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MICROARTHROPOD ECOLOGY AND ECOSYSTEM TYPES: LINKING ADAPTATION TO SOIL AND DIVERSITY OF COMMUNITIES TO ENVIRONMENTAL CONDITIONS IN DIFFERENT GEOGRAPHICAL LOCATIONS

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Everything is everywhere, but,
the environment selects

Baas Becking, 1934

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ABSTRACT

The soil community exhibit high variability in diversity, abundance and structure depending on ecosystems and climate. It is subjected to the integrity of the soil matrix, which constitute their habitat. It is directly involved in the ecosystem functions that constitute the basis for the services that soil provide. Land management often lead to soil degradation, which compromise soil community and ecosystem stability. Soil arthropods are key groups involved in ecosystem processes as decomposition but their role has been neglected in soil organic matter models until recently. Several research questions have been addressed: what are the effects of seasonal microarthropod diversity on ecosystem functions and soil food web stability? Section I focuses on how seasonal changes of arthropods induce changes on carbon cycling and soil food web stability in two beech forests. A modeling process based on the biomass of trophic groups (which includes bacteria, fungi and microarthropods), and environmental characteristics of each study area was implemented by using flow networks. Differences between forests were identified: the soil food web in the area with continental environmental characteristics responded to seasonality by increasing stability, while the soil food web in the area with Mediterranean environmental features increased the resistance and flowing material. Top-predators contributed to enhance the stability of the food webs, whereas fungi and bacteria represented the main groups controlling the cycling of carbon.

Sections II and III focus on the effects of local environmental characteristics on soil arthropods in semi-arid ecosystems. The ecological functioning of semi-arid areas is closely related to the distribution of vegetation, and water cycle. The diversity and functions of soil communities depend on resources and protection provided by vegetation. Pressure exerted by livestock often reduce the capacity of soils to provide their ecosystem functions due to degradation. The main research question was: what are the spatiotemporal patterns of soil arthropods depending on microsites characteristics, livestock pressure, and limiting factors?

Two similar sylvopastoral areas were studied. The first one (section II) is a farmland located in SW Spain. A photo interpretation analysis of an experimental catchment was developed to classify the intensity of livestock pressure. A total of 150 soil samples were collected, half in spring and the other half in autumn. Moreover, half of points were located beneath tree canopies and the other half in open spaces. Soil biological and physicochemical parameters were considered as drivers of arthropod richness, abundance, and adaptation to soil. Results showed higher abundance of arthropods and higher adaptation outside the influence of trees than beneath the tree canopies. Moreover, the classification of livestock pressure revealed

by the photo interpretation analysis showed low correlations with community structure, and with the occurrence of well-adapted arthropod groups.

The section III involved the study of arthropods under drought conditions, and how the community changed during a simulated soil rewetting process. Firstly, 9 points were located in a pasture meadow. A total of 24 sampling points were located in sylvopastoral areas (12 grazed and 12 ungrazed). Then, 40 L of water were added to each sampling point 3 days before the sampling to simulate the soil rewetting process. A spatial transposition of samples to one-dimension scale in reference to the nearest trees was used to track changes in abundance and richness of arthropods. Results elucidated that the response of edaphic arthropods to the rewetting of soils was different depending on the closeness to trees: higher abundance and richness were found away from the trees during the rewetting of soil. Conversely, such values were higher as the closeness to trees increased when soil was dry.

RIASSUNTO

La comunità del suolo è altamente variabile in diversità e abbondanza a seconda del tipo di ecosistema e clima. È coinvolta nella provvisione di funzioni ecosistemiche che costituiscono la base dei servizi forniti dal suolo. Le pratiche di gestione del suolo portano alla degradazione di esso compromettendo la comunità biotica e la stabilità dell'ecosistema. Gli artropodi del suolo sono coinvolti in processi ecosistemici come la decomposizione della materia organica, nonostante il suo ruolo è stato trascurato fino a tempi recenti. La domanda di ricerca è: quali sono gli effetti dei cambiamenti stagionali nella diversità degli artropodi sulle funzioni ecosistemiche e la stabilità delle reti trofiche del suolo? La sezione I si focalizza su come la variabilità in diversità degli artropodi provoca cambiamenti nei flussi di carbonio in due foreste degli Appennini Italiani (nord e sud). A questo scopo, sono state modellate delle reti trofiche quantitative bassate sulle biomasse dei diversi gruppi di organismi (batteri, funghi e microartropodi). Le differenze climatiche di entrambi posti (continentale nel nord, e mediterraneo nel sud) hanno indotto dei comportamenti antagonisti in base ai cambiamenti stagionali: a nord, la risposta della rete trofica è stata indirizzata sull'incremento della stabilità, mentre a sud si è verificato un incremento della resistenza della rete dovuta all'aumento dell'attività metabolica. Addizionalmente, i predatori contribuirono al miglioramento della stabilità in entrambe le foreste, mentre funghi e batteri costituirono i gruppi principali controllando il flusso di carbonio.

Le sezioni II e III si focalizzano sugli effetti delle caratteristiche ambientali locali sugli artropodi del suolo in sistemi semiaridi. Il funzionamento ecologico di queste aree è fortemente relato alla distribuzione della vegetazione e al ciclo idrologico. La diversità e funzioni ecosistemiche del suolo dipendono dalle risorse che la vegetazione provvede. La pressione esercitata dal bestiame riduce la capacità dei suoli di fornire servizi. La domanda di ricerca è: qual è la distribuzione spaziotemporale degli artropodi a seconda delle caratteristiche di ciascun sito, pressione del bestiame e fattori limitanti?

Due aree di studio con caratteristiche ambientali simili sono state studiate. La prima (sezione II) è stata individuata nel sudovest della Spagna. Un'analisi di fotointerpretazione in un bacino sperimentale è stata fatta per determinare la pressione del bestiame. In totale, sono stati individuati di 150 punti di campionamento suddivisi in primavera e autunno, e in base alla vicinanza agli alberi (sotto chioma e fuori chioma). Parametri biologici e chimico-fisici del suolo sono stati considerati come fattori incentivanti delle abbondanze, ricchezza e occorrenza di tratti morfologici sugli artropodi. I risultati mostrarono che maggiori

abbondanze e adattamento sono correlate con aree fuori chioma. La classificazione delle categorie di pressione del bestiame rilevata dall'analisi delle immagini di satellite mostrò una bassa relazione con i descrittori della comunità.

Lo studio degli artropodi sottoposti a siccità estrema e alla simulazione di un processo di umidificazione del terreno si presenta nella sezione III. L'area di studio è localizzata nell'area centrale del Cile. In totale, 33 campioni di suolo sono stati rilevati, e suddivisi in base alla pressione del bestiame fuori chioma e sotto chioma dell'albero. Per lo studio del processo di umidificazione, 40 L di acqua sono stati aggiunti a ciascun punto 3 giorni prima del campionamento. Per tracciare le variazioni di abbondanza e ricchezza della comunità si è sviluppata una trasposizione delle coordinate dei campioni a una dimensione basata sulla distanza dei campioni agli alberi. Valori più alti sono stati trovati lontani dagli alberi durante il processo di umidificazione. Invece, le abbondanze e ricchezze furono più alte vicino agli alberi quando il terreno era secco.

GENERAL INTRODUCTION

Thesis framework

Soils are essential sources of a wide diversity of ecosystem services defined as the goods and ecosystems functions that provide benefit to human populations (Millenium Ecosystem Assessment 2005; Lavelle et al. 2006). They support most agro-sylvo-pastoral production systems through the beneficial services that they mediate: soil formation, nutrient cycling and primary production (Lavelle et al. 2006). Soils are also involved in the regulation of climate by controlling the balance of carbon between the ground (i.e., carbon sequestration) and the atmosphere (i.e., greenhouse gasses exchange), water filtration, mineralization of nutrients, toxins elimination, and protection of plants against pests (Adhikari and Hartemink 2016). Such ecosystem services are the results of feedbacks between the aforementioned components and organic matter dynamics, as well as the soil physical properties (Lal 2004). In addition, those feedbacks are in general regulated by a wide range of organisms whose effects are still relatively poorly explored, especially for the smaller body-sized taxonomic groups (Lavelle et al. 2006).

One of the key component of such organisms are soil invertebrates, which are very diverse (Lavelle et al. 2006) and they are present at almost every ecosystem on Earth (Wu et al. 2011). Recent estimations indicate that soil animals represent the 23% of the total diversity of living organisms described (Decaëns et al. 2006; Lavelle et al. 2006). These facts, together with their dimensions make soil invertebrates the connection between the microscopic organisms such as bacteria, fungi and protozoa, and the macroscopic ones (i.e., macroarthropods, worms, snails and small mammals) through trophic interactions into the context of the soil food web, which at the same time, connects the below- and aboveground worlds (Bradford 2016).

Since soils are one of the most important reservoirs of biodiversity in the world (Lal 2004; Bardgett 2006; Jeffery et al. 2010; Wagg et al. 2014; Coleman and Wall 2015; Adhikari and Hartemink 2016), the soil living community is subjected to the integrity of the soil matrix, which constitute their habitat. Anthropogenic activities often lead to soil degradation and subsequently, to the depletion of the capacity of soils to provide ecosystem services. Such fact is due to the dependency of the soil living community to the physicochemical properties of soils, as well as the biotic interactions resulted from the coexistence of such large range

of organisms. Therefore, the loss of soil biodiversity is related to changes in ecosystem functions (Hooper et al. 2005; Cardinale et al. 2012). Most experiments have manipulated diversity or have assembled different diversities as a treatment variable and documented the response of ecosystem properties and processes, including modifying effects of environmental factors on such relationships (Naeem et al. 1994; Balvanera et al. 2006). In fact, the evidence suggest that initial losses of biodiversity have relatively small impacts on ecosystem functions, but increasing losses lead to accelerating rates of change in ecosystems (Cardinale et al. 2006, 2012). Together with this, the exposition to gradual changes in climate, habitat fragmentation, and unwise land management prompts to catastrophic shifts in ecosystems (i.e., contrasting stable state) that are often difficult restore (Scheffer et al. 2001).

Belowground biodiversity in the context of…

Ecosystem properties structuring soil communities

It is well-known that soil biodiversity is threatened by global anthropogenic changes, such as land-use intensification, deforestation, and nutrient eutrophication, which is cause for concern since biodiversity loss is a major driver of changes in ecosystem function (Yang et al. 2018). In addition, the soil community assembly is shaped by environmental factors, intrinsic population processes, and disturbance and recolonization events operating at different spatial and temporal scales (Chase and Leibold 2003; Soong and Nielsen 2016). In the meta community framework, dispersal, environmental filtering, and biotic interactions are in fact, all known to play a key role, although their relative importance is expected to vary depending on the system analyzed (Caruso et al. 2013). Nonetheless, soil is a continuous matrix formed by pedogenesis, which means that it follows spatial patterns in relation to the parent material, climate, relief, time, living organisms, and the influence of human factor. Into the context of soil formation process, the role of organisms is dependent on the physicochemical architecture of the soil, which offer a vast array of ecological niches to soil organisms (Wardle et al. 2003), and which imply highly fragmented distribution of populations (Bardgett and Van Der Putten 2014). Here it is where spatial autocorrelation becomes important in structuring soil communities (Legrende 1993; Caruso et al. 2012, 2013).

Spatiotemporal characteristics of soil communities

The global biogeography of soil biota is uncertain due to a lack of data on patterns of occurrence across the world (Bardgett and Van Der Putten 2014). Clear relationships

between latitude and species richness do not exist belowground as they do for many taxa aboveground (Bardgett and Van Der Putten 2014). However, for soil animals, the only clear pattern is that diversity is high along most of the latitudinal gradient, and that it drops towards the poles (Bardgett and Van Der Putten 2014). The spatial distribution of soil organisms depends widely on the scale at which they are investigated. At ecosystem, regional or continental scale, soil biota vary in relation to climate, topography and continental isolation (Bardgett and Van Der Putten 2014).

Terrestrial ecosystems are characterized by an irregular input of resources (i.e., seasonality), which are depleted with time, and to which consumer communities respond (Berg and Bengtsson 2007). Soil moisture and pH often show strong spatial patterns related to soil type and topography, but also as a result of the spatial distribution of precipitation and the extraction of water from the soil, that is affected by variation in the architecture of vegetation canopy. As a consequence, the distribution of many soil organisms exhibits temporal patterning (Berg and Bengtsson 2007).

The importance of the scale

Theoretical ecology, and theoretical science more generally, relate processes that occur on different scales of space, time, and organizational complexity. Understanding patterns in terms of the processes that produce them is the essence of science, and is the key to the development of principles for management. To scale from the species to the landscape to the ecosystem and beyond, it must be first understood how information is transferred from the fine scales to broad scales and vice versa. All ecological systems exhibit heterogeneity and patchiness on a broad range of scales, and this patchiness is fundamental to population dynamics, community organization and stability, and nutrient cycling, that are in fact transcendent at every scale. The diversity of organisms represents a balance between regional processes (e.g., dispersal), and local processes, such as biotic interactions and stochasticity. As it was aforementioned, species can subdivide the environment spatially, concentrating on different parts of the same plant, different layers of vegetation, or different microenvironments into the soil; or temporally, partitioning for example, a seasonal gradient. Because the variability and patchiness of the environment affects persistence and coexistence of species, it also affects species' evolutionary responses (extracted from Levin 1992). This suggests that there is no single correct scale or level at which to describe ecosystems, but the scale must be considered in order to determine what ecosystem process is dependent on one another and at what scale their effects become remarkable.

Studying the soil biota is challenging given the enormous differences in the size of different soil organisms, which range from 2 micrometers for bacteria to more than 10 cm for earthworms, and up to a hectare for some soil fungi (Bardgett and Van Der Putten 2014). Also, while microorganisms and some smaller fauna may be dispersed by wind, dispersal of larger-sized soil biota is limited by active movement, which is generally slow, ranging from 10-100 cm per year for nematodes to tens of meters per year for earthworms. On the basis of this scale-dependent perspective, several aims have been proposed on this thesis to study the local environmental characteristics that shape the soil microarthropod communities and their role on ecosystems.

Aims and sections

In this thesis I focus in soil arthropods that have no the capacity to create pores themselves, and thereby depend on existing pore space forming their microhabitat. The overall aim of this dissertation is to investigate the impact of anthropogenic management in different ecosystem types and climate regime on richness, abundance and functions of soil arthropods. The following research questions are addressed: (1) what are the effects of seasonal microarthropod diversity on ecosystem functions and soil food web stability? (2) what are the effects of local environmental characteristics filtering the spatiotemporal patterns of soil microarthropod community depending on livestock pressure, and limiting factors? (3) do spatiotemporal patterns of the soil microarthropod community change depending on the ecosystem type?

Based on the scientific consensus about the positive effects of biodiversity on ecosystem functioning (Hooper et al. 2005), the expectation presented in section I relies in the following factors: the effect of latitude, changes on seasonal diversity of microarthropods, and environmental characteristics of the two beech forests. These aspects are expected to shape the carbon flow and stability of the soil food web, and the relative importance of microarthropod groups. Furthermore, it is expected that the analysis on the dependency of metabolic rates of organisms and environmental factors will show different rates of ecosystem functions such as decomposition, which rates will be quantified by using flow networks. Finally, this section will be able to provide a holistic framework of the two forests ecosystems, and the feedbacks between the biodiversity of the soil food web and ecosystem functioning.

In section II, practices such as livestock management and landscape heterogeneity in semi-arid ecosystems under wet climatic conditions are considered to evaluate the dependency of

microarthropod community assembly on such factors. The structure of the soil habitat (i.e., physicochemical parameters) and biotic interactions are structuring forces of soil biota that depends on the scale (Bardgett 2006; Caruso et al. 2012a; Delgado-Baquerizo et al. 2019). Remote sensing techniques combined with field work, together with statistical modelling are used to disentangle the spatiotemporal patterns of abundance, richness and adaptation of microarthropod communities to the soil environment. The expectation relies in the fact that landscape heterogeneity will shape the adaptation and richness of soil microarthropod communities but the pressure of the livestock will have a stronger effect on taxa abundance.

In section III, a focus on the community variability under drought conditions, and then on the community structure after a simulated soil rewetting process depending on landscape heterogeneity, land use, and livestock pressure in semi-arid areas are considered. Grazing reduces organic inputs into the soil by decreasing litter cover, the soil surface's capacity to capture and store rainfall via surface disturbance and vegetation cover (Maestre et al. 2016), which negatively affect the soil arthropods since they depend on resources and protection provided by plants (Coleman et al. 2005; Meloni et al. 2020). Field work experiments, and statistical modelling combined with spatial analysis are the techniques that have been used in this section. A strong effect of soil water as limiting factor on the arthropod community development was expected. Grazed, ungrazed, and low-intense grazed areas were considered to study the effect of the livestock component and the closeness to vascular plants. The expectation was that the closeness to trees may have a positive effect on organisms' populations both in grazed and ungrazed areas.

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Section I

Soil microarthropod diversity and ecosystem functioning in semi-natural systems: An ecological network perspective on trophic groups, keystone groups and carbon dynamics in beech forests

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Abstract

The quantification of energy fluxes in food webs represents a universal tool for the understanding of relationships between biodiversity and functioning of multitrophic ecosystems. Since the soil food web shows high complexity, the study of single processes or groups of organisms often depicts a partial illustration about the functioning of ecosystems. In such terms, ecological network models are helpful to study how changes in diversity of soil communities and stocks of critical nutrients influence ecosystem processes that depends on abiotic factors through different ecological scales. Soil arthropods are known to be key groups in ecosystem processes as decomposition. Their communities show high spatiotemporal variation, which is leaded by the availability of resources present in the soil habitat. The present section focuses on how seasonal changes of soil arthropod diversity are reflected on the carbon cycling and soil food web stability in two beech forests of the Italian Apennines at different latitude. In addition, the role of arthropod trophic groups was described in relation to carbon cycle in order to identify key groups on the ecosystems under investigation. A modeling process based on the biomass of trophic groups (which includes bacteria, fungi and microarthropods), and environmental characteristics of each study area was implemented by the use of the Ecological Network Analysis routine. Differences between forests and seasons were identified: the soil food web in the area with continental environmental characteristics responded to seasonality by increasing stability, while the soil food web in the area with Mediterranean environmental features increased the resistance by losing biodiversity but also increasing the flowing material. In addition, top-predators contributed to enhance the stability of the food webs, whereas fungi and bacteria represented the main groups controlling the cycling of carbon. On the light of these results, it was inferred that both ecosystems showed antagonistic responses to seasonality. Moreover, it was verified that both bottom-up and top-down trophic forces act in soil food web at the same time due to the high redundancy of these systems.

Keywords: Soil biodiversity; carbon cycling; Ecological Network Analysis; ecosystem functioning; microarthropods.

I-1. Introduction

Forests cover about 30% of Earth's surface and play key ecosystem functions including the regulation of the global carbon cycle (Lal 2004; Fioretto et al. 2018). Given that forest carbon is stored in living plant biomass and necromass, the balance between net primary productivity and detrital decomposition affects the accumulation of soil organic matter, which is mostly composed by carbon (Innangi et al. 2015b; De Marco et al. 2016a). Soil organic matter is highly influenced by the biodiversity of the soil community as well as abiotic factors such as substrate characteristics, litter quality, and climate (García-Palacios et al. 2013; Innangi et al. 2015b; De Marco et al. 2016a; Fioretto et al. 2018). However, the influence of the biodiversity of soil mesofauna communities on such ecosystem processes have been neglected until recently (Soong and Nielsen 2016).

There is unequivocal evidence that biodiversity influences the efficiency by which soil communities capture biologically essential resources, convert those resources into biomass, and decompose and recycle biologically essential nutrients (Hooper et al. 2005; Cardinale et al. 2012; Barnes et al. 2018). Indeed, research on soil biodiversity has highlighted the dependency between trophic interactions among the soil community and the availability and quality of plant-derived soil organic matter resources (De Ruiter et al. 1998; Andrés et al. 2016). For instance, total resource capture and biomass production are generally more stable in more diverse communities (Cardinale et al. 2012), while litter quality can be a driving factor for the different phases of the decomposition process in field (García-Palacios et al. 2013; Innangi et al. 2015b). However, quantitative estimates of the level of biodiversity at which change in ecosystem functions such as decomposition become significant are still lacking (Cardinale et al. 2012).

For the study of such aspects of ecosystem functioning, soil food web models are helpful to understand the effect of environmental conditions on soil communities as they influence assimilation efficiency and respiratory rates of the organisms involved (Lang et al. 2017), as well as the effects of seasonal changes in biodiversity on the distribution of carbon fluxes and ecosystem functions such as decomposition, carbon sequestration, and nutrient translocation (Barnes et al. 2018). In addition, soil food web models are capable to respond how changes in the availability of different nutrients influences the structure of ecosystems (Hillebrand et al. 2014; Trap et al. 2016), the distribution of biomass across populations (Ott et al. 2014), and the rate of energy flux to consumers (Jochum et al. 2017; Barnes et al. 2018). In such terms, Ecological Network Analysis (ENA) allows modelling matter

circulation in ecosystems by keeping track of trophic groups interactions (Ulanowicz 1986, 2004). It depicts ecosystems as composed of compartments (i.e., species, aggregates of species, nutrient pools, etc.), which exchange energy/matter, display losses (i.e., respiration/dissipations) and may be linked to systems outside the boundaries of the area under investigation (e.g., through gross primary production and migrations). ENA includes routines to define the trophic status of the food web, determine the number and magnitude of cycles, and characterize the status of the entire ecosystem (Tobor-Kapłon et al. 2007; Ulanowicz 1986, 2004). In addition, it quantifies some dimensions of functioning and represents a promising tool to investigate their dependence on biodiversity.

This study has been developed in two beech forests from the Italian Apennines. Beech forests are among the most important ones in Europe, growing in a wide range of site conditions extending from humid to semiarid climates and from alkaline to acidic soils (Baldrian et al. 2013; Fioretto et al. 2018). Their soils contain an extensive carbon stock that is predicted to decrease sharply under climate change scenarios (Innangi et al. 2015a; Fioretto et al. 2018). In Italy, beech forests are found at 900-1900 m altitude and are distributed from the Alps to Sicily across two biogeographical regions, the Central-European and the Mediterranean, separated by a boundary running along the Apennines from Northern Liguria to Southern Emilia-Romagna (Pignatti 1979; De Marco et al. 2016).

I-2. Aims

In this section, previously published data (Innangi et al. 2015b; De Marco et al. 2016; Fioretto et al. 2018) have been used along with new data to model a portion of the detrital food web (soil bacteria, fungi and microarthropods) and to investigate whether changes in seasonal microarthropod diversity have effects on carbon cycling and soil food web stability in two beech forest in the Italian Apennines with slightly different environmental characteristics. A holistic ecological framework of both forests was drawn by means of ecological network models, with a focus on the capacity of both systems to develop their ecosystem functions and their dependency on biodiversity of soil mesofauna. For each site, two seasons (spring and fall) were considered. First, the influence of changes in abundance, diversity and composition of microarthropod community on the soil food web stability was investigated. Second, the study on whether carbon circulation at different latitudes changes with seasons depending on trophic group diversity and biomass was determined. Finally, the role of each trophic group with respect to carbon circulation was described.

I-3. Materials and methods

I-3.1. Study area

The study was carried out in two beech forests in the Italian Apennines (Figure I-3-1). The two beech forests from this study have already been used as study areas in three publications. The first one investigated litter decomposition dynamics under field and laboratory conditions (Innangi et al. 2015b). Carbon stock in forest floor and mineral soil was studied by De Marco et al. (2016). The last study dealt with the effects of substrate chemical composition and season on extracellular enzyme activities (Fioretto et al. 2018). This manuscript will partly use the same data base that was published in the aforementioned publications along with new data. All data was collected in a unique sampling survey. An exhaustive description of sites can be found in Innangi et al. 2015, De Marco et al. 2016, and Fioretto et al. 2018. Sites are covered by 75-year-old coppiced beech trees (*Fagus sylvatica* L.) and had been never affected by fire, grazing or clear-cutting (De Marco et al. 2016a). The first site is the Biogenetic Natural Reserve "Guadine Pradaccio" near Parma (Emilia-Romagna region), located within the limits of the National Park "Appennino Tosco-Emiliano" (northern forest, NF). Second site is in the surroundings of lake Laceno near Bagnoli Irpino (Campania region), within the limits of Monti Picentini Regional Park (southern forest, SF). The main characteristics of the study sites are reported in **Table I-3-1**.

***Table I-3-1**: Main characteristics of beech forests in a northern (NF) and a southern (SF) site of Italian Apennines. Values for soil and litter parameters, as well as forest features are means ± SE (n = 36). Meteorological parameters have been gathered for the observation period 2008-2013 from the Meteorological Station of Lagdei (NF) and Meteorological Station of Piano Laceno (SF) located at 1256 m and 1110 m.a.s.l., respectively (modified from De Marco et al. 2016).*

Parameter	Units	NF	SF
Latitude/Longitude		43˚23'N; 10˚01'E	40˚48'N; 15˚07'E
Elevation	m.a.s.l.	1350	1150
Mean annual temperature (MAT)	°C	6.0	8.7
Mean temperature of the warmest month (TM)	°C	15.4	17.4
Mean temperature of the coldest month (Tm)	°C	-2.7	0.3
Annual precipitation (P)	mm	2900	2300
Maximum monthly precipitation (PM)	mm	415	430
Minimum monthly precipitation (Pm)	mm	42	31
Soil type		Lithic Haploborolls	Humic Haplustands
Soil Parental Substrate		Arenaceous, Lithological formation: Macigno	Calcareous covered by pyroclastic material
Slope	degrees	13.98	12.13
Tree density	trees ha^{-1}	1100±55	800±40
Diameter at breast height*	cm	25.4±1.3	34.4±2.2
Basal area	$m^2 ha^{-1}$	55.7	74.3
Litter input	Kg ha^{-1}	2,497±175	4,313±430
Litter stock	Kg ha^{-1}	23,887±212	21,188±269
Litter pH (H_2O)		5.82±0.10	6.18±0.03
Litter organic matter	mg g^{-1} dw	515.2±4.6	639.9±6.8
Soil water content (0-15 cm depth)	%	72.4±10.7	78.2±2.6
Soil bulk density (0-5 cm depth)	g cm^{-3}	1.06±0.06	0.99±0.05
Soil organic matter content (0-15 cm depth)	%	20.2±1.0	22.8±1.2
Soil pH (H_2O)		3.9±0.1	5.6±0.1

* In each forest, tree diameter at breast height and basal area were measured on the trees standing in 10 plots of 100 m^2 each.

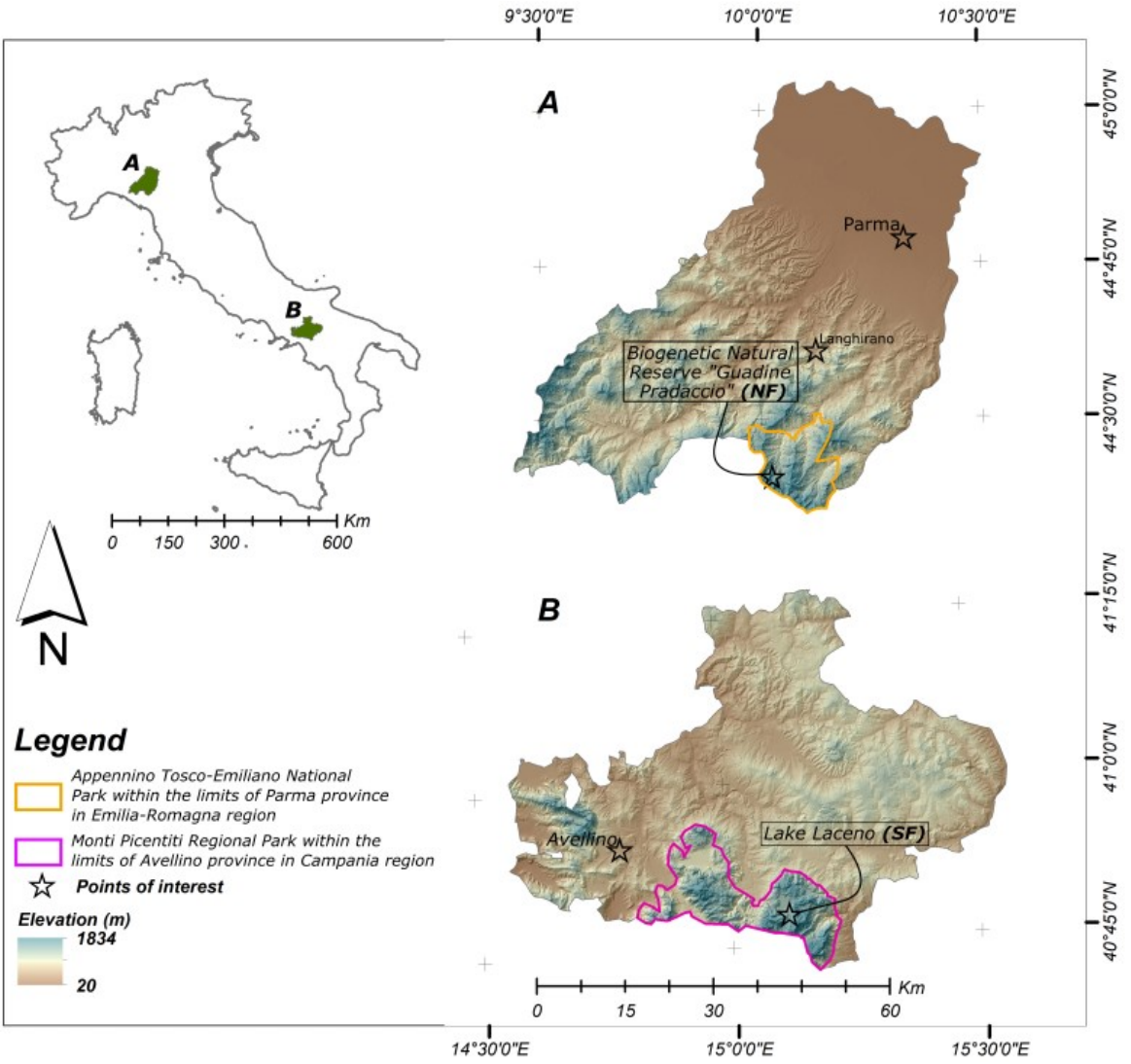

Figure I-3-1: Study areas in the Italian Apennines. (A) The Biogenetic Natural Reserve "Guadine-Pradaccio" (northern forest, NF) in the National Park "Appennino Tosco-Emiliano" (Parma Province, Emilia-Romagna Region). (B) Surroundings of lake Laceno (southern forest, SF) in the Regional Natural Reserve "Monti Picentini" (Avellino Province, Campania Region).

I-3.2. Data

Both sites were sampled simultaneously. The first sampling was carried out in October 2010 (NFA and SFA indicate northern and southern forest in autumn 2010, respectively) and the second in June 2011 (NFS and SFS stand for northern and southern forest in spring 2011, respectively). The data used in this work were gathered from Innangi et al. 2015, De Marco et al. 2016, and Fioretto et al. 2018, and included microbial and fungal biomass, as well as soil and litter parameters. Details about sampling and laboratory analyses can be consulted in the aforementioned works.

New data include soil microarthropod community that was determined in both sites at the same periods. For the characterization of this community, six soil cores (20 × 20 × 20 cm)

at each site and season were sampled following the experimental design of the previously cited works. Then, they were taken to the laboratory for the extraction of organisms. The extraction time lasted 10 days. It was carried out using Berlese-Tullgren funnels (2 mm mesh size) and the organisms were conserved into a solution of 70% ethanol. The extracted microarthropods were identified and counted using a binocular stereomicroscope (40×) Leica M3C. Table I-3-2 shows seasonal abundance of microarthropods per m^2.

Table I-3-2: Means ± SE (n = 24) of microarthropods per square meter collected in each beech forest.

Group	NFA	NFS	SFA	SFS
Acari	5605 ± 1412	6200 ± 1532	3107 ± 261	1932 ± 370
Araneae	21 ± 7	32 ± 11	35 ± 22	- ± -
Pseudoscorpionida	21 ± 7	42 ± 13	64 ± 16	51 ± 20
Isopoda	- ± -	- ± -	21 ± 7	32 ± 9
Diplopoda	42 ± 10	21 ± 7	28 ± 4	34 ± 7
Chilopoda	177 ± 44	42 ± 24	81 ± 24	42 ± 19
Pauropoda	117 ± 28	178 ± 31	- ± -	- ± -
Symphyla	945 ± 303	2067 ± 306	535 ± 66	331 ± 64
Collembola	2484 ± 854	1451 ± 841	1207 ± 374	1787 ± 332
Protura	115 ± 27	21 ± 7	297 ± 74	42 ± 10
Diplura	340 ± 126	42 ± 209	85 ± 43	- ± -
Psocoptera	421 ± 292	42 ± 293	81 ± 300	35 ± 20
Hemiptera	42 ± 10			
Thysanoptera	21 ± 7	42 ± 10	26 ± 7	43 ± 12
Coleoptera				
Adults	152 ± 23	283 ± 31	47 ± 30	89 ± 12
Larvae	446 ± 50	432 ± 68	177 ± 61	92 ± 31
Formicidae	- ± -	38 ± 11	42 ± 13	26 ± 8
Diptera				
Larvae	350 ± 66	149 ± 73	163 ± 54	117 ± 31

I-3.3. Network construction

A flow network answers two major questions: (1) who eats whom? and (2) at what rate? Ecosystems are depicted as graphs, with compartments connected by directional arrows that portray energy/matter flows (e.g., prey-predator interactions). The standing stock biomasses of compartments are expressed here as g C m^{-2}. Square matrices describe the graphs by summarizing all flows from compartments in the rows to those in the columns. Three vectors report exchanges that transgress the boundaries of the system (i.e., gross primary production and immigration are imports, exports record emigration, and respiration/dissipations represent the losses). In this case, all fluxes are measured as g C m^{-2} y^{-1}. This section describes interaction matrices and network construction, decisions about the grouping of taxa, and the calculations made to estimate the metabolic parameters.

Fungal and microbial biomasses were lumped together to form a single group (microbial loop) and then simplify the construction of the networks and to reduce eventual errors linked to the estimation of physiological parameters. The other trophic groups were defined starting

from the taxonomic classification used for microarthropods (Table I-3-2) since there was not a better subdivision in functional groups (i.e., myco-heterotrophs collembolans, saprophagous mites, etc.). Such bias was solved considering all feeding preferences of each taxon in proportion to the availability of prey (i.e., biomass). Organic matter pools were split in two compartments: litter (i.e., fresh organic matter from the forest floor) and detritus (i.e., the entire organic matter pool in the mineral soil). They represent the non-living compartments, whereas all microarthropods and the microbial loop are living compartments. The biomass of the trophic groups was calculated from the number of individuals for microarthropods, from the biomass per gram of soil and litter in the case of the microbial loop, and from the organic matter concentration in soil and litter for the non-living compartments. Since the standard units in network analysis are grams of carbon per square meter, the data were transformed for dimensional consistency (see section I-3.4 for details). Predator-prey relationships and feeding preferences were identified using the literature (Burges et al. 1967; Wallwork 1970; Curry 1994; Killham 1994; Coleman, Crossleu, and Hendrix 2005; Menta 2008; Menta and Remelli 2020). Litter and detritus provide carbon to the various living compartments and receive carbon either from trophic groups in the system (e.g., dead organic material and feces) or in the form of inputs from outside (e.g., litter during the fall). Then, the whole of interactions composed the adjacency matrix (Figure I-3-2).

Figure I-3-2: Adjacency matrix. Here, there are represented all the trophic interactions among every compartment considered in each network model. A value of "1" shows a prey-predator interaction from the row to the column compartments; or intraguild predation if the value is on the diagonal of the matrix. "Zero" value shows an absence of interactions. Asterisks represents non-living compartments. Z represents the import of assimilable matter to the system from the outside, EX represents the exports of assimilable matter from the system to the outside, and R represents the flow of non-assimilable matter from the system to the outside.

	Z	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}	{15}	{16}	{17}	{18}	{19}	{20}*	{21}*	*EX*	*R*
Z	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
{1}	0	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
{2}	0	0	1	1	1	0	0	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0
{3}	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
{4}	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
{5}	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
{6}	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
{7}	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
{8}	0	0	1	1	1	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0
{9}	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0
{10}	0	0	1	1	1	0	0	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0
{11}	0	0	1	1	1	0	0	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0
{12}	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
{13}	0	0	1	1	1	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0
{14}	0	0	1	1	1	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0
{15}	0	0	1	1	1	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0
{16}	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
{17}	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
{18}	0	0	1	1	1	0	0	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0
{19}	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0
{20}*	0	1	1	0	0	1	1	0	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0
{21}*	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0
EX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

{1} MICROBIAL LOOP
{2} ACARI
{3} ARANEAE
{4} PSEUDOSCORPIONES
{5} ISOPODA
{6} DIPLOPODA
{7} CHILOPODA
{8} PAUROPODA
{9} SYMPHYLA
{10} COLLEMBOLA
{11} PROTURA
{12} DIPLURA
{13} PSOCOPTERA
{14} HEMIPTERA
{15} THYSANOPTERA
{16} COLEOPTERA (*adults*)
{17} FORMICIDAE (*adults*)
{18} DIPTERA (*larvae*)
{19} COLEOPTERA (*larvae*)
{20} LITTER* (non-living)
{21} DETRITUS* (non-living)

I-3.4. Standing stock calculations

Values extracted from Innangi *et al.*, 2015, De Marco *et al.*, 2016, and Fioretto *et al.*, 2018 were expressed in terms of biomasses by area (units in g C m^{-2}) and energy flows (g C m^{-2} y^{-1}) as required by the Ecological Network Analysis methodology (Ulanowicz 1986; Fath and Patten 1998). The term "compartment" is often used in reference to the nodes of the networks represented by trophic groups (Ulanowicz 1986; Fath and Patten 1998). Equations and conversion factors were used to transform raw values to units required by ENA (i.e., g C m^{-2} for biomass and g C m^{-2} y^{-1} for flows) (see Table I-3-3). In addition, conversion factors relative to microarthropod compartments, as well as values gathered from the literature useful to calculate microarthropod biomass and C stocks are also reported in that table.

Table I-3-3: Equations used to convert parameters gathered from Innangi et al., 2015, De Marco et al., 2016, and Fioretto et al., 2018 into units required by ENA.

Parameter	Equation	Number
Litter stock	$\frac{g\ C}{m^2} = \frac{kg}{ha} \times \frac{10^3 g\ litter}{kg\ litter} \times \frac{(1 - litter\ water\ content)}{g\ litter} \times \frac{g\ C}{g\ litter\ dw} \times \frac{ha}{10^4 m^2}$	{1}
Litter input	$\frac{g\ C}{m^2\ year} = \frac{kg}{ha} \times \frac{10^3 g\ litter}{kg\ litter} \times \frac{(1 - litter\ water\ content)}{g\ litter} \times \frac{g\ C}{g\ dry\ litter} \times \frac{ha}{10^4 m^2}$	{2}
Detritus stock	$\frac{g\ C}{m^2} = \frac{g\ OM}{g\ soil\ dw} \times \frac{g\ Soil\ dw}{(g\ Soil\ dw + soil\ water\ content)} \times \frac{g\ soil}{cm^3} \times \frac{0.58^* g\ C}{g\ OM} \times \frac{10^4 cm^3}{m^2}$	{3}
Litter microbial biomass (mean value for OL+OF+OH layers)	$\frac{g\ C}{m^2} = \frac{mg\ C}{g\ litter\ dw} \times \frac{g\ C}{10^3\ mg\ C} \times \frac{g\ litter\ dw}{(g\ litter\ dw + litter\ water\ content)} \times \frac{10^{-3}\ kg\ fresh\ litter}{ha} \times \frac{ha}{10^4 m^2}$	{4}
Litter active fungal mycelium (AFM) (mean value for OL+OF+OH layers)	$\frac{g\ C}{m^2} = \frac{mg\ C\ AFM}{g\ litter\ dw} \times \frac{g\ C}{10^3\ mg\ C} \times \frac{g\ litter\ dw}{(g\ litter\ dw + litter\ water\ content)} \times \frac{10^{-3}\ kg\ fresh\ litter}{ha} \times \frac{ha}{10^4 m^2}$	{5}
Litter total fungal mycelium (ATM) (mean value for OL+OF+OH layers)	$\frac{g\ C}{m^2} = \frac{mg\ C\ ATM}{g\ litter\ dw} \times \frac{g\ C}{10^3\ mg\ C} \times \frac{g\ litter\ dw}{(g\ litter\ dw + litter\ water\ content)} \times \frac{10^{-3}\ kg\ fresh\ litter}{ha} \times \frac{ha}{10^4 m^2}$	{6}
Soil microbial biomass (mean value for 0-15 cm depth)	$\frac{g\ C}{m^2} = \frac{mg\ C}{g\ soil\ dw} \times \frac{g\ C}{10^3\ mg\ C} \times \frac{g\ soil\ dw}{(g\ soil\ dw + soil\ water\ content)} \times \frac{g\ soil}{cm^3} \times \frac{10^4 cm^3}{m^2}$	{7}
Soil active fungal mycelium (AFM) (mean value for 0-15 cm depth)	$\frac{g\ C}{m^2} = \frac{mg\ AFM\ C}{g\ soil\ dw} \times \frac{g\ C}{10^3\ mg\ C} \times \frac{g\ soil\ dw}{(g\ soil\ dw + soil\ water\ content)} \times \frac{g\ soil}{cm^3} \times \frac{10^4 cm^3}{m^2}$	{8}
Soil total fungal mycelium (ATM) (mean value for 0-15 cm depth)	$\frac{g\ C}{m^2} = \frac{mg\ ATM\ C}{g\ soil\ dw} \times \frac{g\ C}{10^3\ mg\ C} \times \frac{g\ soil\ dw}{(g\ soil\ dw + soil\ water\ content)} \times \frac{g\ soil}{cm^3} \times \frac{10^4 cm^3}{m^2}$	{9}
Microbial loop stock	$\frac{g\ C}{m^2} = Litter\ microbial\ biomass + litter\ active\ and\ total\ fungal\ biomass + soil\ microbial\ biomass + soil\ active\ and\ total\ fungal\ biomass$	{10}
Microarthropods biomasses	$\frac{g\ C}{m^2} = \frac{individuals}{m^2} \times \frac{g\ dw}{individual} \times \frac{0.446^{**}\ g\ C}{g\ dw}$	{11}

* Carbon content in organic matter (Périé and Ouimet 2008)

** Average carbon content on arthropods (Bowen 1966; Pokarzhevskii et al. 2003)

I-3.5. Estimation of metabolic parameters

The carbon budget of the living compartments responds to the general metabolism equation:

$$I = P + R + E \quad [12]$$

where I is the consumption or total intake, which can be partitioned in production (P), respiration (R) and excretion (E). Consumption and production were quantified for each trophic group by considering standing stock biomass (B), the appropriate conversion factors (e.g., I/B and P/B ratios), the mean temperature during the month of sampling, and the body mass.

Microarthropod compartments

Mean temperature and mean body mass were considered to estimate the assimilation efficiency and respiration rate of each trophic group (see eq. 13), which were calculated according to temperature-body mass dependent regressions for carnivores, herbivores and detritivores (Lang et al. 2017). The assimilation efficiency was computed using the following logistic model:

$$\varepsilon = \frac{e^{\varepsilon_{0,J}} e^{E_{\varepsilon,j}\frac{(T-T_0)}{kTT_0}} m^{a_{\varepsilon,j}}}{1+e^{\varepsilon_{0,J}} e^{E_{\varepsilon,j}\frac{(T-T_0)}{kTT_0}} m^{a_{\varepsilon,j}}} \quad [13]$$

where ε is the assimilation efficiency, ε_0' the normalization constant of the assimilation efficiency, E_ε the activation energy for assimilation efficiency (eV), T the environmental temperature (K), T_0 the temperature normalized to 20°C (293.15 K), k the Boltzmann's constant (8.62×10^{-5} eV K^{-1}), m the body mass (g) and a_ε the allometric exponent for assimilation efficiency. The subscript j refers to the different consumer types.

The effect of temperature and body mass on respiration rates was calculated using the following equation:

$$Rr = Rr_{0\_j} e^{E_{Rr\_j}\frac{(T-T_0)}{kTT_0}} m^{a_{Rr\_j}} \quad [14]$$

where Rr is the respiration rate, Rr_0 is the normalization constant, E_{Rr} the activation energy for respiration (eV), a_{Rr} the allometric exponent for respiration and all other variables are as described above.

A systematic procedure enabled estimating for each trophic group the physiological parameters needed in eq. 13 and 14. A primary source to estimate the fresh body mass of individuals was the database of Lang et al. (2017), which contains information about body mass, temperature and assimilation efficiency in relation to arthropod taxa and feeding habits. Data from Sohlström et al. (2018), which provide information about body mass, weight, length and width in relation to arthropod taxonomical orders and suborders, were also used to estimate the body mass of individuals. In addition, values about dry weight per individual reported on Reichle, (1977) where useful to complete the lacking taxa in the aforementioned databases. Mean temperatures of the sampling months and values gathered form the literature cited above are reported in Table I-3-4 and in Table I-3-5, respectively. The individual body mass was multiplied by the abundance of individuals in each trophic group to calculate the standing stock biomass of the compartments. The assimilation efficiencies were computed based on feeding habits of the organisms (detritivores, herbivores and carnivores) and mean monthly temperatures during samplings (eq. 13). The respiration rates were calculated taking into account the mean temperature during the month of sampling (eq. 14). Production (*P*) and consumption (*I*) were obtained using the relationships with the biomass presented by Curry (1986) and Reichle (1977). The production (*P*) was calculated as the difference between the assimilation efficiency and the respiration rate. The assimilated energy (*As*) was obtained as the sum of (*P*) and respiration (*R*). The consumption (*I*) was defined as the ratio between assimilation efficiency and assimilated energy, and the excretion (*E*) as the difference between *I* and assimilated energy.

Table I-3-4: Average temperatures used for metabolic parameters estimation of living compartments.

Site/month	**Value**
Northern forest	
October (2006-2010)	4.57 ± 1.12
June (2007-2011)	12.59 ± 0.73
Southern forest	
October (2006-2010)	8.77 ± 0.67
June (2007-2011)	11.46 ± 0.51

Table I-3-5: Parameters gathered from the literature that were used to estimate the metabolism of microarthropods groups.

Trophic group	Feeding habit	Dry weight per individual (g) (Reichle 1977)	Dry weight per individual (g) (Lang et al. 2017)	Live mass per individual (mg) (Sohlström et al. 2018)
Acari	Detritivore	0.141	0.005	1.990*
Araneae	Carnivore	0.063	0.005	0.880
Pseudoscorpionida	Carnivore	0.413	0.005	0.5825
Isopoda	Herbivore	-	-	2.68
Diplopoda	Herbivore	0.110	0.004	6.54**
Chilopoda	Carnivore	0.690	0.043	2.51
Pauropoda	Detritivore	0.006	0.016	-
Symphyla	Detritivore	0.089	0.016	0.01; 1.7
Collembola	Detritivore	0.045	0.027; 0.00009⸸	-
Protura	Herbivore	0.003	0.027; 0.00009⸸	-
Diplura	Carnivore	0.081	0.027; 0.00009⸸	-
Psocoptera	Herbivore	0.068	0.027; 0.00009⸸	0.45
Hemiptera	Herbivore	-	0.027; 0.00009⸸	1.523
Thysanoptera	Herbivore	-	0.027; 0.00009⸸	1.33
Formicidae	Detritivore	-	-	1.205
Coleoptera	Detritivore	-	0.027; 0.00009⸸	5.535
Diptera.L	Detritivore	-	-	1.736
Coleoptera.L	Detritivore	-	-	4.006

* Value for Opiliones
** Value for Glomerida
⸸ Minimum weight for the class Insecta

Microbial loop

The estimation of metabolic parameters used for the microbial loop was slightly different from the procedure adopted for the microarthropods. Information on the average wet and dry weight (in grams) of cells, as well as carbon/biomass ratio, average cell density (g ml^{-1}) (Curtis et al 1975), average cell size (in μm^3), (Price and Sowers 2004), and cell dry matter (Bratbak and Dundas 1984) were gathered from the literature and used to calculate the fresh biomass of microbial loop (Table I-3-6). The Arrhenius equation (eq. 15) was used to obtain the average assimilation and respiratory rates (mmol day^{-1}) of cells in relation to the mean temperature of the sampling month:

$$v(t) = Ae\ e^{\left(\frac{-E_a}{RT}\right)} \quad [15]$$

where, *Ae* is the frequency factor, which is the value of *v(t)* when $T = 273.15$ ˚K, E_a is the activation energy of bacteria (kilojoules mol^{-1}), R is the gas constant (8.31 J/K mol), and T is the temperature measured on the Kelvin scale. The respiration was calculated as the 42% of the assimilation (*As*), and the consumption by the ratio *As*/*I*, which is equal to 1 (de Ruiter 1993; Moore et al 1996; Moore et al 2005; Holtkamp et al 2011; de Vries et al 2013; Berg et al 2001). The standing stock of microbial loop (g C m^{-2}) obtained using the equations 4-10 for each site and season was multiplied by C/B ratio (Table I-3-6) in order to obtain the

dry weight of microbial loop by square meter. Then, this value was converted into microbial wet weight using the cell dry matter in Table I-3-6. The next step was to calculate the number of cells by square meter. To this aim, cell size and cell dry weight values (Table I-3-6) were used. Then, the Arrhenius equation was used to estimate the respiration rate of all these cells based on the average temperature of the sampling month. To this aim, it was necessary to firstly calculate the frequency factor (*Ae*) from the Arrhenius equation (**Error! Reference source not found.**), which is the value of the rate when the temperature equals to 273.15 K. This value is defined as follows:

$$Ae = e^{-\left(\frac{Ea}{RT}\right)} \quad \{16\}$$

where parameters are the same than in eq. 15.

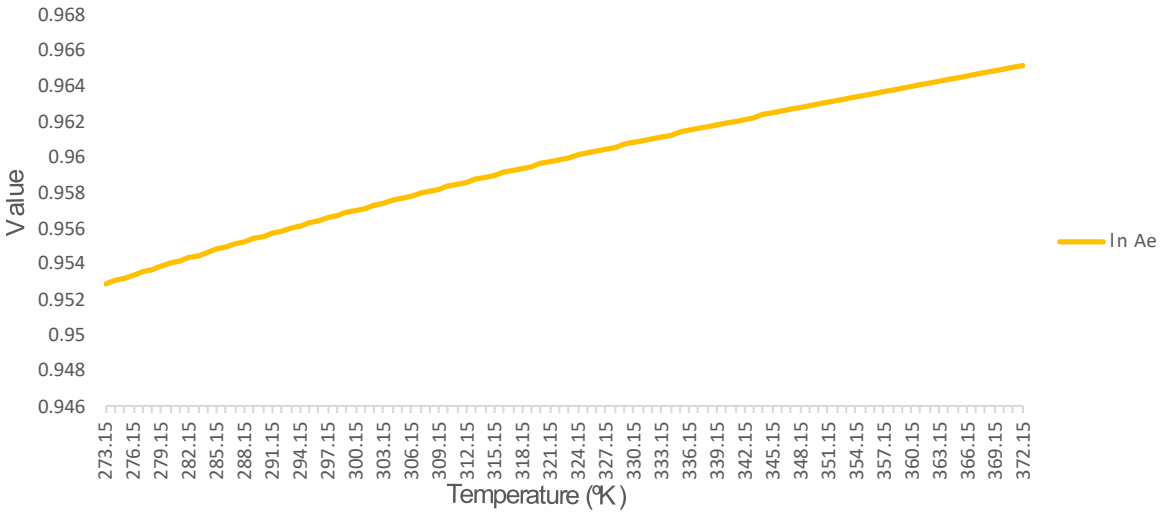

Figure I-3-3: The frequency factor (Ae) function for the microbial loop compartment.

Once *Ae* was obtained, Arrhenius equation was used to determine the respiration rate of cells in mmol cell^{-1} day^{-1}. Then, the rate was converted into g C m^{-2} y^{-1} and subsequently obtained consumption and production rates by using assimilation efficiency and production efficiency ratios.

Table I-3-6: Parameters gathered from the literature that were used to estimate the metabolism of microbial loop.

Parameter	Value	Units	Reference
Cell size	0.0830	μm^3	(Price and Sowers 2004)
Activation energy	110.0	kJ mol^{-1}	(Price and Sowers 2004)
Carbon/B ratio	48.5	% of dry weight	(Bowen 1966)
Cell dry weight	$1 \cdot 10^{-11}$	g	(Curtis *et al.*, 1975; averaged from Bratbak and Dundas, 1984)
Cell density	$7.364 \cdot 10^{-27}$	g mL^{-1}	(Price and Sowers 2004)
Cell dry matter	43.77	%	(averaged from Bratbak and Dundas, 1984)
Carbon in dry cells	47.63	%	(averaged from Bratbak and Dundas, 1984)
Microbial assimilation efficiency	1.0	-	(Ruiter et al. 1993; Berg et al. 2001; Holtkamp et al. 2011; De Vries et al. 2013)
Microbial production efficiency	0.3; 0.4; 0.44; 0.51	%	(Ruiter et al. 1993; Berg et al. 2001; Holtkamp et al. 2011; De Vries et al. 2013)

The next step was to calculate the total flow of metabolic parameters from eq. 12 in relation to the standing stock of each compartment. The results of these calculations are reported in Table I-3-7.

Table I-3-7: Calculated values of the biomasses (B) and metabolic parameters consumption (I), respiration (R), production (P), and excretion (E). Stocks are expressed in g C m^{-2} and fluxes in g C m^{-2} y^{-1}.

Trophic groups	**NFA**					**NFS**					**SFA**					**SFS**				
	B	***I***	***R***	***P***	***E***	***B***	***I***	***R***	***P***	***E***	***B***	***I***	***R***	***P***	***E***	***B***	***I***	***R***	***P***	***E***
Microbial loop	13.0	218.2	153.6	64.52	-	17.32	219.8	154.8	65.01	-	8.223	215.2	151.5	63.65	-	12.98	217.9	153.5	64.47	-
Acari	0.353	165.5	53.86	53.22	58.43	0.391	328.6	115.3	114.5	98.77	0.195	173.8	49.85	49.28	74.69	0.121	183.8	46.74	46.23	90.86
Araneae	0.014	38.72	5.948	5.648	27.12	0.020	77.22	15.66	15.26	46.29	0.023	77.40	11.74	11.44	54.22	-	-	-	-	-
Pseudoscorpionida	0.015	39.09	6.134	5.828	27.13	0.029	85.21	19.66	19.20	46.34	0.044	70.71	18.07	17.57	35.06	0.035	82.44	20.10	19.62	42.72
Isopoda	-	-	-	-	-	-	-	-	-	-	0.006	59.56	4.773	4.615	50.17	0.009	77.35	8.158	7.949	61.24
Diplopoda	0.216	115.9	38.48	37.82	39.58	0.107	162.1	47.92	47.33	66.86	0.143	130.8	40.39	39.78	50.62	0.173	180.1	59.53	58.88	61.69
Chilopoda	0.383	70.29	21.73	21.12	27.43	0.091	78.67	16.38	15.97	46.30	0.176	70.01	17.72	17.22	35.05	0.091	71.61	14.68	14.28	42.64
Pauropoda	0.039	81.79	11.99	11.70	58.08	0.059	161.9	31.96	31.56	98.46	-	-	-	-	-	-	-	-	-	-
Symphyla	0.090	100.2	21.21	20.76	58.20	0.197	242.6	72.28	71.68	98.66	0.051	113.9	19.91	19.56	74.46	0.031	127.5	18.61	18.32	90.64
Collembola	0.156	63.37	30.92	30.41	58.30	0.091	119.6	30.92	30.41	58.30	0.076	126.4	26.15	25.74	74.53	0.112	178.9	44.31	43.82	90.84
Protura	0.005	38.53	2.793	2.707	57.87	0.001	101.1	1.725	1.718	98.11	0.012	88.91	7.394	7.229	74.28	0.002	95.43	2.538	2.485	90.40
Diplura	0.014	54.70	5.855	5.559	27.12	0.002	51.54	2.826	2.718	45.99	0.003	40.85	3.150	2.999	34.70	-	-	-	-	-
Psocoptera	0.021	48.15	7.891	7.608	39.20	0.002	72.82	3.273	3.184	66.36	0.004	57.09	03.537	3.415	50.13	0.002	66.23	2.595	2.518	61.11
Hemiptera	0.009	43.20	4.615	4.427	39.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Thysanoptera	0.003	162.1	2.138	2.041	39.02	0.004	76.22	4.974	4.845	66.40	0.006	59.51	4.749	4.592	50.17	0.006	73.44	6.205	6.038	61.20
Formicidae	-	-	-	-	-	0.005	57.86	5.985	5.782	46.09	0.005	043.43	4.439	4.240	34.75	0.003	50.59	4.176	4.014	42.40
Coleoptera																				
Adults	0.492	162.1	67.61	66.78	27.65	1.792	458.5	206.3	205.4	46.78	0.295	118.1	41.75	41.05	35.25	0.564	210.7	84.25	83.45	43.03
Larvae	0.199	130.7	36.46	35.09	58.34	0.192	240.5	71.21	70.62	98.66	0.079	127.8	26.87	26.45	74.54	0.041	134.9	22.29	21.96	90.68
Diptera																				
Larvae	0.068	92.76	17.48	17.11	58.16	0.028	136.9	19.45	19.16	98.35	0.031	102.8	14.35	14.07	74.39	0.022	120.0	14.83	14.58	90.60
Litter	598.0					598.0					528.0					528.0				
Detritus	5,312					5,312					5,313					5,313				

I-3.6. Quantifying dietary preferences

Dietary preferences quantification for each compartment were estimated considering the following criteria: the higher biomass of a prey there is, the higher predation occurs. Analytically, the equation used was implemented as follows:

$$I_{ij} = \frac{1}{\sum_{i=1}^{n} B_i} \times \sum_{j=1}^{n} I_j \times B_i \quad \{17\}$$

Figure A 1 to Figure A 4 in the Appendix A of this section show the quantified adjacency matrices of each forest and season. Note that these figures and Figure I-3-2 are very similar. The only difference is that "1" values from Figure I-3-2 have been changed by values that represent fluxes meaning the quantity of biomass consumed by a predator compartment from a prey compartment.

I-3.7. Ecological networks analysis (ENA)

Ecological network analysis (ENA) requires networks to be at steady state, which means that the sum of carbon entering each compartment must correspond to the amount of carbon leaving from the compartment. During network construction, the objective was obtaining energy budgets in the near steady-state conditions for all trophic groups. In presence of small deviations from the steady-state condition (below 5%), the balancing of networks was achieved applying the *AVG2* function from the R package *enaR* (Borrett and Lau 2014). Such function implements the algorithm proposed by Allesina and Bondavalli (2003), which has the merit of keeping at minimum the impact on system indices that are caused by changes in flow intensity required to attain steady-state conditions. The carbon flow networks built describe trophic relationships between living groups and trace exchanges that involve the nonliving compartments. They provide a mapping of carbon flows in the soil ecosystems and quantify the amount of carbon per unit of time and space that circulates. Yet the goal of the network analysis was describing the global properties of the soil ecosystem in both study areas. To this aim, Whole-system indices derived from information theory were then applied to study the properties of the networks (Table I-3-8; see Ulanowicz 2004).

Table I-3-8: Whole system indices used to describe the properties of soil ecosystems.

Index	Description	References
Shannon's diversity (*H'*) (calculated on biomass)	It measures the entropy of the system. This includes richness (i.e., quantity of biomass), evenness (equity of biomass distribution), and system's compartments composition. According to theory, increasing levels of diversity permit the ecosystem to maintain their functioning over time. Higher levels of biodiversity	(Shannon and Weaver 1949)

	correspond to high values of H'. H_{max} is the maximum possible value of H'.	
H_r	It is the relative entropy. It gives information about how the biomass is evenly distributed among the compartments ($H_{rl} = H'/H_{max}$). Levels of H_r close to 1 correspond to more equitable distribution of biomass, which is a characteristic of healthier ecosystems.	(Shannon and Weaver 1949)
$H_{central}$	It is the centralization of biomass, or how concentrated the biomass is in a given number of compartments ($H_{central} = 1 - H_r$). The ecological interpretation of $H_{central}$ is the opposite to H_r. The higher the $H_{central}$ is, the lower evenly the biomass is distributed, which results in less resilient ecosystems.	(Shannon and Weaver 1949)
Effective nodes	It is the effective richness of the system. It informs on the number of compartments that encompass the higher portion of total biomass. According to theory, lower levels of effective nodes correspond to ecosystems where functions are accomplished by lower number of compartments. This fact implies that some ecosystem functions should prevail on others, which can impair the balance of energy budget over time in the ecosystem.	(Shannon and Weaver 1949)
Total system throughput (*TST*)	It represents the total amount of carbon exchanged in the system, i.e., total consumption, imports, flows to detritus, and respiration. According to theory, the higher the *TST* is, the more material flowing through the system, and so the more mature the ecosystem is.	(Fath and Patten 1998; Ulanowicz 2004)
Average mutual information (*AMI*)	It quantifies whether specialization or redundancy of multiple, equivalent pathways prevail in the architecture of ecosystem carbon flows. According to theory, increasing levels of specialization (i.e., prevalence of a few main paths for carbon circulation) would prevail in more developed ecosystems (i.e., they correspond to higher values of *AMI*).	(Fath and Patten 1998; Ulanowicz 2004)
Ascendency (*A*)	It is the product of *TST* by *AMI* and represents the fraction of the total activity converted into organized complexity. According to theory, as an ecosystem matures and goes through a series of successional stages, the *A* of the system should increase.	(Fath and Patten 1998; Ulanowicz 2004)
Development capacity (*DC*)	It quantifies the entire potential for development of an ecosystem, and it depends on the amount of stock available and the number of components that share it. It represents the highest possible value of Ascendency (*A*), and together with *TST*, maturity of ecosystems increases as *DC* does.	(Fath and Patten 1998; Ulanowicz 2004)
Overhead (*O*)	It is the portion of carbon that remains once *A* is subtracted from *DC*, i.e., the fraction of development capacity that has not yet been organized. The larger the fraction of overhead is, the more resilient the system is.	(Fath and Patten 1998; Ulanowicz 2004)
Finn cycling index (*FCI*)	It informs on the fraction of carbon that is recycled compared with the total flow. It ranges from zero to one, where zero represents no cycling. E.g., in mature ecosystems, the role of detritus in material regeneration is more important compared to early developmental stages, which corresponds to higher values of *FCI*.	(Finn 1976)
Flow diversity (*H*)	It informs about the diversity of flows between compartments ($H = DC/TST$) and represents the upper limit of *AMI* ($H = AMI_{max}$). Low values of *H* indicate that most of the currency is managed by few	(Baird et al. 1998)

	interactions within the system, and it reaches a maximum if all flows are equal in magnitude. I.e., it measures the diversity with which components of the system are used as food resources by other living components.	
Average path length (*APL*)	It informs on the mean number of compartments crossed by the carbon circulating in the ecosystem. According to theory, increasing number of compartments involved in food chains (i.e., the average length of the food web) are characteristic of mature ecosystems (i.e., they correspond to higher values of *APL*).	(Finn 1976; Fath and Patten 1998; Borrett and Freeze 2011)
Linkage density (*L/n*)	It informs on the complexity of the network based on the average number of edges per node. It directly quantifies the variety of prey that compartments have, and in opposition the degree of specialization of trophic groups. Levels of linkage density close to 1 stands for highly specialized compartments (i.e., low resilient ecosystems)	(Williams et al. 2001)
Connectance (L/n^2)	It is the portion of existing links out of the maximum number of links possible. Higher values of connectance are related to the higher possibilities for any compartment to establishing new linkages (i.e., more diversity of food resources), and so the resilience of the ecosystem.	(Dunne, Williams, and Martínez 2002)

Besides characterizing the whole-system properties, the carbon flow networks can be mapped into a standard straight-chain topology. This structure is called the "Lindeman spine" (Ulanowicz 1995), and allows calculating the transfer efficiencies between discrete trophic levels. The transfer efficiency between any two levels is defined as the amount a given level passes on to the next one, divided by how much it received from the previous level (Patricio et al. 2004).

The overall impact of trophic groups on the whole system (through direct and indirect effects) is the mixed trophic impact (*MTI*). It synthesizes all the effects that a small change in the biomass of a group will have on the biomass of other groups in a system (Morissette and Brodie 2014). The *MTI* routine was used to evaluate the magnitude of positive or negative impacts under the assumption that the diet composition remains constant (Ulanowicz and Puccia 1990; Morissette and Brodie 2014).

I-3.8. Model validation

Consumption rates of litter and detritus were among the aspects investigated with ENA. Model outcomes were compared with independent decomposition rates (k) previously quantified with experiments by Innangi et al. (2015). Decomposition rates refer to the same study sites modelled with ENA and were calculated for the whole soil community during about 1,000 days by using litterbags. They were computed as:

$$k = -\left(ln\frac{M_{(t_x)}}{M_{(t_0)}} \times \frac{1}{t_x}\right) \quad [18]$$

where k is the decomposition rate (days^{-1}), $M_{(t0)}$ the sum of litter and detritus biomass at the initial time and $M_{(tx)}$ the sum of litter and detritus biomass at the final time t_x. Decomposition rates were then calculated for each network using t_x = 365 days since flows of networks are referred to a year. The consumption of every compartment feeding on litter and detritus was summed to obtain the total consumption ($M_{(tx)}$), which was subtracted from the initial biomass ($M_{(t0)}$) of detritus and litter to determine k. Our expectation was to find similarities between the decomposition rates calculated from the networks and those quantified experimentally with the litterbags.

I-3.9. Uncertainty analysis and model comparison

Uncertainty analysis was performed to evaluate the robustness of ENA results. The parameters used were in fact obtained from the literature or calculated as a function of standing stock biomasses, which adds uncertainty to the parametrization of each network (Hines et al. 2015). This choice is justified by the evidence that the biomass of trophic groups is more ecosystem-specific than the respective metabolic parameters (Lohbeck et al. 2015). Uncertainty analysis was carried out to clarify whether some metabolic rates might have disproportionate impact on ENA and to ascertain whether variations in ecosystem properties could be due to altered conditions in the forest or simply to interannual variability. To this aim, 1,000 plausible networks were generated using linear inverse modelling (Hines et al. 2016). The analysis was executed with the *enaR* package (Borrett and Lau 2014) and the plausible networks were built by sampling the strength of each carbon flow in the range ±50% compared to the value in the reference network. All models generated during simulations were at steady state. All plausible networks were modelled with ENA, which enabled obtaining a probability distribution for each index.

Standing stock biomasses of the trophic groups were used to assess the differences in biodiversity between sites and seasons. A set of 1,000 plausible distributions of stocks was generated by randomly sampling values in the symmetrical interval obtained selecting ±50% of the reference biomass of the trophic groups in each network. Diversity measures were calculated using the *Shannondiversity* function from the *enaR* package (Borrett and Lau 2014).

For all distributions of network and diversity indices, the 95% confidence interval was determined and used to make comparisons between sites and seasons. Differences between

the distributions of whole-system indices, trophic efficiency, relative impact of compartments and biodiversity measures on biomasses were investigated with the R package *overlapping* (Pastore 2018). Such package includes a function (*overlap*) that compares the area under the distribution of different variables and assesses area overlap. Distributions were considered significantly different when the overlap did not exceed the 5% of the whole area ($P < 0.05$).

I-4. Results

I-4.1. Biodiversity analysis

In all networks, large portions of total system biomass were concentrated in the microbial loop, which resulted in non-homogeneous biomass distributions. The biomass of microbial loop varied significantly between forests and seasons, while the biomass of all the other compartments remained mainly similar. Such similarities are reflected in the absence of any significant difference found when comparing the biodiversity measures.

The Shannon diversity index (*H'*) showed the lowest value in SFS (Table I-4-1). Higher diversity values were obtained in autumn (0.694 in NFA, 0.639 in SFA) and decreased in spring (0.641 in NFS, 0.444 in SFS). Centrality measures ($H_{central}$) and relative evenness (H_r) indicate that the storage of biomass was more evenly distributed in NFA ($H_r = 0.245$), and more centralized in SFS ($H_{central} = 0.836$). This fact becomes clearer when assessing the effective number of nodes: NFA showed the highest value (2.001), followed by NFS (1.898), SFA (1.895), and at last SFS (1.559).

Table I-4-1: Shannon's diversity metrics calculated on biomasses of trophic groups. N = number of living compartments, H' = Shannon's diversity index, $H_{central}$ = centrality measure, H_r = relative evenness, effective N = effective number of nodes.

Indices	NFA	NFS	SFA	SFS
N	17	17	17	15
H'	0.694	0.641	0.639	0.444
$H_{central}$	0.755	0.774	0.774	0.836
H_r	0.245	0.226	0.227	0.164
Effective N	2.001	1.898	1.895	1.559

Significant differences between the sites were never found (Figure I-4-1). Similar mean values were found in all networks for *H'* (0.6), H_r (0.22) and $H_{central}$ (0.78). They indicate that the biomass was always unevenly distributed. The effective number of nodes indicates that the biomass is distributed in two main types of compartments (i.e., microbial loop vs. all other living groups).

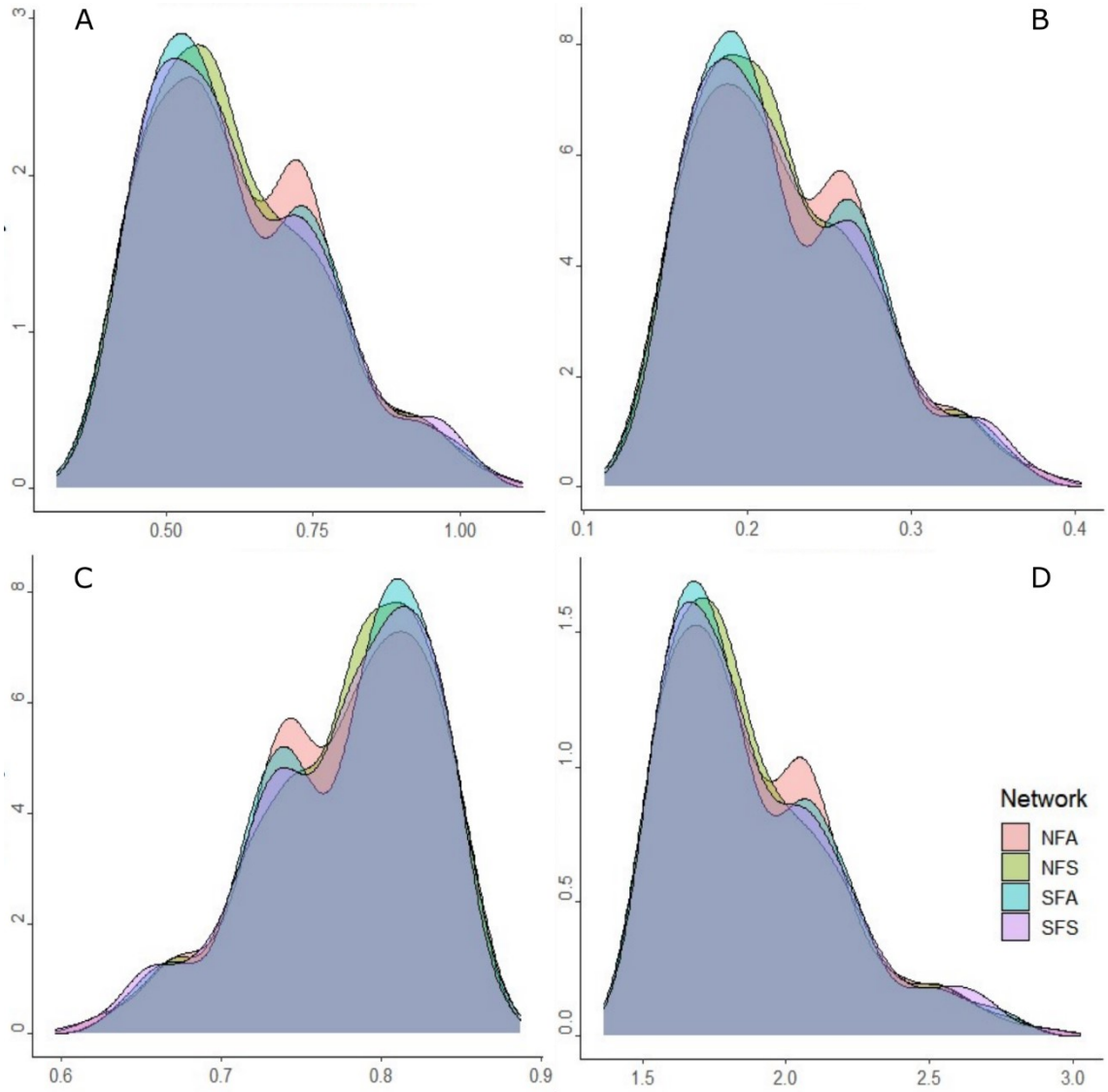

Figure I-4-1: Comparisons between biodiversity indices resulted from the sensitivity analysis. Distributions were obtained by applying enaUncertainty from enaR. A = Shannon's diversity index (H'), B = centrality measure ($H_{central}$), C = relative evenness (H_r), D = effective number of nodes (effective N).

I-4.2. Reference networks

The total biomass of all trophic groups and non-living compartments was comparable among the four networks constructed (≈ 5.93 kg C m^{-2} in NF and ≈ 5.85 kg C m^{-2} in SF). The network structure was similar because the same sources were consulted to identify the dietary habits but the absolute amounts of carbon flowing through the various interactions differed. Moreover, since the metabolic rates were scaled according to temperature, both productivity and respiration of trophic groups varied. Such differences in the flow strengths were reflected by changes at the level of whole-system indices, trophic efficiencies and relative importance of trophic groups.

The number of compartments identified ranged between 15 (SFS) and 17 (all other three networks) living groups and two non-living nodes set to trophic level one (Figure I-4-1). Detritus and litter constitute the basal compartments at trophic level one while all other living groups occupy different continuous trophic levels, which indicates the presence of generalist and omnivore feeding behaviors. Trophic levels around two were occupied by decomposers (microbial loop, Acari, Collembola, Symphyla, Diptera larvae and Pauropoda) and herbivores (Diplopoda, Isopoda, Psocoptera, Hemiptera and Thysanoptera), even though some omnivores could be found (adults and larvae of Coleoptera and Formicidae). The third trophic level was instead occupied by predators (Araneae, Pseudoscorpionida, Diplura and Chilopoda) and by Protura. The trophic structure varied with seasons and depending on the geography. For instance, SFS showed the lowest number of predators (only Pseudoscorpionida and Chilopoda) whereas in the other three networks the third trophic level was occupied by all four predators and Protura.

Overall, the total biomass was about 5.9 kg C m^{-2} including detritus and litter (Table I-4-2). The biomass of microarthropods oscillated between 1.15 g C m^{-2} in SFA and 3.02 g C m^{-2} in NFS (Table I-4-2). The microbial loop was the living compartment reaching highest biomass values in all networks (NFA = 13.0 g C m^{-2}, NFS = 17.3 g C m^{-2}, SFA = 8.2 g C m^{-2} and SFS = 12.9 g C m^{-2}). NFS displayed the highest living biomass accumulation, which consequently resulted in the highest production and respiration values (724.5 g C m^{-2} y^{-1} and 820.6 g C m^{-2} y^{-1}, respectively). However, the overall assimilation efficiency was lower in NFS and SFS compared to NFA and SFA (Table I-4-2). The microarthropods exhibited remarkable seasonal differences in assimilation efficiency, which was lower in spring. The same trend persists for the other physiological parameters, such as respiration (*R*), production (*P*) and excretion (*E*) (Table I-4-2).

Table I-4-2: Biomass, metabolic parameters and assimilation efficiency in soil ecosystems.

Parameter		Units	NFA	NFS	SFA	SFS
Biomass (B)						
	Total	$g\ C\ m^{-2}$	5,925.8	5,931.1	5,849.6	5,854.4
	Non-living	$g\ C\ m^{-2}$	5,910.7	5,910.8	5,840.2	5840.2
	Living	$g\ C\ m^{-2}$	15.08	20.35	9.38	14.20
	Microarthropods	$g\ C\ m^{-2}$	2.08	3.02	1.15	1.21
Average assimilation efficiency (Ae)		%	40.31	39.91	34.93	34.76
Excretion (E) (microarthropod)		$g\ C\ m^{-2}y^{-1}$	700.8	1126.8	877.1	960.1
Intake (I)						
	Total	$g\ C\ m^{-2}y^{-1}$	1,463.2	2,671.9	1,676.5	1,871.3
	Microarthropods	$g\ C\ m^{-2}y^{-1}$	1,245.0	2,452.2	1,461.3	1,653.3
Production (P)						
	Total	$g\ C\ m^{-2}y^{-1}$	393.2	724.5	353.0	408.7
	Microarthropods	$g\ C\ m^{-2}y^{-1}$	328.7	659.5	289.3	344.2
Respiration (R)						
	Total	$g\ C\ m^{-2}y^{-1}$	488.8	820.6	446.5	502.6
	Microarthropods	$g\ C\ m^{-2}y^{-1}$	335.2	665.9	294.9	349.0

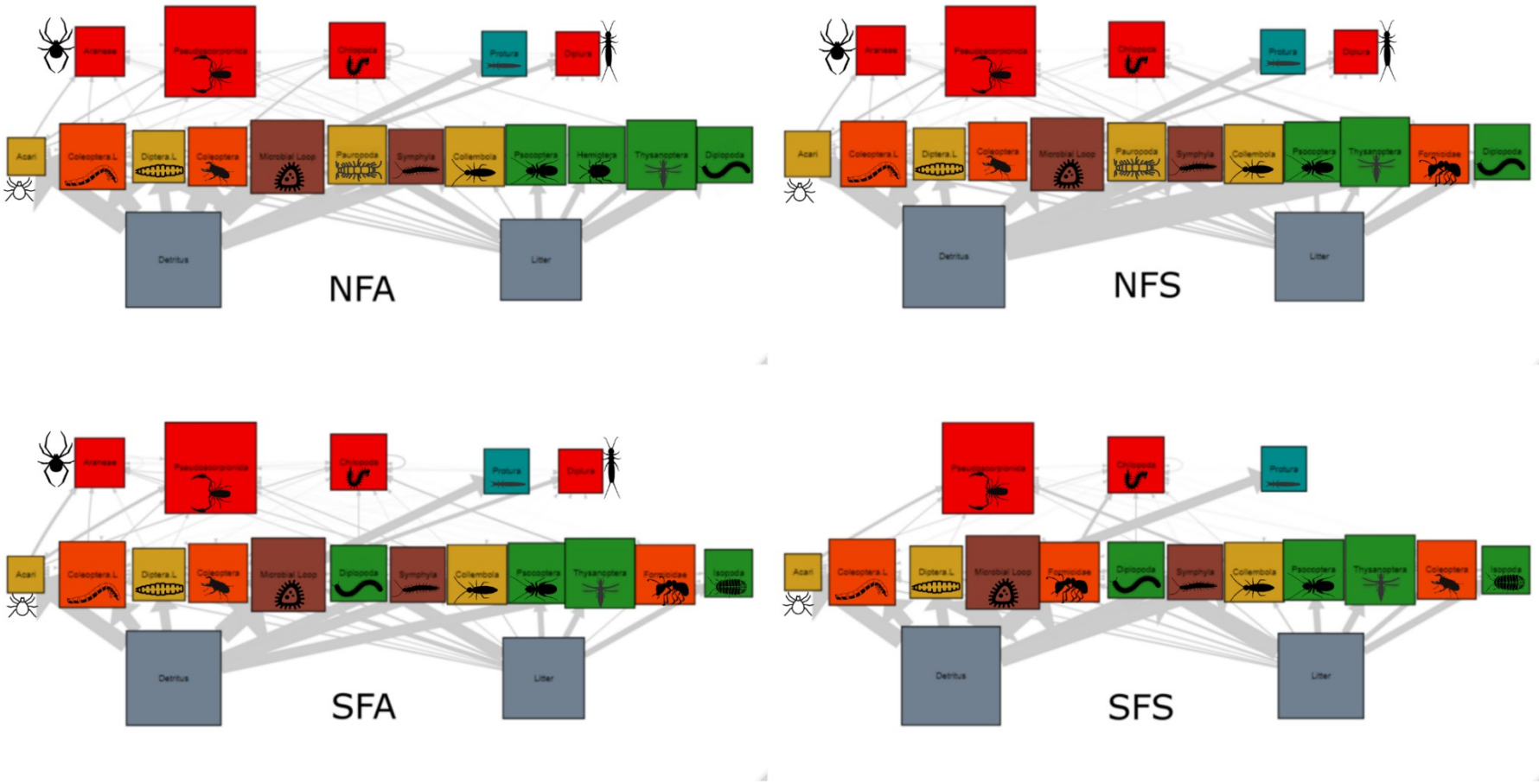

Figure I-4-2: Flow networks illustrating carbon circulation in soil ecosystems. Size of compartments is proportional to their biomass and assimilation efficiency on a logarithmic scale. Compartment colors indicate the feeding habits: red = predators; blue = secondary consumers; green = herbivores; brown = decomposers; yellow = omnivores, mostly decomposers; orange = omnivores; grey = non-living compartments. The nodes are ordered along the y-axis according to the effective trophic level (Scotti et al. 2006). *Arrow-headed interactions indicate the direction of carbon circulation and the thickness reflects the amounts of carbon exchanged. Links representing excretion (i.e., flows to detritus pool) were omitted for the sake of clarity.*

System-level indices and other descriptors used to characterize structure and functioning of the carbon flow networks are in Table I-4-3. The *TST* indicates the size of the system, i.e., total amount of carbon exchanged. Highest *TST* values were found for spring ecosystems. NFS was the largest system (3,270 g C m^{-2} y^{-1}) and NFA the smallest (2,018 g C m^{-2} y^{-1}). The scores of *AMI* show similar flow organization for all networks. The ascendency (*A*) increased from autumn to spring with the highest change found from NFA to NFS (difference = 2,380 g C m^{-2} y^{-1}); in contrast, a smaller difference was obtained when comparing SFA with SFS (52.6 g C m^{-2} y^{-1}). NFS displayed the highest *DC* value (17,528 g C m^{-2} y^{-1}) whereas NFA the lowest (10,886 g C m^{-2} y^{-1}). Evenness in carbon circulation (*O*) depended on the presence of multiple and relatively similar internal paths (redundancy) and on homogeneously distributed respiration losses. Highest overhead was in NFS (11,354 g C m^{-2} y^{-1}) while NFA displayed the lowest overhead (7,093 g C m^{-2} y^{-1}). The relative levels of constraints to carbon circulation (*A*/*DC*) were slightly higher in spring (NFA = 34%, NFS = 35%, SFA = 34%, SFS = 36%). The relative amount of unencumbered complexity (*O*/*DC*) indicated that in all networks about 20% of the carbon flows along redundant paths. Values were lower in the south systems (18.9% and 19.0% in SFA and SFS, respectively) than in the north systems (23.1% and 22.2% in NFA and NFS, respectively).

Table I-4-3: Whole-system indices from ENA and other network descriptors.

Information indexes	**NFA**	**NFS**	**SFA**	**SFS**
Number of nodes (*n*)	19	19	19	17
Number of directed linkages (*L*)	160	172	166	131
Connectance ($Cn = L/n^2$)	0.443	0.476	0.46	0.453
Linkage density (*L*/*n*)	8.421	9.053	8.737	7.706
Number of cycles	28,575	1,386,189	476,051	29,817
Average path length	6.319	6.405	7.251	6.559
Total system throughput (TST) (g C m^{-2} y^{-1})	2,018.4	3,270.6	2,281.5	2,302.1
Average mutual information (*AMI*) (g C m^{-2} y^{-1})	1.879	1.888	1.871	1.881
Ascendency (*A*) (g C m^{-2} y^{-1})	3,793.1	6,173.5	4,268.0	4,330.6
Development capacity (*DC*) (g C m^{-2} y^{-1})	10,886.3	17,528.2	12,422.4	12,027.4
Overhead (O) (g C m^{-2} y^{-1})	7,092.9	11,354.6	8,154.4	7,696.8
Finn cycle index (*FCI*)	0.25	0.249	0.292	0.274
Flow diversity (*H*')	5.393	5.359	5.445	5.225

FCI quantifies the relative amount of carbon recycled. NFA and SFA showed highest FCI scores when compared to their spring counterparts. Southern ecosystems recycled more carbon compared to northern networks. The trophic efficiencies show the percentages of consumption transferred from one discrete trophic level to the next (Figure I-4-3). The trophic chain of spring networks (i.e., Lindeman spine) was shorter than in autumn ecosystems (i.e., one trophic level less) although higher amounts of carbon circulated in spring. Highest efficiency in the transfers from the second to the third trophic level was

found in SFA (23%) while the SFS network showed the lowest percentage (16%). NFS was also the network with the lowest efficiencies for trophic levels III and IV (3% and 1%, respectively) whereas SFA was the ecosystem with the highest efficiencies at trophic levels larger than two (III = 10%, IV = 5%, V = 3%). Approximately 50% of the energy entering the second trophic level returned to detrital compartments (NFA = 49%, NFS = 49%, SFA = 50%, SFS = 54%) and about 30% of the total energy was dissipated by the respiration (NFA = 31%, NFS = 31%, SFA = 26%, SFS = 30%).

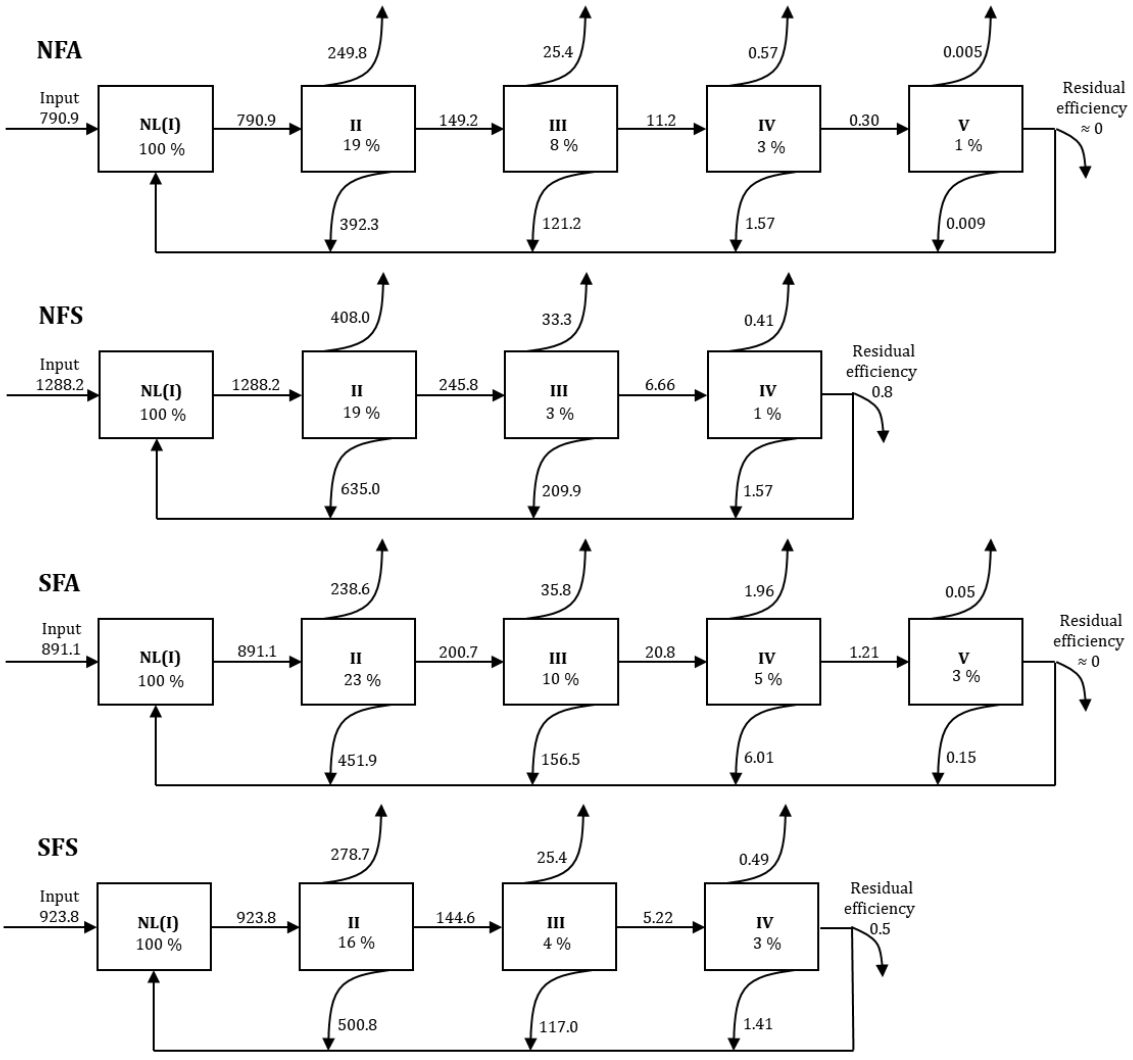

Figure I-4-3: Lindeman spines illustrating ecosystems as chains of discrete trophic levels. All fluxes are in g C m^{-2} y^{-1}. Percentages inside the boxes are the trophic efficiencies for the carbon transfers to the next trophic levels. Input flows from outside represent litterfall while connections between compartments are energetic transfers among trophic levels. Curved arrows in the upper part of the chain stand for dissipations while curved arrows pointing to the lowest link (i.e., the flow entering in NL, which stands for non-living) indicate the carbon that returns to the detrital pool.

I-4.3. Carbon budget

Quantification of the carbon dissipated as CO_2, decomposition (consumption of detritivores and herbivores on detritus and litter), and carbon sequestration (portion of carbon that remains in the soil, quantified by the egestion of trophic groups) are in Table I-4-4. Spring networks display higher rates of decomposition compared to autumn ones. NFS shows the highest decomposition (2,256 g C m^{-2} y^{-1}), followed by SFS (1,608.2 g C m^{-2} y^{-1}). NFA and SFA exhibited similar decomposition rates (1,323.1 and 1,321.7 g C m^{-2} y^{-1}, respectively). NF ecosystems have lower decomposition to decomposers ratios compared to SF ecosystems. Metabolic losses by dissipation (CO_2 emissions) are higher in spring than in autumn, and the highest activity was found in SFA (emissions/B = 108.0). SF attained higher ratios of sequestered carbon per grams of carbon biomass compared to NF ecosystems.

Table I-4-4: Carbon dynamics quantified with networks. Decomposition is the consumption of trophic groups feeding on detritus and litter. Emissions is the sum of all respirations from living compartments. Sequestered carbon is the sum of egestion flows. B is the sum of living biomass (g C m^{-2}).

Parameter	Units	NFA	NFS	SFA	SFS
Decomposition	*g C m^{-2} y^{-1}*	1,323.1	2,256.7	1,321.7	1,608.2
Decomposition/decomposers B	-	90.4	111.8	145.1	114.4
Emissions	*g CO_2 m^{-2} y^{-1}*	1,011.3	1,619.6	1,013.5	1,149.9
Emissions/B	-	67.1	79.9	108.0	81.0
Sequestered Carbon	*g C m^{-2} y^{-1}*	515.1	846.5	614.6	619.2
Sequestered Carbon/B	-	34.2	41.6	65.5	43.6

Values in Table I-4-4 were used to calculate the decomposition rates *k* (Table I-4-4). NFS exhibits the highest rates, followed by SFS, SFA and NFA. Decomposition rates estimated using networks were compared with independent data from experiments. The rates from networks were slightly higher than *k* values reported by Innangi et al. (2015) (Table I-4-4) but orders of magnitude were similar.

Table I-4-5: Comparison between decomposition rates from experiments and network analysis. Experiments refer to Pradaccio (NF) and Laceno (SF) ecosystems (modified from Innangi et al. 2015). Decomposition rates were estimated using network data starting from consumption values. Abbreviations: t = amount of time passed since the beginning of the experiment, t_x = amount of time passed between each measurement; (period considered for the calculation of k), $M_{(tx)}$ = weight lost during the period t_x, k = decomposition rate.

Location	*t* (days)	t_x (days)	$M_{(tx)}$ (%)	*k* (days^{-1})
Pradaccio (NF)	200	200	17.93	0.00099
	400	200	5.27	0.00033
	560	160	5.26	0.00044
	680	120	4.82	0.00058
	1166	1166	50	0.00059
Laceno (SF)	200	200	15.18	0.00083
	400	200	9.44	0.00059
	560	160	7.53	0.00053
	680	120	5.18	0.00066
	1009	1009	50	0.00069
NFA	-	365	18.70	0.00072
NFS	-	365	34.58	0.00151
SFA	-	365	18.54	0.00058
SFS	-	365	27.54	0.00088

I-4.4. Ecological network analysis

Whole-system indices

Significant differences between networks ($P < 0.05$) were found for total system throughput (*TST*), ascendency (*A*), overhead (*O*) and development capacity (*DC*) (**Error! Reference source not found.**). The largest amounts of carbon were exchanged in NFS, which also displayed the lowest recycling rates. The most efficient network (i.e., less redundant pathways) was SFS, as indicated by *A/DC* and *O*/*DC* that significantly deviated from the scores found with the two autumn networks. No differences were instead detected using flow organization (*AMI*), which illustrates that although the various networks differ in terms of potential development (*H'*) they presently display similar organization. Average path length (*APL*) and Finn cycling index (*FCI*) show analogous patterns with SF being the ecosystems with highest degrees of carbon reuse. The highest diversity of fluxes was found in the fall but significant differences were identified only between SFA and NFS, and between SFS and the other three networks.

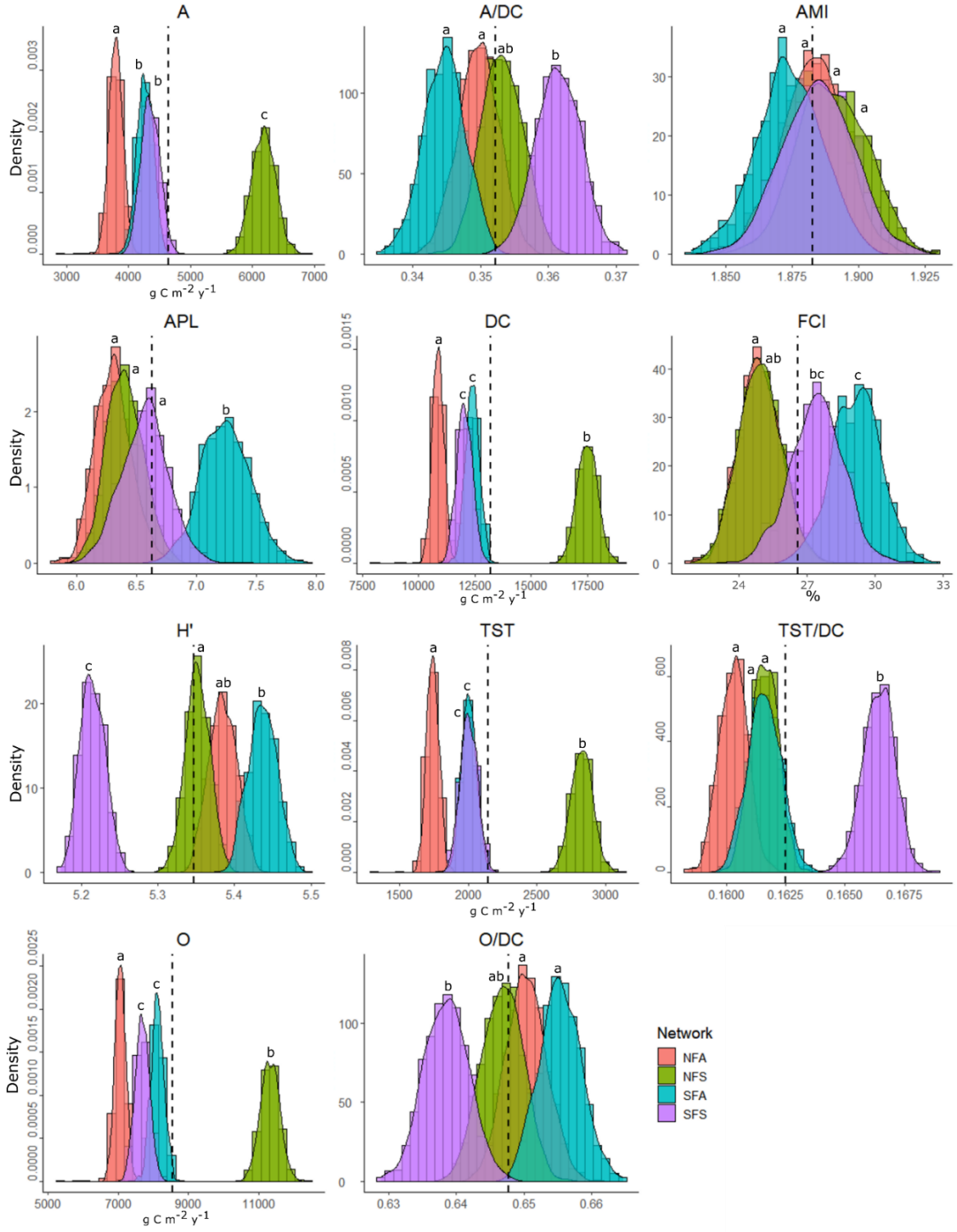

Figure I-4-4: Comparison between whole-system indices. Distributions were obtained by applying enaUncertainty from enaR. TST = total system throughput, AMI = average mutual information, A = ascendency, O = overheads, DC = development capacity, A/DC = relative growth and development, H' = Flow diversity, FCI = Finn cycling index, APL = average path length.

Trophic efficiency

The complex architecture of all networks was simplified by converting them into trophic chains of discrete trophic levels (Figure I-4-5). Decomposers and herbivores were the main consumers feeding at the second trophic level while predators and omnivores occupied levels from the third to the sixth. The highest efficiency was achieved in autumn. In all chains, the second trophic level was the most efficient while the performance decreased moving towards highest trophic levels. Efficiency in SFA was the highest and significantly different from spring systems in trophic levels III to V. NFA followed a similar pattern in levels II and III. SFS and NFS were similar and showed lower efficiencies compared to the other systems in autumn for all trophic levels but such differences were not always significant.

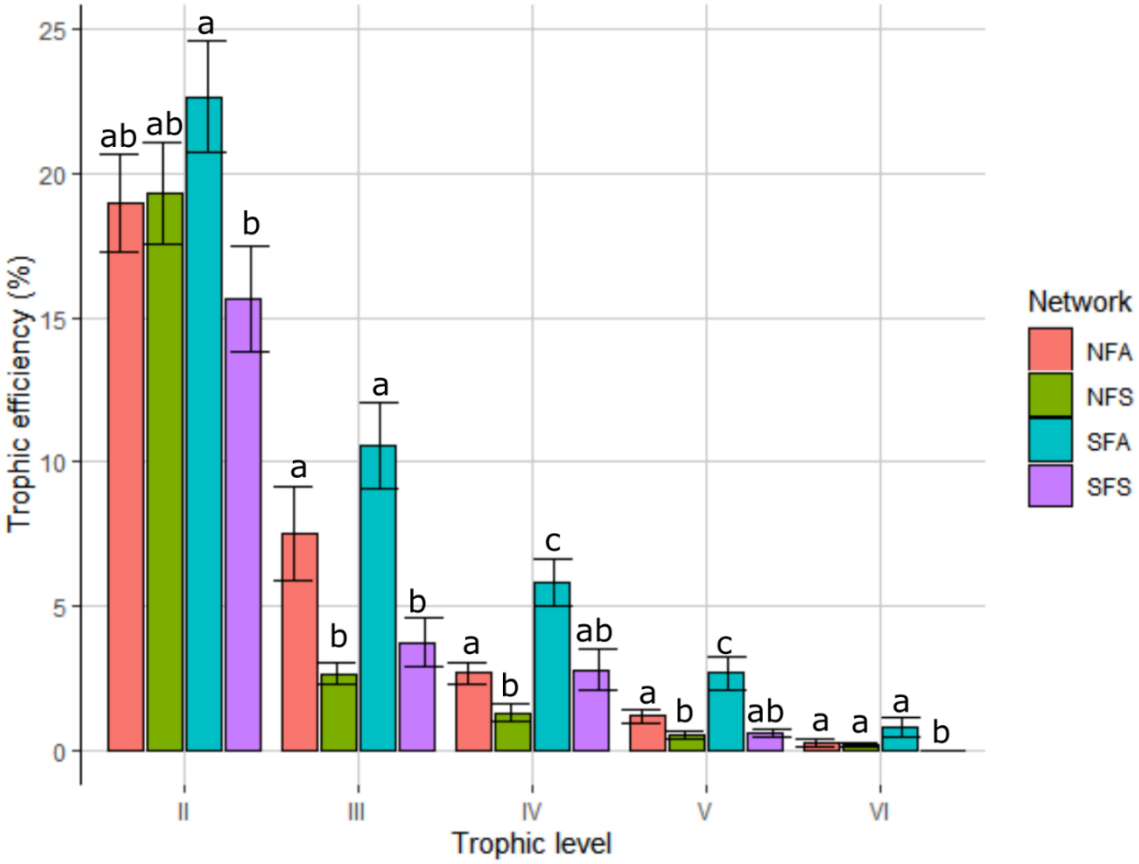

Figure I-4-5: Trophic efficiencies of the linear trophic chains. Distributions were obtained by applying enaUncertainty from enaR. The error bars indicate the standard deviation and efficiency values are shown for consumers. Efficiencies of each trophic level were compared independently, and different letters denote significant differences ($P < 0.05$), which have been obtained by overlapping the tails of the distributions with the function overlap from overlapping R package. By definition, no efficiency was assigned to non-living compartments, then the trophic level I was omitted from the figure for the sake of clarity.

Mixed trophic impact analysis

The impact of each compartment on all others was calculated as the summation of absolute values from the matrix that reports the mixed trophic impacts (Figure I-4-6). Microbial loop, Protura, Acari, and Coleoptera showed the highest overall impact. When present, predators such as Chilopoda, Araneae, Pseudoscorpionida and Diplura did not change their importance along the seasons and in relation to the geographical location. In contrast, other compartments such as Collembola, Symphyla or larvae of Diptera showed lower and more variable impacts depending on seasonality and location.

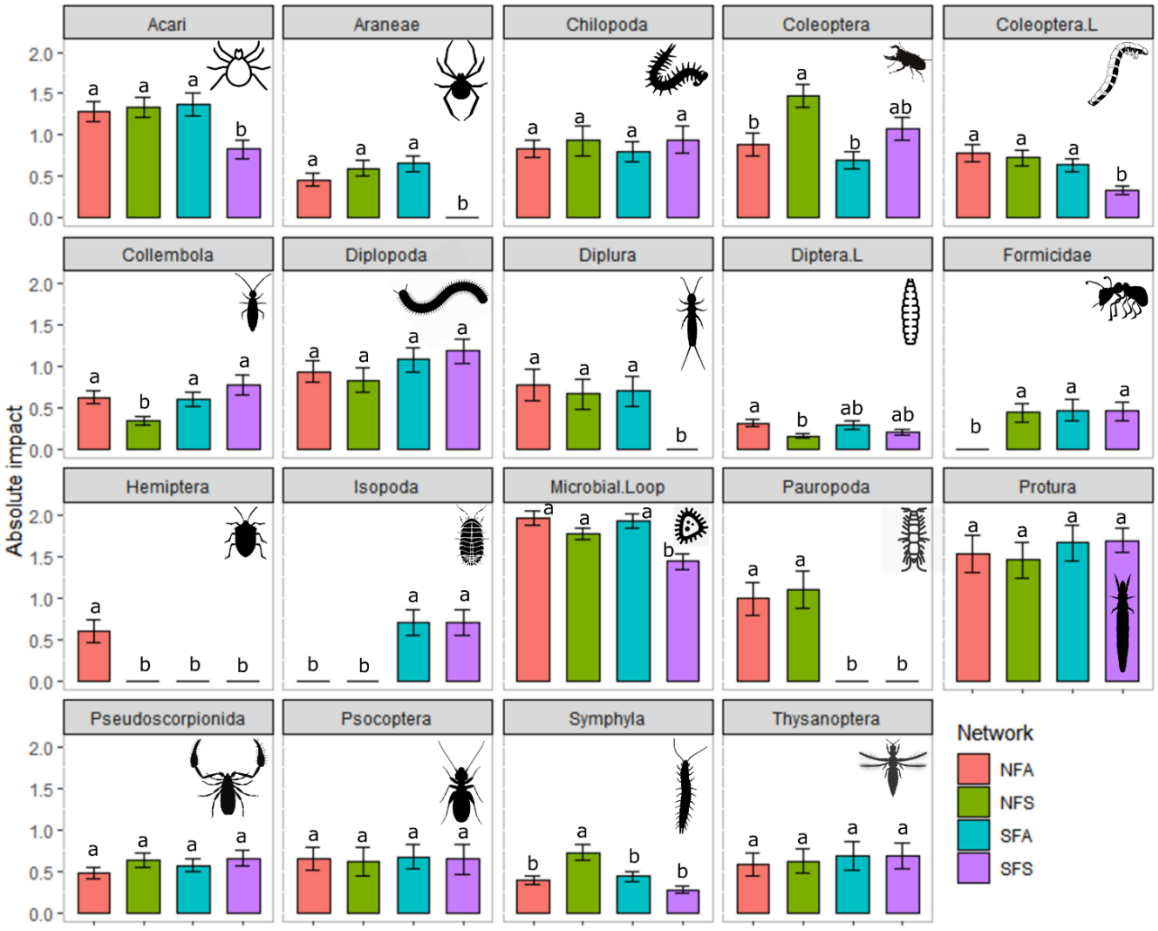

Figure I-4-6: Absolute impacts of trophic groups. Distributions were obtained by applying enaUncertainty from enaR. The magnitude of these impacts was calculated from the matrix of mixed trophic impacts. The error bars indicate the standard deviation of the absolute trophic impact. Different letters indicate significant differences ($P < 0.05$), which have been obtained by overlapping the tails of the distributions with the function overlap from overlapping.

I-5. Discussion

The aim of this section was to find out divergences between soil food webs in relation to climate and site characteristics of the two beech forests that were consistent with the results obtained by De Marco et al. 2016, Innangi et al. 2015, and Fioretto et al. 2018. The focus

was based on the relationships between biodiversity and ecosystem functions, knowing that carbon cycling depends on the seasonal variation of the food web complexity (i.e., number of trophic groups and interactions) (Cardinale et al. 2012; Bardgett and Van Der Putten 2014; Hillebrand et al. 2014; Barnes et al. 2018). The use of flow networks was directed to understand how seasonal variations in diversity and biomass of trophic groups alter the stability of the soil food web, the distribution of carbon fluxes, and the relative importance of taxa.

Taking account of the aforementioned, it was expected that seasonal variations in the microarthropods' community should be reflected in the structural properties of trophic networks such as information indices, transfer efficiency and indirect effects, that are used here as a proxy of ecosystem functioning. Besides, the dependency of such parameters on the environmental characteristics of both sites should trigger differences between the trophic networks. Such fact enabled to tracking how differently similar areas can respond to the seasonal variation of soil communities. The number of trophic groups was the same in all networks except for SFS (Figure I-4-2) and the biomass showed more even distribution in the northern site (Table I-4-1). In both sites, the bulk of biomass was concentrated in less nodes during spring because the microbial loop responds faster to raising temperatures (Creamer et al. 2014) than microarthropods. The increase of biomass in living compartments from autumn to spring was comparable in both forests (Table I-4-2), which resulted in similar increments of exchanged carbon between trophic groups. In NF and SF, the average assimilation efficiency was lower in spring, probably due to higher availability of resources (i.e., litter), even though temperatures were higher. In addition, the higher availability of resources of the south forest was associated with lower assimilation efficiencies compared to the north. The concentration of the biomass in a lower number of compartments and the absence of Araneae and Diplura in SFS might explain the differences between the two locations. Moreover, and together with the higher amounts of litter in soil, carnivore taxa have higher assimilation efficiency rates, which influenced the overall value. Therefore, higher assimilation efficiency is expected in the networks with higher biomass of top trophic levels. In fact, temperature, feeding habits and body mass are crucial factors that determine the assimilation efficiency of soil fauna (Lang et al. 2017; Sohlström et al. 2018; Potapov et al. 2019).

The stability of the food web is quantified through ENA by the overhead (*O*), which represents the redundancy of flows (i.e., multiple and parallel pathways, evenness in the structure of imports, respiration and exports). Therefore, *O* is expected to decline as the

development increases (Tobor-Kapłon et al. 2007). On the one hand, the seasonal changes were wider in the northern forest than in the southern as reflected on absolute indices (*TST*, *A*, *O* and *DC*), which is probably due to the variation of biomass (e.g., increasing biomass of the microbial loop) and community composition (see Table I-4-3 and Figure I-4-4). On the other hand, the consequences of the variation of biomass were stronger for relative indices (*A/DC, H* and *FCI*) in the southern forest. This highlights two different ways of seasonal development between NF and SF ecosystems: the northern forest shows increasing rates of energy transferring throughout unorganized pathways, which is a characteristic response of ecosystems under disturbance (i.e., they increase their levels of redundancy (*O*) to contrast perturbations) probably due to biologic activation after a period of metabolic inactivity during the winter season (Innangi et al. 2015b; De Marco et al. 2016a; Fioretto et al. 2018). In contrast, the southern forest shows lower increases of soil metabolic activity but efficiently transferred throughout less redundant pathways (i.e., increasing levels of organization (*A/DC*)), which reflects that the principal pathways prevailed since the soil community would not reach metabolic inactivity during winter (Innangi et al. 2015b; De Marco et al. 2016a; Fioretto et al. 2018). Specifically, some differences in the community composition between seasons might help explaining the pattern observed in the northern forest. The spring network structure changed compared to the fall network due to the inclusion of Formicidae (omnivores involved in various trophic interactions) and the exclusion of Hemiptera (herbivores with a limited number of trophic links). In these terms, the different community composition might explain the increase of *A* found in spring network (i.e., the higher the number and strength of interactions is, the higher the ascendency is). In fact, the presence of Formicidae increased considerably the number of parallel pathways (i.e., redundancy) as well, and subsequently it contributed to higher development capacity (*DC*). These changes have been described in theoretical models as associated with the progress of ecological succession (Kay et al. 1989; Ulanowicz 2004), which are occurring in the northern forest and would have already reached in the southern forest due to unstopped metabolic activity. In fact, the absolute indices of the southern networks remained stable despite the absence of two top predators during spring, that were present in the autumn community. From the ecological point of view, the substitution of Hemiptera by Formicidae in the NF and the disappearing of Diplura and Araneae in SF may respond to different stages of the seasonal succession: changes in the composition of lower trophic levels (i.e., bottom-up effects in the northern forest) promote the stability of the ecosystem by increasing their resilience in response to changing environmental conditions (i.e., the ecosystem balance itself by increasing the number of parallel pathways). In contrast, changes

in the composition of higher trophic levels (i.e., top-down effects in the southern forest) promote the resistance of the ecosystem by increasing the strength flows (i.e., loss of top predators reduces soil food web stability and carbon cycling). Despite the characteristics of both forests are apparently very similar, both soil food webs seem to operate antagonistically in response to seasons. Taking account of this paragraph and the precedent, these results were consistent with those obtained by Innangi et al. (2015b). In addition, our analysis highlighted (and quantified) the importance of microarthropods on the litter decomposition process through direct and indirect effects on microbial communities. Moreover, the stability of the soil food web (*O*) could be related to the temperatures of both forests due the favorable conditions during the spring of NF compared to the unfavorable conditions during the same season in SF (Innangi et al. 2015b). However, on the light of our results, it seems that the microarthropod top-predators indirectly influence the metabolic activity of microbes through trophic interactions, which resulted in more unstable systems when they lacked.

Since the levels of flow specialization (i.e., *AMI*) in the four networks are similar, it seems that changes in the amounts of carbon circulating play crucial roles for all differences found when comparing sites and seasons. Soil ecologists showed that omnivore organisms are abundant in the soil (Coleman and Wall 2015). Moreover, opportunistic feeding habits are favored by spatial and temporal heterogeneity, which are common in soil ecosystems (Coleman et al. 2005; Berg and Bengtsson 2007). The presence of omnivore and opportunistic taxa may explain the low *AMI* in the four networks. These feeding strategies impose in fact mild constraints to carbon circulation. Rather, they constitute the building blocks responsible for the onset of diverse redundant pathways, which is a characteristic of resilient ecosystems (Ulanowicz 1986). The *AMI* approaches the upper boundary, i.e., flow diversity (*H*), when most of the matter/energy circulation is dominated by a few flows (Rufino et al. 2009). The upper bound *H* is sensitive to network structure and it increases with biodiversity (i.e., with resources availability and/or consumers diversity) (Mann et al. 1989; Baird et al. 1998) or due to the dominance of a few specialized trophic groups that prevail in carbon usage (Kay et al. 1989). It is however difficult to identify the main trophic groups that modify the index (Warwick and Radford 1989). Yet higher values of *H* indicated more interactions in NFA, NFS and SFA than in SFS, which is probably due to the presence of less trophic groups in the latter ecosystem. Still, if *H* values are compared in SFA and SFS, it may be inferred that the top predators (i.e., Araneae and Diplura) could had a critical effect over the diversity of flows, since *H* abruptly increased when they lacked in SFS in an opposite way to *AMI*.

Ulanowicz (1986) suggested that the relative indices of ENA are useful to measure the response of trophic networks to external disturbance or changing conditions in relation to the total budget of energy. The theoretical framework to link variations of values of relative indices and ecological processes has been widely developed in the literature. For instance, Tobor-Kapłon et al. (2007) showed that the perturbations have negative impacts on flow organization, which explains why the ratio *A/DC* increases when the stress declines. The networks of northern and southern forests display divergent behavior but only this latter site exhibited significant differences. The results suggest that the soil ecosystem of the southern forest is subjected to higher environmental variation (Mann et al. 1989; Rufino et al. 2009) but the range of variation of temperatures in northern ecosystem occur in around to lower values, which induces soil metabolic inactivity during the winter period (Innangi et al. 2015b; De Marco et al. 2016a; Fioretto et al. 2018). Subsequently, the northern forest responds to this activation by increasing the rates of activity and redundancy. The lower *A/DC* ratio found in SFS compared to SFA show that a stronger disturbance shapes the architecture of the spring network. The *A*/*DC* results are not confirmed by the trends of decomposition, emissions and carbon sequestered (which were in fact corroborated in the north) but all these properties remained stable in the south ecosystem, which on the contrary is consistent with higher stocks of carbon in mineral soil as described by De Marco et al. (2016). Despite this, differences between the responses of relative indices accounting for structural properties of the networks and carbon dynamics may depend on the choices made during network construction. Our networks depict in fact carbon circulation in a portion of the soil food web, yet changes in the diversity of more sensitive organisms excluded in this study could take place. For example, nematodes are not included in the networks but their response to the increase of microbial loop biomass might lead to underestimate the relevance of bottom-up effect in the NFS (Hunt et al. 1987; De Ruiter et al. 1998; Coleman et al. 2005; Coleman and Wall 2015; Andrés et al. 2016).

The Finn cycling index (*FCI*) quantifies the fraction of matter reused in the system compared to the total amount circulated, adding up the contributions of cycles of different length. Usually, an increase of *FCI* indicates more mature ecosystem status (Odum 1969). However, exceptions exist in the case the raise of cycling occurs via shorter pathways (e.g., in response to nutrient enrichment; see Patricio et al. 2004). Our networks recycle about the 27% of the carbon circulating. Differences between south and north ecosystems are evident. The seasonal variation of *FCI* in the south is wider and the loss of top predators could be responsible for the lower *FCI* found in SFS, which may contribute to higher stocked carbon

(De Marco et al. 2016). Both *FCI* and the average path length (*APL*) follow similar patterns in the four ecosystems, which indicates that the availability of longer paths benefits recycling (Baird et al. 1998).

The analysis of the trophic efficiency reveals the clear relationship existing between biodiversity and ecosystem functioning. The Lindeman spines are longer in autumn than in the spring networks, with the latter displaying lower levels of cycling (i.e., *FCI*). Ulanowicz (1983) observed that the more intense cycling appears to occur in shorter loops in stressed ecosystems (e.g., under the effects of warming and eutrophication). In our systems, cycling was higher in autumn and taxa feeding at lower trophic levels contributed the most to carbon recirculation. Cycling seems to be altered when the availability of resources (i.e., biomass) is lower, thus indicating stress (Odum 1969). In the spring networks, the southern forest recirculates more carbon than the ecosystem in the north despite higher availability of resources in the NFS. This may be also explained by the length of the growing season (178 days in NF compared to 238 in SF) (De Marco et al. 2016). The SFS network also shows more constraints to carbon circulation (i.e., more organized flow structure with lower *O* and higher *A/DC*) compared to the NFS network (higher *O* and lower *A/DC*). Path redundancy enhances the resilience of the ecosystem but reduce the trophic efficiency while a better organization of flows improves the efficiency and recirculation of carbon, especially through the activity of lower trophic levels. Our results show that specific taxa may play crucial roles for carbon circulation in soil ecosystems. The absence of two top predators such as Araneae and Diplura in the SFS network reduced the transfer efficiency and carbon cycling. This finding confirms that the loss of top predators may impair carbon circulation in soil food webs (Barnes et al. 2018). In contrast, it has been suggested that trophic cascades in soil food webs are weak (Laakso and Setälä 1999), but also that initial losses of biodiversity in diverse ecosystems have relatively small impacts on such ecosystem functions (Cardinale et al. 2012) as carbon cycling. This finding may indicate that ENA approach is sensitive enough to these changes; as such it could help identifying early-stage disturbances on ecosystem functions.

The *MTI* analysis informs about the relative importance of trophic groups based on both negative and positive impacts that spread through direct and indirect relationships (Ulanowicz and Puccia 1990). The analysis shows that trophic groups attaining higher standing stock biomasses are the most important (i.e., microbial loop, Acari, Coleoptera and Diplopoda). Protura and Pauropoda display instead disproportionate impacts on the ecosystem if their relatively low biomass is considered (Ruiter et al. 1993; Laakso and Setälä

1999). The microbial loop exhibits highest *MTI* scores in all ecosystems, probably due to the high biomass portion stored by this compartment. The only exception is the SFS network where the Protura are the most important group. Both facts indicate that, in general the distribution of carbon fluxes is controlled by the microbial loop but, under more unfavorable conditions (i.e., SFS) the importance of trophic groups change depending on their specialization (De Ruiter et al. 1998). Protura represent one of the lowest portions of biomass in the soil communities investigated but constantly display very strong impacts over the entire system (i.e., high *MTI*). Most likely, this is because of their trophic specialization since any small variation in Protura biomass directly impair the stock of microbial loop by increasing grazing rates, and then altering the entire cycling of carbon via indirect effects. Unexpectedly, collembolans that together with Acari are the most numerous groups of microarthropods living in soil reach very low impact in all networks. Moreover, the impact of collembolans is lower in spring when their biomass is higher. Collembola are present in almost every soil ecosystem over the Earth (Jeffery et al. 2010; Sha et al. 2015) and are relevant for a variety of soil functions (Menta et al. 2011; Mulder et al. 2011; Coleman and Wall 2015; Orgiazzi et al. 2016). The findings revealed in this section do not exclude that Collembola have important roles for ecosystem functioning but they complement such picture by showing that their impacts on other organisms in the soil community are limited. It is also possible that the importance of collembolans mainly relates to biogeochemical cycles different from the one of carbon, for instance the one of manganese, in which availability both forests are highly dependent (Innangi et al. 2015b; De Marco et al. 2016a). This fact could represent a future direction of investigation.

To validate the analysis, we compared the decomposition rates calculated experimentally (Innangi et al. 2015b) with those estimated using the networks. Results suggest that the estimates of consumption rates on detritus and litter used for the models are accurate (see Table I-4-5). The decomposition rates calculated using the network models were slightly higher than the experimental ones. Such deviations can be explained with the use of different sources (Sohlström et al. 2018; Potapov et al. 2019; Lang et al. 2017; Curry 1986; Reichle 1977) for estimating the assimilation efficiencies of the trophic groups in the networks. Moreover, the decomposition rates calculated with the network approach were estimated for 365 days, them they should be compared with those of the first 200 days from Innangi et al. (2015) because this is the period during which the organic material present in the litterbags lost the less recalcitrant component of litter. The result of the NFS network is particularly high, but this could be due to the huge increment of biomass in the microbial loop, which

increased considerably the consumption on detritus and litter. Nonetheless, results here presented are retained as reliable because they are in the range of decomposition rates determined by Kara et al. (2014) and Jacob et al. (2010), who used similar methodologies to Innangi et al. (2015) in forests with environmental characteristics analogous to the study sites here investigated.

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Appendix A

Figure A 1: Quantitative adjacency matrix of the Northern Forest Autumn (NFA) network. Fluxes are expressed in g C m^{-2} y^{-1}. Z represents the import of assimilable matter to the system from the outside, EX represents the exports of assimilable matter from the system to the outside, and R represents the flow of non-assimilable (respirations) matter from the system to the outside. Value "-" stands for "0" (i.e., absence of interaction), which were omitted in this table and following ones for reading purposes.

	Z	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}	{15}	{16}	{17}	{18}	{19}	EX	R
Z	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	62.7	-	-	-
{1}	-	0.48	0.36	-	-	2.47	-	1.74	0.22	0.26	63.38	35.93	1.16	1.02	0.92	0.36	0.20	0.29	-	-	-	153.6
{2}	-	-	0.0099	13.86	14.21	-	11.95	0.0472	-	0.0071	-	0.9757	-	-	-	0.0097	-	0.0078	-	58.4	-	53.9
{3}	-	-	0.0004	0.5478	0.5614	-	0.4721	-	-	-	-	-	-	-	-	0.0004	-	0.0003	-	27.1	-	5.9
{4}	-	-	0.0004	0.5732	-	-	0.4939	-	-	-	-	-	-	-	-	0.0004	-	0.0003	-	27.1	-	6.1
{5}	-	-	0.0060	-	-	-	7.30	-	-	-	-	-	-	-	-	0.0059	-	0.0048	-	39.6	-	38.5
{6}	-	-	0.0107	-	-	-	12.96	-	-	-	-	-	-	-	-	0.0105	-	0.0084	-	27.4	-	21.7
{7}	-	-	0.0011	1.5330	1.5710	-	1.3211	-	-	0.0008	-	0.1079	-	-	-	0.0011	-	0.0009	-	58.1	-	12.0
{8}	-	-	0.0025	3.5353	3.6229	-	3.0466	-	-	-	-	0.2488	-	-	-	0.0025	-	0.0020	-	58.2	-	21.2
{9}	-	-	0.0044	6.1429	6.2952	-	5.2938	0.0209	-	0.0032	-	0.4324	-	-	-	0.0043	-	0.0035	-	58.3	-	30.9
{10}	-	-	0.0001	0.1809	0.1854	-	0.1559	0.0006	-	0.0001	-	0.0127	-	-	-	0.0001	-	0.0001	-	57.9	-	2.8
{11}	-	-	0.0004	0.5354	0.5487	-	0.4614	-	-	-	-	-	-	-	-	0.0004	-	0.0003	-	27.1	-	5.9
{11}	-	-	0.0006	0.8292	0.8498	-	0.7146	-	-	0.0004	-	0.0584	-	-	-	0.0006	-	0.0005	-	39.2	-	7.9
{12}	-	-	0.0003	0.3776	0.3870	-	0.3254	-	-	0.0002	-	0.0266	-	-	-	0.0003	-	0.0002	-	39.1	-	4.6
{13}	-	-	0.0001	0.1222	0.1253	-	0.1054	-	-	0.0001	-	0.0086	-	-	-	0.0001	-	0.0001	-	39.0	-	2.1
{14}	-	-	0.0138	-	-	-	16.6701	-	-	-	-	-	-	-	-	0.0135	-	0.0109	-	27.7	-	67.6
{15}	-	-	0.0019	2.6620	2.7280	-	2.2940	0.0091	-	0.0014	-	0.1874	-	-	-	0.0019	-	0.0015	-	58.2	-	17.5
{16}	-	-	0.0056	7.8212	8.0150	-	6.7400	-	-	-	-	0.5505	-	-	-	0.0054	-	0.0044	-	58.3	-	36.5
{18}	-	22.0	16.7	-	-	113.4	-	80.0	10.1	12.1	-	-	53.5	47.1	42.3	16.4	9.4	13.2	-	-	-	-
{19}	-	195.7	148.4	-	-	-	-	-	89.9	107.3	-	-	-	-	-	145.3	83.2	117.2	-	-	-	-
EX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

{1} MICROBIAL LOOP
{2} ACARI
{3} ARANEAE
{4} PSEUDOSCORPIONIDA
{5} DIPLOPODA
{6} CHILOPODA
{7} PAUROPODA
{8} SYMPHYLA
{9} COLLEMBOLA
{10} PROTURA
{11} DIPLURA
{12} PSOCOPTERA
{13} HEMIPTERA
{14} THYSANOPTERA
{15} COLEOPTERA (*adults*)
{16} DIPTERA (*larvae*)
{17} COLEOPTERA (*larvae*)
{18} LITTER
{19} DETRITUS

Figure A 2: Quantitative adjacency matrix of the Northern Forest Spring network (NFS). Fluxes are expressed in g C m^{-2} y^{-1}. Z represents the import of assimilable matter to the system from the outside, EX represents the exports of assimilable matter from the system to the outside, and R represents the flow of non-assimilable (respirations) matter from the system to the outside. Value "-" stands for "0" (i.e., absence of interaction), which were omitted in this table and following ones for reading purposes.

	Z	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}	{15}	{16}	{17}	{18}	{19}	*EX*	*R*
Z	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
{1}	-	0.64	0.96	-	-	4.57	-	4.56	0.71	0.35	101.58	48.82	2.05	2.15	1.34	1.62	0.40	0.7027	-	-	-	154.77
{2}	-	-	0.0216	29.61	33.64	-	10.19	0.10	-	0.01	-	1.10	-	-	0.0302	0.0365	-	0.0158	-	98.77	-	115.28
{3}	-	-	0.0012	1.59	1.80	-	0.5461	-	-	-	-	-	-	-	0.0016	0.0020	-	0.0008	-	46.29	-	15.67
{4}	-	-	0.0016	2.21	-	-	0.7617	-	-	-	-	-	-	-	0.0023	0.0027	-	0.0012	-	46.35	-	19.66
{5}	-	-	0.0060	-	-	-	2.8127	-	-	-	-	-	-	-	0.0083	0.0101	-	0.0044	-	66.87	-	47.92
{6}	-	-	0.0051	-	-	-	2.3944	-	-	-	-	-	-	-	0.0071	0.0086	-	0.0037	-	46.30	-	16.39
{7}	-	-	0.0033	4.51	5.13	-	1.5532	-	-	0.0012	-	0.17	-	-	0.0046	0.0056	-	0.0024	-	98.46	-	31.96
{8}	-	-	0.0109	14.94	16.97	-	5.1390	-	-	-	-	0.56	-	-	0.0152	0.0184	-	0.0080	-	98.66	-	72.28
{9}	-	-	0.0051	6.93	7.87	-	2.3839	0.02	-	0.0018	-	0.26	-	-	0.0071	0.0086	-	0.0037	-	58.30	-	30.92
{10}	-	-	0.0000	0.06	0.07	-	0.0220	0.0002	-	0.0000	-	0.00	-	-	0.0001	0.0001	-	0.0000	-	98.11	-	1.75
{11}	-	-	0.0001	0.13	0.15	-	0.0443	-	-	-	-	-	-	-	0.0001	0.0002	-	0.0001	-	46.00	-	2.83
{12}	-	-	0.0001	0.16	0.18	-	0.0550	-	-	0.0000	-	0.01	-	-	0.0002	0.0002	-	0.0001	-	66.37	-	3.27
{13}	-	-	0.0002	0.30	0.34	-	0.1015	-	-	0.0001	-	0.01	-	-	0.0003	0.0004	-	0.0002	-	66.41	-	4.97
{14}	-	-	0.0993	-	-	-	46.75	-	-	-	-	-	-	-	0.1386	0.1677	-	0.0727	-	46.79	-	206.32
{15}	-	-	0.0003	-	-	-	0.1332	-	-	-	-	-	-	-	0.0004	0.0005	-	0.0002	-	46.10	-	5.99
{16}	-	-	0.0016	2.18	2.48	-	0.7498	0.01	-	0.0006	-	0.08	-	-	0.0022	0.0027	-	0.0012	-	98.35	-	19.45
{17}	-	-	0.0107	14.61	16.60	-	5.03	-	-	-	-	0.54	-	-	0.0149	0.0180	-	0.0078	-	98.66	-	71.22
{18}	-	22.17	33.13	-	-	157.55	-	157.30	24.48	12.07	-	-	70.77	74.08	46.23	55.96	13.82	24.25	-	-	-	-
{19}	-	196.96	294.36	-	-	-	-	-	217.45	107.21	-	-	-	-	410.72	-	122.75	215.43	-	-	-	-
EX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

{1} MICROBIAL LOOP
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{13} THYSANOPTERA
{14} COLEOPTERA (*adults*)
{15} FORMICIDAE (*adults*)
{16} DIPTERA (*larvae*)
{17} COLEOPTERA (*larvae*)
{18} LITTER
{19} DETRITUS

Figure A 3: Quantitative adjacency matrix of the Southern Forest Autumn (SFA) network. Fluxes are expressed in g C m^{-2} y^{-1}. Z represents the import of assimilable matter to the system from the outside, EX represents the exports of assimilable matter from the system to the outside, and R represents the flow of non-assimilable (respirations) matter from the system to the outside. Value "-" stands for "0" (i.e., absence of interaction), which were omitted in this table and following one for reading purposes.

	Z	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}	{15}	{16}	{17}	{18}	{19}	*EX*	*R*
Z	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	106.54	-	-	-
{1}	-	0.30	0.24	-	-	0.91	2.01	-	0.16	0.18	88.91	38.71	0.88	0.91	0.17	0.67	0.14	0.18	-	-	-	151.56
{2}	-	-	0.0058	28.43	28.32	-	-	11.88	-	0.00	-	0.92	-	-	0.0040	0.0158	-	0.0043	-	74.69	-	49.86
{3}	-	-	0.0007	3.41	3.40	-	-	1.42	-	-	-	-	-	-	0.0005	0.0019	-	0.0005	-	54.22	-	11.74
{4}	-	-	0.0013	6.42	-	-	-	2.68	-	-	-	-	-	-	0.0009	0.0036	-	0.0010	-	35.06	-	18.08
{5}	-	-	0.0002	0.91	0.91	-	-	0.38	-	-	-	-	-	-	0.0001	0.0005	-	0.0001	-	50.17	-	4.77
{6}	-	-	0.0043	-	-	-	-	8.72	-	-	-	-	-	-	0.0029	0.0116	-	0.0031	-	50.63	-	40.40
{7}	-	-	0.0052	-	-	-	-	10.70	-	-	-	-	-	-	0.0036	0.0143	-	0.0039	-	35.06	-	17.72
{8}	-	-	0.0015	7.40	7.37	-	-	3.09	-	-	-	0.24	-	-	0.0010	0.0041	-	0.0011	-	74.47	-	19.91
{9}	-	-	0.0023	11.04	11.00	-	-	4.61	-	0.0016	-	0.36	-	-	0.0015	0.0062	-	0.0017	-	74.53	-	26.16
{10}	-	-	0.0004	1.73	1.73	-	-	0.72	-	0.0003	-	0.06	-	-	0.0002	0.0010	-	0.0003	-	74.29	-	7.39
{11}	-	-	0.0001	0.50	0.49	-	-	0.21	-	-	-	-	-	-	0.0001	0.0003	-	0.0001	-	34.71	-	3.15
{12}	-	-	0.0001	0.59	0.59	-	-	0.25	-	0.0001	-	0.02	-	-	0.0001	0.0003	-	0.0001	-	50.14	-	3.54
{13}	-	-	0.0002	0.90	0.90	-	-	0.38	-	0.0001	-	0.03	-	-	0.0001	0.0005	-	0.0001	-	50.17	-	4.75
{14}	-	-	0.0088	-	-	-	-	17.90	-	-	-	-	-	-	0.0060	0.0239	-	0.0064	-	35.26	-	41.76
{15}	-	-	0.0002	-	-	-	-	0.34	-	-	-	-	-	-	0.0001	0.0005	-	0.0001	-	34.76	-	4.44
{16}	-	-	0.0009	4.58	4.56	-	-	1.91	-	0.0007	-	0.15	-	-	0.0006	0.0025	-	0.0007	-	74.40	-	14.35
{17}	-	-	0.0023	11.49	11.44	-	-	4.80	-	-	-	0.37	-	-	0.0016	0.0064	-	0.0017	-	74.54	-	26.87
{18}	-	19.41	15.68	-	-	58.65	128.81	-	10.28	11.40	-	-	56.21	58.60	10.65	42.68	9.27	11.53	-	-	-	-
{19}	-	195.50	157.88	-	-	-	-	-	103.51	114.85	-	-	-	-	107.23	-	93.41	116.13	-	-	-	-
EX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

{1} MICROBIAL LOOP
{2} ACARI
{3} ARANEAE
{4} PSEUDOSCORPIONES
{5} ISOPODA
{6} DIPLOPODA
{7} CHILOPODA
{8} SYMPHYLA
{9} COLLEMBOLA
{10} PROTURA
{11} DIPLURA
{12} PSOCOPTERA
{13} THYSANOPTERA
{14} COLEOPTERA (*adults*)
{15} FORMICIDAE (*adults*)
{16} DIPTERA (*larvae*)
{17} COLEOPTERA (*larvae*)
{18} LITTER
{19} DETRITUS

Figure A 4: Quantitative adjacency matrix of the Southern Forest Spring network (SFS). Fluxes are expressed in g C m^{-2} y^{-1}. Z represents the import of assimilable matter to the system from the outside, EX represents the exports of assimilable matter from the system to the outside, and R represents the flow of non-assimilable (respirations) matter from the system to the outside. Value "-" stands for "0" (i.e., absence of interaction), which were omitted in this table for reading purposes.

	Z	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}	{11}	{12}	{13}	{14}	{15}	{16}	{17}	*EX*	*R*
Z	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
{1}	-	0.48	0.41	-	1.86	4.33	-	0.28	0.40	95.43	1.59	1.76	0.47	1.21	0.27	0.30	-	-	-	153.52
{2}	-	-	0.0038	28.78	-	-	7.16	-	0.00	-	-	-	0.0044	0.0114	-	0.0028	-	90.86	-	46.74
{3}	-	-	0.0011	-	-	-	2.08	-	-	-	-	-	0.0013	0.0033	-	0.0008	-	42.72	-	20.10
{4}	-	-	0.0003	2.23	-	-	0.55	-	-	-	-	-	0.0003	0.0009	-	0.0002	-	61.25	-	8.16
{5}	-	-	0.0054	-	-	-	10.21	-	-	-	-	-	0.0062	0.0162	-	0.0040	-	61.70	-	59.54
{6}	-	-	0.0029	-	-	-	5.38	-	-	-	-	-	0.0033	0.0085	-	0.0021	-	42.64	-	14.69
{7}	-	-	0.0010	7.46	-	-	1.86	-	-	-	-	-	0.0011	0.0029	-	0.0007	-	90.65	-	18.62
{8}	-	-	0.0035	26.61	-	-	6.62	-	0.0034	-	-	-	0.0041	0.0105	-	0.0026	-	90.85	-	44.31
{9}	-	-	0.0001	0.40	-	-	0.10	-	0.0001	-	-	-	0.0001	0.0002	-	0.0000	-	90.41	-	2.54
{10}	-	-	0.0001	0.42	-	-	0.10	-	0.0001	-	-	-	0.0001	0.0002	-	0.0000	-	61.12	-	2.60
{11}	-	-	0.0002	1.49	-	-	0.37	-	0.0002	-	-	-	0.0002	0.0006	-	0.0001	-	61.21	-	6.21
{12}	-	-	0.0177	-	-	-	33.21	-	-	-	-	-	0.0203	0.0527	-	0.0130	-	43.04	-	84.25
{13}	-	-	0.0001	-	-	-	0.21	-	-	-	-	-	0.0001	0.0003	-	0.0001	-	42.40	-	4.18
{14}	-	-	0.0007	5.35	-	-	1.33	-	0.0007	-	-	-	0.0008	0.0021	-	0.0005	-	90.60	-	14.83
{15}	-	-	0.0013	9.72	-	-	2.42	-	-	-	-	-	0.0015	0.0038	-	0.0009	-	90.68	-	22.29
{16}	-	19.65	16.56	-	75.50	175.79	-	11.50	16.13	-	64.64	71.69	18.99	49.27	10.81	12.16	-	-	-	-
{17}	-	197.87	166.83	-	-	-	-	115.80	162.45	-	-	-	191.25	-	108.91	122.45	-	-	-	-
EX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

{1} MICROBIAL LOOP
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{16} LITTER
{17} DETRITUS

Section II

Effects of livestock pressure on soil microarthropod community in sylvopastoral systems in the SW of Iberian Peninsula

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Abstract

Sylvopastoral systems, including their soils, play an important role since they represent a large reservoir of biodiversity. Current studies show that the diversity of soil fauna provides multiple ecosystem functions and services across biomes. However, anthropogenic practices often pose a threat to soil fauna because of changes in land use and soil mismanagement. In these terms, rangelands in the southwest of Spain present several problems of soil degradation related to livestock activity and soil erosion, the intensity of which compromises the soil fauna's functions in the ecosystem. Therefore, the aim of this study is to evaluate the response of community metrics and the spatial distribution of soil microarthropods to livestock pressure and vegetation in such ecosystems. A photo interpretation analysis of an experimental catchment used as a study area was developed to identify and classify the intensity of livestock pressure and presence of trees. A total of 150 soil samples were collected throughout 2018 in the three different categories of livestock pressure differencing samples beneath and outside the tree canopies. Soil biological CO_2 efflux and physicochemical parameters (pH, bulk density, organic matter, and water contents) were considered at each sampling point. In addition, such meteorological variables as precipitation, temperature, and evapotranspiration were considered as variables affecting the composition of microarthropod communities in terms of taxa diversity, abundances, and their adaptation to soil environment (evaluated by QBS-ar index). Results showed higher abundance of microarthropods and higher adaptation to soil environment outside the influence of trees rather than beneath tree canopies. Moreover, the classification of livestock pressure revealed by the photo interpretation analysis showed low correlations with community structure, as well as with the occurrence of well-adapted microarthropod groups that were found less frequently in areas with evidence of intense livestock activity. Furthermore, abundances and adaptations followed different spatial patterns. Due to future climate changes and increasing anthropogenic pressure, it is necessary to continue the study of soil fauna communities to determine their degree of sensitivity to such changes.

Keywords: arthropod-based soil quality; community structure; environmental filtering; morphological adaptation; remote sensed image analysis; spatial heterogeneity.

II-1. Introduction

Soils are one of the most important reservoirs of biodiversity in the world (Lal 2004; Bardgett 2006; Jeffery et al. 2010; Wagg et al. 2014; Coleman and Wall 2015; Adhikari and Hartemink 2016). Today, problems such as climate change, an increasing of human population, changes in land use, and land abandonment compromise the diversity and functions of soil biota (IPCC 2014; Smith et al. 2019) and, subsequently, the provision of ecosystem services (Mulder et al. 2011; Wagg et al. 2014; Adhikari and Hartemink 2016; IPCC 2019; Smith et al. 2019) by the soil complex. Moreover, soil functions and healthy soil communities are closely correlated, and together, they are essential for safe and sustainable food production (Mulder et al. 2011), and they also maintain ecosystem stability and resilience (Smith et al. 2019). Furthermore, the diversity of the soil community is often used to provide soil quality indicators, such as the composition and abundance of microarthropod communities (Parisi et al. 2005; Menta et al. 2018). Indeed, it is widely accepted that soil microarthropods are very sensitive to disturbances because of their adaptation to a soil environment (Menta et al. 2014, 2018). Although, the contribution of microarthropods to the total amount of energy fluxes and biogeochemical transformations occurring in the soil is relatively low (Soong and Nielsen 2016), they are a key component in enhancing the resilience and resistance of the soil food web by supporting structural stability (Andrés et al. 2016) since they link microorganisms to macrofauna in the context of an interconnected network (Dam and Heil 2011). Such close correlations between bacterial and fungal channels to mesofauna (Mulder et al. 2011) also determine top-down and bottom-up forces that modify the structure of the entire community and, therefore, the efflux of CO_2 produced by the soil food web during its metabolic activity (Lal 2004).

Many ecological functions have been attributed to soil microarthropod communities (Menta et al. 2011). However, the functions they perform can be compromised via the reduction of biodiversity caused by disturbances in the soil environment (Adhikari and Hartemink 2016). Therefore, the loss of functional groups of microarthropods such as detritivores, which are related to soil carbon cycle could determine the interruption of several steps in the organic matter degradation chain (Wardle et al. 2003; Lindo et al. 2012). In such a context, Mediterranean bioclimatic areas with semi-arid conditions are susceptible to this fact since they have been catalogued as ecosystems under risk due in future climate scenarios to land mismanagement and livestock intensification (Lacetera et al. 2013).

Sylvopastoral systems such as *dehesas* in the Iberian Peninsula are ecosystems subjected to semi-arid conditions that are mainly dedicated to livestock production. In general, the land use is sorted by traditionally-managed rangelands that are characterized by a two-layered vegetation structure: a savanna-like open tree layer (15-40 trees/ha) with an understored pasture in the same land unit (Moreno and Pulido 2009; Schanbel et al. 2013; Lozano-Parra et al. 2014; Fernández et al. 2018). Moreover, pools of soil nutrients are frequently limited due to poor parent material and extremely arid conditions during the Mediterranean summer (Moreno and Pulido 2009; Schanbel et al. 2013). Such systems are particularly subject to abandonment (Pulido et al. 2017; Fernández et al. 2018), soil degradation (Schanbel et al. 2013; Lozano-Parra et al. 2015; Fernández et al. 2018), and subsequent loss of soil biodiversity because of the increase of livestock density and the progressive abandonment of land by farmers. However, patches of vegetation are important for *dehesas* to maintain biodiversity associated with spatial heterogeneity (Moreno et al. 2015). In this context, trees play an important role in regulating environmental features such as soil temperature (Pregitzer et al. 2000; Lozano-Parra et al. 2018b) and moisture (Lozano-Parra et al. 2014); the modification of chemical characteristics such as availability of nutrients (Pulido et al. 2016), and the direct promotion of the development of detritivorous microarthropod communities via the reduction of sunlight availability and litter inputs (Jiménez-Chacón et al. 2018). Moreover, such habitat heterogeneity at multiple spatial scales (Pulido et al. 2016; Fernández et al. 2018) could represent areas for the conservation of biodiversity in farmlands, as indicated by Moreno et al. (Moreno et al. 2015) in which the authors used the term “habitat condition” to refer to areas that sustain certain levels of aboveground biodiversity in rangelands (Fuls 1992). We adapted this concept to our study area in the Iberian Peninsula trying to define combinations of environmental features and elements of the landscape (mostly in reference to vegetation and livestock pressure) that should drive the spatial distribution, structure, abundances, and adaptation to soil of microarthropod communities. In order to clearly define such combinations of factors in this work, we used the term “soil habitat condition” (SHC) (Fuls 1992).

II-2. Aims

For this section, there were defined three central questions: do different intensities of livestock activity induce changes in soil microarthropod communities? Is the structure of a microarthropod community affected by niche environmental factors associated with the presence of trees? And, do the morphological adaptation of microarthropod to such habitats and their abundances follow similar spatial patterns? With regard to these questions, three

aims were defined: first, to determine changes on microarthropod communities associated to seasonality, proximity to trees, and intensity livestock pressure. This aim was based on the hypotheses by which trees, as well as, areas with low livestock pressure should harbor better adapted and numerous communities. Moreover, their seasonal variation should be less wide compared to areas outside the influence of trees and with evidence of high livestock pressure on the ground. Second, to identify the most sensitive biological forms of the microarthropod group to livestock pressure. This aim is based on the sensitivity of soil arthropods to physical disturbances of their habitat. In this case, the occurrence of well-adapted biological forms to soil environment such as Protura, Pauropoda, Diplura, etc, should be less frequent in areas with high livestock pressure outside the tree influence area. And third, to explore the spatial patterns of microarthropod abundance and the occurrence of morphological traits that indicate high adaptation to soil environment. This aim is merely descriptive; the occurrence of morphological traits that indicate high adaptation to the soil habitat varies mostly depending on land use and physical disturbance of soils (Parisi et al. 2005; Menta et al. 2011, 2014). Instead, the abundance of microarthropod populations is related to trophic interactions and availability of resources (Bardgett and Van Der Putten 2014; Barnes et al. 2018), as well as dispersal phenomena, and colonization of habitats by interconnected patches (Chase and Leibold 2003). This aim points out to disentangle whether undisturbed areas in *dehesas* are correlated with areas with high availability of resources and then, becoming more stable habitats for the soil community. Such fact could have implications in practices for soil biodiversity conservation (Decaëns et al. 2006).

II-3. Materials and methods

II-3.1. Study area

Research was conducted on a farmland with agro-silvo-pastoral land use located in province of Cáceres, in the SW of Spain, where an experimental catchment was delimited (Figure II-3-1). The study area (151.6 ha) is representative of a traditionally-managed system, commonly known as a *dehesa*, which is dominated by several vegetation layers including scattered oak trees (*Quercus ilex* L.), a shrub layer (*Retama sphaerocarpa* L.), and a herbaceous layer composed of annual species (grasses such as *Vulpia bromoides* L. [Gray], *Bromus* sp., *Aira caryophyllea* L., and legumes such as *Ornithopus compressus* L., *Lathyrus angulatus* L., and several species of *Trifolium*) (Moreno and Pulido 2009; Lozano-Parra et al. 2014). Climate (Table II-3-1) is typical of the Mediterranean area, with semi-arid conditions characterized by cold winters and a period of hydric stress during the summer. Mean annual precipitation is 524.2 mm. Rainfall events are common in autumn and spring;

however, dry seasons and longer dry periods are frequent. Mean annual temperatures oscillates from 14 to 16 °C.

Table II-3-1: Means ± SD of meteorological parameters calculated for the period 01/01/2013 to 31/12/2018. From: Redarex; Meteorological station: Valdesalor (CC18) which, is approximately 31 km away from the study area; altitude: 382 m.; coordinates UTM H30 X: 730,101, Y: 4,361,000; Extracted from (Junta de Extremadura).

Meteorological Variable	Units	Value
Annual solar radiation	W/m^2	16.59 ± 6.76
Net solar radiation	W/m^2	7.52 ± 4.22
Mean annual temperature	°C	15.02 ± 6.30
Maximum mean temperature of the coldest month	°C	15.84 ± 0.62
Minimum mean temperature of the coldest month	°C	2.41 ± 0.27
Maximum mean temperature of the warmest month	°C	30.60 ± 6.46
Minimum mean temperature of the warmest month	°C	13.61 ± 4.22
Mean annual rainfall	mm	524.2 ± 28.4
Mean annual effective precipitation	mm	249.8 ± 14.4
Mean annual evapotranspiration	mm	1363.1 ± 75.5

Geomorphologically, study area is in old erosion surfaces (Figure II-3-1A), that is formed by schist and greywacke of the Precambrian age (Lozano-Parra et al. 2015). Soils are shallow with a thickness of usually less than 50 cm (Schnabel et al. 2013; Lozano-Parra et al. 2015); soil textures are sandy-loam in low-slope areas and silty-loam in areas with a higher slope. Soils reactions oscillate from 4.3 to 7.3, and they are poor in organic matter (mean values are about 3% in the A horizon) (Lozano-Parra et al. 2015). They are classified as Luvisols and Cambisols (FAO 2006).

Farm management is conventional: livestock walk freely inside the farm, which means that livestock charges per hectare inside the study area are not equally distributed. Moreover, the presence of several "points of reunion", such as eating zones and water reservoirs, influences the frequency of trampling and grazing of surrounding areas close to them. In 2018, the livestock at the farm comprised 1200 sheep and goats (SE area), 50 pigs (NW area), 37 cows, and 1 bull (SW and central areas of the farm).

II-3.2. Determination of the intensity of livestock pressure

The study involved description of the farm management by interpreting orthoimages (0.5 MP size) taken in 2016 by the Spanish National Information Center (Ministerio de Fomento). Parameters such as density of vegetation cover and bare soil area were identified and related to livestock activity (mostly trampling and grazing) (Pulido et al. 2016). For the identification of zones with different grazing and trampling intensities, a supervised object-based image analysis (OBIA) classification (Drăguţ et al. 2010; Ma et al. 2017) was used. The procedure was developed in the eCognition Developer software, avoiding "salt and

pepper effect" that occurs with pixel-oriented classifications (Blaschke et al. 2000; Myint et al. 2011).

Broadly three categories were defined by OBIA based on the effects of livestock activity and the characteristics of the vegetation cover (Figure II-3-1B). Then, the classification was confirmed on the field: (1) SHC_{low}: characterized by a shrub-encroached herbaceous layer, typically 40%-70% *Retama sphaerocarpa* L. cover with a dense tree layer, absence of bare soil and no signs of livestock pressure (i.e. defecation, trampling, or grazed vegetation); (2) SHC_{medium}: herbaceous layer, mostly 10%-40% of *R. sphaerocarpa* L. cover with a sparse tree layer, < 10% of bare soil, and few signs of livestock presence, and (3) SHC_{high}: herbaceous layer with a sparse tree layer but no shrub cover, 50% or more bare soil, and evident signs of livestock pressure. See Figure II-3-2 for an example of the general characteristics of each SHC on the field.

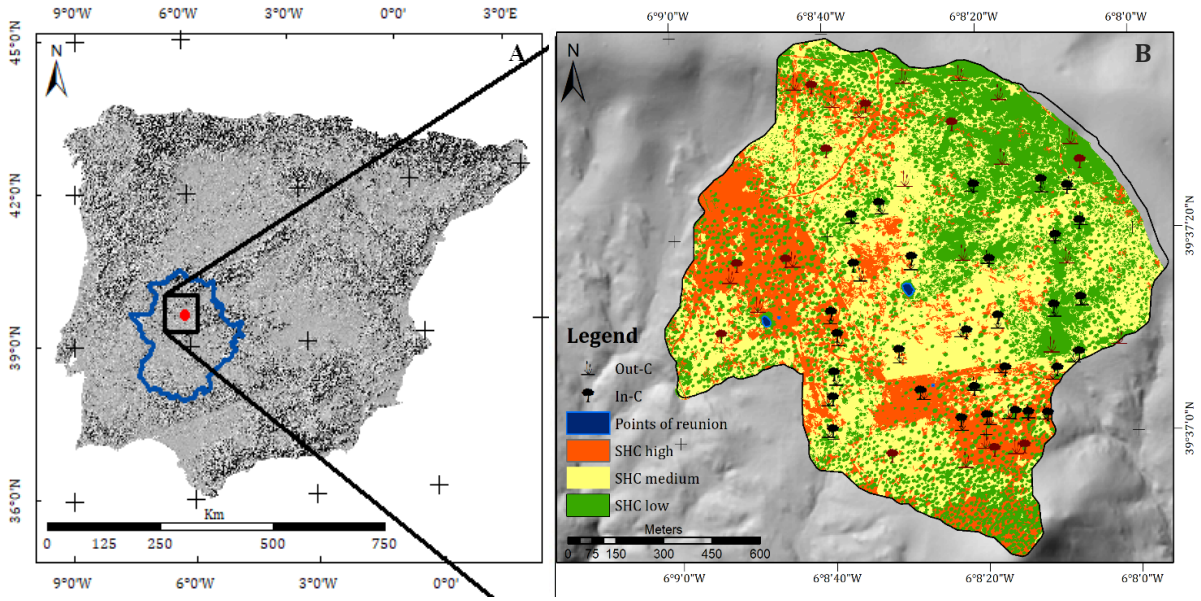

Figure II-3-1: (A) Study area within the Extremadura region (blue boundaries) in the Iberian Peninsula and (B) result of the OBIA classification for the entire experimental catchment. Red indicates the ensemble of characteristics defining the SHC_{high} area, yellow represents SHC_{medium} and SHC_{low} is indicated by green. Sampling point distribution across the SHC categories is also shown: points sampled in spring are black and points added in autumn are indicated by dark red. A tree symbol (in-C; black or dark red) indicates the geographic location of a sampling point beneath the tree canopy; a grass symbol (out-C; black or dark red) indicates the geographic position of sampling points outside the canopy.

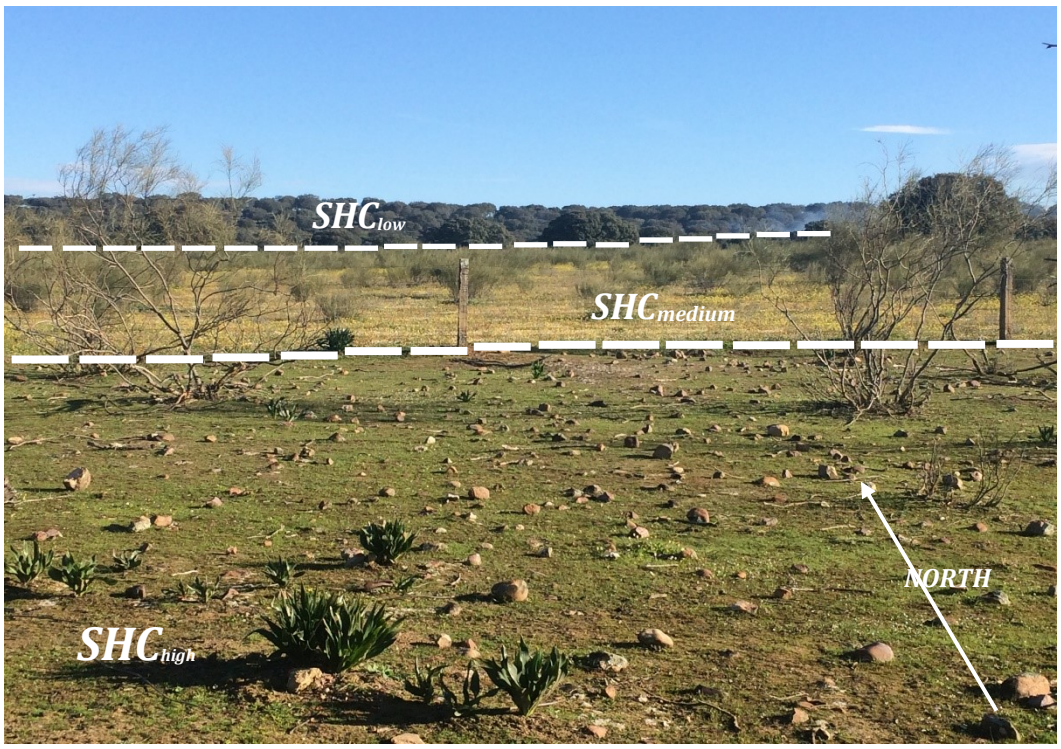

Figure II-3-2: A picture taken in the study area showing the general characteristics of the environments classified as SHC_{high}, SHC_{medium} and SHC_{low}.

II-3.3. Sampling

Two sampling campaigns were carried out in 2018. A total of 60 points were sampled in spring (April), and 90 in the late fall (December). In both campaigns, points were equally distributed among the three SHC categories previously identified by OBIA (Figure II-3-1B). Inside each SHC, half of the points were established beneath the oak canopies (in-C) on the northern cardinal point in relation to the stem. The other half were located outside the canopy (out-C), at least 8 m far away from every tree (stem) (Wardle et al. 2003). Both in-C and out-C points were established considering the presence of herbaceous vegetation cover and avoiding bare soil because it is widely accepted that low densities of soil fauna occur in absence of vegetation (Menta et al. 2014; Meloni et al. 2020). We made this choice to accurately compare the different SHCs because considerable surface of bare ground was only representative of SHC_{high}.

For the spring sampling, 60 PVC cylinders (21 cm ø and 15 cm height) were embedded at each point the day before the beginning of the sampling campaign, as recommended by the LI-COR 8100A protocol of soil CO_2 efflux measurement (LI-COR Inc., 2010). The cylinders were installed up to 10 cm deep, leaving 5 cm of the total height free in order to carry out the measurement correctly. After the insertion of the cylinder in the ground, the stabilization

of the microbial soil community occurs after 12 hours (LI-COR Inc., 2010). Then, sampling was conducted as follows at each point: three repeated measurements of soil CO_2 efflux using a LI-COR 8100A survey device were executed, three measurements of soil moisture were taken in three points beside the cylinder using a TDR device, and finally, three undisturbed soil cores were collected using a steel cylinder at a known volume (100 cm^3) and a soil sample extractor. The soil volumes collected from inside the cylinders used for the soil CO_2 efflux measurement (approx. 3.5 dm^3) were taken to the laboratory, where microarthropod extraction was carried out. Once organisms were collected, soil samples were meshed at 2 mm mesh size. Then, six replicates were picked up to determine the pH and soil organic matter (SOM) content of each sample (3 for pH and 3 for SOM). Due to logistical reasons, measurements of soil CO_2 efflux, pH, water content and bulk density could not be revealed in autumn campaign. At this time, only SOM has been measured in the 90 points sampled.

In the laboratory, pH was determined by dissolving 1 g of soil in 3 g of H_2O using a pH meter. SOM was revealed using the loss-on-ignition method. Soil cores inside the steel cylinders were used to estimate the soil bulk density and gravimetric moisture by the wet-minus-dry weights of the samples in relation to the volume of the undisturbed soil cores (100 cm^3).

II-3.4. Analysis of the microarthropod communities

The analysis of the microarthropod community was based on the QBS-ar methodology (Parisi et al. 2005; Menta et al. 2018). The QBS-ar index (i.e., biological soil quality based on arthropods) evaluates the capacity of a soil to harbor animals that are sensitive to disturbances based on their morphological traits. Therefore, known the number of well-adapted microarthropods to the soil environment at a given time, it is possible to make a judgment about the quality of the soil in a given area (i.e., the higher the number of such organisms is, the higher the soil quality is). The QBS-ar of a soil sample is calculated as the sum of the ecomorphological indices (EMIs) of each biological form. The EMI is a dimensionless score that varies between 1 and 20, and it evaluates the degree of adaptation of the morphological traits that soil animals share by evolutionary convergence. For more details on QBS-ar application, see (Menta et al. 2011, 2014).

In this study, soil microarthropods were extracted from the 150 samples (both spring and autumn) using Berlese-Tullgreen funnels (2 mm mesh size) and conserved in 70 % ethanol solutions. The extraction time was about eight days, depending on the humidity of samples.

Then, the extracted microarthropods were observed under stereomicroscope Leica M3C (40×), counted, identified, and classified as indicated in Table II-3-2. Once analysis of the microarthropod community was completed and raw data were collected, taxa diversity were evaluated via the Shannon's index; a value of QBS-ar was associate with each soil sample, and the numbers of individuals per taxon for each soil sample were obtained.

Table II-3-2: Eco-morphological Indexes (EMIs) scores for each microarthropod taxa. Groups shown are those found in this work.

Taxa	EMI Score
Pseudoscorpiones	20
Opiliones	10
Araneae	1–5
Acari	20
Isopoda	10
Diplopoda	10–20
Pauropoda	20
Symphyla	20
Chilopoda	10–20
Protura	20
Diplura	20
Collembola	1–20
Psocoptera	1
Hemiptera	1
Thysanoptera	1
Zigentomi	10
Embioptera	10
Orthroptera	1–20
Coleoptera	1–20
Hymenoptera	1–5
Diptera	1
Lepidoptera	1
Coleoptera (larvae)	10
Diptera (larvae)	10
Hymenoptera (larvae)	10
Lepidoptera (larvae)	10
Holometabolans (adults)	1

II-3.5. Statistical analyses

Three response variables were considered for this work: abundances, taxa diversity (defined by Shannon's index), and community adaptation to soil environment (defined by the QBS-ar index). A first screening of the data was carried out following the protocol proposed by Zuur et al. (2010). Three categorical predictors were considered: (i) the season in which samplings were accomplished; (ii) the location of each sampling point (in-C: beneath tree canopy, out-C: outside the canopy), and (iii) the SHC representing the intensity of livestock activity surrounding each sampling point.

Initially, a three-way ANOVA test was performed to evince statistical differences among categories. Abundances were log-transformed based on the range of the data and significance

level was established at P = 0.05. A Tukey pairwise test was applied post hoc to highlight the significant differences between pairs of categories. Once seasonal variation of community metrics was statistically confirmed, the rest of the analyses were carried considering seasons separately.

Prior to analysis, collinearity was tested with Pearson's correlation coefficient in order to eliminate variables with identical trends (Zuur et al. 2010). When Pearson's correlation was found to be higher than 0.4999, covariates were considered as collinear and, subsequently, one was excluded from the analysis (Borcard et al. 2011). Methods such as non-metric multidimensional scaling (NMDS) and non-parametric permutational multivariate ANOVA (PERMANOVA) were chosen to study dissimilarities in microarthropod communities. NMDS based on Bray-Curtis distances was used to order the relationships among communities' composition in a specified number of axes (Borcard et al. 2011). A stress level score of ≤ 0.2 was used to account for goodness of fit. PERMANOVA, also based on Bray-Curtis distances, was then used to study environmental variables causing dissimilarity in the community structure (Anderson 2001; McArdle and Anderson 2001). In order to identify the sensitivity of each biological form, NMDS was also applied on each taxon based on the Bray-Curtis dissimilarity index. In order to accomplish these aims, community matrices were split into (1) two log-transformed abundance matrices (60 soil samples [rows] × 27 taxa [columns] in spring; 90 soil samples [rows] × 27 taxa [columns] in autumn); and (2) two EMI value matrices (60 soil samples [rows] × 27 taxa [columns] in spring, and 90 soil samples [rows] × 27 taxa [columns] in autumn) representing the morphological adaptation of biological forms to the soil environment. Environmental factors were summarized in a matrix presenting soil parameters, categorical predictors (SHC and out-C/in-C locations), geospatial characteristics (UTM coordinates, slope, and altitude of each sampling point), and meteorological variables such as maximum, minimum and mean temperature of the sampling day; average of maximums, minimums and mean temperatures of the 20 days prior to the sampling day, effective precipitation of the sampling day, effective cumulative precipitation of the 20 days prior to the sampling day, evapotranspiration of the sampling day, average evapotranspiration of the 20 days prior to the sampling day, and average hydrological balance of the 20 days prior to the sampling day (22 columns in spring and 18 in autumn). A stepwise model selection based on the significance criterion was used to choose the best combination of variables explaining the variance of the data. These analyses were carried out with the *vegan* package (Oksanen et al. 2019) from RStudio.

Generalized additive models (GAMs) were applied to investigate the effects of spatial distribution of niche-environmental factors upon spatial distribution of QBS-ar and total log-transformed abundances. In order to model the dispersion of community metrics across the space, two protocols were executed to run the models: the first, a random effect on "pure" spatial coordinates was used in order to seek spatial dependence of the response variables; on the second, a random effect on ordination coordinates extracted from NMDS replaced the spatial coordinates in order to find the best descriptor of the community metrics variation (Borcard et al. 2011). Stepwise model selection was based on Akaike's information criterion (AIC) (Zuur et al. 2009). The R package *mgcv* (Wood 2011) was used to perform this analysis.

II-4. Results

II-4.1. Soil parameters

Organic matter and water contents, bulk density and pH were measured in the three SHC in both in out-C and in-C locations (Table II-4-1). Averages slightly differed based on SHC categorization. However, decreasing values of organic matter content were found from SHC_{high} to SHC_{low} in out-C locations; differences were less evident when pH, bulk density, and water content were compared. Soil pH was found to be acidic (5.61 to 5.96) inside the study area with no broad variations both in either out-C or in-C. Moreover, bulk density averages in out-C varied slightly around 1.5 g cm^{-3}. However, values of the soil parameters on in-C were smaller in the case of bulk density (≈ 1.2 g cm^{-3}), but far higher for organic matter (≈ 10% compared to ≈ 5% for in-C and out-C, respectively). Instead, water content and soil CO_2 efflux were the less variable parameters considering both out-C and in-C locations (≈ 20% and ≈ 5 µmol m^{-2} s^{-1}, respectively).

Table II-4-1: Mean ± standard deviations of soil parameters. SHC indicates the "soil habitat condition" categories; In-C and Out-C indicate whether values were detected beneath the tree canopy or outside the canopy, respectively.

		SHC_{high}		SHC_{medium}		SHC_{low}	
Parameter	**Units**	**Out-C**	**In-C**	**Out-C**	**In-C**	**Out-C**	**In-C**
Bulk density	g cm^{-1}	1.5 ± 0.1	1.2 ± 0.2	1.5 ± 0.1	1.2 ± 0.2	1.5 ± 0.2	1.2 ± 0.1
Organic matter	%	5.3 ± 2.5	10.3 ± 4.6	1.9 ± 1.8	9.1 ± 4.6	3.8 ± 1.4	9.5 ± 4.1
pH	-	5.8 ± 0.7	6.0 ± 0.8	5.6 ± 0.4	5.9 ± 0.4	5.8 ± 0.2	5.7 ± 0.7
Soil CO_2 efflux	µmol m^{-2} s^{-1}	4.6 ± 2.8	4.9 ± 2.7	4.5 ± 1.4	5.2 ± 1.9	5.2 ± 1.9	5.0 ± 2.2
Water content	%	18.4 ± 5.9	20.8 ± 8.3	22.2 ± 8.8	23.2 ± 8.0	21.8 ± 8.4	23.7 ± 10.5

II-4.2. Environment and diversity

Generally, 113,579 organisms belonging to 27 taxa were individually identified and counted. Collembola, Acari, larvae of dipterans, and larvae of coleopterans were the most frequent

taxa (58%, 35%, 3%, and 1%, respectively) representing 97% of the total abundances. In detail, frequencies varied significantly from spring to autumn ($P < 0.01$), as evidenced by results of the three-way ANOVA showed in Table II-4-2. In spring, collembolans represented 50% of total abundances, which increased to 62% in autumn. Mite populations were higher in spring (44%) than in autumn (32%), and larvae of dipterans and larvae of coleopterans maintained their populations varying from 2% to 3% in the case of dipterans, remaining at 1% in the case of coleopterans. Other taxa such as coleopteran adults, hemipterans, pauropods, thysanopterans, and ants were frequently found but their abundances were lesser. Moreover, diplopods were found only in spring, and isopods conversely only in autumn, as well as individuals belonging to Zygentoma taxon. However, the most important source of variation was the location of each sampling point (in-C or out-C), showing a strong influence on the response variables. Although SHC was not revealed as a significant source of variation by the ANOVA, some taxa, such as diplopods, were found only in SHC_{low} when trees were present. Embiopterans were found in the three SHCs, both in out-C and in-C, during spring campaign, but only in in-C locations during autumn. Proturans and pseudoscorpions followed similar patterns, as they were found in the same categories; but pseudoscorpions lacked in autumn in-C-SHC_{low}. Such variations were also reflected by the QBS-ar and *H'* indices, the values of which differed not only according to seasonality, but also to the location of sampling points ($F = 4.490$ and $F = 6.232$, both significant, respectively) as showed in Figure II-4-1 and Table II-4-2. The highest mean value of QBS-ar was detected in out-C-SHC_{medium}, followed by out-C-SHC_{high}, both in autumn. Generally, higher values of QBS-ar were found in out-C. Instead, mean values of *H'* were closer to 1 in in-C locations in spring, but not in autumn.

See details in the Appendix B: results of the post-hoc Tukey test are showed in Table B 1, mean values of QBS-ar and H' are in Table B 2 and Table B 3, and total abundances are in Table B 4 and Table B 5.

Table II-4-2: Three-way ANOVA on log-transformed abundances, QBS-ar and Shannon's index (H'). Asterisks indicate levels of significance (*) = P < 0.05; (**) = P < 0.01; (***) = P < 0.001. "Location" indicates whether the sampling point was located beneath tree canopies (in-C) and outside the canopy (out-C).

	Abundance		**QBS-ar**		**Shannon's diversity**	
Source of variation	F test	P-value	F test	P-value	F test	P-value
Livestock pressure	2.911	0.058	2.451	0.090	1.532	0.220
Location	14.655	<0.001***	17.464	<0.001***	0.913	0.341
Season	7.644	0.007**	2.057	0.154	0.007	0.932
Livestock pressure × Location	1.233	0.295	1.059	0.350	1.209	0.302
Livestock pressure × Season	1.355	0.262	0.511	0.601	2.247	0.110
Location × Season	0.015	0.902	4.490	0.036*	6.232	0.014*
Livestock pressure × Location × Season	1.718	0.184	1.581	0.210	0.634	0.532

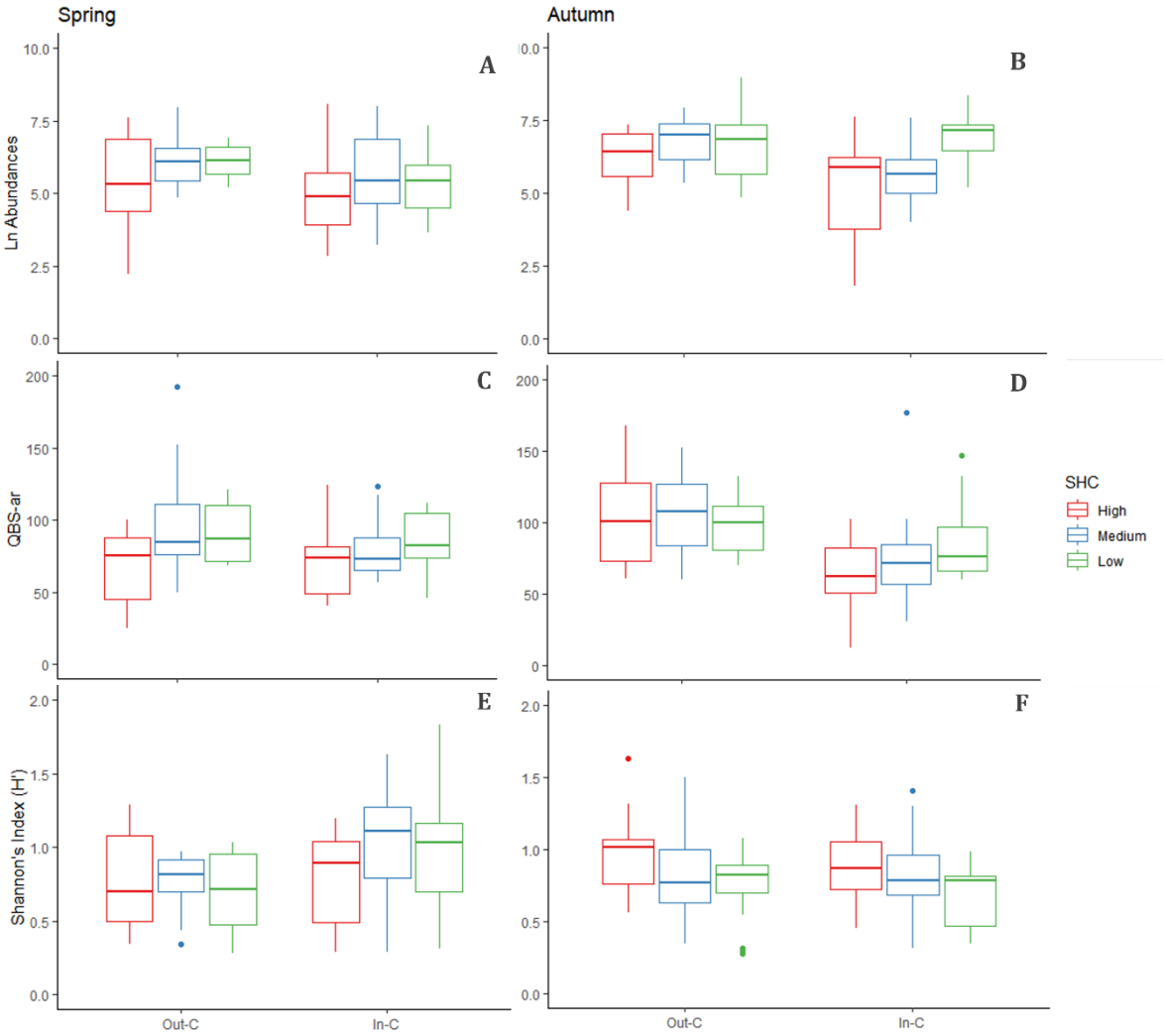

Figure II-4-1: Boxplots showing the distribution of data for each response variable by soil habitat condition (SHC) and location factor (outside the canopy = Out-C or beneath tree canopy = In-C) in both seasons. A and B plots show log-transformed abundances; C and D plots show QBS-ar values; E and F plots show H' index values.

Results of NMDS and PERMANOVA are reported in Figure II-4-2 and Table II-4-3, respectively. The ordination of sampling points based on community abundances showed stress values below the 0.15 threshold (Figure II-4-2A and Figure II-4-2B). However, the occurrence of high EMI scores did not show convergence, as evidenced by stress values above 0.20 (Figure II-4-2C and Figure II-4-2D). The scaling of community abundances was characterized by high overlapping based on categorical predictors (locations and SHC). Nevertheless, more dissimilarity among communities was attributed to locations ($P < 0.05$ and $P < 0.001$ in spring and autumn, respectively) than to SHC, which was significant in autumn ($P < 0.05$) but not significant at all in spring (Table II-4-3). Representation of significant taxa abundances in spring was lower than in autumn, as shown in Figure II-4-2A

and Figure II-4-2B. In spring, such groups as Acari and Coleoptera (adults and larvae) avoided points where values of organic matter and pH were higher, but they also were positively related to high bulk density. Otherwise, Collembola, Thysanoptera, larvae of Diptera and larvae of Coleoptera were positively related to points where soil water content was higher. In autumn (Figure II-4-2B), Collembola, Chilopoda and Pauropoda avoided points where SOM content was higher. Moreover, these groups were significantly related to out-C-SHC_{medium} and out-C-SHC_{low} in autumn. Several environmental variables were significant in both seasons, but after the model selection performed on PERMANOVA, only water content ($P < 0.01$), pH ($P < 0.05$), and soil CO_2 efflux ($P < 0.05$) were deemed significant ($R^2 = 17.4\%$). In the autumn model, environmental variables such as slope ($P < 0.05$), SOM content ($P < 0.01$), effective precipitation ($P < 0.05$), and mean temperatures of the 20 days prior to sampling day ($P < 0.05$) explained a wider percent of the total variance of PERMANOVA ($R^2 = 22.1\%$) when compared to the spring model. It is noteworthy that the location of sampling points was found significant in both abundance models ($P < 0.05$ and $P < 0.001$ in spring and autumn, respectively).

As the NMDS ordinations based on EMI matrices were almost random in both seasons (stress value > 0.2), a clear effect of SHC categories causing differences among sampling points was not determined. Nonetheless, segregation of communities by locations was quite evident in autumn as indicated by PERMANOVA ($P < 0.001$) in Table II-4-3 and Figure II-4-2D. Moreover, the number of significant taxa that fit the scaling based on EMI scores was higher when compared to taxa abundance ordination in both seasons. Once again, variables fitting communities was higher on NMDS than in PERMANOVA being soil water content, the only significant variable related to spring communities after the model selection process ($P < 0.05$). In contrast, the autumn model evidenced the variation of slope ($P < 0.01$), mean temperature of the 20 days prior to sampling day ($P < 0.01$), and the location factor as structuring forces of the community. Despite this, and similarly to abundances, total variances explained by EMI spring and autumn models were low ($R^2 = 8.4$ and $R^2 = 19.7\%$, respectively).

Table II-4-3: PERMANOVA results for matrices of log-transformed abundances and Eco-morphological index scores matrices. Significant results for environmental parameters causing dissimilarity are marked with asterisk: (*) = P < 0.05; (**) = P < 0.01; (***) = P < 0.001. Location indicates if the sampling point was stablished beneath tree canopy (In-C) or outside the canopy (Out-C); SHC indicates the characteristics of the surrounding environment and pressure of the livestock where sampling points were placed; EP(-20) = Effective Precipitation of the 20 days prior to sampling day; T (-20) = Average temperature of the 20 days prior to sampling day.

Community matrix	**Season**	**Source of dissimilarity**	**Df**	**F**	R^2
Log-transformed Abundances	Spring	Location	1	2.674	0.041*
		Water content	1	3.444	0.052**
		pH	1	2.480	0.037*
		Soil CO_2 efflux	1	2.263	0.034*
		Residuals	54		0.836
Log-transformed Abundances	Autumn	Location	1	6.217	0.062***
		SHC	2	2.184	0.044*
		Slope	1	3.173	0.032*
		OM content	1	3.530	0.035**
		T (-20)	1	2.720	0.027*
		EP (-20)	1	2.156	0.022*
		Residuals	78		0.779
EMIs	Spring	Location	1	2.097	0.034
		Water content	1	3.155	0.051*
		Residuals	57		0.916
EMIs	Autumn	Location	1	11.329	0.111***
		Slope	1	5.055	0.050**
		T (-20)	1	3.456	0.036**
		Residuals	82		0.803

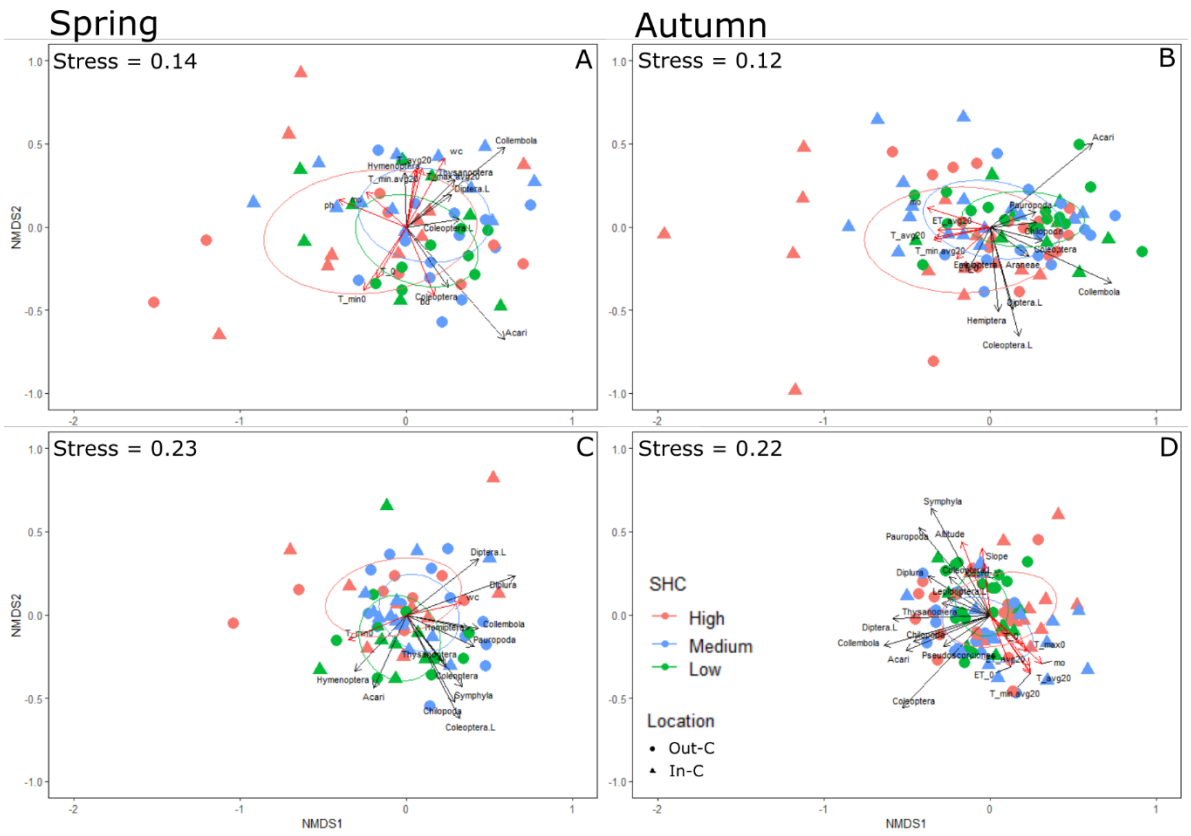

Figure II-4-2: Community composition fitting categorical predictors (SHC and location factor), environmental parameters and taxa (abundances and EMIs). Log-transformed abundance matrices for spring and autumn samplings are shown in graphics A and B, respectively; EMI-values matrices for spring and autumn samplings are shown in graphics C and D, respectively. Black arrows show the fitting of significant taxa, whereas red arrows show the fitting of significant environmental parameters. Location indicates whether the sampling point was established beneath the tree canopy or outside the canopy; SHC indicates the characteristics of the surrounding environment, as well as the pressure of the livestock where sampling points were placed; bd = bulk density; ET_avg20 = average evapotranspiration of the 20 days prior to sampling; mo = soil organic matter content; T_0 = mean temperature of the sampling day; T_avg20 = average temperature of the 20 days prior to sampling; T_max0 = maximum temperature of the sampling day; T_min0 = minimum temperatures of the sampling day; T_min.avg20 = average minimum temperature of the 20 days prior to sampling; wc = soil water content.

II-4.3. Spatiotemporal patterns of abundances and QBS-ar

GAMs demonstrated how both response variables (total abundances and QBS-ar) changed in spring and autumn in relation to the spatial structure of environmental variables (Table II-4-4 and Figure II-4-3). In general, variance explained by the models was very high (R^2 = 87.4% and R^2 = 89.1% for abundances; R^2 = 85.5% and R^2 = 91.8% for QBS-ar in spring and autumn, respectively), the largest effect of which was the contribution of the random effect in NDMS coordinates (F = 21.750 and F = 23.880 for abundances in spring and autumn; F = 12.870 and F = 37.430 for QBS-ar in spring and autumn, respectively). Moreover, the smoothness of the models was conditioned by location factor, where out-C

significantly explained a wider proportion of the variance over the unexplained (F = 7.920 and F = 8.923 in spring and autumn, respectively) rather than in-C. Also, effective precipitation of 20 days prior to sampling day resulted statistically significant in autumn (F = 2.539). Otherwise in autumn, QBS-ar scores followed similar spatial patterns to SOM content in autumn (F = -2.214). It is important to note that smoothing was better when several variables such as pH, SOM and bulk density (spring abundances), temperature (autumn abundances), and effective precipitation (autumn QBS-ar) were available. Despite their insignificant effects on smoothing, AIC obtained better scores when they were present.

Figure II-4-3A and Figure II-4-3B show the spatial patterns of smooth isolines for total abundances. The maximum order of magnitude in autumn (e^4) indicates a higher variation than in spring (e^2). Instead, smooth isolines for QBS-ar reached variations from 0 to 80 in both seasons (Figure II-4-3C and Figure II-4-3D).

Table II-4-4: GAMs result for community metrics in each season. Significant results are shown in bold. Location indicates where sampling stations were located: outside the canopy (Out-C) or beneath tree canopy (In-C); SHC-low/medium/high indicates the characteristics of environment and pressure of the livestock in which points were located; T (-20) = Average temperature of the 20 days prior to sampling day; EP (-20) = Effective cumulative precipitation of the 20 days prior to sampling day.

Metrics	Season	Parameter	F	P	R^2
Log-transformed Abundances	Spring	**s(NMDS1, NDMS2)**	**21.750**	**<0.001**	**0.874**
		Location-out-C	**7.920**	**<0.001**	
		Location-In-C	-0.948	0.348	
		SHC_{low}	-1.705	0.095	
		SHC_{medium}	-1.444	0.156	
		pH	-1.416	0.164	
		OM content	-1.529	0.134	
		Bulk density	-1.536	0.132	
	Autumn	**s(NMDS1, NDMS2)**	**23.880**	**<0.001**	**0.891**
		Location-out-C	**8.923**	**<0.001**	
		Location-In-C	1.742	0.087	
		SHC_{low}	1.899	0.062	
		SHC_{medium}	1.066	0.291	
		T (-20)	-1.605	0.114	
		EP (-20)	**2.539**	**0.014**	
QBS-ar	Spring	**s(NMDS1, NDMS2)**	**12.870**	**<0.001**	**0.855**
		Location-out-C	**35.507**	**<0.001**	
		Location-In-C	-0.873	0.389	
	Autumn	**s(NMDS1, NDMS2)**	**37.430**	**<0.001**	**0.918**
		Location-out-C	**15.892**	**<0.001**	
		Location-In-C	0.107	0.915	
		OM content	**-2.214**	**0.030**	
		EP (-20)	-1.888	0.063	

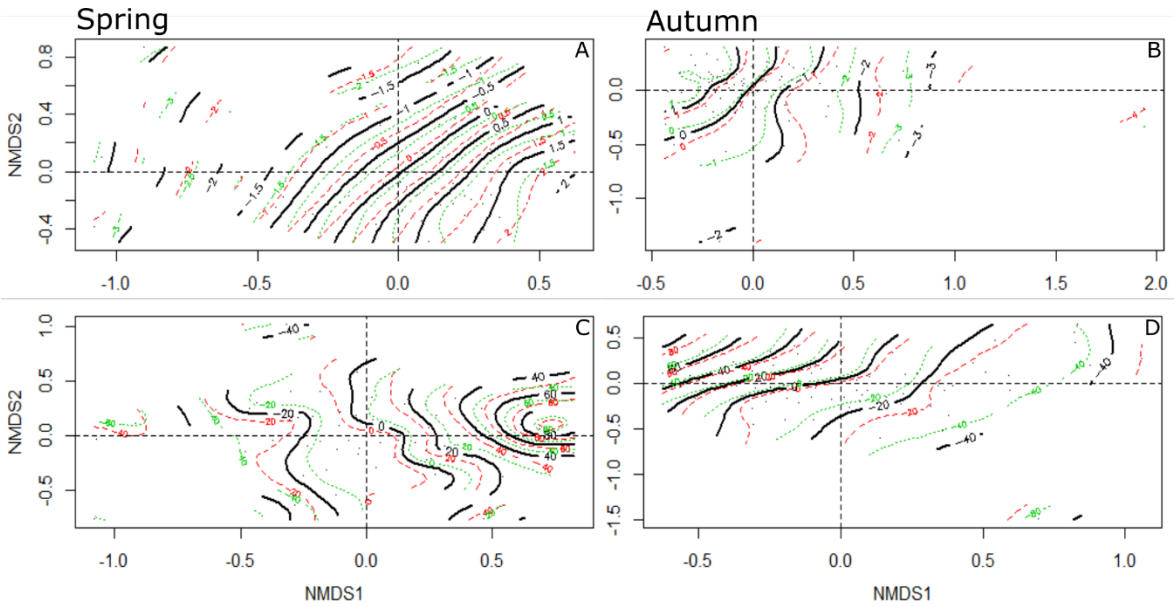

Figure II-4-3: GAM plots representing spatial smoothing of the response variables. (A) GAM model for spring total abundances; (B) GAM model for autumn total abundances; (C) GAM model for spring QBS-ar; (D) GAM model for autumn QBS-ar. Codes represent the quantity by which each response variable varies. Black-solid isolines represent the spatial smoothing that belonged to a determined interval of variation. Red-dashed isolines represent the upper variation of that interval associated with each black solid isoline sharing the same code. Green-dashed isolines represent the lower variation of that interval associated to each black solid isoline sharing the same code.

II-5. Discussion

Understanding the ecosystem processes governing reservoirs of soil biodiversity, and the practices threatening them (e.g., unwise land management), would strongly benefit from characterizing the microarthropod community composition associated with traditionally managed rangelands. Moreover, the use of morphological traits in identifying spatial patterns and diversity of biological forms and relationships with above- and belowground environmental characteristics is a helpful method to detect areas under risk in terms of loss of soil multifunctionality (Wagg et al. 2014; Soong and Nielsen 2016). This need becomes even more urgent since Mediterranean areas are especially sensitive to new climate change scenarios (IPCC 2014). Features of Iberian rangeland ecosystems, such as the patchy distribution of vegetation and the unequal pressure exerted by livestock, may be a major structuring force of soil microarthropod communities at local scales. Nevertheless, several stochastic events (e.g., colonization and extinction) usually more related to regional scales can also take place locally (Gao et al. 2014). The implications of this ensemble of facts on the functioning of such ecosystems are here discussed in order to track the effects of land management on soil biodiversity, and for a better understanding of the mechanisms that enhance its conservation.

II-5.1. The response of the community abundances

The analyses suggest that abundances of microarthropod communities differed in response to the presence of trees and livestock pressure. These differences among community and taxa abundances can be simply explained by the environmental characteristics of each sampling point (Sha et al. 2015). In this context, the analysis based on NMDS allowed us to identify dissimilarities among communities' composition, and sensitivity of taxa populations in relation to spatiotemporal dynamics of niche-environmental parameters. Results suggest that, in general, areas outside the influence of trees harbor higher abundance of microarthropods rather than areas beneath tree canopies. NMDS also reveals a great degree of overlap between locations × SHC categories that could be representative of a geographic dispersal of taxa (at the study area scale) due to the absence of physical barriers and proximity of categories (Gao et al. 2018). It is noteworthy that approximately 80% of variation was undetermined by the multivariate analysis (PERMANOVA), thus, it could be due to other non-spatially structured environmental factors that were not measured in the field (Caruso et al. 2013), or even because of biotic interactions within the microarthropod community due to its spatial aggregation (Tilman 2004; Caruso et al. 2012b). Results of GAM, based on abundances in both seasons, support the results of PERMANOVA. GAM models reflected a clear spatial structure of total abundances, as indicated by approximately 88% of variance explained in both seasons. This indicates that spatiotemporal processes (e.g., dispersal) in relation to local environmental factors drive total abundances of microarthropod communities (Mulder et al. 2008; Caruso et al. 2012b; Dong et al. 2017; Gao et al. 2018). Therefore, soil environmental variables, characteristics of vegetation cover, and livestock pressure alone could not explain by themselves the community aggregation phenomena but a dispersion of total abundances. This fact coincides with Caruso et al. (2013), who concluded that the spatial structure of variables plus the spatiotemporal structure of total abundances reveal that overall abundances are mediated both by dispersal and environmental factors.

Several relationships inferred from NMDS analysis are relevant. Significant taxa, such as Acari, Collembola, Pauropoda, Araneae, and Chilopoda, were related to out-C-SHC_{medium} and out-C-SHC_{low} in autumn, while Acari, Collembola, and Thysanoptera were positively associated with out-C-SHC_{medium} and out-C-SHC_{low} in spring. Such convergence of positive correlations could indicate that lower livestock pressure allows the development of populations and the co-occurrence of microarthropod taxa in the absence of trees, which accords with Mulder et al. (2008). However, an ensemble of biotic and abiotic interactions

could also drive such relationships for instance, soil parameters analyses indicate that trees contribute to rising SOM values, mostly due to litter inputs (Moreno and Pulido 2009), which provide habitat and energy budget to the detrital community. In addition, significant negative relationships between pH, SOM, and abundances of such groups as Acari and Coleoptera in spring, as well as between SOM, and Collembola and Chilopoda (and Coleoptera) in autumn, have been identified. Except for Chilopoda (mainly predators), the other taxa show a wide variety of feeding habits (Coleman and Wall 2015). However, the study presented in this section is limited since the assemblage of communities was performed at a low taxonomical level. Thus, in order to shed light on relationships between feeding habits, environmental parameters, and community structure, an analysis of the functional roles of microarthropods at higher taxonomical level should be performed.

Another inference suggested by results based on NMDS analysis is that Acari and Collembola abundances avoid each other, as mites were more related to out-C, whereas collembolans were more related to in-C areas. However, this affirmation must be put in context: mites and collembolans are dominant and normally coexist in soil. Locally, competition for resources between both taxa (e.g., those with detritivores feeding habits) is expected to benefit some functional groups over others due to negative interactions, as suggested by Caruso et al. (2013) in a study of Antarctic microarthropod communities. As this study lacked a functional characterization of taxa, this affirmation is not sustained by the results. Otherwise, several authors indicate that trees (and litter) in semiarid wood pastures decrease soil evapotranspiration rates (Schnabel et al. 2013; Lozano-Parra et al. 2018b) by sunlight interception (Jiménez-Chacón et al. 2018), and consequently decrease wider fluctuations of soil moisture when compared to open spaces. This causes a response of the entire microarthropod community to light availability as demonstrated by Jiménez-Chacón et al. (2018), who concluded that detritivores preferred darker microsites (e.g., beneath tree canopies). Hence, a higher accumulation of litter and SOM beneath tree canopies, associated with lower rates of evapotranspiration, promoted collembolan abundances and likely inhibited the development of detritivores mites by competition for resources. The opposite occurs in localities where mite populations are greater than collembolans, but these results do not allow for speculation about such dynamics.

II-5.2. The response of the biological forms

In the context of this study, rangeland mismanagement leads to a promotion of undesirable vegetation in terms of livestock profit. However, from the perspective of biodiversity, a

greater number of well-adapted microarthropod communities live in such areas. The measurement of biological forms' adaptation to soil environment involves the evaluation of such traits as depigmentation; reduction of appendages, such as antennae and legs; presence, absence, or reduction of the visual apparatus; presence, absence, or reduction of wings; dimensions; and body shape (Parisi et al. 2005). The higher the score attributed to each trait, the better adapted to a soil environment the organism is. The sums of all these scores serves as the EMI of each biological form. In the same way, the greater the number of biological forms with high scores that lives in the soil, the better quality and stability of the soil (i.e., the less disturbance) (Parisi and Menta 2008). This is the main concept upon which QBS-ar relies and, by definition, it is based on environmental filtering theory. Overall, our analyses suggest that microarthropod communities' evolutive adaptation to their soil environment differed mostly in response to the presence of trees. These differences is in accord with the hypothesis that vegetation cover and environmental characteristics (i.e., habitat degradation caused by livestock pressure) are major forces that structure microarthropod communities even at evolutive level, which accords with the main basis of QBS-ar and environmental filtering theory.

Stress values of the NMDS analysis based on EMI suggest that the goodness of fit on morphological traits was poor. Nevertheless, a clear and significant differentiation between out-C and in-C was identified (stronger in autumn than in spring). In such terms, Meloni et al. (2020) found that abundance and richness of ground arthropods depended on the size and closeness of patches of vegetation in Mediterranean drylands. This fact and the aforementioned result coincide on the positive effect of vegetation on microarthropod communities (trees in the case of this section), and it confirms the hypotheses by which vegetation cover shapes the microarthropod adaptation. NMDS analysis also showed a large degree of overlap between SHC categories, and insignificant effects on EMI communities. Overall, a greater number of taxa showed significant fits to SHC areas and locations. Unfortunately, it is difficult to extract clear inferences in relation to SHC based on these results due to stress values over 0.20. However, disturbances driven by livestock could explain it since several authors consider that well-managed sylvopastoral systems, for instance with livestock charges at 1 AU ha−1 or below (Pulido et al. 2016), could enhance resource allocation within soil food webs (Schon et al. 2008), by, for example, altering the C:N ratio (Peco et al. 2017). This fact supports the niche-environmental hypothesis, and it could explain why SHC_{medium} showed similar patterns to SHC_{low} on QBS-ar values.

Finally, poor values of variance explanation resulted from PERMANOVA. Approximately 87% of the total variance remained undetermined. This implies that the occurrence of morphological adaptation may be related to spatially structured variables or biotic interactions (or both) that were not measured in the field. Results of GAM analyses based on QBS-ar confirm the hypothesis that morphological adaptation also follows a spatially structured distribution. Moreover, it is even stronger than total abundances models. Smoothing patterns also differed from spring to autumn, which were negatively related to the spatial position of trees and SOM in autumn, and only to trees in spring. Therefore, the answer to the third question of this work is that morphological adaptation and abundances did not follow identical, but similar, spatial patterns as confirmed by NMDS, PERMANOVA and, GAM results.

II-5.3. Object-Based Image Analysis and SHC classification

Correlations between microarthropod communities' structure, metrics and evolutive adaptations and SHC classification using OBIA were not as high as expected. This might have been due to the fine scale at which microarthropod populations develop themselves, or to the relatively rapid dynamics of annual grasses. OBIA was chosen as the best candidate to remotely classify objects on the ground when compared to pure pixel classification techniques, but it obviously presents problems regarding the pixel's dimensions of the image. However, OBIA turned out to be a useful technique to identify livestock effects, which would be a useful analysis when performed at larger scales and therefore, to provide indications about soil biodiversity conservation. That being said, it can be confirmed that the results of the analysis corresponded with the areas in which livestock spend more time, as demonstrated in precedent studies about physical-chemical indicators of soil quality (Pulido et al. 2017), impacts of livestock (Pulido et al. 2016), and soil erosion studies (Schnabel et al. 2009; Pulido et al. 2016) realized within the study area.

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Appendix B

Table B 1: Significant comparisons from post hoc Tukey test

Metrics	Factors	Pairs Comparison	Difference	*p*
Ln abundances	Livestock pressure	Low − High	0.568	0.045
	Location	In-C − Out-C	–0.07	<0.001
	Season	Spring − Autumn	–0.051	0.007
	Livestock pressure × Location	High × In-C − Low × Out-C	–1.108	0.009
		High × In-C − Medium × Out-C	–1.147	0.004
		Medium × In-C − Medium × Out-C	–0.9	0.03
	Livestock pressure × Season	Low × Autumn − High × Autumn	0.882	0.038
		High × Spring − Low × Autumn	–1.093	0.032
		Medium × Spring − Low × Autumn	–0.924	0.036
	Location × Season	In-C × Autumn − Out-C × Autumn	–0.651	0.036
		In-C × Spring − Out-C × Autumn	–1.199	<0.001
	Livestock pressure × Location × Season	High × In-C × Spring − Low × Out-C × Autumn	–1.526	0.048
		High × In-C × Autumn − Medium × Out-C × Autumn	–1.427	0.043
		High × In-C × Spring − Medium × Out-C × Autumn	–1.733	0.019
		High × In-C × Spring − Low × In-C × Autumn	–1.781	0.035
QBS-ar	Location	In-C − Out-C	–19.693	<0.001
	Livestock pressure × Location	High × In-C − High × Out-C	–24.222	0.037
		High × In-C − Low × Out-C	–28.101	0.009
		High × In-C − Medium × Out-C	–33.791	<0.001
		Medium × In-C − Medium × Out-C	–23.922	0.027
	Livestock pressure × Season	High × Spring − Low × Autumn	–23.295	0.09
	Location × Season	In-C × Autumn − Out-C × Autumn	–27.661	<0.001
		In-C × Spring − Out-C × Autumn	–24.243	0.002

	Livestock pressure × Location × Season	High × In-C × Autumn − High × Out-C × Autumn	–39.419	0.08
		High × In-C × Autumn − Low × Out-C × Autumn	–34.004	0.051
H′	Location × Season	In-C × Spring − Out-C × Spring	0.197	0.063

Table B 2: Average QBS-ar values ± SD found at each SHC (high, medium and low livestock pressure), in each Location (beneath = in-C and outside the canopy = out-C) during both sampling campaigns.

	Spring		Autumn	
Livestock Pressure	**Out-C**	**In-C**	**Out-C**	**In-C**
SHC_{high}	66.9 ± 28.3	72.1 ± 27.2	104.4 ± 34.2	64.9 ± 23.2
SHC_{medium}	97.1 ± 39.4	80.3 ± 22.2	105.9 ± 27.8	76.8 ± 32.3
SHC_{low}	91.3 ± 22.4	84.8 ± 22.7	98.9 ± 18.4	89.0 ± 31.5

Table B 3: Average Shannon's diversity values ± SD found at each SHC (high, medium and low livestock pressure), in each Location (beneath = in-C and outside the canopy = out-C) during both sampling campaigns.

	Spring		Autumn	
Livestock Pressure	**Out-C**	**In-C**	**Out-C**	**In-C**
SHC_{high}	0.79 ± 0.36	0.78 ± 0.33	0.97 ± 0.27	0.89 ± 0.23
SHC_{medium}	0.76 ± 0.20	1.04 ± 0.41	0.86 ± 0.34	0.83 ± 0.29
SHC_{low}	0.69 ± 0.29	1.00 ± 0.48	0.76 ± 0.26	0.68 ± 0.24

Table B 4: Absolute numbers of microarthropod found at each SHC (high, medium and low livestock pressure), in each Location (beneath tree canopy = In-C or outside the canopy = Out-C) during the first sampling campaign.

	Spring					
	Out-C			In-C		
Taxa	**SHC_{high}**	**SHC_{medium}**	**SHC_{low}**	**SHC_{high}**	**SHC_{medium}**	**SHC_{low}**
Pseudoscorpiones	-	3	-	-	-	3
Opiliones	-	-	-	-	-	-
Araneae	1	-	3	-	2	2
Acari	3,410	3,928	2,882	902	1,116	2,030
Isopoda	-	-	-	-	-	-
Diplopoda	-	-	-	-	-	2
Pauropoda	1	8	1	3	-	-
Symphyla	-	10	3	-	3	-
Chilopoda	2	17	18	4	19	8
Protura	-	1	-	-	-	3
Diplura	30	29	24	3	7	-
Collembola	995	4,368	1,046	3,424	5,584	936
Psocoptera	-	-	-	5	2	7
Hemiptera	1	51	30	14	34	13
Thysanoptera	1	24	7	6	20	8
Zigentomi	-	-	-	-	-	-
Embioptera	1	2	-	6	4	2
Orthroptera	-	-	-	1	-	-
Coleoptera	46	180	28	25	18	12
Hymenoptera	5	26	64	17	153	31
Diptera	-	1	2	2	7	6
Lepidoptera	-	-	1	1	1	-
Coleoptera (larvae)	36	31	30	14	31	34
Diptera (larvae)	29	218	63	64	120	135
Hymenoptera (larvae)	-	-	-	4	-	-
Lepidoptera (larvae)	1	3	1	-	2	2
Holometabolans	-	-	-	-	-	-
Total	4,559	8,900	4,203	4,495	7,123	3,234

Table B 5: Absolute numbers of microarthropods found at each SHC (high, medium and low livestock pressure), in each Location (beneath tree canopy = In-C or outside the canopy = Out-C) during the second sampling campaign.

	Autumn					
	Out-C			In-C		
Taxa	**SHC_{high}**	**SHC_{medium}**	**SHC_{low}**	**SHC_{high}**	**SHC_{medium}**	**SHC_{low}**
Pseudoscorpiones	1	6	1	-	1	-
Opiliones	-	-	-	-	-	-
Araneae	1	5	12	4	3	1
Acari	4,003	5,375	10,370	1,321	2,599	2,498
Isopoda	-	-	-	-	1	-
Diplopoda	-	-	-	-	-	-
Pauropoda	16	383	56	1	29	97
Symphyla	18	9	20	7	1	2
Chilopoda	5	11	2	-	11	1
Protura	2	2	7	-	1	1
Diplura	8	1	-	-	3	1
Collembola	7,079	9,787	13,472	4,708	4,892	10,574
Psocoptera	-	-	-	-	-	2
Hemiptera	102	22	18	243	12	17
Thysanoptera	34	29	11	7	36	13
Zigentomi	-	-	3	1	-	-
Embioptera	-	-	-	7	2	5
Orthroptera	-	-	-	-	-	-
Coleoptera	96	85	29	10	36	32
Hymenoptera	3	17	17	80	58	10
Diptera	31	15	16	7	25	13
Lepidoptera	-	-	-	-	-	-
Coleoptera (larvae)	152	101	92	137	52	69
Diptera (larvae)	1,374	712	226	238	84	71
Hymenoptera (larvae)	-	-	-	-	-	-
Lepidoptera (larvae)	70	16	21	21	4	2
Holometabolans	3	6	1	1	2	1
Total	12,424	16,382	24,310	6,700	7,839	13,410

Section III

Livestock management and trees shape soil arthropod communities in meadows and sylvopastoral areas under semi-arid climatic regime in the central region of Chile

Carlos Lozano Fondón

Javier Lozano Parra

Cristina Menta

Abstract

The ecological functioning of drylands is closely related to the spatial distribution of vegetation as well as to the water cycle. In addition, drylands are critical for the sustain of the 38% of human population, where managed grazing is the most important land use. The diversity and functions of soil communities depends on the resources and protection provided by the vegetation and besides, water present in soil pores represents the medium by which nutrients associated to soil particles become available. The pressure exerted by livestock often reduce the capacity of soils to provide their ecosystem functions due to land surface compaction and vegetation degradation. This ensemble of features shapes the soil arthropod communities, which are highly dependent on such resources and contribute to the functioning of soil ecosystem. This section involved the study of arthropods under severe drought conditions, and how the community changed during a simulated soil rewetting process. The focus relied in what are the spatiotemporal patterns of soil arthropods depending on tree closeness, livestock pressure, and limiting factors? Firstly, 9 points were located in a pasture meadow. A total of 24 sampling points were located in sylvopastoral areas (12 grazed and 12 ungrazed). Then, 40 L of water were added to each sampling point 3 days before the sampling to simulate the soil rewetting process. A spatial transposition of samples to one-dimension scale in reference to the nearest trees was used to track changes in abundance and richness of arthropods. Results elucidated that the response of edaphic arthropods to the rewetting of soils was different depending on the closeness to trees: higher abundance and richness were found away from the trees during the rewetting of soil.

Keywords: arthropods diversity; soil rewetting; grazing; community structure; spatial patterns.

III-1. Introduction

Drylands (e.g., arid, semi-arid, and dry-subhumid ecosystems) are critical terrestrial environments, which are considered to be Earth's largest biome (Prăvălie 2016). They show an Aridity Index (ratio of mean annual precipitation to mean annual potential evapotranspiration) below 0.65 (Maestre et al. 2016), have a climate characterized by infrequent and highly variable rainfall and experience intense solar radiation (Whitford 2002; Maestre et al. 2016), that usually undergo water stress and not continuous cover of vascular plants (Maestre et al. 2016). Drylands occupy the 45% of the total terrestrial surface (Prăvălie 2016; Moreno-Jiménez et al. 2019) and contribute to the sustain of the 38% of human population (Millenium Ecosystem Assessment 2005). About 33 million km^2 of their total surface are destined to managed grazing of domestic animals representing the main land use (Asner et al. 2004; Safriel et al. 2005; Eldridge et al. 2017). In fact, such areas provide essential ecosystem services including soil development, that involves the soil carbon regulation and other nutrient cycles, and primary production for the livestock sustain (Safriel et al. 2005).

Semi-arid bioclimatic areas (e.g., central region of Chile) show high risk of degradation due to grazing pressure (Asner et al. 2004). Into such context, there are still gaps of knowledge about soil biodiversity, the effects of overgrazing on soil organisms, and feedbacks between them and soil multifunctionality. High-intensity grazing is known to reduce organic inputs into the soil by decreasing litter cover, hence reducing litter decomposition, or by diminishing the soil surface's capacity to capture and store rainfall via surface disturbance (Maestre et al. 2016). This imply the reduction of the vegetation cover, where rhizosphere is habitat for the soil biota (Meloni et al. 2020; Meloni and Martinez 2021). For instance, soil arthropod communities are particularly sensitive because they grow intimately associated with plant roots and soil particles. Recently published studies investigated the spatial distribution of their populations in association to roots and bare soil (Meloni et al. 2020; Meloni and Martinez 2021), but less attention has been paid to the effect of soil structure and water dynamics (i.e., soil rewetting processes) on soil arthropods (Erktan et al. 2020). Importantly, only few studies report the response of soil arthropod communities in relation to vascular plants and pastures depending on the intensity of grazing in semi-arid bioclimatic areas (see Lozano-Fondón et al. 2020). Facts, that should be considered in order to lead soil biodiversity conservation practices.

The impacts of grazing on soil biological communities in semi-arid ecosystems depend on grazing intensity, but their consequences are also modulated by local aridity conditions

(Velasco-Ayuso et al 2019). Indeed, the rewetting process of soil is closely related to precipitation and rainfall intensity, that generally occurs in a restricted period of the year. On the one hand, the intensity of precipitation events compromise soil structure (i.e, micro-, and macro-porosity) causing soil erosion, which difficult the access of arthropods to food resources/prey into the soil matrix (Erktan et al. 2020). On the other hand, rewetting processes (that depend on soil texture, as well) modulate trophic interactions occurring among the soil community by segregating micro-habitats and then, affecting soil biogeochemical cycles at local and landscape scales (Erktan et al. 2020). For example, water-filled pores and air-filled pores are habitat for aquatic and non-aquatic organisms respectively, where consumers/resources and predators/prey populations differ depending on their habitus and making difficult the access to resources (Erktan et al. 2020). In addition, such water dynamics influence the volatile transportation in soil, which have implications for arthropod sensing of resources/prey (Brückner et al. 2018). The result of this ensemble of facts is a high aggregation of soil organisms into discrete spots (Bardgett and Van Der Putten 2014), which leads to highly heterogeneous and discontinuous environment where trophic interactions, and subsequently soil ecosystem process are depending on the environmental conditions to take place (Delgado-Baquerizo et al. 2019).

Taking account of the aforementioned, the impact of high-intensity grazing and aridity on soil organisms, and in particular on soil arthropods, is expected to differ depending on their morphological adaptation, and on the micro-habitat where they spend most of their life cycle. Zoologists have classified soil arthropods attending to their morphological traits as follows: (a) epi-edaphic forms, which live mostly in soil surface and have larger dimensions, as well as high movement capacity (Menta and Remelli 2020), (b) hemi-edaphic forms, which live in the soil surface but also spent part of their life cycle into the soil, showing partial depigmentation, and partial reduction of movement and visual organs (Menta and Remelli 2020). And (c) eu-edaphic forms, which are highly adapted to their micro-habitat (i.e., micro-pores), and show high reduction of movement capacity (few cm by day), complete depigmentation, and total loss of visual capacity (Menta and Remelli 2020). Because of the degree of development of traits implicated in their movement, sensing, and visual capacity, some groups of arthropods should be more (or less) sensitive than others to grazing pressure. In addition, morphological traits should be responsible of how rapidly they respond to soil rewetting process.

Additionally, the effects of grazing and soil rewetting on soil arthropods should be dependent on the environmental characteristics of the microsite. For example, it is expected that soil

organisms that are active in semi-arid ecosystems are strongly adapted to such biotic (i.e., food resources, and phenological status of vegetation) and abiotic (i.e., favorable soil physical conditions, and availability of soil water) factors that are available in a particular period of the year (Delgado-Baquerizo et al. 2019; Eldridge et al. 2020; Erktan et al. 2020). Therefore, the understanding of how soil arthropods respond to pressure exerted by livestock, to the addition of water simulating soil rewetting process, as well as to vegetation is essential to disentangle how ecosystem multifunctionality in drylands could respond to future climatic scenarios (Maestre et al. 2016) and what environmental characteristics may be a proxy of reservoir for soil biodiversity (Lozano-Fondón et al. 2020).

III-2. Aims

The study here presented was developed in the semi-arid bioclimatic area of central Chile. The area is located into one of the most productive regions of the country in terms of agriculture-related products. Livestock breeding is a common practice, where sylvopastoral and pasture meadows are usual land uses. On the basis of this, the main hypothesis of this section was stated as the characteristics of the microsite (i.e., closeness to trees, livestock pressure, and presence of herbaceous vegetation cover) should drive the response of arthropods to soil rewetting, and facilitate the maintenance of soil arthropod community structure under extreme drought climatic conditions. Because of the low soil water content, edaphic parameters that are considered to be a proxy of soil water circulation such as the dimension of soil particles, were measured to study if these characteristics could lead to a better circulation of soil arthropods when soil gets rewetted. Since soil physical properties influence the water circulation, and livestock exert a physical disturbance of the soil surface, as well as a decreasing of herbaceous vegetation cover, increasing intensities of livestock pressure should also lead to differences on the structure of soil arthropod communities. Then, the phenological status of the vegetation cover was considered as a proxy of the time that livestock spend on the land. Hence, the aims of this section were: first, to describe the variation of soil arthropod communities as a function of the closeness to trees and edaphic parameters related to soil water circulation depending on the livestock management. Second, to study the effect of the soil rewetting processes on the abundance, richness, and community structure of soil arthropods depending on the livestock management, the closeness to trees, physical edaphic parameters, and the phenological status of herbaceous vegetation.

III-3. Materials and methods

III-3.1. Study area

The study was conducted on the farmland *Agricola y Ganadera Corralillo S.A.,* which is located between the municipalities of *Casablanca* and *Cartagena*, in the *Valparaíso* Province (33˚48'57.45'' S, 71˚41'9.01'' W, Figure III-3-1A). It is an agronomic exploitation of about 16,000 ha, which belongs to *Viña Matetic* brand. The activity integrates the ecological production of agricultural services (mainly vineyards and wine, but also meadows for forage production), as well as cattle breeding (1300 head of cattle: Black Angus 70%, Red Angus 15%, and Ereford 15%). A total of 2500 ha are dedicated to pasture divided in two main land uses (i.e., cropping meadows and sylvopastoral). For meadows, livestock management is considered as extensive with rotation periods of ten to fifteen days that begin in the late autumn (March) and last until the first months in spring (September-October) depending on the rainfall. There are about 100 to 200 head at each rotation, where animals walk freely within the pasture land, and which extension is delimited by farmers (30 to 100 ha). For the sylvopastoral system, livestock walks freely during autumn, winter and spring seasons. In this system, higher number of animals are present at each rotation (about 200 to 300 head of cattle) within areas slightly larger (100 to 300 ha) due the lower forage yield of this land use (about 385 to 634 Kg ha^{-1}, Lozano-Parra, 2019). In summer, livestock feeding needs must be supplied using the integration of fodder, as well as forage yielded from the meadows.

Lozano-Parra et al. (2018a) defined the climate characteristics in the area as representative of semi-arid Mediterranean ecosystems (Csb in accord to the Köppen-Geiger classification, [Rubel & Koppek, 2010]). Average rainfall is under 700 mm, and it is mainly concentrated in the winter season due to the influence of the Pacific Ocean. Average annual temperature oscillates about 11˚C. Summers are dry and warm, meanwhile winters are rainy and temperate. Soils are classified as Luvisols and Calcisols according to FAO, (2006), where concentration of organic matter and potassium are extremely low, and texture is mainly clay-loam.

Into this context, two study areas were chosen as representative of the main pastoral land uses within the limits of the farmland. The first study area is a sylvopastoral system (SpS) (Figure III-3-1B) that is representative of semi-arid Mediterranean *espinares*. Due to land management, vegetation is structured in SpS as follows: a layer of scattered trees (*Acacia caven* Molina and *Prosopis chilensis* Molina) at medium-low cover density (25 – 50%), and

an herbaceous layer mainly dominated by the *Phalaris* genus. The climate characteristics, vegetation structure and management make *espinares* comparable to systems located in other regions around the world such as *dehesas* in Spain, *montados* in Portugal, or rangelands in California (USA). The second study area is a cropped *Phalaris sp*. meadow of about 70 ha (PhM) (Figure III-3-1C), which management is conventional. In other words, ploughing, and the use of pests and herbicides are usual. In addition, fertilization is chemical and usually applied when annual precipitation is low. The seeding of the meadow was in 2012, which was previously ploughed and fertilized. The average yield of the meadow oscillates between 4,000 and 9,000 Kg of dry mass per year. Moreover, the main provision of organic matter to the soil of both study areas comes from the defecation of cattle, as well as from the dead plant material.

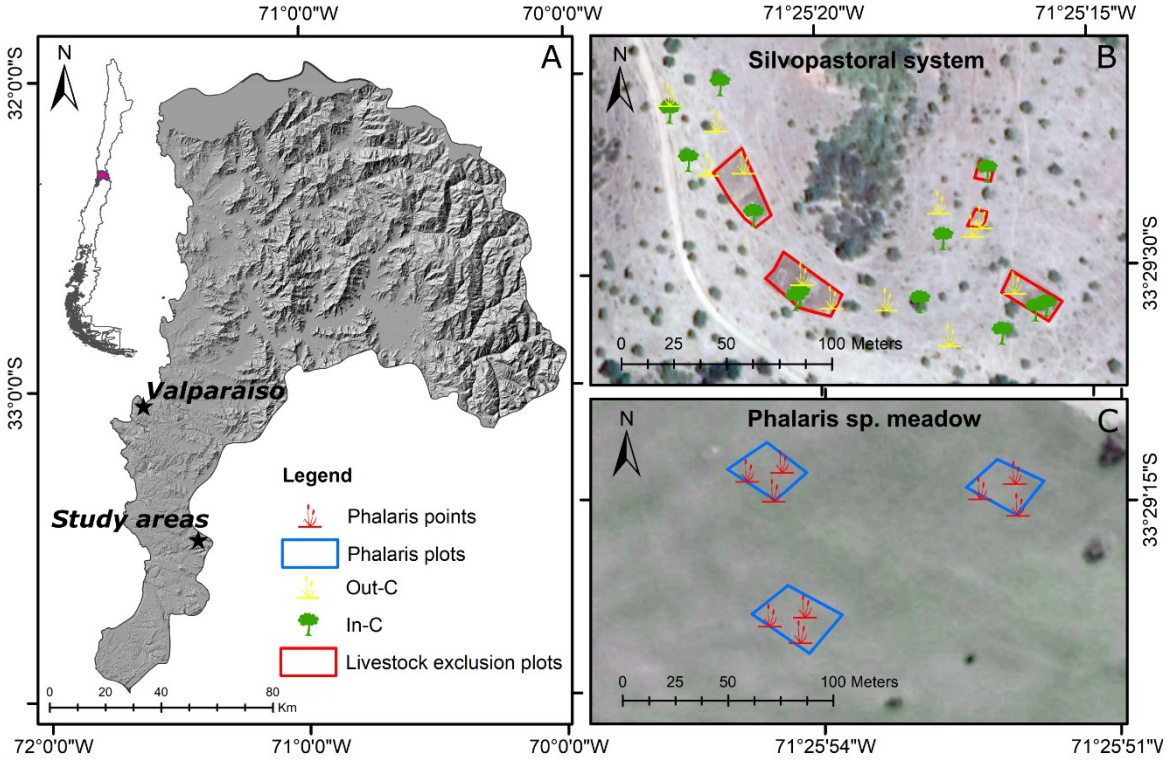

Figure III-3-1: (A) Situation of the farmland Agricola *y Ganadera Corralillo S.A. in the region of Valparaíso, in Central Chile. (B) detail of the sylvopastoral study area (SpS), where in-C represent soil samples collected beneath the tree canopy, and out-C stands for soil samples collected outside the tree canopy (i.e., open space). Red-boundary plots represent livestock exclusion areas. (C) detail of the cropped meadow of Phalaris sp (PhM), where some trees can be appreciated. Blue-boundary plots stand for representative homogeneous areas where soil samples were collected. B and C images were obtained from Google Earth.*

III-3.2. Soil sampling

Sampling was carried out during the spring season of southern hemisphere (November) in both study areas. In order to represent the different conditions in SpS (Figure III-3-1B, Figure III-3-2A, and Figure III-3-2B), sampling points were placed beneath the tree canopy and in open space. Moreover, to study the effect of livestock pressure, half of points were located inside plots that were limited to grazing (three years before the sampling), and the other half on grazed areas. Experimental design was performed as follows: for SpS, six points were placed beneath the tree canopy (in-C), three on grazed areas, and three inside the plots (ungrazed). Besides, six points were placed in open space (out-C), three on grazed areas, and three inside the plots (ungrazed). In order to study the effect of soil rewetting process on the arthropod community, a new sampling was carried out following the same experimental design. This time, 40 L of water were added to each sampling point three days before the collecting of soil cores (Figure III-3-2B). Thus, the total number of samples collected in SpS were twenty-four. For PhM (Figure III-3-1C, and Figure III-3-2C), three square plots (10 × 10 m) were placed within the limits of the meadow at known distance from trees, where three soil samples by plot (a total of nine) were collected at the vertices of a three-side polygon within each plot. For PhM, it was not possible to execute a second sampling with the 40 L water treatment due to the social disturbs that occurred in Chile during that period. In both study areas, soil temperature *h* and water content *w* were measured at the moment of the sampling in three points next to each soil sample by using a MSFS-TDR350 device.

Figure III-3-2: Detail of the various sampling areas. (A) Sylvopastoral system (SpS) ungrazed. (B) Sylvopastoral system (SpS) grazed with the treatment of 40L of water. (C) Phalaris sp. meadow (PhM).

III-3.3. Laboratory analyses and data organization

One soil core per sampling point (3.5 dm^3) was picked up and taken to the laboratory. Cores were placed in Berlese-Tüllgren funnels for arthropods extraction. Once the organisms were extracted, particulate proportion of samples was determined using seven soil sieves (mesh

sizes 4.75 mm, 2 mm, 1 mm, 500 µm, 250 µm, 125 µm, and 63 µm). Samples were weighted before the treatment, and them shook for two minutes using a Retsch AS200 basic shaker. The remaining soil material in the sieves was weighted and then, the particles proportion was calculated using the following equation:

$$t = \frac{S_i - S_0}{X_0} \times 100 \quad \text{[III-1]}$$

where, t is the relative content of particles in percent units, S_i is the weight of the sieve plus the soil content measured in grams, S_0 is the tare of the sieve measured in grams, and X_0 is the initial weight of the soil sample measured in grams. In order to obtain the fractions of particles relative to coarse, sand, loam, and clay, the soil material that remained on the sieves was treated as follows: the clay fraction was obtained as the sum of the soil material present in sieves with mesh sizes of 125 and 63 µm. The loam fraction was the result of sum the soil material in the sieves of 500 and 250 µm mesh size. The sand fraction was calculated as the sum of the soil material present in the sieves of 2 and 1 mm mesh size. Finally, the coarse material was the remaining material in the sieve 4.75 mm mesh size.

Normalized Differential Vegetation Index (*NDVI*) and Normalized Differential Water Index (*NDWI*) were obtained by analyzing remote sensed images form the Sentinel 2 mission. Images, dated on 5th December 2019, were downloaded from the Copernicus web site and then treated by using the software ArcGIS 10.4.

In order to determine the influence of the tree on the soil arthropod communities, the categorical predictors in-C and out-C were transformed into a spatial variable (Figure III-3-3). This decision was based on the methodology utilized by Meloni *et al.*, (2020), and by Meloni and Martinez, (2021), who performed closeness-vegetation descriptors to determine the facilitation phenomena between patches of vegetation and soil arthropod communities in drylands. To this aim, the canopy diameter T (meters), and the average distance to the four nearest trees D (meters) were considered to assign a descriptor based on the distance to the tree x. Therefore, a sample i obtained in the soil beneath the tree canopy shows $T_i \neq 0$ and $D_i = 0$ (no distance from the tree), while a sample j obtained in the soil outside the canopy shows $Tj = 0$ and $Dj \neq 0$. Thus, the x values are the subtraction of T and D of each sample, obtained as

$$x_{i,j} = T_{i,j} - D_{i,j} \quad \text{[III-2]}$$

where *i* and *j* are samples taken beneath the tree canopy and outside the canopy, respectively. According to equation III-2, *x* takes values between $-\infty$ and $+\infty$. Positive values stand for samples taken beneath the tree canopy and negative values represent samples taken in open space. For samples collected in PhM, the procedure was slightly different as the density of trees was lower than in SpS and there were no samples taken beneath tree canopies (Figure III-3-3). In this case, it was considered only the average closeness of each sample to the four nearest trees P_t (meters) present in the meadow. The expectation was to identify whether the soil arthropod community changed as the closeness to trees increases. Then, the relationship was computed as

$$x_j = -P_t \qquad \text{[III-2]}$$

where *j* represents the sample taken in the meadow. Then, *x* (always negative) is expected to approach the zero value as the closeness to the tree increases (Figure III-3-3).

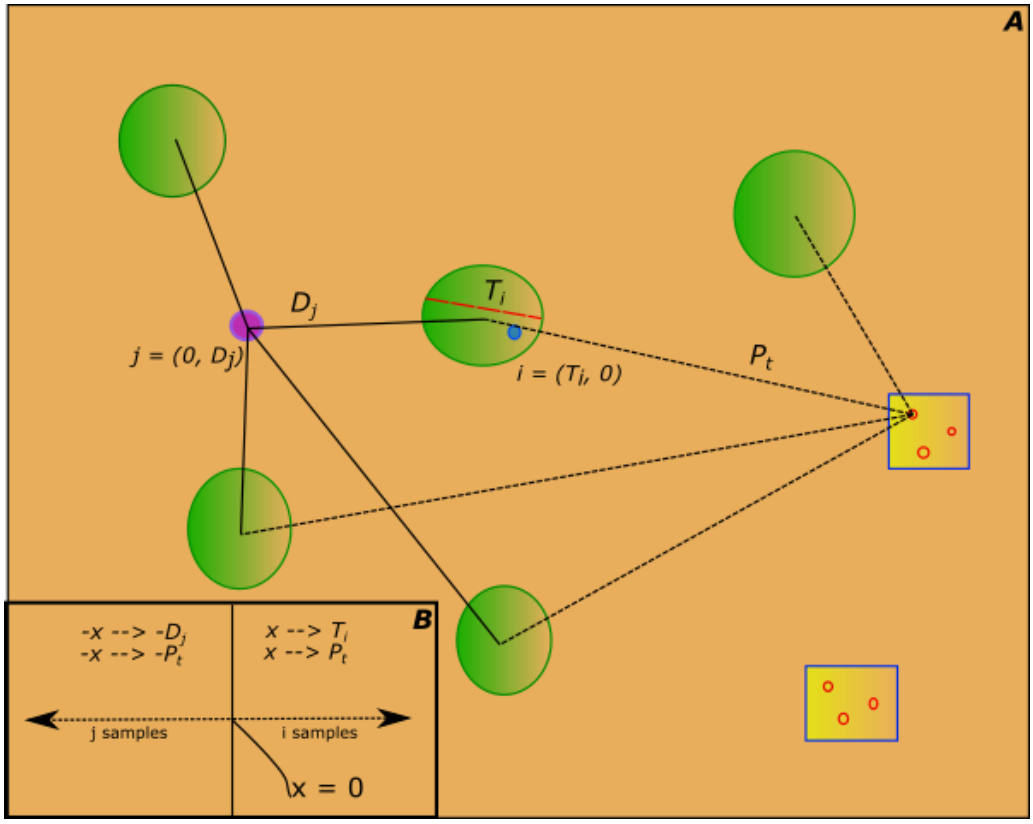

Figure III-3-3: Schematic representation of the sampling and the spatial transposition used in the present section. The panel A merges the schema of both study areas: green ellipses represent the scattered tree layer within the sylvopastoral system (SpS), while blue-boundary squares represent the homogeneous plots in the Phalaris sp. meadow (PhM). The letter j stands for samples taken outside the tree canopy (purple filled circle) and bold black lines connecting it to green ellipses represent the distances that were used to compute the average closeness of such samples to trees (D_j). T_i stands for the canopy diameter with which were associated the samples collected beneath the tree canopy (blue filled circle). Note that j and i samples are composed by two components representing the value of T and D: j samples show zero value in relation to the tree canopy diameter T, while i samples show zero value in relation to the average distance to trees D. Red circles represent the PhM sampling points

and dashed lines stands for the distances used to compute the average closeness to the four nearest trees (P_t). The panel B depicts the 1-d transposition of all samples in terms of a unified and continuous behavior, which is addressed as x-coordinates. The non-zero values of T or P_t determines +x coordinates, while the non-zero values of D or P_t determines -x coordinates. Modified from Meloni and Martinez (2021).

III-3.4. Soil arthropods

The analysis of the soil arthropod community was based on the morphological adaptation of organisms to the soil. Arthropods were extracted from the 33 samples using Berlese-Tüllgren funnels (3 mm mesh size) and conserved in 70 % ethanol solutions. The extraction time was eight days. Then, the extracted arthropods were observed using a stereomicroscope (40×) Leica M3C, counted, identified, and classified as showed in Table III-4-1 attending to their morphological traits. Once counting and identification of the soil arthropods was completed, richness of morpho-biological forms (*S*) was calculated, as well as the abundance (*A*) and associated to each sample. Both richness *S* and abundances *A* were transformed into logarithmic scale (i.e., *ln(S)* and *ln(A)*, respectively) for a better evidence of the independent variables influence (Meloni et al. 2020).

III-3.5. Statistical analyses

Two response variables were considered: abundances *ln(A)*, and morpho-biological forms richness *ln(S)*. A first screening of the data was carried out following the protocol proposed by Zuur et al. (2010). Data were classified attending to the livestock pressure (i.e., heavy grazing for SpS-grazed and no grazing for SpS-ungrazed areas, and medium-intensity grazing in relation to the meadow).

Initially, two one-way ANCOVAs with one covariate at time (i.e., the tree closeness descriptor *x*, and the soil water content *w* before and after the treatment of the sampling points with water) were performed to test statistical differences among the grouping categories and to describe the variability of data attending to both quantitative parameters. For soil water content, there were considered both before and after the treatment of soil with water. The statistical significance was stablished at P = 0.05. Linearity, homogeneity of regression slopes and normality of residuals were tested, this last by using the Shapiro-Wilk test. In addition, a sample-based analysis was performed considering the livestock management factor to examine the individual importance of each explanatory variable for arthropod abundance and richness. To this aim, multiple linear regressions were used. A step-by-step process was followed in order to find the best combination of variables

explaining the variance of data, where the importance of each single explanatory variable relied on the statistical significance.

Finally, the effect of *x* and *w*, as well as the other explanatory variables (i.e., dimension of soil particles, NDVI, NDWI, and soil temperature *h*) were tested on the community composition of each sample by using Canonical Correspondence Analysis (CCA) (Ter Braak 1986). The test was computed with the function *cca* from the *vegan* package (Oksanen et al. 2019). Multicollinearity was firstly checked with the variance inflation factor (VIF). Variables were considered as redundant and then, excluded from the analysis when VIF < 10. The entire statistical analysis was performed with RStudio 1.4.1106.

III-4. Results

In general, 1,380 organisms belonging to 21 groups of edaphic arthropods were individually identified and counted. Mites, springtails, ants, and larvae of coleopterans were the most frequent groups (61%, 15%, 7% and 5%, respectively) representing 88% of the total abundance. Higher abundances and richness were found in the ungrazed areas before and after the soil rewetting process compared to heavily grazed areas in SpS, while in PhM were found higher abundances and richness than in grazed areas before the rewetting (Table III-4-1).

Table III-4-1: Absolute numbers of arthropod found at each land use (i.e., livestock management). SpS = sylvopastoral system, PhM = Phalaris sp. meadow.

	SpS		**SpS** (after water treatment)		**PhM**
Morphological form	**Grazed**	**Ungrazed**	**Grazed**	**Ungrazed**	**Managed grazing**
Pseudoscorpions	-	-	-	2	-
Scorpions	-	-	-	1	-
Epi-edaphic spiders	-	-	1	5	-
Opiliones	-	10	-	-	2
Oribatid mites	16	30	73	133	35
Other mites	125	60	85	276	167
Epi-edaphic collembolans	2	-	6	49	12
Hemi-edaphic collembolans	-	-	135	1	4
Eu-edaphic collembolans	-	-	1	-	-
Woodlice (isopods)	-	-	-	3	-
Millepedes (diplopods)	-	-	-	7	-
Pauropods	-	-	1	2	-
Epi-edaphic coleopterans	-	1	4	14	3
Larvae of coleopterans	4	19	3	36	24
Psocopterans	25	3	12	5	27
Dipterans	1	3	-	7	-
Epi-edaphic hemipterans	-	17	3	5	43
Winged hymenopterans	-	12	-	-	-
Ants	-	1	93	-	-
Larvae of dipterans	-	1	2	-	-
Moths (lepidoptera)	-	-	-	1	-

III-4.1. The response of community descriptors

Statistical differences on soil arthropod abundance and richness of morpho-biological forms were identified in relation to the closeness to the trees depending on the livestock management. In addition, abundance and richness of morpho-biological forms were strongly dependent on the treatment of soil with water but independent of the livestock management (Table III-4-2). The influence of water content on soil arthropods ($F = 12.179$, $P < 0.01$ and $F = 17.418$, $P < 0.001$ for abundances and richness, respectively) was higher than the effect of the interaction tree closeness descriptor with the land use ($F = 3.374$, $P < 0.05$ and $F = 3.650$, $P < 0.05$ for abundances and richness, respectively). In addition, it was identified an influence of the livestock management on soil arthropod richness ($F = 4.707$, $P < 0.05$) since the number of morpho-biological forms was lower in PhM than in SpS.

*Table III-4-2: Results (F and P values) of ANCOVAs on arthropod abundances and morpho-biological forms richness as a function of the factor livestock management and covariates tree closeness descriptor (x) and soil water content (w). A = abundance; S = richness of morpho biological forms; N = 33; *, **, ***: significance codes at 5%, 1% and 0.1%.*

ANCOVAs	***ln(A)***		***ln(S)***	
Covariates and fixed factors	**F**	***p***	**F**	***p***
x	1.079	0.308	1.439	0.141
Livestock management	0.039	0.962	1.629	0.886
x : Livestock management	3.374	0.041*	3.650	0.049*
w	12.179	0.002**	17.418	<0.001***
Livestock management	1.639	0.213	4.707	0.018*
w : Livestock management	0.084	0.920	0.513	0.604

At the sample scale, arthropod abundances were explained by the soil water content ($P < 0.001$) and the dimension of soil particles (i.e., clay $P < 0.05$ and sand content $P < 0.01$). The regression model explained the 39% of the total variance of data and it was significant at 0.1% (Figure III-4-1A). In addition, the closeness to the tree did not explain the variance of abundances data significantly, therefore the variable was removed from the modelling process. Conversely, the richness of the soil arthropod community was related to the closeness to the tree ($P < 0.05$), as well as to the livestock management ($P < 0.01$) and to the water content ($P < 0.001$). The regression for richness of morpho-biological forms explained the 43% of the total variance and it was statistically significant at $P < 0.001$ (Figure III-4-1B).

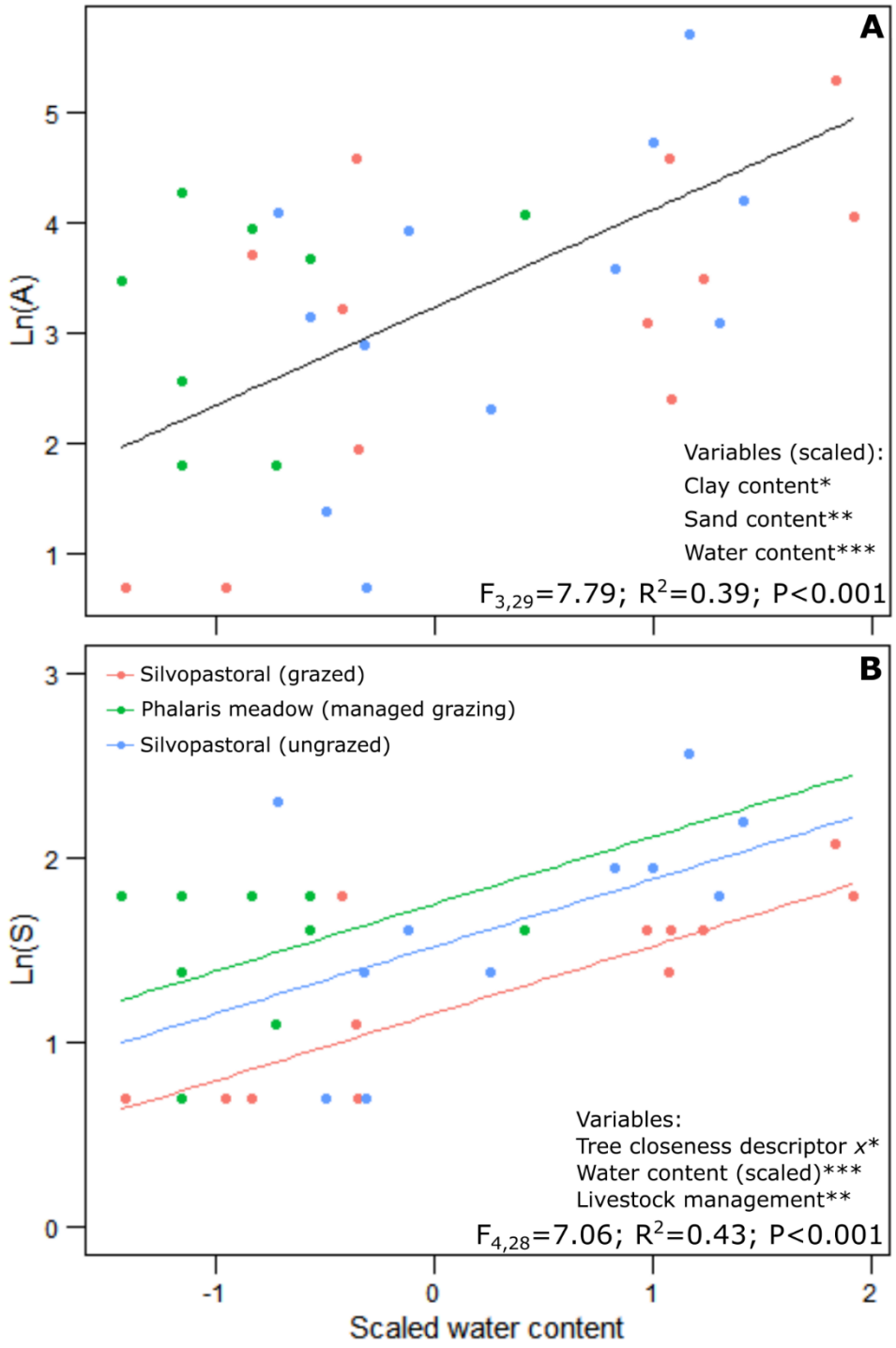

*Figure III-4-1: Relationships between ln-scaled arthropod abundances (ln(A)) (panel A) and richness (ln(S)) (panel B) and the scaled water content as a function of the land use (i.e., livestock management). Linear models were computed taking account the effect of all the explanatory variables, whereas in graphs are reported only the significant variables after the model selection process. The black line in the panel A represents the linear regression between ln(A) and the significant variables water content, clay and sand content. Livestock management was not included in this regression because its effect was not significant. Lines green, blue and red in the panel B stand for the significant regressions of the tree closeness descriptor x and w on the PhM, SpS-ungrazed, and SpS-grazed respectively. N = 33; *, **, ***: significance at 5%, 1% and 0.1%.*

Absolute numbers of abundances and richness were plotted as a function of the closeness to trees (Figure III-4-2). The relationship between such distance and the soil arthropod

community descriptors seems clear, however the results of the ANCOVAs were not as robust as expected. More homogeneous communities were collected in PhM compared to SpS, which values showed higher variances. Though, this variation was the result of the soil rewetting process, where the dimension of soil particles showed statistical significance (Figure III-4-1A). On average, lower abundances (Figure III-4-2A) and richness (Figure III-4-2B) were founded in the PhM-plot located 70 m away from the trees. However, both parameters were similar to those found in SpS before the rewetting. Richness and abundance were slightly higher in the other two PhM-plots located at 40 m of the nearest four trees. On the other hand, the communities collected in SpS showed variation from some individuals to hundreds of them because of the soil rewetting process. Before the rewetting, similar values of abundance and richness were identified both beneath the tree canopy and in open space. Abundance beneath trees in grazed areas showed higher values after the treatment compared to ungrazed areas. In contrast, samples in open spaces showed a similar increment of abundance except for one sample in the ungrazed area. The response to soil rewetting was slightly different for the richness values, which showed higher increases in ungrazed open spaces compared to their respective grazed areas. On the contrary, samples located beneath trees both in grazed and ungrazed areas showed similar increases of morpho-biological forms.

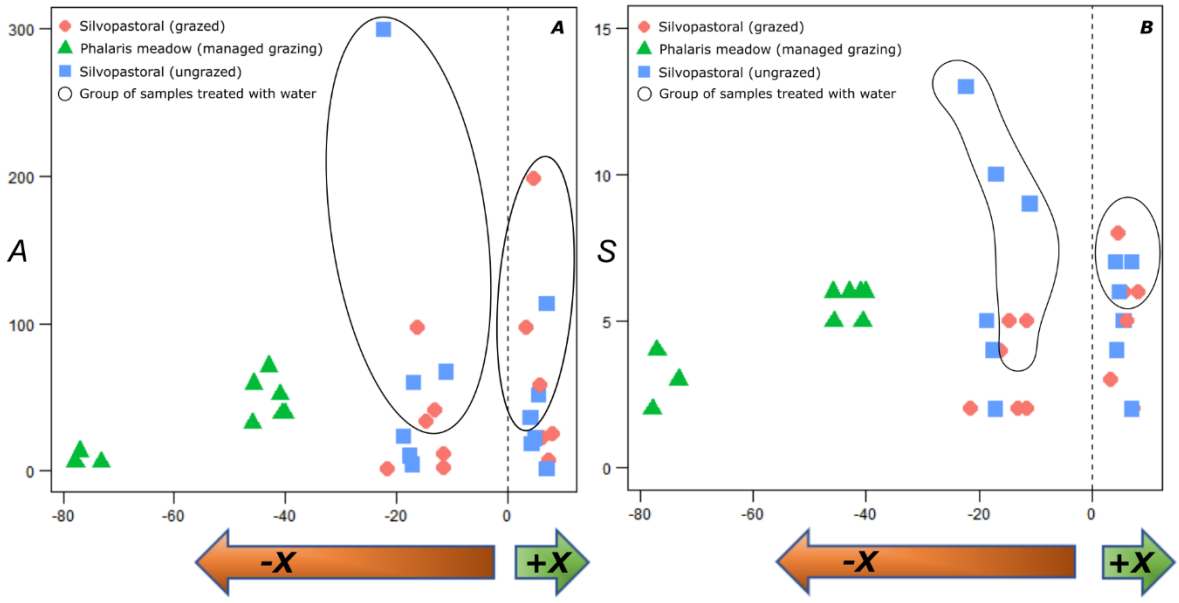

Figure III-4-2: Spatial distribution of the absolute abundance (A) and morpho-biological forms richness (B) of soil arthropods as a function of the closeness to trees descriptor (x), that were observed beneath the grazed and ungrazed tree canopies in the silvolpastoral system (SpS) (positive values of x), in grazed and ungrazed open spaces in SpS (negative values of x), and within plots located in the Phalaris sp. meadow (PhM) (negative values of x).

III-4.2. The response of community structure

The CCA (Figure III-4-3) revealed the general influence of the livestock management on the community composition. The constraining process explained the 48% of total data dispersion, and the dimensions CCA_1 and CCA_2 explained, respectively, the 45% and the 31% of the constrained variation in community composition. Some biological forms such as emi-edaphic collembolans were significantly correlated ($P < 0.05$) to the tree closeness descriptor, silt and clay contents, water content and NDWI, that was a characteristic response of SpS-grazed samples collected beneath trees. Moreover, higher variability of the community composition was related to such areas. Otherwise, higher numbers of ants were also found in such areas but negatively correlated ($P < 0.05$) to the closeness of trees. Epi-edaphic hemipterans were common in the PhM meadow and highly correlated to the sand content, soil temperature and NDVI. Less variable communities were found PhM and SpS-ungrazed samples as showed by the CCA constraining analysis, where high values of sand content, coarse and NDVI were identified. On the other hand, the group of soil parameters determined in samples collected in SpS-grazed were high in water, clay, and silt contents, (factors usually related to water retention capacity in soils).

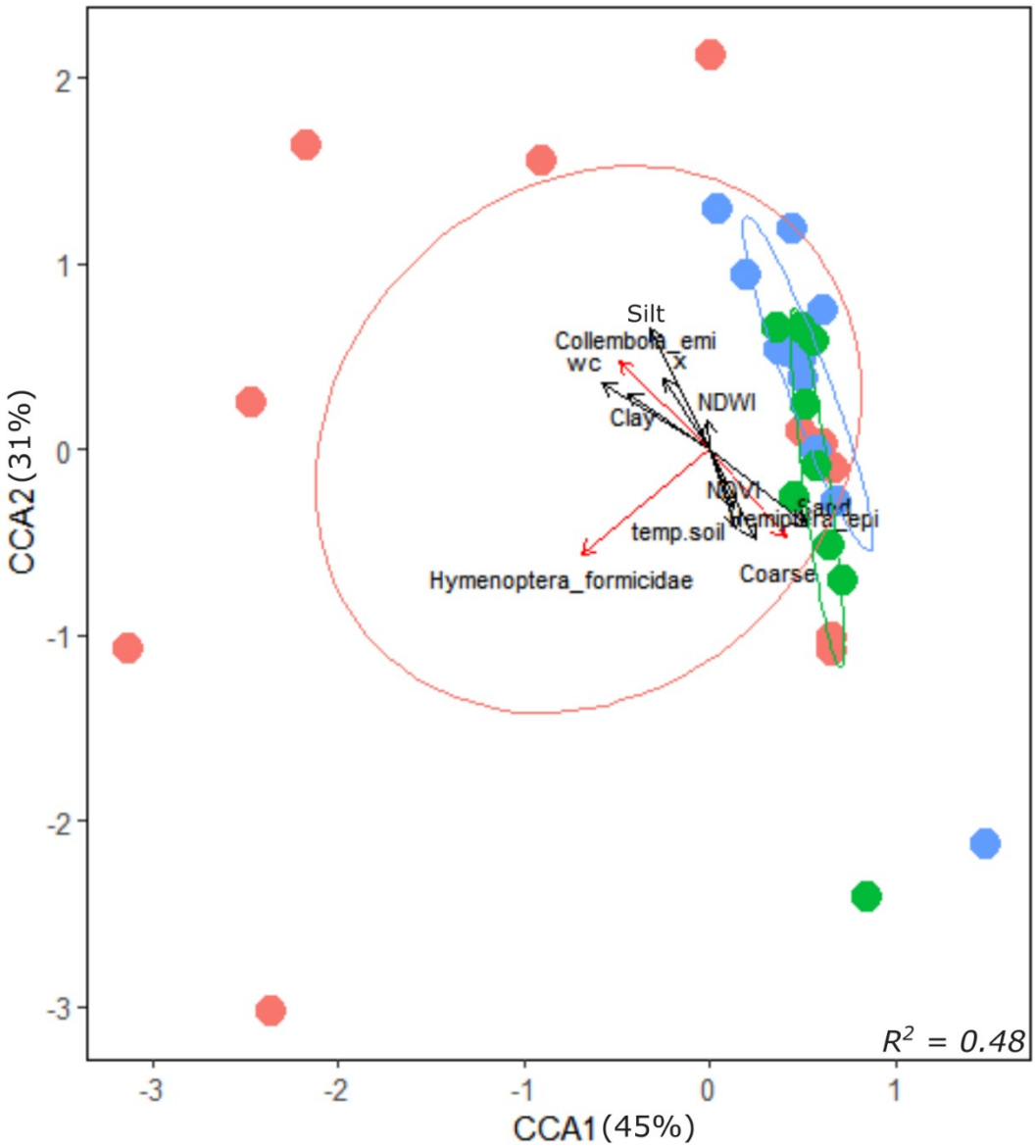

Figure III-4-3: Variation in the composition of soil arthropod communities sampled in the land uses with different livestock management, according to the ordination resulting from Canonical Correspondence Analysis (CCA). Red-filled circles: soil arthropod communities within the SpS-grazed areas; blue-filled circles: soil arthropod communities within the SpS-ungrazed areas; green-filled circles: soil arthropod communities within the PhM area. Red arrows: significant correlations of morpho-biological forms with the ordination axes; black arrows: significant correlations of explanatory variables with the ordination axes.

III-5. Discussion

The present section points out to describe the response of soil arthropod community to the closeness to trees, livestock pressure and soil rewetting processes. Despite the abiotic limitations that characterize Chilean semi-arid systems, the soil arthropod community is diverse and includes key groups, such as oribatid mites, hemi-edaphic collembolans, woodlice, and millepedes, that play critical roles in regulating organic matter demolition and mineralization processes, and that remain active under very dry conditions (Wallwork 1970;

Withford 1996; Meloni et al. 2020). On the contrary, groups such as Pseudoscorpions, eu-edaphic collembolans, and pauropods appeared during the soil rewetting process in ungrazed areas, which could be an evidence of their vertical movement when the environmental conditions in the upper layers of the soil are favorable (Wasserstrom et al. 2016), as well as due to the availability of food resources that became available with the increase of soil moisture (Erktan et al. 2020). Additionally, some investigations have showed that bacteria feeding on root exudates produce volatile compounds informing starving bacteria in their neighborhood about the presence of food resources (Schmidt et al. 2011; Tyc et al. 2017; Erktan et al. 2020). Such fact could modulate the activity of arthropods by sensing that stimulus, which could explain the higher diversity and number of organisms found after the rewetting. The worst condition in terms of abundance and richness was found in the intensively grazed areas before the treatment with water, where only mites, collembolans, psocopterans, and larvae of dipterans were identified. Such fact reveals their high tolerance to drought, which coincides with other studies that identified these groups in arid ecosystems (Cepeda-Pizarro and Whitford 1989; Noble et al. 1996; Wasserstrom et al. 2016). Moreover, heavily grazed areas were associated with the highest variability of abundance and group diversity.

In addition, it is noteworthy the remarkable effect of soil moisture on soil arthropod communities, which only after three days showed a response in terms of abundance and richness. The increase was positive both in SpS-grazed and ungrazed but higher in the areas with herbaceous and vascular vegetation cover. The explanation relies in the fact that the effect of water together with a wetter rhizosphere provided higher availability of resources for the arthropod community (Wasserstrom et al. 2016). Higher uncertainty of the community composition was found in areas with intense grazing (i.e., absence of herbaceous vegetation cover). Whereas, more similar communities of soil arthropods were obtained in areas excluded to grazing and in the meadow. This last, as a consequence of the homogeneous plant cover. However, abundance and richness of arthropods were lower in the grazed meadow than in the sylvopastoral area. This fact could be due to the influence of the dimension of soil particles during the rewetting process, as well as to the low density of trees in such area. The low heterogeneity of grazed meadows landscape was in fact reflected in less variable communities of soil arthropods, which seemed to increase in terms of abundance and richness as the closeness to trees increased. The explanation relies on the fact that soil arthropods depend on resources and protection provided by plants (Coleman et al. 2005; Lozano-Fondón et al. 2020; Meloni et al. 2020). Additionally, Meloni and Martinez

(2021) revealed the existence of a region of maximum uncertainty located in the bare soil of drylands with patched vegetation, which is in accord with our findings related to the high variability of the community composition in open spaces of the sylvopastoral grazed area. This area reveals the bare soil region where soil communities switch, from a simple community, with few organisms and species, to a more diverse community, with larger abundance and species richness (Meloni and Martinez 2021). The authors conducted their experiment on an arid steppe from the SE Spain, where the tree layer lacked and the main vegetation cover was patches of herbaceous plants and identified a range of positive influence of the herbaceous patch which oscillates between 0.35 and 0.50 m far from it in direction of bare soil (1.00 m in extreme cases). Instead, such range of influence could not be defined on the light of the results in due probably to the low number of samples. Nevertheless, the positive correlation between the closeness to tree descriptor and the richness of the communities was stablished, and seemed to be larger in terms of distance compared to patches of herbaceous vegetation. This fact could represent a future research line to disentangle such feedbacks in relation to the pressure of the livestock and factors that limit the growth of soil communities as the soil moisture.

The environmental conditions prevailing at the moment of sampling, which are indeed characteristics of semi-arid ecosystems in the central area of Chile i.e., drought and intense solar radiation, the low availability of organic matter and moisture in the soil (Padarian et al. 2017), the high bulk density related to the effect of livestock (Asner et al. 2004; Padarian et al. 2017) cause environmental filter to the soil arthropod community. For example, interesting findings reported by Synodinos et al. (2015) show that the impact of grazing on vegetation cover change with soil moisture availability: under favorable climatic conditions, vascular plants take advantage over herbaceous vegetation cover and colonize the bare soil. While under dry conditions, the impact of grazing is negative for vascular plants, which leads to soil degradation (Lohmann et al. 2012; Synodinos et al. 2015). Although the focus of that study lacks the diversity of soil communities, the reported effects should show an impact on them since soil organisms are highly dependent on resources provided by plants.

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Section IV

Conclusions

IV-1. Main remarks

The framework of this dissertation focusses on the ecology of soil arthropods, their role on the functioning of ecosystems, and the structuring forces acting on community composition. Here, I present the conclusions that have been inferred after the discussion of results. The study has been developed in four different geographical locations: the ecosystems were representative of forests with continental (northern Apennines) and Mediterranean (southern Apennines) climatic regimes, that were compared between them with a focus on microarthropod diversity and the consequences of seasonal changes of biodiversity on carbon cycling. In addition, study areas in Spain and Chile were representative of sylvopastoral systems that differed in livestock and land management, and vegetation species but their environmental characteristics and climate regime were similar. Both locations have been described as semi-arid Mediterranean areas (Rubel and Koppek 2010; Fernández et al. 2018; Lozano-Parra et al. 2018a, b). A severe drought was occurring in the central area of Chile at the moment of the sampling, whereas the environmental conditions in Spain were particularly wet. Both Chilean and Spanish study areas were oriented to livestock production, which is considered as extensive (Pulido et al. 2016; Lozano-Parra et al. 2018a). Although, the head per hectare under such grazing activity are low, the difference between the Chilean and Spanish study areas relied in the management: in Spain, livestock walked freely during the whole year, and four kinds of livestock coexisted within the limits of the farm (i.e., sheep, goat, cattle, and pigs). Such fact entailed to an heterogenous spatial distribution of the pressure exerted by the livestock, which was determined for the study by the using of remote sensed images. Such heterogenous pressure enabled the occurrence of patches of vegetation varying from bare soil and annual grasses in the heavily grazed areas with presence of trees, to annual grasses and shrubs (but also trees) where livestock spent less time. Chilean sylvopastoral area got more uniform livestock pressure, in other words, definite number of head and rotation times were used by the farmer. Such practices derived in a homogeneous distribution of cattle, which reduced soil degradation rates. The microarthropod community in the study area from Spain showed highly variable community composition in terms of diversity, abundance and adaptation to soil even in heavily grazed areas with respect the communities found in Chile. In fact, the management in the Chilean farm should enhance the diversity of soil communities. Instead, environmental drought

played a crucial role, which prevailed over the anthropogenic factor structuring microarthropod community even after the simulation of soil rewetting in the location of sampling points. In addition, the community composition strongly responded to the presence of trees. Results from Spain and Chile were comparable about tracking the effect of trees, which facilitate the soil community recovering as demonstrated by the diversity values before, and during the soil rewetting process in Chile, as well as the diversity values out, and beneath the tree canopy in Spain. In both areas, the response of community composition to soil moisture was clear. In fact, the spatial structure of soil parameters (i.e., soil organic matter in the Spanish study area, and soil particles proportion in Chile) were crucial factors influencing the diversity and abundance of microarthropods. In addition, both grasses and vascular plants present in both study areas were an important factor on which the diversity of the arthropod community depended on. The reason relied in the fact by which plants (i.e., the radicular systems) provide protection and resources to such communities. Finally, the occurrence of well-adapted biological forms to the soil environment seemed to be more related to the elements of the landscape (i.e., in terms of habitat structure) rather than to spatial variation of soil parameters and absence of indicators of soil physical disturbance. This last consideration may have ecological implications when practices for conservation of biodiversity are applied.

The network models presented in section I points out to the role of microarthropod on carbon circulation in two beech forests from the Italian Apennines that differed in latitude and climate regime. The one from the north was subjected to the continental climate, while climatic characteristics in the southern forest were representative of Mediterranean climate (Innangi et al. 2015b; De Marco et al. 2016b; Fioretto et al. 2018). In such context, the composition of the soil community found at each site was similar in terms of biomass of microarthropods with slight seasonal variation. Nevertheless, such changes showed remarkable effects on carbon flow (i.e., rates of decomposition, carbon sequestration and predation), and stability of the soil food web. The explanation relied both on the climatic characteristics of each system and the loss of several top-predator groups. In fact, microarthropod groups such as Protura (microbivore), Acari (detritivore/predator), Coleoptera (omnivore), Diplopoda (detritivore), and Chilopoda (predator) were identified as keystone groups which importance changed seasonally. Subsequently, it was inferred that the ecosystem process carried by the soil food web depended on the dynamics of such groups, as well as their stability. On the light of these results, the variation of community composition at each studied ecosystem may indicate that the impacts of livestock

management and climate should shape the flows of carbon (and other nutrients) and keystone groups in the Spanish and Chilean study areas. The implications of this on the providing of ecosystem services of semi-arid areas should be studied due the current environmental changes on act.

IV-2. Specific considerations

IV-2.1. Feedbacks between microarthropods' diversity and ecosystem functioning

Results presented in the section I are highly consistent with those presented in Innangi et al. 2015b, De Marco et al. 2016, and Fioretto et al. 2018. On the basis of this, it was demonstrated that *ENA* is able to track the fate of soil carbon and quantify ecosystem functions also in soil systems, since to our knowledge, this is one of the few works developed in soil using this routine.

Northern and southern ecosystems in Italy showed antagonistic behaviors in response to seasonal variation. Together with the acting variables defined by the aforementioned studies, it was concluded that the diversity of microarthropods have implications in carbon cycling (i.e., decomposition and carbon sequestration). These results verified that carbon cycling and ecosystem functions are mostly controlled by the microbial biomass in the two forests but microarthropod top-predators contribute to render stable the entire food web and enhance the cycling of carbon. This fact suggests that both bottom-up and top-down forces acted at the same time in the four ecosystems in the following way: the microbial component of soil ecosystems involves and control the largest portion of carbon budget in soil, meanwhile the microarthropod community contributes to the dispersion of carbon to the other ecosystem compartments. In addition, Protura turned out as the most important among the microarthropod trophic groups showing high impact on carbon circulation in both forests and seasons probably due to their trophic specialization. In contrast, collembolans showed a low impact on carbon circulation in the four networks even though, together with Acari represents the most numerous microarthropod groups in soil ecosystems. However, such result does not exclude that their importance could be higher with respect to other biogeochemical cycles such as the one of manganese, on which both forests were highly dependent (Innangi et al. 2015b; De Marco et al. 2016b; Fioretto et al. 2018).

One of the main conclusions of the studies aforementioned is that decomposition stops in the northern forest while continues in the southern site during the winter season. The analysis of the networks confirms the statement. Nevertheless, based on the values of the overhead

and metabolic activity of the soil food web, it was inferred that the southern forest is more resistant to perturbations, meaning that the principal pathways for the flow of carbon prevail during the whole year. Instead, there is an interruption of the metabolic activity of the soil food web in the winter season in the northern forest. In the same terms, the value of overhead and metabolic activity makes it capable to restore their activity promoting resilience instead of resistance every year.

IV-2.2. Environmental filtering and stochastic distribution of microarthropods abundance and traits

Results of section II suggest that there is a clear effect of spatial heterogeneity and spatially distributed variables (measured and unmeasured in the field) on structuring community metrics and community composition. This study demonstrates several facts: (1) landscape characteristics play a crucial role on the occurrence of evolutive adaptation of microarthropod biological forms; (2) abundances and frequency of occurrence of morphological adaptation did not follow identical, but similar spatial patterns; (3) the effect of environmental characteristics, such as the patchy distribution of vegetation seemed to influence the occurrence of high abundances and taxa diversity, which is likely due to environmental filtering, but the low percentage of variance explained suggested that stochastic dispersal is equally probable. Moreover, environmental filtering better explains the spatial distribution of QBS-ar and community composition based on EMI scores, which coincides with the QBS-ar theoretical framework (i.e., environmental filtering theory). (4) Higher abundances and adaptation to soil environment were related to open spaces rather than areas under arboreal influence. Smoothing of GAM models responded to the spatial positions of trees in terms of overall abundances and QBS-ar in both seasons. Moreover, the contribution of spatial pattern of soil parameters, as well as livestock pressure to GAM models was unexpectedly low for abundances, and almost absent in QBS-ar patterns (with the exception of SOM content in autumn). This indicates that stochastic dispersal in relation to local environmental factors (e.g., non-spatially structured abiotic factors, as well as biotic interactions) drive abundances and adaptation of microarthropod communities. (5) High livestock pressure influenced microarthropod communities' composition and metrics. Values of community metrics that indicate well diversified communities were founded in medium- and low-pressure areas, which suggest that lower livestock activity trends to enhance microarthropod zoocenoses. (6) Finally, the delimitation of SHC areas via OBIA technique showed unexpectedly lower correlations with microarthropod communities'

composition, which was attributed to the dimension of pixels revealed by the remote-sensed images.

IV-2.3. The response of arthropod community to severe drought and soil rewetting depending on environmental conditions

The structure of soil arthropod communities in Chilean semi-arid ecosystems under extreme drought was studied in order to evaluate their variation based on the presence of trees and livestock pressure. In addition, the effect of simulated rewetting process in soil was evaluated depending on the environmental characteristics of the microsite. Firstly, the results elucidated that the response of edaphic arthropods to the rewetting of soils was different depending on the closeness to trees: Higher abundance and diversity of arthropods were found away from the trees during the rewetting of soil. Conversely, abundance and diversity were higher as the closeness to trees increased when soil was dry. This is probably due to the role of trees' radicular system as provider of resources for soil arthropods (e.g., refugee against harsh environmental conditions) but also, lower availability of water is expected in presence of tree's roots when the rewetting process is in act. Such fact suggest that the response of arthropod should be slower in presence of tree's roots. On the other hand, the effect of trees and herbaceous vegetation cover was dependent on the pressure of the livestock. Higher uncertainty in the community composition was identified in intensively grazed areas (i.e., absence of herbaceous vegetation cover), which suggest that the disturbance exerted by the livestock displaces more sensitive taxa but benefits more fitted taxa to harsh conditions. Finally, several important groups related to the demolition of the organic matter were found even when the soil moisture was very low, but the occurrence of such groups was higher in ungrazed areas. Moreover, higher diversity of feeding habits was related to ungrazed areas during the rewetting process, which indicate that roles attributed to arthropods, and so, functions they accomplish in the ecosystem are expected to respond to soil rewetting as follows: quicker responses is expected in areas with herbaceous vegetation cover, while slower responses are expected as the closeness to trees increases. Nevertheless, a long-term study should be performed in order to track these dynamics precisely and what are the feedbacks between them and the ongoing climate change.

IV-3. Future projections

A future direction of investigation could be the implications of the different community composition of each ecosystem on the different biogeochemical cycles. For example, due the deficiency of phosphorous in Chile, a focus on the dynamics of this nutrient depending on the arthropod community composition could reveal how it becomes available for each

trophic level. ENA was used in such terms to study the role of microarthropods in soil ecosystems, with a focus on carbon dynamics. The architecture of networks relied on general taxonomic compartments but future developments should aim at higher taxonomic and functional resolution. Moreover, increasing the frequency of sampling might help to describe accurately changes of biomass, as well as the monitoring of environmental parameters that might drive the response of ENA indices (e.g., by recording temperature and moisture conditions). Moreover, the implementation of experiments to measure arthropod metabolic parameters, such as respiration rates (e.g., by using ^{12}C and ^{13}C stable isotopes), would reduce the uncertainty on network construction. The network approach has the merit of complementing studies of biodiversity that describe changes in biomass or abundance in response to varying environmental conditions. Therefore, networks represent a promising tool to explore the cause-effect mechanisms linking biodiversity (i.e., biomass of trophic groups) to ecosystem functioning (e.g., transfer efficiency between discrete trophic levels, ecosystem stability and number of elements' cycling; see Barnes et al. 2018).

Linking belowground communities to the spectral analysis of remote sensed images could be improved by using UAVs instead of satellite images, since it would permit the reduction of pixel dimensions. Moreover, the using of hyperspectral images instead of multispectral could increase the chances to detect any relationship between them and parameters which are considered to be a proxy of ecosystem functioning. A higher number of bands enables one a higher availability of spectral sign to work with and to find out masked relationships. Moreover, to determine the physiological state of vegetation is highly recommended since the feedbacks between radicular systems of vegetation and belowground communities are dependent on each other.

In relation to sampling methodology, a highly recommended action is to perform experiments during the sampling when a limiting factor is clearly discernible. However, increasing the number of samples must be considered to avoid weak results. For example, a future line of investigation could be the definition of the influence area of trees in sylvopastoral systems for the edaphic community. Such area has been studied for scattered trees that generate fine-scale mosaics (i.e., gradients of available resources availability from beneath the canopy to interstitial areas among trees) (Moreno et al. 2015). Although the relationships between resources availability and soil biodiversity show high dependency (Hooper et al. 2005; Cardinale et al. 2012; Barnes et al. 2018), several questions still remain unanswered. For instance, are the ecological relationships between the tree and the soil community stable during the year or instead, they change seasonally? How the soil

community living under the influence of the tree respond to changes in the availability of resources that are not always available? does the tree benefit soil communities or instead, it may occur ecological competency? Moreover, an identification at high-taxonomical level of soil organisms together with species functional traits definition is recommended. The monitoring of loss of taxonomical and functional diversity under the climate change context can lead to catastrophic shifts on ecosystems (Eppinga et al. 2009; Cardinale et al. 2012; Lohmann et al. 2012; Smith et al. 2019) and therefore, to put in danger their capacity to provide services.

Although little is still known about the soil fauna distribution in many areas of the Earth, completing soil arthropod community studies with other groups of organisms such as bacteria, fungi, nematodes and earthworms in order to define the actual role of arthropods into the soil food web context and nutrient cycling is a very promising research field. The composition of the soil community vary widely across ecosystems and land uses (Jeffery et al. 2010; De Vries et al. 2013), and it has been demonstrated that soil ecosystem functions are dependent on them (Barnes et al. 2018). Therefore, soil biodiversity studies on semi-arid systems become important due the risk of degradation to which such areas are subjected (Asner et al. 2004; Maestre et al. 2016).

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Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems

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Cuando pienso en el mar de porquería
que tragamos cada día
con total filosofía,
soportando esta agonía…

Deglutimos con estúpida alegría
dilatadas groserías
complacientes y vacías
que nos hacen compañía…

Y creemos que sabemos lo que hacemos
pero somos unos memos embobaos

que ya ni vemos.

Y es que hagamos lo que hagamos, la cagamos
pero nos pavoneamos
de que aquí somos los amos.

Juan Abarca (Mamá Ladilla)