

# Romul\_Hum model of soil organic matter formation coupled with soil biota activity. I. Problem formulation, model description, and testing



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## ABSTRACT

For many decades in the late 20th century, the processes involved in the formation of soil organic matter (SOM) (also known as humification) constituted one of the most important areas of scientific inquiry in soil science. However, these processes have not been included in modern models of SOM dynamics, despite their relevance to quantifying carbon stabilisation (i.e., sequestration) in soil. Furthermore, modern models have focussed on mineralisation processes (e.g., mainly microbial heterotrophic respiration) and have not included the important effects of soil fauna that are known as key agents of SOM formation. To address these issues, we developed a modelling approach predicated on the existence of definable stoichiometric relations among the processes leading to SOM formation that are mediated by soil biota (e.g., correlations among biotic respiration, production of faunal excrement, and necromass as sources of SOM formation). Soil respiration, a core rate variable in all SOM models, was associated with the production of faunal by-products in soil food webs as precursors of stable SOM, specifically micro- and meso-faunal excrement, necromass, and earthworm casts. We developed a food-web based module, using a synthesis of decades of published data, to describe micro- and meso-faunal excrement and necromass production. We developed a separate module for anecic earthworms, with explicit representation of processes related to fresh casts. The contributions of these two modules were compiled and integrated with the ROMUL model of SOM dynamics, without changing the structure of the original model. These modules enabled calculation of the proportional contribution of faunal by-products to humification (i.e., recalcitrant SOM formation) and carbon sequestration. Testing of the new version of the model, known as Romul\_Hum, showed consistent accumulation of faunal by-products in the “final” SOM fractions: the well-decomposed SOM of the organic soil horizons and the stable SOM of the mineral soil.

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## 1. Introduction

The modelling of soil organic matter (SOM) and soil carbon (C) dynamics has been intensively developed over recent decades, with

significant progress in terms of understanding the mechanisms and patterns of C emissions, C sequestration, and plant nutrition (e.g., Smith et al., 1997, 1998; Benbi and Richter, 2002; Manzoni and Porporato, 2009). The models used in these assessments have focussed on mineralisation, because their main goal has been to estimate emissions of greenhouse gases (specifically carbon dioxide and nitrogen oxides) or the release of nutrients from the soil for uptake by plants, or both. However, they may not be suitable for assessing C sequestration (stabilisation) in soil because of their focus on the loss, rather than the retention, of C. Furthermore, theoretical approaches to modelling SOM that focus on mineralisation may be flawed if they do not emphasise processes for stabilisation (Manzoni and Porporato, 2009; Schmidt et al., 2011), including

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humification (Chertov and Komarov, 2013). Humification is a process of SOM transformation that leads to long-term storage of organic matter (or C) in the soil and ecosystem as stable humus or recalcitrant organic C. Here, we use the terms “stable humus” and “recalcitrant SOM” synonymously, without a detailed theoretical discussion of the differences between them in terms of soil chemistry. During the 20th century, understanding the processes of humus formation was principally a theoretical problem in soil science, but now it is highly relevant to C sequestration in soil for mitigation of climate change and sustainability of ecosystem productivity (e.g., Kögel-Knabner and Matzner, 2008; Knyazev et al., 2009; Chertov and Komarov, 2013) and should be an integral part of models used to assess C sequestration.

In many modern models, humus is represented as a side product of decomposition (i.e., recalcitrant SOM). It is defined as the slow-decomposing organic matter that remains after decomposition, which is not readily accessible to microorganisms (Kögel-Knabner and Matzner, 2008; Kleber et al., 2011), as opposed to stable humus, which results from active processes, some of which are independent of decomposition. Pathways from labile to stable SOM fractions are included in all simulation models and are usually based on empirical data (e.g., Liski et al., 2005; Manzoni and Porporato, 2009; Braakhekke et al., 2011).

Most modern SOM models focus exclusively on explicit or implicit microbially (primarily bacterially) mediated decomposition, often neglecting the role of micro- and meso-fauna, and earthworms. This focus on microbial processes probably reflects the history of SOM models, which were originally developed for arable, well-mixed mineral soils with no development of organic soil horizons. In these mineral soils, microbiological processes are assumed to dominate, leaving a negligible role for soil fauna (Miltner et al., 2012; Fedotov and Shoba, 2013). As such, recent SOM models have a small number of litter fractions, sometimes without decomposer organisms (Jassal et al., 2004; Liski et al., 2005), with only undifferentiated pools of microorganisms (Parton et al., 1988; Franko et al., 1995; Coleman and Jenkinson, 1999; Bruun et al., 2003; Blagodatsky et al., 2011), or with a generalised representation of soil fauna (Chertov et al., 2001; Kätterer and Andrén, 2001). In the late 1970s and 1980s, Hunt and others (Hunt, 1977b; Hunt et al., 1987; de Ruiter et al., 1993) made significant contributions to understanding and modelling complex faunal food webs (FWs) in the soils of native ecosystems. The early model of SOM dynamics put forth by Hunt (1977a), which had a comprehensive representation of decomposer organisms, was not developed further, but in subsequent decades others have developed FW-based soil models with special reference to soil biota and nitrogen (N) release (Schröter et al., 2003; Holtkamp et al., 2011; de Vries et al., 2013). These models have allowed calculation of soil N and C budgets, but at fixed points, with measured FW and soil data only. Therefore, their predictive capabilities are more limited than those of SOM dynamic models. The wealth of knowledge they provide can contribute to the development of SOM dynamic models that include the effects of micro- and meso-faunal activities. Over a similar time frame (1970s to early 2000s), considerable research focussed on understanding the ecological niches of earthworms and their role in SOM dynamics (Perel, 1979; Lee, 1985; Bohlen and Edwards, 2008), and in the last couple of decades a few models were developed to simulate the effect of earthworms on soil C dynamics (Whalen et al., 1999; Frouz, 2008; Huang et al., 2010). Despite these advances, no models are available to explicitly simulate soil biota as agents of SOM formation, and none are comprehensive, combining the effects of the major soil biota functional groups (microorganisms, micro- and meso-fauna, and earthworms) into a single modelling framework. Therefore, the aim of this work was to integrate the existing ROMUL model of SOM dynamics (Chertov et al., 2001; Komarov et al., 2007) with modules developed to represent the SOM-forming activity of

the main groups of soil biota (Chertov and Komarov 2013; de Vries et al., 2013; Chertov et al. manuscript in preparation [Romul.Hum: parameterisation of food web biota activity]), and a description of the quantification of earthworms' contribution to SOM formation (Chertov et al. manuscript in preparation [Romul.Hum: parameterisation of earthworm activity]). The opportunity to realise this expansion of the ROMUL model is based on substantial achievements of modern experimental soil zoology, microbiology, and soil science and the recent development of methodologies for compiling simulation models.

Variables used to describe the effect of biota on SOM pools in the ROMUL model are generalised, and it has no detailed representation of faunal contributions to SOM formation. However, when this model was fully incorporated into the forest ecosystem model EFIMOD, it allowed for simulation of litter and SOM decomposition and transformation, with release of soil N, for a wide range of environmental conditions and litter qualities (Chertov et al., 2002, 2009; Komarov et al., 2003; Nadporozhskaya et al., 2006; Shaw et al., 2006; Komarov et al., 2007; Kahle et al., 2008; Bhatti et al., 2009; Yurova et al., 2010; Shanin et al., 2011, 2015; Kalinina et al., 2013, 2015; Larocque et al., 2016).

The theoretical background for this work is the concept of biological and ecological stoichiometry (Elser, 2006; Elser and Hamilton, 2007; Elser et al., 2012). This stoichiometric concept has led to a research strategy to integrate various levels of biological and ecological organisation. This strategy focusses on a mathematical methodology instead of the reductionist approaches that dominate in modern biological research. According to the stoichiometry concept, the allometric relations and scaling that prevail in biological systems are investigated and explored in detail (Mulder, 2006; Mulder and Elser, 2009; Mulder et al., 2013).

Twenty years of continuous research and analyses with the ROMUL model revealed the need for a more mechanistic representation of the role of soil fauna in humification and N release with integration of new concepts, approaches, and results from analyses of large datasets. Therefore, we developed a research plan to significantly improve the ROMUL model by including a) the soil forming activities of micro- and meso-fauna and anecic earthworms; b) calculations for SOM-forming processes (humification) and SOM mineralisation mediated by soil biota and, c) a mechanistic representation of N mineralisation using the methodology of food web analysis (Hunt et al., 1987; de Vries et al., 2013). The important role of pot worms (Enchytraeidae) is included in the food web module. The anecic earthworm module will be used as a template to build, in the future, the epigeic and endogeic earthworm modules. The role of meso- and macro-fauna such as ants, termites, insects, woodlice, mollusks, millipedes and centipedes as “litter transformers” are not included in the model described here, but data collection and analyses are underway to elaborate modules to represent the activities of these soil organisms. Therefore, here we use the terms “meso- and macrofauna” to refer to the meso-fauna of food webs and anecic earthworms, respectively.

We endeavour to follow the TRACE protocol (transparent and comprehensive ecological modelling) of model description (Grimm et al., 2014), with one significant modification. This model parameterisation required the analysis and processing of a very large amount of experimental data. Therefore, the work is being presented in three parts: a description of the expanded ROMUL model, Romul.Hum, with its structure and testing (the current article); a description of parameterisation of FW biota activity (Chertov et al., manuscript in preparation [Romul.Hum: parameterisation of food web biota activity]), and a description of the quantification of the contribution of anecic earthworms to SOM formation (Chertov et al., manuscript in preparation [Romul.Hum: parameterisation of earthworm activity]).

## 2. Description of the Romul\_Hum model

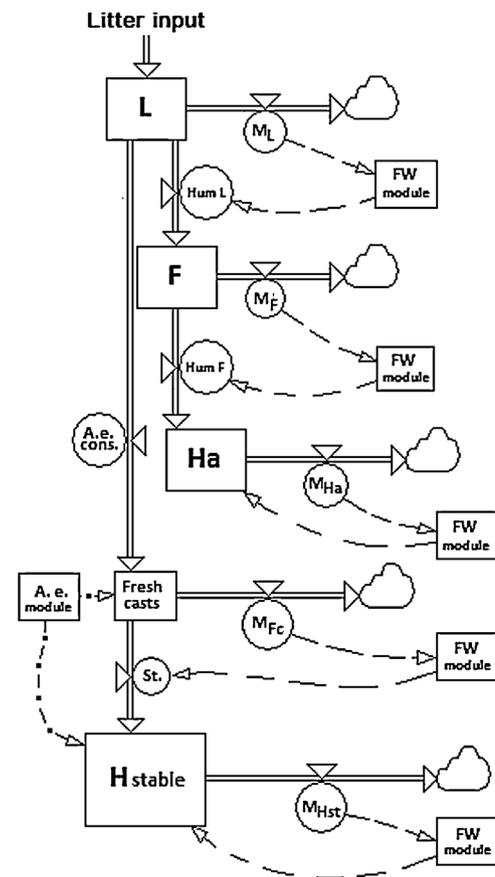
### 2.1. General description

The Romul\_Hum model is based on the ROMUL model of SOM dynamics, described in detail elsewhere (Chertov et al., 2001; Komarov et al., 2007). Briefly, the ROMUL model was designed to allow description of SOM transformations in forest and arable soils. It reflects the activity of three functional groups of decomposer organisms that are responsible for the three main humus forms: Mor, Moder, and Mull (Chertov and Komarov, 1997; Chertov et al., 2001; Zanella et al., 2011; De Nicola et al., 2014). Special attention is given to the processes of SOM transformation, from the L horizon (a pool consisting of untransformed fresh organic debris) through the F horizon (a pool consisting of material that is only partially decomposed, such that its origin can still be determined), to the organic H horizon or the mineral Ah or Ahe horizons (pools with strongly modified or metamorphosed, slowly decomposing [humified] SOM). In the original ROMUL model, three variables reflect the formation of three different SOM pools through the activity of (a) microorganisms, Protozoa, Nematoda, and microarthropods only; (b) the biota of the previous group combined with mesoarthropods; and (c) a full complex of biota from the first two categories combined with earthworms.

In ROMUL, the rate of transformation from L to F in the forest floor was derived from experimental curves of organic debris mineralisation, based on the concept that slowly decomposing SOM forms quickly at the start of mineralisation, which results in a “complex of humic substances intermixed with undecomposed organic debris” (Chertov, 1985; Komarov et al., 2007). Such a complex has been described in numerous morphological studies of humus forms (e.g., Bal, 1970; Pawluk, 1987; Galvan et al., 2006). This complex has a significantly lower rate of SOM mineralisation than the undecomposed organic matter of the L pool. The rate of transformation from F to H pools was based on available data for the maximum rate of SOM transformation by micro- and meso-fauna and by earthworms (Chertov and Komarov, 1997; Komarov et al., 2007). The mineralisation rate of every pool (state variable) was determined experimentally and is dependent on the quality, moisture, and temperature of the organic matter (Komarov et al., 2007). This simplified approach allowed for satisfactory reproduction of the formation of relatively stable SOM but lacked the potential to explore and analyse the degree of humification in response to varying environmental conditions.

Using recently generated data, we expanded the ROMUL model structure to create the Romul\_Hum by adding two modules for SOM formation by soil biotic activity: one for the micro- and meso-fauna (using FWs) and another for anecic earthworms (which will be used as a template to elaborate additional modules for epigeic and endogeic earthworms). These modules allow calculation of faunal-derived by-products and necromass as the precursors of SOM formation. New algorithms to determine available N in relation to the modules for FW biota and anecic earthworms were also incorporated. Details of the analyses related to parameterisation of the modules are presented in two companion papers (Chertov et al., manuscripts in preparation [Romul\_Hum: parameterisation of food web biota activity; Romul\_Hum: parameterisation of earthworm activity]). These new modules will be expanded in the future to include the role of non-Lumbricina macrofauna (e.g., Diplopoda, Diptera, Coleoptera, Isopoda, Formicidae, and Isoptera) and the non-anecic (epigeic and endogeic) Lumbricina.

The Romul\_Hum model has the basic structure of ROMUL with the addition of a pool for the humified organic layer, *Ha*, and modules for food web micro- and meso-fauna and anecic earthworm activity including a pool for fresh earthworm casts,  $M_{fc}$ . The pools,



**Fig. 1.** Overview of the integration of SOM-forming faunal activity into the ROMUL model structure for one above-ground leaf litter cohort, food webs and anecic earthworms, in the Romul\_Hum model. Litter input – above-ground leaf litter fall; L – undecomposed fresh leaf litter in organic layer; F – partially decomposed organic layer of the forest floor or grassland sward; Ha – strongly decomposed (humified) organic layer (H sub-horizon); Fresh casts – fresh casts of anecic earthworms; Hstable – stable humified or recalcitrant SOM in mineral topsoil horizons (Ah or Ahe); FW module – module to calculate micro- and meso-faunal excrement and necromass using soil food webs (including Enchytraeidae); A.e. module – module for calculation of SOM-forming activities of anecic earthworms; A.e. cons. – consumption (ingestion) of organic litter by anecic earthworms; Hum L, Hum F – flow of transformed (humified) material from L to F and from F to Ha pools, respectively;  $M_i$  – mineralisation rates of the corresponding SOM pools; St. – stabilisation of SOM as the fresh casts age; double-lined arrows – SOM flows (mineralisation and transformation processes); dash lines – information links on carbon mineralisation (as heterotrophic respiration  $[R_h]$ ) to FW module, and calculated values of by-products in the corresponding SOM flows; dash-dotted lines – earthworm module link to fresh casts and *Hstable* pools. SOM transfer and loss due to leaching, lateral input and output from internal soil water flow and erosion are not represented in this figure. Details of the ROMUL rate variables and algorithms for the food web and earthworm contributions to SOM formation are summarised in Table 1 and described in detail elsewhere (Chertov and Komarov, 1997; Chertov et al., 2001; Komarov et al., 2007, 2012; manuscripts in preparation [Romul\_Hum: parameterisation of food web biota activity; Romul\_Hum: parameterisation of earthworm activity]).

parameters, and processes of the Romul\_Hum are represented in Fig. 1 and in Table 1.

### 2.2. FW module for calculation of by-products, necromass, and available N

FW parameters were developed to quantify the effect of micro- and meso-fauna on the production of SOM for incorporation into models of SOM dynamics. The biota of FW includes two types of microorganisms (bacteria and fungi), the trophic level of “microbial grazers” (mostly protozoa and nematoda) and a few levels of micro- and meso-arthropods and predaceous protozoa (Hunt et al., 1987). Enchytraeidae are included in the FW structure only

**Table 1**  
Metrics of the Romul.Hum model for one cohort of the above-ground litterfall, including anecic earthworms<sup>a</sup>.

Metric	Symbol	Unit	Values	Notes
Litter or organic debris input	$L_0$	kg[C] m <sup>-2</sup> day <sup>-1</sup>	Various	Values dependent on source of inputs (ecosystem model or user)
SOC of <i>L</i> horizon	$L$	kg[C] m <sup>-2</sup>	Various	Initial values dependent on user input
Coefficient of <i>L</i> mineralisation <sup>b</sup>	$k_1$	day <sup>-1</sup>	0.0001–0.01	Dependent on litter N concentration, temperature, and moisture
SOC of <i>F</i> horizon	$F$	kg [C] m <sup>-2</sup>	Various	Initial values dependent on user input
Coefficient of <i>F</i> mineralisation	$k_2$	day <sup>-1</sup>	0.000496	At 20 °C and 60% soil water field capacity; varies with temperature and moisture
Coefficient of <i>L</i> to <i>F</i> transformation	$k_3$	day <sup>-1</sup>	0.004–0.015	Dependent on litter N concentration, temperature, and moisture
Coefficient of <i>F</i> to <i>Ha</i> transformation by micro- and meso-fauna	$k_4$	day <sup>-1</sup>	0.001–0.002	Dependent on N content in <i>L</i> horizon; for details, see Chertov et al. (manuscript in preparation [Romul.Hum. II. Parameterisation of food web biota activity])
Coefficient of <i>L</i> consumption by earthworms	$k_5$	day <sup>-1</sup>	0–0.007	Dependent on N content in <i>L</i> pool
SOC of <i>H</i> horizon	$Ha$	kg [C] m <sup>-2</sup>	Various	Initial values dependent on user input
Coefficient of <i>Ha</i> mineralisation	$k_6$	day <sup>-1</sup>	0.000157	At 20 °C and 60% soil water field capacity; varies with temperature and moisture
Stable SOC of <i>Ah</i> or <i>Ahe</i>	$Hstable$	kg [C] m <sup>-2</sup>	Various	Initial values dependent on user input
Coefficient of <i>Hstable</i> mineralisation	$k_7$	day <sup>-1</sup>	0.00001–0.0006	Calibrated parameter dependent on soil texture and mineralogical composition
Correction factors for temperature effect	$f_i(T)$	Unitless	0–3.0	Used to modify reference value at 20 °C (i.e., $k_2$ , $k_6$ , $k_7$ )
Correction factors for moisture effect	$g_i(W)$	Unitless	0–1.0	Used to modify reference value at 60% soil water field capacity (i.e., $k_2$ , $k_6$ , $k_7$ )

Abbreviations: N – nitrogen; SOC – soil organic carbon.

<sup>a</sup> See Tables 2 and 3 for parameters specific to the food web and anecic earthworm modules, respectively.

<sup>b</sup> All rates of SOC mineralisation presented as  $k_i$ [SOC.pool] are outputs to the food web module.

**Table 2**  
Metrics of the food web (FW) module for one cohort of above-ground litterfall.<sup>a</sup>

Metrics	Symbol	Units	Values	Notes
Assimilation efficiency of FW biota functional groups <sup>a</sup>	$A$	Unitless	0.01–1.0	Proportion of consumed food assimilated by FW biota
Production efficiency of FW biota functional groups <sup>a</sup>	$P$	Unitless	0.3–0.7	Proportion of assimilated food used for faunal biomass production
Death rate of FW biota functional groups <sup>a</sup>	$D$	year <sup>-1</sup>	0.4–2.2	Inverse of lifespan
Biomass C:N ratio of FW biota functional groups <sup>a</sup>	$CN_{bio}$	Unitless	4–12	Needed to calculate N dynamics in FWs
C:N ratio of the ROMUL pools ( <i>L</i> , <i>F</i> , <i>Ha</i> , <i>Hstable</i> )	$CN_i$	Unitless	8–50	As in the ROMUL model (Chertov et al., 2001)
Rate of SOC mineralisation of every SOC pool [ $S_i$ ] <sup>b</sup>	$Miner_{Si}$	kg[C] m <sup>-2</sup> day <sup>-1</sup>	Various	As in the ROMUL model, where it is denoted as $S_i \cdot k_i$
Parameters of excretion production by FW biota as ratio C excrement to C- $R_h$	$R_{exc}$	Unitless	0–1.0	Unique to each FW pattern
Parameters of dead mass production from FW biota as ratio C necromass to C- $R_h$	$R_{dm}$	Unitless	0–1.0	Unique to each FW pattern
Part of $R_h$ of FW biota in the bacterial energy channel	$G_{BactPart}$	Unitless	0–1.0	Function of F:B ratio
Part of $R_h$ of FW biota in the fungal energy channel	$G_{FungPart}$	Unitless	0–1.0	Function of F:B ratio
Production of faunal excretions in the bacterial energy channel	$M_{ExcBact}$	kg[C] m <sup>-2</sup> day <sup>-1</sup>	Various	Calculated using Eq. (2)
Production of faunal excretions in the fungal energy channel	$M_{ExcFung}$	kg[C] m <sup>-2</sup> day <sup>-1</sup>	Various	Calculated by Eq. (2a)
Production of faunal mortmass in the bacterial energy channel	$M_{DmBact}$	kg[C] m <sup>-2</sup> day <sup>-1</sup>	Various	Calculated by Eq. (3)
Production of faunal mortmass in the fungal energy channel	$M_{DmFung}$	kg[C] m <sup>-2</sup> day <sup>-1</sup>	Various	Calculated by Eq. (3a)
Available N	$N_{avail}$	% of $Miner_{Si}$	<100	Calculated by Eq. (4) and functions dependent on SOC, C:N, and $Miner_{Si}$

Abbreviations: B – bacteria; C – carbon; F – fungi; N – nitrogen;  $R_h$  – heterotrophic respiration; SOC – soil organic carbon.

<sup>a</sup> Some auxiliary parameters and functions not included in this table are described by Chertov et al. (manuscript in preparation [Romul.Hum: parameterisation of food web biota activity]).

<sup>b</sup> This value is postulated to be the  $R_h$  of the entire FW biota:  $R_{hFW_{Si}} = Miner_{Si}$ .

as microbial grazers though they play an important role in small coprolite production (Ponge, 1999). The FWs of the organic and topsoil horizons (the *L*, *F*, *H*, and *Ah* or *Ahe* horizons) were sys-

tematised into six “FW patterns” for three soil horizon groupings (*L*, *F*+*H*, and *Ah* or *Ahe*) and two “energy channels” to separate bacterial and fungal faunal FWs (Chertov et al. manuscript in prepa-

**Table 3**  
Metrics of the anecic earthworm module for one cohort of above-ground litter fall<sup>a</sup>.

Metric	Symbol	Unit	Value	Notes
Assimilation efficiency of earthworms <sup>a</sup>	<i>A</i>	Unitless	0.08–0.70	Proportion of consumed food that is assimilated by earthworms; varies with litter quality
Production efficiency of earthworms	<i>P</i>	Unitless	0.10–0.35	Proportion of the food assimilated that is used for production of earthworm biomass
Annual death rate of earthworms	<i>D</i>	year <sup>-1</sup>	0.17	Inverse of lifespan
Biomass C:N of earthworms	<i>CN<sub>bio</sub></i>	Unitless	4.0	Needed to calculate N dynamics in the earthworm module
Rate of food C ingestion (consumption)	<i>F<sub>ingest</sub></i>	kg[C] m <sup>-2</sup> day <sup>-1</sup>	0–0.3	Input from L, using coefficient <i>k<sub>s</sub></i> and L
Amount of food consumed by earthworms	<i>F<sub>cons</sub></i>	kg[C] m <sup>-2</sup>	0–1.5	Total mass of consumed food
Rate of consumed food assimilation	<i>A<sub>cons</sub></i>	kg[C] m <sup>-2</sup> day <sup>-1</sup>	0–0.5	Rate which consumed food is assimilated, calculated as a function of the assimilation efficiency
Amount of assimilated food	<i>M<sub>Ass</sub></i>	kg[C] m <sup>-2</sup>	Various	Total mass of assimilated food in the earthworm module
Rate of production of earthworm biomass	<i>P<sub>Lumb</sub></i>	kg[C] m <sup>-2</sup> day <sup>-1</sup>	Various	Dependent on N content of assimilated food
Earthworm biomass	<i>B<sub>Lumb</sub></i>	kg[C] m <sup>-2</sup>	Various	Live earthworm biomass
Earthworm death rate	<i>D<sub>Lumb</sub></i>	kg[C] m <sup>-2</sup> day <sup>-1</sup>	Various	Calculated from <i>B<sub>Lumb</sub></i> and <i>D</i>
Earthworm necromass	<i>M<sub>dmL</sub></i>	kg[C] m <sup>-2</sup>	Various	Dead earthworm mass
Coefficient of necromass mineralisation	<i>k<sub>LumbD</sub></i>	day <sup>-1</sup>	0.022	At 20 °C and 60% soil water field capacity; varies with temperature and moisture
Excreted non-assimilated food	<i>M<sub>excr</sub></i>	kg[C] m <sup>-2</sup> day <sup>-1</sup>	Various	Difference between food ingested and food assimilated
Amount of fresh casts	<i>M<sub>fcs</sub></i>	kg[C] m <sup>-2</sup>	Various	Short-term, fast-mineralising SOC pool
Coefficient of mineralisation of fresh casts	<i>k<sub>fcm</sub></i>	day <sup>-1</sup>	0.0183	At 20 °C and 60% soil water field capacity; varies with temperature and moisture
Coefficient of transformation of fresh casts into stable SOM	<i>k<sub>stab</sub></i>	day <sup>-1</sup>	0.033	Output from earthworm module to H_stable pool in the ROMUL model
Coefficient of N fixation in fresh casts	<i>N<sub>fix</sub></i>	day <sup>-1</sup>	0.000001–0.00002	Calibrated parameter

Abbreviations: C – carbon; N – nitrogen; SOC – soil organic carbon; SOM – soil organic matter.

<sup>a</sup> Some auxiliary parameters and functions are not included in this table but are described in Chertov et al. (manuscript in preparation [Romul.Hum: parameterisation of earthworm activity]).

**Table 4**  
Ratios of nitrogen mineralisation rates between the two models (Romul.Hum:ROMUL).

Pool	Nitrogen in litter fall, %			
	0.5	1.0	1.5	2.0
<i>L</i>	3.3	3.8	6.2	7.6
<i>F</i>	0.4	1.1	1.4	1.7
<i>Ha</i>	0.7	0.6	0.9	0.8
<i>Hstable</i> <sup>a</sup>	0.6	1.1	1.0	0.9

ration [Romul.Hum: parameterisation of food web biota activity]). The module parameters are summarised in Table 2, and the general scheme of the algorithms is shown in Fig. 2. Development of the parameters and algorithms, through analyses of experimental data, is described in detail elsewhere (Chertov et al. manuscript in preparation [Romul.Hum: parameterisation of food web biota activity]).

The main parameter used to calculate faunal by-products in the FW modules is mineralised C taken from the ROMUL model for each SOM pool. It was postulated that mineralised C represents C from heterotrophic respiration of the soil biota (*R<sub>h</sub>*) that is the driving variable for the following calculations. The fungi to bacteria ratio (F:B) is calculated to determine the structure of the soil microbiological population using Eq. (1) (Chertov et al. manuscript in preparation [Romul.Hum: parameterisation of food web biota activity]):

$$FB = 1.50 + 0.31 * [CN], \quad (1)$$

where  $n = 38$ ,  $r^2 = 0.33$ ,  $SE = 4.31$ , *FB* is the F:B ratio and *CN* is the C:N ratio of the SOM pool. The F:B ratio is used to split the pool of respired C into bacterial and fungal channels (*R<sub>hbac</sub>* and *R<sub>hfun</sub>*).

The pools of faunal excrement and necromass (*M<sub>Exc</sub>* and *M<sub>Dm</sub>*) are calculated by multiplying the parts of FW *R<sub>h</sub>* belonging to bac-

terial and fungal channels (*G<sub>BactPart</sub>* and *G<sub>FungPart</sub>*) by *R<sub>exc</sub>* and *R<sub>dm</sub>* (Table 2) for every energy channel, respectively (see Chertov et al. manuscript in preparation [Romul.Hum: parameterisation of food web biota activity]):

$$M_{ExcBact} = R_{exc} * G_{BactPart}, \quad (2)$$

$$M_{ExcFung} = R_{exc} * G_{FungPart}, \quad (2a)$$

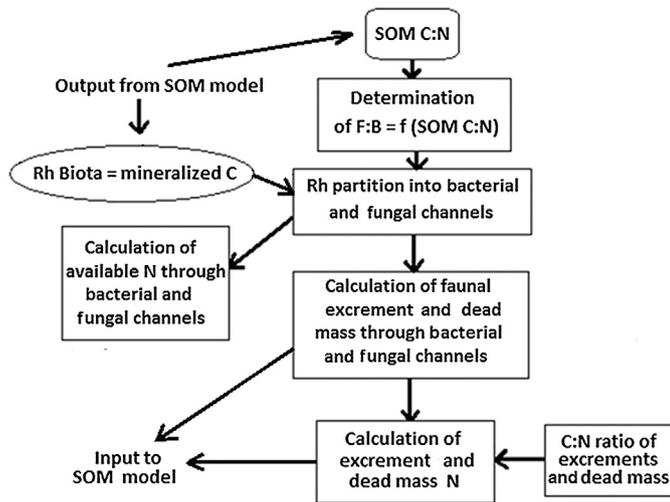
$$M_{DmBact} = R_{dm} * G_{BactPart}, \quad (3)$$

$$M_{DmFung} = R_{dm} * G_{FungPart}. \quad (3a)$$

The N pools of excrement and necromass are calculated by dividing the mass of excrement and necromass, respectively, by their corresponding C:N ratios (see Chertov et al., manuscript in preparation [Romul.Hum: parameterisation of food web biota activity]). The N mineralised by soil biota and available for plant nutrition is calculated in most modern models of SOM dynamics. Here, we calculate this pool using Eq. (4):

$$N_{avail} = R_{hbac} * Y_i + R_{hfun} * Y_j, \quad (4)$$

where *N<sub>avail</sub>* is the pool of total mineral N available for plant uptake; *R<sub>hbac</sub>* and *R<sub>hfun</sub>* are the parts of total respired C (*R<sub>h</sub>*) of the bacterial and fungal channels, respectively; and *Y<sub>i</sub>* and *Y<sub>j</sub>* are the ratios



**Fig. 2.** Food web biota module for calculating faunal excrement, necromass, and available nitrogen (N) for one SOM pool in an organic or organo-mineral layer. Faunal excrement and necromass are integrated through a rate variable (if a pool is being further transformed into another pool) or are integrated back into the same pool if it is the final stage of decomposition (stable humus or recalcitrant SOM). B – bacteria; C – carbon; F – fungi;  $R_h$  – heterotrophic respiration.

of available N to soil respiration of the bacterial and fungal channels, respectively, as determined by functions for available N (see Chertov et al., manuscript in preparation [Romul.Hum: parameterisation of food web biota activity]).

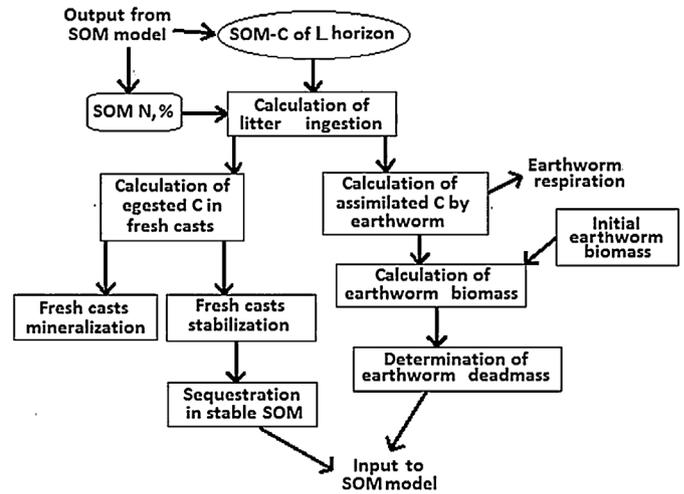
The calculated pools of faunal by-product C and N become inputs to the basic structure of the Romul.Hum model. These values are required to quantify the degree of transformation (humification) of initial litter into stable humus and for the eventual calculation of available N due to soil FW biota activity.

The rate of mineralisation of faunal by-products was postulated to be equal to the rate of mineralisation of the corresponding SOM pool, as determined by the ROMUL model (Chertov, 1985; Chertov et al., 2001). An increase in the C:N ratio of the transformed humified SOM will occur only if faunal by-products decompose faster than corresponding pool, but in reality a significant decrease is observed in the C:N ratio during the process of organic debris decomposition (e.g., Komarov et al., 2007; Berg and McLaugherty, 2008) suggesting that faunal by-products must contribute to stable SOM. With the Romul.Hum model, we have the additional capability to account for the role of the by-products of micro- and meso-fauna activity in forming new SOM. Furthermore, the FW SOM-forming activity is a component of the anecic earthworms' contribution to SOM sequestration, as described below.

### 2.3. Anecic earthworm module for calculation of newly formed SOM

We developed the module for earthworm activity for application in forest, grassland, and other natural ecosystems, assuming no barriers to population growth and spread in a given soil and assuming that earthworm biomass quickly reaches a balance with the available pool of palatable litter. The module parameters are summarised in Table 3, and the general scheme of the algorithms is shown in Fig. 3. Development of the parameters and algorithms, through analyses of experimental data, is described in detail elsewhere (Chertov et al., manuscript in preparation [Romul.Hum: parameterisation of earthworm activity]).

The main input to the earthworm module is organic matter of the forest floor or grassland sward at the early stage of decomposition (i.e., L horizon). All or part of this material can be ingested by anecic earthworms, whereby it is moved into the mineral soil. The



**Fig. 3.** Earthworm module for calculating the soil organic matter (SOM)-forming activity of anecic earthworms. C – carbon; N – nitrogen.

amount of food ingested is calculated using the equation for coefficient  $k_5$  in the ROMUL model (Chertov et al., 2001, manuscript in preparation [Romul.Hum: parameterisation of earthworm activity]).

The initial biomass of anecic earthworms is calculated using Eq. (5):

$$B_{init} = (F_i / CN_{food}) * CN_{bio} / D, \quad (5)$$

where  $B_{init}$  is biomass C of the earthworm population;  $F_i$  is the expected annual consumption of palatable litter;  $CN_{food}$  is the C:N ratio of consumed litter;  $CN_{bio}$  is the C:N ratio of the earthworm biomass,  $D$  is the annual death rate of the earthworms.

The rate of ingestion of food (material from the L horizon) is calculated using Eq. (6):

$$F_{ingest} = k_5 * L * corr(T, W), \quad (6)$$

where  $F_{ingest}$  is the rate of food ingestion,  $k_5$  is coefficient of food consumption by earthworms (Table 1),  $L$  is the pool of undecomposed organic layer (forest floor, sward), and  $corr(T, W)$  is a correction factor dependent on soil temperature and moisture.  $F_{ingest}$  goes into the pool of consumed food,  $F_{cons}$ , in Romul.Hum.

The proportion of ingested material from the L horizon that is assimilated ( $M_{Ass}$ ) is calculated using Eq. (7):

$$M_{Ass} = F_{ingest} * A, \quad (7)$$

where  $A$  is assimilation efficiency (Table 3).

The proportion of  $M_{Ass}$  used for biomass growth in models is usually a fixed value (Whalen et al., 1999). In Romul.Hum this proportion is linked to soil C and N dynamics because N availability to earthworms is often the main limiting factor to their growth. Therefore earthworm growth is dependent on the amount of N in the assimilated food and the C:N ratio of the earthworm biomass ( $CN_{bio}$ ) using Eq. (8)

$$P_{lumb} = (M_{Ass} / CN_{food}) * CN_{bio}, \quad (8)$$

where  $P_{lumb}$  is the amount of earthworm biomass production for one time step, and  $CN_{food}$  is the C:N ratio of the ingested food. Correspondingly, earthworm biomass at time step “t + 1” calculated as in Eq. (9):

$$B_{lumb}(t + 1) = P_{lumb} + B_{lumb}(t) \quad (9)$$

The dead mass of earthworms ( $M_{dmL}$ ) at the time step “t + 1” is calculated using Eq. (10):

$$M_{dmL}(t + 1) = M_{dmL}(t) + D_{Lumb} * B_{lumb}, \quad (10)$$

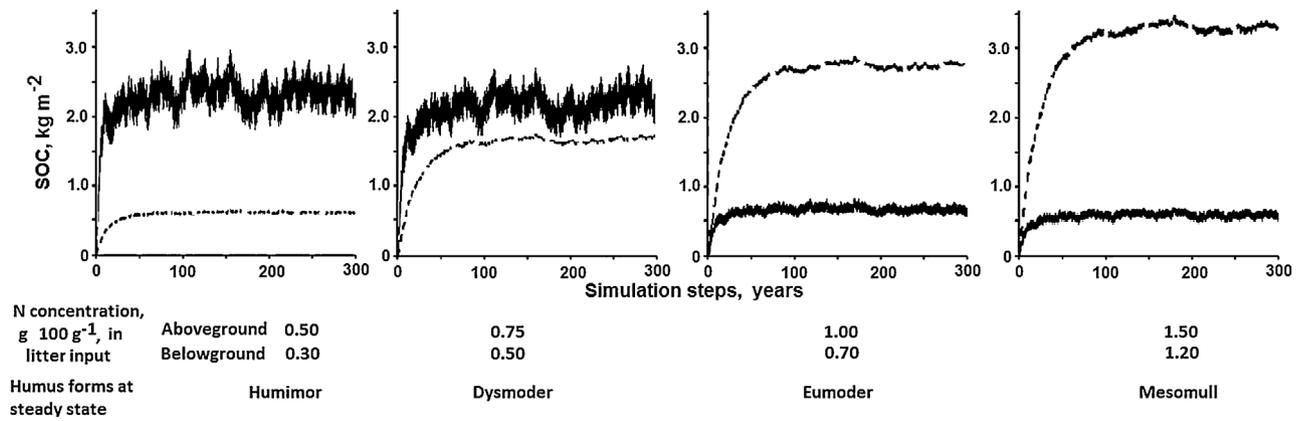


Fig. 4. Simulated development of humus forms at a constant litter input of 3 ton [C] ha<sup>-1</sup> year<sup>-1</sup> with different N concentrations in the southern taiga of eastern Europe. Single line – organic layer; dashed line – mineral topsoil.

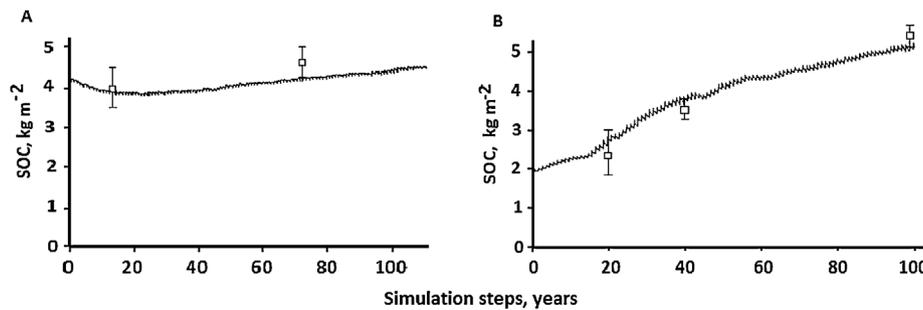


Fig. 5. Validation of Romul.Hum by comparison of simulated soil organic carbon stocks to measured soil organic carbon stocks on sites reclaimed from agricultural land use. A – Haplic Albeluvisol soil, taiga of northeastern Europe (Kalinina et al., 2013); B – Calcisol soil, dry steppe grassland of southeastern European (Kalinina et al., 2015). Lines – simulated data; small quadrat – measured data; vertical bars – standard deviation.

where  $D_{Lumb}$  is the coefficient of the earthworm death rate for one time step.

Death rates are most often reported in annual time steps, but in the Romul.Hum simulations it was recalculated for the daily or monthly time step of the model. Earthworm necromass was assumed to mineralise quickly (to become secondary litterfall), producing carbon dioxide and available N. The mineralisation rate of the dead earthworm mass was based on the assumption that all the necromass was decomposed in two months.

The rate of organic matter excretion for earthworm cast formation ( $M_{excr}$ ) is calculated using Eq. (11):

$$M_{excr} = F_{ingest} * (1 - A). \quad (11)$$

This excreted material goes into a pool of fresh casts,  $M_{fcs}$ . The previous calculations show that the SOM concentration in casts immediately after egestion can increase by 1.8–2.3 fold when the initial SOM C concentration is 2.0% in forest soils with a mull humus form (Phaeozems and Umbric Albeluvisols of eastern Europe) if the soil to litter ratio in ingested material is equal to 15 and the assimilation efficiency ( $A$ ) varies from 0.06 to 0.50 (Chertov, 2016).

Organic matter ingested by earthworms is highly modified and mineralised in the gut within hours. These processes continue in the egested SOM of fresh casts, with the casts being sites of intense mineralisation and transformation that play a crucial role in the formation of stable organic matter, the emission of carbon dioxide, and the release of N. The rate of mineralisation in fresh casts ( $M_{fcs}$ ) is approximated as:

$$M_{fcs} = M_{excr} - (k_{fcm} + k_{stab}) * M_{fcs}, \quad (12)$$

where  $M_{fcs}$  is the pool of fresh casts,  $k_{fcm}$  and  $k_{stab}$  are coefficients for fresh casts mineralisation and stabilisation, respectively, as described in Table 3.

After a short (one-month) phase with a high rate of SOM transformation, the organic C in the fresh casts becomes stabilised. The stabilised C ( $k_{stab} * M_{fcs}$  in Eq. (12)) is eventually incorporated into the stable SOM pool (Hstable, Table 1).

The N dynamics are calculated using the same algorithm as for SOM, where the main sources of N available for plants from the earthworm module are the fresh casts and earthworm necromass. One additional source of N input is biological N fixation in the fresh casts ( $N_{fix}$ ) that is included in the total mineralised N.

The earthworm module is closely linked to the module for FW biota (see Section 2.2), which calculates a pool of by-products for the formation of recalcitrant SOM. This linkage in the fresh casts is the main pathway for formation of stabilised SOM. A diagram of the Romul.Hum model design for one cohort of above-ground litterfall with the anecic earthworm and FW modules is presented in detail in Fig. S1 (Supplementary materials).

### 3. Testing of the Romul.Hum model

The Romul.Hum model was programmed in the dynamic modelling system Powersim Studio Academic 2005<sup>®</sup> and in the Object Pascal in Delphi XE environment with daily and monthly time steps, respectively. However, for ease of presentation, the results were output at annual time steps. The Powersim program was used to compile the structure of the new components in the Romul.Hum and for the preliminary model testing with one cohort of leaf litter fall. The program in Object Pascal was implemented for the long-term model runs with various qualities of litter fall. The testing was

**Table 5**  
Functional groups of soil biota for simulation of humus forms and SOM dynamics.

Soil biota	Humus form		
	Mor	Moder	Mull
microbial energy channels	FC	FC + BC	BC
FW and earthworms in the organic layer	FW	FW + EPI	fw+ epi
FW and earthworms in the mineral topsoil	fw	FW + endo+ ane	ANE + ENDO +FW

Abbreviations: ANE or ane – anecic earthworms; BC – bacterial channel; ENDO or endo – endogeous earthworms; EPI or epi – epigeous earthworms; FC – fungal channel; FW or fw – biota of food webs. Uppercase letters represent a dominant role for a given group; lowercase letters represent a subordinate role.

performed (a) to evaluate the ability of this model to reproduce the main humus forms in forest soils; (b) to validate Romul\_Hum against some independent data; (c) to check the effectiveness of the new algorithms for mineralised N calculated on the basis of the FW approach, and (d) to analyse the simulated results for faunal by-product accumulation in SOM pools.

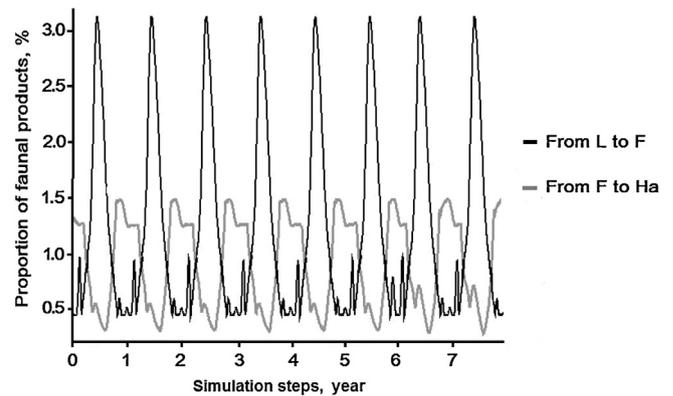
The Romul\_Hum model uses the structure, parameters, and functions of the well-tested, calibrated, and validated ROMUL model, which means we were able to easily examine the behaviour of the new modules in relation to the roles of faunal excretion and necromass in SOM formation.

To examine the model's performance, model runs were executed to simulate humus form development where initial SOM values were assumed to be zero. First, we ran simulations for one cohort of aboveground litter fall with the FW and anecic earthworm modules and then the model was run with the scenarios for above- and below-ground cohorts of litter fall. The simulations were run for a mixed-wood forest on an Albeluvisol soil on moraine loam mesic landforms in the southern taiga of eastern Europe, with a continental climate (mean annual temperature 5 °C, precipitation 650 mm, atmospheric N deposition 5 kg N ha<sup>-1</sup> year<sup>-1</sup>) with scenarios of soil temperature, moisture and litter inputs from measured data (Komarov et al., 2007). We examined the model's behaviour in response to a range of N concentrations in the litter fall input (Fig. 4). The mass of plant litter input was set to 3 ton [C] ha<sup>-1</sup> year<sup>-1</sup> for all soils in the range of N concentrations.

The simulations with one-cohort of aboveground litter input forms a forest floor only when the N content in the litter fall is low, and accumulates a large SOM pool in the mineral topsoil when the N content in the litter fall is high. This is consistent with the typical features of Mor and Mull humus forms, respectively, developed due to the soil forming activities of FW biota and earthworm. The simulations with above- and below-ground litter inputs of different quality produced similar patterns of SOM formation reaching a steady state within 100 years (Fig. 4). These results and a set of additional runs for other soils of the region are in concordance with the observed data (Komarov et al., 2007) where the distribution of C stocks shifts from dominantly in the forest floor to dominantly in the mineral soil as the humus forms shift from mors to moder and then mulls.

We validated the Romul\_Hum by comparing simulated results for humus form development to data collected from soils reclaimed after agricultural land use in two contrasting ecosystems; one in north-eastern Europe (central taiga Albeluvisol, Kalinina et al., 2013) and the other in the semi-arid grasslands of eastern Europe (dry steppe Calcisol, Kalinina et al., 2015). Results from the Romul\_Hum exhibit trends over time similar to the measured values for SOC stocks, and are within the error of the measured values (Fig. 5).

Representation of N mineralisation in the Romul\_Hum model includes new algorithms based on an FW approach (Hunt et al., 1987), while in the ROMUL model a few simple empirical correction factors to C mineralisation were used to assess plant available mineralised N (Chertov et al., 2001). The novel approach resulted in a substantial difference in the prediction of available N between

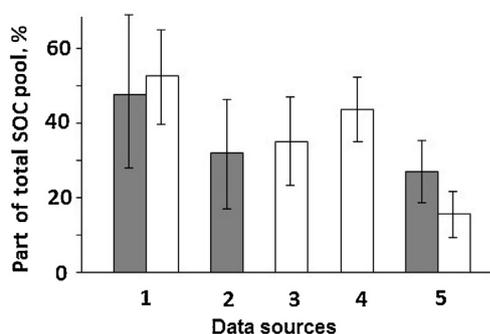


**Fig. 6.** The percentage of faunal by-products involved in flows of soil organic matter between organic layer horizons, simulated for an Albeluvisol using a constant litter input with a nitrogen concentration equal to 1.0%.

ROMUL and Romul\_Hum expressed as the ratio of N mineralisation rates between the two models (Table 4). Values close to 1.0 indicate little change, whereas large values (i.e., 6.2 for the L pool) indicate a substantially higher N mineralisation rate in Romul\_Hum compared with ROMUL (Table 4). The greatest discrepancy occurred for the small pool of undecomposed fresh litter (fast transforming L pool), for which the new model calculated up to seven times more available N compared with the ROMUL model. The difference was smaller for the F pool and was minimal for the large final pools of SOM transformation (Ha and Hstable pools). The sum of available mineralised N for all horizons combined differed by 14% to 17% between the old and new models.

The Romul\_Hum model allowed us to evaluate the contribution of faunal by-products to SOM formation and stabilisation that was one of the most important reasons to elaborate a new version of ROMUL model. The percentage of faunal by-products involved with SOM flows resulting in stabilisation of C fluctuated seasonally (Fig. 6), because it was correlated with litter input, soil temperature and moisture, and the responses of faunal activity to these variables. The amplitude of variations for flow from fresh litter (L pool) to partially decomposed SOM (F pool) increased from 0.5%–1.5% for poor-quality litter (low N, 0.5%) to 0.5%–4.5% for rich litter (high N, 2.0%), with the maximum in summer. The percentage of faunal by-products flowing from the F pool to the humified organic layer (Ha pool) varied from 5% to 10% for poor litter input and from 0.1% to 0.8% for rich litter input, with the maximum in autumn. These patterns reflect differences in the responses of processes, modelled in the Romul\_Hum, to N and climatic factors.

The results of long-term Romul\_Hum model runs show that simulated pools of faunal-derived organic matter in SOM reached a stable-state after approximately 100 years of soil development – the same period of time required for simulated total SOC to reach a steady state (Fig. 4). At the steady state, the percentage of total SOC that is derived from faunal organic matter varies around a mean of 25% where the upper part of the range is represented by Mor humus forms and the lower part of the range by Mull humus forms. In



**Fig. 7.** A comparison of observed stable soil organic carbon (SOC) and simulated faunal-derived organic matter, as a percentage of total SOC. Data sources: 1, Podzolic and Albeluvisolic soils with different humus forms, the Russian northwestern Europe ( $n=47$ , Chertov, 1981); 2, Mor forest floor of Rustic Podzolic soils, St. Petersburg district in Russia ( $n=5$ , recent authors' data); 3, Haplic Albeluvisolic soils, Russian northeastern Europe ( $n=14$ , Kalinina et al., 2013); 4, Calcisolic soils, Russian southeastern Europe ( $n=13$ , Kalinina et al., 2015); 5, simulated faunal-derived organic matter ( $n=4$ , this study). Estimates from Chertov (1981) are based on the insoluble residue after alkaline extraction and hydrolysis. Estimate from Kalinina et al. (2015) are based on clay associated organic matter. Dark columns – SOC of organic layer, white columns – SOC of mineral topsoil.

organo-mineral topsoil, the percentage of total SOC that is derived from faunal organic matter varies from 12 to 19% (Fig. 7).

We compared these simulated results for the percentage of total SOC derived from faunal organic matter with measured estimates of stable SOC in various soils ( $n=79$ ) based on the postulate that faunal derived organic matter is the precursor of stable (resistant) SOC (Fig. 7). From this we conclude that faunal by-products can represent up to 50% of the stable SOC pool in various soils and that this percentage is higher in the soil organic layers than in the mineral topsoil.

The results for faunal by-products in SOM pools (Figs. 4–7) illustrate the ability of the Romul.Hum model to simulate different patterns of the dynamics of these by-products and their accumulation in SOM pools of different humus forms. Faunal by-products were more highly concentrated in the final pools (*Ha* and *Hstable*) than in the pools through which they flowed (*F*). Rich litter inputs led to a high percentage of faunal by-products in a relatively small *F* horizon pool. The litter quality did not influence the percentage of faunal by-products in the stable humus, but it did affect the size of the whole pool.

#### 4. Discussion

Recent evaluations of the ability of various models to predict soil C stocks (Todd-Brown et al., 2013; Shaw et al., 2014) have shown that calls to the soil modelling community to develop approaches that include missing agents and processes are justified (Smith et al., 1998; Chertov and Komarov, 2013). Few SOM models used today include a representation of SOM stabilisation mechanisms that have been well articulated in observational studies (e.g., Fox et al., 2006; Kögel-Knabner and Matzner, 2008) but have not necessarily been quantified in a way that is amenable for use in models. Here, we have addressed the missing processes of humification (a stabilisation mechanism) and development of humus forms and the missing biological agents (from bacteria and fungi to mesofauna and earthworms).

The challenge of including the degree of SOM transformation (humification) has not been emphasised in simulation modelling, despite its relevance to C sequestration. Hunt (1977a) represented SOM transformation over time ( $n$ ) as “SOM<sub>*n*</sub> → active decomposers + inactive decomposers → SOM<sub>*n+1*</sub>” where “decomposers” included all soil biota. This pathway is inferred in most other SOM models, including CENTURY (Parton, 1996), RothC (Coleman and

Jenkinson, 1999), and CANDY (Franko, 1997). Sometimes, the explanation for SOM transformations from fast to slowly decomposing pools is short and is qualified as “abstract” (e.g., Braakhekke et al., 2011: pp. 1715 and 1718). In the ICBM model, for example, Andrén and Kätterer (1997) used only a “humification factor,” which was dependent on litter quality.

In most models, the agents of SOM transformation are not “decomposers” as intended by Hunt (1977a); instead, “active SOM” is interpreted as microbial biomass that directly transfers SOM from one pool to the next (Manzoni and Porporatto, 2009). Alternatively, Kuka et al. (2007), in their model of SOM dynamics in microaggregates, used dissolved organic C as the driver for the transfer of transformed organic matter between various pools. The direct role of microbial biomass as a primary source of transformed, relatively resistant SOM (humus) was pointed out by Ågren and Bosatta (1998) in their Q model. None of these approaches have included quantifying pathways that take into account all of the soil biota that are of principal importance for C sequestration and ecosystem function.

In the ROMUL model, and now the Romul.Hum model, the pools are not abstract but rather are related to the well-defined horizons of the humus forms. The development of humus forms has been reasonably well described in observational studies (Klinka et al., 1981; Bal, 1982; Baritz, 2003; Jabiol et al., 2013) and studies linking observations to site productivity and soil function (Zanella et al., 2011; De Nicola et al., 2014). In spite of macro- and micromorphological evidences of the prominent role of soil fauna in SOM formation (Zanella et al., 2011; Ponge, 2015 and many others) there is a lack of quantitative data on the rate of formation and pools of fauna-derived organic matter in SOM. Previously, an attempt was made to assess the input of faunal by-products with litter fall only (Chertov, 2016). Until now, no attempt has been made to develop a quantitative model that simulates the processes (including humification) and agents (the full suite of soil biota) leading to the observed humus forms and their characteristics. From our synthesis of the literature, we have developed such a model (Romul.Hum), which produces behaviour consistent with observational studies. For the first time, the Romul.Hum model provides the opportunity to evaluate faunal by-products as drivers of SOM formation.

The results of testing the Romul.Hum model, as described in Section 3, show that a significant percentage of the stable SOC fraction of various soils could be comprised of faunal by-products even if a part of the faunal-derived matter stays in the occluded SOC (Fox et al., 2006). These outcomes are similar to results obtained for 14 FWs, as processed by Chertov (2016). In the transitional SOM pools (*L* and *F*), the percentage of faunal by-products quickly reaches a plateau (as a function of substrate quality); in contrast, in the stable pools (*Ha* and *Hstable*), that percentage increases over a longer period and reaches a relative steady state if litter inputs are constant and environmental conditions do not change. We speculate that the percentage of faunal by-products would increase without fresh litter inputs to the soil because of the continued activities of soil biota. These dynamic patterns are in agreement with micro- and macromorphological observations on the accumulation of humified matter in H and Ah horizons during development of humus forms (Bal, 1970; Galvan et al., 2006; Zanella et al., 2011) and sequestration of recalcitrant SOM in the Ah horizon (Kögel-Knabner and Matzner, 2008). In addition, the internal dynamics of faunal by-products (recalcitrant SOM) is consistent with the concept of the SOM decomposition continuum described by Ågren and Bosatta (1998).

Results from initial assessments of the Romul.Hum model and analyses of data for quantitative soil fauna parameters (Chertov et al., manuscripts in preparation [Romul.Hum: parameterisation of food web biota activity; Romul.Hum: parameterisation of earthworm activity]) enabled us to propose a framework to specify the

main biotic drivers of humus forms, and therefore SOM development (mineralisation and formation of stable SOM) (Table 5).

Because the Romul.Hum is modular it can be expanded to include additional pools, agents and processes. For example, new modules can be created to account for root litter dynamics (Shanin et al., 2015) in the organic layer (required for modelling the activity of epigeic earthworms) and in the mineral topsoil (required for modelling the activity of endogeic earthworms).

The Romul.Hum model not only made it possible to evaluate the proportion of faunal by-products contributing to SOM formation but also distinguished the dynamics along different pathways of humification and SOM sequestration, as follows:

1. Transformation of rapidly mineralising fresh plant debris (*L* pool) in the organic layer into partially decomposed organic matter (*F* pool), consisting of 0.5%–4.5% faunal by-products with a mineralisation rate that is significantly lower than for the *L* pool. This process is positively correlated with litter N content. Given that this process is driven by FW biota, it forms the partially resistant organic matter that is a precursor of stable SOM (i.e., an acid-soluble fraction of the *F* pool) (Fox et al., 2006; Ekschmitt et al., 2008).
2. Transformation of SOM in the *F* pool to the slowly mineralising SOM of the humified organic layer (*Ha*). This flow has widely varying amounts of faunal by-products (ranging from 0.1% to 10%) and is dependent on hydrothermal conditions.
3. Transfer of the litter at the early stage of decomposition into the mineral topsoil by anecic earthworms, accompanied by transformation of SOM by the FW biota in the earthworm gut and in fresh casts, into stable SOM. This process demonstrates the interaction of FW biota and earthworms functioning as a zoogenous–microbial complex (Byzov, 2005; Rakhleeva et al., 2011) and resulting in SOM sequestration and stabilisation. The intensive FW activity and high heterotrophic respiration rates in fresh casts reflect the high production of micro- and mesofaunal excrement within earthworm excreta, where there is a high potential for formation of recalcitrant SOC. This aspect warrants further investigation as discussed by Chertov (2016). In particular, the FW necromass could represent relatively fast decomposing organic matter.
4. Internal sequestration processes in the humified SOM pool (*Ha*) of the organic layer, with consistent accumulation of faunal by-products due to the activity of FW biota. An asymptotic decrease in the mineralisation rate (down to zero) in old SOM is theoretically possible here and it is consistent with the “limit value” concept of Berg and McLaugherty (2008). Such a decrease would be dependent on an increase in the ash content of the SOM, particularly with iron and aluminum sesquioxides and ash phytoliths that can bind with and stabilise SOM (Song et al., 2014).

## 5. Conclusions and future directions

The development of the Romul-Hum model shows that SOM-formation mediated by soil biotic activities can be included in simulation modelling of soil systems. Here, we have described a model for above-ground litter inputs with FW biota and anecic earthworms, which represents an important step toward explicit representation of all soil biota and their role in SOM stabilisation (sequestration); agents and processes that are not represented in soil models commonly used for coarse-scale C assessments. Model results will be further tested and validated with experimental data on the production and mass of faunal excrement and necromass. Work is now under way to investigate 1) root litter input to the organic layer and the role of epigeic earthworms; 2) root litter input to the mineral topsoil and the role of endogeic earthworms; and

3) litter-consuming macroarthropods (Diplopoda, Isopoda, etc.) as litter transformers (Striganova and Chernobrovkina, 1992; Lavelle, 1997). This work will contribute to our larger strategic goal of modelling the full soil profile system (O, A, B, and C horizons) to simulate dynamic processes involving organic matter, biota, and the mineral matrix for a wide range of environmental conditions, with reference to the classic soil-forming factors articulated by Dokuchaev and Jenny (Jenny, 1994).

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2016.08.007>.

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