |
| Soil vertical position| Boolean    | Below soil surface : 1/0 and/or above soil surface : 1/0                     | Literature    |

Table 2: Description of traits and proxies of traits used in the study.
* Food webs dataset and body mass measurements were provided by [Digel et al. 2014]. Body mass was difficult to obtain from the literature; therefore, for the independent interactions dataset we estimated body mass from body size, using documentation protocols described in [Andrassy 1956], [Freckman 1982] and [Ganihan 1997].
Simulations and analyses

We simulated community dynamics of the 48 food webs until equilibrium (reached after at least 150 time steps), then we removed tropho-species one at a time and ran again the simulation until equilibrium (50 extra time steps). We then calculated tropho-species removal effect on other components (fungi, bacteria, detritus, producers, consumers and nitrogen). The effect of a species \( j \) on component \( i \), \( A_{ij} \), was considered as the inverse of its removal effect, calculated as the relative change in mass of each component induced by the removal. This effect was calculated as:

\[
A_{ij} = -\frac{B_0_i - BR_{ij}}{B_0_i},
\]

(7)

where \( B_0_i \) is the biomass of component \( i \) at equilibrium in the entire community, and \( BR_{ij} \) is the biomass of component \( i \) at equilibrium in the community without species \( j \).

We also calculated per capita effects by dividing the per population effects of the removed tropho-species by its biomass in the entire community, at equilibrium.

We tested whether tropho-species removal per population and per capita effect on other component biomass could be determined by tropho-species trophic and functional attributes. To do so, we used Random Forest algorithms (RF) [Breiman, 2001] to assess which traits and trophic characteristics explained tropho-species effects. RF is a machine learning algorithm, which, using decision tree-like processes, finds the best combination of variables and variable coefficients to explain the response variable. This method effectively handles with the non-linear relationships that were expected in our investigations. We assessed the importance of each species properties in the explanation of their per population and per capita effects on the five components. Explanatory variables used were food web identity, removed species traits, mean and minimum functional distance, mean trophic similarity, number of resource and number of consumer. We estimated functional distance between species by calculating Gower distances [Gower, 1966] on the matrix of species traits and taxonomy. Taxonomy was
considered as the scores of each species from the two first axes of the Principal Coordinates Analysis (PCoA) conducted on taxonomic distances between species obtained with the R package ”ade4” [Dray and Dufour 2007]. To calculate functional distances, the sum of the relative weight of each variable equaled one when they were divided into more than one column (e.g. taxonomy). We added an index of taxonomic distance to overcome the lack of time calibrated phylogenies and the challenge of accounting for a wide range of organisms simultaneously (from bacteria to arthropods). Trophic similarity was calculated as the percentage of shared resources and consumers for each pair of species. To assess RF accuracy, we calculated the adjusted $R^2$ between observed effects and predicted effects (Rpo). Additionally, we assessed which species led to the maximum positive and negative effects on each component.

All of the analyses were performed with R [R Core Team 2015] and the package ”party” [Hothorn et al. 2006, Strobl et al. 2007 2008].
Results

Most tropho-species did not affect the biomass of other consumers, producers, detritus and microbes (fungi and bacteria), but certain tropho-species had the highest effects in most food webs (figure 2).

Nitrogen availability was not affected by any tropho-species (effects consistently < 0.06). Fungi biomass, however, responded greatly to the majority of tropho-species removals (75% of effects had an absolute value > 0.1). Tropho-species per population and per capita effects on each component were accurately predicted by their traits and trophic properties ($Rpo > 0.70$), except for their effects on fungi which were highly dependent on food web identity. The main properties that predict species effects were their number of resources,
mean trophic similarity, diet, body mass, C:N ratio, mobility and toughness (table 3). Herbivores, and especially species with a low body mass, toughness and similarity (mainly nematodes) decreased producers and consumers biomass (table 4). In most food webs, small herbivorous-detritivorous species with a C:N ratio of 5, including enchytraeids, Sarcoptiformes (mites), and Symphypleona (springtails), had the highest negative per population and per capita effects on detritus and bacteria. In general, detritivorous mesofauna had negative per population and per capita effects on detritus, bacteria and fungi. However, various mesomicrobivores often had high positive per capita effects on fungi. Small to medium strict carnivores with low resource similarity and/or a high number of prey, such as chilopods, Sarcoptiformes and Parasitiformes (mites) had the highest positive per capita and per population effects on each component (except N) in the majority of food webs. However, some of them also had the highest negative per population effects on consumers.

| Property               | Population                  | Capita                     | Total |
|------------------------|-----------------------------|----------------------------|-------|
|                        | Det | Bac | Fun | Cons | Prod | N     | Det | Bac | Fun | Cons | Prod | N     |
| Food web               | X   | X   |     |      |      |       | X   |     |     |      |      |       |
| Number of consumer     |     |     |     |      |      |       |     |     |     |      |      |       |
| Number of resource     |     | X   |     |      |      |       | X   |     |     |      |      |       |
| Resource similarity    | X   |     | X   |      |      |       | X   |     |     |      |      |       |
| Consumer similarity    | X   |     | X   | X    |      |       | X   |     |     |      |      |       |
| Functional distance    | X   |     |     |      |      |       |     |     |     |      |      |       |
| Diet                   | X   |     | X   | X    |      |       | X   |     |     |      |      |       |
| Body mass              |     |     | X   | X    |      |       | X   |     |     |      |      |       |
| Mobility               |     |     | X   |     | X    |      |     |     |     | X    |      |       |
| Toughness              | X   |     |     | X    | X    |      |     |     |     |     |      |       |
| C:N                    |     |     | X   |     | X    | X    |     |     |     |     |      |       |
| Rpo                    | 0.78| 0.90| 0.50| 0.88| 0.89| 0.83  | 0.78| 0.90| 0.50| 0.89| 0.88| 0.82  |

Table 3: Variables explaining 80% of species per population and per capita effects on each component and on N. Rpo is the adjusted R square of the regression between observed and predicted effects. Det stands for detritus, Bac for bacteria, Fun for fungi, Cons for consumer, Prod for producer, and N for nitrogen.

The different effects a species can have on others were synthesized using motifs inspired by Stouffer [2010] to show relationships between trophic position and species effects (table...
5). A consumer usually negatively affected its resource (motif a) but could also be beneficial when it also consumed a resource’s competitor (b). Motifs a and b were observed mainly when fungi responded to fungivorous oribatids, and when the latter responded to their predators (Chilopoda). A resource usually decreased its consumer when it decreased a more productive resource, or when they also competed with each other (c), instead of increasing it (d). Motifs c and d concerned mainly the effects of herbivorous nematodes and macrocarnivores. Competitive species (exploitation) decreased their competitor (e,g), which occurred mainly between herbivores, detritivores and microbivores. We found numerous cases of apparent competition, especially due to herbivorous nematodes (f,g). Motif h occurred when species that produce a large amount of detritus favored fungi. We found several cascading effects in the food webs resulting from carnivores (Chilopoda, Coleoptera) which decreased microbivores and detritivores, then increased detritus and fungi (i). Cascading effects also stemmed from intraguild predation (j). These results highlight how direct effects can combine with indirect effects.

Increasing nitrogen leaching (i.e. lower fertility) changed the magnitude of species effects (table 4). However, changes in species effects, from high to low fertility, did not increase or decreased linearly. Therefore, the species which have maximum negative and positive effects in food webs were different. In general, effects of carnivores on basal species (producers, detritus, microbes) tended to be lower. In contrast, intermediate species effects (detritivores, fungivores and herbivores) and, especially, mesofauna tended to be higher. We also observed increasing occurrence and mean effect values of motifs c, e, f, i and j, which may indicate an increase in resource competition, apparent competition and top-down cascading effects in low fertility systems.
### Table 4: Number of food webs in which a tropho-species of a particular body mass class (BM) and diet had the highest negative effect (min) and the highest positive effect (max) on each components at high fertility. At low fertility, we noted the difference in the number of food webs in which the tropho-species had the highest effects, in comparison to high fertility.
| Class  | Diet  | Status | Representation | Observation percentage |
|-------|-------|--------|----------------|------------------------|
|       |       |        |                |                        |
| Mean per pop effect | -0.4 | 0.5 | -0.2 | 0.3 | -0.4 | -0.4 | -0.4 | 0.5 | 0.3 | 0.2 |
| Mean per cap effect | -309.7 | 746.1 | -28.2 | 12.8 | -2.7 | -28.4 | -4.9 | 11.7 | 11.8 | 21.5 |
| Count | 7357 | 1681 | 3122 | 868 | 1590 | 3935 | 6129 | 289 | 1224 | 302 |
| BM class | Diet | Role |                |                        |
| micro | C | fc | 3.8 | 5.7 | 12.3 | 13.7 | 7.9 | 8.2 | 8.9 | 0 | 3.3 | 0 |
|       | rp | 3.4 | 6 | 1.6 | 11.2 | 0.6 | 4 | 2.6 | 0 | 7.8 | 1.3 |
| D | fc | 3.8 | 5.6 | 10 | 13.4 | 7.9 | 7 | 8.8 | 0 | 0 | 0 |
|       | rp | 0 | 0.1 | 1.5 | 0 | 0.6 | 0 | 1.8 | 0 | 0.4 | 0 |
| F | fc | 4.3 | 8 | 11.8 | 14.1 | 7.9 | 7.2 | 9 | 0.5 | 0.3 |
|       | rp | 0 | 0.1 | 1.5 | 0 | 0.6 | 0 | 1.8 | 0 | 0.4 | 0 |
| H | fc | 5.8 | 5.6 | 30.7 | 24 | 8.7 | 41.8 | 15.2 | 0 | 7.3 | 0 |
|       | rp | 0.05 | 0.2 | 1.5 | 0 | 0.8 | 0 | 2.6 | 0 | 0.7 | 0 |
| meso | C | fc | 28.3 | 25.8 | 10.7 | 12.4 | 10.9 | 2.2 | 19.2 | 12.1 | 23.9 | 60.3 |
|       | rp | 11.1 | 9.3 | 29.8 | 54.0 | 16.8 | 21.2 | 29.9 | 5.2 | 5.1 | 51.7 |
| D | fc | 25.4 | 23.6 | 12.7 | 15.8 | 59.8 | 21.4 | 48.6 | 73 | 3 | 12.3 |
|       | rp | 11.9 | 2.5 | 8.2 | 2 | 43.6 | 9.6 | 32.4 | 1.7 | 11.4 | 6.3 |
| F | fc | 27.3 | 40.5 | 6.8 | 11.5 | 24 | 6.8 | 25.9 | 7.3 | 2.0 | 20.2 |
|       | rp | 9.4 | 6.1 | 12.3 | 26.7 | 41.6 | 11.1 | 33.7 | 5.2 | 10.3 | 41.7 |
| H | fc | 14.3 | 14.6 | 10 | 1.5 | 31.8 | 21.2 | 32.2 | 15.6 | 0.2 | 1.3 |
|       | rp | 4.3 | 2.9 | 2.9 | 9.4 | 20.4 | 2.4 | 16.9 | 0 | 4 | 5.3 |
| macro | C | fc | 46.8 | 31.9 | 45.7 | 55.1 | 20.8 | 22.3 | 21.9 | 5.5 | 53.1 | 27.2 |
|       | rp | 27 | 11.2 | 68.5 | 34 | 13.2 | 43.3 | 14.1 | 4.5 | 8.2 | 26.5 |
| D | fc | 11.9 | 21.2 | 9.4 | 19.6 | 24.2 | 18.5 | 21.6 | 19.4 | 0.7 | 13.6 |
|       | rp | 11 | 1.1 | 2.7 | 1.4 | 24.5 | 8.8 | 30.5 | 2.4 | 20 | 17.2 |
| F | fc | 12.6 | 23.4 | 9.6 | 18.2 | 21.7 | 18.5 | 21.5 | 0 | 0.5 | 1 |
|       | rp | 9.2 | 3.4 | 2.2 | 4.7 | 15.3 | 7.6 | 28.3 | 4.5 | 16.2 | 24.5 |
| H | fc | 13.8 | 9.5 | 14.4 | 18.4 | 22 | 23.7 | 21.3 | 2.1 | 10.4 | 3.6 |
|       | rp | 9.1 | 1.4 | 9 | 4.8 | 8.4 | 0.4 | 19.1 | 0 | 2.9 | 0 |
| fungi | NA | rp | 16.7 | 65 | 0 | 0 | 0 | 0 | 15.4 | 10.8 | 0.7 | 88.2 | 43.2 | 18.2 |
| detritus | NA | rp | 7.6 | 6.5 | 0 | 0 | 0 | 0 | 4.7 | 0 | 0 | 13 | 0 |
| bacteria | NA | rp | 10.6 | 0 | 0 | 0 | 2.4 | 0.2 | 0 | 2.1 | 0 | 0 |
| producer | NA | rp | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 5: Motifs showing how species can directly and indirectly affects other species. Plain arrows are direct effects, and dotted arrows are indirect effects. Blue arrows represent a positive effect and red ones are negative. The framed letter is the focus species and the bold letter is the target species. D stood for detritus, and F for fungi. We counted only effects greater than 0.1 or less than -0.1 which concerned 26,498 pairs among the 221,055. We also calculated the percentage of observations of each species involved in each motif. Sums of percentages are not equal to 100 as species can be omnivores. D= detritivores, C=carnivores, F=fungivores, H=herbivores, fc= focus species, rp= response species.
Discussion

Models of community dynamics are useful tools to better understand the functioning of complex systems such as soil food webs. Using a model based on metabolic theory and stoichiometry, we revealed the potential effects of species extinction with changing functional and community structure. While soil food webs were particularly resistant to species extinction, we were able to outline which tropho-species affect the most community productivity. However, we found that the determination of species effects based on traits and topological position were also contingent on community properties.

We identified several traits that underlie species effects on other species and detritus within the community. As expected, species diet was the main factor explaining differences in species effects. Herbivores had the greatest effects on the overall food web by decreasing producers biomass and hence other herbivores. Since producers generate the litter that supports a detritus-based food web, herbivores decreased the biomass of detritivores and their relative consumers. Body mass was the second most important trait explaining species effects. Non-carnivores with low body mass had greater effects on the various food web components than larger species with the same diet. Species with low body mass have greater metabolic rates per unit of biomass, and therefore consume a greater amount of resource per unit of biomass than larger species. Herbivorous nematodes, which have the lowest body mass, had the greatest effects on the overall food web, similar to findings from Hunt and Wall [2002]. Their large effect, however, suggests that the model might miss some regulation mechanisms of this particular tropho-species or that their low taxonomic resolution overemphasizes their contribution to producer regulation. Because body mass is also related to trophic position, carnivores with the greatest effects were not necessarily the smallest Schneider et al., 2012 Laigle et al., 2018. For instance, carnivorous mites had important effects because they consumed nematodes, and then had the opposite effects of
herbivorous nematodes. Species toughness and mobility were also found to be important traits underlying species effects. However, we presume that this contribution mainly stems from the fact that nematodes are soft and have low mobility. Thus, the combination of body mass and diet partly explained observed species effects on the overall food web.

In our study, we considered observed interactions in real communities, allowing us to show that species effects are also contingent on network structure. Past studies that investigated species effects used simplified soil food webs [Hunt et al., 1987, de Ruiter et al., 1993, Hunt and Wall, 2002] or based their work on food webs in which interactions were determined based on species’ body mass [Brose et al., 2005, Berlow et al., 2009]. However, the network structure is not necessarily realistic in the earlier study while results essentially derive from the community body mass distribution in the latter one. We found that body mass predicted species effects well because it determines species metabolic rate and, in part, species interaction. However, we found that trophic similarity explained also a great proportion of species effects. Prey species with a low consumer similarity had significant effects on their relative consumers as they comprised a large portion of their consumers diet [Eklöf and Ebenman, 2006, Montoya et al., 2009]. This property can also explain the important effects of nematodes and enchytraeids, which had the lowest consumer similarity among all herbivores. Carnivores with the greatest effects consumed a wide range of resources, as also found by Sole and Montoya [2001] and Dunne et al. [2002], but also have a low resource similarity and possess small body sizes (e.g. Chilopoda, Parasitiformes). These carnivores directly decreased their most abundant prey, indirectly favoring less abundant ones, hence increasing food web productivity through the regulation of competitive forces [Paine, 1969, Power et al., 1996]. Because the body mass of a carnivore partly determines its prey, its value relative to body mass of other species should capture a carnivore’s importance in a food web [Schneider et al., 2012]. Further, Laigle et al. [2018] showed how functionally close species tend to be trophically similar. However, the low importance of functional distance in our study highlights that we are missing traits that adequately represent trophic similarity.
These results suggest that the determination of species effects, or key stone species must refer to a specific network structure.

The precision and realism of our stoichiometrically explicit model demonstrate the variability in species effects based on soil fertility and litter composition. First, fungi responses to species could be explained only by food web identity, and certainly by community detritus dynamic. Second, the C:N ratio was an important variable explaining species effects. Species with a lower C:N than their resources need to consume more than species with a higher C:N to fulfill their N requirements. Because they are small detritivores with a low C:N ratio, micro (enchytraeids) and mesofauna (Sarcoptiformes and Symphypleona) had the greatest negative effects on detritus, and consequently on bacteria, which agrees with previous findings. [Huhta et al., 1998, Verhoef and Brussaard, 1990, Laakso and Setälä, 1999]. We can imagine a change in detritivore species importance in the decomposition process according to detritus C:N (vegetation C:N) and thus soil fertility. Third, we showed that decreasing soil fertility (i.e. soil N content) can influence species effects by increasing competition pressure. In our case, competition was higher at intermediate trophic levels because producers, detritus and microbes were not identified to species level. Therefore, soil fertility modifies competition between species and the ratio between the C:N ratio of consumers and basal resources, both affecting species effects. The determination of species effects or key stone species then depend on the level of soil fertility or basal resource availability in a given food web.

The inclusion of detritus in simulations of soil food web dynamics, as originally proposed by Moore et al., 2004, enhanced species indirect effects in the simulations. While the importance of indirect effects is commonly accepted, their consideration is often limited to competition regulation [Brose et al., 2005, Berlow et al., 2009, Montoya et al., 2009]. In our study, detritus-induced indirect effects limited the explanation of species effects on fungi because fungi respond to species detritus production and quality as well as competition
pressure from detritivores, and consumption by fungivores. Fungivores and fungi regulation by their relative consumers has been shown empirically, but their effects from excretions on the community are less studied [Hanlon and Anderson, 1979, Visser, 1985, Salminen et al., 1997]. While we confirm that soil species richness limits the effects of species extinction because of compensatory mechanisms, we add that increasing detritus flows enhance indirect effects in communities. Microbes adaptability to detritus availability can further buffer species extinction effects on nitrogen availability. These results are consistent with the empirical studies of Mikola and Setälä [1998] and Laakso and Setälä [1999] who found that negative effects of consumers on their resource do not cascade to nitrogen availability. We contend that the high resistance of soil communities to extinction stems from adaptability and compensatory mechanisms present in detritus-based food webs.

Conclusions from such numerical experiments are contingent on the model structure, with some results being more robust than others to its assumptions. Low resolution of basal species is one of the limitation that should be overpass to further improve the realism of our study. Indeed, we think that if producer and microbial species were identified, and species-to-species interactions more finely documented, we could better specify the role of microbivores and herbivores. Some herbivores could favor plants that produce a nitrogen-rich litter which would then favor mineralization. In addition, the coarse resolution of detritus gathering as well as their interactions with detritivores hide potential complementarity among detritivores. Complementarity and facilitation along the decomposition process were documented by several studies and may surpass competition [De Oliveira et al., 2010, Hedde et al., 2010]. Mesodetritivores, mesofungivores and microbes are the main nitrogen producers in soil food webs, and thus their interactions deserve to be more documented [Brose and Scheu, 2014].

In this study, we showed that species effects depend on a combination of traits relative to other the traits of other species comprising the community. We also highlighted that
explicitly accounting for detritus, and carbon and nitrogen flows emphasizes the importance of feedbacks and indirect effects in detritus based food webs. We highlighted for the first time how important it is to assess a species contribution to ecosystem functioning in regard to the community structure and ecosystem properties. Therefore, network trophic and functional structure, as well as detritus quality within the ecosystem, should be integrated in studies to improve the understanding of soil community functioning and to better target conservation efforts.

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