Soil carbon cycle responses to global change and its prediction by modelling links between key biotic and abiotic processes in terrestrial ecosystems

Respuestas del ciclo del carbono del suelo al cambio global y su predicción mediante la modelización de vínculos entre procesos bióticos y abióticos clave en los ecosistemas terrestres

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PhD Thesis, 2020

"***Nullius*** *addictus iurare* ***in verba*** *magistri,*

quo me cumque rapit tempestas, deferor hospes."

Quintus Horatius Flaccus

It’s gonna be legen… wait for it

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ABSTRACT

Global change, defined as the set of environmental changes (e.g. climate change and/or land use change) resulting from anthropogenic activities and their impacts on Earth system functioning, is threatening the terrestrial biodiversity conservation and thus the ecosystem services provided by nature. It is therefore of upmost importance to anticipate the potential consequences of global change on natural communities. This requires improving our ability on understanding the functioning and potential vulnerability of natural communities, as well as on predicting future ecosystem responses to global change and their impact on key ecosystem-provided services such as carbon (C) sequestration. However, given the inherent complexity in the functioning, interactions, and levels of organization of the natural communities that form ecosystems, predicting how ecosystems will respond in the face of global change remains challenging. In order to deal with such complexity, it is essential to use mechanistic models for the integrative simulation of multiple processes and their potential feedbacks in order to simulate as realistically as possible how ecosystems will respond to environmental disturbances.

The soil system is probably the less known biosphere compartment and the one whose responses to global change are more uncertain, despite being the most biodiverse terrestrial ecosystem on the planet and playing an essential role as C sink (i.e. second C sink after the oceans at global scale). Nevertheless, an increasingly critical mass of knowledge on different key aspects of the soil system (e.g. on the role of C and nutrients flow through the complex soil food webs) is currently starting to become more available. Also, there is growing evidence on the role of key functional groups on soil functioning in general and on C cycling in particular, such as e.g. the ecosystem engineer species that transform the physical structure of the soil, the detritivore species that fragment the soil organic matter (SOM), facilitating thus the task of the decomposer species that mineralize the organic matter, or the bacterivore and fungivore species that control the population of the decomposers. However, current state-of-the-art biogeochemical models are mostly based on empirical approaches that do not take into account the large ecological complexity of the soil system, or important aspects of its functional diversity, which directly relate to important aspects of soil functioning, soil chemistry or soil physical structure.

The simplistic representation of the complex soil processes considered in empirical models is evidenced for example by the fact that these models tend to underestimate litter decomposition rates in arid and semiarid ecosystems (drylands). This has a large impact on global estimations of C emissions and soil C sequestration, because those ecosystems represent a substantial part of all emerged lands. Specifically, the mechanisms of litter decomposition which play a critical role in drylands (i.e. water-limited ecosystems) have not been yet integrated into prediction models, despite their evident contribution to global C emissions and soil C sequestration. Such mechanisms of litter decomposition refer to the abiotic degradation of litter induced by solar radiation (photodegradation), or the biotic litter decomposition induced by non-rainfall

water sources (e.g. dew). Accordingly, it can be expected that the inclusion of those mechanisms into soil C cycling prediction models will lead to a remarkable improvement in the accuracy of the predictions made with those models. Although specific mechanistic models exist for the simulation of some of these processes and functions, it is still necessary to combine them all for the integrated simulation of the soil processes that regulate the C cycle. It is also important to further study key processes in the soil C cycling that are highly susceptible to global change, such as litter decomposition, by developing new experiments in order to better understand which factors control the soil C cycling in drylands, and its potential vulnerability to global change driven disturbances, such important as climate change or the change in land uses.

In this PhD thesis, the complexity of the soil system has been reviewed and integrated in a new model concept. The three main aims of this PhD thesis were to: 1) develop a new mechanistic soil model, called KEYLINK, by integrating soil diversity characteristics such as the trophic structure and functional complexity, both playing a crucial role in the soil physical structure and in the stabilization of SOM in terrestrial ecosystems; 2) develop within the KEYLINK model a mechanistic representation of the processes associated with litter decomposition in drylands, given their critical contribution to global C emissions and soil C sequestration, hence providing a second version of KEYLINK adapted to these terrestrial ecosystems; and 3) develop experiments to understand regional patterns and factors that control litter decomposition in Mediterranean systems (i.e. drylands), with special emphasis on studying the effects of climate and litter intraspecific variability on litter decomposition.

This PhD thesis gathers an extensive bibliographic review to explore the published information on the role of soil biodiversity on soil C cycling in general, and on how the existing knowledge on the soil trophic organization and functional diversity may help improving current biogeochemical modelling in particular. All this information has been essential for the development of KEYLINK, a new mechanistic process-based soil model that integrates the soil physical structure, the soil hydrology and the soil functional diversity for the simulation of soil C cycling at ecosystem scale. The evaluation of the new model was carried out by simulating several scenarios of disturbances resembling scenarios of global change. Results show the ability of the KEYLINK model to represent, in an integrative way, the role of biological phenomena, such as trophic cascades (e.g. how scenarios of local extinction of predators may impact soil physical structure (porosity)), on the soil C sequestration or C emissions. These results put into perspective the relevance of taking soil biodiversity and its organizational complexity into account when predicting future responses of the terrestrial ecosystems to global change derived environmental disturbances. They also highlight the fact that the soil physical structure is a key aspect to explain the physical and physico-chemical stabilization of SOM. In addition, the integration of soil hydrology not only contributes to a better representation of the organic matter stabilization, but also facilitates the coupling of this soil model with vegetation models, contributing to an improvement in the simulation of the soil hydrological cycle and the

availability of water in the soil system. The resulting simulations also showed how global change could alter leaf litter decomposition mechanisms, especially in drylands, and determine different effects depending on different soil C stocks (i.e. different litter layers). Specifically, the KEYLINK simulations showed how the solar radiation incidence at the soil level, which depends on the structure of the vegetation, could affect the rates of litter decomposition and determine the dominant mechanisms (abiotic vs. biotic) that control litter degradation. More in detail, the results of the simulations showed that the spatial fluctuation in the amount of radiation reaching the soil, due to changes in vegetation cover, may determine shifts between the prevalence of abiotic litter degradation (photodegradation) in more exposed places, and the prevalence of biotic litter degradation (degradation induced by dew) in more shaded places under vegetation.

All the above described model development, of a more theoretical-mathematical nature, has been complemented with two field experiments of leaf litter decomposition. These experiments have been carried out in the Iberian Peninsula, where eight holm oak woodlands have been considered in order to cover a climatic gradient. The purpose of these experiments was to study how climate and the intraspecific variability of litter quality regulate the rates of litter decomposition of a Mediterranean widely distributed tree species such as holm oak (*Quercus ilex*). Our study showed that, at a regional scale (i.e. the Iberian Peninsula), the vegetation structure (as understory cover) could play a more critical role over litter decomposition than climate. On the other hand, we found that climate, together with soil pH, exerted an indirect effect over litter decomposition shaping the intraspecific variability in holm oak litter quality, which affected decomposition rates in a similar magnitude than the environmental variability throughout the regional scale of the Iberian Peninsula. Therefore, the intraspecific variability, indirectly controlled by climate, could be a key driver of soil C cycle responses to future changes in climate, and should be taken into account to predict rates of litter decomposition by models.

To conclude, in order to improve the predictions on the soil C cycle responses to climate change and land use change, it is of upmost importance to develop mechanistic models that integrate the different levels of the complex soil system, such as its functional biodiversity and its structure. The KEYLINK model presented in this thesis is a very good example and it has shown how such an integrative representation of the soil could significantly improve the prediction potential of global change effects on soil C sequestration in terrestrial ecosystems. KEYLINK is already a functional tool that allows us to better understand the complexity of the soil system in general, and more in particular, the role of soil biodiversity on soil functioning and on soil C sequestration. Additionally, KEYLINK is also a very accessible tool, which allows new mechanisms (e.g. photodegradation, dew induced degradation) to be easily included and implemented within its functioning, and can be easily coupled to other models (e.g. vegetation models). The experimental evidences showed in this PhD thesis point at the relevance of the intraspecific variability in litter quality, which could contribute to the improvement of predictions of climate change effects on soil C cycle. Future versions of

KEYLINK can be further improved to progress in our capacity to simulate and predict key soil functions and their role on terrestrial ecosystem responses to global change.

RESUMEN

El cambio global, definido como el conjunto de cambios ambientales (por ejemplo del clima o cambios de uso del suelo) que resultan de la actividad humana y sus impactos sobre el funcionamiento del sistema planetario, amenaza la conservación de la biodiversidad terrestre y de los servicios ecosistémicos que obtenemos de la naturaleza. Por ello es de máxima importancia anticipar las potenciales consecuencias del cambio global en las comunidades de la naturaleza. Para ello es necesario mejorar nuestra capacidad de entender el funcionamiento y potencial vulnerabilidad de las comunidades naturales, así como nuestra capacidad de predecir futuras respuestas ecosistémicas ante el cambio global y sus impactos sobre servicios ecosistémicos clave tales como el secuestro de carbono (C). Sin embargo, y ante la inherente complejidad en el funcionamiento, las interacciones y los niveles de organización de las comunidades naturales que conforman los ecosistemas, predecir cómo responderán los ecosistemas frente al cambio global sigue siendo un desafío. Para poder afrontar esta complejidad, es esencial usar modelos mecanicistas para simular de forma integrada numerosos procesos y las potenciales retroalimentaciones entre ellos, pudiendo así simular de la manera más realista posible cómo los ecosistemas responderán ante perturbaciones medioambientales.

El sistema suelo es probablemente el compartimento de la biosfera más desconocido y cuyas respuestas al cambio global son más inciertas, a pesar de ser el ecosistema terrestre más biodiverso del planeta que juega un papel esencial como sumidero de carbono (el segundo más importante a escala global, solo superado por los océanos). Sin embargo, una creciente masa crítica de conocimiento sobre diferentes aspectos clave del sistema suelo, tales como el papel del flujo de C y nutrientes a través de las redes tróficas del suelo, es cada vez más accesible. También existe una creciente información sobre el papel de grupos funcionales de organismos clave en el funcionamiento del suelo en general y en el ciclado del carbono en particular, como por ejemplo las especies ingenieras del ecosistema que transforman la estructura física del suelo, las especies de detritívoros que fragmentan la materia orgánica del suelo y facilitan así la tarea de los descomponedores que mineralizan la materia orgánica, o las especies de bacterívoros y fungívoros que controlan las poblaciones de descomponedores. Sin embargo, los actuales modelos biogeoquímicos están mayormente basados en aproximaciones empíricas que no tienen en cuenta la enorme complejidad ecológica del sistema suelo, o aspectos importantes de su diversidad funcional, que se relacionan directamente con el funcionamiento del suelo, la química del suelo o la estructura física del suelo.

La representación simplista de los complejos procesos del suelo considerada en los modelos empíricos se evidencia por ejemplo en el hecho de que estos modelos tienden a subestimar las tasas de descomposición de la hojarasca en los ecosistemas áridos y semiáridos. Esto tiene un enorme impacto en las estimaciones globales de emisiones de C y de secuestro de C en suelos, ya que estos ecosistemas suponen una parte sustancial de todas las tierras emergidas. Específicamente, los mecanismos de descomposición de

la hojarasca que juegan un papel fundamental en los ecosistemas donde el agua es limitante todavía no han sido integrados en los modelos de predicción, a pesar de su evidente contribución global a las emisiones de C y el secuestro de C en suelos. Esos mecanismos de descomposición de hojarasca incluyen la degradación abiótica de la hojarasca inducida por la radiación solar (fotodegradación), o los procesos bióticos de descomposición de hojarasca usando aportes de agua que no provienen de las lluvias, como por ejemplo el rocío. Cabe esperar que la inclusión de esos mecanismos en modelos de predicción del ciclo de carbono en suelos suponga una notable mejoría en la precisión de las predicciones generadas por esos modelos. A pesar de la existencia de modelos mecanicistas específicos que simulan algunos de estos procesos y funciones, aún es necesario combinarlo todo para la simulación integrada de los procesos del suelo que regulan el ciclo de carbono. También es importante estudiar más a fondo los procesos clave en el ciclado del C en suelos que son altamente susceptibles al cambio global, tales como la descomposición de hojarasca, llevando a cabo nuevos experimentos que permitan entender mejor qué factores controlan el ciclado de C en suelos de ecosistemas áridos y semiáridos, y su potencial vulnerabilidad ante alteraciones provocadas por el cambio global tan importantes como el cambio climático o el cambio en los usos del suelo.

En esta tesis doctoral se ha revisado la complejidad del sistema suelo para integrarla en un nuevo concepto de modelo. Los tres objetivos principales de esta tesis fueron: 1) el desarrollo de un nuevo modelo mecanicista de suelo, llamado KEYLINK, integrando características de la diversidad del suelo como la estructura trófica y su diversidad funcional, cuyo papel es crucial para la estructura física del suelo y la estabilización de la materia orgánica del suelo en los ecosistemas terrestres; 2) el desarrollo en el modelo KEYLINK de una representación mecanicista de los procesos relacionados con la descomposición de hojarasca en ecosistemas áridos y semiáridos, dada su crítica contribución a las emisiones de C y el secuestro de C en suelos a escala global, aportando una segunda versión del modelo KEYLINK adaptada a este tipo de ecosistemas terrestres; y 3) el desarrollo de experimentos para entender los patrones y factores regionales que controlan la descomposición de la hojarasca en los ecosistemas semiáridos mediterráneos, con especial énfasis en estudiar los efectos del clima y de la variabilidad intraespecífica de la hojarasca sobre su descomposición.

En esta tesis se presenta una extensa revisión bibliográfica de los antecedentes sobre el papel de la biodiversidad del suelo en el ciclado de C en el suelo en general, y particularmente sobre cómo el conocimiento que existe sobre la organización trófica y la diversidad funcional puede ayudar a mejorar los modelos biogeoquímicos actuales. Toda esta información ha sido esencial para el desarrollo de KEYLINK, un nuevo modelo mecanicista basado en procesos del suelo, que integra la estructura física del suelo, la hidrología del suelo y la diversidad funcional del suelo para la simulación del ciclado de C en suelos a escala de ecosistema. La evaluación del nuevo modelo fue llevada a cabo simulando varios escenarios de perturbaciones en el ecosistema similares a escenarios de cambio global. Los resultados muestran la capacidad del modelo KEYLINK para representar de forma integrada el papel de fenómenos biológicos, como

las cascadas tróficas (por ejemplo cómo escenarios de extinción local de depredadores del sistema pueden afectar a la estructura física del suelo), sobre el secuestro de C en el suelo o las emisiones de C. Estos resultados ponen en perspectiva la importancia de tener en cuenta la biodiversidad del suelo y la complejidad de su organización a la hora de predecir futuras respuestas de los ecosistemas terrestres ante perturbaciones medioambientales derivadas del cambio global. También se extrae de estas simulaciones que la estructura del suelo es clave para explicar la estabilización física y físico-química de la materia orgánica del suelo. Además, la integración de la hidrología del suelo no solo contribuye a una mejor representación de la estabilización de la materia orgánica, sino que también facilitará el acoplamiento de este modelo de suelo con modelos de vegetación, contribuyendo a una mejora en la simulación de la hidrología del suelo y del agua disponible en el suelo. Las simulaciones resultantes también mostraron cómo el cambio global puede alterar los mecanismos de descomposición de la hojarasca, especialmente en ecosistemas áridos y semiáridos, y con efectos diferenciados entre los distintos reservorios de C en el suelo (como diferentes capas de la hojarasca). Específicamente, las simulaciones realizadas con KEYLINK mostraron cómo la incidencia de radiación solar sobre el suelo, que depende de la estructura de la vegetación, puede afectar a las tasas de descomposición de hojarasca y determinar la dominancia de los mecanismos (abióticos vs. bióticos) que controlan la descomposición de la hojarasca. Concretamente, los resultados de las simulaciones mostraron que la fluctuación espacial en la cantidad de radiación que incide sobre el suelo, debido a cambios en la cobertura vegetal, puede determinar cambios entre la prevalencia de la degradación abiótica de la hojarasca (por fotodegradación) en lugares más expuestos, y la prevalencia de la descomposición biótica de la hojarasca (inducida por rocío) en los lugares más sombreados bajo la vegetación.

Todo el trabajo de modelización descrito anteriormente, de carácter más teórico-matemático, ha sido complementado con dos experimentos de descomposición de hojarasca. Estos experimentos se han llevado a cabo en la península ibérica, donde se han tomado ocho encinares en un gradiente climático. El propósito de estos experimentos fue estudiar cómo el clima y la variabilidad intraespecífica de la calidad de la hojarasca regulan las tasas de descomposición de la hojarasca en una especie arbórea ampliamente distribuida por la cuenca mediterránea, como es la encina (*Quercus ilex*). Nuestro estudio mostró que, a escala regional (de la península ibérica), la estructura de la vegetación (como la cobertura del sotobosque) puede tener un papel más relevante que el clima. Por otro lado, encontramos que el clima, junto con el pH del suelo, ejerció un efecto indirecto sobre la descomposición de la hojarasca, determinando la variabilidad intraespecífica en la calidad de la hojarasca de encina, que afectó a las tasas de descomposición en una magnitud similar a la variabilidad ambiental a lo largo de la escala regional de la península ibérica. Por tanto, esa variabilidad intraespecífica, controlada indirectamente por el clima, puede ser un motor clave de las respuestas del ciclo de C en suelos ante futuros cambios en el clima, y debería tenerse en cuenta en los modelos a la hora de predecir las tasas de descomposición de la hojarasca.

En conclusión, para poder mejorar la predicción de las respuestas del ciclo del carbono en los suelos al cambio climático y al cambio en los usos del suelo, es de máxima importancia desarrollar modelos mecanicistas que integren las diferentes partes del complejo sistema que es el suelo, como su biodiversidad funcional y su estructura. El modelo KEYLINK que se presenta en esta tesis es un buen ejemplo, y ha mostrado cómo esa representación integral del suelo puede mejorar significativamente el potencial de predicción de los efectos del cambio global sobre el secuestro de C en suelos en los ecosistemas terrestres. KEYLINK es ya una herramienta funcional que nos permite entender mejor la complejidad del sistema suelo en general, y más en particular, el papel de la biodiversidad del suelo en el funcionamiento y secuestro de C en el suelo. Además, KEYLINK es una herramienta muy accesible, que permite que nuevos mecanismos (por ejemplo la fotodegradación o la descomposición estimulada por rocío) se implementen fácilmente, y puede ser acoplado fácilmente a otros modelos (por ejemplo modelos de vegetación). Las evidencias experimentales mostradas en esta tesis doctoral indican la relevancia de la variabilidad intraespecífica en la calidad de la hojarasca, que puede contribuir a la mejora de las predicciones de los efectos del cambio climático sobre el ciclo de C en suelos. Futuras versiones de KEYLINK pueden ser mejoradas para avanzar en nuestra capacidad para simular y predecir funciones clave del suelo y su papel en las respuestas de los ecosistemas terrestres al cambio global.

GENERAL INTRODUCTION

Background

Global change, which refers to the alterations in the earth system (e.g. climate, land use, etc.) associated with human activities, is expected to alter key ecosystem processes that regulate the terrestrial carbon (C) cycle, as soil organic matter (SOM) stabilization and SOM and litter decomposition (Allison *et al*., 2013). This is because the rates at which these processes occur determine the capacity of soils to sequester C (soil organic matter stabilization) and the rates of soil CO_2 emissions to the atmosphere (Paustian *et al*., 2000), which is a key feedback to climate change. On the other hand, projected increases in temperature together with altered precipitation regimes under climate change scenarios (IPCC, 2007) will result in increasing aridity in many regions, and its impact on soil functioning is still uncertain (e.g. Curiel Yuste *et al*., 2011; 2014). Moreover, other drivers of global change as changes in land management (e.g. tillage or no-tillage, livestock, wood extraction) alter ecosystem structure, which also influences soil functioning and the capacity of soils to sequester C (Paustian *et al*., 2000).

The role of biodiversity on soil functioning

All evidences suggest that these perturbations associated with global change are and will be affecting the structure and diversity of the biological communities that conform the soil system, which are amongst the most diverse communities on earth (Emmerling *et al*., 2002) and are composed by organisms belonging to all kingdoms of life, i.e. Prokaryota (i.e. Archaea and Bacteria), Fungi, Protista, Animalia and Plantae (as traditionally classified). Soil biodiversity is structured in different trophic levels within the food web, through which most of the C incorporated in soils flows (e.g. Andrés *et al*., 2016) before being stabilized by different processes (Six *et al*., 2002; Liang *et al*., 2011) or released as an end metabolic product, especially CO_2, which is the result of the aerobic oxidation of soil organic matter (SOM). However, state-of-the-art tools used to predict future scenarios of soil C sequestration have not yet managed to find a way to represent how this large biodiversity and its structural complexity is linked to the cycling of carbon in soils.

All this taxonomic diversity could be further classified according to different key functions, e,g. microbial communities (including prokaryotes and fungi) are the ultimate responsible of degrading litter and SOM (Allison *et al*., 2013). Other functional groups in the soil system play also relevant roles that are commonly neglected in SOM models; e.g. predators control the demography of all other fauna, affecting all the trophic interactions among the food web; and engineer species can affect all the soil processes and C fluxes, because they shape ecosystem structure by influencing pore formation, bioturbation and stabilization of SOM (Lavelle *et al*., 1997; 2007); soil faunal saprotrophs enhance microbial decomposition process by litter fragmentation, facilitating microbial accessibility to labile C compounds and nutrients otherwise physically or chemically not accessible in litter (Yang *et al*., 2012). The complexity of soil food webs and the roles that all functional groups play controlling other soil processes are crucial factors for soil C cycling and SOM stabilization, but the lack of representation of that ecosystem complexity in SOM models might be one of the

reasons why the predictive capacity of those models is generally limited (Vereecken *et al*., 2016).

The extreme complexity of those ecosystem processes and their interactions and feedbacks (**Fig. 1**) require complex mathematical tools in order to make predictions of ecosystem responses under any hypothetical scenario. Ecosystem mechanistic models are tools which mathematically represent the ecosystem functioning, and simulate how, from certain initial conditions, the represented processes will shape future scenarios in the ecosystem. Hence, mechanistic models allow us to deal with such complexity. Those models are developed using empirical knowledge and also theoretical approaches, and therefore, the accuracy of predictions relies on how deep is our understanding of ecosystem processes. Thus, in order to improve global change predictions accuracy, we need to improve our knowledge on key soil processes associated with C cycling, as it is the case for SOM and litter decomposition, and subsequently improve mechanistic representation in modelling approaches to improve predictions.

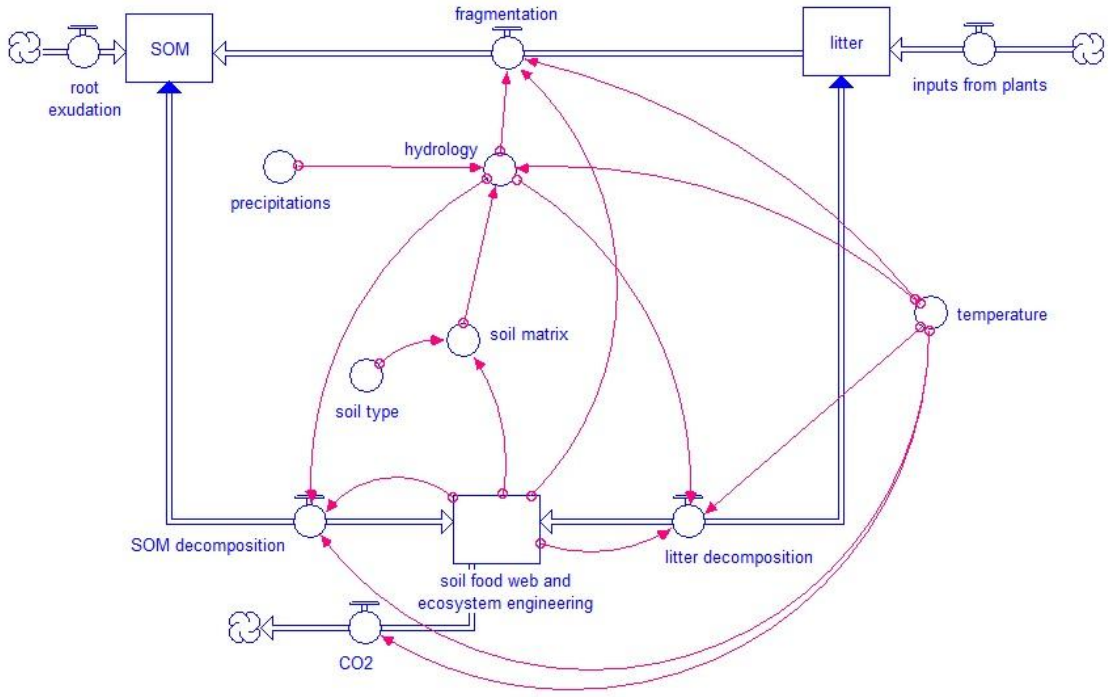

Figure 1. Ecosystem complexity and its impact in the soil C cycle. Square boxes represent pools of organic matter. Wide double-line arrows, with a circle within the arrow, represent fluxes between pools (blue arrowheads show bidirectional fluxes). Isolated circles represent abiotic factors affecting ecosystem processes, and red narrow arrows connect each factor or pool with the ecosystem parts (at the arrowheads) that are regulated by them.

Different modelling paradigms of SOM turnover and stabilization

At present, there are different 'schools' for representing SOM turnover and stabilization, with many overlapping views. Main concepts are reviewed (in chapter 1) from three main 'soil views': 1) the SOM pools-view, depicting SOM pools and their chemical characteristics as the central part of the soil (with structural and microbial effects as secondary determinants); 2) the soil structure view, emphasizing the soil structure and the role of the soil engineers thereon as the main determinant; and 3) the soil food web view, representing soil microbial and faunal food webs and their role in the flow of C and N. Moreover, main interactions between SOM, soil structure and soil biota are discussed in chapter 1, concerning soil aggregation, fate of casts, structural effects of soil engineers and the important interactions between fine roots, mycorrhizal fungi and SOM. By integrating the key processes and pools from each of these views, a new, integrative concept has been created to represent the soil, which can be included into existing models to improve them. Because of the very strict relation between accessibility of SOM, structure and soil water, it is also included a review on the soil water modelling.

Traditionally, biogeochemical models simulate and predict soil carbon cycling based on the classical paradigm of SOM pools-view, representing organic matter flowing in a cascade of C pools with increasing recalcitrance (**Fig. 2**), in which decomposition rates (k) depend on the chemical properties of the C pool and are regulated by environmental factors as temperature and humidity. Examples of those widely used models applying this paradigm are RothC (Jenkinson and Rayner, 1977), CENTURY (Parton *et al*., 1987; Paustian *et al*., 1992) or Yasso (Liski *et al*., 2005; Tuomi *et al*., 2011).

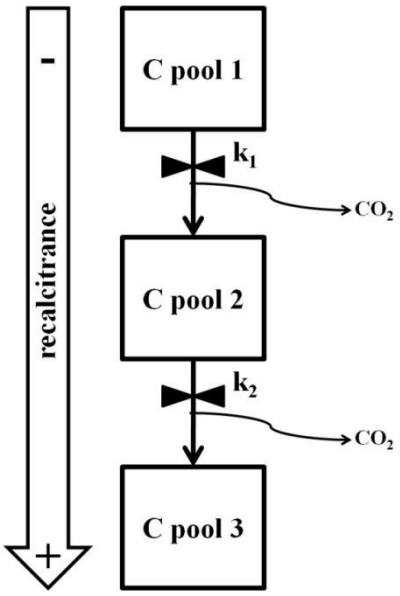

Figure 2. Simplified conceptual scheme of the classical SOM pools-view, representing organic matter turnover as a cascade of C pools with increasing recalcitrance. Organic matter in each pool is degraded at a decomposition rate (k), releasing CO_2 during the process.

A new mechanistic process-based soil model (KEYLINK) is presented in this thesis (see chapter 2), in which those three 'soil views' have been integrated in the same modelling framework, constituting an ambitious step forward to a new generation of ecosystem models. The KEYLINK model includes the representation of the soil physical structure (i.e. soil porosity), the soil hydrology and the soil food web, simulating their interactions and feedbacks, and allowing to better represent their role controlling SOM stabilization and soil C emissions.

The challenge of understanding and modelling mechanisms of litter decomposition in drylands

Soil hydrological predictions are particularly relevant in drylands, where most ecological processes (as litter decomposition) are limited by water availability (Bosco *et al*., 2016). Moreover, most empirical and mechanistic models of litter decomposition have been developed based on mesic ecosystems processes, and therefore their predictions tend to fail when applied to drylands (Adair *et al*., 2017). This is partially explained because soil microbial communities need water to conduct litter and SOM decomposition, hence models tend to simulate low rates of biotic degradation of litter under drought conditions; however, in drylands, microbial communities are adapted to drought, so they are more resilient than mesic populations (Curiel Yuste *et al*., 2011; 2014) and can conduct their metabolisms under suboptimal conditions. For instance, decomposers in drylands can use non-rainfall water sources (e.g. dew) to maintain some biotic degradation of litter (Gliksman *et al*., 2017) even under extreme drought conditions. Therefore, these local adaptations to low water availability and the subsequent humidity-enhanced decomposition of litter is a crucial process that gains relevance in drylands.

There are also strong evidences of the crucial and underestimated role of abiotic processes on litter degradation (Adair *et al*., 2017), as the degradation mediated by solar radiation (hereafter photodegradation) (Austin and Vivanco, 2006; Rutledge *et al*., 2010), or the thermal degradation due to high temperatures, which also have large contributions to CO_2 emissions (Lee *et al*., 2012) mainly from arid and semiarid ecosystems (hereafter drylands). Photodegradation largely affects litter decomposition in drylands, by direct breakdown of organic matter (Liu *et al*., 2018) but also indirectly, by facilitation biotic degradation controlled by moisture availability, as dew-induced degradation (Almagro *et al*., 2017; Gliksman *et al*., 2017). Solar radiation interacts also with vegetation coverage, which determines the fraction of radiation reaching the soil and hence the litter, and thus, ecosystem structure, which is strongly associated with how ecosystems are managed, is another factor that must be taken into account for photodegradation modelling. All this potential degradation of SOM in arid and semiarid systems remains underestimated in many models, though few models have recently begun to take this into account, e.g. DayCent (Chen *et al*., 2016). Hence, increasing the accuracy of predictions largely depends on our ability to simulate potentially important process of abiotic litter degradation and associated biotic processes, and their role in C emissions from and C sequestration in arid and semiarid systems.

Those typical SOM degradation dryland processes (e.g. photodegradation or humidity-enhanced decomposition of litter) could explain, at least partially, the discrepancies between experimental results of litter decomposition in drylands and the lower decomposition rates predicted by models (Adair *et al*., 2017; Gliksman *et al*., 2017). Therefore, they must be included in global C cycle modelling. A second version of the new model KEYLINK has been also developed to include the mentioned dryland mechanisms of litter decomposition (see chapter 3). This second version was parameterized for a Mediterranean ecosystem, and those dryland processes of litter decomposition were simulated for several scenarios of increasing temperatures and decreasing precipitations, together with changes in vegetation cover, in order to evaluate the model predictions of soil C cycle responses to global change.

Regional-scale drivers of litter decomposition in Mediterranean ecosystems

There is no doubt that litter decomposition, as one of the main sources of CO_2 emissions to the atmosphere (Lee *et al*., 2012), is a crucial process that must be well understood, and particularly in drylands, where models fail to simulate it correctly (Adair *et al*., 2017). Moreover, these systems will be especially vulnerable to climate change, as they are expected to suffer severe disturbances by increases in temperatures and aridity (Giorgi and Lionello, 2008). However, to date there is still large uncertainties on which controlling factors determine rates and variability of litter decomposition in drylands; hence, improving modelling simulations of C dynamics in drylands requires a deep understanding of the key processes controlling litter decomposition. More experimental research is, therefore, needed to deepen the drivers and processes of litter decomposition. Additionally, plant can alter their chemistry and recalcitrance in response to climatic stress (Ford *et al*., 1979; Gindl *et al*., 2000), which implies that under global change scenarios litter quality of the species might be altered (León-Sánchez *et al*., 2020). In particular, in Mediterranean forests with low tree diversity, local adaptation and phenotypic plasticity driven by climatic variability and, more particularly, under varying water regimes, result in very high intraspecific variability in leaf functional traits of the dominant tree species (Ramírez-Valiente *et al*., 2010). Because of that, to study at which extent intraspecific variability in litter quality may affect decomposition rates at regional scales could help to predict future responses of the soil C cycle to future changes in climate and land use.

Holm oak (*Quercus ilex*) is the tree species most widely distributed in the Iberian Peninsula, covering a wide regional climatic gradient. This wide distribution of holm oak points to this tree as a good model for the study of the potential role of litter intraspecific variability and climate as drivers of regional variability in litter decomposition rates. In chapter 4 two experiments on holm oak litter decomposition in Mediterranean forests are presented addressing that issue. Experiments were designed to improve our knowledge on litter decomposition controlling factors such as climate or intraspecific variability in litter quality, taking into account the regional variability of these factors within the area of distribution of this species in the Iberian Peninsula.

AIMS AND STRUCTURE OF THE THESIS

This thesis constitutes a contribution to improving our ability to predict soil C cycling under global change scenarios, by 1) exploring the state-of-the-art in our understanding of the soil system, by confronting classical versus modern views of, e.g., how soil biota or mechanisms of SOM stabilization should be represented in models according to scientific evidences; 2) using the gained knowledge to develop, calibrate and implement a new mechanistic process-based soil model, called KEYLINK; 3) developing a second version of the KEYLINK model including key mechanisms of litter decomposition in drylands; and 4) developing regional-scale experiments to deepen large scale trends and drivers of litter decomposition in semiarid ecosystems. The main goal is to provide this new state-of-the-art predictive tool as a stand-alone model, which captures soil complexity and can be used to simulate C dynamics in the soil of any terrestrial ecosystem. Another important goal is to develop this model so that its subsequent coupling to other models (e.g. vegetation models) can be relatively easy. This is an important goal to further improve the soil representation in ecosystem-scales simulations. KEYLINK model is intended to introduce some novel concepts into soil modelling, as the physical and physico-chemical protection of SOM within soil particles, going beyond the more traditional concepts of SOM degradability regulated only by its chemical properties, as its recalcitrance. For that purpose, KEYLINK model links key parts of the soil system, from different soil sciences as the community ecology of the soil food webs, the geology of soil structure and the ecohydrology. Therefore, this new model could become a powerful tool for C cycle predictions in terrestrial ecosystems.

This thesis is structured in four chapters, preceded by general introduction and methodology, and followed by the general discussion and conclusions. The chapters and their contents are structured as follows.

Chapter 1 – Towards a more integrative soil representation for inclusion in ecosystem scale models

A review is presented on factors controlling SOM stabilization and turnover, as the soil structure, soil hydrology and soil organisms that are part of the food webs. Interactions between soil structure and engineer species are key processes shaping water and C flows through the soil, which highlight the crucial roles played by soil fauna and microbial communities controlling litter and SOM turnover in soils, but this remains neglected in many ecosystem models used to predict soil C cycle. The integration of soil structure with the role of soil biodiversity is needed for a better understanding of soil processes, and for that it is also presented the background of previous modelling approaches to include those processes into models. This chapter constitutes a first step towards the improvement of soil representation in ecosystem modelling, presenting a new model concept.

Chapter 2 – KEYLINK, a new mechanistic soil model

In order to improve predictions of SOM and litter decomposition in soils, a new mechanist process-based soil model (KEYLINK) has been developed. This model includes soil food web, variability in soil structure and ecohydrology as main processes controlling C cycle in the soil. The background reviewed in the previous chapter has been included in KEYLINK model, simplifying the food web in 9 functional groups: bacteria, non-mycorrhizal fungi, mycorrhizal fungi, bacterivores, fungivores, detritivores, engineer species (which shape soil structure), herbivores and predators. On the other hand, soil structure has been represented through the pore volume between soil particles, which determines water flow through the soil and trophic interactions in the food web. The first version of the model was calibrated for a Scots pine forest in Brasschaat (Belgium). In order to evaluate the model outputs, six different scenarios were simulated, showing potential ecosystem responses under altered conditions. The main hypothesis here is that the modelling of interactions between soil structure, hydrology and soil food web offers an improved way to represent SOM and litter turnover, required for a new generation of ecosystem models.

Chapter 3 – Drought and abiotic degradation of litter modeled as key drivers of C dynamics in drylands with a second version of KEYLINK model

This chapter presents a second version of the new model, adapted for drylands. This is because litter decomposition in drylands is controlled by some mechanisms (e.g. photodegradation) that are negligible in mesic ecosystems. Hence, models that do not include those specific processes tend to underestimate litter decomposition in these ecosystems. *KEYLINK drylands* version includes the key role of solar radiation and drought stress in soil C dynamics. Shortwave radiation from the solar radiation reaching the top litter layer promotes abiotic degradation of litter (photodegradation), which may also potentially affect microbial communities exposed to light (photoinhibition) if communities are not adapted to this intense shortwave radiation; then, *KEYLINK drylands* allow the user to simulate litter decomposition with or without potential photoinhibition of microbial communities under high exposition to solar radiation. Additionally, vegetation cover determines the fraction of solar radiation reaching the soil, and that is included in this new version, allowing to simulate also the effects on soil C dynamics of different land managements that shape vegetation structure. Moreover, the drought-related mechanisms have been further developed in this version, including also key adaptations of microbial communities such as the use of non-rainfall water sources. *KEYLINK drylands* has been calibrated for a Mediterranean-type ecosystem in Ramat Hanadiv (Israel). As in the previous chapter, simulation outputs are presented showing the responses predicted by the model under different scenarios, in order to test the hypothetical high relevance of the dryland mechanisms on litter decomposition.

Chapter 4 – The roles of climate and litter intraspecific variability on decomposition of holm oak litter in the Mediterranean region

The last chapter is an experimental approach to investigate potential regional-scale drivers of litter decomposition in drylands. The study was developed in eight holm oak (*Quercus ilex*) forests distributed over a broad geographical and climatic gradient in the Iberian Peninsula. Moreover, being interspecific variations in litter quality one of the main drivers of decomposition rates, we here explored the potential relevance of the intraspecific variability of litter quality using holm oak as a model-species, very representative in the Mediterranean landscape. Climate and land management were tested as potential factors shaping that intraspecific variability in litter quality, and their roles as controllers of rates of litter decomposition. Therefore, another novel approach of this thesis is to study the roles played by climate and land management shaping C cycle in drylands, e.g. through their potential effects on intraspecific variability in litter quality. Additionally, we analyzed the importance of plant-microbes co-evolutionary trends leading to a faster decomposition of the litter in its environment of origin (at 'home') than in a foreign environment ('away'), a hypothesis known as *home field advantage* (HFA). Overall, the main goal of this study was to contribute with empirical data to future improvements in soil modelling.

GENERAL METHODOLOGY

Modelling part

Model development

The new mechanist process-based soil model, KEYLINK, has been developed from the background reviewed in chapter 1, integrating the simulation of the soil food web with the soil structure, hydrology and their interactions controlling organic matter dynamics (**Fig. 3**). In chapter 2 all the mathematical development of the model is presented.

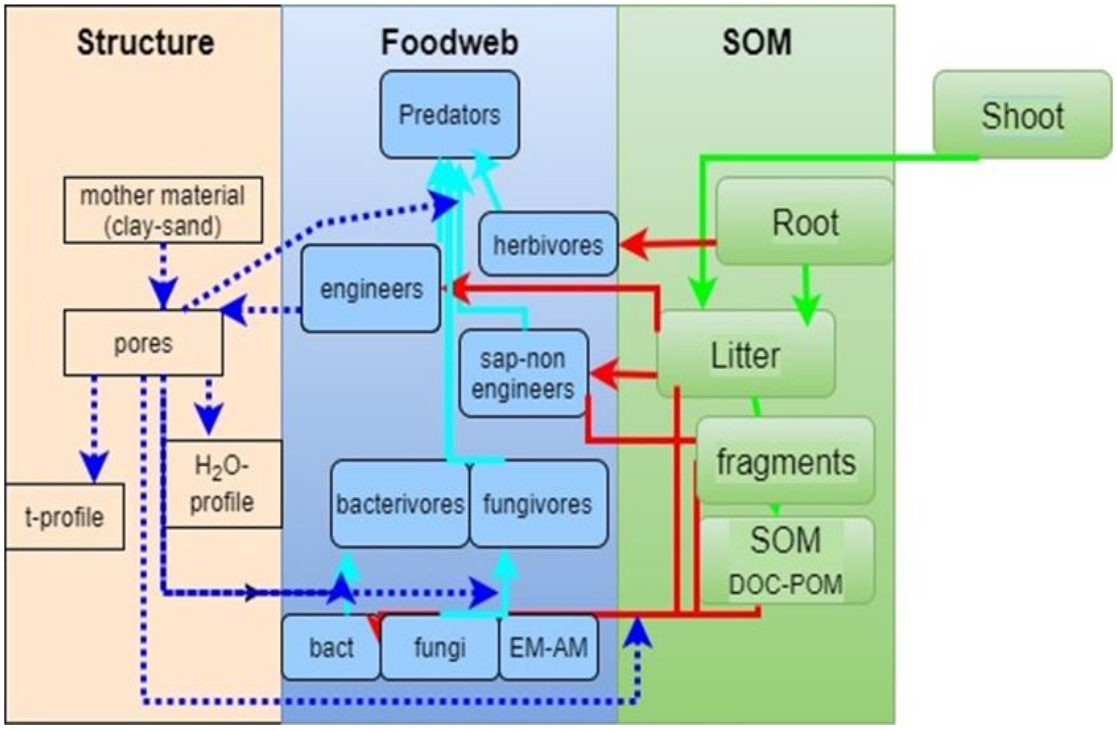

Figure 3. Model concept scheme. Soil structure and soil food web controlling soil organic matter (SOM) dynamics. C pools include inputs from plants, litter, SOM, dissolved organic C (DOC) and particulate organic matter (POM), with green arrows indicating C fluxes between those pools. Red arrows indicate C fluxes entering in the food web (including saprotrophs (sap), bacteria (bact) and mycorrhizal fungi (EM-AM)). Light blue full arrows indicate C fluxes among the food web. Dashed arrows indicate soil structure effects on hydrology, soil temperature (t) profile, or C fluxes, and also the engineering feedback to soil structure.

The new model has been programmed in Python, as a free downloadable code that can be easily used, and even modified by any user in case someone wants to replace any function. All code files are available at https://github.com/Plant-Root-Soil-Interactions-Modelling/KEYLINK, together with the text files that provide the input parameters that can be changed to simulate different scenarios. Soil C pools in the model have been represented in 13 categories (**Table 1**), including 9 functional groups in the soil food web.

Number	Symbol	C pool
1	B_b	bacterial biomass
2	B_f	fungal biomass
3	B_{myc}	mycorrhizal biomass
4	B_{bvores}	biomass bacterivores
5	B_{fvores}	biomass fungivores
6	B_{det}	biomass detritivores
7	B_{eng}	biomass engineers
8	B_{hvores}	biomass herbivores
9	B_{pred}	biomass predators
10	L_{surf}	aboveground litter
11	SOM	total soil organic matter
12	B_{root}	biomass roots
13	R	respiration (CO_2)

Table 1. Carbon pools in the KEYLINK model. Pools of the soil food web (1 – 9) represent different functional groups. Organic matter pools (10 and 11) and roots (12) are C sources for the food web. Respiration (13) is an output flow from all the food web groups.

Model parameterization

The first version of KEYLINK model has been parameterized for a Scots pine forest stand situated in Brasschaat, in the Campine region in Belgium (51°18' N and 4°31' E). The soil is sandy but with high ground water table so trees are generally not water-limited, but the topsoil is often dry. The soil is acidic (pH 3.5). The trees were planted around 1930 and formed a rather sparse vegetation in 1999, with leaf area index (LAI) ranging from 2.1 to 2.4.

For this model run, we used the following input data from the stand (**Table 2**). In this case, we did not use measured or modeled growing trees but constant input of aboveground and belowground litter to show how the KEYLINK model works by itself. Brasschaat forest data concerning the top 90 cm of soil was analyzed in 1999 by Janssens *et al*. Earthworm biomass is extremely low due to the low pH, it was not measured since 1993 by Muys, but these data are used since there is no reason to expect there was a marked change.

Variable	Unit	Value	Reference
Earthworm biomass	g C m^{-3}	200	Muys (1993)
pH		3.5	Janssens *et al*. (1999)
Sand	%	93	Janssens *et al*. (1999)
Initial SOM	g C m^{-3}	11470	Janssens *et al*. (1999)
Initial litter	g C m^{-3}	2680	Janssens *et al*. (1999)
Fine root biomass	g C m^{-3}	400	Janssens *et al*. (2002)
Fine root litter	g C m^{-3}	300	Janssens *et al*. (1999)
Fine root growth rate	g C m^{-3} $year^{-1}$	210	Janssens *et al*. (2002)
Annual litter fall	g C m^{-3} $year^{-1}$	400	Horemans *et al*. (2017)
Fine root turnover	g C m^{-3} $year^{-1}$	740	Based on Janssens *et al*. (2002)
C input to mycorrhiza	g C m^{-3} $year^{-1}$	197	Assumed based on Deckmyn *et al*. (2014)
Microbial C as HWC	g m^{-3}	1338.21	Gaublomme *et al*. (2006)

Table 2. Initial input data. Data from Brasschaat Scots pine forest (Belgium). Microbial C pool was estimated as hot water extractable C (HWC).

Data availability on soil pools, biology and functioning is generally low, and it is currently not possible to find a dataset describing in detail, and with small error margins, the temporal evolution of all different soil biological compartments and SOM pools. Available data are often incomplete, or based on rough estimates, e.g. from semiquantitative DNA analysis for microbial abundance in soils. To deal with this issue, a quite pragmatic approach combining different estimates from different sources is appropriate for most datasets where the soil is not the key focus, but a means to improve the simulation of an ecosystem.

Model calibration

Once the model is parameterized for an ecosystem, the next step is to optimize that model, calibrating the fit of its simulations to the ecosystem data. The optimization included in the KEYLINK model follows a Bayesian procedure as described by Van Oijen (2008). The Bayesian method allows the determination of model parameters and their uncertainties by combining (1) prior information about parameter values and uncertainty and (2) experimental observations of output variables. The prior parameter information can be obtained directly from measurements or it can be derived from the literature. We calibrated the model applying the Bayes' Theorem that in a simplified form can be written as:

$$p(\theta \mid D) = c \cdot p(D \mid \theta)\, p(\theta), \qquad (1)$$

where $p(\theta \mid D)$ is the posterior distribution of the parameter value θ, c a constant $(1/p(D))$, $p(D \mid \theta)$ is the likelihood function for θ and the factor p(θ) the prior distribution for θ (Van Oijen *et al*., 2005). The data likelihood function is determined by the probability errors in observations. We assumed that errors are uncorrelated and normally distributed with zero mean (Van Oijen *et al*., 2005). To avoid rounding errors, the logarithm was determined as follows:

$$\log L_i = \sum_{j=1}^{n} \left(-\frac{1}{2} \left(\frac{D_j - f(\theta_j)}{\sigma_j} \right)^2 - \frac{1}{2} \log(2\pi) - \log(\sigma_j) \right) \qquad (2)$$

Where D_j is the observed data in sampling year j, $f(\theta_j)$ is the simulated value, and σ_j the standard deviation of the model error. Practically, the posterior parameter distribution was estimated in a non-analytical way following Van Oijen *et al*. (2005). Model calibration was run more than 20000 times (for each version, the first and the second adapted to drylands) with different parameter settings sampled from the prior parameter distribution, using the version of Markov Chain Monte Carlo (MCMC) known as the Metropolis-Hastings random walk with reflection algorithm (Christian and Casella, 1999; Van Oijen, 2008).

The goal is to walk through parameter space (prior distribution) in such a way that the collection of visited points forms a sample from of the calibrated parameter values (posterior distribution). This Bayesian calibration scheme generates a chain of accepted parameter values and corresponding model output.

A pragmatic assumption is that the starting values of the C pools (including the soil fauna initial biomass) are at steady state for a given data (most often spring or summer). The simplest calibration of any ecosystem can be done by assuming these 11 carbon

pools (litter, SOM and the 9 functional groups in food web) need to be stable over the simulated years, e.g. for 9 years that gives us 99 data points by taking the same value for each C pool every year (**Table 3**). Initial litter, SOM and biomasses of bacteria, fungi and engineers were taken from the references cited in **Table 2**. For other C pools, data were estimated using measured data for previous C pools and similar proportions between C pools as in the Swedish pine forest in Persson *et al*. (1980); predator biomass was assumed to be the 20% of all biomass in their consumed C pools. Errors were assumed as a percentage of biomass, 10% for predators, 12.5% for litter and SOM, and 20% for the rest C pools.

C pool	Value (g C m^{-3})	Error (g C m^{-3})
$\mathbf{B_b}$	15.1	3.02
$\mathbf{B_f}$	15.1	3.02
$\mathbf{B_{myc}}$	160	32
$\mathbf{B_{bvores}}$	0.1	0.02
$\mathbf{B_{fvores}}$	0.8	0.16
$\mathbf{B_{det}}$	0.6	0.12
$\mathbf{B_{eng}}$	0.2	0.04
$\mathbf{B_{hvores}}$	0.2	0.04
$\mathbf{B_{pred}}$	0.4	0.04
$\mathbf{L_{surf}}$	2680	335
SOM	11470	1433.75

Table 3. Calibration data. Data of C pools (see **Table 2**) used for the model calibration. Values were used once per year during calibration at days 180, 545, 910, 1275, 1640, 2005, 2370, 2735 and 3100.

It is common to apply a correction ("burn-in") deleting part of the posterior, e.g. the first half of the runs, to avoid the effect of the starting distribution (Gelman and Shirley, 2011). A Latin Hypercube Sample (LHS) (Mckay *et al*., 1979) was taken from the posterior after the burn-in, which consisted in a representative sample of one hundred parameter vectors. LHS was used for all further model runs, so every run was performed with 100 different parameter sets.

Model implementation

Although coupling KEYLINK to real or simulated data of the aboveground ecosystem would yield more realistic results, in this exercise we used KEYLINK as a stand-alone model with quite constant input (e.g. litter, plant water uptake) to minimize the feedback effects and give a clear view on the model behaviour. This is a model evaluation, not a full model validation.

After calibration to the Brasschaat dataset, a set of scenarios was performed to evaluate the model: I. Basic results; II. Sensitivity to initial soil structure; III. Changing initial litter CN ratio; IV. Changing initial litter recalcitrance; V. Changing soil pH; VI. Excluding predators.

Scenario I was done with the reference input parameters (**Appendix 2**), and used as a basal one to be compared with the other five alternative scenarios: scenario II with higher clay content in the soil (clay 15%); scenario III with lower litter CN ratio (40); scenario IV with lower litter recalcitrance (20%); scenario V with higher pH (5.9); and scenario VI without predators by setting its initial biomass to 0 (B_{pred} = 0).

In each one of the five alternative scenarios, input parameters were the same than in the basal scenario, except for the parameter changed to generate the new scenario (see **Appendix 2**). All the six scenarios were run 100 times using the LHS, as mentioned before, consisting each run in a simulation of 10 years at a daily time-step (3653 days). Then, averages of biomass were calculated for each C pool among the 100 simulations of 10 years, for each scenario, comparing the effects of disturbances on average values.

KEYLINK drylands

The second version, KEYLINK drylands, was parameterized for a Mediterranean-type shrubland in the Ramat Hanadiv Nature Park, on Carmel Ridge in Israel (32º30' N and 34º550' E), at 120 m above sea level. The soil is red brown Terra rosa over hard limestone. Reference data for the calibration was used from a litter decomposition experiment conducted during one year in that ecosystem by Gliksman *et al*. (2017). Climatic variables from Ramat Hanadiv meteorological station were downloaded at http://www.meteo-tech.co.il/hanadiv_new/hanadiv_en.asp, for the same time period of the experimental data (from March 17, 2012, to March 27, 2013); variables were daily values of precipitation (mm), mean and minimum temperatures (ºC), maximum relative humidity (RH, %), and daily solar insolation (MJ m^{-2}). The calibration followed the same mathematical methods explained before for the previous version of the model, but using as reference data the results from the mentioned litter decomposition experiment (see chapter 3 for a detailed methodology). After the calibration, the same climatic parameters from Ramat Hanadiv meteorological station were downloaded for a period of ten years (from March 1, 2009, to February 28, 2019), and used to run 10 years of simulation for each scenario, evaluating the model predictions of changes in litter decomposition mechanisms in response to changes in temperature, precipitation regime or vegetation cover.

Experimental work

Litter decomposition experiments

Finally, litter decomposition experiments were conducted in eight holm oak forests and open woodlands (Spanish 'dehesas') distributed over a broad geographical and climatic gradient in the Iberian Peninsula (**Fig. 4**), in the Spanish provinces of León, Navarra, Lérida, Madrid, Cáceres, Ciudad Real, Almería and Alicante. The site in Ciudad Real was placed in the Cabañeros National Park, the site in Alicante was in the Font Roja Natural Park, and the site in Cáceres was a private land near to Monfragüe National Park. Those eight sites were chosen to represent broad gradients of climate, management and soil properties along Spain, with warmer and drier weathers in the South, and more acidic soils in the West. Regional climate varied from oceanic (Navarra) to semiarid (Alicante), being continental Mediterranean in most cases, with typical hot and dry summers, and rainfalls mainly concentrated during spring and autumn.

Figure 4. The eight holm oak forests selected for the litterbag experiments. Names indicate the Spanish province of each forest. In red, Cabañeros National Park (province of Ciudad Real), where a common garden experiment was placed, and the forest of origin of the uniform holm oak litter used in the litterbags distributed by the forests in the other seven provinces (in blue).

The litter decomposition experiments followed the litterbag methodology (Bocock and Gilbert, 1957). Holm oak leaf litter from the experimental sites was incubated in the field inside litterbags (**Fig. 5**), and collected during one year (from autumn 2016 until autumn 2017) after four, eight and twelve months, allowing to calculate the decomposition rates for all intervals between the beginning of the experiments and the three sampling times. The litterbags were made of green polypropylene of 20×20 cm side and 1.9×1.9 mm mesh size, and each litterbag was filled with 5g of litter from a single procedence site. Two experiments were conducted during the same year: a common garden experiment (1), and a gradient experiment (2).

The common garden experiment (1) was set up in Cabañeros National Park (Ciudad Real), using litterbags filled with litter from ten origins, i.e. all the sites except Madrid, and four litter types from four origin plots in Cabañeros (characterized by different land managements and ungulate grazing pressures), testing the effects of intraspecific variability in *Q. ilex* litter quality on litter decomposition rates. The characteristics of each litter origin site were used to evaluate the factors controlling variability in *Q. ilex* litter quality.

Figure 5. Litterbags on the field, in the experimental site in the province of Cáceres, at the beginning of the experiments in 2016.

The experiment 2 was conducted over the climatic and land use gradient in the Iberian Peninsula to study the roles of climate and forest structure controlling litter decomposition rates. For that, uniform holm oak litter from Cabañeros was translocated inside litterbags to the other seven sites. Additionally, in three of those sites (i.e. León, Navarra and Cáceres) extra litterbags were placed with local litter (i.e. litter collected in the same site). This allowed to compare litter decomposition rates of local and translocated litter, testing the HFA hypothesis.

Initial chemical composition of litter was analyzed for all litter procedences, determining the recalcitrant fractions (% dry mass) of lignin, cellulose and hemicelluloses according to Van Soest method (Van Soest, 1963), and the nutrient content (mg g^{-1}dry mass) for carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), iron (Fe), zinc (Zn), copper (Cu) and sodium (Na) by inductively coupled plasma optical emission spectroscopy (ICP-OES) determination. Another two variables were calculated for the structural C (sC), as the sum of lignin, cellulose and hemicellulose, and its complementary the non-structural C (nsC), i.e. the labile compounds.

Statistical analyses are explained in detail in chapter 4. Briefly, all the potential explanatory variables of litter decomposition rates in each experiment, i.e. litter quality in experiment 1, and climate and forest structure in experiment 2, were tested with Spearman pairwise correlations. Subsequently, linear mixed-effect models (LME) were done to find the best predictors of decompositions rates, as well as the predictors of intraspecific variability in *Q. ilex* litter quality. These results were combined in a structural equation model (SEM) to represent the ecosystem complexity controlling litter quality and, therefore, decomposition rates.

Chapter 1

Towards a more integrative soil representation for inclusion in ecosystem scale models

ABSTRACT

The relatively poor simulation of the below-ground processes is a severe drawback for many ecosystem models, especially when predicting responses to climate change and management that impact nutrient and water-availability through effects on the soil. For a meaningful estimation of ecosystem production and the cycling of water, energy, nutrients and carbon, the integration of soil processes and the exchanges at the surface are crucial. It is increasingly recognized that soil biota play an important role for soil organic carbon and nutrient cycling, for soil structure and hydrological properties through their activity, and for metabolic and plant uptake processes of nutrients, such as mycorrhizal processes.

Main biological actors and soil functions are reviewed, and to what extent they can be included in ecosystem models. Key issues in improving ecosystem-scale soil representation in models are the representation of the soil food web, the impact of soil faunal engineers on soil structure, and the related effects on hydrology and soil organic matter (SOM) stabilization as related to its accessibility by microbial organisms.

Finally, we describe a new core model concept (KEYLINK) that integrates insights from SOM models, structural models and food web models to simulate the living soil at an ecosystem scale.

INTRODUCTION

Soils are multi-scale complex systems with long-lasting resilience as well as rapid response to disturbance, but with limited regeneration and buffering capacities after mismanagement. Soil degradation is caused by industrial and agricultural activities, deforestation, overgrazing, pollution, and overexploitation for fuelwood (Oldeman *et al*., 1991). Decline of soil organic matter (SOM) threatens soil fertility, productivity and food security, as well as the stabilization or reduction of atmospheric CO_2 levels (Gobin *et al*., 2011). It also accelerates the loss of above and belowground biodiversity across ecosystems.

Mechanistic models can be useful both to increase our understanding of this complex system, by integrating knowledge gained from numerous experiments, and to allow predictions of how soils could change in future and in response to, e.g., management and/or climatic changes.

For stand/ecosystem predictions, a very limited number of soil empirical models are generally used, mainly based on CENTURY, RothC, and Yasso (Campbell and Paustian, 2015). Essentially, these models describe the soil as consisting of homogeneous horizons, where SOM transformation occurs in a cascade from easily degradable to passive or stable SOM based on its chemical complexity/degradability (**Figure 2** in the general introduction). Equations are based on first-order kinetics (depending on pool size) where decay-rate constants are controlled by the initial litter quality (mostly represented as CN ratio or recalcitrance) and modified by temperature and humidity. This representation can adequately be parameterized to simulate a stable soil under unchanging conditions, but cannot explain differences in functioning between soils concerning C and nutrient cycling, plant nutrition and hydrological processes, nor represent changes due to climate, management or pollution. It is also more representative of well-mixed arable lands than of natural soils that have developed horizons.

In recent years, insights into how soils function has increased and the knowledge to improve ecosystem-scale soil modelling is available. Recently, research on SOM dynamics has made substantial progress by new conceptual approaches and methodological developments, e.g. biogeochemical and physical analyses, molecular and microbial ecology, and novel visualization tools. Vereecken *et al*. (2016) reviewed the key soil processes and the existing models, covering different scales and from a wide range of soil science disciplines. They clearly demonstrate the need to include the contributions of the different ecological compartments involved in SOM dynamics, e.g. microbes and fauna, and a revised and more realistic representation of SOM stabilization processes, SOM degradability and SOM pools, in order to obtain a wider understanding of the soil.

Schmidt *et al*. (2011) highlighted the importance of the microbial biomass as key actors in SOM turnover and stabilization. There is increasing evidences that SOM stabilization depends more on accessibility by decomposers than by chemical composition of the

SOM itself (Schmidt *et al*., 2011; Cotruffo *et al*., 2013). In addition, Filser *et al*. (2016) and Lavelle *et al*. (2016) showed the importance of including some representation of soil fauna. The most important aspect appears to be the engineering actions by specific faunal groups (earthworms, ants, termites) that not only incorporate plant residuals into the soil and mix up soil layers (bioturbation) but also change the soil structure by creating biopores and biostructures (e.g. casts, aggregates) that greatly affect soil hydrology and/or the activities of other soil organisms. Furthermore, it is also increasingly evident that understanding the architecture of the complex soil food webs is key to determine the functioning of soil biota and their influence on SOM dynamics (e.g. de Vries *et al*., 2013).

The importance of soil structural modifications on SOM stabilization mediated by soil biota has stimulated the development of models including the explicit representation of structural effects on SOM, which improve predictive capacity without explicit representation of soil fauna (Kuka *et al*., 2007). Komarov *et al*. (2017) and Chertov *et al*. (2017a, b) recently proposed a new, complex, mechanistic soil model which incorporates many of these ideas (ROMUL), which however, requires very detailed parameters and measurements, which hinders its application at large scales and its coupling to ecosystem models.

Main new insights in soil science are reviewed here, with special emphasis in the role of soil biota as a major factor influencing the structure of soils, the dynamics of C and N, as well as the soil hydrological cycle. Key processes that can be included in ecosystem models are discussed. To that end, the latest knowledge of key soil processes is reviewed, in terms of chemical SOM concepts, more structurally based concepts, insights into the fine root and mycorrhizal fungal interactions, as well as the key soil faunal actors and how they interact in the soil food web, at a stand-scale. Existing models for nutrient (mainly nitrogen, N) and water availability to plants, as well as soil C sequestration and leaching, are assessed. Finally, a new model concept is proposed, by extracting the most relevant processes and the minimal community complexity required to understand and predict the overall functioning of the soil concerning C and nutrient cycling from SOM and hydrological functioning. Prediction of the faunal food web or microbial biomass is not the goal of this model concept, but a means to improve predictions of soil C and nutrient cycling and hydrology, as well as our understanding of soil functioning in relation to climate change and management.

REVIEW ON KEY POOLS, PROCESSES, AND EXISTING MODELS

Classical and new paradigms of SOM turnover and stabilization

Soil organic matter is derived from decomposition and transformation of plant (above- and belowground litter) and animal remains (detritus) and organic products (e.g. root exudates). The fate of SOM is primarily determined by a complex interplay of its chemical properties, the composition and activities of soil organisms, abiotic conditions, and different stabilization mechanisms in soil (Stockmann *et al*., 2013; Paul, 2016).

Traditional soil models used to predict biogeochemical cycling such as RothC (Jenkinson and Rayner, 1977), CENTURY (Parton *et al*., 1987; Paustian *et al*., 1992) or Yasso (Liski *et al*., 2005; Tuomi *et al*., 2011) define soil organic matter as a cascading number of pools with different intrinsic decomposition rates. Intrinsic decomposition rates can usually be associated with pools having specific chemical and physical properties, and are modified by abiotic parameters such as temperature and moisture (Liski *et al*., 2005; Dungait *et al*., 2012). Such models are good at describing the decay of litter and have been well validated with data derived from litterbag studies (Liski *et al*., 2005). While pools associated with labile, easy degradable compounds (e.g. sugars) have a fast decay, pools associated with lignified compounds have a slow decay. Several models assume SOM pools associated with the most recalcitrant compound groups (e.g. humic substances and lignin) and chemical protection (e.g. SOM-clay complexes) to account for a long-term stabilization of organic matter in soil (Smith *et al*., 1997).

However, the concept of long-term SOM stabilization due to chemical recalcitrance has been increasingly questioned (Schmidt *et al*., 2011; Dungait *et al*., 2012; Cotrufo *et al*., 2013; Lehmann and Kleber, 2015). There is a growing evidence showing that patterns of spatial inaccessibility against decaying soil organisms, or stabilization by interaction with mineral surfaces and metal ions (von Lützow *et al*., 2006) seem to play a more important role in long term stabilization of SOM than chemical recalcitrance (Kleber *et al*., 2011; Schmidt *et al*., 2011; Lehmann and Kleber, 2015). Modern analytical methods could not prove humic substances to be persistent in soil (Schmidt *et al*., 2011; Lehmann and Kleber, 2015). It rather seems that SOM is a continuum of decomposing substances and even recalcitrant humic compounds can decay rather quickly (Lehmann and Kleber, 2015). In fact, it is increasingly accepted that chemical recalcitrance is primarily important in early stages of litter decomposition (von Lützow *et al*., 2006; Marschner *et al*., 2008). Decay rates of plant litter for example, are usually inversely related to their lignin to N ratios, suggesting slow decomposition at high lignin contents (Melillo *et al*., 1982; Zhang *et al*., 2008; Prescott, 2010). Furthermore, recent studies have highlighted that, rather than plant litter *per se*, microbial products from the transformation of plant litter are the largest contributors to stable SOM (Mambelli *et al*., 2011; Cotrufo *et al*., 2013; Gleixner, 2013).

The accessibility of the SOM to microbes due to pore size and the capacity of microbes to oxidize SOM based on the strength of the organo-mineral bondings are two different

mechanisms involved in SOM stabilization and SOM dynamics, but it is possible to model the stabilized SOM as either one of these fractions, because they are closely linked. Organic matter (OM) bound to a clay mineral can be simulated as chemically stabilized, or can be seen as in such close contact to the mineral that there is no space for microbes and microbial exoenzymes to physically reach the OM. It can therefore be said that the most important mechanism for SOM stabilization over longer time scales is the physical separation of organic compounds from the organisms able to degrade or transform them, e.g. in anoxic or dry pore space areas or within aggregates (von Lützow *et al*., 2008). Soil structure and its dynamics are thus the most important factors controlling SOM turnover and sequestration, whereas chemical recalcitrance is only a secondary determinant.

While traditional ecosystem models represent physical and chemical stabilization of C in the soil as an implicit property of the most passive (inert) SOM pool, only a few models explicitly account for stabilization mechanisms for SOM (e.g. adsorption, aggregate inclusion) (Stockmann *et al*., 2013). Almost all models relate clay content to the stable SOM pool. However, the Struc-C model (inspired by RothC), for example, describes the interaction among organic matter and soil structure through the incorporation of aggregation and porosity submodules (Malamoud *et al*., 2009). Also Stamati *et al*. (2013) introduced a coupled C, aggregation, and structure turnover (CAST) model to simulate macro- and micro-aggregate formation and the stabilization of particulate organic matter (POM). Chemical protection by adsorption onto mineral surfaces is dynamically represented in the COMISSION model (Ahrens *et al*., 2015). However, aggregate formation modelling remains a difficult issue at the stand scale because many of the processes occur at a much smaller scale.

The CIPS model (Kuka *et al*., 2007) modified the classic empirical SOM pools taking into account soil structure effects. It is based on a quality-driven primary stabilization mechanism (recalcitrance of SOM) and a process-driven secondary stabilization mechanism (site of turnover) of SOM in soil. In addition to the division of SOM into the qualitative pools on the basis of chemical measurability, it takes into account different turnover conditions depending on pore space and accessibility for microbial biomass. The main assumption of the CIPS model is that the biological activity is not evenly distributed through the whole pore space. The pore space classes (i.e. micro-, meso- and macropores) used in the model are marked by wilting point, field capacity and pore volume. Because of the poor aeration in the micropores they show very low biological activity, leading to a strong protection of the C localized in this pore space. This results in the reduction of the turnover activity, related to soil temperature, humidity, soil texture, relative air volume and distance to the soil surface. Simulation results show that the bulk density variations have a severe impact on C storage (Kuka *et al*., 2007). Besides a validation of the CIPS model for long term experiments representing a wide range of soils and site conditions (Kuka *et al*., 2007), it was shown that the conceptual pool of inert SOM (used in many models) can also be described as the amount of C situated in micropores. Consequently this new approach is more generally applicable

than the soil texture based approaches (Körschens, 1980; Rühlmann, 1999) applied so far, where clay content is used to estimate the stable SOM pool.

Dissolved organic matter as key element of the SOM dynamics

Another key element of the SOM dynamics is the dissolved organic matter (DOM), being a very important component of the C cycle of the soil. Most DOM is derived from litter and humus degradation (Kalbitz *et al*., 2000; Guggenberger and Kaiser, 2003). Recent studies showed that subsurface DOM is linked to recent plant material, whereas in deeper layers it consists of older, more processed substrates, mainly derived from microbial turnover (Kaiser and Kalbitz, 2012). Besides the OM derived from decaying litter and microbial turnover, direct exudation from plant roots can be an important source of organic C in the soil, up to 7% of photosynthates (Haller and Stolp, 1984), with very important effects on the surrounding zone. Due to its mobility, DOM is important for the C and nutrient transport in and between ecosystems and for the contribution to soil forming processes (Kalbitz *et al*., 2000; Kaiser and Kalbitz, 2012).

Modelling perspectives for DOM

Because DOM can leach from soils and can move between soil layers, it is, therefore, important to model DOM separately. A number of models such as LIDEL (Campbell *et al*., 2016) include the explicit simulation of DOM. A detailed dynamic model (DyDOC) for predicting metabolic transformations of SOM components and the transport and sorption of DOM in different soil horizons with different soil properties was developed and tested by Tipping *et al*. (2001, 2012). DyDOC models within each soil layer the transport of water, metabolic transformations of organic matter, and sorption of potential dissolved organic C (DOC), though it does not include soil biology. DOC can be controlled by sorption to minerals and co-precipitation with Al (or Ca), all governed by the soil acidity (Guggenberger and Kaiser, 2003). For this reason, mineral weathering rate should be considered in the models predicting DOC solubility.

However, the pathways, sorption and desorption processes of the different compounds of DOM and essential nutrients like nitrogen and phosphorous are extremely complex, and as such hard to include in a simple soil model. There are detailed surface complexation and ion-exchange models which deal with these processes (Weng *et al*., 2008; Duputel *et al*., 2013). Models for soil weathering and for adsorption processes that ultimately explain the soluble nutrients available to plants exist, but are complex and require many parameters, e.g. PhreeqC (Parkhurst and Appelo, 2013). In Bortier *et al*. (2010) a relatively simple empirical model within the soil model ANAFORE is used to distinguish adsorbed and soluble P based on pH, without concretely simulating different base cations. Dzotsi *et al*. (2011) developed a more complex model for P availability that goes beyond the scope of this PhD thesis as it requires extensive parameterization.

Each soil type has associated a distinctive physicochemical environment and development pathway of the soil profile, which affects the chemical composition and stability of soil organic C (SOC) in mineral horizons (Rumpel *et al*., 2004; Rumpel and

Kögel-Knabner, 2011), by affecting both the living conditions and activity of soil decomposers but also through a distinctive physical and chemical protection. One of the main soil forming processes involved in chemical SOM stabilization, especially in deep mineral soils, is the 'podzolization', which involves a transport of DOM, Al and Fe in solution from the surface to deeper horizons. The process consists of a phase of mobilization and of immobilization of these compounds (Lundström *et al*., 2000). General conditions that favour podzolization are the absence of sufficient neutralizing divalent cations due to the presence of parent materials with low amounts of weatherable minerals (Ca^{2+}, Mg^{2+}), an impeded decomposition of plant litter due to low temperatures and high rainfall conditions that favour the transport of DOC (along with Al/Fe) down the profile (Van Breemen and Buurman, 2002). Moreover, the nutrient poor status and high acidity typical of this soil type tends to decrease faunal activity which subsequently impedes vertical mixing of the soil and favours vertical differentiation and accumulation of partially decomposed plant residues in the topsoil (Rumpel *et al*., 2002; Van Breemen *et al*., 2002). Although few studies have reported data on C stability comparing different soil types, some of the published information suggests that stabilization processes may be soil-type specific and therefore depend on pedological processes (Rumpel *et al*., 2004; Rumpel and Kögel-Knabner, 2011).

Integrating soil hydrological cycle into biogeochemical modelling

There is a close interaction between SOM, soil structural stability, water/gas balance, and the size and connectivity of pores as ecological habitats in soil. On one hand, water content, water potential and water activity are key parameters controlling biological activity. Water is essential for all soil processes (chemistry, biology, physical transport of DOM and nutrients) and the physical separation of habitats at low water contents supports the vast diversity of soil microorganisms. In turn, microorganism activities may stabilize (Six *et al*., 2004) or destabilize aggregates and hence affect soil porosity or, under extensive microbial growth, may even result in pore clogging (Seki *et al*., 1998); they thus affect structural soil properties and water flow through the soil matrix. They also influence the chemical composition of soil by formation, transformation and degradation of SOM as well as by inducing weathering of minerals (Uroz *et al*., 2009). Soil processes associated with C and water cycling are thus closely interlinked (Six *et al*., 2004).

Water availability or water activity in soil is limited by water potential, which in soil is mainly controlled by the adhesion forces to solid particles (matric potential), which, together with the cohesion forces between water molecules, drives capillarity. Water matric potential is considered to be a major controlling factor of SOM turnover (Thomsen *et al*., 1999). It affects the physiology of microorganisms and many critical mass transfer processes in the pore space: diffusion of soluble organic matter, exoenzymes and gasses, and motility of microbial cells (Or *et al*., 2007). These mass transfer processes can limit microbial access to organic matter at low water contents and, as a consequence, affect its turnover rate. However, soils are adaptive systems and within microbial communities, organisms have developed different strategies to

mitigate the effect of these barriers (Torsvik and Ovreas, 2002; Mills, 2003; Allison, 2005).

Modelling perspectives for soil hydrology

A large number of soil models of varying levels of complexity and dimensionality are now available to describe the basic physical and chemical processes affecting water flow and solute transport in the subsurface environment. Many models that describe the soil-plant-atmosphere continuum still use simple capacity based soil water flow models to quantify the terms of the water balance. The main motivation for using these capacity based models is their simple parameterization. They describe water flow in soils as mainly driven by gravitational forces where each soil layer spills over to the lower soil compartment once a critical soil moisture content has been reached (spilling bucket models). This critical soil moisture content is often defined as field capacity and is routinely measured in soil surveys. Soil water storage capacity of a specific compartment can be thus emptied by downward flow, surface runoff, deep drainage, and evapotranspiration processes. Since gravitation is the dominant potential controlling water flow, specific parameterization needs to be included in order to account for capillary rise from a groundwater table into the root zone and lateral flow processes (Guswa *et al*., 2002). However, this method tends to overestimate soil water in the top layer and underestimate drainage.

More advanced soil models nowadays use Richards' equation and the convection-dispersion equation (Jury and Horton, 2004) to describe water and solute movement through soil. Soil models describing water flow based on Richards' equation provide more flexibility in incorporating the full complexity of water flow in the soil-plant-atmosphere continuum and its impact on spatially distributed abiotic and biotic processes, including capillary rise, though at a high computational cost. Many of these processes are characterized by a large spatial and temporal variability with locally distributed hot spots and hot moments. However, these more advanced 3D features are harder to parameterize. To address parameterization difficulties, PedoTransfer Functions (PTFs) have been developed that allow predicting soil properties and soil parameters that control abiotic and biotic processes. Soil horizons, texture, qualitative structural and morphological information, organic matter content, pH, redox and mineral concentrations are soil properties that can be used in PTFs to quantify soil properties and gain information on functions, e.g. soil hydraulic functions, mineralization constants, sorption properties and ecosystem functions such as providing water and nutrients to plants and regulating biogeochemical cycles (Bouma, 1989; McBratney *et al*., 2001; Vereecken *et al*., 2016; Van Looy *et al*., 2017).

The presence of macropores and other structural heterogeneities can generate flow instabilities and cause preferential flow and transports (Hendrickx and Flury, 2001; Jarvis *et al*., 2016; Beven, 2018). Due to preferential flow, water and solutes may move faster and deeper into the soil profile than what would be predicted by Richards' equation, so models using this equation tend to underestimate leaching. These macropores are in many cases the consequences of biotic processes, such as earthworms

burrowing and growing roots. Modelling approaches for preferential and non-equilibrium flow and transport in the vadose zone were reviewed by Šimůnek *et al*. (2003). Extensions have been made to consider preferential flow and transport in models based on Richards' equation (Šimůnek *et al*., 2003; Köhne *et al*., 2009). Yet, these models contain several uncertainties due to a lack of observational data at the pore scale and to the inherently dynamic macropore system in soils being subject to physical (swell/shrink, freeze/thaw), biological (variations in soil faunal and microbial activity, root growth, rhizosphere processes) and man-made disturbances (e.g. tillage practices). Continuous advances in both numerical techniques and computation power are now making it increasingly possible to perform comprehensive simulations of non-equilibrium flow processes in the vadose zone. Such simulations, especially if paired with exhaustive field data sets (e.g. by data assimilation), are vital for better understanding and quantifying the effects of heterogeneities, fractures and macropores on flow and transport at the field scale (van Genuchten *et al*., 1997; Šimůnek, 2003).

Challenges in predicting soil water flow and solute transport beyond laboratory scale include: soil parameterization, handling structured soils including preferential flow, handling soil heterogeneity, temporally changing properties (e.g. soil bulk density, structural properties, etc.), and description of root water uptake. Thus, it is clear that although the importance of soil structure and water are proven, their inclusion in models is hampered because of the lack of data on soil structure and the difficulties in measuring and simulating soil water. An approach to integrate soil structure and its related effects on soil water flow is presented in chapter 2, allowing to simulate the subsequent effects of hydrology on SOM accessibility and turnover.

The role of the soil food web

The soil comprises a rich and very diverse community of organisms. To be able to cope with this high diversity, species have been grouped into functional groups, under the assumption that if species occur at the same location in the soil and share the same resources and predators, they should perform the same function. Research has so far focused on the importance of each one of these functional groups to the ecosystem, but this highly specialized information is not integrated into the more plant-based ecosystem models.

It has long been known that litter decay is faster in presence of a more complete soil fauna (comparison between small and larger mesh size litterbags) (reviewed by Frouz *et al*., 2015). Also, the major roles of soil engineers for bioturbation are well described (Rasse *et al*., 2006; Filser *et al*., 2016), which add to the effect of soil fauna to decomposition processes. Recent publications have shown the importance of the diversity of soil organisms in relation to soil functioning and stability, both in the laboratory and in the field (reviewed by Deng, 2012; Wagg *et al*., 2014). It has been shown that an intact soil food web is important for ecosystem functioning influencing decomposition, nutrition retention and nutrient cycling (Bengtsson *et al*., 1996; Phillippot *et al*., 2013). In addition, the soil food web is sensitive to management. Ploughing, soil compaction, removing litter and obviously the use of insecticides are

deleterious to the soil faunal community (Wardle *et al*., 1995; Yeates *et al*., 1997), with repercussions for soil processes. Such major negative effects on soil organisms are ignored in the most widely used models, that thus cannot realistically simulate these management effects.

To develop a model that is as simple as possible, it is important to review all soil network biotic inhabitants to determine which can be defined as keystone species, and which can be grouped together to reduce the web complexity. In the following sections, we therefore review the main players of the soil, i.e. microorganisms (size 1 – 100 µm), microfauna (< 0.1 mm), mesofauna (0.1 – 2 mm) and macrofauna (> 2 mm), as well as fine roots (< 2 mm) that are the main primary source of soil C. Simulating larger vertebrate fauna (mice, moles, rabbits, some birds) is beyond the scope of this thesis. All size groups of soil fauna include organisms of different trophic level and functional significance. Nevertheless, microbivore soil fauna are usually small-sized members of micro- and mesofauna, whereas ecosystem engineers belong to the macrofauna. In this review we will classify the organisms mainly by function and food source, not by size, but we describe for each functional group which organisms belong to it. All biota effects on the main soil functions necessary to simulate SOM and nutrient flows are described. **Table 1** summarizes how the different functional groups impact on porosity as linked to aggregation (meso- and micropores), macroporosity, SOM turnover, nutrient availability, and C influx into the soil. Since the goal is to understand how to include these organisms in a model we also review, where possible, data on the biomass of the group and of their contribution to the C cycle.

	Main functions						
Biota	micro- and meso-porosity	macro-porosity	SOM turnover	SOM input	fragment.	Plant nutrient uptake	bioturbation
Bacteria	++		+++			***	
Fungi	++		+++		+	***	
Mycorrhizal fungi	++		++	++	+	+++	
Bacterivores	**		***			*	
Fungivores	**		***			*	
Predators	**	*	**	*	*	*	*
Engineers	++	+++	+		+++	*	+++
Detritivores			+		+++	*+	+
Fine roots	+	++		++		+++	
Herbivores		*		**	++		

Table 1. Importance of different functional groups of soil biota on key soil processes linked to ecosystem functioning. Fragmentation is abbreviated as fragment. Cross symbols (+), in red, represent direct effects, while asterisk symbols (*), in blue, represent indirect effects. More symbols and more intense colour indicate a stronger effect (either direct or indirect).

Soil microorganisms

The soil microorganisms, including bacteria, archaea, fungi and protozoa are the primary enzymatic degraders of organic matter, which ultimately determines both the rate at which nutrients become available to plants and the amount of C stored in soils (Mambelli *et al*., 2011; Cotrufo *et al*., 2013; Gleixner, 2013).

Mycorrhizal fungi

Mycorrhizal fungi are a group of soil fungi that form symbiotic relationship with vascular plants (Smith and Read, 2008). Mycorrhizal fungi provide host plants with nutrients and improve biotic and abiotic stress tolerance (Smith *et al*., 2015; Pozo *et al*., 2015), often leading to increased plant diversity and productivity of the host plants (van der Heijden *et al*., 2008; 2015). Mycorrhizal fungi require C from their host plants to grow and form hyphae (mycelium) extending into the soil to take up water and nutrients (mainly N and P) that are subsequently transferred to their plant hosts (Smith and Read, 2008). While the nutrient to C exchange rates are highly variable, on average in gaining

ca. 75% of their required N, plants trade 15% – 30% of their C. For the fungi, this represents their entire required C at a cost of 40% of their N (Hobbie and Hobbie, 2006; Smith and Read, 2008). The C transfer from the plant to the mycorrhizal hyphae can occur quickly, contributing up to 30% of the total respiration in soil (Söderström and Read, 1987).

Structurally, there are several different types of mycorrhizal interactions (mycorrhizae). The most common types are the ectomycorrhizas (EM fungi), with high number of taxa and a low number of plant partners but dominant in many ecosystems; arbuscular mycorrhiza (AM fungi) with a low number of taxa but a high number of plant partners; and ericoid (ErM fungi) and orchid mycorrhizas (OrM fungi), which are restricted to plants in the Ericaceae and Orchidaceae families respectively. With an estimated 5 billion tons of C flux from plants to AM fungi per year (Bago *et al*., 2000), they make up a significant proportion of the belowground labile C pool (de Vries and Caruso, 2016). In one gram of forest soil, tens to hundreds (50 – 800) of meters of EM mycelia can be found, representing 20 – 30% of the total soil microbial biomass (Söderström, 1979; Leake *et al*., 2004; Ekblad *et al*., 2013). Mycelial biomass corresponding to EM fungi can range from 100 to 600 kg ha^{-1} (Wallander *et al*., 2004; Cairney, 2012; Hendricks *et al*., 2016) or up to 1.5 Pg of AM fungal biomass globally (Treseder and Cross, 2006). Mycorrhizal fungi also contribute to soil structure and aggregation (Lehmann and Rillig, 2015) while senescing hyphae provide C to the soil (Wilson *et al*., 2009). They also play a role in water absorption and transport (Johnson *et al*., 2012) even between multiple trees or seedlings (Warren *et al*., 2008).

For the plants, AM fungi are thought to be more important for uptake of P and mineral or other readily available N, whereas some EM and ErM fungi are able to break down SOM to obtain nutrients, mainly N (Moore *et al*., 2015; de Vries and Caruso, 2016). Thus, mycorrhizal fungi can play key roles in mobilizing organic N trapped in the SOM for plant primary production (Rineau *et al*., 2013; Shah *et al*., 2016). The EM fungal mycelium can retain in its biomass high proportion of N (Lindahl *et al*., 2007) which can prevent up to 50% of nitrate leaching losses; reductions of organic N and P leaching have also been reported. The uptake and immobilization of N by EM fungi may also aggravate and stabilize a state of strong N limitation in nutrient poor forests (Näsholm *et al*., 2013; Franklin *et al*., 2014). It has also been proposed that EM fungi compete with the decomposer community for organic N and restrain activities of saprotrophs (Bödeker *et al*., 2016). This is known as the Gadgil effect (Fernandez and Kennedy, 2015) and results in a decrease of the nutrient content of SOM, reduced SOM decomposition and an increase in soil C (Orwin *et al*., 2011; Averill *et al*., 2014; Averill, 2016).

Modelling perspectives for mycorrhizal fungi

EM and AM fungi are the most common types of mycorrhiza and it is therefore reasonable to include them in general soil/ecological models (Treseder, 2016). Several models have been developed to include mycorrhizal symbiosis (reviewed by Deckmyn *et al*., 2014), but they are rarely included in ecosystem models. Examples of models at

an ecosystem level are the MoBilE and Mycofon models (Meyer *et al*., 2010; 2012) that have been implemented into a forest growth model, the C accumulation model MySCaN by Orwin *et al*. (2011), an AM fungal distribution model proposed by Schnepf and Roose (2006), the mycorrhiza C partitioning model described by Staddon (1998), and the EM forest model by Franklin *et al*. (2014). These models represent the symbiotic trade of C and mineral nutrients between plants and fungi, which is modelled in different ways. The most parsimonious approach is based on the assumption that fungi only transfer N that is taken up in excess of their own N demands to the plants (Näsholm *et al*., 2013; Franklin *et al*., 2014). Recently, de Vries and Caruso (2016) have developed a conceptual model for the soil food web considering the ability of EM fungi to decompose SOM by extracellular enzymes (Read and Perez-Moreno, 2003; Phillips *et al*., 2014), previously only attributed to non-mycorrhizal fungi. Using a mechanistic model, Baskaran *et al*. (2017) showed that capacity of EM to decompose SOM leads to reduced soil C, increased tree growth and a shift in the balance between microbial groups.

In summary, while the key role of mycorrhizal fungi in providing nutrients to plants in exchange for C is relatively well understood, this is not true for effects of mycorrhizal fungi in SOM decomposition. Because of the global importance of mycorrhizal symbiosis and the large C and nutrient fluxes involved, more research on these effects are urgently needed. As far as the uptake of nutrients is concerned, it is not unrealistic to simulate mycorrhizal fungi as 'part' of the plant fine roots. However, the main drawback is that only mineral N and P can be taken up by the plant, whereas in reality mycorrhizal fungi can also obtain nutrients from recalcitrant SOM and thus play a vital role in the SOM dynamics of the soil (Deckmyn *et al*., 2014).

Non-mycorrhizal fungi

Fungi are an important component of the soil ecosystem functioning, especially regarding the organic matter decomposition (van der Wal *et al*., 2013). Fungi can be of two distinct forms: spherical cells (yeasts) or long thread like structures called hyphae or mycelium (filamentous fungi). Filamentous fungi are of particular importance in terrestrial ecosystems as they allow an extended exploration of soil via their hyphal system, penetrating solid substrates (van der Wal *et al*., 2013). Hyphae are also very efficient in the translocation of water since they can help bridging air-filled pores (Curiel Yuste *et al*., 2011) and nutrients across nutrient-poor patches and to supply growth limiting elements to zones of metabolic activity (Frey *et al*., 2000; Gupta and Germida, 2015). Their abundance averaged 1×10^5 cm^{-3} soil (Bardgett and van der Putten, 2014). It was estimated that about 1.3 to 10.9 µg of fungal biomass is formed per g soil per day, corresponding to about 0.06 to 0.48 µg N immobilized into fungal biomass (Bottomley *et al*., 2012). Filamentous fungi are fundamental to C decomposition of terrestrial organic matter; it was estimated that fungal respiration can account for 65% of the total microbial soil respiration (Joergensen and Wichern, 2008). The major function of fungi in soil is the degradation of more recalcitrant SOM. Their ability to decompose this fraction of the SOM is due to a combination of morphological

(hyphal growth form) and physiological (extracellular enzymes) characteristics (van der Wal *et al*., 2013).

Bacteria and Archaea

Prokaryotic abundance can vary between 4 to 20×10^9 cells cm^{-3} soil (Bardgett and van der Putten, 2014). Several studies have shown that at least half of the soil microbial populations are respiratory active (Lennon and Jones, 2011). Bacteria were found to contribute about 35% of the total heterotrophic soil respiration (Joergensen and Wichern, 2008), and their contribution relative to fungi depend mainly on the chemical composition of the SOM. The classic understanding about the distribution of the microorganisms (especially Bacteria and Archaea) is that everything is everywhere (Baas-Becking, 1934). However, recent studies showed that, contrasting with the classic understanding, bacterial species are restricted in their global distributions due to variations in climatic, soil and plant conditions (Bardgett and van der Putten, 2014). The common view is that there is a high functional redundancy within the soil communities for nutrient mineralization, and changes in community structure rather than changes in species richness play a role in soil and ecosystem functioning (Bardgett and van der Putten, 2014). Nevertheless, for most ecosystem scale purposes the classic understanding is adequate.

Bacteria also play a central role in the production and immobilization of inorganic and organic N. Moreover, microbial biomass contributes directly to the pool of soil organic N through its death and turnover (Bottomley *et al*., 2012). It is estimated that about 0.28 to 28 μg N is assimilated into bacterial biomass (into protein) per g soil and per day (Bottomley *et al*., 2012). Much of the organic material is degraded by microorganisms carrying out aerobic respiration. However, when organic matter is transported to zones in the soil where oxygen is low or inexistent, it will be mineralized by anaerobic processes by bacteria. In soils where sulphate and/or other electron acceptors are low, CO_2 will be reduced anaerobically by bacteria, producing methane, the end product of CO_2 reduction. Global methane emissions reach 600 Tg CH_4 $year^{-1}$, and it is estimated that water-saturated soils such as peat and rice soils contribute to about 55% of the total methane emissions (Le Mer and Roger, 2001).

Because of their size (0.3 – 5 μm), bacteria often reside in pores and inner surface of aggregates as micro-colonies of about 2 – 16 cells (Gupta and Germida, 2015). Higher colonization of bacterial cells is restricted to hot spots with higher available C, such as the rhizosphere or the outer surface of freshly formed aggregate (Foster, 1988). Several studies reported an influence of the physicochemical characteristics (water potential, nutrient and oxygen availability) on the ecology of the bacterial community (Six *et al*., 2004), which links well with the concepts of the structural availability of SOM.

SOM mineralization: bacteria versus fungi

The ratio of fungal to bacterial biomass is highly variable (between 0.007 and 0.34) among different biomes (de Vries *et al*., 2006; Fierer *et al*., 2009). Generally, forests ecosystems have a higher fungal to bacterial biomass ratio than grasslands. Particularly

high fungal to bacterial ratio was observed in temperate coniferous forest soils, whereas deserts had the lowest ratio (Fierer *et al*., 2009). Land use changes and agricultural intensification have been shown to shift a fungal-dominated to a bacterial-dominated food web (de Vries *et al*., 2006). For example, in a study comparing the resistance and resilience of the soil food web to drought, the fungal-based food web of an extensively managed grassland and the processes of C and N it governs were more resistant to drought than the bacterial-based food web of an intensively managed wheat field (de Vries *et al*., 2013). Modelling of these two systems revealed that the fungal-based network had a greater evenness that mitigated C and N loss, which made the system more adaptable to drought than the bacterial-based food web (de Vries *et al*., 2013).

Through evolution, bacteria and fungi have undergone niche differentiation in the decomposition of organic materials. Typically, fungal hyphae are better adapted to nutrient-poor niches in soil than bacteria in searching for the heterogeneously distributed nutrient resources (Boer *et al*., 2005). A classic view is that during evolution of terrestrial microbial life, fungi have become specialists in decomposing structurally complex organic matter, such as lignin (recalcitrant litter and SOM), while on the other hand, bacteria have been able to maintain a significant role in the degradation of simple substrates (Boer *et al*., 2005). However, for both complex and simple substrates, competition between fungi and bacteria exists, especially for limiting nutrients such as N (Bottomley *et al*., 2012).

Plant roots exude substantial amounts of simple and easily degradable organic molecules. Classically, due to the high abundance of bacteria in the rhizosphere, it was assumed that these easily degradable plant exudates were almost exclusively degraded by bacteria (e.g. Jones, 1998). However, using stable isotope probing, a significant contribution of fungi in the degradation of root exudates was observed (Treonis *et al*., 2004). These studies also revealed that fungi are the most the active group in the degradation of easily degradable compounds in acid soils and at high substrate loading rates, probably due to their superior osmotic stress tolerance (Griffiths *et al*., 1998). Moreover, the degradation of cellulose, the most abundant organic compound on Earth (30 – 50% of plant dry mass), can take place in both aerobic and anaerobic conditions. Aerobic cellulose degradation is widespread within the fungal and bacterial communities (Boer *et al*., 2005; Baldrian and Valášková, 2008). Both aerobic bacteria and fungi produce hydrolytic enzymes, which convert cellulose into glucose (Mansfield and Meder, 2003). Competition for cellulose between fungi and bacteria is high. However, it is considered that most of the degradation of cellulose is performed by fungi, the hyphal growth strategy being particularly well adapted to access the cellulose fibres, which are often embedded in a matrix of other structural polymers, such as hemicellulose and lignin. Contrastingly, in anoxic environments, due to bacterial tenure of cellulosomes allowing enzyme activities to take place directly in their cell, bacteria are almost exclusively responsible for the cellulose degradation (Lynd *et al*., 2002). On the other hand, lignin degradation is largely, but not exclusively, done by white-rot fungi (Leonowicz *et al*., 1999) though ligninolytic capabilities that have been reported for Proteobacteria (Bandounas *et al*., 2011; Tian *et al*., 2014) and Actinobacteria

(Abdel-Hamid *et al*., 2013). The decomposition of lignin needs specialized enzymes (Bödeker *et al*., 2009), and occurs strictly under aerobic conditions. However, most studies dealing with lignin degradation focus on single strains under laboratory conditions, and therefore a better understanding of lignin degradation and involved C fluxes through the microbial food web is still needed, in particular under field conditions.

Modelling perspectives for fungi and bacteria

Litter decay rates depend on litter chemistry (e.g. lignin content), but also on microbial activity and the amount of microbial biomass. The recognized importance of microbes in the formation of stable SOM has led to the introduction of a new generation of biogeochemistry models such as MIMICS (Wieder *et al*., 2014; 2015) and LIDEL (Campbell *et al*., 2016). These models explicitly represent the soil microbial community and its role in SOM dynamics; dead microbial biomass is the main contributor to SOM, and litter enters the SOM pool primarily via its transformation/incorporation by microbes (Wieder *et al*., 2014; 2015; Campbell *et al*., 2016; Grandy *et al*., 2016). Microbial activity is modified by temperature and a variable growth efficiency parameter. There has been some effort to include microbial biomass (Neill and Gignoux, 2006), microbial activity (Todd-Brown *et al*., 2012) and diversity (Treseder *et al*., 2012) into soil carbon models which confirms the interest of including microorganisms in soil C and N dynamics models. Incorporating information about microbial diversity is, however, controversially discussed (Nannipieri *et al*., 2003; McGuire and Treseder, 2010; Nielsen *et al*., 2011; Graham *et al*., 2014). The diversity of soil microorganisms (e.g. species richness and relative contribution of each species to the community composition) is vast, with a high level of functional redundancy in C and N transformations, which makes it difficult to explicitly integrate the microbial diversity in soil C and N models (Louis *et al*., 2016). Also the soil module of the ANAFORE model (Deckmyn *et al*., 2011) incorporates microbial decay, but the described SOM pools are similar to traditional models such as CENTURY (i.e. accessible versus recalcitrant, or slow, intermediate and fast pools).

Bacteria and fungi are known to have specific affinities to decompose plant litter and other SOM compounds, and they are often modelled as separate pools, because their physiological differences induce contrasting C and N stoichiometries, and their relative abundance influences C and N dynamics at the ecosystem scale (Waring *et al*., 2013; Louis *et al*., 2016). Concerning size, bacteria, because of their smaller size (< 1 µm), can access SOM in smaller pores than hyphal fungi (5 – 10 µm diameter). Some models have attempted to include microbial functional types in C and N models. In these models, selected groups of microorganisms with distinct functional traits have been integrated (Fontaine and Barot, 2005; Perveen *et al*., 2014; Riley *et al*., 2014; Wieder *et al*., 2014). Active decomposers in soils consist of heterotrophic aerobic bacteria and fungi having copiotrophic (nutrient rich environment) and oligotrophic growth strategies (Goldfarb *et al*., 2011). Including only three functional groups of microbes (mycorrhizal and non-mycorrhizal fungi and bacteria) substantially underrepresents observed functional diversity in soils (Goldfarb *et al*., 2011), but the use of multiple

SOM decomposing microbial functional groups have not been explored to date, which would be necessary to develop more complex models (De Graaff *et al*., 2015). Recently, Lehmann and Kleber (2015) argued that the development of models built on microbial ecology should omit any emphasis on substrate quality and especially the proposed large 'humified' organic compounds. They suggested instead moving beyond conceptual pools having different turnover times and combining soil physical principles into soil biological processes.

In our view, in many cases it can be enough to distinguish between fungi and bacteria assuming the former are more oligotrophic and the latter copiotrophic. Based on the very fast lifecycle of bacteria, and the 'everything is everywhere' hypothesis that states that when conditions change the bacterial community will change as well, the bacterial community can switch to an anaerobic life style. Simulating the fungal/bacterial ratio is important because of their differential contribution to SOM decay, and can be related to differences in pH sensitivity and ability to decay recalcitrant SOM similar to the approach in ROMUL (Chertov *et al*., 2017a, b). Since the reaction of microbes to changes in their environment is extremely fast, calculating population dynamics is less relevant at the time scales interesting for ecosystem studies. Assuming they are, at any given time, in balance with the available C sources is a reasonable assumption. It is clear that for soils with significant periods or layers in anaerobic conditions, this ought to be included in models, as the role of bacteria is fundamentally different under anaerobic conditions, but for most ecosystems it can be ignored. Moreover, the important role of bacteria in the N cycle as denitrifiers or N-fixing bacteria can be modelled, and this would certainly be necessary if closing the N budget of an ecosystem is required (Treseder *et al*., 2012; Levy-Booth *et al*., 2014).

Microbivores

Microbivores are animals that feed on the soil microflora, i.e. bacteria, Archea and fungi. Proper simulation of their effects in a food web SOM model is crucial because they are the primary controls of bacterial and fungal biomass and activity. A recent review revealed that, although on average, the presence of active bacterivores reduces soil microbial biomass by 16%, they increase soil respiration by 29%, plant biomass by 27%, and shoot N and P contents by 59% and 38%, respectively (Trap *et al*., 2016). In other words, the flow of C and N through soil, and possibly other elements, from the bacterial and fungal pools to the SOM pool and to plants is controlled by the size, activity and efficiency of microbivores.

Microbivores are generally divided between bacterial feeding and fungal feeding animals. Bacterial feeding organisms are generally small (mostly microfauna) and include notably nematodes such as Cephalobidae and free-living protozoans such as amoebae and flagellates (Blanc *et al*., 2006). Fungal feeders include families of nematodes which use a stylet or spear to penetrate fungal hyphae of saprophytic or mycorrhizal fungi (Yeates *et al*., 1993). Mites and collembolans (mesofauna) are also important grazers of bacteria and fungi, but not exclusively, as they also consume other food sources such as plant litter (Brussaard, 1997). In general, larger animals will tend to ingest plant litter and soil together with microbes. Pausch *et al*. (2016), using ^{13}C

labelling, found 51mg C bacterial feeders and 68mg m^{-2} fungal feeders in an arable maize field.

Although microbivores have probably little impact on soil structure, the opposite is not true, as soil structure is thought to have a large influence on the predation potential of microbivores. For example, Cephalobidae nematodes have a much higher impact on bacterial community composition and biomass in large pores than in the bulk soil, presumably because bacterial feeding nematodes cannot access pores smaller than 10 μm (Blanc *et al*., 2006). Likewise, microbial biomass and diversity is highest in microaggregates while nematode abundance and diversity is highest in large macroaggregates (Zhang *et al*., 2013). It is therefore likely that changes in soil structure with both SOM content and activities of soil fauna engineers induce a feedback mechanism on microbivores. As far as DOM is concerned, there are several studies showing that microbivore soil fauna can increase the rate of N leaching (Williams and Griffiths, 1989; Setälä *et al*., 1990; Toyota *et al*., 2013). Similarly, Liao *et al*. (2015) compared microbial feeding fauna-accessible and non-accessible litterbags and found that microbivores decreased the CN ratio in DOM. One possible explanation is that faunal grazing can reduce microbial immobilization of N (Carrera *et al*., 2011). This change in CN ratio of DOM can affect the rate of decomposition in the soil.

Modelling perspectives for microbivores

Microbivore functions in soils should be taken into consideration in our efforts to improve SOM models for predicting soil fertility and C sequestration. Many of the needed parameters have been evaluated for some organisms, but the number of studies is still too limited to reliable quantify the overall effect of microbivores on ecosystem functioning (Trap *et al*., 2016). Nonetheless, initial values from these studies might be enough to start exploring their effects on soil C, N and P dynamics. Predicting microbivore effects in specific environments remains difficult (Trap *et al*., 2016), but a first effort targeting generic simulation of effects would be of great value. The diversity of soil fauna feeding on the microorganisms and, at least for some of them, the non-specificity of their diet pose two challenges in terms of modelling. First, it is not clear if a common parameterization can be used for one generic pool of microbivores. For example, do fungal and bacterial feeders have a similar CN ratio, respiratory quotient, generation time and mortality rate? Although it is certainly not the case, standard parameters across a wide spectrum of organisms should be investigated. For example, microbivore composition has been reported to affect neither trophic-level biomass nor the response to increased resource availability (Mikola, 1998). The second challenge is that larger soil fauna, i.e. mesofauna, do not feed exclusively on the soil microflora but might also digest litter, thereby creating an overlap between potential model pools of detritivores, on the one hand, and microbivores, on the other hand. The modelling concept based on nutrient stoichiometry developed by Osler and Sommerkorn (2007) is also relevant for microbivore microorganisms as well as for larger soil faunal predators.

It is clear that the microbivore fauna require more attention in our studies, so their role can be adequately represented in SOM models. Given the current limited data, they can

be simulated as a link between the microbial biomass and the larger predators and detritivores. These links and their importance in terms of SOM flows are largely determined by pore size distribution, and we would suggest therefore to simulate only the micro-fauna microbivores in simple models.

Predators

Soil ecosystems include predators within each of the body size classes of soil fauna (micro-, meso- and macrofauna). These three levels of body size also form a hierarchy where larger animals prey on smaller animals as well as on prey of their own size. For instance, the main microfauna groups, nematodes and Protista, have predators preying within and among them including Protozoa feeding on nematodes and vice-versa (Geisen, 2016). Isotopic studies have demonstrated that predators form a soil fauna group of their own, i.e. an isotopic niche (Korobushkin *et al*., 2014), including spiders, Gamasida and nematodes, preying on microbivores, detritivores and herbivores. Even the neanurid collembolans are classified as predators, thus inhabiting the same isotopic niche as the before mentioned predators. Predation in the soil challenges our conception of a boundary between aboveground and belowground biota. Aboveground predators, such as spiders, beetles and harvestmen in fact feed on preys traditionally considered to be soil organisms. While predatory mites, spiders and beetles are ubiquitous, centipedes are rare in conventional agricultural systems, but enjoy the conditions offered in biological agriculture. One of the consequences seems to be that under conventional agriculture there is sometimes a higher impact of pest species (herbivores) because of the lack of predators (Kladivko, 2001). Soil predators can obviously influence the entire food web by creating important secondary effects. For example, bacterivorous nematodes have been shown to increase plant P uptake by different mechanisms. Nematode predators can decrease bacterial grazing and thus increase mineralization by bacteria, because of the higher bacterial turnover. They can also have a hormonal effect on plant roots increasing branching and therefore P uptake capacity of the plants (Ranoarisoa *et al*., 2018).

Modelling perspectives for predators

To our knowledge, there are no ecosystem models that include soil faunal predators, apart from the Romul-Hum extension to the ROMUL model (Chertov *et al*., 2017a, b), where for forest soils six food web topologies were used to simulate C and N flow in different soils. In this model approach, the predators are not a dynamic pool but a fixed part of the soil food web depending on soil characteristics. It is clear that more data are necessary to validate the population dynamics of predators and subsequently their effect on SOM dynamics. However, some important effects of differences in management cannot be simulated without including the predators. The model framework described by Osler and Sommerkorn (2007) shows how using nutrient stoichiometry could be an effective and simple way to include the influence of predation on the C and N cycling. The main concept of their framework is that soil fauna with a high C-efficiency and prey with a similar CN ratio contribute to the mineral N, while inefficient assimilators that consume prey with a higher CN ratio would contribute more to the DOM pool. Given the larger size and longer life-spans of many predators, simulating their effects as

'in balance' with the environment seems unrealistic. To allow effects of management, or drought periods/flooding in a more realistic fashion, including a dynamic pool of predators seems a worthwhile extension to existing ecosystem models for many environments.

Herbivores

Herbivores eat living plant material, such as leaves, flowers, stems and roots. Herbivores exert an influential role in plant community dynamics (Bever, 2003), which in turn determines the amount and quality of plant litter entering into the soil and the density and tissue quality of roots. Herbivores have an effect on the amount of SOM via different actions. About 50% of net primary production occurs belowground, in the form of roots, while the largest part of aboveground primary production enters the soil in the form of litter. Although aboveground herbivores have an effect on SOM via the return of plant tissue to the soil, the most important herbivores for SOM models are root herbivores.

Root herbivores are a diverse soil fauna feeding group. An important root-feeding microfauna group is constituted by the plant-feeding and plant parasitic nematodes. They feed mainly on plant juices and tap into the root. The density of plant-feeding nematodes varies greatly among ecosystems, but due to their sort life cycle and fast reproduction they can significantly affect plant communities, including a severe reduction in the crop yields (Yeates *et al*., 1993). Symphyla and prostimatid mites belong to the mesofauna and are also considered root feeders. However, the most influential root herbivores are found in the macrofauna, and include Diptera larvae (mainly midges), caterpillars and some major groups of beetles, such as click beetles and curculionids (mainly their larvae). The highest recorded average density of Symphyla (plant-feeding Myriapoda) is around 10.8×10^3 m^{-2} (Belfield, 1956). The few other sources generally report lower densities, around 200 individuals m^{-2}. With an average individual dry weight of 81 µg, this translates in an annual mean biomass estimate of 58 mg m^{-2} (Reichle, 1977). Prostigmatid mites are very abundant in temperate coniferous forest (about 2×10^6 individuals m^{-2}; 300 mg dry weight m^{-2}), and less abundant in tundra systems (about 5000 indidivuals m^{-2}; 10 mg dry weight m^{-2}, Petersen, 1982), with a mixed oak forest in between (Lebrun, 1971). An average dry weight of about 0.5 µg (range 0.2 – 4.0 µg) is assumed in most data sets, resulting in an average biomass ranging between 10 mg m^{-2} (tundra and temperate deciduous forest) and 50 mg m^{-2} in tropical grasslands (Petersen, 1982). Diptera larvae are the most important meso- and macrofauna root herbivores. Their average biomass ranges between 10 mg dry weight m^{-2} in tropical grasslands to 0.47 g dry weight m^{-2} in tundra ecosystems (Petersen, 1982). No data are available for caterpillar or root-feeding beetle (larvae). Being of larger size, beetle densities will be much lower on average than Diptera densities. Based on average biomass estimations for predaceous beetles (Carabidae and Staphylinidae), i.e. ranging from 10 mg m^{-2} to 0.12 g m^{-2} (Petersen, 1982), the biomass of root feeding beetles (Elateridae and Curculionidae) will probably be in the same range.

Modelling perspectives for root herbivores

The number of studies on consequences of root herbivore-plant interactions is still too limited to quantify the effect of root herbivores on ecosystem functioning (Eissenstat *et al*., 2000). However, the available information is enough to start exploring the effects of introducing root herbivores in SOM models on soil C and nutrient dynamics. Predicting root herbivore effects in a specific environment remains difficult, due to a number of often unknown factors, i.e. species composition, actual density, ecological efficiencies (which can deviate considerable between modes of feeding), and population turnover rates or generation times, but a first effort targeting generic simulation of effects would still be of great value. At an ecosystem level, fine root turnover is one of the most important C sinks, and the fate of fine roots (whether they die or are eaten) could potentially have a major effect on the simulated C balance (Brunner *et al*., 2013).

Detritivores

Mesofauna detritivores

Mesofauna detritivores feeding on decomposing organic matter (plant and animal remains), also called saprophages, include enchytraeids, collembolans, large groups of mites, some small-sized Diptera larvae, Protura and Diplura. The first three groups have been recognized as having major ecological importance in terms of abundance and biomass whereas the rest have been subjected to very little specific research and will not be further included. As a whole, their primary role shifts between promoting physical or chemical changes of the organic material ingested, depending on the group of species (Wallwork, 1970). These transformations mainly occur at the top layers (organic soil horizons but also in the litter layer, under stones, etc.) due to their limited burrowing abilities.

Enchytraeids

General population density estimates range from 10,000 to 300,000 individuals m^{-2} (O'Connor, 1967; Briones *et al*., 2007), with the majority occupying the upper layers (the 0 – 4 cm can concentrate > 70% of the total population; Briones *et al*., 1997). The main factors controlling their population sizes and vertical distribution are temperature and moisture. There are no quantitative reliable estimates of enchytraeids' consumption and digestion rates or agreement on their preferred food sources. As a rule of thumb it is believed that they feed on organic matter (20% of their diet), bacteria (40%) and fungi (40%) (Didden, 1993). Like earthworms, they burrow through the soil and ingest the soil. More recently, C dating techniques performed on field populations have established that they feed on organic matter that has been deposited into the soil 5 – 10 years before (Briones and Ineson, 2002). Importantly, temperature-driven increases in their population size results in a greater competition and thus, when biomass reaches a value of 2.1 g m^{-2} (Briones *et al*., 2007), consumption of older organic matter substrates increases and consequently, also a greater release of non-labile C occurs (Briones *et al*., 2009). Interestingly, in certain ecosystems, such as coniferous moder soils, their metabolic contribution has been estimated to be 11% (O'Connor, 1967) and is

comparable to that exhibited by woodland earthworm populations (8 – 10%) (Satchell, 1967).

Collembolans

Collembolans are important as epigeic decomposers (Ponge, 1991). Although they tend to be numerically exceeded by mites in many ecosystems, they can be the most abundant arthropods. As many as 53,000 m^{-2} (equivalent to 330 mg m^{-2}) have been found in a limestone grassland (Hale, 1966). However, their numbers fluctuate seasonally and with food availability, and for example, 670,000 individuals m^{-2} have been recorded in a permanent moist soil in Antarctica covered by the alga *Prasiola crispa* (Collins *et al*., 1975). Predation seems to be the primary regulatory factor of their population sizes (Wallwork, 1970). As many hexapods, they accumulate a high proportion of fat in their bodies (54% of dry weight or 24% of live weight) which increases with age (Anderson and Healey, 1972). Importantly, they shed their exoskeleton several times as they grow (up to 60 times in their lives) and in exuvia representing 2 – 3% of body weight (Anderson and Healey, 1972), which could be an important source of nutrients for other soil organisms.

Mites

Although the majority of mites are considered to be panphytophages (Luxton, 1972), more recent work (Schneider *et al*., 2004) indicated that besides fungal feeders and predators, there are larger groups that can be defined as primary and secondary decomposers and hence, having a preference for litter at different decomposition stages as well as coprophagous (feeding on fecal material) (Petersen and Luxton, 1982). Mites can colonise all soil horizons, including the mineral layers, and can reach up to 10^6 individuals m^{-2} in temperate mixed forests (Orgiazzi *et al*., 2016). These high densities are the result of their fast life cycles, which in the case of small species could be several generations per year (Mitchell, 1977). Their role in soil mixing is small compared to other invertebrates but they play an important role in humus formation and mineral turnover (Hoy *et al*., 2008). They produce fecal pellets, which help to distribute organic matter and are prone to microbial attack.

Quantitative contribution of detritivores to SOM transformations

The bulk of plant-derived C enters the soil only when the vegetation dies. A fraction of it is transformed by the decomposers through breaking down the organic substrates and assimilated into their tissues; another fraction is released as fecal material and/or exuvia, respired as CO_2 and finally deposited as dead bodies (Petersen and Luxton, 1982). There are very few estimates of how much organic material is ingested, digested, assimilated and respired by individual groups. In one year, detritivores (including earthworms) may consume 20 or 30% of the total annual input of organic matter (Macfadyen, 1963; Kitazawa, 1967); certain species, such as blanket bogs enchytraeids, are responsible for processing 40% of the total litter input (Standen, 1973). Even fewer attempts have been made to measure how much of the ingested organic matter has been assimilated. Overall, it has been suggested that the range of assimilation efficiencies is

wide (1 – 65%), with oligochaetes being the least efficient (Petersen and Luxton, 1982). Under laboratory conditions, the measured metabolic activity of enchytraeids and collembolans per unit of dried weight seems to be twice that of oribatid mites (compiled by Wallwork, 1970). In certain ecosystems where these organisms are dominant, their contribution could have a great influence. For example, in moorland soils, 70 – 75% of the total energy is assimilated by the dominant enchytraeids (Heal *et al*., 1975), whereas in mixed deciduous woodlands dipteral larvae accounted for 6.6%. A certain amount of energy ingested is metabolized and most of it is dissipated in respiration. Temperature has a strong influence on their respiratory metabolism and for example, in a laboratory incubation of a grassland soil (Briones *et al*., 2004), Q_{10} significantly increased and was ca. 25% greater in the presence of enchytraeids (Q_{10}=3.4) than in their absence (Q_{10}=2.6), and reached even higher values when the enchytraeids were incubated in a peatland soil (Q_{10}=3.9; Carrera *et al*., 2009).

In the field, the whole picture gets complicated because estimates change with population densities (and hence, with biomass and age structure) that are known to fluctuate with seasons (and thus, with variations in ambient temperature and moisture conditions). A good quantitative assessment was provided by Petersen and Luxton (1982), who concluded that soil detritivores are reasonably efficient in assimilating organic matter (40 – 50%) and have a community growth efficiency of 10 – 20%; 45 – 85% of the assimilated energy is dissipated in respiration, with only 15 – 50% being allocated to growth and reproduction. In addition, coprophagy is important since allows a better reutilization of organic substrates that were not fully digested on first consumption.

Furthermore, the role of soil animals on the retention of other nutrients can also be crucial: McBrayer (1977) estimated that 70% of the N released during litter decomposition is immobilized by soil invertebrates. Similarly, MacLean (1980) indicated that up to 1 mg P and 10 mg N m^{-2} are found in dipteran adults emerging from tundra soils, forming a major redistribution mechanism in these nutrient-poor soils. On the other hand, these soil organisms can also increase the mobilization of C, N and P. Thus, enchytraeids have been seen to have a predominant role in C fluxes and significant amounts of CO_2 and dissolved organic C (DOC) are released when these animals are present (Briones *et al*., 1998a; 2004; Carrera *et al*., 2009; Carrera *et al*., 2011). They are also influential for the leaching of dissolved organic N (DON), ammonium and phosphorus (Briones *et al*., 1998b). Similarly, significant increases in the leaching of ammonium, nitrate and calcium occurred as a consequence of collembolan grazing (Ineson *et al*., 1982).

Macrofauna detritivores

Macrofauna detritivores include soil organisms that are larger than 2 mm, such as earthworms, and ants, termites and their colonies. They excavate the soil in search for plant remains, soil organic matter and mineral particles. The engineering capacities of this group will be discussed further, but they also have an important role in the C cycle. Macrofauna detritivores can reach very high densities and biomasses. For example,

earthworms are abundant as long as the climate is humid and warm enough, at least during a part of the year. When soils contain enough organic matter (for endogeic earthworms that ingest soil and digest SOM) and primary production is high enough (for epigeic and anecic earthworms that eat plant litter), earthworms can be very abundant (i.e. more than 10^6 individuals ha^{-1}) and their biomass can be as high as 1000 kg ha^{-1} (Lavelle and Spain, 2001). Endogeic earthworms may ingest more than their own weight of soil each day, so that depending on their abundance and climate they may process all the soil in 5 years or less.

Modelling perspectives for detritivores

Mesofauna detritivores have not been included into ecosystem scale models so far, and information at this scale is scarce. Nonetheless, their impact on the ecosystem has been shown to be significant (Filser *et al*., 2016). It is not possible for a simple SOM model to distinguish the different mesofauna detritivores. However, parameterization of the saprotroph pool can mimic the differences between them. In the simplest case, this can be seen as a fixed relative abundance of the various species that determines the 'average' parameters. Besides maximal growth rate and respiration, CN ratio and response to temperature (Q_{10}) are important to characterize this group, as is the production of excrements, exuvia and exoskeletons that need not be addressed separately but can be an important flux. From the review it seems clear that distinguishing only between C used for growth and C respired is not an adequate representation. Although the concept of recalcitrance has been questioned, it can still be used here to allow some chemical changes by detritivores, that slow decay and favor fungal decay above bacterial decay. For macrofauna detritivores, quite a number of models have been developed that often focus on their engineering capacity, so these models are discussed in that section.

Fine roots

The rhizosphere, the area of soils conformed by the fine roots and the microorganisms directly associated with them, has been shown to be of great importance to soil C and nutrient dynamics (Kriiska *et al*., 2019). Byproducts from fine root activity, e.g. exudates produced by fine roots as well as the biomass and necromass of fine roots are the base food for a large community of soil microorganisms and soil fauna (e.g. detritivores, herbivores). Nowadays, the definition of 'fine roots' is under discussion, as the commonly used 2 mm threshold (Finér *et al*., 2007) is not a functional criterion. In this regard, despite the fact that fine root turnover is a significant and dynamic C sink, in most models it is simulated very simply as a constant rate. Root turnover can be increased by 50% by grazing (Eissenstat *et al*., 2000). Furthermore, the direct input of DOC from fine roots is important for leaching and for all interactions with soil microbiota.

The root litter usually remains underestimated. Live roots contain high concentrations of soluble and easily decomposable organic substrates (e.g. glucose, malate, cellulose, peptides such as glutamate), whereas root necromass is rich in organic constituents

(lignin, suberins) characterized by lower decomposition rates (due to recalcitrant substances) (Grayston *et al*., 1997; Rasse *et al*., 2005). The composition of the roots is considered to be relatively similar to the above-ground parts, showing a similar pattern of relative compounds abundance between deciduous (higher in nutrients and soluble compounds) and coniferous (higher in lignin and liposoluble) species. On the other hand, root and hyphal exudates particularly rich in readily available constituents may induce a small but significant increase in litter decomposition, indicating an active role of the rhizosphere in soil priming (Kuzyakov *et al*., 2000; Rasse *et al*., 2005). However, differences in fine root activity (production and mortality) and decomposition among ecosystem types are not well known (Coleman and Hendrix, 2000), and even less is known regarding the impact of species on the amount and composition of root exudates. Furthermore, once different above and below-ground C inputs enter the mineral soil, pedogenic processes and soil-inherent stabilization mechanisms may interact altering their stabilization, especially in subsoil horizons where interaction with the mineral phase is considered a dominant stabilization mechanism (Rumpel *et al*., 2004; Rumpel and Kögel-Knabner, 2011).

Modeling perspectives for fine roots

In many ecosystem models, fine roots are still simulated as a single pool with a single turnover rate though data on fine root distribution are available (Finér *et al*., 2011). Furthermore, when root growth is not well defined over the soil layers, nutrient and water uptake is obviously not simulated realistically over the layers as well. Novel root architecture models and tomography techniques have facilitated the development of three-dimensional functional-structural models as reviewed by Dunbabin *et al*. (2013). The description of root water uptake has been advanced though more complex approaches that explicitly describe water flow in both the soil and inside the root system (Javaux *et al*., 2008; Schröder *et al*., 2009). Yet the impact of specific rhizosphere hydraulic properties on the root water uptake at the plant scale is generally not considered, except for instance in Schwartz *et al*. (2016). Models that simulate root growth and nutrient uptake processes, like R-SWMS or SimRoot, enable calculation of nutrient uptake as the roots grow and receive photosynthates from the shoot (Postma *et al*., 2017). Examples of coupling of the root growth model RootBox with soil models are presented e.g. in Schnepf *et al*. (2012), who simulated root system phosphate uptake from a rhizotron as affected by root exudation. In most of those models, root architecture is used to compute volumetric sink terms for water or nutrient uptake. Few examples exist that explicitly simulate the roots as physical objects with uptake prescribed via the boundary conditions at the root surfaces (e.g. Leitner *et al*., 2010). However, these improved descriptions are not yet sufficiently incorporated into larger scale models (Hinsinger *et al*., 2011; Vereecken *et al*., 2016). Recent initiatives in this way already include soil resistance, plant root distribution and climatic demand, to upscale to the macroscale (Javaux *et al*., 2013). There remains an overall lack of spatially explicit models that properly describe soil C and nutrient dynamics at different spatial scales (Manzoni and Porporato, 2009). How macropores are used by roots and

how roots create macropores or induce compaction are still challenging questions (Lesturgez *et al*., 2004) which only start to be included in models (Landl *et al*., 2017).

Modelling soil food webs

Soil food web modelling has mainly been used to calculate the flow of C and nutrients through soil and to investigate the role of the various functional groups in these flows. This kind of modelling requires knowledge about the architecture of the food web ('who eats who'), the biomass of the functional groups and physiological information, such as generation time, growth and death rates and metabolic efficiencies. The importance of these types of models in explaining N and C stocks was already shown in the late 80's and 90's (e.g. Berg *et al*., 2001); however, this knowledge did not find its way into the basically plant-centred ecosystem models. Nonetheless, Berg *et al*. (2001) and Schröter *et al*. (2003) used such food web models at a forest ecosystem scale to show the importance of functional groups for predicting C and N dynamics in the soil.

To model the C and nutrient fluxes, many food web models first calculate the feeding rates among the functional groups. Next, using metabolic efficiencies, i.e. assimilation and production efficiencies, and CN ratios of consumer and resource, C and N mineralization are derived from the feeding rates of functional groups. The equations used to calculate the feeding rates follow the approach of 'inverse modelling', which goes back to O'Neill (1969) based on the conservation of matter and energy and the assumption that system is at steady-state. This approach has been applied first to soil food webs by Hunt *et al*. (1987) and later by de Ruiter *et al*. (1994), Berg *et al*. (2001) and Schröter *et al*. (2003).

Alternatively to a steady-state description, different approaches exist for modelling the growth of a species population within a food web. The first approach is to simulate an increase in population towards the carrying capacity of the system. This yields stable and reliable results, but does not allow for a strong influence of management or climate on the carrying capacity, so it is not so different from assuming a steady-state. Other models opt for a more Richards' shaped growth curve, where growth rate goes to a maximum, allowing a direct link between resource and species and a dynamic representation of climate and management effects. To be sensitive to climate change, a daily timestep is most appropriate at a stand scale. Daily faunal pool sizes can be calculated as a set of linear equations for each pool including growth, turnover and respiration. A dynamic representation of all populations is thus possible. However, we have found no models using such an approach at an ecosystem scale, although current computational power should allow this. The new ROMUL model (Chertov *et al*., 2017a, b) has a detailed representation of soil fauna in 15 groups. This is the first model (to our knowledge) including data of the faunal food web, including necromass and respiration, on the C and N cycle of a soil. The biota is assumed to be at steady-state and climate and management only empirically affect them.

Interactions between SOM chemistry - structure and soil biota

The processes involved in SOM stabilization are strongly controlled by soil biota. The role of microorganisms on soil aggregate formation, stabilization and eventually degradation is well-known. In fact, bacteria and fungi are considered to be the most important soil microorganisms involved in the formation and stabilization of aggregates, especially at the microscale (Gupta and Germida, 2015; Costa *et al*., 2018). Mycorrhizal fungi are known to influence the movement of SOM into mineral soil (Frouz *et al*., 2001; Ponge, 2003) but also the formation and stabilization of aggregates. Ectomycorrhizal fungi affect soil aggregation (reviewed in Rillig and Mummey, 2006) through changes in the root architecture by 1) covering fine roots with fungal mantles (Smith and Read, 2008), 2) producing hydrophobins in the mycelium and rhizomorphs (e.g. Tagu *et al*., 2001; Mankel *et al*., 2002) that help adherence to different soil surfaces, 3) enmeshing and entangling soil primary particles, organic materials and small aggregates, and 4) oxidizing of biomolecules present in SOM that leads to the formation of aggregates of organic matter (Kleber and Johnson, 2010; Kleber *et al*., 2015). In sandy soil, only hyphal networks are able to tie the abundant sand particles to form stable aggregates (Six *et al*., 2004). Bacteria can also have a profound influence on soil aggregation (Six *et al*., 2004). Like fungi, bacteria produce exopolysaccharides, which act as glue and help organic residues to attach to clays, sands and other organic material, resulting in the formation of new micro-aggregates (Degens, 1997).

In addition, other functional groups, such as microarthropods, are assumed to affect SOM stabilization; most likely by influencing organo-mineral interactions (e.g. by effects on soil chemistry and leachate) and aggregate formation (e.g. by necromass, eggs as aggregate starting point) (Maaß *et al*., 2015; Soong and Nielsen, 2016). Similarly, it has been shown that earthworms can play a central role in physical stabilization of newly generated organic matter through soil aggregate formation (Pulleman *et al*., 2005; Rillig and Mummey, 2006; Six and Paustian, 2014; Bottinelli *et al*., 2015) and cast formation (see below).

Casts

When macrofauna is present, a substantial part of litter is turned into macrofauna excrements that are either holo-organic (such as faeces of millipedes) or in form of organo-mineral aggregates (such as faeces of earthworms). They can be deposited in the soil or at the surface in large quantities (**Fig. 1**), and in the case of some species of earthworms the surface aggregations of intact and fragmented litter together with defecated soil around the openings of the earthworm burrows are called “middens”, and represent important microhabitats for microbial activities.

Figure 1. Casts over the soil surface in a Spanish holm oak forest, near Arascues (province of Huesca).

Several authors have shown that microbial activity increases during and shortly after faunal feeding but then decreases and may be lower in faunal faeces than in the non-ingested litter (Lavelle and Martin, 1992; Frouz *et al*., 1999; Tiunov and Scheu, 2000; Frouz and Šimek, 2009). The increase in microbial activity in fresh faeces is often attributed to litter fragmentation (Gunnarsson *et al*., 1988; Kaneda *et al*., 2013), which increases surface area and may thereby increase microbial access to the litter. Artificial litter fragmentation experiments have shown, however, that litter fragmentation alone may enhance or suppress microbial activity (Gunnarsson *et al*., 1988; Kaneda *et al*., 2013). The reasons for the decrease in decomposition rate and hence in the stabilization of SOM in the older faeces of soil fauna are also variable. Some macrofauna species, such as earthworms, consume soil organic matter together with the soil particles. These results in the binding of SOM in aggregates, which may slow decomposition and help stabilize SOM (Lavelle, 1988; Six *et al*., 2004; Gunina and Kuzyakov, 2014). In the case of macrofauna that mainly consumes litter without soil, the reduced decomposability of their faeces is associated with changes in their chemistry compared to that of the original litter. The faeces are usually depleted in easily available polysaccharides, degraded by invertebrate enzymes (Frouz *et al*., 2002), and are enriched in lignin (Hopkins *et al*., 1998; Frouz *et al*., 2015). Because the easily available substances are not present in faeces, the decomposition rate is reduced (McInerney *et al*., 2001; Bossuyt *et al*., 2005). The content of soluble phenols decreases after passage through the gut of litter-feeding fauna (Coulis *et al*., 2009; Špaldoňová and Frouz, 2014; Frouz *et al*., 2015), which may be caused by precipitation with proteins, making phenols insoluble (Frouz *et al*., 2015) but at the same time also reduce N availability. Although earthworms are typically the main group contributing to faunal-mediated aggregation, faecal pellets produced by micro-arthropods have also been recognized as important contributors to aggregate formation (Maaß *et al*., 2015),

either by promoting porosity or by filling the pore space between particles and hence, impairing fungal growth and decomposition. For earthworm casts at the surface, aggregate degradation by rain can have a significant impact on their stability and the subsequent leaching of nutrients (Decaëns *et al*., 1999), and similar effects have been found for termite mounds (Jouquet *et al*., 2011).

Soil structural modifications by engineers

By definition, ecosystem engineers are organisms that have measurable impacts on the physical properties of their environment, either through their activities or their mere presence (Jones *et al*., 1994). Such organisms are thus often very influential for the functioning of ecosystems and tend to affect all organisms and their activities with which they share a common environment. Note that engineers are also important because they can create heterogeneity in physical, chemical and biological features at various spatial scales (Barot *et al*., 2007a; Jouquet *et al*., 2007; Jiménez *et al*., 2012; Raynaud *et al*., 2013), and likely strongly influence the functioning of food webs (Sanders *et al*., 2014). Three concurrent and interrelated processes are behind the engineering capacity of soil organisms, but generally considered separately for practical reasons: i) biopore formation, ii) bioturbation (soil mixing), and iii) fauna-mediated aggregation (discussed above for casts).

Biopore formation

Many soil organisms can be considered as ecosystem engineers and are very influential for soil processes (Lavelle *et al*., 1997; 2007). Indeed, soil biota requires space and connectivity between pores to move through the soil, to forage for nutrients and carbon-based energy sources, water and living space (e.g. plant large roots and macrofauna such as earthworms, ants or termites). This can be achieved either by pushing aside soil aggregates or by ingesting soil (e.g. in earthworms), creating the so-called biopores that remain after roots death or the passage of fauna. Some soil macrofauna is particularly influential for soil structure through their engineering activities, such as ants (Folgarait, 1998), termites (Dangerfield *et al*., 1998) and earthworms (Lavelle, 1988; Lavelle *et al*., 2007). As an example, values between 0.013 and 0.024 m^3 earthworm burrows m^{-3} of soil have been reported (Bastardie *et al*., 2005), that can persist for very long periods in the soil.

Bioturbation

By burrowing through the soil and dragging litter, soil engineers mix mineral and organic materials from the different horizons in a process known as bioturbation. The extent and type of bioturbation largely depend on the ecological behaviour, body size and population density of the different species, and earthworms are a good example to illustrate this. Earthworms are traditionally classified into three main ecological groupings (Brown, 1995): epigeic, endogeic and anecic species. Epigeic and anecic earthworms consume fresh litter at the soil surface, whereas endogeic earthworms ingest more mineral soil creating a network of galleries and soil aggregates of various sizes (earthworm casts). While epigeics and endogeics move horizontally in their respective

layers, anecic earthworms create permanent or semi-permanent vertical galleries. Therefore, the latter group plays a more important role in mixing the soil and incorporating litter into the soil profile. Taken together, earthworms are thus very influential for soil structure (Blanchart *et al*., 1999) and subsequently for water drainage, aggregate stability, mineralization and leaching of mineral nutrients (Edwards *et al*., 1989; Jouquet *et al*., 2008).

It is generally considered that bioturbation tends to stabilize SOM by promoting physical protection (see Filser *et al*., 2016), although the deep burial of litter or casts is an often overlooked mechanism that could significantly contribute to carbon persistence in soils, also favoured by the more stable conditions (Špaldoňová and Frouz, 2014). However, some authors have highlighted that in some systems, wetter conditions in the deeper layers might accelerate SOM turnover (Rasse *et al*., 2006). To elucidate this, more information is needed regarding the decomposition rates of buried casts and C sequestration processes in earthworm burrow walls (Zhang *et al*., 2013). Similarly, ants and termites build nests by gathering different organic and mineral materials, creating SOM hotspots. This creates soil physical and chemical heterogeneity (Lovegrove and Siegfried, 1989; Dean *et al*., 1999; Jouquet *et al*., 2002). Little is known on the horizontal transportation carried out by termites during the construction of their fungus-growing chambers or those by ants with their anthills. Both ants and termites bring food to their nests (which are locally partially returned to the soil as faeces) and create fungal gardens in some chambers, so that these nests often constitute patches enriched in organic matter and mineral nutrients (Dangerfield *et al*., 1998; Folgarait, 1998).

In agroecosystems, plant residues are artificially incorporated in soil by tillage, but in natural ecosystems, besides bioturbation by fauna, the processes incorporating those materials into the soil are rather limited (i.e. soil flooding and consequent burial by mud, burial by mineral particles brought by wind or water erosion, or cryoturbation). This is why, when macrofauna is absent, litter mostly accumulates in soil surface, and can only reach deep soil after its physical fragmentation into small pieces and washing down by percolating water. Hence, faunal activity determines to a large extent if organic matter and processes such as decomposition mostly happens on the soil surface or in deeper soil horizons, and thus affects the amount and quality of organic matter incorporated into the soil.

Soil engineer models

Most models on soil engineers focus on the effect of earthworms on mineral soils. Some models only tackle the demography of earthworms or their movements (Martin and Lavelle, 1992; Klok *et al*., 2006; Pelosi *et al*., 2008; Vorpahl *et al*., 2009), to predict their impact on soil functioning. Other models such as the Multi Agent System model, SWORM, simulate the movements of individual earthworms within a soil profile and the consequences for soil structure (Blanchart *et al*., 2009). Barot *et al*. (2007a) modeled at a larger scale (about 100 m^2) the feedbacks between earthworm demography and soil aggregates. Another analytical model (Barot *et al*., 2007b) allows predicting the impact of earthworm on mineral nutrient stocks and primary production, from the impact of

earthworms on fluxes of mineral nutrients within the ecosystems and losses of nutrients from the ecosystem (e.g. through leaching). More recently, a simulation model was developed to predict the impact of an invasive earthworm on the dynamics of soil C taking into account earthworm effects on microorganisms (Huang *et al*., 2010). In the future, this model may help predicting the speed of earthworm invasion. A food web model and the activities of anecic earthworms are incorporated in the ROMUL model (Chertov *et al*., 2017a, b; Komarov *et al*., 2017). There are few models tackling the impact of other soil engineers such as ants or termites on soils, except for the work by Dangerfield *et al*. (1998) on termites.

DISCUSSION

The goal of this effort is to integrate the current views on the central role of soil biota on soil SOM and water dynamics into a new mechanistic model, the KEYLINK model. The challenge faced was to minimalize model complexity while retaining enough detail to predict and analyse effects of changes in climate and management of a very wide range of soils (grasslands, forest, agricultural soil, organic and more mineral soils) including the key processes and the key species according to the most recent insights.

From our extensive review our main conclusion is that placing chemical recalcitrance at the centre of a soil model is not the best representation of soil functioning. Instead we propose soil structure as the central part of our soil model, since structure determines 'accessibility' for the dynamic soil faunal pools in terms of pose sizes and body sizes of soil fauna (**Fig. 2**), but also the hydrological properties (soil water flow) of a soil. Our key assumptions are:

- Litter and SOM decomposition are active processes, conducted by microbes and soil fauna and thus dependent on the consumer pool size.
- Decomposition depends on accessibility (function of pore size distribution and the related local soil water content and aeration) and secondly on the quality of the decomposing material.
- Pore size distribution determines the accessibility to all soil biota, but also the hydrology and the availability of O_2.
- Soil water flow depends on soil pore distribution which is also a function of the activity of soil engineers and aggregation by soil biota
- In soils where soil engineers are important (most mineral soils) it is essential to simulate their effect on biopore formation and bioturbation; for some organic soils their effect is less important.
- Mycorrhizal fungi need to be represented in the model concerning their interaction with the plant (important input of C to the soil), decay of SOM and effect on aggregation.
- In many cases a real food web, with dynamic faunal and microbial pools, is necessary, e.g. to simulate management or climate change effects. The diversity and number of trophic levels changes with soil types/ecosystems. When there are not enough data however, and when changes are slow (stable situation), a representation with constant pools of soil fauna can be considered.
- Special attention needs to be paid to the simulation of fine root turnover which should either include herbivory or herbivory should be simulated.

- Modelling aggregation in detail is beyond the scope of an ecosystem model; the most important effects of aggregation can be included through the concept of the pores (aggregation increasing micropore fraction and reducing mesopore fraction) as influenced by engineers (casts), bacteria and fungi.

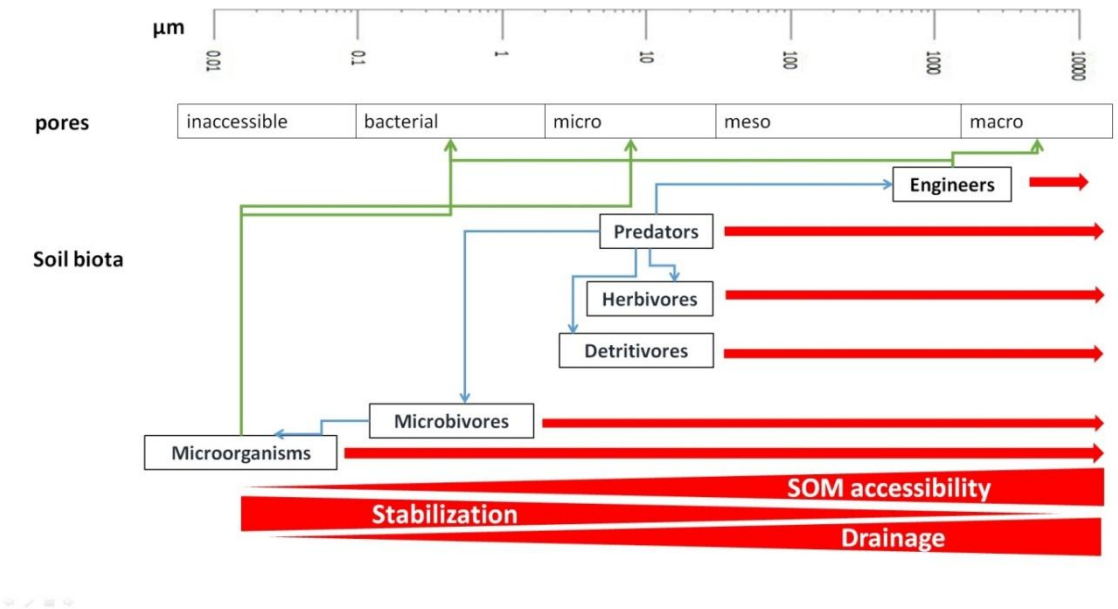

Figure 2. Interactions among the soil food web and with soil structure. Pore size distribution is presented in five categories: inaccessible pores, bacterial pores, micropores, mesopores and macropores. Green arrows indicate engineering effects on soil porosity; red arrows indicate the accessibility range to pore classes for each biota group; and blue arrows indicate predation interactions. Red triangles show the expected responses to soil structure in water drainage and SOM accessibility and stabilization.

To use the KEYLINK concept, a good hydrology model with multiple soil layers is necessary. For soils where, besides the water availability, distinct horizons are present with very different characteristics, each horizon should be simulated separately, but in other cases it can be adequate to use layers only for the hydrological calculations.

We define different pore sizes, based on measurability and accessibility by soil fauna as well as hydrological concepts. The initial pore size distribution can be calculated from water retention measurements. Soil structure is dynamic: it can be modified by bioengineers, by aggregation (by bacteria and fungi) which glue together soil particles thus, by organo-mineral interactions (function of clay content and SOM) but also by precipitation (destroying macropores and aggregates) and management (increasing bulk density). In a multi-layers soil system, bioturbation by soil engineers can be a major factor.

Concerning size and the main decomposing biota, a distinction between larger particulate material (fresh litter, fragments, and necromass) and SOM is required. Within SOM, dissolved DOM and particulate POM need to be simulated separately to allow leaching, but can be simulated as in balance with each other. Fungi and bacteria have different capabilities to decay litter; therefore, we need to add enough description

of the initial litter quality. The average recalcitrance (defined here as % non-hydrolysable compounds) and CN ratio are enough for a main division between these three pathways. SOM need not be further divided into pools. However, SOM is distributed across the pore space and depending on the pore size distribution it is more or less accessible. Accessibility is defined by pore size distribution by calculating the surface area of each pore fraction at each timestep, and distributing SOM by this area.

We opted for a minimal complexity but able to explain the best understood faunal and food web effects, allowing the important distinction between the bacterial and fungal pathway as well as incorporating the potential feedback effects of management in reducing food web complexity. The main division is based on function, not family or size:

- Non-mycorrhizal fungi
- Bacteria
- Mycorrhizal fungi
- Fungivores and bacterivores (or total microbivores)
- Predators
- Root herbivores
- Detritivores (non-engineers)
- Engineer detritivores

The different roles of all biota are summarized in **Table 1**. Engineers are part of the food web, and in addition create biopores and casts (changing accessibility by reducing pore size within the cast), and bioturbate the soil.

In our view, the most simple soil model can ignore all changes in chemistry apart from the initial litter quality, and decay is calculated from pore size distribution and environmental parameters (in combination with consumer pool size). However, for a more complete model, all biota can change 'recalcitrance' and CN ratio of the material they consume by producing faeces that are more stable. All biota respire and become necromass that enters the SOM. The interaction between the biota is shown in **Figure 3**. Since the goal is to simulate the response of the soil functioning to climate and management, the soil fauna need to be responsive to both. We suggest calculating the faunal pools as a set of linear equations with the change in the pool size dependent on growth, respiration (depending on temperature), faeces (including exoskeletons), and turnover (natural death and predation). Growth can be calculated as a function of maximal growth rate, resource availability (as a function of pore sizes) and quality, and environmental parameters (temperature and pH). The CN ratio and sensitivity to pH and temperature, as well as respiration rates and faecal production need to be included for each biota.

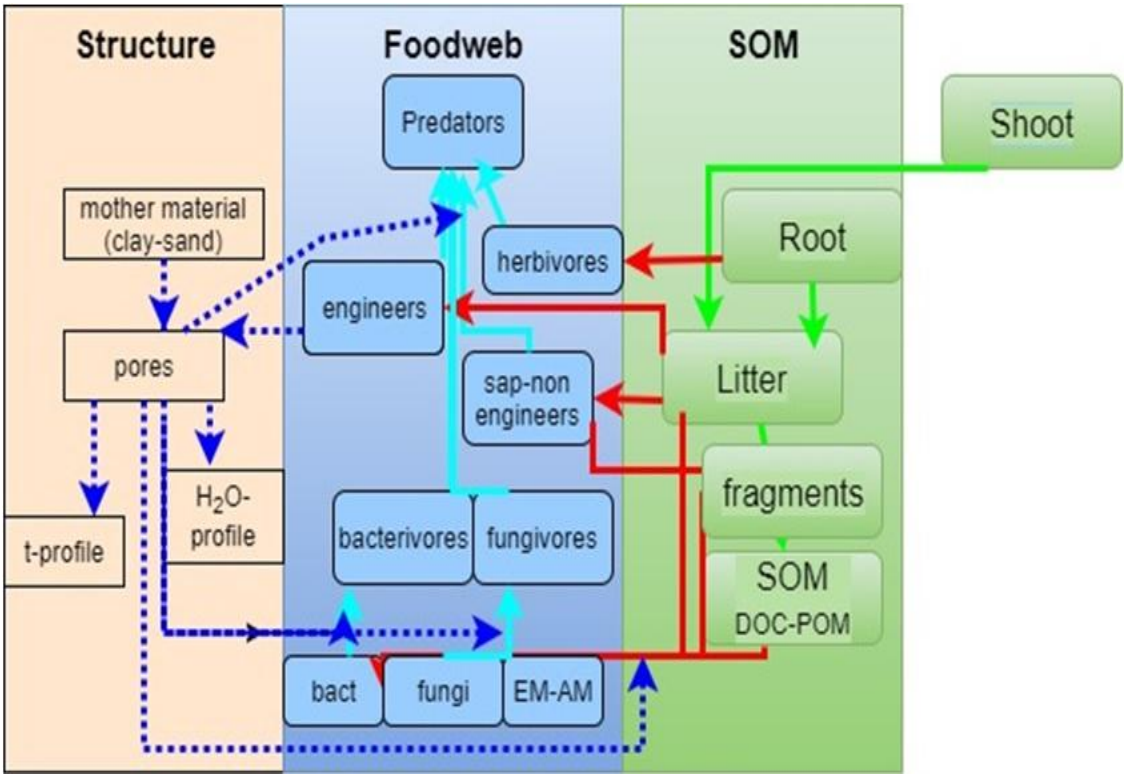

Figure 3. Model concept scheme. Soil structure and soil food web controlling soil organic matter (SOM) dynamics. C pools include inputs from plants, litter, SOM, dissolved organic C (DOC) and particulate organic matter (POM), with green arrows indicating C fluxes between those pools. Red arrows indicate C fluxes entering in the food web. Light blue full arrows indicate C fluxes among the food web. Dashed arrows indicate soil structure effects on hydrology, soil temperature (t) profile, or C fluxes, and also the engineering feedback to soil structure.

This very general model concept should be at least parameterized and implemented differently according to the specific ecosystem, but will allow comparison across these different systems (which is not possible using most current models that focus on specific ecosystems).

In organic soils, a focus on chemical decomposition can yield adequate results if the different pathways are included in an active way (microbes divided between bacteria, fungi and mycorrhizal fungi with different characteristics and efficiencies for transforming different food sources). For such soils, it is important to know at least the CN ratio and the 'recalcitrance', and to include the interaction between mycorrhizal fungi and plants. Inclusion of faunal effects (the composition will depend on C content and hence pH) and improved hydrological description (requiring structural description of the soil) should be able to improve the modelling results. For very wet soils (e.g. peatlands) it is clear that a correct distinction between anaerobic and aerobic processes should be included.

In the case of mineral or organo-mineral soils, the incorporation of pore distribution in the mineral layers will better describe the (in)accessibility of SOM due to physical inaccessibility (only bacteria can access the smallest pores, and they cannot be

consumed by bacterivores in those pores) or to water or oxygen availability. Here, the role of soil ecosystem engineers would be crucial. In reality, the structural diversity of a soil is extremely important. A precise model will need to include a full 3D description of the rhizosphere which is beyond the scope of an ecosystem model at the scale we envisage. However, some aspects can be included by simulating root exudates as 100% accessible.

Concerning nutrients, the described model concept is limited to the nutrients available from SOM decay and ignores mineral weathering. Improved understanding of the interactions between the different soil biota and the soil geochemistry could enhance this concept, for example including the weathering effect of mycorrhizae (Andrews *et al*., 2011), but available studies are as yet limited. For less soluble nutrients such as P depending on the parent material, pH and concentration of base cations, a more chemical approach (including the simulation of pH depending on mother material) might be necessary but hard to parameterize at an ecosystem scale, although an empirical approach as used in Bortier *et al*. (2018) could be added, for example for podzol soils where nutrient availability is low.

For the faunal food web, we have chosen to represent functional groups, instead of species. For the parameterization of these groups, average values of the main species can be used, as described in the sections above.

We describe a single layer here, but it is the goal to simulate the distinct horizons of a soil, since using average values when the soil horizons are strongly differentiated induces large errors. For hydrological simulations, distinct soil layers need to be distinguished even if their composition is similar.

CONCLUSIONS

Recent technological advances such as high-throughput DNA sequencing and stable isotopes analyses have greatly increased our knowledge and understanding on the key soil processes and how they interlink. Yet, the key interactions between major actors in the soil are often ignored in widely used soil models, and are only represented in complex models, focussing only on specific processes but not on ecosystem functioning. Our model concept KEYLINK is a novel and simple yet integrative representation of the latest insights from different 'schools' of soil description and analyses. By including and linking the major faunal groups, the description of the soil pore space and the active decomposition of SOM, a dynamic link between management, climate and soil functioning is attainable. More insight into the interaction between the different soil biota and the soil chemistry and structure is required to improve and validate this concept.

The KEYLINK model has been implemented (see chapter 2) and data are available to allow its development. However, full validation of the concept requires some crucial data which are missing in many experiments. For example many studies on ecosystems do not include soil fauna data at all, or only the diversity but not the abundance or biomass. While earthworms have been quite intensively studied, the effect of termites and ants on soil C dynamics are less known. On the other hand, experiments focussing on soil fauna often do not include crucial data concerning the ecosystem such as litter quantity and quality, and fine root biomass and turnover. Soil structure and hydrology are very seldom described in detail, in many cases limited to sand and clay content and bulk density. Concerning hydrology, preferential flow through biopores is seldom taken into account. For a better representation of N availability, models on nitrifying/nitrogen fixing bacteria would be necessary. For many other nutrients (including P), representation of the mineral weathering and the adsorption/desorption including a dynamic pH model would be required, but in many cases data are lacking to parameterize such models.

To evaluate our concept, data from isotope studies could be of great value, especially if they include the faunal food web as well as the microbial composition, the fine roots and the mycorrhizal fungi. The strength of our concept goes beyond getting a more reliable prediction of soil processes. It is clear that, due to the limited available data for many sites, in many cases a very simplistic representation of the soil can, with site-specific parameterization, yield a reasonable fit to measured data. Indeed, given enough parameters and pools, and limited validation data, almost any model can 'fit'. However, existing models, in which the growth of plants is limited by soil nutrient and water content only, create the false impression that adding nutrients and water is enough to have a well-functioning ecosystem. This is in contrast to all recent findings concerning the importance of a well-functioning soil ecosystem, including a diverse soil fauna that efficiently buffers the nutrient and water availability. Therefore, we believe that our model concept stimulates viewing the soil as a complex live system that needs to be protected in its diversity so it can fulfil all ecosystem functions.

Chapter 2

KEYLINK, a new mechanistic soil model

ABSTRACT

In the KEYLINK model, we integrate new knowledge on soil structure and its importance for soil organic matter (SOM) stabilization and hydrology, with the existing concepts on SOM pools, and elements from food web models, i.e. those from direct trophic interactions among soil organisms. KEYLINK is, therefore, one of the first and most ambitious attempts to integrate soil functional diversity and food webs in predictions of soil carbon (C) and soil water balances. In addition, this mechanistic process-based model can be coupled to other ecosystem models and improve their predictions as an alternative to the widely used more chemically based models. We present a selection of equations that can be used for most models as well as basic parameter intervals for, e.g., key pools, functional groups' biomasses and growth rates. Parameter distributions can be determined with Bayesian calibration, and here an example is presented for food web growth rate parameters for a pine forest in Belgium. We show how these added equations can improve the functioning of the model in describing known phenomena. For this, five test cases are given as simulation examples: changing the input quality (CN ratio and recalcitrance), excluding predators, increasing pH and changing initial soil porosity. These results overall show how KEYLINK is able to simulate the known effects of these parameters and can simulate the linked effects of biopore formation, hydrology and aggregation on soil functioning. Furthermore, the results show an important trophic cascade effect of predation on the complete C cycle with repercussions on the soil structure as soil engineers are predated, and on SOM turnover when predation on fungivore and bacterivore populations are reduced. In summary, in contrast with broadly used first order kinetic models, KEYLINK shows how soil functional diversity and trophic organization and their role in shaping both C and water cycling in soils should be considered in order to improve our predictions on C sequestration and C emissions from soils.

INTRODUCTION

Soil models used in ecosystem-scale modelling need to be relatively simple and fast at performing calculations. Nonetheless, C and nutrient turnover and hydrology are extremely important for determining ecosystem productivity and C sequestration in the ecosystem. The oldest and still most widely used soil models (Century, RothC) emphasize the C flow from easily degradable to stable organic compounds using first-order kinetics to describe their decay rates (Campbell and Paustian, 2015). The relevance of chemical recalcitrance, used in those models, is accepted in the early stages of litter decomposition, but that approach has been questioned on the long term SOM stabilization (Schmidt *et al*., 2011), highlighting the relevance of other processes as the physical protection of SOM within soil matrix (as discussed in the general introduction).

More recently, the importance of the microbial biomass in C turnover has been introduced in models such as MIMICS (Wieder *et al*., 2014; Wieder *et al*., 2015) and LIDEL (Campbell *et al*., 2016). However, soil fauna and especially soil engineers, sensu Jones *et al*. (1994), have also been shown to play a key role in determining C and nutrient turnover and hydrology of soils (Filser *et al*., 2016; Lavelle *et al*., 2016), and there is a need to include their contributions to SOM dynamics into soil modelling (Vereecken *et al*., 2016). This information has been used in detailed soil models (Chertov *et al*., 2017a), but is not incorporated into larger-scale ecosystem models. The main difficulty is the lack of data concerning the soil, either physical, chemical or biological, and the different methods used, making parameterization of any model unsure. The goal of the KEYLINK model is to consider the soil including the main mechanisms concerning the effects of soil fauna on litter and SOM transformations and hydrology, without increasing the number of parameters beyond what is currently available on most well-measured ecosystems.

The core model concept is the strong link between soil fauna, soil structure and turnover. The decay of fresh litter is dependent on the recalcitrance and CN ratio of the litter, though different faunal groups have specific sensibilities to recalcitrance and CN ratio. For SOM, the turnover depends on the accessibility, linked to the pore size distribution, the aeration and H_2O in the pores and the aggregation (based on the model by Kuka *et al*., 2007). Both SOM and litter turnover depend on temperature and humidity. Soil fauna, specifically soil engineers, directly affect pore distribution besides an important effect on bioturbation. Pore distribution affects hydrology which again affects all soil processes.

Structural effects

Pore size distribution determines accessibility for trophic interactions of soil fauna and soil microorganisms (**Fig. 1**), both by size and by aeration and H_2O; soil fauna changes pore size distribution and produces cracks and fissures in the soil. In the model, pore size distribution is divided into the following five categories:

- **Inaccessible pores** (< 0.1 µm in diameter)**:** pores around inaccessible C (within the micro-aggregate, organo-clay interaction). Water is held here but is not available to plants (measured from wilting point). The volume of inaccessible pores is related to the clay content and type.
- **Bacterial pores** (0.1 – 2 µm)**:** the pores within macro-aggregates and pores in loam, accessible only to bacteria. Engineer saprotrophs (e.g. earthworms) can also use SOM in these pores (and in all the following pore categories) because they eat directly all soil.

- **Micropores** (2 – 30 µm): pores not accessible to macrofauna, mesofauna and most predators, but accessible to microfauna bacterivores and fungivores, fungi, mycorrhiza and bacteria. Water is held at field capacity but available to plants. In sandy soil and within macro-aggregates (> 250 µm), pores fall in this category.
- **Mesopores** (30 µm – 1.5 mm): pores where most soil fauna can penetrate (not macrofauna) between large macro-aggregates (>1 mm) or formed by fine roots. Mesopore volume can be determined in the field from drained water capacity (but this includes macropores). These pores are well aerated also at field capacity, but can dry out below field capacity.
- **Macropores** (> 1.5 mm): cracks or biopores formed by soil engineers. They are of vital importance for soil hydrology as preferential flow through these pores has a major impact on infiltration rate. These are the first pores to have O_2 when water level is above field capacity, but dry out quickly below field capacity. Macroporosity is hardly measurable with typical lab measurements or the retention curve but visual assessment is possible.

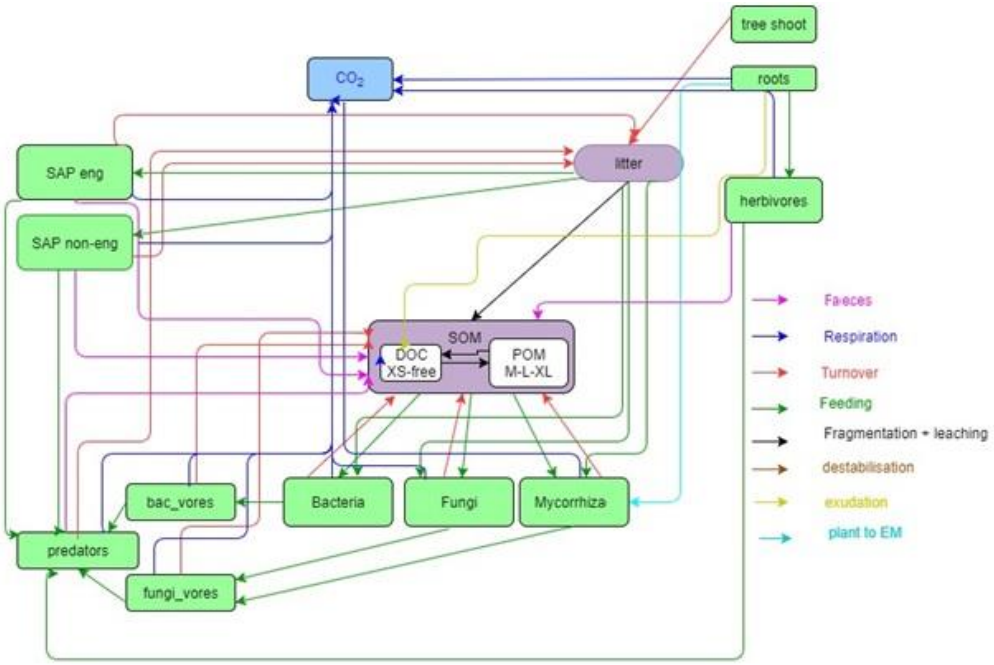

Figure 1. Pools and fluxes. Scheme of C pools (food web, litter and SOM) with their interactions. All pools, soil, microorganisms and fauna are represented in the model in the same units (g C m^{-3}). The arrows represent carbon fluxes between the pools; each arrow is represented by a term in the model equations. POM is particulate organic matter (medium (M), large (L) and extra large (XL) sizes), and DOC is dissolved organic carbon (extra small (XS) or free). Engineer species are represented as "SAP eng", while "SAP non-eng" are the detritivores. EM stands for ectomycorrhiza.

The scientific background for the model has been described in chapter 1. Here, the related processes are formulated mathematically. We show how this model is parameterized for a forest stand where soil fauna was never studied in detail, but many other soil and stand characteristics are well established. Finally, we show how the model can simulate several known mechanisms of soil faunal effects such as changes in litter recalcitrance affecting fungal/bacterial ratio, changes in pH affecting earthworm populations, effects of soil engineers on bioturbation and hydrology, and importance of microbivores and predators in the soil fauna food web.

METHODOLOGY

The initial values of soil porosity in the model simulations can be calculated from measured soil water retention curves, or even using models such as Saxton *et al*. (1986) that yield field capacity, porosity and wilting point from the C, clay and sand contents, or using measured bulk density (D_b). Following Malamoud *et al*. (2009), the percentage of total porosity ($P_{\%}$) can be computed from D_b and soil particle density (D_S) as shown in equation 2. D_S can be measured or is calculated from D_m = soil mineral particle density (2.65 g cm^{-3}) and D_{SOM} = organic particle density (1.35 g cm^{-3}) as:

$$D_s = \frac{100}{\frac{\%\,SOM}{D_{SOM}} - \frac{100 - \%\,SOM}{D_m}} \qquad (1)$$

$$P_{\%} = \frac{D_s - D_b}{D_s} 100 \qquad (2)$$

Water flow

We advise using our model in combination with a detailed water model including preferential flow through macropores as well as good representation for matrix flow (s.a. Richards' equation). However, we show in this paper how it can be used with a simpler representation of water flow but still allowing the important dynamic interactions between pore sizes and hydrology that are fundamental to the model. A spilling bucket approach is used at a daily time-step, where water drains from a layer into the underlying layer when its water content is above field capacity in the soil matrix. However, in contrast to conventional spilling bucket models, we allow water to flow faster through macropores (before the soil matrix is saturated). Net precipitation (P_{net}) is calculated as:

$$P_{net} = P - E \qquad (3)$$

where P is precipitation (mm day^{-1}) and E is evapotranspiration (mm day^{-1}). The daily loss of water by evapotranspiration is calculated using an equation for potential evapotranspiration based on Thornthwait (1948). Infiltration (I) is assumed to be equal to the part of precipitation entering the soil. Infiltration and runoff (P_{runoff}, mm day^{-1}) must equal P_{net} .

$$I + P_{runoff} = P_{net} \qquad (4)$$

Infiltration is composed of water entering the soil matrix, water filling the macropores and water draining from macropores. Water that enters macropores remains in the macropore domain or enters the layers below. The fraction of infiltration entering macropores depends on the surface area of the macropores (SA_{macro}), assumed cylindrical. Assume measured or derived maximal infiltration rate (I_{maxMat}, mm day^{-1}) of the soil matrix. Maximal infiltration rate through macropores (I_{maxPor}, mm day^{-1}) is calculated from the volume of the pores (PV_{macro}), assumed not limiting at daily scale, plus infiltration capacity of the layer (n+1) in which the macropores end.

$$I_{maxPor} = PV_{macro} + I_{maxMat\ (n+1)} \qquad (5)$$

If $P_{net} > (I_{maxPor} + I_{maxMat})$ runoff is calculated as:

$$P_{runoff} = P_{net} - (I_{maxPor} + I_{maxMat}) \qquad (6)$$

after which calculations continue using P_{net} - P_{runoff} as net precipitation.

If $I_{maxMat} < P_{net} < (I_{maxPor} + I_{maxMat})$ the soil matrix is filled at a rate equal to the maximum infiltration rate, all other water is lost either through the macropores to the next layer or by filling macropores. If $I_{maxMat} > P_{net}$ the soil matrix is filled with water, traditional spilling bucket, but an equivalent volume is lost through macropores to the bottom layer depending on the surface area of the macropores. The total soil water volume of soil layer n, SW_n, is then limited by the total pore volume of the layer and the water already filling the pores, and is calculated as:

$$SW_n = SW_n + \min(PV_n - SW_n, I_{maxmat}(1 - SA_{macro}), Pnet(1 - SA_{macro})) \quad (7)$$

For drainage (D) to the bottom layer, the spilling bucket approach is used plus a portion of water that goes straight through the macropores, calculated from the surface area of the macropores.

$$D_n = P_{net} SA_{macro} + P_{net} - \min(PV_n - SW_n, I_{maxmat}(1 - SA_{macro}), P_{net}(1 - SA_{macro})) \quad (8)$$

For each pore size class the fraction water filled is calculated from the water content: so always one pore size is partially saturated and all others are either saturated or dry within one layer.

C flow

The KEYLINK model combines soil organic matter modelling with soil food web modelling. The model conceptualized in **Figure 1** has 13 carbon pools, visualised by boxes. Above and belowground litter is assumed to be provided from an external source (*tree shoot* in **Figure 1**) not covered by this model. It could be given through experimental data or an external model, e.g., a tree growth model that delivers the input of litter into the litter pool. All simulations presented here were made with constant C inputs (**Appendix 2**). *Exudation* is an input of organic carbon released from roots into the soil organic matter pool. Every live pool has a respiration rate (R) and a turnover rate (death). On consuming a C pool, a fraction of this pool always becomes faeces and enters the SOM pool except for the microbial pools, i.e. microbes and microbivores. SOM can be distributed in different fractions, particulate organic matter (POM) and dissolved organic matter (DOM), which can gain relevance in the addition and simulation of other nutrient cycles and processes as leaching. However, here, as a first version of the model, we present a simplification using SOM as a uniform pool. The growth (G, g C m^{-3}) of a biomass pool (B, g C m^{-3}) is described according to Monod kinetic,

$$G = \Sigma(g_{max}\left(\frac{Sf_a}{K_s+S}\right))B \quad (9)$$

where g_{max} is the maximal rate of growth. Substrate (S, g C m^{-3}) is the consumable pool, litter, SOM or biomass of soil organism, that consumer pool (B) can use but corrected by its available fraction (f_a). All fluxes of consumed C from each S are summed. K_s is related to substrate quality, it gives the content required to get half the maximal growth. This is not related to the amount that will be consumed, because consumed C equals growth + faeces, but shows how dense the material needs to be 'found' by the consumer. Availability of a S to a consumer (as f_a) is calculated using the fraction from

total porosity volume that is accessible for the consumer, by size, minus its fraction that is completely flooded or dry. This availability introduce a novelty concept, the physical recalcitrance, highlighting the role that soil structure plays affecting C fluxes in the soil, because SOM decomposition rates modelling use to rely on its chemical recalcitrance, from now on referred just as 'recalcitrance'. But physical recalcitrance has proven to be also relevant for the calculation of SOM decomposition rates (von Lützow *et al*., 2008), and soil matrix also affect other biotic interactions through the food web by this availability concept.

Rate of increase of a population of meso- or macrofauna depends on generation time (r, K strategies), age distribution of the population, different life stages. Models exist for some soil fauna species only (Osler and Sommerkorn, 2007; Chertov *et al*. 2017a). To offer a solution that can work for both the microbial biomass and the meso- and macrofauna, we use g_{max} as the maximal rate of increase in number (N) of any population, $dN/dt = g_{max}$ when resources are non-limiting and assuming the population structure is stable and optimal, equal to what is often stated as the intrinsic growth rate of a species (Birch, 1948).

The net rate of change of a biomass pool is the sum of growth (G), respiration (R) and turnover (death, D_t), and possibly predation (P_d), all in g C m^{-3}:

$$\frac{dB}{dt} = G - R - D_t - P_d \qquad (10)$$

R is a function of temperature, through respiration rate (r), and biomass, assuming the same temperature sensitivity as growth; this is somewhat different to how it is seen in many models where a food source is turned over with a specific efficiency. From a more faunal point of view, this makes sense: a food source is ‘consumed’; the consumed material is partly excreted and partly assimilated and spent on respiration and growth (i.e. biomass formation).

$$R = rB \qquad (11)$$

While the death rate d (day^{-1}) is constant.

$$D_t = dB \qquad (12)$$

Predation depends on biomass of predator or microbivore and is calculated from the growth of the predator (G_{pred}) plus the fraction of the prey allocated to faeces (f_{faec}).

$$P_{d_{prey}} = G_{pred}\,(1 + f_{faec}) \qquad (13)$$

Effect of H_2O

Drought or saturation of a pore leads to reduced availability of the C in the pore for its food web consumers. First, the overall effect of hydration is calculated as a modifier (m_{H2Otot}) in function of volumetric soil moisture (V) and pore volume (P_{vol}) (after Freytag and Luttich, 1985).

$$m_{H2Otot} = \begin{cases} 4\frac{V}{P_{vol}}\left(1 - \frac{V}{P_{vol}}\right) & \text{for } \frac{V}{P_{vol}} < 0.5 \\ 1 & \text{for } \frac{V}{P_{vol}} > 0.5 \end{cases} \qquad (14)$$

The activity is always in the pores that are not water-logged therefore the pore size class that is partially filled with water, and the pore size above that is assumed not yet completely dry (after Kuka *et al*., 2007).

$$m_{H2O} = \frac{P_{volA}}{P_{volA} + P_{volW}} m_{H2Otot} \quad \text{for the pores partially filled,} \quad (15)$$

$$m_{H2O} = \frac{P_{volW}}{P_{volA} + P_{volW}} m_{H2Otot} \quad \text{for the pores one class above,} \quad (16)$$

where P_{volW} is the water filled pore volume and P_{volA} is the aerated pore volume. The availability (a) of a substrate to a consumer is defined by the inherent availability of the pore size to the consumer, multiplied with m_{H2O}. For surface litter these calculations are not possible since the surface litter is not in the soil matrix. However, on days without precipitation, litter humidity is assumed to be related to the soil humidity below, therefore the m_{H2O} calculated for the microbial biomass is used.

Simulating the variability in g_{max}

The maximum growth of biota is influenced by different environmental factors. Each one can lead to a modifier ($m \in [0, 1]$) on g_{max}. It is easy to change, add or turn off specific modifiers according to the soil studied. Here we present a modelling framework focused on abiotic controls of growth rates, but there is room for new add-ons as for example a density-dependent microbial turnover. While interaction processes affected by the demographic density of microbial communities (e.g. competition, space constraints) can play also a significant role controlling growth and decomposition rates and improve its modelling (Georgiou *et al*., 2017), our aim in this work is to link the key roles of fauna and soil structure in C cycle modelling, and together with the hydrology can simulate constraints in biotic interactions, which are also relevant controls in microbial growth and activity.

Simulating the effect of temperature (T)

To simulate the effect of T on growth rate through a temperature modifier (m_T), we use a Q10-shaped curve between maximum tolerable temperature (T_{max}) and minimum temperature for consumers activity (T_{min}), set as a default at 0°C (Franko, 1989), but unlike many models, we assume a plateau above the optimal temperature (T_{opt}).

$$m_T = \begin{cases} 0, & T < T_{min} \text{ or } T > T_{max} \\ Q^{(T-T_{opt})/10}, & T_{min} < T < T_{opt} \\ 1, & T_{opt} < T < T_{max} \end{cases} \quad (17)$$

However, temperature also increases respiration (R). To simulate this temperature effect, we assume the same Q10 function but without the plateau; in this way, when T is above the optimum, R increases while growth does not. At some point these lines will cross and cause a net reduction in biomass.

Effect of pH on growth

A good example of an optional effect is the effect of pH: for a system close to a threshold, simulating pH can be very important, assuming a good knowledge of the system. But for well-buffered systems, it is an unnecessary increase in complexity. g_{max} decreases at low pH for bacteria but increases for fungi. For this example, we put the thresholds at 8 for fungi and 3 for bacteria inducing a 10 fold reduction in g_{max} for a change in pH of 1.

$$m_{pH} = 1/((pH - 8)10) \quad \text{for fungi if } pH > 8 \quad (18)$$

$$m_{pH} = 1/((3 - pH)10) \quad \text{for bacteria if } pH < 3 \quad (19)$$

In any other case for bacteria or fungi, $m_{pH} = 1$. For engineer saprotrophs, their optimal g_{max} changes (becoming g_{maxEng}) with pH according to the following equation:

$$g_{maxEng} = \begin{cases} 0, & \text{if } pH < 3 \\ \left(\frac{g_{max}}{2}\right)(pH - 3), & \text{if } 3 \leq pH < 5 \\ g_{max}, & \text{if } pH \geq 5 \end{cases} \quad (20)$$

Effect of recalcitrance and CN on g_{max}

Overall consumption of an organism that can consume different pools is computed by simply adding them up. However, litter is not necessarily as 'palatable' depending on CN ratio, if not enough N then it is needed to consume more, and recalcitrance, if low in energy it is needed to consume more, through modifiers m_{CN} and m_{rec}. This is simulated by changing g_{max}. The equation for m_{rec} is not necessary and only important if enough data on litter quality is available or the users are interested into looking into the effects of changes in litter quality. The litter pool can be consumed by both bacteria and fungi, and of course also detritivores. Depending on the CN ratio, the competition between these two is different; this is simulated by the g_{max} of the bacteria being more variable with CN ratio. The sensitivity is described by the parameter p_{mCN}, between 0 and 1.

$$\text{fungi: } m_{CN\,fung} = \min\left(1, \left(\frac{CN_{fung}}{CN_{lit}}\right)^{p_{mCN\,fung}}\right) \quad (21)$$

$$\text{bacteria: } m_{CN\,bact} = \min\left(1, \left(\frac{CN_{bact}}{CN_{lit}}\right)^{p_{mCN\,bact}}\right) \quad (22)$$

For litter recalcitrance (Rec_{lit}), a linear equation instead of a power is chosen so that decay of the recalcitrant litter is 0 if $p_{mRec} = 1$ and is unaffected if $p_{mRec} = 0$.

$$\text{fungi: } m_{rec\,fung} = \min(1, 1 - p_{mRec\,fung}\, Rec_{lit}) \quad (23)$$

$$\text{bacteria: } m_{rec\,bact} = \min(1, 1 - p_{mRec\,bact}\, Rec_{lit}) \quad (24)$$

Adding up all these modifying effects on g_{max}

We assume a complete additivity of the effects, so the different modifiers on g_{max} are multiplied to get the overall effect, m_{tot} in equation 25. Another optional approach could be to use only the most limiting effect, setting m_{tot} equal to the lowest modifier and ignoring the rest.

$$m_{tot} = m_{CN}\, m_{rec}\, m_{pH}\, m_{H2O} \qquad (25)$$

Closing the C budget

The reduction in a substrate equals the growth of the consumer plus the C that goes to faeces (excrements) and to respiration. Fraction to excrement (f_{faec}) is a parameter of the consumer and assumed constant. However, one consumes more and a larger fraction becomes faeces at a lower substrate quality, for the meso- and macro fauna, because microbes do not produce excrements; the sensitivity of f_{faec} to CN ratio is expressed by the modifier m_{faec}. This is however only relevant for the detritivores and engineers (equation 26) that eat SOM and litter which can contain extremely variable amounts of nutrients; for the predators and herbivores we assume the variability is minimal. For the microbes, it was calculated as an effect on g_{max}.

$$f_{faecEff} = f_{faec} + m_{faec}\, \frac{CN_{SOM} - CN_{eng}}{CN_{SOM}}\, f_{faec} \qquad (26)$$

Closing the budget of recalcitrance and N

KEYLINK can be run with or without a detailed N model, but if a detailed N model is included, it is important to close the N budget; if not the following equations need not be used. Including a closed recalcitrance budget if N is not included seems an unlikely choice since N is more important than recalcitrance as a driver. Respiration reduces the C of the biomass pool of the organism. The associated N goes into excretion for larger fauna; for microbes, it is mineralised to ammonium (i.e. plant available mineral N) unless it is necessary for growth, if the CN ratio of the SOM is higher than that of the biota after deducting respiration. For microbes growth on a source not containing enough N is possible but the ratio respiration to growth will increase to close the budget.

$$g_{max} = R + \frac{CN_{SOM}}{CN_{bact}} R \qquad (27)$$

When there is no N simulated, this equation will stop almost all bacterial growth, because litter has a much higher CN ratio. In this case, we recommend to replace equation (27) by calibrating the m_{CN}. The faeces recalcitrance and CN ratio are calculated from the difference between consumer and consumed source for the larger fauna. To close the N cycle it is important that the consumer cannot grow if there is not enough N to build its tissues: faeces can have a lower or higher N content depending on the fraction to faeces (f_{faec}), which increases if N is limiting. This is only relevant for detritivores and engineers, because the others eat each other at constant CN ratios. Under N limitation, N consumed plus available from respiration surplus needs to equal N used for growth.

$$\frac{(1+ f_{faecCN})C_{SOM}}{CN_{SOM}} = \frac{g_{max}}{CN_{eng}} \quad (28)$$

$$f_{faecCN} = \frac{g_{max}\ CN_{SOM}}{CN_{eng}\ C_{SOM}} - 1 \quad (29)$$

$$f_{faecEff} = \max(f_{faec}, f_{faecCN}) \quad (30)$$

For recalcitrance of SOM, if enough data are available to include this, assume faeces are twice as recalcitrant as the consumed pool. Recalcitrance of each faunal group is an input constant.

Calculations regarding engineers

Soil changes made by engineer species depend on their body width, but in the model this is simplified using initial parameters for engineers' effects that must be chosen based on an average width (see **Appendix 2**); the model then simulates their daily effects using their biomass. Bioturbation is a function of engineer biomass (B_{eng}, g C), which calculates organic matter moving to deeper layers: litter moving (g C_{lit}/g C_{eng} day) from litter layer to end of burrow, and SOM moving by mixing of soil between layers (g C_{SOM}/g C_{eng} day). In this first version of the model, with only one soil layer, bioturbation works as a C output flow, but in future versions with more layers it could be upgraded to C flows between them.

Burrow volume (PV_B, l/m^3) is a function of engineer biomass and the ratio of pore volume to engineer biomass (VE_{ratio}, l/g C_{eng} m^3) but towards a maximum (PV_{Bmax}):

$$PV_B = \min(dPV_{Bmax}, dVE_{ratio}\ B_{eng}) \quad (31)$$

where d is layer depth (m). On the other hand, burrow turnover happens at a constant rate, with average burrow lifespan of 10 years; porosity decreases and burrows become mesopores. This could be improved in future versions including perturbations as the possible effect of heavy rain.

Porosity calculations

The pore volume is distributed in five classes by pore size. Initial pore size distribution is given or measured as the total pore volume (PV, l m^{-3}) in each class. The link between aggregation and porosity is hard to quantify. Regelink et al. (2015a) showed for different soils that overall soil porosity is the sum of the textural porosity determined by the proportion of clay, sand and silt fractions and aggregation porosity. They conclude that micropores, which they define <9 µm, are mainly situated within the aggregates, while mesopores are situated between dry-sieved aggregates. While Regelink *et al*. (2015a) have shown that total micro and mesoporosity (<1000 µm) increases with total aggregate content, Grosbellet *et al*. (2011) have provided evidence that pores in the range 30 – 300 µm decrease with aggregation. Despite of the generally lower ranges for mesopores (9 – 1000 µm) described for soil physics (Lal and Shukla, 2004; Regelink *et al*., 2015a), we want mesopores to be physically accessible to mesofauna body size (ca. 100 – 2000 µm), so we consider that mesopores ranging 30 – 1500 µm are a reasonable compromise. Based on that, we decided to hypothesize that aggregation increases bacterial and micro- porosity while decreasing mesoporosity.

However, we want to emphasize that further experimental studies are needed to establish robust relationships between aggregation and pore size distribution.

Aggregates are not calculated as a pool, but the effect of aggregation is included in the calculation of porosity as described below. The following three porosities contribute to total porosity:

- Textural porosity (PV_{text}): measured or calculated from % clay and sand.
- Additional aggregation porosity (PV_{Ag}): all porosity in surplus of textural, can be estimated, for example from PTF (PedoTransfer Function) or calculated empirically from SOM and fungal biomass, i.e. mycorrhiza and other fungi, max 2% porosity extra (equation 33). Aggregation (Ag) is the fraction (0–1) of the SOM aggregated calculated as (based on the data from Malamoud *et al*., 2009):

$$Ag = \min\left(1, \frac{c\left(B_{fung} + B_{myc}\right)}{B_{SOM}}\right) \qquad (32)$$

  with an empirical parameter c = 10. The aggregation porosity is then calculated as:

$$PV_{Ag} = k\, Ag\, B_{SOM} \qquad (33)$$

  with k = coefficient (2 l g C^{-1} m^{-3}) based on empirical data (Regelink *et al*., 2015a, b).

- Bioporosity (PV_B): biopores created by engineers. Pore formation by engineers increases macroporosity, increasing soil layer thickness, but at the same time reduces mesoporosity as engineers push soil aside and produce casts that are denser than average soil. The relative importance of these two effects depends on the engineers' activity patterns, and is reflected by the parameter $f_{PV} \in (0, 1)$, which gives the fraction of the change in biopore volume that increases macroporosity. Therefore, the counterpart of the biopore volume $(1 - f_{PV})\, PV_B$ is 'compensated' by a decrease in mesoporosity.

Conceptually, the total soil porosity is then the sum of:

$$PV_{tot} = PV_{text} + PV_{Ag} + f_{PV}\, PV_B \qquad (34)$$

In the model, pore volume is calculated for each pore size separately.

The volume of micropores (PV_{micro}) and bacterial pores (PV_{bact}) increases with increasing aggregation. Apart from creating additional porosity depending on the total amount of aggregated SOM (eq. 33), aggregation also increases the relative micro- and bacterial pore volume at the expense of (textural) mesoporosity (PV_{meso}), therefore not increasing total porosity. This effect is controlled by available pore space between mineral particles (i.e. textural mesoporosity) and we assume that half of this mesoporosity can be affected by aggregation. In both cases, we assume that the increase in porosity due to aggregation is divided equally among micropores and bacterial pores. The pore volume in different size classes is calculated as:

$$PV_{macro} = PV_{textmac\ ro} + PV_B \qquad (35)$$

$$PV_{meso} = PV_{textmeso} - \left(1 - f_{PV}\right)PV_B - \frac{Ag}{2} PV_{textmeso} \qquad (36)$$

$$PV_{micro} = PV_{textmicro} + k\frac{Ag}{2} B_{SOM} + \frac{Ag}{4} PV_{textmeso} \qquad (37)$$

$$PV_{bact} = PV_{textbact} + k\frac{Ag}{2} B_{SOM} + \frac{Ag}{4} PV_{textmeso} \quad (38)$$

Volume of inaccessible pores is assumed to be constant and equal to $PV_{textinac}$.

These changes are calculated daily to give a dynamic feedback to the hydrology and to the distribution of each C source among pore classes, affecting its availability.

Leaching

Water leaving one soil layer (n) is moved to the layer below (n+1). Dissolved organic and inorganic compounds are a complex matter to simulate since they are strongly dependent on the pH and the mother-material, i.e. clay and Ca rich or not. Nonetheless, in many systems simulating leaching of N and DOM is highly relevant. Unless better data are available, we suggest the following, semi-empirical method:

DOM can be simulated in relation to the CO_2 released, high 'activity' in the soil, as total respiration (R_{tot}) by the fraction of respiration from DOM (f_{DOM}), similar to the concepts used in the LIDEL model, in addition to the directly exuded DOM (C_{Exud}). Assuming a short half-life of DOM and semi-empirically, because daily concentration is not 'equal' to daily production but is linearly related to the daily production, we consider:

$$DOM = C_{Exud} + f_{DOM} R_{tot} \quad (39)$$

DOM has a short half-life but the dissolution is even faster (hours). We assume the daily concentration is in equilibrium between dissolved and adsorbed (DOM_{ad}) depending on adsorption coefficient K_D of the soil (m^3 kg^{-1} soil). Similar to the modelling in Orchidee-SOM (Cammino-Serrano *et al*., 2018) we assume:

$$DOM_{ad} = K_D DOM \quad (40)$$

In addition depending on the minerals and pH, more or less DOM and mineral N will be dissolved. More clay means less mobile DOM, and lower pH is also a cause of less mobile DOM.

$$K_D = a_{KD} - b_{KD} pH + c_{KD} fClay \quad (41)$$

with values 0.001226, 0.000212 and 0.00374 respectively for a_{KD}, b_{KD} and c_{KD}, from Cammino-Serrano *et al*. (2018).

Calculation order

Sequence of function sets used by the model to calculate all carbon fluxes and ecosystem changes:

a) Calculate the pore size fractions in 5 classes and the associated pore surface areas
b) Calculate the water volume of the relevant pore size
c) Use the precipitation leaching to calculate DOM leaching
d) Calculate for each biota group the accessibility of each of the pools it consumes
e) Calculate the g_{max} depending on temperature, H_2O, CN, pH and recalcitrance
f) Solve the 12 differential equations for increase/decrease of all C pools
g) Update all C pools

h) Calculate the new CN and recalcitrance of each pool
i) Calculate engineering effect
    a. Update macropores
    b. Update SOM from bioturbation
j) Calculate other changes in pore size distribution from weather or management

KEYLINK core model consist in steps from d to i; steps a, b, c and j are add-ons that could be replaced by other models (e.g. water flow model) coupled to KEYLINK. Steps a-c are used to calculate the distribution of porosity between the pore classes, the hydrology and daily soil water content (distributed among pore classes), and then step d calculates how that is affecting the availability of each C source to its consumers. That couples soil structure and hydrology with trophic interactions, allowing the resolution of differential equations for C fluxes.

Model coding and output

KEYLINK consists of a relatively limited, freely downloadable Python code (available at: https://github.com/Plant-Root-Soil-Interactions-Modelling/KEYLINK) that is very easy to modify and calibrate towards specific questions or ecosystems, and to link to existing ecosystem models. Each of the modifiers on growth, i.e. temperature, pH, H_2O, recalcitrance and CN, as well as the primal shape of the growth equations can be adapted. The inputs in the current version are read from data-files but are easy to link to a mechanistic model. The output of the current version consist of all daily C pools as well as the main C fluxes. KEYLINK is also available as a stand-alone executable model, allowing it to be called from models in other languages. A single run of ten years could take less than one minute (depending on computing power). We advise using at least a hundred runs to reach a more representative result; this takes approximately one hour from a dataset of a hundred input parameter sets. In this version, the average results over the hundred runs are calculated but also all daily outputs of each run are saved.

Input parameters of species

The KEYLINK model framework is conceptualized as an adaptable framework. Each user needs to determine for their specific site and questions the main drivers and pools required. Depending on the dataset, it is in general better to use less pools and equations if sparse data are available. Moreover, KEYLINK is not a soil fauna model and was not designed to simulate specific soil fauna species in detail. The soil fauna groups used consist of a wide range of species, for which average data are used. Species categories have been described in chapter 1.

Microbes and meso-macro fauna have a temperature curve using an optimum, minimum and maximum temperature. Each soil biota group also has its own maximum growth rate, CN ratio, respiration rate and size. Death rate (D_t) is the inverse of turnover, mostly given in days. In **Appendix 2** we briefly review main input parameters. We propose setting Ks, the concentration of the food source at which growth rate is half the maximum, equal to the existing concentrations for all meso-and macro fauna, so assuming growth could double at unlimiting food source. But for microbial biomass the difference between growth of bacteria on a petri-dish unlimited in nutrients compared to

field data of soil microbes clearly indicates that g_{max} in the soil is not comparable to laboratory data; if such data of g_{max} are used, the Ks should be increased considerably.

Calibration for Brasschaat pine forest

Calibration methodology was explained in the general methodology. We show here the results from a calibration towards data measured and assumed, using proportions between fauna groups in Persson *et al*. (1980), in the Brasschaat Scots pine stand in Belgium. This forest stand is relatively well described in many publications concerning the trees and the total ecosystem fluxes, but less concerning the soil and very little was measured on soil fauna. We use this forest as an example of how the KEYLINK model can be used to improve our understanding of the system even when detailed soil data are limiting.

The parameters g_{max} and Ks and R are linked (increasing g_{max} has a similar effect to decreasing Ks or R). However, g_{max} or R ranges can be found in literature relatively easily. Therefore, we use fixed values for Ks (see **Appendix 2**) and parameterize g_{max} within the known limits. In this way, the number of parameters to be calibrated is 9, which is a reasonable number for most cases where limited data to calibrate towards are available. Of course, a user could decide to optimize more parameters if more data are available. A useful 'rule of the thumb' is limiting the number of parameters to the square root of the number of calibration data available (Jörgensen, 2009), which means we can get a reasonable result for 9 parameters assuming 81 data points.

In our case, no measurements were available and information in the literature was scant. Therefore, we deliberately defined wide ranges for the prior values of each parameter to cover all the possible values found in the literature (Chuine, 2000; Linkosalo *et al*., 2008). For species for which no prior parameter information was available, we assumed parameter values equal to the mean value of the range. The initial uncertainty of each parameter is quantified in terms of a prior probability distribution with lower and upper bounds. Because of lack of detailed knowledge, we assumed the distribution as uniform and non-correlated.

The g_{max} values were optimized using the prior range for g_{max} (**Table 1**). The data used to calibrate against were chosen to give a 'standard' procedure, so limited to biomass of the different C pools, including all available data s.a. soil respiration, soil humidity would improve the run for Brasschaat, but would not be a representative run for the model. Other parameter settings, e.g. sensitivity to CN and recalcitrance, were based on model runs of the Brasschaat site by Deckmyn *et al*. (2011).

gmax	Lower bounds	Upper bounds
Bacteria	0	10
Fungi	0	6
Mycorrhiza	0	6
Bacterivores	0	4
Fungivores	0	4
Detritivores	0	0.5
Engineers	0	0.5
Herbivores	0	0.5
Predators	0	0.5

Table 1. Lower and upper bounds for the g_{max} prior probability distribution, for each one of the nine functional groups in the food web.

We ran the model for the time period 1999-2008, because this was the period in which the forest was still clearly dominated by Scots pine; since then a transition to more deciduous trees has been taking place. We calibrated towards stable C pools over the ten years for all C pools, with an allowed error margin of 20% for all faunal pools, except 10% for predators, and 12.5% for litter and SOM. Daily climate data (temperature and precipitation) were used. The full range of input data can be found in **Appendix 2**, except climate data, which can be downloaded with the model. Choosing to calibrate towards one (see for example chapter 3) or more pools can yield different results, and it depends on the end-user's goal which calibration is preferred.

RESULTS AND DISCUSSION

The model was run ca. 21000 times with different parameter settings sampled from the prior parameter distribution. A burn-in was applied deleting the first half of the posterior distribution of accepted parameter sets of the 9 g_{max} values. Then, a Latin Hypercube Sample (LHS) was taken with 100 parameter vectors for g_{max} (**Table 2**).

	Best g_{max}	LHS g_{max}	Posterior g_{max}
Bacteria	0.972	1.310 ± 0.852	1.346 ± 0.832
Fungi	0.183	1.376 ± 0.915	1.422 ± 0.888
Mycorrhiza	0.854	1.547 ± 0.861	1.552 ± 0.848
Bacterivores	0.090	1.468 ± 0.877	1.555 ± 0.882
Fungivores	0.026	1.271 ± 0.882	1.409 ± 0.907
Detritivores	0.023	0.270 ± 0.162	0.241 ± 0.150
Engineers	0.390	0.255 ± 0.145	0.253 ± 0.145
Herbivores	0.448	0.247 ± 0.136	0.251 ± 0.141
Predators	0.199	0.252 ± 0.132	0.258 ± 0.144

Table 2. Resulting best g_{max} from the posterior and g_{max} (averages ± standard deviation) from the Latin Hypercube Sample (LHS) and the posterior distribution (after the burn-in) of the KEYLINK model calibrated for the Brasschaat Scots pine forest.

The optimization clearly showed the strong link between the different groups of soil biota, e.g. a high g_{max} for bacteria was coupled to a high g_{max} for bacterivores. Running the model 100 times using the LHS of the g_{max} values resulted in predictions with a quite wide range. The alternative five scenarios compared to the basal one can show very different results concerning specific C pools (**Table 3**).

Mycorrhiza, herbivores and detritivores are relatively uncoupled, though influenced by predators, and follow the yearly climate curves. The bacterial and fungal biomasses are very strongly linked. The high g_{max} of bacteria allows steep peaks, which are generally followed by peaks in bacterivore biomass. As we used constant litter input into the soil and used a calculated constant fraction of potential evapotranspiration as water uptake from the soil, it cannot be expected that these results follow the normal annual trends in fluctuations of those fluxes. But for more realistic simulations the model can be coupled with other models that give that information as outputs, or with measured datasets.

Average SOM shows a decreasing trend in the first years, which is not found in data on the forest. This appears to be linked mainly to the microbial biomass and growth rate. Choosing parameter sets that result in a stable SOM on average within a range of measured values (about 11000 g/m^3) is a recommended criterion. Bacterial g_{max} and the final SOM, after ten years, in the Latin Hypercube Sample have a weak but significant correlation (**Fig. 2**), that shows too low values of SOM for bacterial g_{max} above 1.5; so this seems to be a threshold in that parameter, which is crucial for SOM stability and should be below that threshold.

C-pools	basal	rec 20%	CN_{lit} 40	pH 5.9	B_{pred} 0	clay 15%
Bacteria	67.9±13.2	72.2±13.6	70.6±13.0	66.2±13.0	11.4±4.3	73.0±13.1
Fungi	95.9±12.5	96.7±12.2	96.9±12.5	94.1±12.3	49.0±7.8	77.8±11.3
Mycorrhiza	63.2±4.7	63.9±4.6	62.1±4.5	62.9±4.6	38.5±2.8	65.5±5.4
Bactvores	5.7±2.5	6.1±2.5	5.8±2.6	3.2±1.3	6.3±2.8	6.8±2.9
Fungivores	85.7±9.9	89.9±10.0	86.2±9.9	82.7±9.6	124.6±13.1	89.6±10.1
Detritivores	29.4±10.4	28.3±10.0	29.3±10.3	23.9±9.7	294.2±26.6	25.1±10.2
Engineers	0.03±0.02	0.03±0.02	0.03±0.02	0.07±0.03	0.38±0.06	0.03±0.02
Herbivores	7.36±0.97	7.43±0.97	7.38±0.97	7.24±0.96	30.60±1.07	7.74±0.99
Predators	122.1±12.0	127.1±12.4	124.9±12.3	122.2±12.0	0.0±0.0	117.1±11.3
Litter	2382.7±158.4	2110.1±153.5	2247.3±158.5	2430.5±156.6	1047.6±150.2	2448.5±160.9
SOM	6157.8±317.1	6105.2±310.2	6111.8±313.6	6086.9±317.2	3987.1±191.3	6589.0±309.3

Table 3. Effect of changes in input parameter on the average C-pool (in g C m^{-3}) size over 10 years. Averages and standard errors from 100 runs of ten years with the Latin Hypercube Sample parameter sets. The "basal" column has the results using reference input parameters (**Appendix 2**), and the other columns show the results with lower litter recalcitrance (rec 20%), lower input litter CN ratio (CN_{lit} 40), higher pH (5.9), excluding predators (B_{pred} 0) and a higher clay content in the soil (clay 15%), respectively.

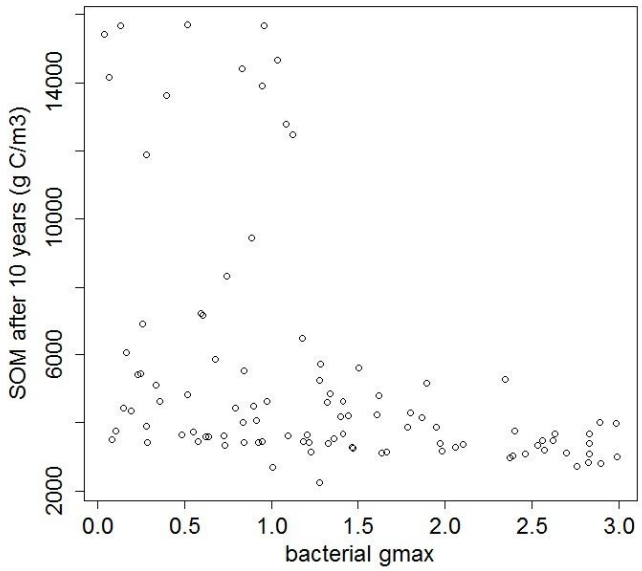

Figure 2. SOM and bacterial g_{max} regression. Each point represents the final SOM (in g C m^{-3}) after 10 years of simulation with the basal scenario and an initial bacterial g_{max} (maximal growth rate) from the Latin Hypercube Sample (p-value <0.0001, R^2= 0.1662).

All C-pools tend to reach stability after the first years, suggesting the model is well-balanced; however, stability values seem to be more sensitive to changes in g_{max} parameters for some pools (e.g. SOM). The set-up of the model, where we only calibrate the faunal g_{max}, does not allow calibration towards different ratio of litter and SOM decay. This depends on the uncalibrated parameter fragmentation, the sensitivity to recalcitrance, but also the temperature used for the litter and SOM. Here we used the same temperature while in reality, since we use data from the top 1 m of soil; a lower temperature for SOM compared to surface litter would be more realistic.

An overview of all C-pools under the different simulation scenarios shows how changing one input parameter at a time influences the results. It must be born in mind that KEYLINK was run as a stand-alone model; linking it to a model or more detailed data of the aboveground ecosystem would greatly influence the results, but would not allow clear interpretation of the model functioning due to feedbacks. To further elucidate these effects and to show some of the potential outputs the model can give, we show a few of the most interesting fluxes (**Table 4**).

	units	basal	rec 20%	CN_{lit} 40	pH 5.9	B_{pred} 0	clay 15%
R_{bact}	g C m^{-3}	1516±319	1625±334	1613±328	1463±317	174±64	1585±310
R_{fun}	g C m^{-3}	2831±362	2859±356	2851±364	2789±362	1596±241	2409±339
R_{myc}	g C m^{-3}	1307±117	1333±115	1300±118	1306±120	781±61	1388±136
Bact SOM turnover	g C m^{-3}	7633±1586	8159±1666	7840±1582	7260±1573	1311±489	8077±1555
Bact litter turnover	g C m^{-3}	607±122	669±132	686±132	598±122	40±18	669±126
Eng litter turnover	g C m^{-3}	22.5±15.2	22.4±15.2	20.4±13.7	33.3±17.1	189.1±38.9	23.2±15.5
B_{fungi}/B_{bact}	-	2.34	2.23	2.25	2.37	7.69	1.96
SWC	l m^{-3}	140.3±1.8	140.8±1.8	140.5±1.8	140.2±1.8	131.8±1.2	318.9±1.6

Table 4. Effect of changes in input parameter on major output fluxes over 10 years. The first three rows show bacterial, fungal and mycorrhiza respiration (R) fluxes (g C m^{-3}), respectively. The next three rows show the total turnover (g C m^{-3}) on an organic matter pool carried out by bacteria (Bact) or engineers (Eng) over 10 years. The penultimate row shows the fungi to bacteria ratio. And the last row is soil water content (SWC, l m^{-3}). Columns show average values and standard errors from 100 runs of ten years from the Latin Hypercube Sample, with a basal scenario using reference input parameters (**Appendix 2**), and the same changes from it as in **Table 3**.

The fungal/bacterial ratio (FB) is an important descriptive of an environment. The difference in sensitivity to pH, CN and recalcitrance of bacteria and fungi explain the differences found in populations.

FB = 1.5 + 0.31CN (forest) or FB = - 0.31 + 0.03CN (Chertov *et al*., 2017a; from Mulder *et al*., 2009).

Our results fit into this range (0.23 to 7.08) since the two equations yield very different results at the measured CN of Brasschaat (18). The model reacts as expected to changes in CN and recalcitrance reducing litter decay and increasing fungal to bacterial ratio with lower quality litter input. Increasing clay content resulted in an obvious increase in water content and a decrease in SOM decay while fungal/bacterial ratio decreased.

The Brasschaat forest is sandy, with low pH and recalcitrant litter; as expected, this is an environment not suited to earthworms. The model correctly simulated extremely low values of engineer biomass. Increasing the pH increased the engineers pool, e.g. earthworms population, but this remained too low to have a significant impact on the system. This is quite realistic as neither litter quality nor soil quality are ideal for earthworms. Obviously, to calibrate the specific parameters concerning earthworms the Brasschaat forest is not an ideal site.

The run without predators showed the most interesting results because the interactions between the different food web parts are apparent. Decay is reduced as fungi and bacteria are consumed by bacterivores and fungivores. This is partially compensated by an increase in engineer populations. Exclusion of predators, setting the starting biomass of that pool at 0, showed how the model tracks its crucial role in the ecosystem (**Fig. 3**). Predators produce a top-down trophic cascade on the food web, e.g. on herbivores and roots, but despite of the decrease in bacteria and fungi without predators due to this phenomenon, SOM and litter were also lower without predators. This could be explained by the effect of predators on soil matrix through engineering species, as we discuss in the next section; so the model successfully tracked soil food web dynamics and also their interactions with soil porosity. The effect of larger soil predators (e.g. Araneae, Carabidae, Formicidae) slowing down SOM decomposition and enhancing its stabilization has been previously found in experiments (Kajak, 1995), as well as mycorrhiza effect on porosity by making aggregates (Siddiky *et al*., 2012). Therefore, KEYLINK model seems to fit with the expected food web and C dynamics, and could serve to improve the biogeochemical cycles modelling, as is needed for larger scale predictions (Grandy *et al*., 2016), by coupling it with other ecosystem models.

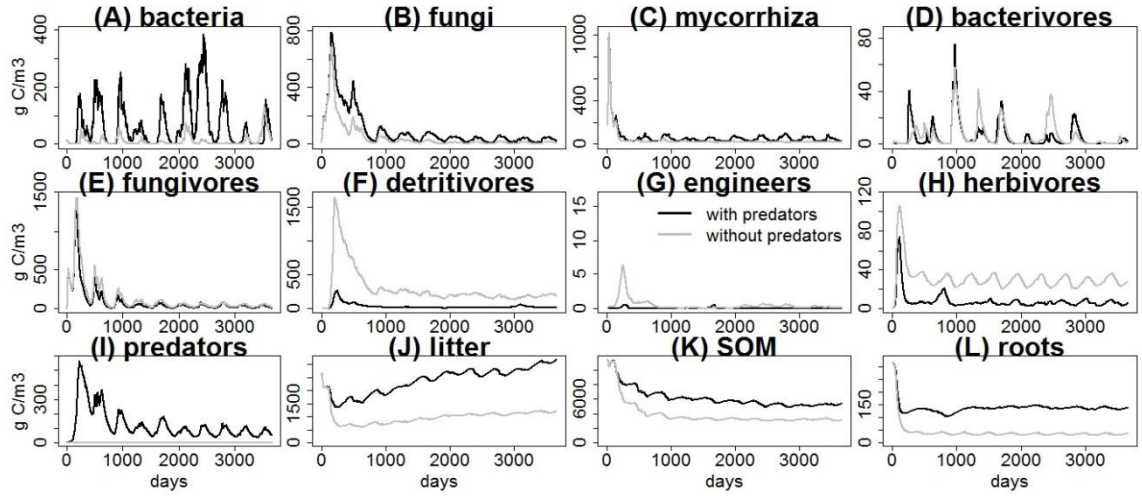

Figure 3. C pools daily biomass averages and predation effect. Averages of C pools (in g C m^{-3}) among 100 simulations of ten years using the Latin Hypercube Sample, with predators (black) and excluding them (grey).

Hydrology is influenced by aggregation and by macropore formation by soil engineers. The increased macroporosity increases infiltration rate with reduced water-logging and runoff. Predators have a clear indirect effect on soil porosity by eating engineer species, and also microbivore species, which leads to changes in soil hydrology (**Fig. 4**). Bacterial pores and micropores variations in volume are positively correlated, while mesopores variations are negatively correlated with both; the higher volume in mesopores, the lower in the two other classes, and the faster the water drains from the soil layer. That is what we can expect to happen in real soils, so the model seems to simulate appropriately those dynamics. The increase in macro and mesoporosity volumes without predators, so with higher engineers, resulted in a decrease of soil water content of 6 % (increasing the pore aeration), and under those conditions the availability of SOM and litter for bacteria and fungi could be increased, explaining why SOM and litter are lower even with lower bacteria and fungi. These results also indicate that the model runs reach an equilibrium in C pools, soil porosity and hydrology after ca. 1000 days.

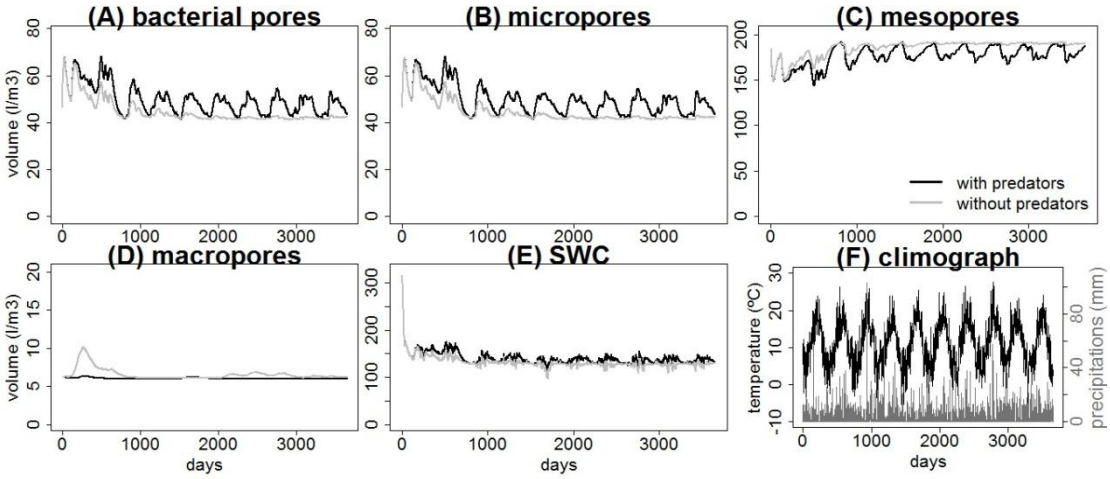

Figure 4. Daily volume averages of soil water content (SWC) and pore size classes in the soil matrix, and climograph. Means of volume (in l m^{-3}) among 100 simulations of ten years using the Latin Hypercube Sample, with predators (black) and excluding them (grey); graphs **A**-**D** for pore size classes, **E** for SWC, and climograph (**F**) of the weather data from Brasschaat between 1999 and 2008, showing daily temperature (black) and precipitations (grey). The innaccesible pore size class is not shown because it was not affected by predators exclusion.

CONCLUSIONS

KEYLINK is a relatively simple, fast and easily modified soil model that can be used as a stand-alone model to understand soil systems, or linked to detailed aboveground data/models to predict SOM turnover. Model evaluation showed that KEYLINK is capable of simulating properly not only the soil food web and C pools dynamics, but also how they interact with soil porosity and hydrology, which is one of the main goals of this new model. The results from the evaluation scenarios showed that SOM turnover is driven not only by microbial biomass, but also by soil structure and hydrology. Moreover, microbial biomass is strongly regulated by the presence/absence of the other soil fauna. Especially the effects of the predators and the soil engineers are extremely significant for our understanding of soil functioning. Furthermore, since management can differentially affect the larger soil fauna, KEYLINK can be of great use to investigate potential effects of management changes on soil SOM, nutrient turnover and hydrology.

This model shows degradability of SOM can be adequately simulated from accessibility in relation to pore space instead of the existing concepts of slow and fast pools. This allows a closer link to the soil structure and soil fauna which we consider closer to the actual, and follows the concepts as first described by Kuka *et al*. (2007), but applied here in a wider framework and including the hydrology.

For a full validation or better calibration of the model, datasets are required including basic data on the aboveground, e.g. litter input, water uptake, root growth and turnover, in combination with relatively detailed data on soil structure, i.e. pore size distribution, and hydrology and soil biota, e.g. biomass of bacteria, fungi, mycorrhyzal fungi and main meso-and macrofauna. All these data are found but very seldom at one site.

In conclusion, KEYLINK is a first step towards a new generation of ecosystems models that include functional diversity, trophic structures and ecological processes as important factors shaping soil/ecosystem carbon and water cycling. Future versions, fed by more detailed data, will be needed to be further developed in order to improve our current predictive capacity.

Chapter 3

Drought and abiotic degradation of litter modeled as key drivers of C dynamics in drylands with a second version of KEYLINK model

ABSTRACT

Improving current predictions on carbon (C) fluxes from terrestrial ecosystems and C sequestration in ecosystem soils under global change scenarios largely relies on how accurately we can represent processes in ecosystem models. In this regard, it is well known that models generally fail to correctly predict soil C dynamic in drylands, e.g. underestimating CO_2 emissions. This is mainly because current models lack the representation of key mechanisms of litter degradation, such as photodegradation of litter and microbial degradation enhanced by non-rainfall water sources, that are important in drylands. Based on the importance of drylands for the global C cycle, it is urgent to improve our current predictive capacity by including those mechanisms in ecosystem models. Here we present a second version of the mechanistic process-based soil model KEYLINK, that has been adapted to simulate ecosystem processes under drought conditions by including those relevant mechanisms of litter decomposition in drylands. This second version was calibrated for a Mediterranean-type ecosystem in Ramat Hanadiv (Israel). Different global change scenarios (e.g. changes in temperatures, precipitations, vegetation structure) were simulated using the new KEYLINK version, showing the potential impact of including these new mechanisms on C emissions and sequestration in dryland soils.

INTRODUCTION

Soil CO_2 effluxes, resulting among other things from the aerobic oxidation of litter and soil organic matter (SOM), release approximately ten times more CO_2 to the atmosphere than anthropogenic emissions from fossil fuel burning and industrial sources (Adair *et al*., 2008; Lee *et al*., 2012). However, the large contribution from degradation of litter and SOM to ecosystem C emissions remains underestimated by as much as 26% in predictions by models with respect to actual data (Adair *et al*., 2017). That discrepancy can be explained because most models were developed based on observations obtained from mesic ecosystems, in which climate (especially temperature and precipitations) and litter quality generally explain most of the temporal and spatial variability of litter decomposition. Hence, those models ignore mechanisms such as microbial degradation of litter using non-rainfall water sources (Gliksman *et al*., 2017), or abiotic litter degradation driven by solar radiation (King *et al*., 2012) and high temperatures (Lee *et al*., 2012), which seem to be negligible in mesic ecosystems, but become very relevant in arid and semiarid ecosystems (hereafter drylands) (Moorhead *et* al., 1999; Collins *et al*., 2008; Bonan *et al*., 2013; Bradford *et al*., 2016).

Drylands represent nearly 45% of the emerged lands, and constitutes one of the larger soil C reservoirs of the planet (Hewins *et al*., 2019), so the consequences of underestimating C emissions from drylands are very relevant at global scale. It is also expected that under global change many mesic ecosystems will become drier, and the extension of drylands could extend beyond the 50% of the total emerged lands by the end of this century (Feng and Fu, 2013; Huang *et al*., 2016). Moreover, projected increases in UV radiation, due to ozone depletion (Song *et al*., 2013), and expected climate change induced increases in temperature together with decreases in precipitations (IPCC, 2007) suggest that this currently neglected mechanisms of SOM and litter degradation could gain more relevance in the future (Lee *et al*., 2012).

Photodegradation

Among processes that become very relevant in drylands (hereafter dryland mechanisms), one of the main candidates that contribute to explain the mentioned underestimations in predictions for litter decomposition in drylands is the abiotic degradation of organic compounds by direct exposure to solar radiation, known as photodegradation (Hewins *et al*., 2019). Some efforts have been already done to include photodegradation into litter decomposition modelling, e.g. in CENTURY (Parton *et al*., 1987) and its version DayCent-UV (Chen *et al*., 2016). Although the underlying mechanisms that produce this photodegradation process are still under research and the specific carbon compounds affected by photodegradation remain unclear (King *et al*., 2012), some hypothesis suggest that radiation can break litter chemical bonds, especially on more recalcitrant components as lignin (Austin and Ballaré, 2010; Lee *et* al., 2012; Hewins *et al*., 2019). Among all solar radiation, litter compounds are expected to react more to UV-B (280-315 nm), but chemical bonds are affected also by UV-A (315-400 nm) and shortwave visible light. That has two main consequences: the direct emission of gasses (e.g. CO_2, CO, CH_4), and the change in litter quality from

recalcitrant components to more labile ones (Brandt *et al*., 2009; Austin and Ballaré, 2010; Foereid *et al*., 2010; Lee *al*., 2012). However, some modelling results did not support that correlation between lignin content and photodegradation (Adair *et al*., 2017). What is clear is that photodegradation change litter quality, increasing litter degradability, with a higher effect for longer periods of dry season and exposure to radiation (Ma *et al*., 2012). That change in litter quality by radiation produces a priming effect, facilitating microbial decomposition when litter becomes wet (Foereid *et al*., 2010), and there are also evidences of positive feedbacks between abiotic photodegradation and biotic microbial decomposition of litter even at daily scale (Gliksman *et al*., 2017). There is a need to include those new findings into SOM modelling, which can serve to improve predictions of litter decomposition in drylands and hence predictions of C storage and C emissions from soils, with many applications for efforts to mitigate climate change through land management (Campbell and Paustian, 2015).

Photoinhibition

UV radiation reaching the litter could also affect negatively microbial communities on the top layer, decreasing decomposition rates (King *et al*., 2012), by the inhibition of microbial activity or reduction of microbial growth, and altering the microbial community composition (Song *et al*., 2013). However, some microbial communities (mainly in drylands) can be adapted to resist high radiation (Wang *et al*., 2015). So it is an open discussion if UV radiation must be considered a direct limiting factor for microbial degradation. UV could inhibit decomposition not only by direct effects on microorganisms, but also by affecting their extracellular hydrolytic enzymes (EHE) that mediate in SOM and litter decomposition, especially in higher latitudes, as evidence shows that EHE are more sensitive to temperature increases in higher than in lower latitudes (German *et al*., 2012). Both new experimental frameworks and new modeling approaches could also contribute to shed light on the potential importance of photoinhibition on litter decomposition.

Changes in canopy cover

Plant coverage over soil is a factor that determines the amount of radiation reaching the litter, so it is a crucial parameter to estimate any solar radiation driven effect in the soil. Many factors can contribute to changes in ecosystem canopy cover, e.g. anthropogenic factors such as changes in land use, deforestation, afforestation, reforestation (Song *et al*., 2018), or natural disturbances such wind throw, insect outbreaks or forest fires (Williams *et al*., 2007; Witte *et al*., 2011; Jenkins *et al*., 2014; Allen *et al*., 2015; Buma, 2015; Hauser *et al*., 2016; Schoennagel *et al*., 2017). Under more intense drought scenarios, canopy cover could be reduced not only by tree death, but also by increases in canopy transparency and leaf shedding due to forest dieback processes (Hevia *et al*., 2019). Forest dieback affects also to soil microbial communities (Curiel Yuste *et al*., 2012) and could enhance the decoupling in C and N biogeochemical cycles (Rodríguez *et al*., 2019).

Moreover, solar radiation reach the soil also through the canopy, and modelling that transmittance of radiation is a complex matter that might need further modelling efforts including several parameters, as density and thickness of the vegetation layer, its absorptive, sun beam incidence angle, seasonality, or terrain relief among others (Nyman *et al*., 2017). And those parameters are not independent, especially in drylands, so those calculations need their own model.

Hence, future changes in canopy cover will vary the radiation interception, and in drylands that could have a more significant effect for the ecosystem C balance than the expected effects from the climate-induced changes in temperature or precipitation (Austin and Vivanco, 2006), so canopy cover can be a helpful addition to ecosystem modelling of C cycle, allowing to simulate many scenarios associated with global change, such as changes in radiation due to changes in land use or to climate-induced forest dieback.

Microbial adaptations to water limitations in drylands

In ecosystems where water constrains biological activity, organisms have different niches in function of their drought sensitivity and/or its capacity to adapt to drought, and this shapes how communities are distributed and organized (Engelbrecht *et al*., 2007). Therefore, the tolerance to drought is different in each ecosystem, and could affect ecosystem responses to climate change. Drought sensitivity is a key trait, with many potential impacts on crop yields (Lobel *et al*., 2014), and the risk of large C losses from Amazon forests under increasing droughts (Phillips *et al*., 2009). Modelling drought requires to define which conditions are necessary to produce drought stress on organisms, and that has to take into account the different drought sensitivities of organisms adapted to each ecosystem and climate.

For instance, in drylands, microorganisms that are adapted to drought conditions can use non-rainfall water sources, as fog, dew or even direct adsorption of water vapor from the atmosphere (Wang *et al*., 2017), to keep a humidity-enhanced microbial degradation of litter. In fact, small increases in soil moisture under dry conditions lead to higher increases in litter decomposition rates than larger rainfall events under moister conditions (Lee *et al*., 2014). However, modelling the incidence of non-rainfall water sources entails complexity, because it depends on several meteorological factors, as temperature (T), relative humidity (RH), wind speed, or wind direction (Gultepe *et al*., 2009; Lekouch *et al*., 2012), and that could lead to overparameterization in ecosystem models. Therefore, the inclusion of those processes into ecosystem models should be simplified.

Second version of KEYLINK model

A key difference between KEYLINK model and many other models that simulate organic matter (OM) decomposition is that while other models use to calculate litter and SOM decomposition using decomposition rates (k) based on how environment affects directly biotic and abiotic decomposition drivers, in KEYLINK the biotic drivers have trophic interactions within the food web, as well as react to environmental conditions.

Daily OM decomposition is calculated by the biomass of decomposers and the activity they can conduct on OM divided in different pools with different microclimates, and its availability within the soil, including physical protection in inaccessible pores and pores that are totally flooded or too dry.

KEYLINK simulates a complete food web simplified in functional groups, which shows how microbial communities and OM pools are affected by processes as trophic cascades (see chapter 2). In the second version, called "KEYLINK drylands", the model has been adapted to simulate also some dryland mechanisms (e.g. photodegradation, humidity-enhanced microbial degradation of litter), as well as other factors discussed before, as changes in canopy cover. It was parameterized for a Mediterranean shrubland in Israel, and a calibration of photodegradation parameters were conducted using data from a litterbag experiment in that ecosystem (Gliksman *et al*., 2017). The Python code is also freely downloadable (available at: https://github.com/Plant-Root-Soil-Interactions-Modelling/KEYLINK). Finally, different global change scenarios were simulated in order to evaluate model outputs, and the predicted relative contributions of different litter decomposition mechanisms to C fluxes in dryland ecosystems.

METHODOLOGY

New model version: *KEYLINK drylands*

KEYLINK previous version has been upgraded with the following additions:

Canopy cover

In order to allow simulations for different types of ecosystems (e.g. forests, shrublands, grasslands, crops) with different plant coverages, the model has an input parameter to fix the fraction of soil that is covered by plants, i.e. under canopy cover ($cc \in [0, 1]$).

While radiation usually penetrates the plant coverage and a reduced energy reach the soil through the canopy, the model does not calculate that diffusion of radiation through canopy, so cc must be interpreted as the fraction of soil that is totally shadowed by plant coverage. If information is available to recalculate cc as a lower fraction than current canopy, i.e. totally shadowed soil, by using another specific model for that purpose (Nyman *et al*., 2017), it would be better to use that value; but if that is not available, we suggest to use directly the fraction of canopy or plant cover as an approach to radiation that cannot reach the soil.

Exposed litter

Leaf fall tends to pile up litter layers, so only the top layer is exposed to some factors as solar radiation or dew. In the model, an input parameter, in text file KL_drylands (**Appendix 3**), is used to fix the minimum litter biomass (g C/m^2) to fully cover a square meter of soil surface (B_{full}, from Chen *et al*. (2016)). Assuming a homogeneous distribution of litter over the soil, B_{full} will depend on leaf type (and its specific leaf area); it can be easily determined experimentally for any type of litter, spreading certain litter mass until it covers totally as much surface as possible, and then that ratio mass/surface can be used to calculate B_{full}.

If litter mass in the pool is lower than B_{full}, there is bare soil, and the fraction of litter mass over B_{full} is the complementary of bare soil; this will be used to calculate how much radiation reaching the soil are not affecting litter because it goes directly to bare soil, and all litter will be a single top layer. But if litter mass is equal or higher to B_{full}, then all solar radiation that reach the soil will affect the litter. Moreover, in that latter case there are more than one litter layer, and litter pool is divided into two subpools: the exposed litter, on the top layer, equal to B_{full}; and the unexposed litter, the rest of the litter that is below the top layer. Radiation absorbance by litter is represented by the parameter c_{abs}, calculated in equation 1 when litter biomass (B_{lit}) at time t is lower than B_{full}, and in other case $c_{abs} = 1$.

$$c_{abs}(t) = \frac{B_{lit}(t)}{B_{full}} \qquad (1) \qquad \text{Chen } \textit{et al}. \text{ (2016)}$$

The fraction of the exposed litter (i.e. top layer) over the total litter pool (expLit) equals 1 when there is only a top layer, and in any other case it is calculated as the fraction of B_{full} over B_{lit}.

UV radiation reaching the litter

Daily total solar radiation (rad, in MJ/m^2) is given as an input in the meteorology data input file. The model includes an input parameter to set the fraction of UV radiation from total solar radiation; nevertheless, it can be used to give any fraction of solar radiation to be used for photodegradation (**Appendix 3**). The fraction of UV in solar radiation reaching the soil can vary in ranges as 2% – 9.4%, depending on several atmospheric conditions as gases concentrations, clouds and dust in the wind (Escobedo *et al*., 2009), but in the model it is simplified as a fixed fraction (f_{UV}).

However, it is necessary to take into account also another factors as the canopy cover (cc), and if there is bare soil (calculated with c_{abs}). So only the part of top litter layer that is not under the canopy will be affected by UV radiation, and the total energy absorbed by litter (UV_{lit}, in kJ/m^2) at time t is calculated in equation 2.

$$UV_{lit}(t) = 10^3 \, rad(t) f_{UV} \, c_{abs}(t) \, (1 - cc) \quad (2)$$

Photodegradation

While other authors suggest to use three-pool models for litter (Adair *et al*., 2008), in KEYLINK model litter was a single mass pool with two parts, the recalcitrant fraction (rec) and the more labile fraction. In this new version, litter pool is subdivided in another two parts: exposed litter on the top layer, and unexposed litter below the first; each one is divided again in two fractions, the recalcitrant and the labile ones, which are different for exposed and unexposed litter. So daily calculations run using a litter pool subdivided in four fractions with different litter qualities, and exposed to different decomposition drivers.

Due to the lack of knowledge of the underlying mechanisms of photodegradation, a simplistic representation of photodegradation could be a better option than to elaborate a more complex modelling of photodegradation impacts (Adair *et al*., 2017). Thus, a linear correlation between the litter recalcitrance in the top layer (rec_{top}) and the effect of radiation is applied, based on Chen *et al*. (2016), with two parameters, the intercept (p_0) and slope (p_1) for equation 3, provided in an input file (**Appendix 3**), used to calculate the litter mass degraded by radiation unit (dr, in µg C/kJ), and then equation 4 calculates the litter mass photodegraded each day (phd, g C/m^2).

$$dr(t) = p_0 + p_1 \, rec_{top}(t) \quad (3)$$

$$phd(t) = 10^{-6} \, UV_{lit}(t) \, dr(t) \quad (4)$$

phd is divided in two fractions, one that goes directly to CO_2 emissions, as a C loss that changes litter CN ratio, and the rest is subtracted from rec_{top} and added to the complementary labile fraction, changing litter recalcitrance. How much photodegraded litter is emitted as CO_2 depends on another input parameter (see **Appendix 3**). The priming effect of radiation on microbial decomposition results from those changes in litter quality.

Photoinhibition

In order to allow the simulation with and without microbial photoinhibition and death by radiation, those processes have been included but can be deactivated through a switch parameter (**Appendix 3**). These optional processes could be used to simulate scenarios with both options and to compare both results with empirical measurements. Moreover, even if microbial communities in drylands are adapted to exposition to high UV radiation, maybe other microbial communities from mesic ecosystems are not adapted, so it could be useful to activate photoinhibition for scenarios on mesic ecosystems in which dryland mechanisms gain relevance under global change scenarios (Grünzweig *et al*., in preparation).

First version of KEYLINK already included the fraction of average daily sunlight hours in each month ($f_{sun} \in (0, 1)$), and it is used in this version to adapt night-day processes to daily step simulations. Radiation effects are multiplied by f_{sun} to be applied only to light hours, while night processes are multiplied by $(1\text{-}f_{sun})$.

Here we keep it simple and assume all radiation driven responses are linearly affected by UV, until a maximum at certain radiation (max_{rad}, in MJ/m^2) given as input parameter (**Appendix 3**). The fraction of effective photoinhibition ($p_{inh} \in [0, 1]$) is calculated for each time (t) in equation 5. It is applied to calculate the daily decomposition activity on exposed litter ($dec_{exp} \in (0, 1]$) in equation 6, and the daily microbial biomass (mb) dead by radiation (p_{death}, $g\ C/m^2$) in equation 7.

$$p_{inh}(t) = \frac{rad(t)}{max_{rad}} \qquad (5)$$

$$dec_{exp}(t) = cc + (1 - cc)(1 - f_{sun}(t)p_{inh}(t)) \qquad (6)$$

$$p_{death}(t) = topm(t)\ mb(t)p_{inh}(t)f_{sun}(t) \qquad (7)$$

where topm is the fraction of microbial biomass on the top litter layer, calculated in equation 8 assuming a homogeneous distribution of microbes over all available OM, i.e. all litter and all available SOM, which is SOM pool biomass (B_{SOM}), except unavailable SOM ($SOM_{unavail}$) by physical protection within inaccessible pores, and multiplied by its availability on the accessible pores for microbial communities in function of soil hydrology ($avail_{SOM}$).

$$topm(t) = \frac{expLit(t)B_{lit}(t)}{B_{lit}(t) + avail_{SOM}(t)(B_{SOM}(t) - SOM_{unavail}(t))} \qquad (8)$$

Drought

In the first version of KEYLINK, C sources were available for their consumers only in soil pore classes that were partially filled with water, but they were unavailable in all pores totally flooded or totally dry. But in drylands we expect some faunal activity even in dry pores, due to biological adaptations to partially tolerate drought, so in this new version, only the fractions of C sources that are in completely flooded pores remain unavailable, and all C sources in partially-humid and dry pores are available, but

subjected to an added "drought effect" over the C consumption, which constrains all biological activity in the soil in function of soil water availability (SWA). This drought correction to the C consumption is applied *a posteriori* to the different fluxes among the trophic web, once the pore C availability and the subsequent reduction in trophic interactions are calculated. That drought stress on functional groups is added multiplying all fluxes by a factor named *drought modifier* (dm ∈ [0, 1]). This correction is applied also to the consumption of the litter pool, in which the water availability is assumed to be similar to SWA.

Drought stress is calculated through the fraction of soil water content (SWC) in the volume of all soil pore classes except inaccessible pores, as SWA, based on empirical measurements of soil respiration under drought conditions (Curiel Yuste *et al*., 2003; 2005). Drought sensitivity (ds) is given as an input parameter that accounts for the minimum percentage of SWA needed to completely avoid drought, and should be estimated as an average from all organisms among the food web. If SWA value is higher than ds/100, then dm = 1. When temperature is 0ºC or lower, dm = 0. And for the rest, dm is calculated as:

$$\mathrm{dm(t)} = 10\mathrm{SWA(t)} - 10^{-1}\mathrm{ds} + 1 \qquad (9)$$

being replaced by 0 if the value is negative.

Dew

Dew formation and its use by microbes to decompose litter have been added to the model. In order to make it easier for users, the only new input data required for dew calculations are two daily weather variables: minimum temperature (T_{min}) and maximum relative humidity (RH_{max}), because dew is calculated for night hours, so it requires weather at night conditions. Using RH_{max} and the two input parameters of intercept (d_0) and slope (d_1) (**Appendix 3**) in temperature-RH equation 10 (adapted from Beysens *et al*. (2005)), it is transformed in equation 11 to calculate the dew point temperature (T_{dew}), i.e. the maximum temperature to allow dew formation.

$$\mathrm{RH(t)} = \mathrm{d_1 T(t)} + \mathrm{d_0} \qquad (10)$$

$$\mathrm{T_{dew}\,(t)} = \frac{\mathrm{RH_{max}\,(t)} - \mathrm{d_0}}{\mathrm{d_1}} \qquad (11)$$

Then for each night it is calculated the dew incidence (i_{dew}), if $0 < T_{min} < T_{dew}$, there is dew ($i_{dew} = 1$), and otherwise $i_{dew} = 0$. This is applied to correct the dm for humidity-enhanced microbial degradation of litter, being replaced by the moisture effect on decomposition (med), which multiplies all C fluxes from top litter layer to microbial decomposers:

$$\mathrm{med(t)} = \mathrm{dm(t)f_{sun}\,(t)} + \Big(\mathrm{dm(t)\big(1 - i_{dew}\,(t)\big)} + \mathrm{i_{dew}\,(t)}\Big)\,(1 - \mathrm{f_{sun}\,(t)}) \qquad (12)$$

med is always equal or higher than dm, because med = dm during the day (f_{sun}), and it can be equal to dm or higher during the night ($1-f_{sun}$) in function of if dew is absent or present respectively.

Calibration of KEYLINK drylands version for a Mediterranean-type ecosystem

The Mediterranean shrubland in Ramat Hanadiv, Israel (described in the general methodology), was parameterized using available data in literature (see **Appendix 3**). Calibration was conducted using as reference the litterbag experiment by Gliksman *et al*. (2017), with six sampling times along one year of field incubation. Experimental results were standardized using the decomposition rate of the final sample to calculate estimated values for each sampling time following a negative exponential function (**Table 1**, see also equation 1 in chapter 4 for details on decomposition rates). Moreover, in the model, litter is represented as a dynamic pool with inputs and outputs, but the calibration used as reference litterbag data without inputs, so the Bayesian procedure was applied comparing reference data to an isolated duplicate of the litter pool, with the same initial litter mass, and accounting only for the outputs from the simulated litter pool (simulating a litterbag experiment). The scarce reference data available allowed to calibrate very few parameters, and here we show as example a calibration of two parameters for photodegradation, the intercept (p_0) and slope (p_1) in equation 3. The prior probability distribution ranged between 0 and 500 for the intercept (p_0), and between -10 and 60 for the slope (p_1). After the calibration, a Latin Hypercube Sample (LHS) of 100 parameter vectors was taken, and the average values from the LHS were used to simulate the scenarios for the model evaluation.

Days	Litter (g C m^{-2})	Error (g C m^{-2})
35	73.36	0.8127
65	70.38	0.8586
97	67.33	0.8855
201	58.31	1.4678
270	53.01	2.6763
376	45.78	2.2943

Table 1. Calibration data. Values of remaining mass from the initial litter (77 g C m^{-2}) after six field incubation periods.

Simulation of global change scenarios

The evaluation of this version followed a different approach than the previous (in chapter 2). Here we used the model to simulate single-run scenarios of 10 years, under a full-factorial design of increasing temperatures, decreasing precipitations and different conditions of canopy cover. In total, 80 scenarios were simulated: five conditions for daily mean and minimum temperatures, "+0ºC" (current temperature), and adding 2, 4, 6 and 8ºC; four precipitation regimes, the current regime (100% of daily precipitations), and reductions to 80, 60 and 40% of the current water inputs; and canopy covering 0, 25, 50 and 75% of the soil.

The effects of those changes on litter decomposition processes were analyzed, first comparing the change in the annual rate of litter decomposition (ld, g C m^{-2} $year^{-1}$), by the average litter mass degraded per year among the ten years of simulation, in the total litter pool (ld_{pool}) and in the top layer only (ld_{top}). Results show values of litter decomposition from the total litter pool, and also from the fraction of the top litter layer. Litter degradation outputs were divided in three complementary categories: abiotic degradation induced by light, i.e. photodegradation (phd_{CO2}, the fraction of phd from equation 4 that goes directly to CO_2 emissions), biotic degradation induced by dew (bd_{dew}), and biotic degradation using rainfall water (bd_{rain}). phd_{CO2} and bd_{dew} are fluxes from top litter layer only, while bd_{rain} comes from both litter layers.

$$ld_{pool} = phd_{CO_2} + bd_{dew} + bd_{rain} \qquad (13)$$

$$bd_{dew} = \left(\frac{ld_{top} - phd_{CO_2}}{D}\right) \sum_{i}^{D} \left(1 - \frac{dm\,(i)}{med\,(i)}\right) \qquad (14)$$

Using dm from equation 9 and med from equation 12, and being D the total number of simulated days (i) in which med > 0; in days with med=0 there is no biotic degradation of litter. Then, the relative contributions of photodegradation (C_{phd}) and dew-induced decomposition (C_{dew}) to ld_{pool} were calculated as:

$$C_{phd}\,(\%) = 100 \left(\frac{phd_{CO_2}}{ld_{pool}}\right) \qquad (15)$$

$$C_{dew}\,(\%) = 100 \left(\frac{bd_{dew}}{ld_{pool}}\right) \qquad (16)$$

The contributions of photodegradation and dew-induced degradation to litter decomposition in the top layer were calculated replacing ld_{pool} with ld_{top} in equations 15 and 16.

Finally, another set of 80 scenarios were simulated following the same method, but deactivating photoinhibition processes (results from those simulations in **Appendix 3**).

RESULTS

More than 20000 runs were done for the model calibration, each time with a different parameter vector (for the calibrated parameters). A 13.86% of those runs constituted the posterior distribution of vectors with values for the two calibrated parameters. The LHS of the posterior distribution resulted in the following average values (± sd): photodegradation equation (3) intercept p_0 = 97.36 ± 19.19, and slope p_1 = 16.52 ± 17.29. Those results indicate that more reference data is needed in order to reach parameter convergence, particularly for p_1. Therefore, model calibration should be improved when more data is available.

Global change scenarios

The 80 simulated scenarios (with photoinhibition activated) showed that annual litter decomposition tend to decrease with increasing temperatures and decreasing precipitations; for example, without canopy cover, an increase of 2ºC in soil temperature and a decrease of 20% in precipitations could reduce litter decomposition from 43.35 to 35.76 g C m^{-2} $year^{-1}$, a 17.51% reduction in decomposition rates according to this simulations (**Table 2**), while in the top layer the reduction would be only a 2.63% (from 23.6 to 22.98 g C m^{-2} $year^{-1}$). Under 75% of canopy cover, the decrease in decomposition rates for the same conditions (2ºC warmer and 20% lower precipitations) was 24.7%, with 6.78% decrease in the top layer. The contribution of dew-induced litter decomposition mechanism increased under warmer and drier scenarios (**Table 3**), as well as the photodegradation contribution (**Table 4**).

On the other hand, reductions in canopy cover increased litter decomposition rates (**Fig. 1**), due to an increase in photodegradation, which reduced the relative contribution of biotic decomposition and, therefore, the contribution of dew-induced decomposition to total litter degradation (**Fig. 2**). The relevance of photodegradation without canopy increased from 39.68% until 48.1% for an increase of 2ºC and a 20% reduction in precipitations, and even under a 75% of canopy cover, photodegradation relevance increased from 13% to 17.26% (**Fig. 3**).

The simulation of the same scenarios deactivating photoinhibition resulted in similar results, but with a slight increase in biotic degradation, as expected due to the lack of simulated negative effects of radiation on microbial communities. Although photoinhibition does not affect to the abiotic process of photodegradation, the relative contribution of photodegradation to total litter decomposition was slightly lower without photoinhibition, due the increase in biotic degradation of litter (**Appendix 3**).

		ld_{pool}					ld_{top}				
cc	**Precip**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**
0%	**100%**	43.35	39.73	31.94	25.93	24.18	23.6	23.27	22.97	22.77	22.85
	80%	41.75	35.76	28.72	25.04	23.93	23.45	22.98	22.74	22.74	22.85
	60%	37.01	32.15	26.18	24.09	23.47	22.81	22.69	22.62	22.7	22.85
	40%	30.12	26.02	23.96	23.33	23.05	22.29	22.39	22.52	22.73	22.91
25%	**100%**	39.92	36.23	28.25	22.14	20.37	19.86	19.48	19.15	18.94	19.02
	80%	38.29	32.14	24.93	21.23	20.12	19.69	19.17	18.91	18.9	19.02
	60%	33.41	28.45	22.39	20.27	19.65	18.98	18.85	18.78	18.86	19.02
	40%	26.37	22.21	20.13	19.5	19.22	18.43	18.53	18.68	18.89	19.08
50%	**100%**	36.49	32.71	24.53	18.35	16.56	16.12	15.69	15.33	15.1	15.19
	80%	34.83	28.53	21.18	17.43	16.3	15.94	15.36	15.07	15.07	15.19
	60%	29.79	24.74	18.6	16.45	15.83	15.16	15.01	14.94	15.03	15.2
	40%	22.61	18.41	16.31	15.68	15.4	14.56	14.68	14.84	15.06	15.25
75%	**100%**	33.08	29.19	20.85	14.55	12.75	12.39	11.91	11.52	11.27	11.37
	80%	31.38	24.91	17.42	13.63	12.49	12.19	11.55	11.24	11.23	11.36
	60%	26.18	21.04	14.81	12.64	12.01	11.35	11.17	11.1	11.2	11.37
	40%	18.86	14.6	12.49	11.85	11.57	10.7	10.83	11	11.23	11.43

Table 2. Annual litter decomposition (g C m^{-2} $year^{-1}$) in the total litter pool (ld_{pool}) and in the top litter layer (ld_{top}) under different global change scenarios of increasing temperatures and decreasing precipitations (Precip), for four canopy coverages (cc).

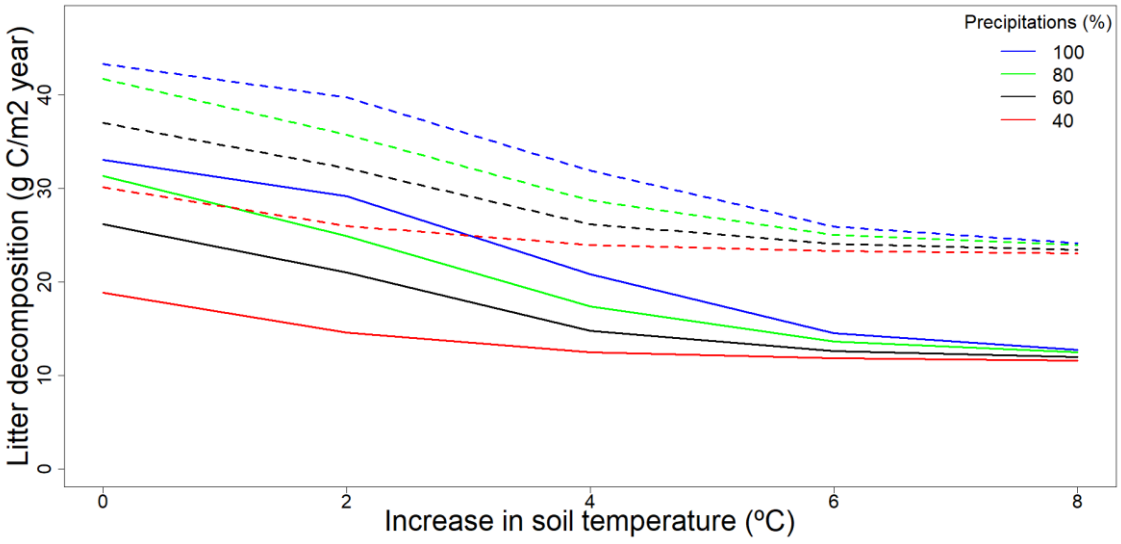

Figure 1. Annual litter decomposition in total litter pool under different global change scenarios. All simulated scenarios for precipitations and soil temperatures are represented, for the two most contrasted canopy cover scenarios: 75% (full lines) and 0% (dashed lines).

		ld_{pool}					ld_{top}				
cc	**Precip**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**
0%	**100%**	11.34	12.73	16.12	20.18	22.53	20.84	21.74	22.41	22.98	23.84
	80%	11.94	13.85	17.58	20.97	22.85	21.25	21.54	22.2	23.1	23.94
	60%	12.68	15.11	19.34	21.96	23.49	20.57	21.41	22.38	23.3	24.12
	40%	14.98	18.55	21.35	23.11	24.37	20.24	21.55	22.71	23.72	24.52
25%	**100%**	13.4	15.14	19.74	25.62	28.97	26.93	28.17	29.13	29.95	31.02
	80%	14.15	16.7	21.94	26.8	29.44	27.51	28	28.93	30.11	31.14
	60%	15.24	18.5	24.52	28.29	30.38	26.83	27.93	29.24	30.39	31.38
	40%	18.57	23.59	27.58	29.97	31.63	26.57	28.27	29.72	30.94	31.87
50%	**100%**	15.84	18.08	24.48	33.3	38.37	35.86	37.69	39.18	40.46	41.82
	80%	16.81	20.28	27.83	35.18	39.12	36.74	37.67	39.1	40.71	41.99
	60%	18.44	22.93	31.83	37.56	40.62	36.23	37.79	39.63	41.12	42.31
	40%	23.36	30.72	36.74	40.19	42.51	36.27	38.51	40.38	41.83	42.92
75%	**100%**	18.8	21.73	30.88	45.03	53.39	50.19	53.28	55.92	58.11	59.9
	80%	20.07	24.91	36.27	48.24	54.71	51.64	53.73	56.22	58.54	60.15
	60%	22.53	28.91	42.89	52.43	57.36	51.98	54.44	57.22	59.2	60.61
	40%	30.07	41.57	51.52	57.01	60.59	52.99	56.06	58.49	60.18	61.38

Table 3. Dew-induced litter decomposition contribution (%) to annual litter decomposition in the total litter pool (ld_{pool}) and in the top litter layer (ld_{top}) under different global change scenarios of increasing temperatures and decreasing precipitations (Precip), for four canopy coverages (cc).

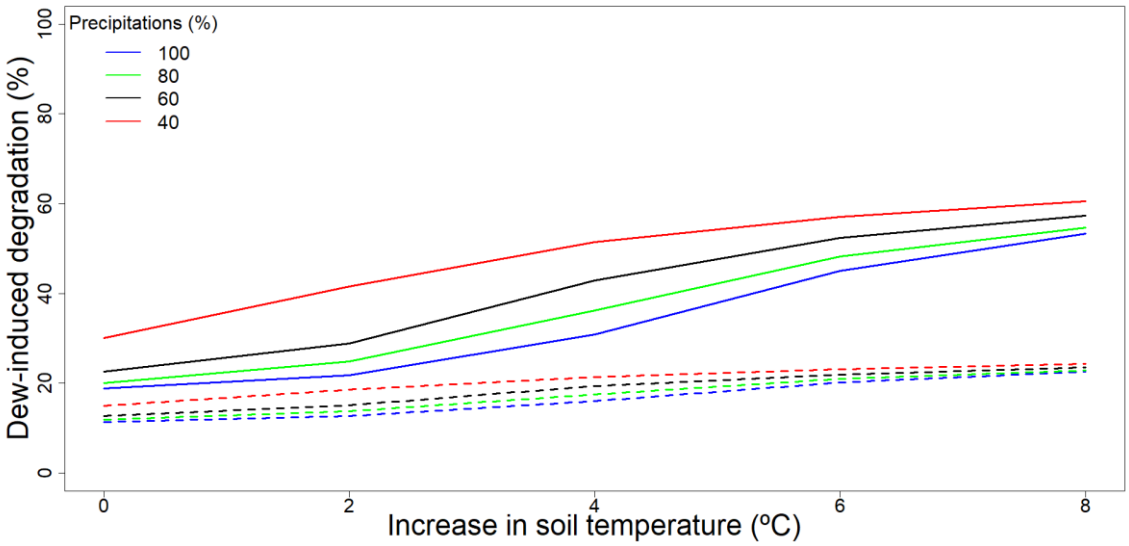

Figure 2. Contribution of dew-induced decomposition (%) to litter decomposition in total litter pool under different global change scenarios. All simulated scenarios for precipitations and soil temperatures are represented, for the two most contrasted canopy cover scenarios: 75% (full lines) and 0% (dashed lines).

		ld_{pool}					ld_{top}				
cc	**Precip**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**
0%	**100%**	39.68	43.29	53.85	66.33	71.12	72.89	73.92	74.89	75.53	75.25
	80%	41.2	48.1	59.89	68.67	71.85	73.36	74.84	75.62	75.64	75.26
	60%	46.47	53.49	65.7	71.4	73.27	75.42	75.81	76.04	75.76	75.25
	40%	57.09	66.1	71.79	73.73	74.62	77.15	76.82	76.35	75.67	75.08
25%	**100%**	32.32	35.6	45.66	58.26	63.32	64.96	66.22	67.36	68.12	67.8
	80%	33.69	40.13	51.74	60.75	64.11	65.51	67.29	68.23	68.25	67.82
	60%	38.61	45.34	57.62	63.63	65.64	67.94	68.44	68.7	68.37	67.8
	40%	48.92	58.07	64.07	66.14	67.1	70	69.6	69.05	68.27	67.61
50%	**100%**	23.57	26.29	35.05	46.85	51.92	53.34	54.8	56.1	56.93	56.59
	80%	24.69	30.15	40.6	49.33	52.74	53.95	56	57.06	57.08	56.61
	60%	28.87	34.75	46.24	52.26	54.32	56.71	57.29	57.57	57.21	56.59
	40%	38.03	46.72	52.73	54.85	55.85	59.05	58.57	57.95	57.1	56.38
75%	**100%**	13	14.73	20.62	29.56	33.72	34.7	36.11	37.34	38.14	37.82
	80%	13.7	17.26	24.68	31.54	34.42	35.26	37.23	38.26	38.27	37.84
	60%	16.43	20.43	29.04	34.01	35.79	37.89	38.48	38.74	38.4	37.82
	40%	22.8	29.44	34.44	36.27	37.15	40.18	39.7	39.09	38.28	37.63

Table 4. Photodegradation contribution (%) to annual litter decomposition in the total litter pool (ld_{pool}) and in the top litter layer (ld_{top}) under different global change scenarios of increasing temperatures and decreasing precipitations (Precip), for four canopy coverages (cc).

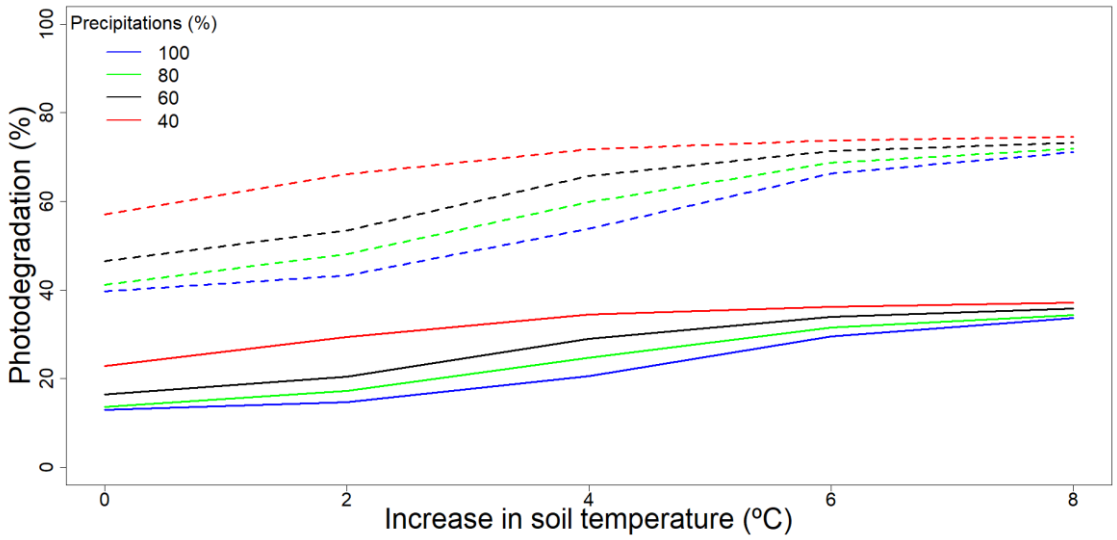

Figure 3. Contribution of photodegradation (%) to litter decomposition in total litter pool under different global change scenarios. All simulated scenarios for precipitations and soil temperatures are represented, for the two most contrasted canopy cover scenarios: 75% (full lines) and 0% (dashed lines).

DISCUSSION

The simulated climate change scenarios showed that both increases in temperature and decreases in precipitation reduce decomposition rates, mainly constraining rainfall-induced biotic degradation of litter, which is aligned with evidences on drought effects on litter decomposition (e.g. Curiel Yuste *et al*., 2003; 2011; Xiao *et al*., 2014).

On the other hand, the relative contributions of dew-induced decomposition and photodegradation increased under drier scenarios, as expected since also rainfall-induced biotic degradation decreased. Our simulations support the relevance of photodegradation and dew-induced litter decomposition in drylands, accounting for a large proportion of the litter decomposition in the scenarios of precipitation presented (from 20 to 60% of total decomposition), which is in agreement with the observed role of non-rainfall-induced biotic decomposition in drylands (Wang *et al*., 2017). Moreover, our results show that the role of those dryland mechanisms over total litter decomposition could increase considerably under drier and warmer scenarios.

Although litter decomposition rates decreased with increasing aridity, decomposition rates in the top litter layer where much more stable than in the total litter pool, which means that the reduction in rainfall-induced biotic degradation in the top litter layer could be mitigated by dew-induced decomposition, and also by the priming effect of photodegradation reducing litter recalcitrance. Hence, our results suggest that the decomposition of the top litter layer will not necessarily change with changes in precipitation or temperature. However, more empirical data is needed to calibrate properly parameters as those for dew incidence, in order to simulate accurately the effects of changes in temperature and RH on dew formation.

The confluence of precipitation scenarios under high increases in soil temperature suggest that, at high temperatures, the faster loses of water from soil by evaporation makes less relevant the changes in soil water content by changes in precipitation. Thus, even under current precipitation regimes, if soil temperature increases following the global warming trend (IPCC, 2007), rainfall could lose relevance for biotic decomposition of litter in dryland soils, becoming much more relevant the humidity-enhanced mechanisms of litter decomposition. Here we have shown the contribution of dew to litter decomposition, but other non-rainfall water sources should be taken into account as well, as fog or the direct adsorption of water vapor from the atmosphere by microorganisms (Wang *et al*., 2017).

The considerable complexity in forest structure in Mediterranean forests may cause very complex spatial heterogeneity in rates and drivers of litter decomposition, with different expositions to radiation under the canopy and in forests gaps. Spatial heterogeneity is a crucial factor shaping litter decomposition rates (see chapter 4), which is particularly remarkable in open woodlands, which are a very representative ecosystem structure in drylands (Maranon, 1988). In our study, changes in radiation interception by vegetation cover had higher impact on simulated litter decomposition processes than changes in

precipitations or temperatures, which supports the high relevance of light-induced degradation of litter in drylands.

Moreover, such influence of solar radiation on abiotic litter decomposition supports the crucial role of radiation, and its potential effects on other processes that controls litter decomposition (e.g. photoinhibition of microbial activity and microbial death by radiation) should be considered. On the other hand, the effect of radiation facilitating microbial decomposition of litter by reducing litter recalcitrance is already included in the model, as discussed below. The results of simulated scenarios shown in this chapter, including photoinhibition processes, compared to the alternative results from simulations of the same scenarios without photoinhibition (shown in **Appendix 3**), suggest that direct radiation effects on microbial communities could negatively affect litter degradation. How photoinhibition may affect litter degradation under future climate change is still uncertain (King *et al*., 2012; Song *et al*., 2013; Wang *et al*., 2015), but under warmer and drier scenarios it is likely that during daylight, when also biotic degradation is low, microbial communities will be small in the litter layer. However, this photoinhibition during daylight may also have a legacy effect by reducing the microbial biomass during night when dew-stimulation of microbial activity becomes important. In any case, the net effect of radiation was a decrease in soil C stabilization, because the increase in total litter degradation due to photodegradation was higher than the decrease in biotic litter decomposition due to photoinhibition.

The remarkable increase in annual litter decomposition under higher exposition to radiation (**Fig. 1**) support the crucial relevance of photodegradation, not only due to the release of C emitted as CO_2, but also due to the priming effect of radiation facilitating microbial decomposition, due to a decrease in the recalcitrance of the top litter layer. In the simulated scenarios, the photodegraded litter mass that was emitted as CO_2 was a 48%, and that flux is what results from applying the percentages of photodegradation contribution (**Table 4**) to annual litter decomposition (**Table 2**), which means that the remaining 52%, i.e. photodegraded litter that was not released, constituted a considerable mass of recalcitrant litter that became labile. Even simulating photoinhibition, the priming effect of radiation on microbial decomposition through decreasing litter recalcitrance was more relevant. Shifts in dominance between photodegradation (abiotic) and dew (biotic) processes occurred under scenarios of contrasting radiation interception, i.e. more abiotic degradation in open areas with more radiation incidence, while litter decomposition in areas of higher plant cover and hence less radiation incidence was clearly dominated by biotic processes. This indicates that climate change may exacerbate the spatial complexity in drivers of litter decomposition in spatially complex systems.

Other potentially important factors should be added in future versions though, e.g. how changes in vegetation cover affects microclimatic conditions on the litter layer (Heithecker and Halpern, 2006; Wang *et al*., 2014), which are not currently included. We expect that plant coverage could reduce climatic stress by reducing temperatures and hence evaporation of the uppermost litter layer, hence further promoting biotic degradation over photodegradation by increasing microclimatic humidity and the access of microbes to non-rainfall water sources. Our results, nonetheless, imply that land management shaping vegetation structure is very relevant for litter decomposition processes and, therefore, management practices might be crucial for the regulation of C emissions from soil and for C sequestration in soils, particularly in drylands.

CONCLUSIONS

In summary, our results show that increasing temperatures can substantially reduce water availability in dryland soils, constraining rainfall-induced microbial degradation of litter, and subsequently reducing litter decomposition rates. Representation in models of litter decomposition in drylands suggest, on the other hand, that other mechanisms of litter decomposition, i.e. photodegradation or dew-induced biotic degradation, could gain importance under drier and hotter scenarios. Dew-induced degradation of litter was a substantial fraction of all biotic degradation of litter simulated in drylands, and under extreme drought conditions it could be even more relevant than rainfall water inputs. We also observe that ecosystem structure, which in many cases depends strongly on anthropic interventions (land use and/or management intensity) may determine the radiation incidence and hence the role of photodegradation and dew-induced biotic degradation as dominant drivers of litter decomposition in drylands.

We are aware that a proper representation of litter decomposition in drylands still requires much work, and it will be challenging to integrate all the mechanisms that seem to be relevant in drylands. There is still a lack of strong data sets to back up our results, and other potentially important processes which has not been included in this version of KEYLINK, such is the abiotic thermal degradation of litter (Lee *et al*., 2012), needs of more empirical evidence before could be parameterized into the model. Also, the potential differential sensitivity to drought of different soil functional groups should be carefully evaluated because it might cause a sensitive transformation of the trophic fluxes with unknown effects over key functions. For instance, we expect that increases in drought will be more negative for soil fauna than for soil microbial communities, due to the ability of microbes to partially avoid drought stress using non-rainfall water sources. Therefore, even if drought constrains microbial activity, the trophic cascade effects through the food web (as discussed in chapter 2), when microbivores suffer higher drought stress, could lead to increases in microbial populations in soils, increasing decomposition rates. This could be particularly relevant in mesic ecosystems that, under climate change, could be exposed to drier conditions, being microbial communities more able than soil fauna to adapt to those conditions and avoid drought stress, which could lead to unexpected increases in litter decomposition rates with increasing drought (Grünzweig *et al*., in preparation). More data is, therefore, needed on how sensitive to drought could be different trophic levels and functional groups, and how this may affect soil functioning and the relative contribution of abiotic and biotic processes of degradation to total litter decomposition rates.

Chapter 4

The roles of climate and litter intraspecific variability on decomposition of holm oak litter in the Mediterranean region

ABSTRACT

Litter decomposition is a key ecosystem process with high impacts on ecosystem carbon (C) budgets and CO_2 emissions. Although rates of litter decomposition are generally controlled by climate and litter quality, there are still many uncertainties about mechanisms controlling litter decomposition rates in drylands. Our goal was to understand the relevance of those environmental factors (climate and litter quality) over litter decomposition from an evergreen tree species, holm oak (*Quercus ilex* L.) widely distributed in the Mediterranean area. More specifically, we were interested in understanding at which extent potential intraspecific variability in leaf litter quality of holm oak litter across its distribution over the Iberian Peninsula could determine decomposition rates relative to climate, which also experienced a large gradient within the peninsular distribution of this species. For that purpose, two litterbags experiments have been designed: 1) a litterbag experiment with leaves from different peninsular procedences was installed in a common garden experiment to study the role of intraspecific litter quality on litter decomposition rates; and 2) a litterbag experiment with leaves from a single location (Cabañeros National Park) was installed at different locations, covering the whole climatic gradient of distribution of this species in the Iberian Peninsula, with mean annual temperatures (MAT) ranging from 10.34 to 15.37ºC, and mean annual precipitation (MAP) ranging from 282.41 to 916.67 mm. Despite the large gradient in temperatures and precipitations, no direct effects of climate over the variability of litter decomposition were observed in the peninsular gradient of experiment 2. Instead, understory vegetation, which is determined by factors such as historical management, system degradation or climate, was the main factor controlling litter decomposition at regional scale (Iberian Peninsula). On the other hand, the large intraspecific differences in litter chemistry found at the peninsular level determined in experiment 1 levels of litter decomposition rates variability as high as the peninsular gradient from experiment 2. Litter decomposition rates in experiment 1 were determined by the interaction between litter recalcitrance (lignocellulosic content) and litter Mn content, which supports recent evidences on the importance of Mn in the decomposition of structural leaf C. Structural equation model (SEM) further shows how intraspecific differences in leaf recalcitrance and Mn were strongly shaped by the historical environmental conditions of the litter's procedences: recalcitrance (lignocellulosic content) was favored by harsher climatic conditions (drought and cold), while litter Mn concentration in leaf litter was favored by drought and soil acidic (low pH) conditions. Hence, our study highlights: (1) the importance of intraspecific variability in litter quality, responsible for a variability in litter decomposition rates comparable to that observed in a regional gradient of climate and management; (2) the lack of direct effects of climate over litter decomposition in a peninsular gradient, but its importance, together with other abiotic conditions (pH) in shaping the decomposability of litter; and (3) the role of understory vegetation, which buffers the harsher environmental conditions imposed by the Mediterranean climate and accelerates rates of litter decomposition.

INTRODUCTION

Global carbon (C) fluxes are one of the main drivers of climate change, being crucial to understand ecosystem processes that regulates those fluxes (see chapter 3). Litter and soil organic matter (SOM) decomposition is particularly relevant among these processes, because it links above-ground and below-ground processes in ecosystems (Meier and Bowman, 2008), which is crucial for ecosystem stability (Yang *et al*., 2014). Understanding litter and SOM decomposition in drylands will be crucial for global change predictions, especially under future scenarios with increases in aridity, which can lead to decoupling of above-ground and below-ground processes, affecting C cycle and feedbacks to climate change (Bardgett *et al*., 2013).

Litter decomposition processes occur at different rates depending on many factors, such as temperature, precipitations, litter chemical composition (litter quality), solar irradiation, microbial community adaptations to soil nutrients availability, etc. (Austin and Vivanco, 2006; Zhang *et al*., 2008; Janssens *et al*., 2010). Litter quality is considered the main driver regulating litter decomposition at global scale (Zhang *et al*., 2008), due to compounds as lignin which are highly resistant to microbial degradation, and only can be decomposed by some extracellular enzymes produced by specialized biota, mainly fungi (Austin and Ballaré, 2010). While litter quality effects on litter decomposition rates have been studied mainly between different species (e.g. Carrillo *et al*., 2011; Riutta *et al*., 2012; Slade and Riutta, 2012), some studies have shown the importance of intraspecific differences in litter quality on rates of litter decomposition (e.g. Madritch *et al*., 2006; Semmartin and Ghersa, 2006). Intraspecific variability in litter quality might be particularly important in ecosystems and regions with low tree diversity, as happens in many European forest ecosystems and particularly in the Mediterranean basin. The potential role of intraspecific variability in litter quality might be, therefore, a source of uncertainty that has been underestimated in global studies and models (Incerti *et al*., 2011; García-Palacios *et al*., 2016), despite the fact that modifications of the environment induced by global change may lead to changes in litter quality and other functional traits among species, but also into the same species (Quested *et al*., 2007; Jin *et al*., 2011).

Moreover, microbial communities under or near each plant species are expected to be adapted to that species litter quality, as a consequence of plant-microbes co-evolutionary trends, decomposing it faster than litter from other species growing further away, which means that litter decomposition rates are expected to be higher in its procedence site (i.e. at home) than translocated to other sites (i.e. away). That is called the *home field advantage* (HFA) hypothesis (Gholz *et al*., 2000; Austin *et al*., 2014), which has been found to happen mainly between different species (Ayres *et al*., 2009), despite it is not a general trend and other authors did not find evidence supporting HFA (e.g. John *et al*., 2011; Aponte *et al*., 2012). Being under doubt the HFA even between different species, it would be even less expectable to observe a HFA effect between single-species forests, but a possible HFA should be tested for a single-species like

holm oak (*Quercus ilex* L. subsp. *ballota*), which substantial intraspecific variability in leaf chemistry and functional traits.

Climate plays also an important controlling role over litter decomposition. Microbial communities that decompose litter respond directly to weather conditions during the decomposition process, i.e. litter decomposition generally peaks under warmer and wetter conditions (Gliksman *et al*., 2017; Gregorich *et al*., 2017). However, litter decomposition rates respond differently to extreme conditions in each climate, e.g. in temperate ecosystems extremely high precipitations could decrease decomposition due to anaerobic conditions, while in tropical ecosystems litter decomposition increase even with high rainfall (Austin and Vitousek, 2000). In drylands, litter decomposition is constrained mainly by drought, and increasing aridity together with altered precipitation regimes are expected in future climate change scenarios (see chapter 3), which might alter ecosystem C budgets and CO_2 emissions. Therefore, there is a need to improve our knowledge on climatic controls over litter decomposition, especially in drylands, in order to improve mechanistic models and predictions.

Although it is generally the combination of climate, litter quality and biological activity what usually explains the variation in litter decomposition better than any single factor (Zhang *et al*., 2008), other environmental factors generally underestimated might also represent a source of uncertainty that models are not accounting for. For instance, changes in environmental conditions due to changes in aboveground vegetation dynamics and plant-soil interactions, which might be controlled by local-scale factors such as land management, could have higher relevance on litter decomposition than climate itself (Bradford *et al*., 2014). Indeed, anthropogenic interventions on forests ecosystems modifies their structure (Boulangeat *et al*., 2014), and with it, the environmental conditions that determine litter decomposition such as the microclimatic conditions, the incidence of radiation or the nutrient concentration in soils (Fraterrigo *et al*., 2005; Heithecker and Halpern, 2006; Gliksman *et al*., 2018).

Holm oak forests and open woodlands (Spanish 'dehesas') have great relevance in the Iberian Peninsula from ecological and economical perspectives, due to the biological diversity they host and all the diversity of ecosystem services they provide, e.g. wood, livestock, recreational, etc. (Díaz *et al*., 1997; Vicente and Alés, 2006). Holm oak is actually the tree species with broader distribution in the Iberian Peninsula, with intraspecific differences in leaf functional traits and composition over a broad climatic, geological and land use gradient (Castro-Díez *et al*., 1997; De Rigo and Caudullo, 2016). Such environmental variability has been proven to affect plant chemistry and recalcitrance in other species (Ford *et al*., 1979; Gindl *et al*., 2000). Therefore, the role of *Q. ilex* intraspecific variability can be very relevant to regulate litter decomposition rates in response to global change.

In order to study the discussed potential drivers of decomposition rates, and to assess their contribution to litter decomposition in Mediterranean holm oak forests, we have conducted a common garden experiment (1) at one site with leaf litter from different

procedence sites, studying the effects of litter quality, and testing the following hypothesis:

H1: There is a large intraspecific variability in *Q. ilex* litter quality, that has important effects controlling litter decomposition rates.

Another field litterbag experiment (2) was conducted on a broad geographical gradient, in seven sites contrasting the effects of climate and forest structure on litter decomposition, allowing to test two hypotheses:

H2: Climate is the main driver of oak litter decomposition over the Iberian Peninsula, being temperature and precipitation positively correlated with decomposition rates.

H3: Forest structure affect decomposition rates mainly due to tree canopy cover, which lead to a decrease in decomposition rates.

Moreover, analysis of the translocation treatment over decomposition rates on these experiments will show if there is any HFA effect between different *Q. ilex* forests:

H4: Local litter decomposition rates should be higher than those for foreign litter translocated from other site, and than those for the local litter translocated away, according to HFA hypothesis.

METHODOLOGY

Sites description and litter collection

Eight holm oak (*Q. ilex*) stands, distributed across the Iberian Peninsula (**Table 1**), were used for this study. The sites were distributed throughout the entire distribution area of this species in the Iberian Peninsula, in the Spanish provinces of León, Navarra, Cáceres, Lérida, Madrid, Ciudad Real, Almería and Alicante (**Figure 4** in general methodology). In function of the percentage of tree crown coverage per hectare (hereafter 'canopy'), which is related to land use, these forests were divided in three categories: open woodlands ('dehesas', canopy ≤ 30 %), abandoned forests (30 % < canopy ≤ 60 %) and closed forests (canopy > 60%).

Understory vegetation structure was assessed in each forest (except Cabañeros) during autumn 2015, in 27 circles of 10m diameter, each one around each of 27 holm oak trees studied per site (García-Angulo *et al*., submitted). The understory percentage cover, including shrubs and grasses (the remaining fraction was bare soil and/or stones) was estimated by consensus among four different observers. Canopy cover was estimated using orthophotos (Sevilla *et al*., 2016) (http://signa.ign.es/signa/Pege.aspx) analyzed with the SigPacviewer (Spanish Ministry of Agriculture, Food and Environment). Litter from Ciudad Real was collected from litter traps during spring and summer 2016. From the other sites (except Madrid), senescent leaves were collected from trees during the samplings conducted in autumn 2015 (Garcia-Angulo *et al*., submitted).

Var.	Unit	Alic	Alme	Cáceres	CR	León	Lérida	Madrid	Navarra
Lat	ºN	38.67	36.89	39.88	39.33	42.45	41.83	40.38	42.73
Long	ºW	0.54	2.62	6.05	4.32	5.97	1.45	4.19	1.75
Alt	m	1068.81	995.6	421.98	727.87	934.59	661.42	702.1	671.5
Land use		forest	aband	woodl	aband/woodl	forest	forest	woodl	aband
Canopy	%	90.11	43.99	9.94	54.89 / 9.5	78.38	63.50	26.77	47.56
Shrubs	%	29.63	51.22	36.11	NA	20.22	33.96	11.15	54.74
Grass	%	6.74	10.67	39.15	NA	5.89	45.78	42.59	31.89
Und	%	36.37	61.89	75.26	NA	26.11	79.74	53.74	86.63
MAT	º C	13.83	13.66	15.37	13.84	10.34	13.08	12.88	10.62
MAP	mm	519.16	282.41	740.09	475	488.35	568.78	600.95	916.67
pH		7.69	7.77	5.17	(*)	5.30	7.51	6.13	7.23
soil P	$g\ m^{-2}$	10.13	7.02	36.64	NA	18.75	12.56	40.82	11.77
T_{01}	º C	11.54	13.28	11.75	7.17	10.68	11.78	9.95	10.36
T_{12}	º C	17.1	18.27	14.5	16	13.44	14.26	13.07	12.7
T_{23}	º C	20.26	21.76	23.76	22.07	19.7	20.4	22.68	18.65
P_{01}	mm	281.1	190.7	249.2	204.4	184.8	270	192.2	294.9
P_{12}	mm	91.4	78.1	157.3	96.9	197.5	265.6	100.2	341
P_{23}	mm	106.9	67.2	61.8	74.2	72.9	156.2	86.7	171.4

Table 1. Study sites in eight Spanish provinces (e.g. Alicante (Alic), Almería (Alme), Ciudad Real (CR)). Descriptive variables: latitude (Lat), longitude (Long), altitude (Alt), land use (with three categories: woodland (woodl), abandoned (aband) and forest), canopy, shrubs and grass covers, understory (Und), mean annual temperature (MAT), mean annual precipitation (MAP), soil pH, total P in soil (soil P), and weather variables during litterbag incubation intervals, temperature (T) and precipitation (P) during the first four months (T_{01}, P_{01}), the next four months until the second litterbag sampling (T_{12}, P_{12}), and the last four months (T_{23}, P_{23}). In Cabañeros National Park (Ciudad Real), land use and canopy cover are divided in two for the different land managements, abandoned forest (CF) and open woodland (CW) respectively; (*) soil pH in each one of four experimental sites (for ungulate exclusions (E) and controls (C) in both land managements) in Cabañeros: CFC = 6.3; CFE = 6.25; CWC = 6.44; CWE = 6.36.

Experimental design

Experiment 1

In order to test the effects of intraspecific variability in litter quality over decomposition rates (H1), we used *Q. ilex* leaf litter from different sites (those in **Table 1** except Madrid) in a common garden experiment in the Cabañeros National Park (province of Ciudad Real, Spain, see CR in **Table 1**). The experiment was set up in a plot of 50x100 m into the dehesa, on November 2016 in two different sites within the plot, each one placed in the south side of a holm oak tree. In each site, we constructed an equilateral triangular metallic fence of 6 m side and 2 m tall (as in **Figure 1**), to avoid perturbations

by wild animals as deer and wild boar, because the Park has an issue of ungulates overpopulation.

Figure 1. One of the litter decomposition experimental plots in Cabañeros National Park (Ciudad Real, Spain), with fences surrounding the litterbags, at the beginning of the experiments in autumn 2016. This plot was placed in the forest of Cabañeros, being the set up similar to the plots placed in the dehesa.

Inside each one of the two fences, we placed six litterbags per each one of the six different litter procedences, those from the provinces of León, Navarra, Lérida, Cáceres, Almería and Alicante. This set up allowed us to test whether litter decomposition was affected by intraspecific variability among forest in different regions (H1); moreover, to test the effects of intraspecific variability in the litter at local scale, we also included local litter from Ciudad Real coming from four different plots in Cabañeros National Park, i.e. from two types of uses (abandoned forest and open woodland), and including or excluding ungulates at each use; thus, from Cabañeros we used 4 different types of litter: (1) from a forest with ungulate exclusion (CFE), (2) from a control forest (CFC), (3) from an open woodland with ungulate exclusion (CWE) and (4) from a control open woodland (CWC). Each type of litter was placed in its procedence plot following the same design than translocated litter, into metallic fences in the south side of a *Q. ilex* tree.

The litterbags, made as described in the general methodology, were systematically distributed over the soil and covered with metallic meshes (as in **Figure 2**), within the area surrounded by the metallic fences mentioned above. In total there were 120 litterbags, 12 replicates per each one of ten litter procedences, six procedences translocated from other forests, and four procedences from Cabañeros itself.

Figure 2. Litterbags placed in one of the experimental plots in Cabañeros National Park (Ciudad Real, Spain), in the forest, inside the fences and covered with metallic meshes. Litterbags were distributed in 4 groups, one per replicate, and inside each group there were three litterbags for the three sampling times (litterbags showed in this picture are more than those explained in the methodology, because some of the litterbags were used for another experiment not included here).

Experiment 2

In order to test how litter decomposition rates responds to a regional gradient of climate (H2) and land uses (H3) in Mediterranean forests, *Q. ilex* leaf litter originally from the forest of Cabañeros was distributed across the other seven plots of the studied regional gradient (**Figure 4** in the general methodology). In the autumn of 2016, in each forest we selected four *Q. ilex* trees from among the trees measured in the autumn of 2015 (Garcia-Angulo *et al*., submitted). In the south side of each one of those four trees we set up 3 litterbags (one litterbag per sampling period, see below "samplings" section) with the uniform litter over the soil and covered with metallic meshes. In total there were 84 litterbags, 12 in each forest.

HFA (H4) was tested in three of those forests (León, Navarra and Cáceres), where another additional 12 litterbags were disposed with local litter from the forest itself, 3 litterbags per each one of the same 4 trees and under the same metallic meshes than the litterbags with the uniform litter; and comparisons with that same litter translocated to the common garden experiment in Cabañeros, as well as with litter from Cabañeros incubated in its procedence and in those three other sites, were also used to test HFA.

Samplings

Litterbags were collected from all sites at three different times during the 12 months after the experimental set up, i.e. after ca. four, eight and twelve months of incubation in the field. At each sampling, four litterbags (replicates) per treatment were collected. The first sampling was conducted during the winter (January-February 2017), the second by the end of the spring (May-June 2017), and the third at the beginning of the autumn (September-October 2017).

Ancillary data

Historical climate at each site was defined with the mean annual temperature (MAT, ranging from 10.34 to 15.37ºC) and mean annual precipitation (MAP, ranging from 282.41 to 916.67 mm) for the time period 1950-2007, by interpolating data in 1km grid database published by Felicísimo *et al*. (2011). Monthly weather values (mean temperature and total precipitation) from each site during the 12 months of the experiments was taken from a global climatology gridded dataset, CRU TS v.4.03 at 0.5º resolution (Harris *et al*., 2014), being subsequently grouped in three intervals of four months for every litterbag incubation period; values for other intervals were calculated from those results, e.g. for the total incubation period of one year, mean temperature was the mean between the values of temperatures in the three intervals of four months, and total precipitation was the sum of the three values of precipitation for every four months.

Litter mass decay was analyzed for the three removal times, and C, N, P, K, Ca, Mg, Mn, Fe, Zn, Cu and Na contents were analyzed also in samples from the first and the third removal times, i.e. after four and twelve months of incubation in the field.

Additionally, data on soil characteristics in each site from experiment (2) was available from other study (García-Angulo *et al*., submitted), and here we used soil pH and total soil P, measured from the same sampling campaign during autumn 2015. During this campaign, soil samples of the first 10 cm depth were taken using a cylinder (5 cm diameter), under holm oak influence, i.e. under tree canopy and with a 0.5m radius from the trunk; 27 soil samples were taken from each forest, near the trunk of the same 27 holm oak trees in the center of the squares used to assess understory coverage, being subsequently mixed every 3 samples in a composited soil sample, resulting in 9 composited samples per site that were analyzed. All soil samples were homogenized and sieved (2 mm mesh size). Soil pH was analyzed from a saturated soil paste (Kalra, 1995) using a CRISON micropH 2001 (Hachlange Spain, S.L.U., Barcelona, SP), and total P in soil was determined by ICP-OES (PerkinElmer 4300 DV, PerkinElmer Inc., Wellesley, MA, USA). In Cabañeros, which was not included in the mentioned study, the same sampling method was applied at the four different plots described above. Only data on soil pH was available in soils from Cabañeros.

Decomposition rates are expressed by the constant k from the exponential decomposition model commonly used to represent litter decay curves (Zhang *et al*., 2008; Kampichler and Bruckner, 2009):

$$M_t = M_0\, e^{-kt} \qquad (1)$$

where t is incubation time (days), M_0 is litter mass at the beginning of the experiment, and M_t is litter mass at removal time t. k was calculated for all time intervals between all times, the beginning of the experiment (t_0) and the three litterbag removal times (t_1, t_2 and t_3 respectively). For each interval, k is labeled as k_{ij}, representing the interval between times i and j, where $i \in \{0, 1, 2\}$, $j \in \{1, 2, 3\}$, $i < j$. Therefore, six types of k were calculated, but most of the results here focus on the k_{03}, which corresponds to the longest time interval of the experiment (one whole year), hence being k_{03} the most integrative coefficient of decomposition rates over the four seasons, and because main results were consistent among time (i.e. for most k_{ij}).

We can compare litter mass decomposition rates among: i) different litter qualities in the common garden (H1); ii) differences associated with a regional gradient of climate (H2) and land uses (H3), using the uniform litter from Cabañeros; and iii) differences associated with HFA using local litter versus translocated litter from three procedences of experiment 2 and local litter from Cabañeros and litter from those same three procedences in experiment 1 (H4).

Statistical analyses

All statistical analyses were carried out in R v. 3.5.1 (R Core Team, 2016). Differences among litter qualities (experiment 1) and among sites (experiment 2) were represented by principal component analysis (PCA). Normality distribution of variables was tested with the Shapiro-Wilk normality test, and due to the lack of normality in many variables, correlations between them were analyzed with non-parametric Spearman pairwise correlation coefficients (r).

In order to find which explanatory variables are the best predictors of the observed decomposition rates, and also to find the best predictors of those variables, linear mixed-effects models (LME) were done with R package nlme (Pinheiro *et al*., 2019). In models for common garden experiment (1), litter procedence site nested in local (from Cabañeros) versus translocated litter were used as random effects, while in models for gradient experiment (2) the random effect was the litter incubation site. Distribution of model residuals was tested with the Shapiro-Wilk normality test, being those without normality (i.e. models explaining Mn content in leaves) transformed by the natural logarithm of the response variable; therefore, only models with normally distributed residuals (p-value > 0.05) have been used, and among them, those models with lower Akaike information criterion (AIC) were selected; when AIC differences were not significant between models with lower AIC, the simplest model was selected. Interactions have been tested only for independent variables (Spearman correlation p-

values > 0.05). Once the best predictor variables were determined, all their possible combinations in models were compared using the R software package "MuMIn" (Barton, 2019), being selected the resulting best combination of variables and interactions according to that analysis, based on the corrected AIC (AICc) for small sample sizes.

Variance among time of Mn content in litter was analyzed with t-Student test, comparing Mn concentration between the beginning of experiment 1 and the litterbag removal times 1 and 3, and also between those two sampling times.

Ecosystem complexity controlling litter decomposition was represented with a structural equation model (SEM), using R software package "piecewiseSEM" (Lefcheck and Freckleton, 2016). Best LME models resulting from previous analyses for experiment 1 were used to construct the SEM, representing the litter quality predictors of the observed variance in k_{03}, as well as the effects of land use, climate and soil pH from procedence sites controlling intraspecific variability in holm oak litter quality. The goodness of fit of our SEM was calculated with the Fisher's C statistic and the AIC coefficient.

HFA hypothesis (H4) was tested using equations adapted from Vivanco *et al*. (2018). Here we calculated the translocation effect as the difference between k in the decomposition of the same original litter in litterbags incubated in different sites (the procedence site "home" and other site "away"), and the litter quality effect as the difference between k in the decomposition in the same site of local litter versus translocated litter from the "away" site:

$$\text{Away effect (\%): } 100\ (k_{home} - k_{away})/k_{home} \qquad (2)$$

$$\text{HFA effect (\%): } 100\ (k_{local} - k_{trans\ located})/k_{local} \qquad (3)$$

Equation 2 was applied to gradient experimental sites of León, Navarra and Cáceres, being k_{home} the decomposition rate of local litter in each one of those forests, and k_{away} the rate for the same litter translocated to the common garden experiment in Cabañeros; equation 2 was also applied to local litter in Cabañeros compared with that litter translocated to those three sites in the gradient experiment. This could show a potential HFA between sites (i.e. "away effect") if results are significantly higher than zero, but if responses to reciprocal transplantations are significant but positive for one site and negative for the other site, that could indicate that climate or forest structure are the main causes of those results, rather than HFA. On the other hand, equation 3, applied to the same four sites and both experiments, shows a more classical HFA analysis, which would be supported also by results significantly higher than zero. Results from both analyses were tested with t-Student, to determine if the observed differences are significant or not. Both effects were also compared with a one-way analysis of variance (ANOVA).

RESULTS

Common garden (experiment 1)

As expected, intraspecific variability in chemical composition of *Q. ilex* litter was lower within Cabañeros than among the different sites across the Iberian Peninsula. Between sites, differences in litter quality were quite high, as observed by the low overlapping among sites in the PCA (**Fig. 3**). Remarkably, there was a clear differentiation in litter quality between forest and woodland sites in Cabañeros, showing the relevance of land management for litter quality.

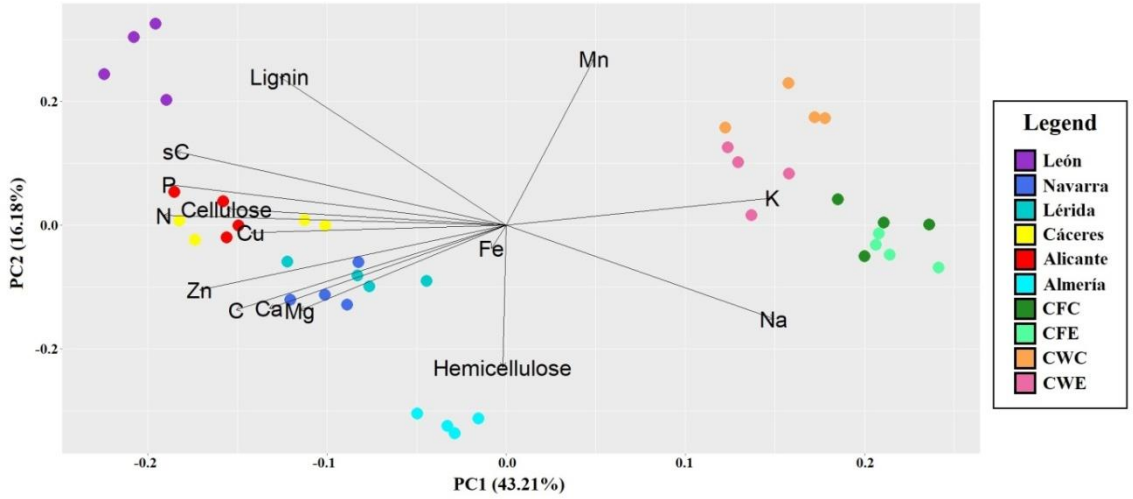

Figure 3. PCA for intraspecific variability in *Quercus ilex* litter quality. Variables include lignin, cellulose, hemicellulose, their sum as structural C (sC), and the elements C, N, P, K, Ca, Mg, Mn, Fe, Zn, Cu and Na. Samples consist in four replicates from each site, i.e. León (purple), Navarra (dark blue), Lérida (cyan), Cáceres (yellow), Alicante (red), Almería (turquoise), and the four sites inside Cabañeros: control forest (CFC, dark green), exclusion forest (CFE, light green), control open woodland (CWC, orange) and exclusion open woodland (CWE, pink).

Litter decomposition rate after one year (k_{03}) was correlated with the initial contents in lignin, cellulose, sC, nsC, C, N, P, K, Ca, Mn, Zn, Cu and Na (**Appendix 4**). A negative correlation between sC and k_{03} was the strongest one observed (Spearman r = - 0.7, p-value < 0.0001), being sC also correlated to the rest of those components except Mn, which was independent from sC (p-value = 0.0656); Mn had a positive correlation with k_{03} (Spearman r = 0.36, p-value = 0.0241).

The analysis of mixed models with package MuMIn, for the explanatory variables of the observed decomposition rates, showed that the best model was the one that uses sC and Mn but without interaction between them (AIC = -590.85, df = 6, marginal R^2 = 47.26%, conditional R^2 = 47.26%) (**Fig. 4**).

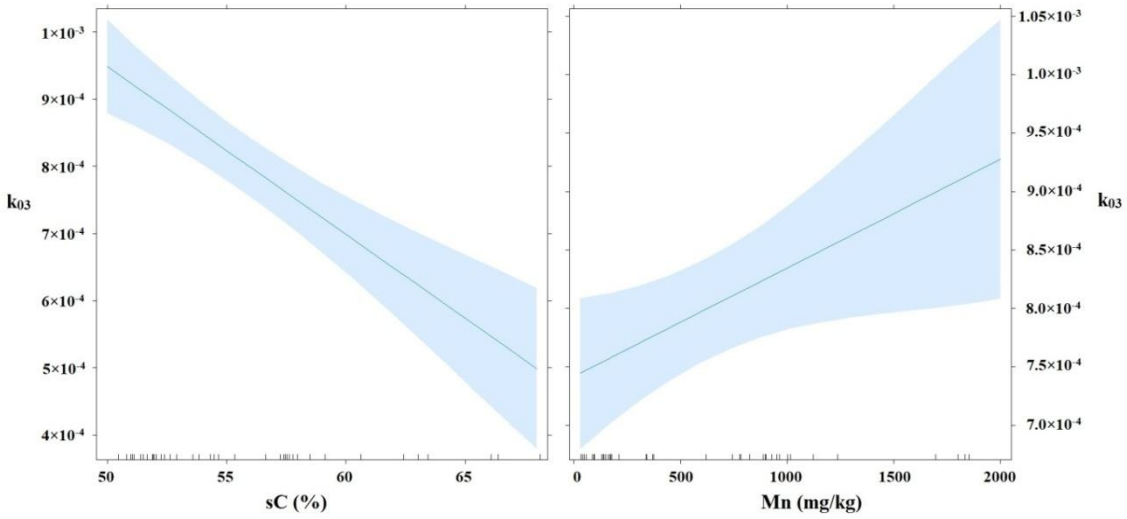

Figure 4. Correlations between k_{03} and its explanatory variables: sC and Mn litter contents. LME model equation: $k_{03} = 2.1378\times10^{-3} - 2.4955\times10^{-5}sC + 9.31\times10^{-8}Mn$.

Moreover, mixed models also show that sC was best explained by climate, with a mixed model using MAT, MAP and their interaction (MAT:MAP) (**Fig. 5**), with the same random factors than the model for k_{03} (AIC = 163.58, df = 7, marginal R^2 = 51.32 %, conditional R^2 = 93.09 %). sC decreases with increases in MAT, especially under drier conditions.

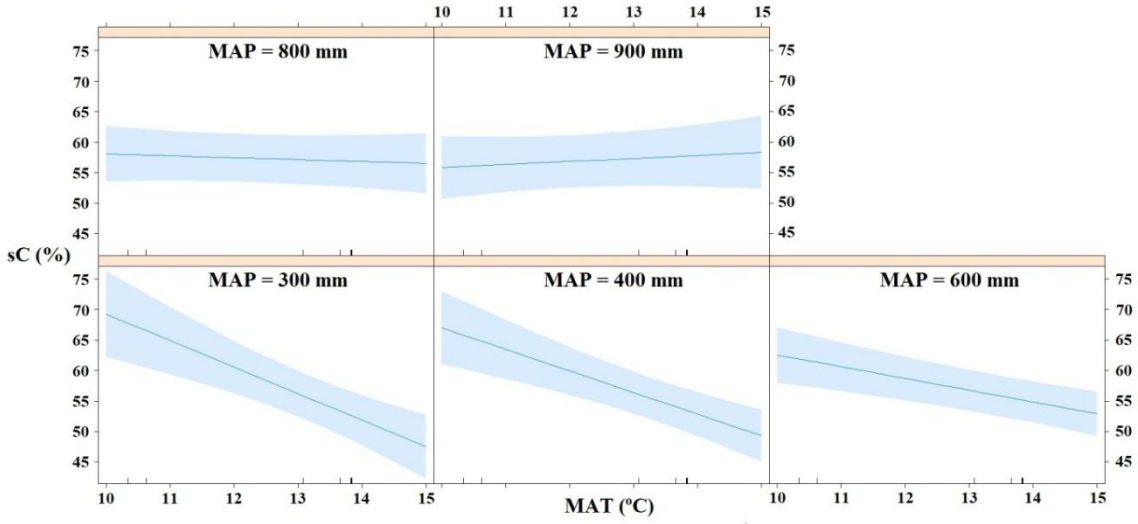

Figure 5. Correlations between structural C (sC) and its predictors: mean annual temperature (MAT), mean annual precipitation (MAP), and their interaction (MAT:MAP). LME model equation: sC = 143.4944 – 6.7581 MAT – 0.1029 MAP + 0.0081 MAT:MAP.

On the other hand, concentration of Mn in leaves was best explained by soil pH, MAP and their interaction (pH:MAP) as fixed factors (**Fig. 6**) (AIC = 9.51,df = 7, marginal R^2 = 87.54 %, conditional R^2 = 98.29 %). Leaf Mn content increases when pH decreases, especially under drier conditions; but for high rainfall (MAP) Mn content in leaves tend to decrease, being attenuated the pH effect.

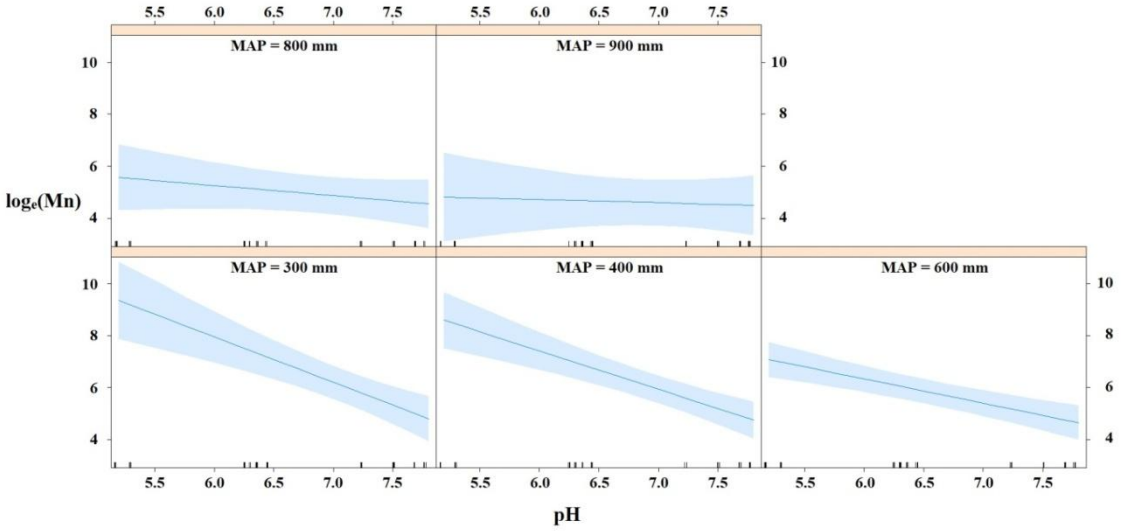

Figure 6. Correlations between the natural logarithm of manganese, $\log_e$(Mn), and its predictors: soil pH and mean annual precipitation (MAP), with their interaction (pH:MAP). LME model equation: $\log_e(Mn) = 26.4888 – 0.0241$ MAP + 0.003 pH:MAP.

Regarding Mn changes in litter through time, only weak significant differences were found for Mn litter from León after four months (p-value = 0.0308) and between four and twelve months (p-value = 0.0445), and a stronger difference was found for Mn in litter from the control forest in Cabañeros between four and twelve months (p-value = 0.0026); for all other time intervals and litter types, changes in Mn concentration were not significant. Therefore, Mn concentrations in litter were almost similar through the incubation time of one year in the common garden.

SEM confirmed results obtained in mixed models for the common garden experiment: litter decomposition rates after one year were explained mainly by litter recalcitrance (sC) and Mn concentration, which, on the other hand, could be predicted by a combination of site environmental factors, including climate (both MAT and MAP) and soil pH (**Fig. 7**).

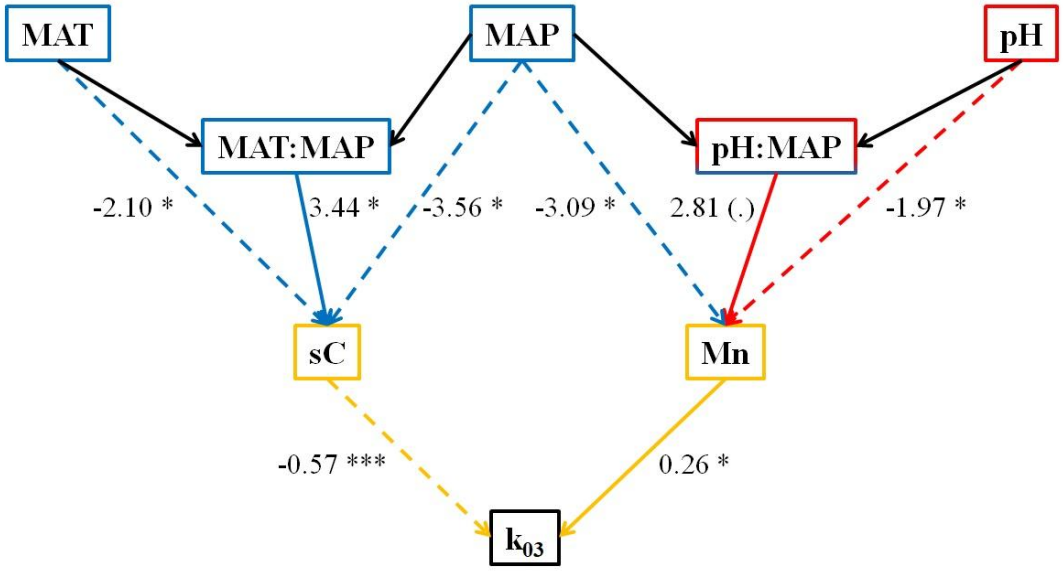

Figure 7. Structural model of litter decomposition drivers though litter quality (AIC = 57.45; AICc = 120.94; BIC = 91.22; Fisher's C = 17.45). Climate (in blue) includes mean annual temperature (MAT) and mean annual precipitation (MAP); and soil (in red) by pH. Interactions between MAT and MAP (MAT:MAP), and also between pH and MAP (pH:MAP) are included. Litter quality (in orange) includes the response variables to the previous factors, i.e. structural C (sC) and Mn (transformed by the natural logarithm), which at the same time are the predictors of litter decomposition rates after one year (k_{03}). Full arrows stand for positive relationships among variables, while dashed arrows indicate negative relationships; numbers near each arrow indicate the estimated coefficients for each relationship, with their significance: *** for p-values < 0.001, * for p-values < 0.05, and (.) for a p-value = 0.067.

Gradient (experiment 2)

The analyses of intersite variability throughout the Iberian Peninsula, accounting for differences between sites as in climate and forest structure, showed a large environmental variability (**Fig. 8**).

Among all the variables tested, decomposition rate after one year (k_{03}) was mainly correlated with forest structure, and mainly with a positive correlation with understory (Spearman r = 0.68, p-value < 0.0001). So the best model to explain the decomposition rate after one year was a mixed model with understory as fixed factor (**Fig. 9**) (AIC = -436.79, df = 4, marginal R^2 = 43.74%, conditional R^2 = 43.74%). Understory was negatively correlated with canopy cover (Spearman r = -0.39, p-value = 0.039, **Appendix 4**), supporting the land use controls on understory structure, but mainly it was explained by its positive correlation with MAP (Spearman r = 0.64, p-value < 0.001).

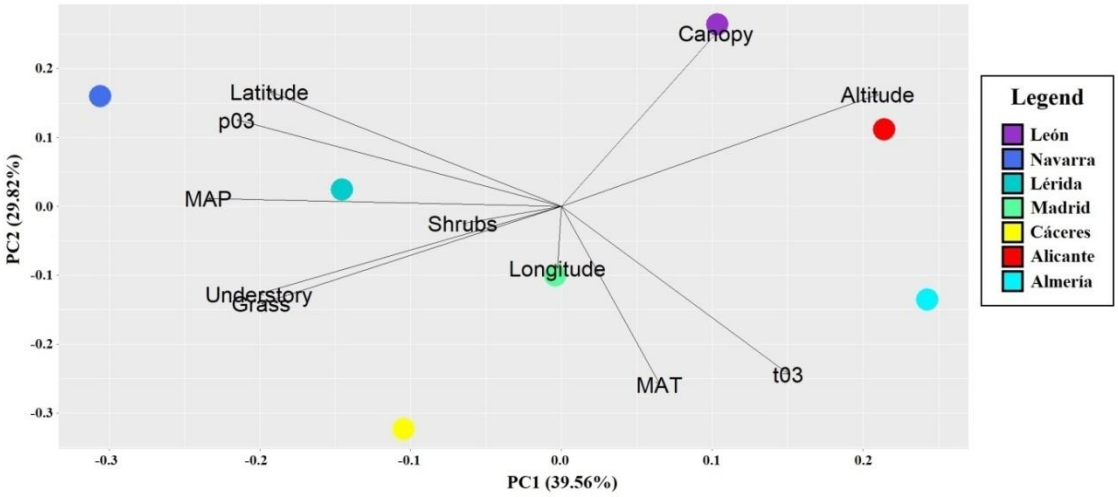

Figure 8. PCA for intersite variability in climate and forest structure. Altitude, latitude and longitude are also included. Climate include mean annual temperature (MAT), mean annual precipitation (MAP), and the weather during the litterbag experiment, mean temperature (t_{03}) and total precipitations (p_{03}) after one year of incubation in the field. Forest structure includes vegetation cover divided in tree canopy, shrubs and grass, and also with understory cover. Sites are represented by a circle averaging the four samples per site: León (purple), Navarra (dark blue), Lérida (cyan), Madrid (light green), Cáceres (yellow), Alicante (red) and Almería (turquoise).

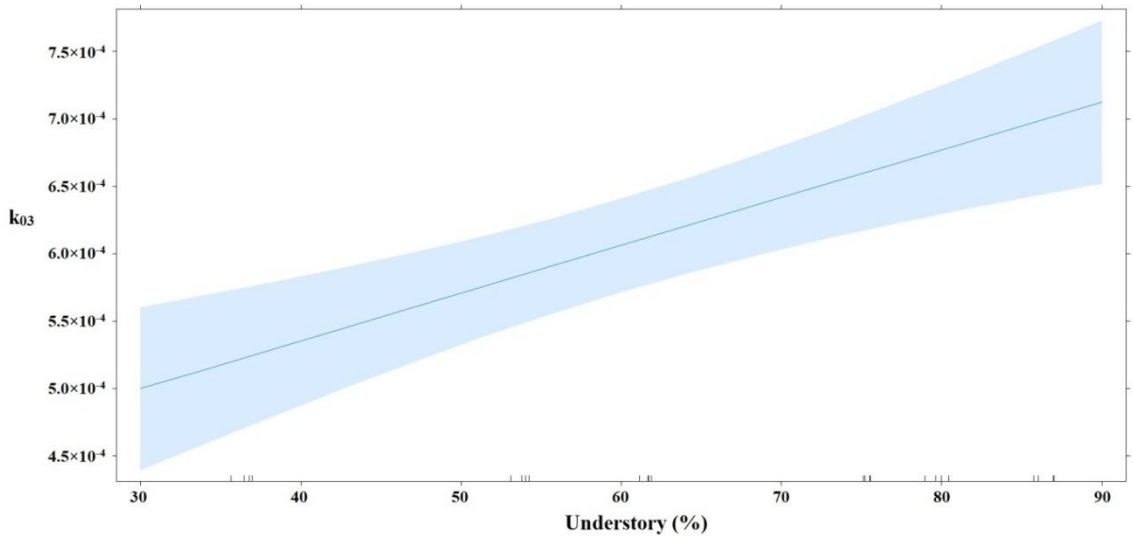

Figure 9. Correlation between litter decomposition rate after one year (k_{03}) and understory cover. LME model equation: $k_{03} = 3.9331\times10^{-4} + 3.5477\times10^{-6}$ Understory.

HFA

Differences in litter decomposition rates comparing local litter versus translocated litter (equation 3) incubated in the same place (for both experiments 1 and 2) resulted in apparent higher rates for local litter than for translocated litter in all locations, average changes ranging from 9.57 to 22.98%; and the "away" treatment (combining experiments 1 and 2) resulted also in apparent higher rates for litter decomposition incubated in its procedence site than in another "away" site, except for León. Nevertheless, most differences were not significant (**Table 2**), and in general neither HFA (p-value = 0.1646) nor away treatment (p-value = 0.5057) had clear effects, being both also similar between them as resulted from a one-way ANOVA (p-value = 0.7178).

Procedence site	Away site	HFA effect			Away effect		
		mean (%)	sd (%)	p-value	mean (%)	sd (%)	p-value
Cabañeros	León	22.98	13.92	0.2363	45.15	3.26	**0.0011**
Cabañeros	Navarra	22.22	23.57	0.4610	15.41	4.75	0.0623
Cabañeros	Cáceres	13.63	10.45	0.3277	23.82	3.25	**0.0072**
León	Cabañeros	15.58	3.05	**0.0197**	-18.57	20.72	0.4812
Navarra	Cabañeros	9.57	5.06	0.1890	17.05	24.05	0.5710
Cáceres	Cabañeros	21.93	3.90	**0.0151**	11.57	10.05	0.3789

Table 2. Changes in litter decomposition rates (k_{03}) due to intraspecific variability in litter quality (HFA) and away treatment. Changes in k_{03} due to litter quality (third column) were calculated comparing decomposition of local litter from the procedence site (first column) with decomposition of translocated litter from away site (second column), both incubated in the procedence site (equation 3). Changes in k_{03} due to away treatment (sixth column) were calculated comparing decomposition of litter from the procedence site incubated in its procedence site and in the away site (equation 2). t-Student test were done (shown p-values) for every comparison (row) testing if any effect differed significantly from zero. Significant p-values are highlighted in bold.

Environment and litter intraspecific variability effects on decomposition

Differences among sites and between litter qualities had a similar effect on litter decomposition rates (**Fig. 10**), suggesting that the intraspecific variability in litter quality has a relevance on holm oak litter decomposition comparable to that of the environmental variability at regional scale.

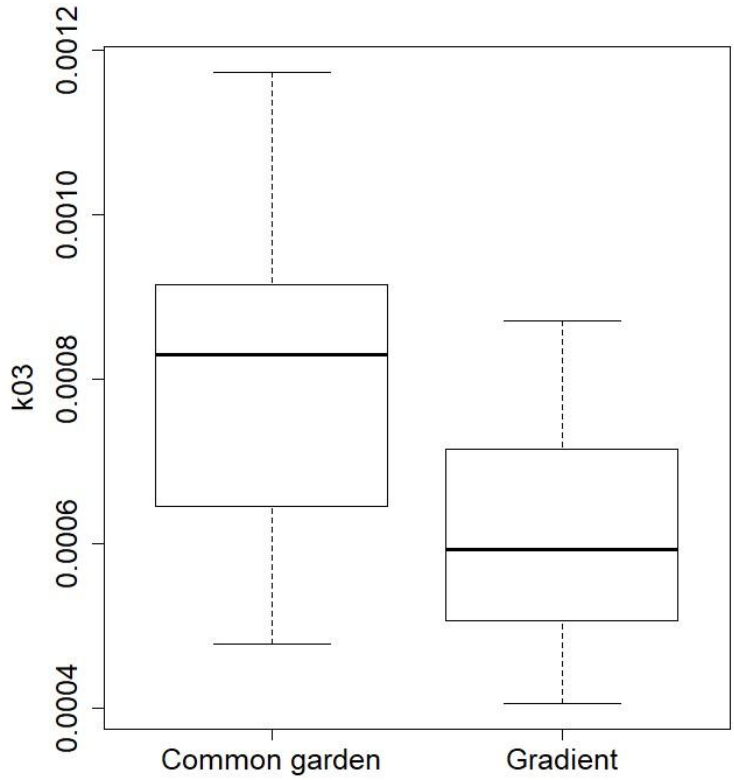

Figure 10. Comparison of variances in litter decomposition rate after one year (k_{03}) between both experiments.

DISCUSSION

Factors controlling litter decomposition in a regional environmental gradient

Our study shows that in the regional climatic gradient of the study, variables associated with forest structure rather than climate controlled rates of litter decomposition. Although precipitations and temperatures tend to be positively correlated with litter decomposition rates (Austin and Vitousek, 2000; Salinas *et al*., 2011; Bothwell *et al*., 2014), those variables did not explain the observed variability of k_{03} in our experiments. Positive correlation between understory and k_{03} suggests that under grass and shrub vegetation, environmental conditions, likely microclimatic conditions (e.g. relative humidity and temperature on litter layer) were more favorable for litter decomposition, independently of the climatic conditions of the site.

Consequently, litter decomposer community in Mediterranean holm oak forests seem to be decoupled from historical and current climate, and rather affected by vegetation structure, and more precisely by the degree of understory cover. It is likely that understory vegetation modifies surface conditions towards a more favorable environment for the decomposer community and/or the soil fauna, e.g. buffering temperatures and decreasing evaporation, hence providing a shelter for soil organisms and a more copiotrophic environment (more belowground biomass available) for their proliferation. Understory intercept radiation, hence decreasing temperatures and hence evaporation rates from litter surfaces during warm days (Wang *et al*., 2014). Since microbial communities in drylands are generally adapted to the stressful drought conditions (Curiel Yuste *et al*., 2011; 2014), and their extracellular enzymes tend to show greater sensitivity to changes in soil moisture (Averill *et* al., 2016), slight modification of the microclimatic conditions under the vegetation cover could counteract the stress of water deficit in drier sites, which is aligned also with evidences on the role of dew-induced litter decomposition (Gliksman *et al*., 2017), as discussed in chapter 3. That could explain why, contrary to H2, precipitations and temperatures during the experiment were not correlated with decomposition rates in our study.

Moreover, understory vegetation tend to have positive effects on the abundance and diversity of the soil fauna (Bokhorst *et al*., 2014), which has also a relevant role controlling litter decomposition (see chapters 1 and 2), so that could also explain the higher litter decomposition rates associated with the understory. Given the observed regional impact of understory vegetation over the turnover of litter in these very representative Mediterranean ecosystems, future studies should be designed to deepen the potential impact of the understory vegetation over the micro-environmental conditions that determine litter decomposition.

Understory vegetation had a main positive correlation with precipitation (MAP) but presence of understory vegetation (grass, shrubs and seedlings) in holm oak systems also responds to other, more anthropic factors, such as the land use (grasses proliferate in open woodlands used for livestock with respect to those used for wood extraction, hunt, etc.), the management intensity (lack of thinning in abandoned lands; Garcia-

Angulo *et al*., submitted), or the history of natural disturbances of the stands such as number or intensity of fires, which determines the level of degradation and tree regeneration capacity of the system (Schoennagel *et al*., 2017). In our case, understory cover was also negatively correlated with canopy cover, which suggests that more intensively managed sites (less density of trees) are more subjected to colonization by pioneer species of grasses and shrubland. This colonization was further stimulated under wetter, more favorable climatic conditions. Hence, we here highlight that rates of litter decomposition in this peninsular gradient were directly independent from the local climatic conditions, and rather by vegetation structure (understory cover), which exerts a strong control over the micro-environmental conditions that determine rates of litter decomposition in the soil surface. Understory cover was, on the other hand, mainly shaped by land use and management intensity together with climate. This is a result that should be taken into account since most terrestrial ecosystems, particularly in the Mediterranean basin, are or have been subjected to a long history of anthropic influences and fires.

Intraspecific variability in litter quality as an underestimated factor of variance in litter decomposition rates

We found a considerable intraspecific variability in litter stoichiometric composition and litter quality. Indeed, elemental composition, as well as structural and non-structural C concentrations in litter differed substantially in our peninsular gradient, which highlights some important regional variability that should be explored; it may also result in strong, and so far underestimated, impacts over regional-scale magnitude and variability of carbon and nutrient dynamics, even in systems apparently similar in vegetation composition. It is known that *Q. ilex* shows a large intraspecific variability in structural and functional traits in response to environmental conditions (e.g. Bussotti *et al*., 2002), which explains the observed variability in litter quality. Such variance in leaf litter quality and decomposability within a species with such a broad distribution implies that changes in the environmental conditions among the distribution range of holm oak could lead to large impacts on soil C cycling.

Indeed, we here show that these substantial intraspecific differences in litter quality were also reflected in remarkable differences in litter decomposition rates, comparable to those obtained in the peninsular gradient (**Fig. 10**). As expected for such a sclerophyllous litter (Barbeta and Peñuelas, 2016), initial leaf recalcitrance (i.e. structural C) was the main factor inhibiting litter decomposition, even more than lignin or cellulose alone. This might be explained because both lignin and cellulose, as recalcitrant compounds, slow down litter decomposition, resulting more relevant for decomposition rates the difference between litter labile and recalcitrant fractions than differences among those different types of recalcitrant compounds.

Together with litter recalcitrance, Mn content in leaves was another main driver of litter decomposition. It is known that Mn plays a very important role as an electron acceptor during redox reactions in soils (Bolan *et al*., 2003), and there is strong evidence that Mn redox cycle is coupled to litter decomposition, because its oxidation is directly involved

in the process of oxidative degradation of aromatic structures in lignin (Keiluweit *et al*., 2015). Mn concentrations are crucial for fungal degradation of lignin because they regulate the production and activity of enzymes implicated in the depolymerization of lignin, as the manganese peroxidase (Wariishi *et al*., 1991; Perez and Jeffries, 1992; Berg *et al*., 2007).

Mn relevance for litter decomposition could differ in function of litter species during different stages of the decomposition process. While some studies shown that Mn seems to gain relevance on the long term decomposition after the first years (Berg *et al*., 2007), even for some oak species litter (Aponte *et al*., 2012), other studies have shown that oak litter decomposition rates could be controlled by Mn even during the first stage of the process (Davey *et al*., 2007). Our results support the high relevance of Mn in holm oak leaves even during the first year of litter decomposition.

Despite the fact that decomposition rates for local litter seems to be generally higher than those for translocated litter, we could not find enough statistical evidence to support a clear HFA effect, at least for the one-year period of our experiment. It is likely that for more recalcitrant litter as is the case for this sclerophyllous leaves, more time is needed to detect potentially significant local advantage trends in litter decomposition (Gao *et al*., 2016), but for the time-span of our experiment our results only allow for rejection of the HFA hypothesis (H4). These results support previous evidence of the absence of HFA in oak litter (Aponte *et al*., 2012). Thus, no clear advantage was found either for microbial communities decomposing local litter instead of translocated litter with different litter quality, or for litter being decomposed in its procedence site instead of in another forest.

Our results show that the observed intraspecific variability of litter quality, that largely determines rates of litter decomposition, was strongly shaped by the climatic conditions of the leaf litter procedence. For instance, structural C concentration, a measure of the recalcitrance of the litter, was favored under harsher climatic conditions, e.g. low precipitation and temperature (**Fig. 5**), meaning that sC, and particularly lignin, was largely synthesized in leaves to protect them against stress under low temperatures and water deficit (Moura *et al*., 2010). Hence, and as it has been observed for other evergreen Mediterranean *Quercus* species (*Q. suber*, Ramírez-Valiente *et al*., 2015), our study confirms that climatic constrains in this gradient may shape intraspecific changes in litter chemistry that may determine their decomposability in this peninsular gradient.

On the other hand, Mn leaf litter concentration was favored under low soil pH, which, in the gradient of the study is generally associated with the parent material that dominates the western part of the Peninsula (Costa *et al*., 1997). Mn is an essential plant nutrient, with a relevant role in redox processes as an activator or cofactor for many enzymes, including processes required for photosynthesis, as the photosynthetic water oxidation (Renger and Wydrzynski, 1991). It is uptaken from soil by plants as Mn^{2+} and transported to leaves, where it accumulates (Loneragan, 1988). Leaf Mn concentration has been found to be associated with the uptake of other nutrients, particularly phosporous (P, Lambers *et al*. 2015), through the exudation of carboxylates by roots for

P acquisition, which chelates Mn and reduce Mn^{4+} to Mn^{2+} which is the soluble form of Mn taken up by plants (Jauregui and Reisenauer, 1982). Hence, under acidic conditions, when P is generally adsorbed in mineral soil particles and no readily available for plant uptake (Devau *et al*., 2009), exudation of carboxylates by plants may also have enhanced the availability of micronutrients like Mn as a side effect (Godo and Reisenauer, 1980). The strong negative correlation between soil pH and total P in the soil (Spearman r = -0.9429, p-value < 0.0001, **Appendix 4**) suggests that P sequestration in soils decrease with pH, and therefore P availability for plants could decrease with decreasing pH. The negative effect of pH on Mn litter concentration was exacerbated under drier conditions (**Fig. 6**), potentially suggesting that liberation of soluble forms of Mn (Mn^{2+}) mediated by carboxylates exudation under low pH conditions, could be neutralized by lixiviation of these mobile forms under high precipitations regimes with respect to drier sites. This explanation is further supported by the fact that concentrations of Mn in litter from procedences with higher precipitations were similar, independently of the soil pH.

CONCLUSIONS

This study shows complex interactions in the controls of litter decomposition from one very representative Mediterranean tree species in a regional climatic gradient. In this regional gradient, we could not detect a direct effect of historical climatic conditions or current weather on litter decomposition rates. Instead, understory cover, which is a variable mainly related to forest structure and hence, land use and management intensity, was the best predictor for decomposition rates of uniform litter over a broad geographical and climatic gradient, obscuring the expected role of climate. It is likely that the presence of understory vegetation alters the microclimatic conditions that favor decomposers of litter.

Climate affected litter decomposition rates mainly through indirect influences on understory cover and *Q. ilex* leaf litter quality and decomposability. The high intraspecific variability observed in litter quality of *Q. ilex*, which subsequently affects litter decomposition rates, responded to environmental abiotic (climate and pH) differences in the litter procedence, i.e. litter was more recalcitrant (more structural carbon) under colder and drier conditions, and had more Mn under drier and more acidic conditions (low pH), when probably P and Mn liberated insoluble forms but not leached. Variability in rates of leaf litter decomposition related with climate-driven intraspecific differences in litter quality was of the same order of magnitude as the observed variability associated with the regional climatic gradient of the study. In this regard, this study also identified a mechanism of litter decomposition determined by the role of Mn as an important element that favors oxidation of complex structural molecules like lignin.

In conclusion, our study supports that, at a regional scale, land use and management intensity shaping vegetation structure could play a more relevant role over litter decomposition than climate, which exerted more indirect effects over leaf chemistry and intraspecific variability in holm oak litter quality (together with soil pH). Such intraspecific variability in litter quality was found to affect decomposition rates in a similar magnitude than the environmental variability throughout the regional scale of the Iberian Peninsula. Therefore, that intraspecific variability, controlled by climate, could be a key driver of soil C cycle responses to future changes in climate and should be taken into account to predict current rates of decomposition by models.

GENERAL DISCUSSION

The cycling of C in soils involves many biotic and abiotic processes, and yet much of them remain not included in current state-of-the-art models, which generally represents empirical relations that oversimplified the ecological complexity behind it. This is the case, for instance, of the processes associated with or controlled by the complex soil trophic web, despite the large evidence of their crucial role in e.g. SOM and litter decomposition (e.g. García-Palacios *et al*., 2013) or the flow of energy, C and nutrients in the system (e.g. DuPont *et al*., 2009; Andrés *et al*., 2016). How the biological community is structured in soils, the flux of matter and energy through its different trophic levels or the functions they are responsible for, largely determines the dynamics of C and nutrients in soils.

Beyond the traditional concept of SOM decomposition controlled mainly by its chemical recalcitrance (Marschner *et al*., 2008), our review on this issue has highlighted the knowledge gap related to the role of physical and organo-mineral stabilization of SOM and, therefore, the relevance of soil structure for the prediction of soil carbon cycle responses under global change. This concept of 'physical recalcitrance', representing the accessibility of organic matter to decomposers, may drive SOM stabilization even more than its chemical properties, because microbial enzymes much reach the SOM first, but its protection in aggregates and/or organo-mineral complexes within soil particles constrains its accessibility by decomposers and, therefore, the rates of potential SOM degradation, which are determined secondly by its chemical properties. Moreover, soil hydrology, together with soil structure, also plays a role determining SOM accessibility and food web interactions. These links between abiotic and biotic processes should be included in ecosystem scale models to improve the accuracy of their predictions.

The review on the state-of-the-art on our knowledge of soil ecology and functioning presented in chapter 1 has led to the elaboration of a new model concept, integrating soil structure, soil food webs and ecohydrology in a new mechanistic process-based soil model, KEYLINK, for predictions of soil C cycle in terrestrial ecosystems. The development of this model, showed in chapter 2, constitutes a first step towards a new generation of ecosystem models, and to our knowledge, it is the most ambitious attempt until now to integrate soil functional biodiversity in the prediction of soil C cycling. In the dramatic biodiversity crisis we are experiencing nowadays (Singh, 2002), we need to account for the large functional diversity of soils (Emmerling *et al*., 2002) and its organizational complexity to better understand how climate change will affect soils and ecosystem functioning in the future. New models are, therefore, required to integrate the many factors (e.g. climate, litter quality, soil food webs, soil structure, soil hydrology) controlling key functions (e.g. C sequestration, CO_2 emissions). This next generation of ecosystem models, such as KEYLINK, that integrate all those ecosystem processes, could serve for substantial improvements in predictions of soil carbon cycle responses under global change.

The results presented in chapter 2 support the importance of integrating the links between trophic structure, functional biodiversity and soil structure, showing, for instance, the impact of classical trophic cascade effects on soil C stabilization when predators are excluded from the food web (**Figure 3** in chapter 2) or other more counterintuitive predictions, as the increase in SOM and litter decomposition without predators even when microbial decomposer populations where lower. This was because the increase in engineers population, due to the trophic cascade effect from excluding predators, changed the soil structure, increasing macro- and mesoporosity and decreasing bacterial- and microporosity (**Figure 4** in chapter 2), which reduced the physical protection of SOM as a direct consequence of the lower volumes in the smaller pore size classes. Moreover, that increase in macro- and mesoporosity led to a faster water flow through the soil to deeper layers (water output in the model), resulting in lower soil water content in the simulated layer and, therefore, in a higher aeration of the pores that were flooded in the presence of predators. Both processes produced an increase in soil C accessibility, which could explain the observed decrease in SOM stabilization in the simulated scenario for predator exclusion. This result remarks the relevance of modelling links between key biotic and abiotic processes in terrestrial ecosystems.

The scenarios simulated for chapter 2 showed how changes in the food web structure (e.g. excluding predators) affected litter decomposition and SOM stabilization more than any other tested change in soil properties (texture) or even litter quality, which is remarkable because most models representing litter and SOM decomposition mainly focus in the role of organic matter quality, neglecting the role of soil fauna, despite it has been proven to play a crucial role on SOM stabilization (Fox *et al*., 2006; Frouz, 2018). If these predictions are confirmed, we could move forward to a more reliable representation of C dynamics in soil models.

There is, however, room for improvement of how the SOM, soil food webs and/or the soil functional diversity are represented in KEYLINK. For instance, the simplified representation of faeces being added to SOM does not account for potential impacts of faeces on microbial activity (Frouz, 2018), beyond the increase in total SOM. Future versions should include better representations of SOM and its different components (e.g. POM, DOM); although DOM was included in the developed functions for KEYLINK (equation 41 in chapter 2), in the simulations presented in this thesis SOM remained simplified as a single pool, but that could be improved accounting for different dynamics of each type of SOM. We also need to take into account potential differences in the sensitivity of different functional groups to stressors, e.g. how water deficit or land use affects different trophic levels and functional groups. Moreover, the representation of different soil layers should be also further developed, particularly for the simulation of dryland soils, integrating the seasonality of soil fauna that migrates to deeper and wetter soil horizons during summer to avoid drought stress (Garcia-Pausas *et al*., 2004).

It is also clear that more empirical data on the soil system and the different integrated parts is needed to further parameterize and validate these new modelling efforts. Therefore, it is clear that the presented versions of the KEYLINK model in chapters 2 and 3 still need more development and more data to conduct full validations, but they are already functional and can be used, for example, to formulate hypothesis to be tested with new experiments, e.g. about soil structure and food web interactions, and their role controlling soil C dynamics (see **Figures 3** and **4** in chapter 2). In fact, a contribution of this new model is the identification of knowledge gaps that require new experiments with multidisciplinary research approaches to the whole ecosystem, integrating e.g. soil fauna, C cycle, hydrology and soil structure. Once those knowledge gaps are filled up, the representation of soil processes in ecosystem models could be improved.

The inclusion of simple parameterizations of vegetation or land use effects could greatly help the coupling of KEYLINK to other ecosystem models, which is also one of the main purposes of this modelling framework. Coupling KEYLINK to vegetation models should allow a better representation of the importance of the plant-soil interactions in the overall ecosystem functioning and ecosystems cycling of C and nutrients. This has been partially done in KEYLINK, by modelling the effect of vegetation on radiation interception and hence the role of photodegradation, as well as other plant-soil interactions as C inputs from vegetation which, however, remain represented in a too simple way, because all the vegetation complexity that controls those C inputs to the soil cannot be modeled in detail in a stand-alone soil model. The addition of other potentially important effects of vegetation on soil processes, as the impacts of vegetation cover on the microclimatic conditions on soil surface (e.g. soil temperature, dew incidence, etc) could improve our simulations of C cycle. In a future version, the model KEYLINK will be available also directly coupled to a vegetation model, the ANAFORE model (Deckmyn *et al*., 2008), as the first attempt to systemically coupled a belowground and an aboveground mechanistic model.

We did a further effort towards improving the poor representation in current state-of-the-art models of important mechanisms of SOM decomposition specific for drylands, such as photodegradation (King *et al*., 2012; Lee *et al*., 2012) and dew-induced biotic litter decomposition (Gliksman *et al*., 2017). The climate change scenarios simulated with the version of KEYLINK for drylands, showed in chapter 3, support the idea that under future conditions, with increasing temperatures and altered precipitation regimes, dryland mechanisms of litter decomposition will gain relevance as drivers of decomposition, and therefore, their inclusion into C cycle modelling is crucial for predictions of soil C sequestration and CO_2 emissions. Ecosystem structure and radiation interception will play a critical role in explaining complex spatial patterns in drivers of litter decomposition under drier and hotter conditions, e.g. when radiation is intercepted by vegetation, microclimatic conditions will favored dew-induced litter decomposition over photodegradation, while dew effect becomes considerably less than that of photodegradation when vegetation do not intercept radiation (**Figures 2** and **3** in chapter 3). Although there is still much work to do for including those dryland mechanisms in current climate change predictions at global scale, and for the

development of accurate representations of those mechanisms in models, the KEYLINK drylands model presented here constitutes a remarkable contribution to the field of C cycle modelling in drylands, integrating some dryland mechanisms with the previous discussed model concepts of physical protection of SOM, hydrology, soil food web and soil structure interactions.

Despite the clear relevance of dryland mechanisms on litter decomposition under drought conditions, more detailed research must be conducted in order to provide insights into photodegradation, dew-induced litter decomposition or photoinhibition, to facilitate model calibration and further inclusion into ecosystem models. Moreover, other dryland mechanisms should also be considered for inclusion in ecosystem scale models, as the abiotic degradation of litter induced by high temperatures (thermodegradation), which also requires more empirical data (Day *et al*., 2019). In future versions of KEYLINK, processes such litter thermodegradation could be added, as well as other non-rainfall water sources apart from dew, as fog or the direct water adsorption from the atmosphere by microbial decomposers (Wang *et al*., 2017).

Complementing, therefore, the reviewed knowledge (chapter 1) and the integrated model development (chapters 2 and 3) we further conducted experimental research to advance in the understanding of the main factors controlling litter decomposition in drylands. Using as a model litter from a tree species with broader distribution in the Mediterranean area, the holm oak (*Quercus ilex*), our experimental design has given us a new perspective on key processes associated with climate change with a potential influence on the carbon cycle in arid systems and very specifically on the decomposition of leaf litter. We here show how climate-driven variability in structural carbon (sC) and manganese (Mn) concentration of leaf litter was a major driver of variability of decomposition in the peninsular gradient of the study, comparable to the observed variance in the decomposition of holm oak litter incubated in a broad gradient of climate and forest structure (**Figure 10** in chapter 4). In particular, the structural C was the best predictor of litter decomposition rates, agreeing with the common hypothesis that litter recalcitrance is the main chemical factor shaping decomposition rates (Meentemeyer, 1978). Under the particular Mediterranean conditions of the Iberian Peninsula, in gradients of aridity and temperature, vegetation increases lignin concentration in leaves to protect them against desiccation and/or low temperatures. Independently from structural C, Mn content in holm oak litter, which is mainly a function of the pH of the system, played also a relevant role in litter decomposition, has it has been previously reported (Berg *et al*., 2007; Davey *et al*., 2007; Aponte *et al*., 2012; Keiluweit *et al*., 2015). Our findings showed that Mn controlled litter decomposition even in the short term of the process, during the first year, and despite the lack of significant variations in Mn content during that period. Therefore, at a regional scale, intraspecific changes in litter quality due to plant responses to their local environment should be considered to determine and predict variability in litter decomposition, especially in scenarios of climate and land use changes, where parallel changes in litter quality may affect decomposition process.

On the other hand, the observed absence of correlation between weather conditions and litter decomposition rates in the aridity gradient of the study (chapter 4) indicates some short of adaptation of decomposers communities to water limitations in this Mediterranean areas, which is something that has been observed in the past (Curiel Yuste *et al*. 2011; 2014). The potential role of climate seems to be strongly modulated by vegetation structure, as observed by the unexpected role of understory vegetation as the best predictor of regional variability in litter decomposition rates in the broad climatic gradient used in the study. We here hypothesized that in these semiarid environments, understory vegetation plays an important role in buffering the harsh environmental conditions imposed by the generally hot and dry conditions and the sparse overstory vegetation. This speculative explanation should be further studied in future experiments. Hence, at regional aridity gradient of the study, the role of climate on litter decomposition seems to be more related to indirect effects over leaf quality than to direct effects over decomposers.

These experimental results further emphasize, as discussed before, how models should integrate the effects of vegetation cover on soil environmental conditions. Moreover, the differentiation between tree canopy cover and understory cover effects on litter decomposition could be a valuable addition for soil C modelling, especially in arid systems where spatial complexity of vegetation distribution is very high. Such additions could be approached with a soil model as KEYLINK once it is coupled to a vegetation model, which will further entail the possibility of simulating dynamic feedbacks between soil and vegetation cover.

In conclusion, the modelling and experimental works developed in this thesis have highlighted the key roles of biotic and abiotic processes of litter and SOM decomposition in terrestrial ecosystems, showing the necessity and advantages of accounting for soil biodiversity and soil structure in a more integrative representation of the soil system into ecosystem models. These advances might improve the accuracy of the predictions of soil carbon cycle responses to global change.

GENERAL CONCLUSIONS

The main conclusions derived from this PhD thesis are listed below:

1. Recent advances in knowledge on soil complexity and the parts integrating it allow us to understand better the soil as a living system, in which its structure, hydrology and food webs interact between them regulating SOM stabilization.

2. Despite the growing evidence on the role played by those different parts of the ecosystem on C and water cycles in soils, existing models tend to represent only a lower fraction of soil complexity, neglecting the relevance of the interaction among its different parts. Hence, it is necessary to develop new more integrative ecosystem models that represent the complexity of that system.

3. Soil physical structure is key to understand C cycle in soils. Particularly, soil particle aggregation and the subsequent porosity determines organic matter accessibility to its consumers and also trophic interactions, and the physical and physico-chemical protection of organic matter might be even more relevant than its chemical composition to determine its decomposition rates.

4. The inclusion of hydrology is a relevant add-on to soil C cycle models, together with soil structure, because soil structure determines water flow through the soil, affecting organic matter accessibility. This add-on simulating soil hydrology facilitates the coupling of models of different ecosystem parts, giving feedback from simulation of soil water flow to vegetation models and vice versa.

5. The new mechanistic soil model, KEYLINK, is already an available tool for the integrated simulation of all those parts of the soil of terrestrial ecosystems, which will continue to be developed and improved, in order to advance in our ability to predict soil C cycle responses to disturbances as global change. We hope this becomes a useful resource for the research on the complex functioning of the terrestrial ecosystems.

6. KEYLINK evaluation shows how food web, soil structure and hydrology interact, affecting organic matter decomposition. Particularly, population growth parameters of soil organisms and flow of C through trophic cascades, further regulated by soil structure effects on substrate or prey accessibility for each functional group, are key regulating SOM stabilization.

7. Engineer species play a key role, even simulated at low densities, they have crucial impacts on soil structure and the related processes. Changes in pH or in predators' demography have remarkable effects on engineer species, leading to changes in soil structure, water availability and the physical protection of organic matter.

8. Predators are an essential functional group for demographic control of the food web; the conducted simulations show that the decrease or absence of predators, e.g. by local functional extinction, can lead to reductions in C sequestration capacity in soils.

9. Under simulated climate change scenarios, both increase in temperatures and the alteration in precipitation regimes lead to increasing aridity, decreasing biotic litter decomposition due to the lower soil water availability. In the top litter layer, this leads to an increase in the contribution of degradation mechanisms as photodegradation and the biotic decomposition using dew as water source.

10. Vegetation structure, particularly tree canopy, has a remarkable effect on top litter layer decomposition rates, by blocking solar radiation and, therefore, reducing photodegradation. This indicates the relevance of forest management, particularly in drylands, where photodegradation has a remarkable contribution to total litter decomposition.

11. The observed relevance of simulated microbial litter decomposition using dew, which allowed microbial communities to partially avoid drought stress, can be a population filter causing potential imbalances of the trophic web in the face of increases in aridity, if fauna is harmed more severely by droughts than microorganisms. Consequently, under scenarios of increasing soil aridity, a threshold could be reached, causing an increase in biotic litter decomposition, contrary to what would be expected. This could also explain partially why observed litter decomposition in drylands is higher than what is predicted by models.

12. Multidisciplinary experiments should be designed to obtain a more complete and integrative picture of the different parts and processes of the soil system, allowing to improve and validate such integrative models as KEYLINK, which are necessary to improve the accuracy of our predictions of ecosystem responses to environmental disturbances.

13. Holm oak litter shows a remarkable intraspecific variability at the regional scale of the Iberian Peninsula. Effects on litter decomposition rates of this intraspecific variability were comparable in magnitude to the effects associated to the large regional variability in environments throughout the peninsula. Litter concentrations of recalcitrant compounds (i.e. lignin, cellulose and hemicellulose) and of Mn were the best explanatory variables for observed litter decomposition rates, being those rates positive and negatively related to Mn and litter recalcitrance, respectively.

14. Although no direct effect of climate on holm oak litter decomposition was found at regional scale, we found that climate is a crucial factor shaping holm oak litter recalcitrance and chemical composition: 1) litter recalcitrance was higher in colder sites with lower precipitations, because lignocellulosic tissues are associated to protection against extreme climatic conditions, and 2) Mn content was higher in litter from forests with more acidic and dry soils where phosphorus (P) is limiting, and the leaching of its mobile form is lower.

15. Vegetation structure has a considerable effect on holm oak litter decomposition, which was higher in forests with higher understory (i.e. shrubs and grass) cover. On the other hand, weather conditions (temperatures and precipitations) during the experiment throughout the Iberian Peninsula did not explain the observed decomposition rates. These two results together suggest that vegetation modulates microclimatic conditions on the litter layer, mitigating the direct effect of regional climate.

16. The observed effects of vegetation cover on litter decomposition rates should be integrated into soil models, particularly for coupling soil and vegetation models, as it will happen in the next versions of the KEYLINK model. The integration of those processes, together with the developed modelling representing dryland mechanisms of litter decomposition, may offer an important improvement in our capacity to predict future changes in C emissions from terrestrial ecosystems in response to global change.

CONCLUSIONES GENERALES

Se enumeran a continuación las principales conclusiones que se derivan de esta tesis:

1. Recientes avances en el conocimiento de la complejidad del suelo y de las partes que lo integran nos permiten comprender mejor el suelo como un sistema vivo, en el que su estructura, la hidrología y las redes tróficas interaccionan entre sí para regular la estabilización de la materia orgánica en el suelo.

2. A pesar de la creciente evidencia del papel que tienen esas diferentes partes del ecosistema para los ciclos del C y del agua en los suelos, los modelos existentes suelen representar solo una mínima parte de la complejidad del suelo, obviando la relevancia que tiene la interacción entre sus diferentes partes. Por tanto, es necesario desarrollar nuevos modelos ecosistémicos más integradores que representen la complejidad del sistema.

3. La estructura física del suelo es clave para entender el ciclo del C en suelos. Concretamente, la agregación de las partículas del suelo y la consiguiente porosidad entre ellas determina la accesibilidad de la materia orgánica para sus consumidores y también las interacciones tróficas, a tal punto que la protección física y físico-química de la materia orgánica puede ser aún más relevante que su composición química para determinar sus tasas de descomposición.

4. La inclusión de la hidrología es un importante añadido a los modelos de ciclo de C en suelos, junto con la estructura del suelo, puesto que dicha estructura determina los flujos de agua por el sistema, que a su vez afectan a la accesibilidad de la materia orgánica. Esta adición simulando la hidrología del suelo también facilita el acoplamiento de modelos de diferentes partes del ecosistema, aportando retroalimentación de la simulación del flujo de agua en el suelo a los modelos de vegetación y viceversa.

5. El nuevo modelo mecanicista de suelo, KEYLINK, es ya una herramienta disponible para la simulación integrada de todas esas partes del suelo de los ecosistemas terrestres, que se seguirá desarrollando y mejorando, para avanzar en nuestra capacidad de predecir las respuestas del ciclo de carbono en los suelos ante perturbaciones como el cambio global. Esperamos que se convierta en un recurso útil para la investigación del complejo funcionamiento de los ecosistemas terrestres.

6. La evaluación de KEYLINK muestra cómo interaccionan la red trófica, la estructura del suelo y la hidrología, afectando a la descomposición de la materia orgánica. Concretamente, los parámetros de crecimiento poblacional de los organismos del suelo y el flujo de C a través de cascadas tróficas, modulados por los efectos de la estructura del suelo sobre la accesibilidad de alimento para cada grupo funcional, son clave para regular la estabilización de la materia orgánica en el suelo.

7. Las especies ingenieras juegan un papel fundamental, incluso simuladas a bajas densidades tienen impactos cruciales sobre la estructura del suelo y los procesos que dependen de ella. Alteraciones como la variación del pH o de la demografía de depredadores afectan notablemente a las especies ingenieras del sistema, provocando alteraciones en la estructura del suelo, la disponibilidad de agua y la protección física de la materia orgánica.

8. Los depredadores son un grupo funcional imprescindible para el control demográfico en la red trófica; las simulaciones llevadas a cabo indican que su disminución o ausencia, por ejemplo por extinción funcional local de especies depredadoras, puede conllevar a pérdidas en la capacidad de los suelos de secuestrar carbono.

9. Bajo escenarios simulados de cambio climático, tanto el aumento de temperaturas como la alteración de los regímenes de precipitaciones en ecosistemas áridos conducen a un aumento de la aridez, reduciendo la descomposición biótica de la hojarasca por la reducción en el agua disponible en el suelo. Esto conlleva a que, en la capa superficial de la hojarasca, aumente la contribución de mecanismos de descomposición como la fotodegradación y la descomposición biótica usando agua del rocío.

10. La estructura de la vegetación, particularmente del dosel arbóreo, tiene un notable efecto sobre las tasas de descomposición de la hojarasca superficial, al bloquear parte de la radiación solar reduciendo así la fotodegradación. Esto indica la relevancia que tiene el manejo forestal particularmente en los ecosistemas áridos, donde la fotodegradación contribuye notablemente a la descomposición total de la hojarasca.

11. La importancia observada de la descomposición microbiana de la hojarasca usando agua de rocío, que en las simulaciones permitió a las comunidades microbianas evitar parcialmente el estrés por sequía, puede suponer un filtro poblacional que provoque potenciales desajustes de la red trófica ante incrementos en la aridez, si la fauna se ve perjudicada más severamente por las sequías que los microorganismos. Por consiguiente, en escenarios de incremento en la aridez del suelo, se podría alcanzar un punto de inflexión que genere un aumento de la descomposición biótica de la hojarasca, contrario a lo que cabría esperar. Esto también podría explicar en parte por qué la descomposición observada de la hojarasca en ecosistemas áridos es superior a las tasas predichas por los modelos.

12. Hace falta diseñar experimentos multidisciplinares que ofrezcan una imagen más completa e integradora de las diferentes partes y procesos que conforman el sistema del suelo, lo que permitirá seguir mejorando y validar modelos tan integradores como KEYLINK, que son necesarios para mejorar la precisión de nuestras predicciones de respuestas ecosistémicas ante perturbaciones.

13. La hojarasca de encina muestra una notable variabilidad intraespecífica a escala regional en la península ibérica. Los efectos de esa variabilidad intraespecífica sobre las tasas de descomposición fueron comparables en magnitud a los efectos asociados a la gran variabilidad regional de ambientes a lo largo de la península. Las concentraciones de compuestos recalcitrantes (lignina, celulosa y hemicelulosa) y de Mn en la hojarasca fueron las variables que mejor explicaron las tasas de descomposición observadas, estando estas positiva y negativamente relacionadas con el Mn y la recalcitrancia de las hojas, respectivamente.

14. Si bien no se encontró ningún efecto directo del clima sobre la descomposición de la hojarasca de encina a escala regional, comprobamos que el clima es un factor determinante para explicar la recalcitrancia y la composición elemental de la hojarasca de encina: 1) la recalcitrancia de la hojarasca fue más alta en sitios con menores temperaturas y precipitaciones, ya que los tejidos lignocelulósicos están asociados a protección contra condiciones climáticas extremas, y 2) el contenido en Mn fue mayor en la hojarasca proveniente de bosques con suelos más ácidos y secos donde el fósforo (P) es limitante, y la lixiviación de su forma móvil es menor.

15. La estructura de la vegetación tiene un considerable efecto sobre la descomposición de la hojarasca de encina, que fue mayor en bosques con mayor cobertura de vegetación del sotobosque (arbustos y herbáceas). Por otro lado, las condiciones meteorológicas (temperaturas y precipitaciones), durante el experimento a lo largo de la península ibérica, no explicaron las tasas de descomposición observadas. Estos dos resultados en conjunto parecen indicar que la vegetación modula las condiciones microclimáticas a las que se ve expuesta la hojarasca, atenuando el efecto directo de la climatología regional.

16. Los efectos observados de la cobertura vegetal sobre las tasas de descomposición de la hojarasca deben ser integrados en los modelos de suelo, especialmente de cara al acoplamiento entre modelos de suelo y de vegetación, como sucederá en las próximas versiones del modelo KEYLINK. La integración de estos procesos, junto con la modelización que se ha desarrollado para representar mecanismos de descomposición de hojarasca en ecosistemas áridos, pueden ofrecer una importante mejora en nuestra capacidad de predecir futuros cambios en las emisiones de carbono por parte de los ecosistemas terrestres en respuesta al cambio global.

Appendix 1 – Additional information

Funding

This thesis was funded by FPU PhD grant program of the Spanish Ministry of Education, and the field work was funded by the R&D project VEroNICA (Vulnerability of Mediterranean Holm-Oak forests to Climate Change: Mechanisms and impact of historical management on ecosystem services; CGL2013-42271-P) and the R&D project IBERYCA (The role of plant-microBiota Interactions in the Resilience and Collapse of Mediterranean holm oAks; CGL2017-84723-P), both granted by the Spanish program for the promotion of scientific and technical research of excellence, of the Spanish Ministry of Economy, Industry and Competitiveness. The modelling work was funded by the COST Actions FP1305 (BioLink) and ES1406 (KEYSOM), supported by COST (European Cooperation in Science and Technology, www.cost.eu), and their Short Term Scientific Mission (STSM) programs. This research was also supported by the Basque Government through the BERC 2018-2021 program, and by the Spanish Ministry of Science, Innovation and Universities through the BC3 María de Maeztu excellence accreditation (MDM-2017-0714).

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Pictures

Cover page

Picture taken by Omar Flores in the open woodland (dehesa) of Cabañeros National Park (Ciudad Real, Spain), on autumn 2016, showing a male deer behind an holm oak tree.

General methodology

Figure 5: picture of litterbags in one of the experimental plots in the Spanish province of Cáceres, at the beginning of the gradient litterbag experiment; taken by Omar Flores on autumn 2016.

Chapter 1

Front page: holm oak seedling growing in the soil of the Natural Park "Hoces del río Riaza", in Segovia (Spain); taken by Omar Flores on autumn 2016.

Figure 1: picture of casts over the soil in a Spanish holm oak forest, near Arascues (province of Huesca); taken by Omar Flores on autumn 2015.

Chapter 2

Front page: landscape of the Natural Park "Hoces del río Riaza", in Segovia (Spain); taken by Omar Flores on autumn 2016.

Chapter 3

Front page: twilight over the open woodland (dehesa) in Cabañeros National Park (province of Ciudad Real, Spain); taken by Antonio Mas and Omar Flores on summer 2019.

Chapter 4

Front page: open woodland (dehesa) in Cabañeros National Park (Ciudad Real, Spain); taken by Omar Flores on autumn 2017. In the distant horizon it is seen the hills where is located the forest included as an experimental site. The picture also shows two female deer with a cub under the shadow of a holm oak tree.

Figure 1: picture of one of the experimental plots in the holm oak forest of Cabañeros National Park (Ciudad Real, Spain); taken by Omar Flores on autumn 2016.

Figure 2: picture of litterbags at the beginning of the experiment in Cabañeros National Park (Ciudad Real, Spain); taken by Omar Flores on autumn 2016.

Back cover page

Pictures of holm oak forests at sundown, taken by Omar Flores. First picture was taken at the Cabañeros National Park (Ciudad Real, Spain) on autumn 2016. Second picture was taken in Toledo (Spain), on autumn 2015.

Appendix 2 – KEYLINK model

Review of input parameters and carbon pools

Respiration

Due to the lack of the experimental data, it is mostly not possible to distinguish between (1) the standard metabolism and metabolism in the active state; (2) the ecological groups within the taxa.

To convert O_2 consumed into carbon respiration losses, for all the animal groups it is assumed that:

(1) Respiratory quotient RQ (volumetric ratio V_{CO2}/V_{O2}) is 1.0, where V_{O2} – volume of oxygen consumed, V_{CO2} – volume of carbon dioxide produced; thus 1 mm^3 O_2 corresponds to 1 mm^3 CO_2. This is a simplification, in fact RQ values can be lower (sometimes much lower); however, few realistic estimates are available.

(2) $C_R = 12V_{CO2}/22.4$, where C_R – carbon respired (g); V_{CO2} – volume of CO_2 respired (l).

Group	T °C	Respiration rates, mm^3 O_2 g^{-1} live weight h^{-1}	Arbitrary mean, mm^3 O_2 $g^{-1}h^{-1}$	Q_{10}
Nematoda	20	450 – 4600	2000	~ 3-4
Enchytraeidae	20	100 – 1500	500	~ 2-3
Lumbricidae	20	40 – 240	100	~ 2
Isopoda (Oniscoidea)	20	90 – 1600	300	~ 2.5
Oribatei	10	40 – 480	150	~ 3.5
Oribatei	15	70 – 700	250	~ 3
Mesostigmata (Gamasina only)	10	180 – 1600	500	~ 3-4
Mesostigmata (Gamasina, Uropodina, Trachytina)	10	100 – 1600	400	~ 3
Araneida	20	20 – 1600	250	~ 2-3
Diplopoda	20	20 – 900	150	~ 2
Chilopoda	20	100 – 800	250	~ 3
Collembola	10	50 – 1300	400	~ 3
Collembola	15	50 – 2700	600	~ 3
Carabidae, im.	15	80 – 1300	350	~ 3
Staphylinidae, im.	15	150 – 850	400	~ 3-4
Coleoptera, larvae	15	70 –2500	550	~ 3
Coleoptera, larvae	20	80 –2600	750	~ 3
Diptera larv.	20	200 – 2200	800	~ 2-3

Table 1. Respiration rates of soil invertebrates. Rough estimates (an adaptation of available data from 105 literature sources and own measurements by A.V. Uvarov).

CN ratios

CN ratios are an important input for the model. Data can be readily found for many soil animal species. The CN ratio of root herbivores has been reported to be lower than their food sources. The average C to N ratio of microfauna is about 10 (range between 7.5-12, Anderson *et al*. 1981; Hunt *et al*. 1987). Soil arthropods typically have a C content of about 50% and a N content around 10%, leading to a CN ratio of about 5. According to Hunt *et al*. (1987), Prostigmata have a CN = 8. Based on information provided in Pokarzhevskii *et al*. (2003), the CN ratio of adult Scarabaeid beetles is 5.43 and of Diptera larvae CN = 4.46. No information is given for the Symphyla, but their relatives, Chilopoda, have a CN = 4.89. For fungi and bacteria a wide range of values have been found but in general bacteria have a lower CN ratio. Chertov *et al*. (2017a) use an empirical model to calculate local CN ratio based on the SOM CN. Ferris *et al*. (1997) provide CN values for bacterial feeding nematodes, i.e. 5.9, and for the populations of *Escherichia coli* they grew on, i.e. 4.1.

Input parameters for Brasschaat forest (Belgium) run

Each table represents an input file for the simulations (specific names of each text file are given between brackets). This set of parameters was used to simulate the basal scenario.

Pool	Initial biomass (g C m^{-3})
Bacteria	15.1
Fungi	15.1
Mycorrhiza	160
Bacterivores	0.1
Fungivores	0.8
Detritivores	0.6
Engineers	0.2
Herbivores	0.2
Predators	0.4
Litter	2680
SOM	11470
Roots	320

Table 2. Initial C in each pool ("KL_initC_pools"). For the scenario excluding predators ("B_{pred} 0"), the initial biomass of predators was set to 0.

Month	Average temperature (ºC)	Monthly total sunlight hours
Ja	3.3	**59**
Feb	3.7	77
Mar	6.8	114
Ap	9.8	159
May	13.6	191
Jun	16.2	188
July	18.4	201
Aug	18.0	190
Sept	14.9	143
Oct	11.1	113
Nov	6.8	66
Dec	3.9	45

Table 3. Monthly data on temperature and sunlight ("KL_climateParams"). Monthly average temperatures and total sunlight hours in the simulated site.

	Units	Bact	Fung	Myc	Bvores	Fvores	Detrvor	Eng	Herbv	Pred
g_{max}	gC gC^{-1} day^{-1}	1.24	0.6	0.44	1.4	0.8	0.178	0.109	0.135	0.096
Ks	g m^{-3}	5500	5500	5500	7.5	7.5	5500	5500	160	2
death	gC gC^{-1} day^{-1}	0.05	0.01	0.04	0.02	0.02	0.0013	0.0065	0.005	0.005
resp	gC gC^{-1} day^{-1}	0.03	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0.01
faeces		0	0	0	0	0	0.3	0.3	0.3	0.3
CN		4	8	9	6	9	5	5	8	8
recalc		0.2	0.4	0.5	0.6	0.8	0.9	0.9	0.1	0.1
pmCN		0.8	0.3	0.3	0	0	0	0	0	0
pmRec		0.9	0.75	0.8	0.8	0.8	0.5	0.5	0.8	0.8
T min	ºC	0	0	0	0	0	0	0	0	0
T opt	ºC	25	25	25	25	25	15	15	15	15
T max	ºC	40	40	40	40	40	40	40	40	40
Q10		2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5

Table 4. Faunal parameter values used for the Brasschaat run ("KL_FaunalParams"). Each column is a food web pool: bacteria (bact), fungi (fung), mycorrhiza (myc), bacterivores (Bvores), fungivores (Fvores), detritivores (detrVor), engineers (eng), herbivores (herbv) and predators (pred). Each row is a parameter vector: g_{max} and Ks used for the showed simulations, death and resp are the rates of death and respiration, feces is the equivalent fraction of growth that is transformed to feces, CN (ratio) and recalcitrance (recalc) of each pool, pmCN and pmRec are the sensibility parameters to CN and recalcitrance (for equations 23-26 in the paper), the minimum (min), optimum (opt) and maximum (max) temperatures (T) for the growth of each population, and the Q10.

Variable	Units	Value
Depth of soil layer	m	1
Bulk density	kg m^{-3}	1463
alpha (van Genuchten)	kPa^{-1}	1.2
n (van Genuchten)		1.7
m (van Genuchten)		0.3
Ksat (van Genuchten)		10
pH		3.9
Initial litter CN ratio		38.6
Initial SOM CN ratio		18
Drainmax	mm day^{-1}	7
Volume of inaccessible pores	l m^{-3}	45
Volume of bacterial pores	l m^{-3}	37
Volume of micropores	l m^{-3}	37
Volume of mesopores	l m^{-3}	200
Volume of macropores	l m^{-3}	6

Table 5. Parameters of soil characteristics ("KL_initSoil"). Litter CN ratio here refers to initial litter quality in the litter pool. pH was set to 5.9 for the alternative scenario “pH 5.9”. And for the alternative scenario “clay 15%”, the volumes of the five pore classes were the following (respectively): 142, 80, 80, 200, 6.

Variable	Units	Value
VE_{ratio}	l g^{-1}	1
f_{PV}	0.5	0.5
Turnover of burrows	day^{-1}	0.01
PV_{Bmax}	l m^{-3}	25
Litter fragmentation	day^{-1}	0.05
m_{faec} for engineers		0.2
m_{faec} for detritivores		0.3
Bioturbation	% SOM g C_{Eng}^{-1} day^{-1}	0.05
Litter moved by engineers	% litter g C_{Eng}^{-1} day^{-1}	0.01

Table 6. Parameters for engineers and detritivores activity ("KL_engineerParams"). Rows show ratio of pore volume to engineer biomass (VE_{ratio}), fraction of volume that is made by extra porosity (f_{PV}), the daily turnover of burrows, maximum burrow volume (PV_{Bmax}), fraction of litter fragmentation, sensitivity of % faeces to CN ratio (m_{faec}) for engineers and detritivores, bioturbation and litter moved as the daily amount of SOM and litter (respectively) that engineers bring to deeper layers.

Variable	Units	Value
Simulation time	days	3653
Initial soil water	%	100
Initial mineral N	g N m^{-3}	5
Root growth	g C m^{-3} day^{-1}	0.575
Root turnover	g C m^{-3} day^{-1}	0.003
Litter input	g C m^{-3} day^{-1}	1.32
Litter CN ratio		60.3
Recalcitrance of litter	%	40
C input to mycorrhiza	g C m^{-3} day^{-1}	0.54
Fraction N from myc to plants		0.9
Fraction effective evapotranspiration		0.7

Table 7. Model run options ("KL_runparams"). The C fraction of N from mycorrhiza ("myc") to plants is the fraction (0-1) of the N input to mycorrhiza that they receive from plants (and the rest comes from the soil). Litter CN ratio here refers to the litter quality of input litter added daily to the litter pool, which was set to 40 for the alternative scenario "CN_{lit} 40". And the recalcitrance of litter was set to 20 for the alternative scenario "rec 20%".

Model outputs

After each simulation, together with graphs automatically created by the model showing daily variations in all C pools, soil water content and soil porosity, KEYLINK creates a new text file named "keylinkoutput" in the same folder, and when it already exists, a new simulation overwrites that file, so we recommend to copy it in other folder or to change its name before every new simulation in order to keep all results. This text file has a row for each simulated day, and C pools biomass and some C fluxes (g C m^{-3}) in 21 columns, in the following order: (1) bacteria, (2) fungi, (3) mycorrhiza, (4) bacterivores, (5) fungivores, (6) detritivores, (7) engineers, (8) herbivores, (9) predators, (10) litter, (11) SOM, (12) roots, (13) cumulative CO_2 emissions, (14) daily respiration from bacteria, (15) from fungi and (16) from mycorrhiza, (17) C flux from SOM to bacteria, (18) C flux from litter to bacteria, (19) total SOM eaten, (20) total litter eaten, and (21) litter eaten by engineers.

Results from the calibration for the Brasschaat forest (Belgium)

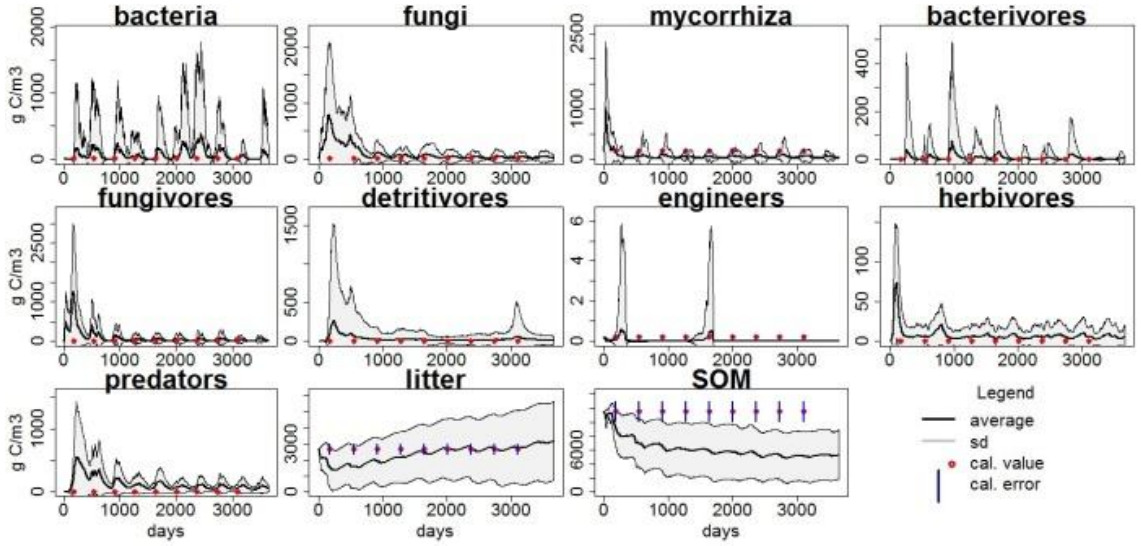

Figure 1. Fit of the simulated pools to the calibration data. Each graph shows the daily variation (through ten years of simulation) in each C-pool (g C m^{-3}) with averages (in black) and standard deviation (sd, in grey) using the 100 simulations with the parameter sets of maximal growth rates (g_{max}) from the Latin Hypercube Sample. Reference data for calibration (see **Table 3** in the general methodology) are shown for each pool as calibration values (cal. value, red dots) and their respective errors (cal. error, blue lines).

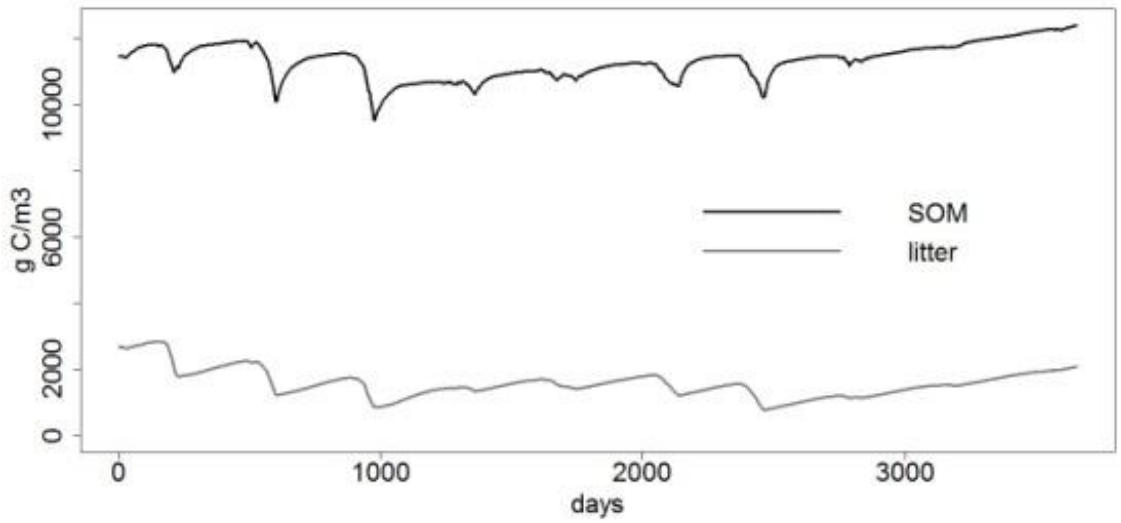

Figure 2. SOM (black) and litter (grey) along ten years of simulation with KEYLINK. Both C pools are shown in g C per soil cubic meter, along ten years on a daily temporal step of simulation. This simulation was done using the following set of g_{max} (maximal growth rate) values for each population: bacteria (0.895), fungi (0.85), mycorrhiza (0.575), bacterivores (0.95), fungivores (0.8969), detritivores (0.58747), engineers (0.37656), herbivores (0.45418), predators (0.258569). This parameter set was chosen, from the posterior distribution of the Bayesian calibration, as one of the best simulations using as criterion only the SOM stability.

Appendix 3 – KEYLINK drylands

Input parameters

Table 1 shows the new input parameters added in the second version of the KEYLINK model (chapter 2), in order to simulate soil processes that are characteristic from drylands. Other input files are shown below. C pool biomasses were estimated based on dryland literature for earthworms (Cortez, 1998; Vijver, 2005), microorganisms (Kushwaha *et al*., 2000) and SOM (Sainju *et al*., 2006). Root biomass was estimated for the same plant species of the reference litter experiment in Israel, but from available data on oat (*Avena*) roots on a Nordic agroecosystem (Pietola and Alakukku, 2005). Other parameters (e.g. pH, soil N, bulk density, litter quality) were estimated from other studies conducted in Ramat Hanadiv Park and other drylands in Israel (Dirks *et al*., 2010; Gabay *et al*., 2011; Angel *et al*., 2013; Dovrat *et al*., 2014; Stavi and Argaman, 2016; Bar, 2017; Gliksman *et al*., 2017; Dovrat and Sheffer, 2019). The input files not shown here had the same values used for the first version of KEYLINK, except Q10, which was set in 2 for all functional groups.

Variable	Symbol	Units	Value
Recalcitrance of SOM	rec_{SOM}	%	2.22
Increase in litter recalcitrance from exposed to unexposed litter layers	in_{rec}	%	3.8
Minimum litter biomass to fully cover soil surface	B_{full}	g C / m^2	83.4
Canopy cover fraction	cc		0
UV fraction in solar radiation	f_{UV}		0.06
Fraction of photodegraded litter emitted as CO_2	F_{litCO2}		0.48
Minimum radiation to reach maximum effects of radiation	max_{rad}	MJ/m^2	30
Equation 3 intercept	p_0	µg C / kJ_{UV}	97.36
Equation 3 slope	p_1	µg C / kJ_{UV} % rec_{lit}	16.52
Equation 10 intercept	d_0	% (RH)	68.8
Equation 10 slope	d_1	% (RH) / ºC	0.18
Switch parameter to activate (1) or deactivate (0) photoinhibition	ap		1
Minimum biomass in each pool	min_B	g C / m^3	1
Drought sensitivity	ds	%	32

Table 1. New input parameters for KEYLINK drylands version. The canopy cover (cc) was changed to 0.25, 0.5 and 0.75 for the different scenarios of vegetation structure.

The climate change scenarios simulated were generated from the weather data downloaded from the meteorological station on Ramat Hanadiv (see general methodology), adding 2, 4, 6 or 8 ºC to daily temperatures, and multiplying daily rainfall inputs by 0.8, 0.6 and 0.4, in the core of the model.

Pool	Initial biomass (g C m^{-3})
Bacteria	219.1
Fungi	219.1
Mycorrhiza	53.8
Bacterivores	21.9
Fungivores	27.3
Detritivores	13.7
Engineers	4.6
Herbivores	6.8
Predators	7.4
Litter	77
SOM	5500
Roots	107.5

Table 2. Initial C in each pool ("KL_initC_pools").

Month	Average temperature (°C)	Monthly total sunlight hours
Ja	13.5	192.2
Feb	13.8	205.9
Mar	15.9	235.6
Ap	18.6	270
May	21.1	328.6
Jun	23.4	357
July	26.2	368.9
Aug	27	356.5
Sept	25.5	300
Oct	22.9	279
Nov	19	234
Dec	14.8	189.1

Table 3. Monthly data on temperature and sunlight ("KL_climateParams"). Monthly average temperatures and total sunlight hours in the simulated site.

Variable	Units	Value
Depth of soil layer	m	0.5
Bulk density	kg m^{-3}	850
alpha (van Genuchten)	kPa^{-1}	1.2
n (van Genuchten)		1.7
m (van Genuchten)		0.3
Ksat (van Genuchten)		10
pH		7
Initial litter CN ratio		54.1
Initial SOM CN ratio		8
Drainmax	mm day^{-1}	0.01
Volume of inaccessible pores	l m^{-3}	27.5
Volume of bacterial pores	l m^{-3}	48.5
Volume of micropores	l m^{-3}	48.5
Volume of mesopores	l m^{-3}	40
Volume of macropores	l m^{-3}	3

Table 4. Parameters of soil characteristics ("KL_initSoil"). Litter CN ratio here refers to initial litter quality in the litter pool.

Variable	Units	Value
Simulation time	days	3652
Initial soil water	%	100
Initial mineral N	g N m^{-3}	0.474
Root growth	g C m^{-3} day^{-1}	0.294
Root turnover	g C m^{-3} day^{-1}	0.0015
Litter input	g C m^{-3} day^{-1}	0.3
Litter CN ratio		54.1
Recalcitrance of litter	%	9.37
C input to mycorrhiza	g C m^{-3} day^{-1}	0.54
Fraction N from myc to plants		0.9
Fraction effective evapotranspiration		0.9

Table 5. Model run options ("KL_runparams"). The C fraction of N from mycorrhiza ("myc") to plants is the fraction (0-1) of the N input to mycorrhiza that they receive from plants (and the rest comes from the soil). Litter CN ratio here refers to the litter quality of input litter added daily to the litter pool.

Model outputs

Together with the output text file "keylinkoutput" generated in the first version, this new version creates another three output text files, with values of variables in a row for each simulated day:

I. "keylink_soil": in the columns it includes the pore volumes of all pore size classes in the soil, from the smaller to the larger, and the sixth column shows the soil water content.

II. "keylink_dryland_variables": the first three columns show respectively (1) the drought modifier (dm), (2) the incidence of dew (i_{dew}) and (3) the moisture effect on decomposition (med); next columns show (4) the litter mass in exposed (top) and (5) unexposed (buried) layers; the following columns show (6) the fraction of photoinhibition (p_{inh}), (7) the litter mass photodegraded to CO_2, (8) the litter mass of recalcitrant compounds that become labile by photodegradation, (9) the input litter from plants (including leaves and roots), (10) the bioturbation of litter by engineers, (11) the litter fragmentation, (12) the bioturbation of SOM by engineers, and finally, the last 5 columns (13-17) show the water content in each pore size class from the smaller to the larger.

III. "keylink_stock_fluxes": this file shows litter and SOM inputs and outputs from the food web, in the following order: (1) litter outputs by biotic decomposition; (2) litter inputs (from faunal death mass); (3) SOM outputs by biotic decomposition; (4) SOM inputs from faunal faeces and death mass from microorganisms and microbivores; and the last two columns are two complementary parts of the first with litter outputs: (5) biotic decomposition from the top litter layer, and (6) biotic decomposition from the buried (unexposed) litter layer.

Alternative results without photoinhibition

The same 80 global change scenarios presented in chapter 3 were simulated deactivating photoinhibition processes. Results are shown below.

		ld_{pool}					ld_{top}				
cc	**Precip**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**
0%	**100%**	49.35	44.48	35.57	28.87	27	27.81	26.66	25.87	25.54	25.6
	80%	47.05	39.96	31.85	27.9	26.72	26.98	26.1	25.53	25.48	25.59
	60%	41.35	35.57	29.04	26.84	26.21	25.88	25.48	25.34	25.42	25.59
	40%	33.17	28.82	26.68	26.07	25.79	24.91	25.04	25.21	25.45	25.64
25%	**100%**	45.44	40.51	31.43	24.62	22.72	23.52	22.36	21.58	21.24	21.3
	80%	43.11	35.85	27.65	23.64	22.43	22.69	21.8	21.23	21.18	21.29
	60%	37.29	31.43	24.8	22.56	21.93	21.58	21.18	21.04	21.12	21.29
	40%	29	24.58	22.41	21.78	21.49	20.61	20.74	20.91	21.15	21.34
50%	**100%**	41.53	36.52	27.28	20.38	18.45	19.22	18.07	17.28	16.94	17
	80%	39.17	31.78	23.45	19.38	18.15	18.4	17.5	16.94	16.88	16.99
	60%	33.17	27.29	20.56	18.29	17.64	17.28	16.88	16.74	16.82	16.99
	40%	24.83	20.34	18.13	17.49	17.2	16.31	16.44	16.61	16.85	17.04
75%	**100%**	37.62	32.54	23.14	16.13	14.17	14.93	13.78	12.99	12.64	12.71
	80%	35.23	27.71	19.25	15.12	13.87	14.11	13.21	12.64	12.58	12.69
	60%	29.12	23.13	16.32	14.01	13.35	12.99	12.58	12.44	12.52	12.69
	40%	20.65	16.1	13.85	13.2	12.9	12.02	12.15	12.32	12.55	12.75

Table 6. Annual litter decomposition (g C m^{-2} $year^{-1}$) (without photoinhibition) in the total litter pool (ld_{pool}) and in the top litter layer (ld_{top}) under different global change scenarios of increasing temperatures and decreasing precipitations (Precip), for four canopy coverages (cc).

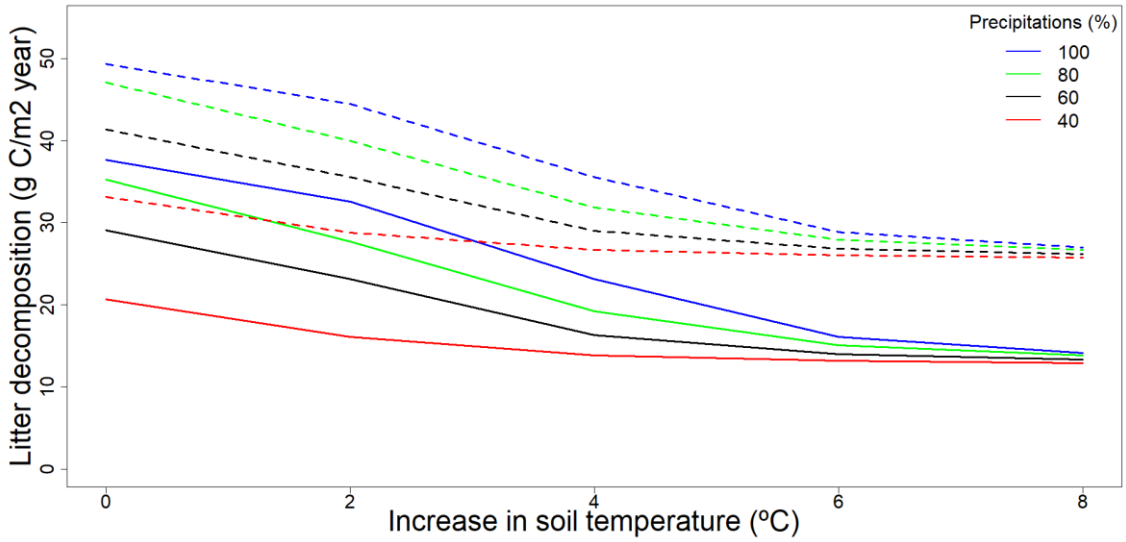

Figure 1. Annual litter decomposition in total litter pool under different global change scenarios (without photoinhibition). All simulated scenarios for precipitations and soil temperatures are represented, for the two most contrasted canopy cover scenarios: 75% (full lines) and 0% (dashed lines).

		ld_{pool}					ld_{top}				
cc	**Precip**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**
0%	**100%**	16.52	17.73	21.77	27.14	29.99	29.32	29.59	29.93	30.68	31.62
	80%	16.59	19.07	23.83	28.14	30.39	28.93	29.2	29.73	30.82	31.73
	60%	17.57	20.59	26.17	29.43	31.19	28.07	28.75	30	31.08	31.96
	40%	20.59	25.3	28.84	30.85	32.23	27.42	29.12	30.53	31.61	32.41
25%	**100%**	17.96	19.49	24.65	31.83	35.63	34.71	35.29	35.9	36.89	38.01
	80%	18.13	21.26	27.46	33.22	36.19	34.43	34.96	35.75	37.08	38.14
	60%	19.49	23.31	30.65	35.01	37.3	33.68	34.6	36.14	37.41	38.41
	40%	23.56	29.67	34.35	36.93	38.67	33.15	35.16	36.8	38.04	38.94
50%	**100%**	19.67	21.63	28.4	38.47	43.89	42.49	43.71	44.84	46.26	47.62
	80%	19.97	23.99	32.38	40.53	44.73	42.5	43.56	44.83	46.53	47.79
	60%	21.91	26.86	36.98	43.2	46.37	42.05	43.42	45.43	46.97	48.14
	40%	27.53	35.86	42.45	45.99	48.33	41.89	44.36	46.33	47.74	48.76
75%	**100%**	21.73	24.3	33.5	48.6	57.14	54.74	57.37	59.7	62	63.74
	80%	22.22	27.53	39.46	51.96	58.54	55.47	57.75	60.09	62.43	63.99
	60%	24.97	31.7	46.61	56.4	61.27	55.99	58.26	61.13	63.1	64.44
	40%	33.11	45.32	55.56	60.94	64.43	56.89	60.06	62.5	64.1	65.21

Table 7. Dew-induced litter decomposition contribution (%) to annual litter decomposition (without photoinhibition) in the total litter pool (ld_{pool}) and in the top litter layer (ld_{top}) under different global change scenarios of increasing temperatures and decreasing precipitations (Precip), for four canopy coverages (cc).

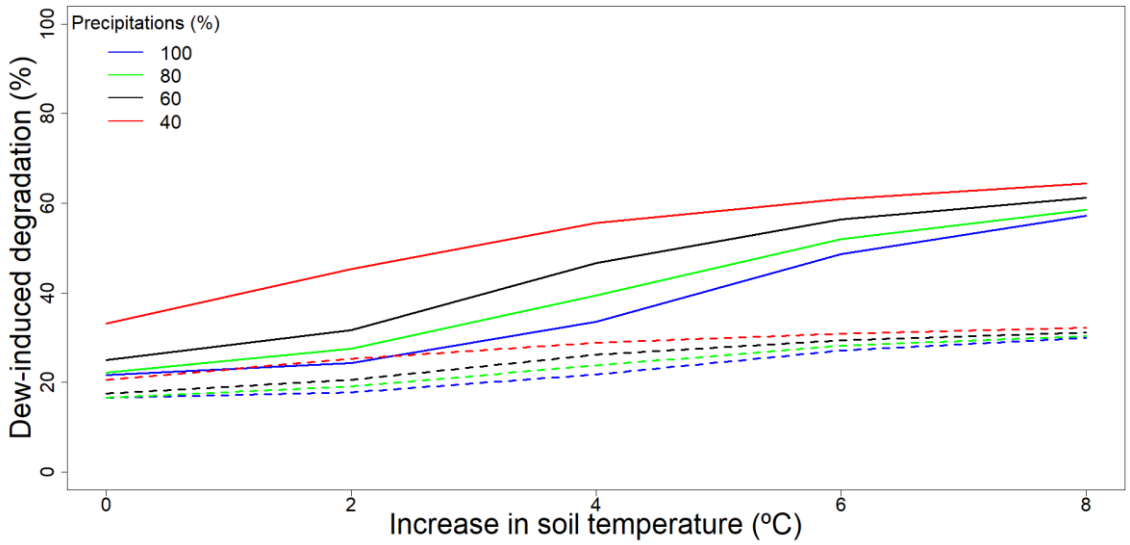

Figure 2. Contribution of dew-induced decomposition (%) to litter decomposition in total litter pool under different global change scenarios (without photoinhibition). All simulated scenarios for precipitations and soil temperatures are represented, for the two most contrasted canopy cover scenarios: 75% (full lines) and 0% (dashed lines).

		ld_{pool}					ld_{top}				
cc	**Precip**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**	**+0ºC**	**+2ºC**	**+4ºC**	**+6ºC**	**+8ºC**
0%	**100%**	34.85	38.66	48.36	59.58	63.69	61.85	64.52	66.47	67.34	67.17
	80%	36.56	43.04	54	61.64	64.37	63.74	65.89	67.36	67.5	67.21
	60%	41.59	48.34	59.21	64.08	65.6	66.46	67.51	67.88	67.66	67.21
	40%	51.84	59.66	64.45	65.97	66.68	69.04	68.68	68.21	67.58	67.06
25%	**100%**	28.39	31.85	41.04	52.39	56.76	54.85	57.68	59.78	60.72	60.55
	80%	29.92	35.98	46.65	54.56	57.49	56.84	59.17	60.74	60.9	60.58
	60%	34.59	41.03	52	57.17	58.82	59.76	60.9	61.31	61.08	60.59
	40%	44.48	52.47	57.56	59.22	60.01	62.58	62.18	61.68	60.99	60.43
50%	**100%**	20.7	23.54	31.52	42.2	46.61	44.73	47.58	49.76	50.75	50.57
	80%	21.95	27.06	36.67	44.37	47.37	46.73	49.13	50.77	50.94	50.61
	60%	25.93	31.51	41.82	47.03	48.75	49.76	50.94	51.37	51.12	50.61
	40%	34.64	42.28	47.43	49.17	50	52.71	52.29	51.76	51.04	50.45
75%	**100%**	11.43	13.21	18.58	26.66	30.34	28.79	31.2	33.11	34	33.84
	80%	12.2	15.52	22.34	28.44	30.99	30.47	32.55	34.02	34.17	33.88
	60%	14.76	18.59	26.35	30.69	32.21	33.1	34.17	34.56	34.34	33.88
	40%	20.82	26.71	31.03	32.57	33.33	35.78	35.4	34.91	34.26	33.73

Table 8. Photodegradation contribution (%) to annual litter decomposition (without photoinhibition) in the total litter pool (ld_{pool}) and in the top litter layer (ld_{top}) under different global change scenarios of increasing temperatures and decreasing precipitations (Precip), for four canopy coverages (cc).

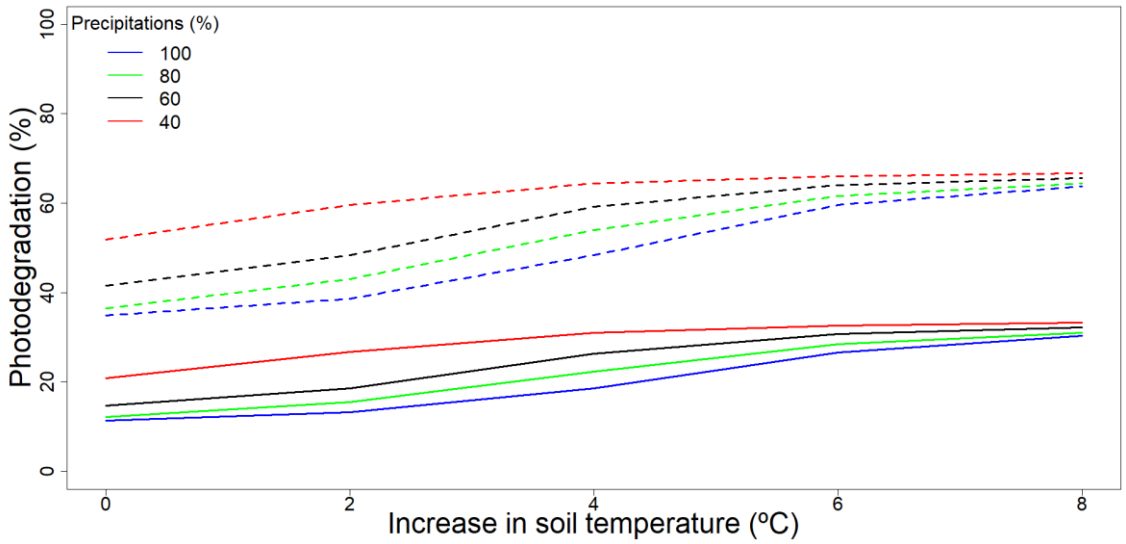

Figure 3. Contribution of photodegradation (%) to litter decomposition in total litter pool under different global change scenarios (without photoinhibition). All simulated scenarios for precipitations and soil temperatures are represented, for the two most contrasted canopy cover scenarios: 75% (full lines) and 0% (dashed lines).

Appendix 4 – Experimental work

Litter quality and decomposition rates

Common garden

Litter	C (%)	N (%)	P (mg/kg)	K (mg/kg)	Ca (mg/kg)
León	50.52±0.58	1.86±0.09	1032.21±65.21	1270.01±139.44	8555.61±451.01
Navarra	49.95±0.55	1.64±0.12	687.33±33.46	1112.06±147.04	11010.23±342.76
Lérida	50.84±0.46	1.61±0.17	679.10±27.45	2271.89±156.92	10449.04±322.93
Cáceres	55.51±1.51	1.40±0.06	998.56±32.76	3072.59±316.15	7402.21±162.76
Alicante	53.93±0.63	1.48±0.11	732.89±49.42	1763.67±184.27	12198.30±1095.25
Almería	54.45±1.58	1.33±0.15	565.57±20.52	1833.60±139.99	10440.20±396.13
CFC	48.52±0.29	1.03±0.03	226.42±36.79	2750.92±182.97	6222.90±315.78
CFE	47.91±0.52	0.95±0.09	326.37±111.71	3352.63±138.88	6978.95±267.02
CWC	47.96±0.29	0.98±0.06	371.98±32.48	3029.06±466.34	7037.21±949.43
CWE	47.82±0.25	1.06±0.05	562.88±132.65	3498.69±687.97	9002.95±676.81

Table 1. Litter quality (elements). Initial C, N, P, K and Ca contents (averages±sd, n=4) for all the litter types in the common garden experiment.

Appendix 4

Litter	Mg (mg/kg)	Mn (mg/kg)	Fe (mg/kg)	Zn (mg/kg)	Cu (mg/kg)	Na (mg/kg)
León	1555.74±57.41	1795.11±69.14	208.36±27.42	30.90±1.77	7.54±3.42	39.11±1.85
Navarra	832.36±23.15	104.33±22.30	246.02±19.88	33.77±1.02	5.42±2.11	83.96±7.90
Lérida	1175.52±79.13	173.63±33.60	273.16±13.88	28.94±1.41	5.97±1.99	72.78±3.20
Cáceres	1480.58±97.50	356.53±18.72	313.32±68.58	37.34±3.85	11.57±7.30	90.17±17.04
Alicante	1547.91±31.67	46.17±10.79	408.59±78.02	27.15±0.62	6.12±0.90	73.71±4.58
Almería	2244.09±78.38	156.15±14.50	330.80±63.98	27.34±0.77	4.64±0.45	147.64±1.75
CFC	957.96±65.51	796.33±130.31	232.13±28.33	18.92±0.89	1.84±0.62	158.76±7.00
CFE	942.51±145.12	864.08±74.82	276.47±32.24	22.65±2.35	3.19±1.45	200.20±72.95
CWC	873.58±66.22	1053.97±123.17	372.00±69.27	12.02±1.72	1.37±0.26	98.66±17.33
CWE	940.23±59.06	904.24±164.50	279.10±32.09	16.49±2.69	2.48±0.56	95.13±13.72

Table 2. Litter quality (elements). Initial Mg, Mn, Fe, Zn, Cu and Na contents (averages±sd, n=4) for all the litter types in the common garden experiment.

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Litter	Lignin (%)	Cellulose (%)	Hemicellulose (%)	sC (%)	k_{01}	k_{02}	k_{03}
León	30.57±2.95	26.88±0.13	8.56±1.08	66.01±1.94	7.62E-04±5.50E-04	6.67E-04±2.47E-04	6.60E-04±1.66E-04
Navarra	18.19±1.94	27.54±0.32	11.78±1.59	57.51±0.23	1.16E-03±2.81E-04	7.60E-04±1.09E-04	6.71E-04±2.54E-04
Lérida	19.00±1.13	27.49±0.64	11.54±1.13	58.02±0.77	1.23E-03±2.71E-04	8.66E-04±1.37E-04	7.42E-04±8.72E-05
Cáceres	22.29±0.77	28.39±0.28	5.37±0.69	56.05±1.29	1.19E-03±1.77E-04	8.16E-04±1.69E-04	7.37E-04±1.30E-04
Alicante	29.90±2.32	26.91±0.43	4.34±1.27	61.14±2.04	8.14E-04±1.79E-04	5.20E-04±1.20E-04	6.24E-04±1.40E-04
Almería	14.29±0.38	26.23±0.56	13.30±0.38	53.82±0.72	1.37E-03±3.67E-04	1.00E-03±2.30E-04	8.25E-04±1.82E-04
CFC	17.40±1.41	24.84±0.62	9.11±1.72	51.35±0.45	1.70E-03±3.35E-05	1.07E-03±4.19E-05	9.41E-04±4.97E-05
CFE	16.52±0.84	24.88±0.29	9.62±0.91	51.02±0.51	1.44E-03±2.18E-04	1.27E-03±2.40E-04	1.03E-03±1.17E-04
CWC	21.27±0.73	27.11±0.33	3.74±0.72	52.11±0.47	1.19E-03±1.25E-04	1.21E-03±1.17E-04	9.14E-04±8.66E-05
CWE	19.10±1.08	25.68±0.66	7.74±1.83	52.51±0.92	1.20E-03±1.52E-04	1.01E-03±1.31E-04	8.50E-04±6.04E-05

Table 3. Litter quality (recalcitrance) and decomposition. Initial lignin, cellulose and hemicellulose contents and their sum as structural C (sC), and the decomposition rates (k) for all the litter types in the common garden experiment (averages±sd, n=4), for incubation times during four (k_{01}), eight (k_{02}) and twelve (k_{03}) months.

Gradient

Site	k_{01}	k_{02}	k_{03}
León	4,33E-04±2,18E-04	4,54E-04±7,42E-05	4,67E-04±4,93E-05
Navarra	7,57E-04±5,78E-05	6,97E-04±7,15E-05	7,20E-04±7,34E-05
Lérida	7,60E-04±2,06E-04	7,34E-04±1,75E-04	6,32E-04±1,10E-04
Madrid	6,91E-04±1,06E-04	9,01E-04±3,37E-05	5,81E-04±1,18E-04
Cáceres	8,45E-04±1,69E-04	6,84E-04±1,14E-04	6,49E-04±7,30E-05
Alicante	9,59E-04±1,70E-04	7,59E-04±8,20E-05	5,32E-04±5,64E-05
Almería	8,15E-04±8,93E-05	7,17E-04±1,59E-04	6,61E-04±1,40E-04

Table 4. Litter decomposition in the gradient experiment. Decomposition rates (k) of the uniform litter from Cabañeros, for incubation times during four (k_{01}), eight (k_{02}) and twelve (k_{03}) months. in all sites of the gradient experiment (averages±sd, n=4).

Appendix 4

Correlations between variables and mixed models

Common garden

	k_{01}	k_{02}	k_{03}	Lig	Cel	Hem	sC	nsC	C	N	P	K	Ca	Mg	Mn	Fe	Zn	Cu
k_{02}	0.00	-																
k_{03}	0.00	0.00	-															
Lig	0.00	0.00	0.00	-														
Cel	0.01	0.00	0.00	0.01	-													
Hem	0.05	0.75	0.73	0.00	0.36	-												
sC	0.00	0.00	0.00	0.00	0.00	0.83	-											
nsC	0.00	0.00	0.00	0.00	0.00	0.83	0.00	-										
C	0.05	0.00	0.00	0.13	0.00	0.52	0.00	0.00	-									
N	0.00	0.00	0.00	0.01	0.00	0.26	0.00	0.00	0.00	-								
P	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	-							
K	0.03	0.00	0.00	0.30	0.04	0.06	0.00	0.00	0.01	0.00	0.01	-						
Ca	0.00	0.00	0.00	0.49	0.02	0.18	0.00	0.00	0.00	0.00	0.00	0.00	-					
Mg	0.11	0.01	0.07	0.17	0.41	0.84	0.01	0.01	0.00	0.01	0.00	0.06	0.03	-				
Mn	0.30	0.00	0.02	0.35	0.06	0.11	0.07	0.07	0.00	0.03	0.16	0.02	0.00	0.17	-			
Fe	0.29	0.81	0.71	0.47	0.67	0.03	0.75	0.75	0.27	0.18	0.98	0.06	0.27	0.18	0.05	-		
Zn	0.06	0.00	0.00	0.26	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.01	0.26	-	
Cu	0.01	0.00	0.00	0.05	0.00	0.49	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.67	0.00	-
Na	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.05	0.58	0.61	0.00	0.00

Table 5. P-values for Spearman correlations between litter decomposition rates (k) and litter quality variables. Decomposition rates are presented for incubation times during four (k_{01}), eight (k_{02}) and twelve (k_{03}) months. Litter quality variables include lignin (Lig), cellulose (Cel), hemicellulose (Hem), structural C (sC), its complementary non-structural C (nsC), and eleven chemical elements.

Appendix 4

	k_{01}	k_{02}	k_{03}	Lig	Cel	Hem	sC	nsC	C	N	P	K	Ca	Mg	Mn	Fe	Zn	Cu
k_{02}	0.71																	
k_{03}	0.78	0.85																
Lig	-0.58	-0.48	-0.46															
Cel	-0.43	-0.46	-0.47	0.40														
Hem	0.31	0.05	0.06	-0.77	-0.15													
sC	-0.60	-0.76	-0.70	0.62	0.58	-0.04												
nsC	0.60	0.76	0.70	-0.62	-0.58	0.04	-1.00											
C	-0.32	-0.57	-0.52	0.24	0.48	0.10	0.62	-0.62										
N	-0.44	-0.70	-0.61	0.39	0.55	0.18	0.87	-0.87	0.57									
P	-0.55	-0.71	-0.67	0.62	0.62	-0.16	0.84	-0.84	0.65	0.79								
K	0.35	0.56	0.47	-0.17	-0.32	-0.30	-0.71	0.71	-0.43	-0.74	-0.44							
Ca	-0.51	-0.62	-0.56	0.11	0.36	0.21	0.67	-0.67	0.45	0.62	0.48	-0.67						
Mg	-0.25	-0.39	-0.29	0.22	0.13	0.03	0.43	-0.43	0.69	0.41	0.48	-0.30	0.34					
Mn	0.17	0.46	0.36	0.15	-0.30	-0.25	-0.29	0.29	-0.55	-0.35	-0.23	0.36	-0.71	-0.22				
Fe	-0.17	0.04	-0.06	0.12	0.07	-0.35	-0.05	0.05	0.18	-0.22	0.00	0.30	0.18	0.22	-0.32			
Zn	-0.30	-0.62	-0.50	0.18	0.63	0.27	0.66	-0.66	0.69	0.73	0.76	-0.51	0.40	0.38	-0.41	-0.18		
Cu	-0.43	-0.66	-0.47	0.31	0.53	0.11	0.68	-0.68	0.71	0.68	0.74	-0.42	0.45	0.55	-0.41	-0.07	0.79	
Na	0.53	0.63	0.58	-0.69	-0.57	0.22	-0.88	0.88	-0.38	-0.75	-0.77	0.55	-0.54	-0.31	0.09	0.08	-0.47	-0.54

Table 6. Coefficients (r) for Spearman correlations between litter decomposition rates (k) and litter quality variables. Decomposition rates are presented for incubation times during four (k_{01}), eight (k_{02}) and twelve (k_{03}) months. Litter quality variables include lignin (Lig), cellulose (Cel), hemicellulose (Hem), structural C (sC), its complementary non-structural C (nsC), and eleven chemical elements.

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Appendix 4

Fixed variables for k_{03}	Random variables	df	AIC	BIC	R^2 marginal	R^2 conditional	p-value residuals
Lignin	Home/Site	5	-585.24	-576.80	0.10	0.37	0.64
Cellulose	Home/Site	5	-582.47	-574.02	0.08	0.29	0.62
sC	Home/Site	5	-587.39	-578.94	0.39	0.39	0.90
N	Home/Site	5	-585.41	-576.96	0.36	0.36	0.13
P	Home/Site	5	-586.48	-578.04	0.38	0.39	0.48
Ca	Home/Site	5	-582.13	-573.69	0.07	0.28	0.15
Na	Home/Site	5	-583.89	-575.44	0.09	0.32	0.47
Lignin*Ca	Home/Site	7	-586.07	-574.25	0.43	0.43	0.33
Lignin*Mn	Home/Site	7	-585.47	-573.65	0.43	0.43	0.75
sC+Mn	**Home/Site**	**6**	**-590.85**	**-580.71**	**0.47**	**0.47**	**0.42**
sC*Mn	Home/Site	7	-588.86	-577.03	0.47	0.47	0.42

192 **Table 7.** Mixed models for k_{03} (common garden), with litter origin site ("Site") nested in local vs. translocated litter ("Home") as random factors; for one fixed variable only models with marginal $R^2 > 5$ % are shown, and for more than one fixed variables only models with marginal $R^2 > 40$ % are shown. Model selected as the best is in bold.

	sC	Mn	Canopy	MAT	MAP
Mn	0.07	-			
Canopy	0.00	0.12	-		
MAT	0.00	0.23	0.00	-	
MAP	0.00	0.01	0.08	0.14	-
pH	0.30	0.00	0.48	0.01	0.38

Table 8. P-values for Spearman correlations between structural C (sC), Mn and litter origin site data: tree canopy cover, mean annual temperature (MAP), mean annual precipitation (MAP), and soil pH.

Appendix 4

	sC	Mn	Canopy	MAT	MAP
Mn	-0.29				
Canopy	0.53	-0.25			
MAT	-0.66	0.20	-0.55		
MAP	0.61	-0.41	0.28	-0.24	
pH	0.17	-0.65	0.12	-0.41	-0.14

Table 9. Coefficients (r) for Spearman correlations between structural C (sC), Mn and litter origin site data: tree canopy cover, mean annual temperature (MAP), mean annual precipitation (MAP), and soil pH.

Fixed variables for sC	Random variables	df	AIC	BIC	R^2 marginal	R^2 conditional	p-value residuals
Canopy	Home/Site	5	168.06	176.50	0.23	0.94	0.11
MAT	Home/Site	5	167.48	175.92	0.23	0.94	0.07
MAP	Home/Site	5	171.43	179.87	0.00	0.94	0.13
MAT*MAP	**Home/Site**	**7**	**163.58**	**175.40**	**0.51**	**0.93**	**0.10**
Canopy*MAP	Home/Site	7	171.19	183.01	0.48	0.94	0.10
MAT*MAP+Canopy	Home/Site	8	162.22	175.73	0.66	0.93	0.11

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Table 10. Mixed models for structural C (sC), with litter origin site ("Site") nested in local vs. translocated litter ("Home") as random factors. Model selected as the best is in bold.

Fixed variables for $\log_e$(Mn)	Random variables	df	AIC	BIC	R^2 marginal	R^2 conditional	p-value residuals
MAP	Home/Site	5	25.80	34.25	0.04	0.98	0.62
pH	Home/Site	5	16.55	25.00	0.52	0.98	0.64
pH+MAP	Home/Site	6	14.32	24.45	0.70	0.98	0.69
pH*MAP	**Home/Site**	**7**	**9.51**	**21.34**	**0.88**	**0.98**	**0.65**

Table 11. Mixed models for Mn normalized by natural logarithm transformation, with litter origin site ("Site") nested in local vs. translocated litter ("Home") as random factors. Model selected as the best is in bold.

Appendix 4

Gradient

	k_{01}	k_{02}	k_{03}	Canopy	Shrubs	Grass	Understory	t_{01}	t_{02}	t_{03}	p_{01}	p_{02}	p_{03}	MAT
k_{02}	0.00	-												
k_{03}	0.04	0.16	-											
Canopy	0.82	0.17	0.03	-										
Shrubs	0.12	0.46	0.00	0.27	-									
Grass	0.68	0.01	0.04	0.00	0.86	-								
Understory	0.29	0.47	0.00	0.04	0.00	0.00	-							
t_{01}	0.12	0.48	0.52	1.00	0.02	0.86	0.36	-						
t_{02}	-	0.58	0.97	0.47	0.06	0.10	0.59	0.00	-					
t_{03}	-	-	0.89	0.04	0.72	1.00	0.36	0.00	0.00	-				
p_{01}	0.03	0.20	0.05	0.36	0.02	0.14	0.00	0.47	0.72	0.14	-			
p_{02}	-	0.22	0.12	0.59	0.04	0.14	0.00	0.47	0.06	0.00	0.00	-		
p_{03}	-	-	0.20	0.06	0.06	0.27	0.00	0.47	0.27	0.00	0.00	0.00	-	
MAT	0.00	0.18	0.43	0.14	0.27	0.36	0.59	0.00	0.00	0.00	0.27	0.27	0.72	-
MAP	0.67	0.28	0.02	0.02	0.20	0.00	0.00	0.01	0.00	0.04	0.00	0.00	0.00	1.00

Table 12. P-values for Spearman correlations between litter decomposition rates (k) and site characteristics in climate and forest structure. Decomposition rates are presented for incubation times during four (k_{01}), eight (k_{02}) and twelve (k_{03}) months. Temperatures (t) and precipitations (p) during the experiment are included for the same intervals than k rates. Historical climate in each site was described by mean annual temperature (MAT) and mean annual precipitation (MAP). Forest structure is represented by vegetation cover divided in tree canopy, shrubs, grass, and the sum of shrubs and grass covers as the understory variable.

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Appendix 4

	k_{01}	k_{02}	k_{03}	Canopy	Shrubs	Grass	Understory	t_{01}	t_{02}	t_{03}	p_{01}	p_{02}	p_{03}	MAT
k_{02}	0.56													
k_{03}	0.40	0.27												
Canopy	-0.04	-0.27	-0.42											
Shrubs	0.30	-0.14	0.59	-0.21										
Grass	0.08	0.47	0.39	-0.54	0.04									
Understory	0.21	0.14	0.68	-0.39	0.75	0.64								
t_{01}	0.30	-0.14	0.13	0.00	0.43	0.04	0.18							
t_{02}	-	-0.11	-0.01	0.14	0.36	-0.32	-0.11	0.86						
t_{03}	-	-	0.03	-0.39	0.07	0.00	-0.18	0.61	0.75					
p_{01}	0.41	0.25	0.37	0.18	0.43	0.29	0.61	-0.14	-0.07	-0.29				
p_{02}	-	-0.24	0.30	0.11	0.39	0.29	0.64	-0.14	-0.36	-0.68	0.61			
p_{03}	-	-	0.25	0.36	0.36	0.21	0.57	-0.14	-0.21	-0.61	0.86	0.89		
MAT	0.59	0.26	0.16	-0.29	0.21	0.18	0.11	0.57	0.71	0.82	0.21	-0.21	-0.07	
MAP	0.08	0.21	0.44	-0.43	0.25	0.54	0.64	-0.50	-0.57	-0.39	0.64	0.68	0.61	0.00

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Table 13. Coefficients (r) for Spearman correlations between litter decomposition rates (k) and site characteristics in climate and forest structure. Decomposition rates are presented for incubation times during four (k_{01}), eight (k_{02}) and twelve (k_{03}) months. Temperatures (t) and precipitations (p) during the experiment are included for the same intervals than k rates. Historical climate in each site was described by mean annual temperature (MAT) and mean annual precipitation (MAP). Forest structure is represented by vegetation cover divided in tree canopy, shrubs, grass, and the sum of shrubs and grass covers as the understory variable.

Fixed variables for k_{03}	Random variable	df	AIC	BIC	R^2 marginal	R^2 conditional	p-value residuals
Shrubs	Site	4	-430.84	-425.51	0.30	0.32	0.23
Understory	**Site**	**4**	**-436.79**	**-431.46**	**0.44**	**0.44**	**0.19**
Canopy	Site	4	-427.18	-421.86	0.16	0.32	0.22
Shrubs+Canopy	Site	5	-433.95	-427.29	0.42	0.42	0.09
Shrubs*Canopy	Site	6	-434.64	-426.65	0.47	0.47	0.11

Table 14. Mixed models for k_{03} (gradient), with litter incubation site ("Site") as random factor. Model selected as the best is in bold.

GLOSSARY

a: availability of a substrate to a consumer.

Ag: aggregation, i.e. fraction of the SOM aggregated by microbes.

AIC: Akaike information criterion.

AICc: corrected AIC (for small sample sizes).

AM: arbuscular mycorrhizal fungi.

ANOVA: analysis of variance.

ap: switch parameter to activate or deactivate photoinhibition.

$avail_{SOM}$: SOM availability on the accessible pores for microbial communities in function of soil hydrology.

B: biomass.

bact: bacteria.

B_b: bacterial biomass (g C/m^3).

B_{bvores}: biomass of bacterivores (g C/m^3).

bd_{dew}: biotic degradation of litter induced by dew.

B_{det}: biomass of detritivores (g C/m^3).

bd_{rain}: biotic degradation of litter using rainfall water.

B_{eng}: biomass of engineers (g C/m^3).

B_f: fungal biomass (g C/m^3).

B_{full}: minimum litter biomass to fully cover a square meter of soil surface (g C/m^2).

B_{fung}: fungal biomass (g C/m^3) (also B_f).

B_{fvores}: biomass of fungivores (g C/m^3).

B_{hvores}: biomass of herbivores (g C/m^3).

B_{lit}: litter biomass (g C/m^2).

B_{myc}: mycorrhizal biomass (g C/m^3).

B_{pred}: biomass of predators (g C/m^3).

B_{root}: biomass of roots (g C/m^3).

B_{SOM}: SOM pool mass (g C/m^3).

Bvores: bacterivores.

c_{abs}: radiation absorbance by litter.

cc: canopy cover fraction.

Cel: cellulose.

C_{Exud}: directly exuded DOM.

C_{dew}: relative contribution (%) of dew-induced decomposition to total litter decomposition.

CF: forest in Cabañeros National Park (Ciudad Real, Spain) (Cabañeros-Forest).

CFC: control forest in Cabañeros (Cabañeros-Forest-Control).

CFE: ungulate exclusion into forest in Cabañeros (Cabañeros-Forest-Exclusion).

CN_{bact}: CN ratio in bacteria pool.

CN_{eng}: CN ratio in engineer pool.

CN_{fung}: CN ratio in fungi pool.

CN_{lit}: CN ratio in litter pool.

CN_{SOM}: CN ratio in SOM pool.

C_{phd}: relative contribution (%) of photodegradation to total litter decomposition.

CR: Ciudad Real (Spanish province).

C_R: carbon respired.

CW: open woodland in Cabañeros National Park (Ciudad Real, Spain) (Cabañeros-Woodland).

CWC: control open woodland in Cabañeros (Cabañeros-Woodland-Control).

CWE: ungulate exclusion into open woodland in Cabañeros (Cabañeros-Woodland-Exclusion).

D: drainage.

d: soil layer depth (m).

d_0: intercept for temperature-RH linear equation 10 (chapter 3).

d_1: slope for temperature-RH linear equation 10 (chapter 3).

D_b: bulk density.

dec_{exp}: daily decomposition activity on exposed litter.

D_j: observed data in sampling year j.

D_m: soil mineral particle density.

dm: drought modifier.

D_n: drainage of soil layer n.

DOC: dissolved organic carbon.

DOM: dissolved organic matter.

DOM_{ad}: adsorbed DOM.

DON: dissolved organic nitrogen.

dr: litter mass degraded by radiation unit (µg C/kJ).

D_s: soil particle density.

ds: drought sensitivity (%).

D_{SOM}: organic particle density.

D_t: death (turnover).

E: evapotranspiration.

expLit: fraction of the exposed litter (i.e. top layer) over the total litter pool.

EHE: extracellular hydrolytic enzymes.

EM: ectomycorrhizal fungi.

eng: engineers.

ErM: ericoid mycorrhizal fungi.

f_a: available fraction (of a consumable pool).

FB: fungal/bacterial ratio.

f_{DOM}: fraction of respiration from DOM.

f_{faec}: fraction of prey allocated to faeces (not assimilated by predator).

f_{faecCN}: CN ratio in faeces.

$f_{faecEff}$: effect of faeces on microbes.

$f(\theta_j)$: a simulated value with parameter θ at year j.

F_{litCO2}: fraction of photodegraded litter emitted as CO_2.

f_{PV}: fraction of the change in biopore volume that increases macroporosity.

f_{sun}: fraction of average daily sunlight hours in each month.

f_{UV}: fraction of UV in solar radiation reaching the soil.

Fvores: fungivores.

G: growth.

g_{max}: maximal rate of growth.

g_{maxEng}: gmax for engineers.

G_{pred}: growth of predator pool.

θ: any parameter value in the model.

H1: hypothesis 1 (and the same applies to any other number after an H).

Hem: hemicellulose.

HFA: home field advantage (hypothesis).

HWC: hot water extractable C.

I: Infiltration.

ICP-OES: inductively coupled plasma optical emission spectroscopy.

i_{dew}: dew incidence.

I_{maxMat}: maximal infiltration rate (into soil matrix).

I_{maxPor}: maximal infiltration rate through macropores.

in_{rec}: increase in litter recalcitrance from exposed to unexposed litter layers.

IPCC: Intergovernmental Panel on Climate Change.

k: decomposition rate.

k_{away}: k of litter translocated to other site away from its origin site.

K_D: (DOM) adsorption coefficient of the soil.

k_{home}: k of litter incubated in its origin site.

k_{ij}: decomposition rate for the incubation period between the times i and j; e.g. k_{03} represents the decomposition rate between the beginning of the experiment and the third removal time, i.e. after one year of incubation in the field.

KL: abbreviation of the name of the model (KEYLINK) used in the input text files.

k_{local}: k of litter from the same site in which was incubated (equivalent to k_{home}).

K_s: content required to get half the maximal growth.

$k_{translocated}$: k of litter from a different site than the one in which was incubated.

LAI: leaf area index.

ld: annual rate of litter decomposition (g C m^{-2} $year^{-1}$).

ld_{pool}: ld in the total litter pool.

ld_{top}: ld in the top litter layer.

LHS: Latin Hypercube Sample.

L_i: likelihood function at calibration step i.

Lig: lignin.

LME: linear mixed-effects model.

L_{surf}: aboveground litter (g C/m^2).

m: modifier (to account for an effect in the model).

M_0: litter mass inside a litterbag at the beginning of the incubation experiment.

MAP: mean annual precipitation.

MAT: mean annual temperature.

max_{rad}: minimum solar radiation to reach the maximum effects of radiation on soil processes (MJ/m^2).

mb: microbial biomass.

MCMC: Markov Chain Monte Carlo (method).

m_{CN}: modifier for the effect of CN ratio.

m_{CNbact}: m_{CN} for bacteria.

m_{CNfung}: m_{CN} for fungi.

med: moisture effect on decomposition.

m_{faec}: sensitivity of f_{faec} to CN ratio of the consumable pool.

m_{H2Otot}: modifier for the effect of hydration.

min_b: minimum biomass in each pool.

m_{pH}: pH modifier.

m_{rec}: modifier for the effect of organic matter recalcitrance.

$m_{recbact}$: m_{rec} for bacteria.

$m_{recfung}$: m_{rec} for fungi.

M_t: litter mass inside a litterbag at removal time t.

m_T: temperature modifier.

m_{tot}: total effect of modifiers on g_{max}.

nsC: non-structural carbon (i.e. labile C).

OM: organic matter.

OrM: orchid mycorrhizal fungi.

P: precipitation.

$P_{\%}$: percentage of total porosity.

p_0: intercept in linear equation 3 (chapter 3) for dr.

p_1: slope in linear equation 3 (chapter 3) for dr.

PCA: principal component analysis.

P_d: predation.

$p(D|\theta)$: likelihood function of the parameter value θ.

p_{death}: death of microbial biomass by radiation (g C/m^2).

P_{dprey}: biomass removed from a prey pool due to predation.

$p(\theta)$: prior distribution of the parameter value θ.

$p(\theta|D)$: posterior distribution of the parameter value θ.

phd: litter mass photodegraded each day (g C/m^2).

phd_{CO2}: fraction of phd that goes directly to CO_2 emissions.

Photodegradation: abiotic degradation of organic compounds by direct exposure to solar radiation.

p_{ij}: total precipitations for the incubation period between the times i and j.

p_{inh}: fraction of effective photoinhibition.

p_{mCN}: sensitivity to CN ratio (of the consumable pool).

$p_{mCNbact}$: p_{mCN} for bacteria.

$p_{mCNfung}$: p_{mCN} for fungi.

p_{mRec}: sensitivity to organic matter recalcitrance.

$p_{mRecbact}$: p_{mRec} for bacteria.

$p_{mRecfung}$: p_{mRec} for fungi.

P_{net}: net precipitation.

POM: particulate organic matter.

Precip: precipitations.

Pred: predators.

P_{runoff}: runoff (from precipitation).

PTFs: PedoTransfer Functions.

PV: total pore volume.

PV_{Ag}: additional aggregation porosity.

PV_B: burrow volume (bioporosity).

PV_{bact}: volume of bacterial pores.

PV_{Bmax}: maximum PV_B.

PV_{macro}: volume of macropores.

PV_{meso}: volume of mesoporores.

PV_{micro}: volume of micropores.

PV_n: total pore volume of soil layer n.

P_{vol}: pore volume.

P_{volA}: aerated pore volume.

P_{volW}: water filled pore volume.

PV_{text}: textural porosity.

$PV_{textmacro}$: textural macroporosity.

$PV_{textmeso}$: textural mesoporosity.

PV_{tot}: total soil porosity.

σ_j: standard deviation of the model error at year j.

R: respiration.

r: Spearman pairwise correlation coefficient.

rad: daily total solar radiation (MJ/m^2).

rec: recalcitrance (%) of organic matter.

Rec_{lit}: litter recalcitrance.

rec_{SOM}: SOM recalcitrance (%).

rec_{top}: litter recalcitrance (%) in the top layer.

RH: relative humidity.

RH_{max}: daily maximum relative humidity.

RQ: respiratory quotient.

R_{tot}: total respiration.

S: substrate, a consumable pool (i.e. litter, SOM or biomass of prey organisms).

SA_{macro}: surface area of the macropores.

sap: saprotrophs.

sC: structural carbon.

SEM: structural equation model.

SOC: soil organic carbon.

SOM: soil organic matter.

$SOM_{unavail}$: unavailable SOM physically protected in inaccessible pores.

SWA: soil water availability (SWC except water in inaccessible pores).

SWC: soil water content.

SW_n: soil water volume of soil layer n.

T: temperature.

T_{dew}: dew point temperature.

t_{ij}: mean temperature for the incubation period between the times i and j.

T_{max}: maximum temperature.

T_{min}: minimum temperature.

topm: fraction of microbial biomass on the top litter layer.

T_{opt}: optimal temperature (for a soil functional group).

UV: ultraviolet (radiation).

UV_{lit}: energy absorbed by litter (kJ/m^2).

V: volumetric soil moisture.

VE_{ratio}: ratio of pore volume to engineer biomass.

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Acknowledgements

“I don't know half of you half as well as I should like;

and I like less than half of you half as well as you deserve.”

John Ronald Reuel Tolkien

…dary.

Acknowledgements

This thesis would not have been possible without the leading of two researchers to whom I cannot thank enough all their support, teachings and friendship: Jorge Curiel Yuste and Gaby Deckmyn.

Jorge has been an awesome supervisor, who showed me the light beyond the Dark Side of the thesis, saving me from the anger and suffering that were close to making me give up. There is no word in Elvish, Entish or the tongues of Men to express my gratitude to Jorge. More advisors like him are needed in science to train new generations of scientists, and I just hope that one day I can do such a good job on that as the one Jorge has done for me.

And I owe a similar thanks to Gaby Deckmyn, who trained me on modelling, which was my final goal with this thesis. In the words of Sir Isaac Newton, she has been one of the Giants in whose shoulders I stand, and all my future contributions to science are going to grow from the knowledge that Gaby gave to me.

But beyond the science, both Jorge and Gaby have shown me values as hospitality and the relevance of team work. For that and for everything, they have my eternal gratitude.

The beginning of this thesis was possible thanks to Fernando Valladares, who offered me the possibility to join his work group, and who have taught me many valuable lessons on science communication and rhetoric. I hope to be able to keep the same energy that he has for science, and I wish him all the best and health for years to come.

Working in the group of Valladares in the National Museum of Natural Sciences (MNCN-CSIC) has been an experience in many senses. Although I had to suffer the deplorable conditions that sadly we all have to face in Spanish science, the wonderful people I have met there make the overall experience positive. Daniel García Angulo became a friend from the very beginning, and it has been a pleasure to work hand in hand with him and to share our hobbies. “In the game of thesis, you win or you die”, and I won because I have Daniel as an ally. I hope our different paths will cross again many times.

On the other hand (of the office), I share these years with two wonder women. First, Ana-Maria Hereş; I can say that I survived to her tree core samplings, but barely. It was amazing how she could take tree cores where others failed. And her skills with languages are equally amazing. I’m glad to have contributed to teach her Spanish. But mostly, a true friendship bond us. And secondly, but not less important, Alicia Forner Sales, who is the lab’s wonder woman by excellence. Everyone who has worked in that lab owes something to Alicia, and I am not an exception. She is always there for anyone who needs help, and that is our blessing and her curse. There were so many things in which I had her help that I cannot remember all, but she deserves great thanks for all.

I wish I could have more time to express properly all the acknowledgements that I owe to so many people, but I hope they already know that, even if I write only a few words for them, or even if they are included only as part of a group, I thank them more than what I can say now. But still, I will say many things.

It is obvious for anybody who have read this thesis that Cabañeros National Park was crucial for my research, and I have to thank the workers of that Park for all their help, but mostly that was possible thanks to Mario Díaz, and all the work that he has done during so many years in Cabañeros, allowing me to take advantage of it; and I also appreciate some other contributions of Mario, as the knowledge I gained on ethology. Regarding the office work, the friendly people from the eighth floor at the ICA (including those already mentioned) generated a family atmosphere that make it easier to go to work (even for those whose night live difficult to see the sunlight at working hours); days at work were much happier thanks to Cristina Crespo Bastias, who always had a smile to shed light on the darkness of our caves. I can say the same about Bárbara Carvalho, despite the worst moments that we had with our theses, it was always pleasant to talk with her, easing the load of such work. Sometimes the thesis results quite boring, but then new interesting challenges give you the strength to continue, and among all the good things of working with Raquel Benavides, she contributed to that, asking me for programming solutions to some analyses that I really enjoyed.

At the beginning of my thesis I was lucky to meet Teresa Morán López, whose thesis was an example of an interesting work that inspired me. And Ciro Cabal was another example that there is always a way to keep in science, despite the healthy envy that he inspires now because of the facilities he has for his thesis in the first world. To Jorge Durán and Xandra Rodríguez, for their contribution to the start of my thesis, and their advices when this thesis was just a "seedling". Moreover, I have learned interesting things on ecology issues beyond the scope of my work by talking with Elena Concepción, as the issues with environmental policies for land management, so I wish I could have more opportunities to talk with her about her research. I had another example of interesting work in Sandra Magro, who showed me a world beyond science. I thank also Jesús Villellas, among other things, for his advices on mixed models analysis and about post-doc grants. And to Andrés Bravo for the months in which I had a better place to live and work, thanks to him. Also to Margot Kaye for her lessons on writing science, and for the book she gave me, which is a very useful tool for improving all the papers I expect to write.

There were so many good moments with colleagues, both at work and after works; I remember interesting talks with Irene Marin Fores, even during party times. I remember also interesting conversations with Esteban Manrique, at work or even in the way to work. And I received help in field work from many people, as Belén Acuña Míguez, who has now all the load of being the PhD student in the lab, and I wish her the best on it. I also thank the field and lab work with many others: Matheus Maza, for the adventures on the field, and the "secreto" in Andalucía that awaits for him to come back; Clara García for the field work in Cabañeros, and the adventure lived on a winter

night caught in the middle of nowhere in Cabañeros; Pilar Sánchez for her help with the first sampling of the litterbags; Manuel Azurmendi and Pedro Pablo Platero were a great help in the lab, and I'm sure they became two real experts in making litterbags; Julia Eggert for both lab and field work even during her holidays; and Guido Pellis for the field work, I was lucky to have his help for the war against soil stones. And especially to Xochiltt Izamar, for her help during some of the hardest times, the long days working with the litter, and for everything else. To Ludmila, for our efforts doing science in both Portuguese and Spanish, which was a challenge that we handled quite well; to Mariana Iguatemy, for those nice months we had her with us; and to Paula Gil Hernández, whose presence contributed also to the friendly working environment. And also to Marina, Lucía, Teresa, and to all other students and people who have worked in the department. To Mikel Calle and the rest of the PhD students and postdocs at ICA and MNCN with whom I have share corridors, meetings, and mainly the eighth floor occasionally when they came to our Photocopier Kingdom.

When I had technical issues preparing experimental stuff, there was no better help than David López Quiroga, a remarkable technician and a tireless worker. I also remember Miguel Fernández and all the laughs during field work, and our jokes at regional scale. And during the last year, I received valuable backup from Antonio Mas Barreiro, whose company and help during the last field works were appreciated, from dawn to nightfall on The Cabañeros Shire, and I know that our friendship, if necessary, will bring us to Mount Doom.

Many people at CSIC were helpful, as Octavio. Also those in the MNCN communication department, as Azucena, Xiomara and Pilar among others, for our collaborations in science dissemination; and I also appreciate all the people which whom I collaborated in other science dissemination projects and events, e.g. Somos Científicos, Pint of Science, La Noche del Conocimiento, etc. Particularly to Armando del Romero, Miguel Sancho, Leticia Herrera and the rest of the people involved in the IPLS project.

Part of my work during these years sadly could not be included in this thesis, but I thank a lot to Antonio Encina and people from the Plant Physiology group at University of León for their help during the month I spent working in their lab; and I thank to Juan Carlos García-Gil and Pedro Soler (ICA-CSIC) for providing me with the herbaceous litter, which experimental results could not be included here, but I hope to use them later. I also want to mention other people from the University of León as many professors, particularly (but not only) to those from the Ecology group (e.g. Reyes Tárrega, Francisco García Criado), because I learned so much with them during my bachelor's degree in biology, and also during my collaboration grant with Leonor Calvo and Elena Marcos. I also thank to other professors at the universities UAM and UCM, particularly to Jesús Barandica for the lessons on modelling, who showed me the way in which I am now; and to Francisco Martín Azcárate, Javier Seoane and Violeta Hevia for our collaboration on ants; to the professors with whom I made the collaboration in teaching, as Pablo Aceves, and particularly to Cristina Mata, with whom I enjoyed so

much the “teaching experience”; and to Salvador Mollá and José González (Pepe) for their help with the bureaucratic procedures, among others.

I thank all the people from PLECO group, University of Antwerp (Belgium), for all the months that I spent with them, which were only the prelude of the coming years. Particularly, Reinhart Ceulemans, Nadine and Laura were very helpful; I am happy to have met such good friends and colleagues as the following: Maral, for being such friendly, closer than the distance at which we lived there; Dajana, who was really nice; Kevin, also very friendly guy; Jonas, whose interesting “lunch time” presentation I still remember, and with Erik, thanks to both for organizing the presentations; Inge and Cristina, for the free time we enjoyed with the group; Johanna, for the time we spent at the office and with her lovely dogs; Miguel, for his hospitality and advices; both Ivan (Nijs and Janssens), who are great examples of successful science careers… they are too many in PLECO, and I still have to learn many names, but I appreciate all of them. Particularly, I thank Olga Vindušková her advices and help with the manuscript, and to Matteo Campioli for the strong motivation he gave me to end this thesis once and for all, and for his trust in me offering me the opportunity to become a PLECO member. And to Irene Ramírez Rojas, the last only because she was the first friend I had there, even before any of us went there, and for all the time we enjoyed in Antwerp. I look forward to spend the next years with all of these nice people.

My acknowledgements also to all the people who have contributed to the BioLink and KEYSOM COST Actions, as Andrea Schnepf and Juan J. Jiménez, because this thesis is upon your shoulders too. On the other hand, to Ana Rey for her contributions to the designing of the experiments; and to Daniel Gliksman and José Grünzweig for their expert contributions about dryland mechanisms for the model development.

I remember also many people that I am glad to have met at conferences, scientific meetings and under many other circumstances during these years. It would be a neverending story to mention all of them, “*but that’s another story and shall be told another time*”, as Michael Ende would say.

Moreover, I want to thank other friends that have been part of my life during these years, as many from Mensa, for the interesting conversations on science and many other matters, for the doubts I could clarify (e.g. asking in GIEncia), and all the time spent together, especially playing werewolf; they are too many, but they know who they are. Also to the rest of my friends, those in Madrid, as Víctor and Bea, or in León, as Sandra and Antonio. To my brother, Javier Flores, for the times we enjoyed playing games, allowing me to forget the stress of the PhD; and to the rest of my family for cheering me up. Finally, above all, my thanks to my parents, Francisco Javier Flores and Maria José Rodríguez, because they have always been there for me, and because all their support to my studies and needs during all my life and particularly during these years is one of the reasons I got here.

To all of you, and to all the people who are not mentioned but remembered, thank you very much. May the Model be with you.

"If I have seen a little further it is by standing on the shoulders of Giants."

Sir Isaac Newton

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