UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LA DIVERSITÉ FONCTIONNELLE SUR PLUSIEURS NIVEAUX TROPHIQUES: L'INFLUENCE DES ESPÈCES D'ARBRES EXOTIQUES SUR LES COLLEMBOLES DE LA LITIÈRE

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RÉSUMÉ

L'émergence de nouvelles communautés est de plus en plus fréquente dans le contexte des changements globaux, notamment via l'introduction d'espèces exotiques. Bien que l'utilisation des traits fonctionnels dans les études de biodiversité a permis de mieux comprendre la répercussion de ces nouveaux assemblages d'espèces sur le fonctionnement de l'écosystème, elle reste limitée lorsqu'appliquée aux niveaux trophiques supérieurs aux végétaux. En effet, l'influence des changements de la litière forestière sur les invertébrés du sol reste encore méconnue (p.ex. : origine, traits). Cette étude avait donc pour but de (1) pousser le concept de redondance fonctionnelle en vérifiant si des espèces d'arbres congénères de provenance différente (exotique vs indigène), mais ayant toutefois des traits similaires, résultent en filtres écologiques similaires pour l'assemblage des communautés de collemboles. Ensuite (2), les mécanismes potentiels menant à la structuration des communautés ont été explorés via l'étude de la covariation entre les traits de la ressource consommée et des consommateurs (litière – collemboles). Pour ce faire, des échantillons de litière et de sol ont été récoltés durant l'été 2015 dans deux plantations expérimentales (Auclair-Cloquet) du réseau IDENT (*International Diversity Experiment Network with Trees*). L'analyse fonctionnelle de la litière (capacité de saturation d'eau, résistance foliaire, épaisseur foliaire, N, C/N, lignine, cellulose, hémicellulose, respiration microbienne) et des collemboles (longueur des mandibules, longueur de la plaque molaire, ouverture buccale, développement apical, avantage mécanique, capacité de déploiement et ratio mandibule/tête) a ensuite été réalisée. Nos principaux résultats ont démontré que (1) les traits de la litière étaient déterminants pour les communautés de collemboles, contrairement à l'origine biogéographique de la litière et (2) qu'il y a avait un appariement entre les traits de la litière et les traits mandibulaires des collemboles. Toutefois, il a été observé que l'effet de la litière dépendait du contexte environnemental étant donné les différences observées entre les deux sites. L'ensemble de ces résultats suggère que les communautés de collemboles sont influencées de façon *bottom-up* par la qualité de leur ressource et que l'origine en soi de la litière ne représente pas un filtre écologique pour celles-ci.

Mots clés : origine biogéographique, détritus, mésofaune, appariement de traits, mandibules

INTRODUCTION

Percevoir l'humanité comme une force « géophysique » et nommer l'époque géologique actuelle en son honneur (Anthropocène) reflète bien l'importance de l'empreinte humaine sur l'environnement global (Steffen *et al.* 2011). Cette pression est perceptible via les différents changements globaux qui perturbent les écosystèmes via l'altération de la biodiversité globale (pollution, réchauffement climatique, espèces envahissantes, surexploitation des ressources, modification du paysage, etc.; MEA 2005). De ces changements émerge le concept des « nouveaux écosystèmes », lesquels diffèrent de ce qu'ils étaient historiquement via entre autres l'arrivée d'espèces exotiques et la conséquente disparition d'espèces indigènes (Hobbs *et al.* 2006). Considérant l'augmentation exponentielle de l'établissement d'espèces exotiques et l'impossibilité de revenir aux écosystèmes historiques (Ricciardi *et al.* 2007, Hobbs *et al.* 2011), ces nouveaux assemblages d'espèces représenteraient la nouvelle normalité (Marris *et al.* 2013). Ce faisant, ce concept implique que les stratégies d'aménagement devraient être orientées vers l'impact des espèces sur leur écosystème, et ce peu importe l'origine biogéographique de celles-ci (Davis *et al.* 2011, Miller et Bestelmeyer 2016). Toutefois, le débat est chaud et ouvert sur ces fameux nouveaux écosystèmes, lesquels ne sont pas unanimement acceptés au sein de la communauté scientifique. Par exemple, certains s'inquiètent que ce nouveau paradigme pourrait diminuer les initiatives et le financement lié à la protection des milieux naturels (Murcia *et al.* 2014). De plus, l'ajout et/ou la perte d'espèces peuvent altérer les processus clés de l'écosystème et donc, les services qui en découlent (Chapin *et al.* 2000, Cardinale *et al.* 2012, Hooper *et al.* 2012, Tilman *et al.* 2014). Cependant, de telles altérations ne sont pas nécessairement négatives pour le fonctionnement de l'écosystème; les espèces exotiques peuvent en effet induire une augmentation de la biodiversité locale, d'où le « paradoxe de la conservation de la biodiversité » (Vellend 2017). Les espèces exotiques semblent en effet avoir des influences variées (c.-à-d. positive, neutre ou négative) sur leur nouvel écosystème. Cela suggère que l'origine même des espèces n'est pas le facteur déterminant de ces effets de diversité et que d'autres caractéristiques comme les traits fonctionnels pourraient être plus impliquées.

L'écologie fonctionnelle s'est montrée très utile au cours des dernières décennies afin de cerner les mécanismes expliquant l'assemblage des communautés et les processus de l'écosystème (Díaz et Cabido 2001, de Bello *et al.* 2010, Handa *et al.* 2014, Cadotte *et al.* 2015). Cette discipline repose sur l'étude des traits fonctionnels lesquels sont définis comme étant toute caractéristique morphologique, phénologique, physiologique ou comportementale affectant la performance d'un individu (Violle *et al.* 2007, Pey *et al.* 2014b). Ceux-ci reflètent les propriétés des communautés de l'écosystème (Bengtsson 1998; McGill *et al.* 2006; Moretti et Legg 2009; Vandewalle *et al.* 2010; Wurst *et al.* 2012). Les espèces partageant des traits similaires peuvent être regroupées dans un groupe fonctionnel (Keddy 1992). Il semble logique d'assumer qu'un grand nombre de groupes fonctionnels dans un écosystème a une influence positive sur le fonctionnement de celui-ci. Toutefois, certaines études ont démontré que la composition fonctionnelle c.-à-de. l'identité des groupes) pouvait avoir un plus grand effet sur les procédés de l'écosystème que la richesse fonctionnelle c.-à-de. le nombre de groupes) (Hooper et Vitousek 1997; Handa *et al.* 2014). Ainsi, l'addition et/ou la perte d'espèces avec leurs traits fonctionnels respectifs ont un impact aléatoire sur des procédés particuliers de l'écosystème (Tilman *et al.* 1997). Cette implication des traits dans le fonctionnement de l'écosystème pourrait expliquer la variété d'effets des espèces exotiques sur leur nouvel écosystème respectif.

L'un des facteurs influençant la performance des espèces végétales exotiques est la pression de consommation qu'elles subissent, laquelle semble être directement influencée par les traits des espèces. À cet effet, deux hypothèses sont suggérées au sein de la littérature afin de déterminer l'influence potentielle des espèces exotiques sur leurs consommateurs. Tout d'abord, l'hypothèse du *enemy release* (HER) évoque qu'une espèce introduite devrait expérimentée une diminution de sa régulation par ses consommateurs, ce qui mènerait à une augmentation de sa distribution et de son abondance (Keane et Crawley 2002). Le phénomène des espèces envahissantes est directement lié à l'HER. Ces espèces ont des traits fonctionnels bien particuliers associés à leur caractère invasif et diffèrent donc grandement des espèces indigènes qu'elles remplacent (Van Kleunen *et al.* 2010), ce qui pourrait expliquer cette diminution de la pression de consommation sur celles-ci. Deuxièmement, il y a l'hypothèse du changement d'hôte : s'il est considéré que les consommateurs ont évolué avec leur ressource en fonction de leurs traits, il peut être supposé qu'ils pourraient consommer une ressource exotique ayant des traits similaires à la ressource d'origine (espèces congénères; Connor *et al.* 1980, Keane et Crawley 2002). Ces hypothèses reflètent toutes deux l'importance des traits fonctionnels dans les interactions trophiques et conséquemment le fonctionnement de l'écosystème, suggérant que l'origine en soi n'est pas un facteur déterminant. Toutefois, la majorité des études portant sur les espèces exotiques vise à vérifier l'HER en scénario d'invasion, ce qui ne permet pas de distinguer les effets d'origine de ceux reliés aux traits fonctionnels étant donné qu'ils sont confondus (Buckley et Catford 2016). Considérant que les études testant l'hypothèse du changement d'hôte sont rares (Connor *et al.* 1980, Wein *et al.* 2016), cette question mérite d'être approfondie. Ceci serait particulièrement intéressant en contexte d'aménagement forestier où l'utilisation d'espèces exotiques est parfois privilégiée (Sax *et al.* 2005).

La litière forestière est un filtre environnemental pour les décomposeurs du sol, notamment les collemboles, étant donné son influence sur la qualité de la ressource et l'environnement physique de ceux-ci (Hättenschwiller *et al.* 2005). Malgré leur faible contribution à la respiration et la biomasse animale totale du sol, les collemboles jouent un grand rôle via la structuration du sol par leurs pelotes fécales et leur alimentation sur le microbiote, d'où leur implication dans les activités de décomposition (Hopkin 1997; Rusek 1998; Cortet *et al.* 2003). Bien que la litière soit l'une des composantes de leur alimentation (p.ex. : Ponge 2000), il est incertain si les collemboles consomment celle-ci pour ses nutriments ou seulement pour ses microbes. En fait, la perception du rôle qu'occupent les collemboles dans l'écosystème est souvent simplifiée à leur fongivorisme (Rusek 1998, Addison 2003). Contrairement à cette vision écologique restreinte, les collemboles ont des régimes variés selon les espèces (Hopkin 1997, Rusek 1998, Addison 2003, Malcicka *et al.* 2017). Il est toutefois difficile de déterminer les possibles interactions trophiques des collemboles étant donné la faible compréhension de la biomécanique de leurs pièces buccales, malgré la morphologie détaillée dans la littérature (Manton et Harding 1964, Goto 1972). Certes, il serait logique que des mandibules plus complexes, développées et fortes soient liées à la consommation de matière plus récalcitrante (aiguilles des conifères, champignons) tandis que des mandibules plus faibles et simples soient associées à la consommation de litière palatable et de bactéries (Bankonyi 1989, Chen *et al.* 1997, Santorufo *et al.* 2014). Certains traits mandibulaires pourraient être liés directement à la consommation de litière : la force mandibulaire pourrait être corrélée avec l'épaisseur et la résistance des feuilles de la litière (sauterelles; Ibanez *et al.* 2013, Le Provost *et al.* 2017, carabes; Brousseau *et al.* 2017). Aussi, ces traits de litière pourraient être corrélés négativement avec la capacité de déploiement mandibulaire des collemboles : afin de fragmenter la litière avant l'ingestion, les mandibules pourraient devoir effectuer des petits mouvements rapides et non pas des longs mouvements amples (lesquels seraient potentiellement associés à une action de raclage). Toutefois, l'influence de la litière sur les collemboles serait probablement plus indirecte via son influence sur les microbes. Par exemple, une litière décidue favorise plus l'activité bactérienne qu'une litière récalcitrante (Scheu 2005, de Vries et Caruso 2016) et donc potentiellement l'abondance des collemboles ayant des mandibules associées à la consommation de bactéries. Ces corrélations hypothétiques sont schématisées dans la Figure 0.1. Il est nécessaire d'approfondir les connaissances à ce sujet afin d'améliorer la capacité de prédiction de l'assemblage des communautés de collemboles face aux changements environnementaux et conséquemment l'influence potentielle sur le fonctionnement du sol.

But et objectifs de recherche

Le but de ce projet était de (1) déterminer l'influence respective de l'origine biogéographique et des traits de la litière forestière sur les communautés de collemboles et (2) d'essayer de comprendre les mécanismes de l'influence de la litière en utilisant une approche fonctionnelle sur plusieurs niveaux trophiques. Pour réaliser ce deuxième point, cette étude devait initialement intégrer la qualité de la litière, les biomasses fongiques et bactériennes ainsi que les traits mandibulaires des collemboles afin de distinguer les effets indirects et directs de la litière (Fig. 0.1). Des difficultés méthodologiques liées à la détermination des biomasses microbiennes ont toutefois été éprouvées au cours du projet: la méthode FungiResp (Sassi *et al.* 2012, Campbell *et al.* 2003) s'est révélée difficilement applicable aux litières forestières suite à de nombreux essais en laboratoire à l'été et l'automne 2016 (p.ex.: type et concentration d'inhibiteur, concentration de substrat, méthode d'ajout et d'homogénéisation des produits, différents types fonctionnels de feuilles, etc.). Ainsi, seule la respiration basale totale (sans ajout de substrat ou d'inhibiteur) a été considérée dans les analyses, ce qui ne permettait pas de valider les hypothèses prédites lors de la mise sur pied du projet (Fig. 0.1). Cette respiration fût plutôt considérée comme un trait fonctionnel de la litière. L'influence de la litière sur les communautés microbiennes n'a donc pu qu'être supposée indirectement en fonction de la littérature. Au final, cet objectif du projet s'est avéré à être orienté sur l'exploration des associations de traits entre la litière et la communauté de collemboles ainsi que sur la validation de l'utilité des mesures de traits mandibulaires.

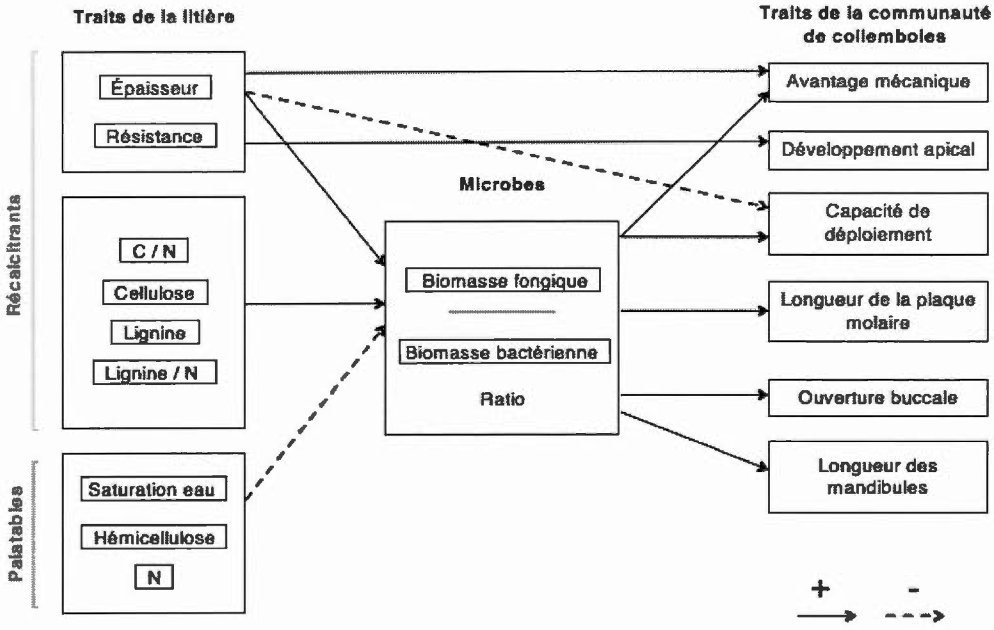

Figure 0.1 Schéma conceptuel des hypothèses initiales sur les corrélations de traits entre la litière et les collemboles.

L'étude ci-jointe est présentée sous forme d'articles scientifiques répartis en deux chapitres, lesquels seront éventuellement soumis pour publication, d'où l'emploi de la langue anglaise;

1) Le premier chapitre avait pour objectif de déterminer si l'influence des traits fonctionnels de la litière forestière était plus déterminante que le genre de celle-ci

sur la composition de la communauté de collemboles. Il s'agissait donc de comparer l'influence d'espèces d'arbres congénères exotique et indigène, ayant des traits similaires, mais d'origine biogéographique différente (Européenne vs Nord-Américaine). Pour ce faire, l'étude s'est déroulée dans deux plantations expérimentales jumelles du réseau IDENT (*International Diversity Experiment Network with Trees*). La litière et la couche superficielle du sol ont été collectées dans 14 traitements (12 monocultures et 2 polycultures). Les résultats ont été obtenus suite à l'analyse fonctionnelle de la litière ainsi que l'identification des collemboles à l'espèce suite à l'extraction Tullgren-Kempson des échantillons.

2) Le deuxième chapitre visait plutôt l'exploration des mécanismes potentiels menant à la structuration des communautés de collemboles en vérifiant l'hypothèse qu'il existe une la relation fonctionnelle entre ceux-ci et la ressource qu'ils consomment (ici la litière). Pour ce faire, des protocoles de mesures de traits mandibulaires ont été développés puis appliqués sur les espèces échantillonnées dans les plantations IDENT (monocultures). Ensuite, il a été vérifié s'il existait une corrélation entre ces données et les traits de la litière.

Étant donné la très mince littérature portant sur l'effet réel de l'origine biogéographique d'une espèce sur la structuration des communautés et sur les traits mandibulaires des collemboles, l'ensemble des résultats obtenus dans le cadre de cette étude contribueront à améliorer la compréhension de la dynamique des communautés du sol, mais aussi de leur réponse face aux changements globaux. Les résultats feront non seulement écho au débat actuel entourant les nouveaux écosystèmes, mais à l'effort international visant à développer l'approche fonctionnelle aux invertébrés.

CHAPITRE I

LEAF LITTER TRAITS, BUT NOT BIOGEOGRAPHIC ORIGIN OF TREES, INFLUENCE COLLEMBOLA COMMUNITY ASSEMBLY ON THE FOREST FLOOR

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1.1 Abstract

Aim: Shifts in the ranges of non-native species and resulting novel communities can modify biotic interactions and ecosystem processes. Within forest soils, little is known about how changes in biogeographic origin or traits of leaf litter resources might influence soil invertebrate consumer communities. We tested the functional redundancy of novel tree communities by verifying (1) if six pairs of congeneric non-native (European origin) and native (North American) tree species bearing similar leaf litter traits resulted in similar ecological filters influencing the assembly of Collembola communities and (2) to which extent traits of the leaf litter resources correlated with Collembola community composition.

Location: Single- and six-species plots in Auclair (Quebec, Canada) and Cloquet (Minnesota, USA) sites of the International Diversity Experiment Network with Trees (IDENT).

Methods: Collembola communities extracted from litter and soil samples were characterized at the species level. Litter resource quality was measured through functional traits (N, cellulose, hemicellulose and lignin concentrations, lignin/N, C/N, thickness, toughness, water saturation capacity and microbial basal respiration).

Results: Litter biogeographic origin (i.e. native versus non-native) did not influence Collembola community composition, but litter genus, which generally reflected trait differences, did. A significant study site by litter genus interaction was observed, probably driven by intra-specific trait variation (e.g. N) and different environmental conditions (e.g. soil moisture) between sites. Additionally, a 0.4 correlation between an integrated index of litter traits and Collembola community composition was observed at Cloquet, but not at Auclair.

Main conclusions: Our strongly site-dependent results highlight the importance of considering context-dependency in functional studies. With the social acceptability of novel ecosystems still hotly debated, our empirical evidence suggests that a functional trait approach may be indeed as relevant as, and complementary to studying biogeographic origin to understand the ecological consequences of changing communities.

Keywords: biodiversity, exotic species, functional diversity, IDENT, mesofauna, springtails

1.2 Introduction

With global change due to anthropogenic activities, historical distributions of species are changing faster than ever through species losses, range shifts and new introductions (Ricciardi 2007). Deliberate (e.g. forest plantations) and unintentional (e.g. biological invasion) introductions reshape species combinations and ecosystem properties, thus leading to novel ecosystems (Hobbs *et al.* 2006). Given that alteration is inevitable under human legacy, the "novel ecosystem" concept suggests that management decisions should be based on functions conferred by species in altered ecosystems, regardless of their biogeographic origin (Miller & Bestelmeyer 2016). This concept has been hotly debated in environmental conservation (e.g. Kattan *et al.* 2016), partly because critics and proponents disagree on strategies regarding non-native species management (Davis *et al.* 2011, Simberloff 2011). There is however unanimity that biogeographic origin should not be the only criterion for management options of non-native species, because the relevance of their impact depends on the stage along the introduction–naturalization–invasion–impact continuum (Larson *et al.* 2016). As non-native does not mean invasive, the question remains whether species biogeographic origin on its own really matters. Surprisingly, few empirical studies have addressed this so far despite the actual debate surrounding it. Studies focusing on non-native species generally contain too many confounding factors to isolate solely the influence of biogeographic origin on ecosystems (Buckley & Catford 2016). The differential performance of introduced species may in fact depend on characteristics of the source environment (to which they have evolved), introduced species traits, recipient community species traits and characteristics of the recipient environment (Buckley & Catford 2016). One way to isolate these factors would be to compare the influence of congeneric species (with similar traits), but with different biogeographic origin, in the same recipient environment. Using such an experimental approach, Wein *et al.* (2016) reported no influence of tree biogeographic origin on leaf herbivory, but it is to our knowledge the only empirical evidence from a study designed like this so far.

Ecosystem novelty is not only characterized by the presence of species outside their natural range of distribution, but also by new ecosystem properties emerging from these new species (thus trait) assemblages (Hobbs *et al.* 2006). The advent of functional ecology in recent decades has led to clear evidence that species traits influence ecosystem functioning ("effect traits") (e.g. Handa *et al.* 2014) and that traits themselves are filtered by environmental conditions ("response traits") allowing individuals to perform in a given ecosystem (e.g. Cadotte *et al.* 2015). However, functional studies generally are limited to a single trophic level (i.e. plants), strongly limiting our understanding of complex interactions. Forests represent complex ecosystems where function results from interactions among and across biotic and abiotic components. A more holistic approach is thus needed in functional studies: the inclusion of animals and microbes is essential to better assess trophic interactions and community assembly (Wardle *et al.* 2004). For example, adopting a bottom-up perspective, plant traits could be used to predict first order consumer communities for which plants provide the food resource (Lavorel *et al.* 2013).

Collembola (springtails) are small invertebrates predominant in leaf litter and soil that are known to have great diversity (> 650 known species in North America; Christiansen & Bellinger 1998), high abundance and fast-response to environmental changes (Hopkin 1997), particularly in response to forest management (Malmström *et al.* 2009). Considering the important role of Collembola in litter decomposition and soil structuration (Hopkin 1997), our understanding of how changing forest composition would modify leaf litter resources and the consequences of such changes for Collembola communities is essential. Changes in leaf litter can impact Collembola communities through 1) abiotic filters (by influencing their physical habitat; Ponge *et al.* 1993) and 2) resource-driven effects (Hopkin 1997). Litter can indeed be consumed by Collembola (i.e. observed in gut content; Ponge 2000), but it is unclear whether it is for leaf nutrients, or indirectly, to consume associated microbes. Despite litter being an important above-ground resource, recent evidence shows that their feeding may be more root-oriented than previously thought (e.g. rhizosphere microbes and direct consumption of roots; Larsen *et al.* 2007, Pollierer *et al.* 2007, Endlweber *et al.* 2009, Fujii *et al.* 2016). However most studies to date have been limited to understanding litter quality influence on Collembola species with a limited number of traits such as C/N ratio (Illieva-Makulec *et al.* 2006) or with a plant functional group approach (Salamon *et al.* 2004). Although a recent urban environment study investigated how multiple litter traits relate to Collembola community composition (Santorufo *et al.* 2014), other studies including multiple traits have been limited to predicting abundance of the total Collembola community with no regard for composition (e.g. Badejo *et al.* 1998). Beyond C/N ratio, other traits that could influence Collembola through litter palatability and/or associated microbial communities might include leaf thickness (Santorufo *et al.* 2014), water saturation capacity (Makkonen *et al.* 2011) and concentrations of lignin, cellulose, hemicellulose (Coûteaux *et al.* 1996), condensed tannins and cations (Makkonen *et al.* 2011).

Relatively little is known about how Collembola communities might respond to novel plant communities. To date, studies on Collembola response to non-native tree species, have not had the purpose of isolating biogeographic origin, but rather have focused on contrasting *Eucalyptus* plantations with native *Quercus* dominated forests (Sousa *et al.* 2000) or with native grasslands (Rieff *et al.* 2016) to determine potential changes in soil quality after plantation. In one study where native (*Alnus* sp. and *Populus* sp.) and non-native litter species (*Acacia* sp. and *Eucalyptus* sp.) were contrasted, Pereira *et al.* (1998) concluded that physico-chemical litter traits had a stronger effect on Collembola-mediated decomposition than biogeographic origin of species, but non-native and native species were functionally different (e.g. polyphenol content) making it impossible to isolate origin effects. Similarly, Makkonen *et al.* (2011) demonstrated by a global reciprocal transplant experiment that litter decomposition by mesofauna was quality-driven and not origin-driven across four different biomes (subarctic, temperate, Mediterranean or tropical). However again, it was difficult to dissociate origin from biome-specific traits.

The aim of this study was to verify (1) if tree biogeographic origin influences Collembola community composition when comparing congeneric tree species bearing similar functional traits and (2) to which extent litter traits allow us to explain Collembola community composition. We first hypothesized that for both single-species and mixed-species litter communities, litter genus will influence Collembola community composition more than tree biogeographic origin, as genus of litters will more likely influence key Collembola distribution factors (e.g. resource quality and microhabitat) than biogeographic origin on its own. Secondly, given our previous hypothesis and the assumption that tree genus should be associated with particular litter traits, we expected to observe a correlation between the Collembola community and litter traits.

1.3 Material and methods

1.3.1 Experimental site and design

The study was conducted in the AuCl experiment of the International Diversity Experiment Network with Trees (IDENT), a network of Biodiversity – Ecosystem Functioning experiments in North America and Europe (Tobner *et al.* 2014). The two study sites, which were planted at the same time with trees grown from the same nurseries, were located in Auclair (Au), Québec, Canada (47.7° N, 68.6° W) and Cloquet (Cl), Minnesota, USA (46.7° N, 92.5° W). These high-density tree experiments were established in 2010 on 0.34 ha low-input abandoned pasture with loam soil (Au) or a previously forested site with sandy loam soil (Cl) (http://www.treedivnet.ugent.be.html). Further site description including climate and soil variables on the AuCl experiment are provided in Annex 1.1. With the aim of allowing for multi-site studies, both sites were identically designed with one, two and six-species treatments for a total of 48 randomized treatments (n=4) (Tobner *et al.* 2014). Plots were distanced from each other by one meter and consisted of 49 trees (7 x 7 trees with 40 cm intervals) (Tobner *et al.* 2014). Species pool of the AuCl experiment was composed of 6 North American temperate tree species (*Acer saccharum*, *Betula papyrifera*, *Larix laricina*, *Quercus rubra*, *Picea glauca* and *Pinus strobus*) and 6 congeneric European temperate tree species (*A. platanoides*, *B. pendula*, *L. decidua*, *Q. robur*, *P. abies*, *P. sylvestris*) (Tobner *et al.* 2014). Here, North American species are considered as native and European species as non-native. Based on wood density, seed mass and leaf N content, native and non-native congeneric species were functionally more similar than non-congeneric species, thereby allowing to use tree genus as a proxy for tree functional identity (Tobner *et al.* 2014). For this study, we subsampled a subset of plots: all twelve single-species treatments and two six-species mixtures, one composed of native species and the other of non-native species (Fig. 1.1). These 14 treatments were replicated four times at each site for a total of 112 sampled plots.

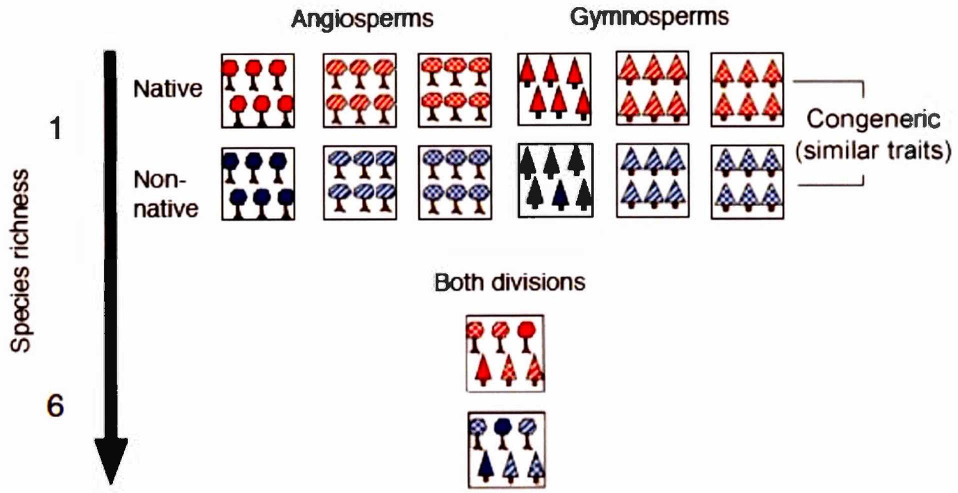


Figure 1.1 Schematic representation of selected treatments in AuCl experimental design (adapted from Tobner *et al.* 2014 with permission).

1.3.2 Litter sampling and litter trait measurements

Considering that the original experimental design was based on traits of the living trees, functional traits were measured on freshly senesced leaf litter to verify that congeneric litters were indeed more similar than non-congeneric litters. In October 2015, freshly senesced leaves were collected on single-species plots at both sites and on at least five random trees per plot after gentle shaking of the trunks. Senesced evergreen needles were collected throughout the field season in June, July and August 2015. All leaves per species per site were then pooled together and mixed homogeneously before trait measurements: leaf water saturation capacity (% H_2O d.m.), leaf thickness (mm), leaf resistance to fracture (g $mm^{2\ -1}$), N concentration (% d.m.), cellulose, hemicellulose and lignin concentrations (% o.m.), C/N and lignin/N ratios. For microbial basal respiration rate (μg CO2-C g^{-1} h^{-1}), litter was manually collected on the forest floor at five random positions per plot and air-dried until

MicroResp analyses (Campbell *et al.* 2003). Here we consider the mean litter microbial basal respiration rate per species (across blocks) as a litter species functional trait. Details about trait measurements are provided in Annex 1.3.

1.3.3 Environmental variable measurements

Soil moisture measurements were taken at each plot center during Collembola sampling with a FieldScout TDR 300 moisture meter (n=3); additional measures for single-species plots at both sites were taken in June 2015 and October 2015. Litter layer mean height (to the nearest mm) was measured prior to Collembola sampling with a ruler from the top of the soil to the top of the litter layer for each subsample. In order to assess if there was any difference in soil microbial resource abundance across treatments within an experimental site, soil microbial biomass (μg microbial-C g^{-1}) was determined for Auclair plots. During Collembola sampling, a superficial layer of soil (0-2 cm) was collected in a sterile tube at three random positions per plot and then frozen at -20 °C. Soils were adjusted to 45 % of their water holding capacity and pre-incubated for 7 days at 25 °C before MicroResp analyses with glucose addition (Campbell *et al.* 2003).

1.3.4 Collembola sampling

Collembola were sampled in July (Au) and August (Cl) 2015. For each plot, two subsamples were randomly collected at its center to minimize any edge effect, yielding a total of 224 subsamples. Adequate sampling effort was determined by preliminary sampling tests at Auclair in June 2015. At each subsample site, litter was collected manually in a 15 x 15 cm quadrat. At the center of the quadrat, soil was extracted with a split soil core sampler (diameter 5.08 cm x depth 5 cm). Both litter and soil were transferred in hermetic containers and kept at 4 °C for transport to the laboratory for a maximum of 48 hrs. Litter and soil subsamples were then pooled together prior to Tullgren (Au) or Kempson (Cl) extraction during which the temperature was gradually increased during 7 days (20 °C to 50 °C) and fauna collected in 70 % ethanol. Collembola were cleared in lactic acid at 60 °C to better see structures needed for identification (e.g. chaetotaxy and post-antennal organ). Patterns and coloration were carefully noted before this step. Identification to the species level was done with a Leica DM1000 LED phase contrast microscope (800x) by using the keys of Christiansen & Bellinger (1998), Fjellberg (1998, 2007) and Hopkin (2007). Bellinger *et al.* (1996-2016) was used as complementary information to these keys. Cleared specimens were all slide-mounted in Hoyer's medium (50 ml distilled water – 30 g gum arabic – 200g chloral hydrate – 20 ml glycerol). Damaged specimens were identified only to the family or genus level (< 3 %) and excluded in further analyses. Other exclusions included four samples for which Collembola total abundance equaled zero (*B. Pendula* (block A) and non native six-species mixture (block D) in Auclair and *A. saccharum* (block A) and *P. abies* (block D) in Cloquet). Given the small size of *Megalothorax minimus* (< 0.4 mm), this species was also excluded from the analyses due to possible sampling bias as some individuals may not have been detected.

1.3.5 Statistical analyses

Variation of environmental variables depending on study site, litter genus and litter origin was analyzed with ANOVAs and post-hoc Tukey HSD test (normality confirmed with Shapiro-Wilk test). The variation of litter traits and Collembola species among and across congeneric tree species was visualised with principal component analysis ordinations (PCA) after trait data standardization and species abundance Hellinger transformation (Legendre & Legendre 2012). Prior to variance analyses, Collembola species abundances were transformed in Hellinger distance (Legendre & Gallagher 2001). PERMANOVAs nested by blocks were then used to test the effect of litter genus, litter biogeographic origin, study site and their interactions on Hellinger distance of Collembola species abundances by site and across sites (9999 permutations) (Anderson & Walsh 2013). We ensured that homogeneity of variance was respected with a multivariate analogue of Levene's test.

To explore association between litter traits and Collembola species matrices, procruste analyses were used (Peres-Neto & Jackson 2001). As we did not have all trait measurements for six-species mixtures (e.g. microbial biomass), procruste analyses included monocultures only. Considering the low number of shared species and high intraspecific trait variation of litters between sites, we decided to ordinate PCA and execute procrustes analyses on each site separately or on species common to both sites.

All statistical data analyses were performed in R (v. 3.2.1) (R Development Core Team, Vienna, Austria) with RStudio environment (v. 0.99.903) (RStudio Inc., Boston, USA). Vegan package (v. 2.4-0) by Oksanen *et al.* (2016) was used for Hellinger transformation / distance (decostand/vegdist), litter trait standardization (decostand), PCAs (rda), homogeneity of variance test (betadisper), normality test (shapiro.test), ANOVAs (aov/TukeyHSD), PERMANOVA model (adonis) and procrustes analyses (protest).

1.4 Results

1.4.1 Litter trait variation of congeneric species

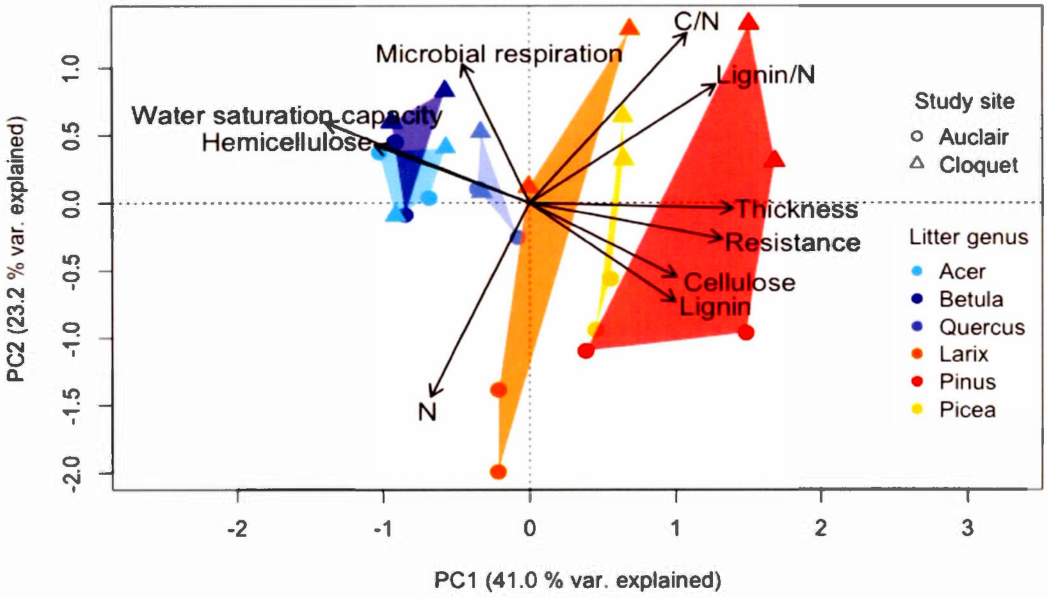


Figure 1.2 Principal component analysis (PCA) ordination of centered and standardized litter traits (arrows) arranged by study site (shape) and litter genus (colored polygon).

The first two PCA axes explained 63.2 % of the variation in litter trait scores (Fig. 1.2). The first axis likely explained the variation due to genera (41.0 %) given the horizontal deciduous-evergreen gradient (Fig. 1.2). The second axis likely explained intra-specific variation in litter traits between sites (23.2 %) (Fig. 1.2): mean N concentration was higher at the Auclair (1.25 ± 0.24 % d.m.) than Cloquet site (0.82 ± 0.17 % d.m.) and conversely mean microbial respiration was lower at the Auclair (27.43 ± 5.24 μg CO_2-C g^{-1} h^{-1}) than Cloquet site (61.26 ± 7.88 μg CO_2-C g^{-1} h^{-1}). Intra-specific variation between sites for a given species was not observed on physical traits (resistance, thickness and water saturation capacity) and was greater for gymnosperm than angiosperm species (as shown by polygon areas in Figure 1.2).

Larix species situated themselves in the middle of the deciduous-evergreen gradient: they exhibited gymnosperm intra-specific variation, but traits showed greater resemblance to angiosperm species (Fig. 1.2). Despite litter trait variation for *Pinus* and *Larix* congeneric species being greater than for other genera (Fig. 1.2), congeneric species generally had more similar litter traits than non-congeneric species. However, variation across sites was strong, demonstrating clear intra-specific trait variation for leaf litters. See Annex 1.4 for all specific traits values.

1.4.2 Environmental variables

Soil moisture was almost double at the Auclair (19.6 ± 1.7 % H_2O d.m.) than Cloquet (10.4 ± 1.5 % H_2O d.m.) site ($p < 0.01$, see Annex 1.1), which is coherent with their respective soil texture (loam vs sandy-loam). At the time of sampling, trees at Auclair were bigger than at Cloquet despite their same age (field observations). Some treatments also had a particularly thin litter layer (mean height < 1 cm) (Auclair: *Betula* sp. / Cloquet: *Acer* sp. and *Quercus* sp.; see Annex 1.2). Soil microbial biomass, measured only in Auclair, did not vary by litter genus, origin or origin by genus.

1.4.3 Collembola communities and treatment effects

Across both sites, 1831 individuals were identified to species. Total richness across sites was 57 species of Collembola, with 34 species sampled at Cloquet (n =758) and 37 species sampled at Auclair (n =1073; see Annex 1.5). The most dominant species sampled at Auclair (i.e. highest relative abundances) were *Lepidocyrtus fernandi* (58.0%), *Parisotoma notabilis* (7.1%) and *Entomobrya* sp.2 (5.7%). At Cloquet, dominant species included *L. violaceus* (21.4%), *L. paradoxus* (15.6%), *E. nivalis* (16.9%) and *Mesaphorura silvicola* (13.5%). Only 14 species were shared between both sites.

On the total variance explained by our model, study site had the strongest influence on Collembola community composition ($R^2 = 0.21$), followed by litter genus ($R^2 = 0.07$) (Table 1.1). As well, these factors interacted significantly with each other ($R^2 = 0.07$) indicating that the influence of litter genus on Collembola community was different at both sites (Table 1.1, Fig. 1.3). This observation was concordant with the intraspecific trait variation observed between sites (Fig. 1.2). Indeed, distinct PERMANOVAs for each site on Hellinger distance matrices (9999 permutations) showed a stronger litter genus influence in Cloquet ($R^2 = 0.19$, $p < 0.001$) than in Auclair ($R^2 = 0.15$, $p < 0.05$). Litter biogeographical origin had no influence on Collembola community composition (no significant litter origin × genus interaction; Table 1.1, Fig. 1.3). Collembola communities of single- and six-species treatments answered similarly to the factors included in the model (see black vs colored dots in Fig. 1.3).

1.4.4 Litter traits and Collembola community composition

As litter genera showed differences in their functional traits (Fig. 1.2) and Collembola community composition varied by tree genus (Table 1.1), we tested the direct relationship between litter traits and Collembola community composition. The procrustes analyses demonstrated a significant 0.4 correlation between litter traits and Collembola community composition at Cloquet (Table 1.2). This relationship was however not observed at Auclair (Table 1.2). These observations highlighted similar patterns as those observed when testing treatment effects with our PERMANOVA models: litter genus had a stronger effect on Collembola community composition at the Cloquet than Auclair site.

Table 1.1 PERMANOVA of the Hellinger distance for AuCl Collembola community composition in relation to study site, litter origin, litter genus and their interactions (9999 permutations, nested by block). Df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; F = F value by permutation. Treatments included in analyses were single- and six-species mixtures.

Factor	Df	SS	MS	F	R^2	P
Litter genus	6	5.55	0.93	1.56	0.066	***
Litter origin	1	0.44	0.44	0.74	0.005	ns
Study site	1	17.23	17.23	28.96	0.206	**
Site*Genus	6	5.74	0.96	1.61	0.069	***
Origin*Genus	6	3.80	0.63	1.07	0.045	ns
Origin*Site	1	0.54	0.54	0.91	0.006	ns
Origin*Site*Genus	6	3.54	0.59	0.99	0.042	ns
Residuals	79	47.01	0.60		0.561	

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significant

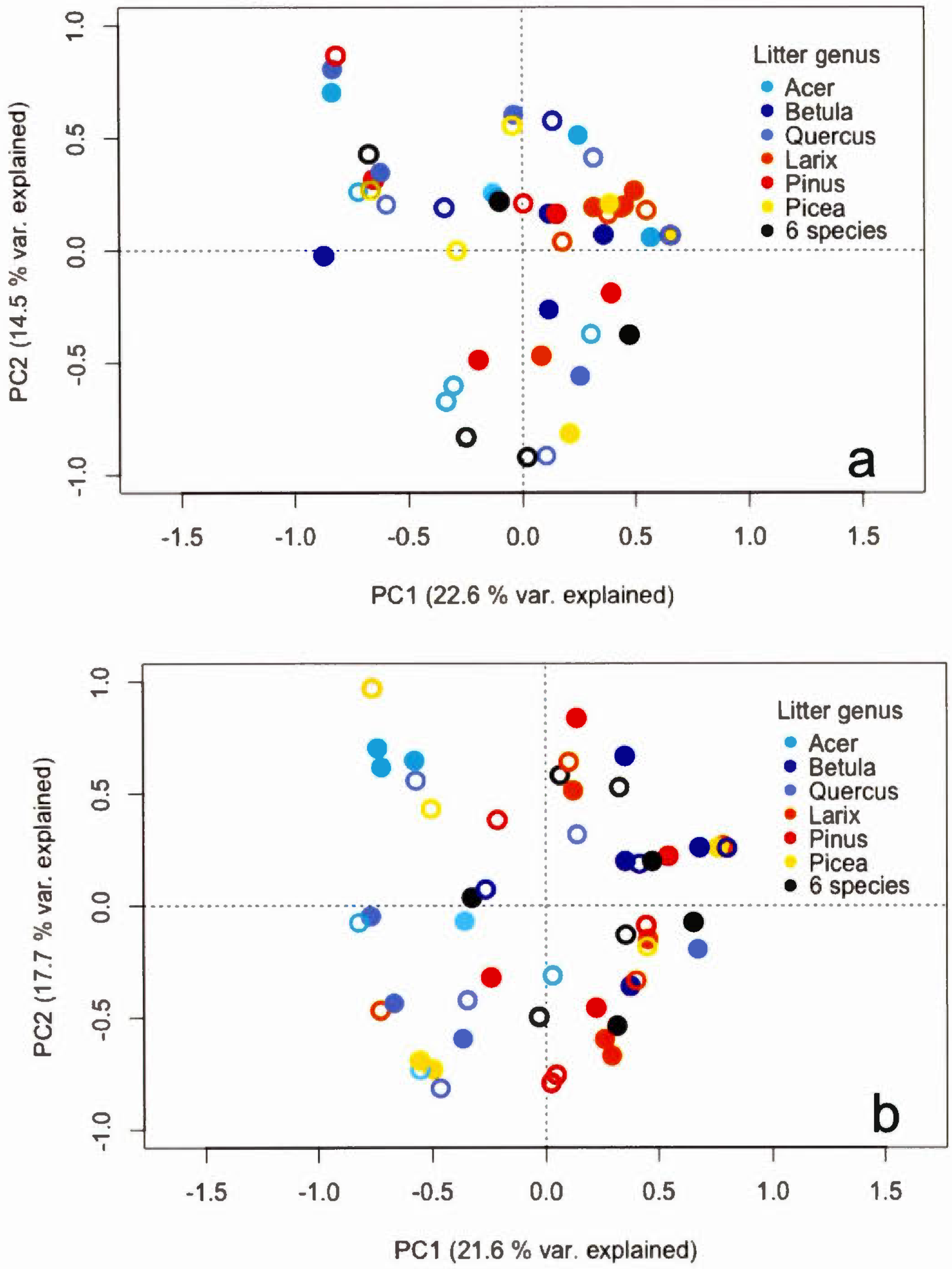


Figure 1.3 Principal component analysis (PCA) ordination of Collembola species abundances of a) Auclair (Au) and b) Cloquet (Cl) arranged by litter genus (color) and origin (open: native / closed: non-native). Hellinger transformation was applied to data before analyses.

Table 1.2 Procrustes correlation between AuCl Collembola community composition (transformed with Hellinger) and litter traits by site. SS = Sum of squares. Permutations = 9999. Prior to analyses, six-species mixtures were excluded, litter traits were standardized and the Collembola species matrices were Hellinger-transformed.

Site	SS	Correlation	P
Auclair	0.90	0.32	ns
Cloquet	0.85	0.39	**
Both sites (shared species only)	0.83	0.41	***

*** P < 0.001, ** P < 0.01, * P < 0.05, ns not significant

The correlation between litter traits and Collembola community composition observed at the Cloquet site (Table 1.2) was clearly driven by the deciduous (right quadrants) or evergreen character of the litter species (left quadrants; as shown by variation on the first axis of Figure 1.4a). Correlations between Collembola species and evergreen litters were stronger than those with deciduous litters (length of arrows). For example, *Lepidocyrtus* species and *Neanura muscorum* were correlated with lignin concentration, *E. nivalis* with C/N ratio and *Pogognathellus flavescens* with cellulose concentration (Fig. 1.4a). *Dicyrtoma fusca* and *Isotomiella minor* were rather associated with thick and resistant litters (Fig. 1.4a). On the other hand, correlations with traits for which high values are associated with deciduous litters (water saturation capacity, microbial respiration and higher N concentration) were observed for *Micranurida pygmaea, Isotoma viridis, I. subviridis, Mesaphorura macrochaeta* and *M. silvicola* (Fig. 1.4a).

Despite the absence of significant correlation between litter traits and the Collembola community at the Auclair site, we observed a significant 0.4 correlation when shared species from both sites were combined (Table 1.2). Contrary to the analysis in Cloquet only (Fig. 1.4a), N concentration and microbial respiration on the first axis were inversely correlated (Fig. 1.4b). Collembola community association with either deciduous litters (lower quadrants) or evergreen litters (upper quadrants) was again observed on the second axis (Fig. 1.4b). *L. fernandi* was a rare species in Cloquet (0.2 %), but the most dominant species in Auclair (58 %) and was mainly sampled in *Larix* treatments (59 %). Given the high N concentration in *Larix* litter at Auclair and its intermediate cellulose concentration (Fig. 1.2), it is not surprising that *L. fernandi* was strongly correlated with these traits (Fig. 1.4b). We observed some consistency between Cloquet and shared species results (Fig. 1.4). *Mesaphorura* species (*M. macrochaeta, M. silvicola*) were consistently associated with deciduous litters at both sites through correlations with water saturation capacity and microbial respiration (Fig. 4b, yet with N and hemicellulose at Cloquet; Fig. 1.4a). Isotomidae species were also mainly related to deciduous litters : 1) *I. viridis* correlated with water saturation capacity and microbial respiration, 2) *I. subviridis* tended to be more related to high hemicellulose concentration, while in contrast, 3) *Parisotoma notabilis* was associated with leaf recalcitrance given its correlation with cellulose concentration (Fig. 1.4). Another species clearly related to evergreen litters (high C/N and lignin/N ratios) was *E. nivalis*. Yet, the most consistent covariation observed across procruste analyses was between *N. muscorum* and lignin concentration (Fig. 1.4).

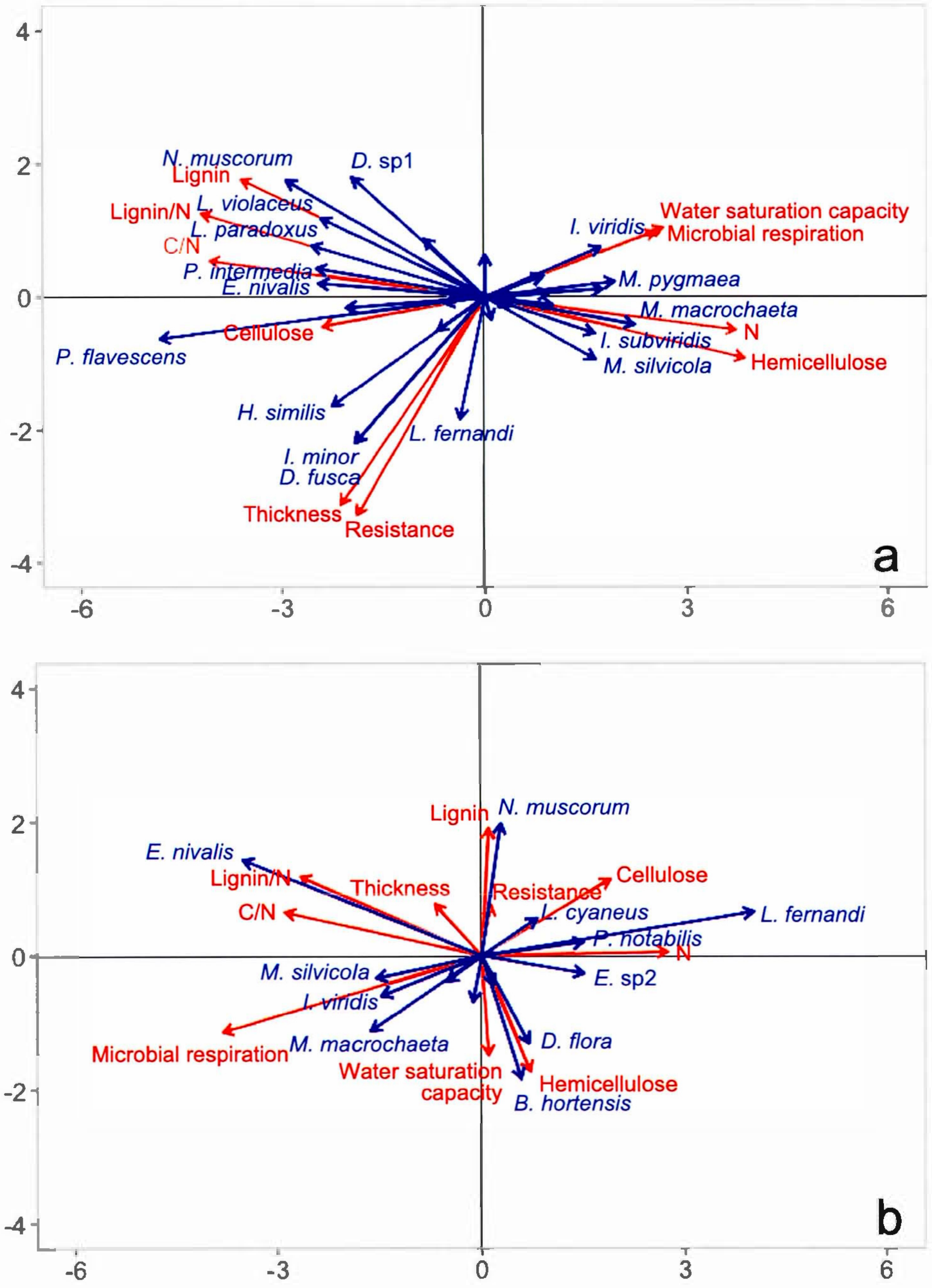


Figure 1.4 Procrustes correlation between Collembola species (blue) and litter traits (red) of a) Cloquet and b) both sites (shared species) monocultures. Permutations = 9999. Prior to analyses, species abundances were Hellinger-transformed and litter traits were standardized (correlation = 0.4, $p < 0.05$).

1.5 Discussion

1.5.1 Litter influence on Collembola community assembly is not origin-driven but partly due to a site-dependent genus effect

Our results confirmed our first hypothesis: across all tested tree community types, there was no evidence of biogeographic origin of the leaf litter resource on Collembola community composition, in contrast to litter genus which showed strong effects in predicting the consumer community (Table 1.1, Fig. 1.3). No impact of the biogeographic origin of the resource was also observed in a recent study on invertebrate herbivores feeding on congeneric native and exotic leaves (Wein *et al.* 2016). These results are consistent with Connor *et al.* (1980) who demonstrated that phytophagous insect consumers can switch resources if an introduced plant species is closely related to its native resource (e.g. congeners), regardless of biogeographic origin. Additionally, our experimental design allowed us to assess another dimension associated to species occurring outside of their biogeographical range: potential invasiveness. Collembola community response to invasive and native congeneric species was compared through *Acer* treatments; *Acer saccharum* (Sugar maple) being the native species and *Acer platanoides* (Norway maple), in addition to being non-native, is also one of the most invasive tree species in forests of eastern North America (Paquette *et al.* 2012). Although we report no litter biogeographic origin influence on Collembola in *Acer* experimental monocultures, we recognize that our results do not imply that a Norway maple invasion in a natural forest would not affect Collembola community composition. In contrast to our experimental plots where a complete replacement of sugar maple occurred, Norway maple invasions are creating new plant species assemblages by displacing numerous species and reducing their regeneration (Martin 1999, Paquette *et al.* 2012). Recent research on "novel ecosystems" have thus emphasized the importance of focusing on the function of species (Hobbs *et al.* 2006, Davis *et al.* 2011, Buckley & Catford 2016, Miller &

Bestelmeyer 2016) and their invasive character (Larson *et al.* 2016) instead of uniquely origin for management decisions.

Considering that tree genera were well defined by their litter traits (Fig. 1.2), we interpreted the observed genus effect as a proxy for leaf litter trait influence on Collembola communities. Nonetheless, we acknowledge that this influence could either be associated with abiotic- and/or resource-driven effects as the experimental design did not allow us to distinguish their respective contributions. One limitation of our interpretation is that tree genera were most likely also related to other traits for which we do not have measurements (e.g. roots) despite their potential influence on distribution of Collembola species having other tree-derived resources as part of their diet (Ponge 2000). However, even if we can not dissociate effects of above- and belowground traits, we could consider genus as a proxy for all genus-related traits, which still reflects a useful functional approach for determining Collembola community assembly. The low proportion of variance of the Collembola communities explained by litter genus (thus tree traits) in comparison to study site (Table 1.1) is not surprising as these communities are also shaped from local species pools each with numerous abiotic and biotic filters (Keddy 1992) such as soil characteristics and species interactions (Wardle *et al.* 2004).

Despite the identical experimental design at both sites including source trees from common tree nurseries, site-specific effects may have been due to intra-specific variation in some litter traits (N and microbial respiration; Fig. 1.2), different environmental conditions (Annex 1.1) or different local species pools of Collembola (Annex 1.5). Interestingly, the variance explained by litter genus within each site was more than two times higher than across sites, which highlights not only the potential of a trait-based approach to predict a higher trophic community, but the importance of context dependency. While local species pools varied, we observed a consistent response of Collembola communities to litter treatments across sites (biogeographic origin and genus), reaffirming the strength of 'filtering effects' despite the context dependency. For example, dominant species at both sites were different, yet within the *Lepidocyrtus* genus (which generally regroups drought-tolerant epigeic species with similar environmental preference; Salmon *et al.* 2014). One final source of variation between sites may have been methodological as we were constrained by the use of slightly different extraction methods for Auclair (Tullgren) and Cloquet (Kempson) that might have influenced the number of total individuals collected in each site. However, given that the most efficient extraction method (i.e. Kempson, due to its capacity to maintain better gradients of humidity and temperature through the sample; Edwards 1991) resulted in lower total abundance at Cloquet, it is unlikely that this contributed to much variation.

Interestingly, the similarity of how Collembola communities of one- and six-species mixtures varied according to the studied factors (i.e. litter genus, litter origin and study site; Table 1.1, Fig. 1.3), suggests additive effects of the litter species when comparing trait and biogeographic origin effects. Despite a lower number of six-species replicates in the experiment, this observation suggests that one could expect similar results for monocultures and multi-species forests, reinforcing the above conclusions for real-life scenarios.

1.5.2 Understanding tree genus effect on Collembola through litter traits

Our second hypothesis was partially confirmed as we observed a correlation between Collembola community and litter traits at Cloquet, but not at the Auclair site (Table 1.2, Fig. 1.4a). This difference might be the consequence of different resource utilization at each site. Soil moisture and soil type are important determinants of microbial activity and decomposition (Bardgett *et al.* 1999, Butenschoen *et al.* 2011), but can also affect root structures (Bauhus & Messier 1999, Tobner *et al.* 2013) and associated root-derived carbon sources to the soil. Collembola are known to have a plastic diet (Ponge 2000) and to migrate vertically depending on numerous factors such as soil moisture (Detsis 2000). Hassall *et al.* (1986) showed that this migration could be driven by resource availability rather than moisture on its own due to microbial blooms after heavy rain. Contrary to the traditional perception, Collembola diet might actually be more root- than litter-driven (Larsen *et al.* 2007, Pollierer *et al.* 2007, Fujii *et al.* 2016) with a preference for root-derived C and N and the capacity to switch to litter C in unfavorable soil conditions (Endlweber *et al.* 2009). Thus, a limitation of a favorable environment in Cloquet with drier and sandier soil might have strengthened the influence of litter resources on Collembola communities in comparison to Auclair. On the other hand, the absence of correlation between Collembola community and litter traits in Auclair, despite a clear litter genus effect, may have been related to the use of root C rather than litter C by Collembola. The significant correlation between litter traits and shared Collembola species between sites may be explained by the mostly epigeic and hemiedaphic ecology of these shared species, except for *Mesaphorura* species (Lindberg & Bengtsson 2005, Malcicka *et al.* 2017). These species likely depended on litter as their main resource (Hopkin 1997), irrespective of whether or not the soil was a favorable environment.

If resource filters were indeed different at both sites, the site-dependent genus effect may be the consequence of root traits not necessarily being coordinated with leaf traits (Withington *et al.* 2006, Tobner *et al.* 2013, Weemstra *et al.* 2016). Even if the deciduous and evergreen character is related to some root traits (Bauhaus & Messier 1999, Alvarez-Uria & Körner 2011), it might not be the main factor driving interspecific variance in root traits contrary to our interpretation of leaf litter traits in the study. For example, Comas & Eissenstat (2004) showed an association of root traits with growth rate: fast-growing species were characterized by roots with lower phenolic content, smaller diameter and higher branching than slow-growing species. One might hypothesize that roots with less chemical defence (low phenolic content) as well as a morphology susceptible to facilitate ingestion (small diameter) and encounters (longer roots with a great degree of branching) might be more conducive to Collembola feeding. *Larix* for example is known to be a fast-growing tree species contrary to *Acer*, *Quercus, Pinus* and *Picea* species (Tobner *et al.* 2013) and could have bore root traits more favorable to Collembola feeding, possibly explaining the similarity in Collembola communities associated with both *Larix* species at Auclair (Fig. 1.3a). These favorable root traits, combined with a thicker and moister *Larix* litter layer (Annex 1.2), could have provided an ideal environment for both epigeic and edaphic species. On the other hand, Withington *et al.* (2006) demonstrated that *Larix* species had conservative root traits despite their fast growth rate. These contrary results reflect that our interpretation remains speculative given the current difficulties to demonstrate a "fast-slow" plant economic spectrum such as described by Reich (2014; Weemstra *et al.* 2016). Different results observed across studies might be due to the fact that root traits are depending on a great number of environmental constraints, thus may be more context-dependent and consequently difficult to relate to leaf traits (Weemstra *et al.* 2016).

Beyond site-specific responses, several interesting observations regarding the Collembola community - litter trait covariation were made. Firstly, stronger correlations with recalcitrant *Pinus* and *Picea* litter (Fig. 1.2, Fig. 1.4a) may indicate that Collembola species need to be more specialized to consume these resources in comparison to palatable resources, thus it could be expected that their consumption traits (i.e. mouthparts) should be less diversified in more recalcitrant treatments. This assumption was however not confirmed by a meta-analysis of Le Provost *et al.* (2017) who showed no correlation between variance of grasshopper incisor strength and mean leaf toughness. The trend observed in our results is probably more due to the association of edaphic species such as *M. pygmaea* and *Mesaphorura* species (Malcicka *et al.* 2017) to deciduous litters. Given that edaphic species are supposed to live mainly in the soil (Hopkin 1997), it would explain the weaker correlations with litter traits. Presumably, we could expect higher correlations with root traits for these species. Secondly, bigger species (e.g. *P. flavesencens* and *E. nivalis*) were associated with evergreen litters except *I. viridis* suggesting that these species have more developed and/or stronger mouthparts since mouthpart dimensions might be associated with body size (Chen *et al.* 1997). However, the correlation of *I. viridis* with deciduous litters might rather indicate that body size is not a good proxy for feeding traits given the possible different diets in a given body size range. Finally, some strong correlations between particular species and traits indicate that using multiple traits could actually lead us to better understand the interactions between consumers and their resources. For example, *N. muscorum* is consistently associated with evergreen litters (Fig. 1.4), which is consistent with Cakir and Makineci (2013) who showed that *Neanuridae* were more abundant in *Pinus* than *Quercus* treatments. However, our results revealed that this species is well correlated with litter lignin concentration in both sites (Fig. 1.4b), which presumably indicates that its preferred food is highly associated with lignin. Such information is valuable to increase modelling predictive capacity; for example, Brousseau *et al.* (2017) demonstrated that predator/prey trait-matches combined with phylogenetic information successfully predicted ground beetle-prey interactions.

1.6 Conclusion

Our study on Collembola communities in dense, young plantations of native and exotic tree communities showed that community assembly was not driven by biogeographic origin of litter resources, but partially driven by their litter traits. Our results provide empirical evidence to the "novel ecosystem" concept premise stating that the impact of a species in a given ecosystem is linked to its functions rather than to its origin (Hobbs *et al.* 2006). Still, considering the scarce number of studies on non-native species trying to correct biases related to species traits and environment (Buckley & Catford 2016), further efforts to understand the full range of biogeographic origin are needed. Future efforts might include a similar experimental design but in an array of different scenarios (e.g. longer time sequence study, influence on vertebrates, specialist vs generalist consumers comparison, top-down vs bottom-up effect of non-native species, different polyculture combinations, etc.). Nonetheless, the clear influence of litter traits on Collembola communities opens the path to multi-trophic functional studies to better understand above- and belowground interactions. Further efforts to better understand trait-matching between resource (litter and roots) and consumers (e.g. mouthparts) will be important to better predict responses of soil communities and their role in key ecosystem functions in face of changing plant communities. Finally, these results highlight context-dependency in experimental biodiversity studies (Wardle 2016), but more importantly the need to better understand this context dependency as it can totally modify filters influencing community assembly (Wardle *et al.* 2004) and induce intraspecific trait variation. To this extent, multi-site studies such as IDENT allow to identify these dependencies, allowing us to better understand how changing biodiversity, including non-native species, will affect ecosystem functioning in a range of real world scenarios (Eisenhauer *et al.* 2016).

1.7 Annexes

Annex 1.1 Site-specific description of field environmental characteristics of the AuCl experiment including various climate and soil variables.

	Auclair (QC, CAN)	**Cloquet** (MN, USA)
Coordinates	47.7° N, 68.6° W[a]	46.7° N, 92.5° W[a]
Altitude	333[a]	383[a]
Former land use	Low-input abandoned pasture[a]	Forest[a]
Mean annual temperature (°C)	3.4 ± 5.5 [b]	4.3 ± 5.5 [c]
Mean annual precipitations (mm/month)	88.5 ± 20.8 [b]	35.2 ± 19.7 [c]
Soil type	Loam[a]	Sandy-loam[a]
Mean litter layer height (cm)	2.0 ± 0.6 [d]	1.8 ± 0.7 [d]
Mean soil temperature (°C)	NA	6.97 ± 4.19 [e]
Mean soil moisture (% H_2O d.m.)	19.5 ± 3.4 [d]	10.6 ± 2.8 [d]
Mean soil microbial biomass (µg microbial-C g^{-1})	132.8 ± 22.6 [d]	NA
Mean soil pH	4.56 ± 0.14 [f]	5.58 ± 0.15 [g]

[a] As described in http://www.treedivnet.ugent.be.html and Tobner *et al.* (2014)

[b] Calculated from average monthly data between 2005 to 2015 at Edmunston, NB, Canada (~ 44km from Auclair; Environment Canada)

[c] Calculated from average monthly data between 2005 to 2015 at Cloquet, MN, USA (Weather Underground)

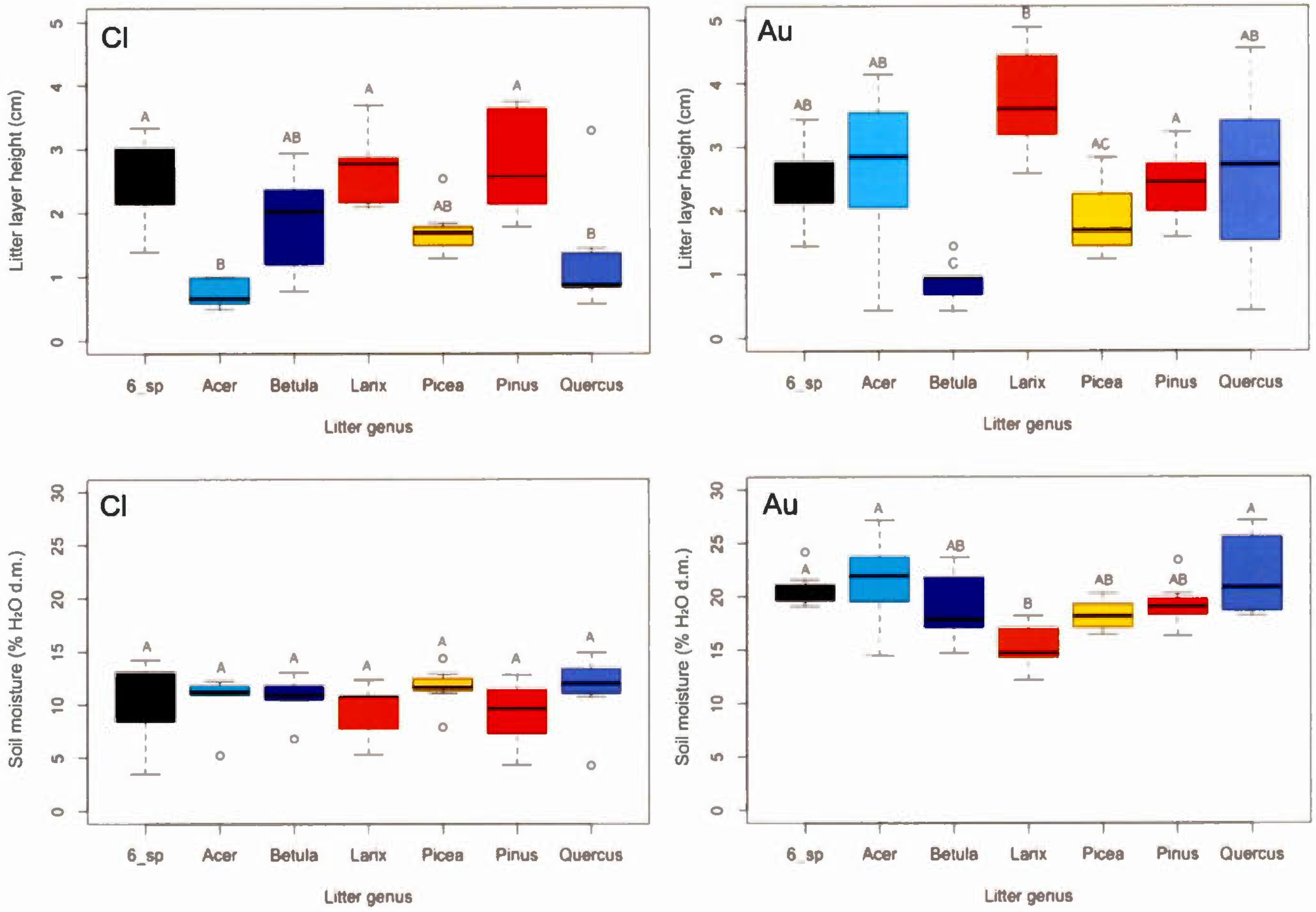
[d] Method is explained in "Material and methods" section of the paper

[e] Calculated from average 2015 monthly data at Cloquet experimental site

[f] Measured with a water-based method on 12 samples taken across blocks in September 2017

[g] Measured with a water-based method on 64 samples taken across blocks in October 2013

Annex 1.2 Soil moisture (% H_2O d.m.) and litter layer height (cm) by tree genus and site (Au = Auclair, Cl = Cloquet). Letters represent post-hoc Tukey results ($p < 0.05$)



Annex 1.3 Functional trait measurement methods of leaf litter per tree species per site.

Trait (units)	Replication	Instrument and/or protocols
C and N concentration (% dry-leaf mass)	3	At least 5 leaves were pooled together to grind to a fine powder with a ball mill (Retsch). A replicate was a subset of this mixture. C and N concentrations were measured with an elementary analyzer EA1108 (Thermo Scientific).
Hemicellulose, cellulose and lignin concentration (% organic matter)	1 to 3	At least 5 leaves were pooled together to grind with a 1 mm cutter mill (Wiley). A replicate was a subset of this mixture. Hemicellulose, cellulose and lignin concentrations were obtained after a series of chemical digestions (NDF, ADF, ADL) with a Fiber Analyzer 2000 (Ankom). Organic matter was determined after ashing at 550°C during 5 hrs. More details in Van Soest *et al.* (1991). Number of replicates depended on available litter for analyses.
Water saturation capacity (% H_2O dry-leaf mass)	≥ 10	Based on this formula: $(W - D) / (D) * 100$ Where: D = Dried leaf mass after 48 hrs in oven at 65°C W = Wet leaf mass after 48 hrs immersion in distilled water. Adapted from the LDMC measurement protocol in Pérez-Harguindeguy *et al.* (2013).
Leaf thickness (mm)	≥ 15	Sub-replicates (3-5) were taken per leaf and at least 15 leaves were analyzed. Measured with a QuantuMike 293-180 digital micrometer (Mitotuyo). More details in Pérez-Harguindeguy *et al.* 2013.
Leaf toughness or "resistance to fracture" ($g\ mm^{2\ -1}$)	≥ 15	Sub-replicates (3-5) were taken per leaf and at least 15 leaves were analyzed. Measured with a Medio-Line 403000 pressure dynanometer (Pesola). More details in Pérez-Harguindeguy *et al.* (2013).
Microbial basal respiration (μg CO2-C g^{-1} h^{-1})	2 to 24	Moisture content was adjusted at 45 % of water holding capacity after grinding (coffee mill) and sieving of all litter material (1 mm Retsch test sieve). To limit size heterogeneity, only litter pieces ≥ 0.6 mm were used (second sieving). Preincubation lasted 7 days at 25 °C. More details see Campbell *et al.* (2003). Number of replicates depended on available litter for analyses.

Annex 1.4 Mean litter trait values and standard deviation for the 12 tree species of Auclair (Au) and Cloquet (Cl). NA= North American origin (native) and EU = European species (non-native).

Species	Origin	Site	Thickness mm	Resistance g mm$^{2\ -1}$	WSC % H_2O d.m.	N % d.m.	C/N	Cellulose % o.m.	Hemicellulose % o.m.	Lignin % o.m.	Lignin/N	MR µg CO2-C g^{-1} h^{-1}
A. saccharum	NA	Au	0.095 ± 0.01	5 ± 1	377.651 ± 33.606	0.98 ± 0.01	45.53 ± 0.09	33.1 ± 0.53	3.75 ± 0.27	12.47 ± 0.47	12.72	21.029 ± 5.946
A. platanoides	EU	Au	0.077 ± 0.009	3 ± 1	383.51 ± 19.926	0.92 ± 0.02	48.68 ± 1.01	39.3 ± 1.72	15.94 ± 1.18	9.99 ± 0.29	10.86	28.769 ± 2.563
A. saccharum	NA	Cl	0.135 ± 0.007	5 ± 1	232.783 ± 17.067	0.91 ± 0.03	49.18 ± 1.3	26.54 ± 0.44	4.38 ± 0.1	12.12 ± 0.27	13.32	55.024 ± 9.747
A. platanoides	EU	Cl	0.115 ± 0.01	4 ± 1	237.533 ± 21.114	1.62 ± 0.02	27.5 ± 0.26	31.65 ± 1.23	7.48 ± 1.81	14.64 ± 0.47	9.04	86.328 ± 15.096
B. papyrifera	NA	Au	0.117 ± 0.012	3 ± 1	367.94 ± 27.023	1.38 ± 0.01	33.76 ± 0.08	31.32 ± 0.65	4.81 ± 1.02	16.7 ± 2.56	12.1	53.394 ± 1.396
B. pendula	EU	Au	0.13 ± 0.009	2 ± 1	384.723 ± 36.062	0.93 ± 0.01	49.98 ± 0.45	33.39 ± 0.1	12.38 ± 1.67	12.45 ± 1.1	13.39	34.69 ± 0.817
B. papyrifera	NA	Cl	0.152 ± 0.015	3 ± 3	352.124 ± 30.811	1.07 ± 0.01	44.09 ± 0.26	25.11 ± 0.43	7.8 ± 0.84	14.75 ± 0.5	13.79	69.054 ± 15.836
B. pendula	EU	Cl	0.138 ± 0.012	2 ± 1	398.826 ± 20.641	0.73 ± 0.02	64.59 ± 1.47	33.27 ± 1.03	5.13 ± 0.27	13.98 ± 0.58	19.15	56.422 ± 18.98
Q. rubra	NA	Au	0.12 ± 0.007	7 ± 1	289.602 ± 38.462	0.92 ± 0.01	51.41 ± 0.16	42.64 ± 0.62	10.46 ± 0.61	16.17 ± 0.66	17.58	38.669 ± 10.649
Q. robur	EU	Au	0.117 ± 0.007	6 ± 1	286.161 ± 24.788	0.93 ± 0.01	49.56 ± 0.14	43.14 ± 0.35	2.23 ± 0.41	16.03 ± 1.89	17.24	24.076 ± 1.064
Q. rubra	NA	Cl	0.141 ± 0.01	5 ± 1	244.33 ± 21.924	0.87 ± 0.02	51.6 ± 1.28	39.93 ± 0.39	8.63 ± 0.96	17.1 ± 0.13	19.66	82.512 ± 14.596
Q. robur	EU	Cl	0.154 ± 0.01	4 ± 1	282.001 ± 24.14	1.04 ± 0.01	42.29 ± 0.31	39.67 ± 0.39	1.88 ± 0.1	14.72 ± 0.3	14.15	67.918 ± 12.707
L. laricina	NA	Au	0.071 ± 0.18	2 ± 1	192.642 ± 16.773	1.85 ± 0.01	26.72 ± 0.13	42.19 ± 0.44	2.44 ± 0.09	24.77 ± 0.07	13.39	26.085 ± 2.21
L. decidua	EU	Au	0.088 ± 0.021	2 ± 1	218.937 ± 25.81	2.46 ± 0	19.81 ± 0.02	36.6	0	34.62	14.07	25.362 ± 5.717
L. laricina	NA	Cl	0.137 ± 0.017	3 ± 1	251.538 ± 51.215	0.92 ± 0.05	48.17 ± 2.45	35.78 ± 0.35	3.6 ± 0.68	26.71 ± 0.25	29.03	60.376 ± 15.654
L. decidua	EU	Cl	0.128 ± 0.012	2 ± 1	255.903 ± 35.845	0.48 ± 0.02	99.74 ± 2.98	39.05 ± 0.61	0.45 ± 0.31	26.65 ± 0.27	55.52	77.549 ± 20.763
P. glauca	NA	Au	0.273 ± 0.46	16 ± 5	148.521 ± 7.605	1 ± 0.01	47.42 ± 0.17	38.86 ± 1.21	2.91 ± 0.17	22.85 ± 1.38	22.85	22.478 ± 2.558
P. abies	EU	Au	0.201 ± 0.031	17 ± 5	138.212 ± 7.301	1.2 ± 0.01	39.17 ± 0.02	44.9 ± 0.80	4.17 ± 0.29	22.61 ± 0.44	18.84	20.329 ± 0.787
P. glauca	NA	Cl	0.284 ± 0.05	17 ± 6	164.594 ± 27.208	0.6 ± 0.01	77.96 ± 0.88	35.39 ± 0.32	4.53 ± 0.42	20.65 ± 0.16	34.42	55.815 ± 20.055
P. abies	EU	Cl	0.239 ± 0.02	10 ± 2	200.053 ± 28.256	0.64 ± 0.01	73.35 ± 0.46	39.75 ± 1.36	1.86 ± 1.15	22.23 ± 0.23	34.73	41.164 ± 6.73
P. strobus	NA	Au	0.232 ± 0.034	17 ± 5	115.494 ± 12.491	1.41 ± 0.01	34.69 ± 0.13	35.63 ± 0.47	2.62 ± 0.45	25.94 ± 0.18	18.4	18.983 ± 2.474
P. sylvestris	EU	Au	0.477 ± 0.078	43 ± 15	85.399 ± 9.752	0.97 ± 0.01	50.05 ± 0.18	47.96 ± 0.84	2.59 ± 0.3	21.6 ± 0.73	22.27	15.308 ± 2.322
P. strobus	NA	Cl	0.223 ± 0.04	11 ± 3	113.201 ± 10.447	0.38 ± 0.02	131.75 ± 6.95	37.51 ± 0.59	0.93 ± 0.39	26.26 ± 0.18	69.11	42.054 ± 7.835
P. sylvestris	EU	Cl	0.497 ± 0.056	50 ± 17	166.069 ± 17.693	0.55 ± 0.03	88.6 ± 4.45	42.8 ± 0.08	1.73 ± 0.27	19.77 ± 0.11	35.95	40.885 ± 8.294

Annex 1.5 List of 57 Collembola species sampled by study site in AuCl experiment. Individuals not matching with any species described in the available taxonomic keys were classed in "morpho-species" based on morphologic characteristics (e.g. *Arrhopalites* sp. 1) *Excluded from analyses.

Family	**Study site**		
	Auclair (n=37)	Cloquet (n=34)	Shared species (n=14)
Bourletiellidae	*Bourletiella hortensis*	*Bourletiella hortensis*	*Bourletiella hortensis*
Dicyrtomidae		*Dicyrtoma fusca*	
Entomobryidae	*Corynothrix borealis*	*Entomobrya* sp.2	*Entomobrya* sp.2
	Entomobrya sp.1	*Entomobrya comparata*	*Entomobrya nivalis*
	Entomobrya sp.2	*Entomobrya nivalis*	*Lepidocyrtus cyaneus*
	Entomobrya sp.3	*Heteromurus nitidus*	*Lepidocyrtus fernandi*
	Entomobrya sp.4	*Lepidocyrtus cyaneus*	
	Entomobrya nivalis	*Lepidocyrtus fernandi*	
	Lepidocyrtus beaucatcheri	*Lepidocyrtus paradoxus*	
	Lepidocyrtus cyaneus	*Lepidocyrtus violaceus*	
	Lepidocyrtus fernandi	*Lepidocyrtus* sp.1	
	Pseudosinella alba	*Pseudosinella rolfsi*	
	Sinella sp.1		
Isotomidae	*Desoria flora*	*Desoria* sp.1	*Desoria flora*
	Desoria trispinata	*Desoria flora*	*Isotoma subviridis*
	Folsomina sp.1	*Folsomia bisetosa*	*Isotoma viridis*
	Folsomia stella	*Folsomia fimetaria*	*Isotomiella minor*
	Isotoma subviridis	*Isotoma subviridis*	*Parisotoma notabilis*
	Isotoma viridis	*Isotoma viridis*	
	Isotomiella minor	*Isotomiella minor*	
	Parisotoma notabilis	*Parisotoma notabilis*	
		Pseudanurophorus	
Hypogastruridae	*Schaeffaria duodecimocellata*	*Choreutinula americana*	
	Willemia intermedia	*Hypogastrura* sp.1	
		Willemia	
Katiannidae	*Sminthurinus conchyliatus*	*Polykatianna intermedia*	
Neanuridae	*Friesea mirabilis*	*Micranurida pygmaea*	*Neanura muscorum*
	Neanura muscorum	*Neanura muscorum*	
Neelidae	*Megalothorax minimus**		
Onychiuridae	*Hymenaphorura similis*	*Hymenaphorura similis*	*Hymenaphorura similis*
	Onychiurus sp.1	*Oligaphorura pingicola*	
	Proisotoma immersa	*Thalassophorura*	
	Proisotoma minima		
	Protaphorura armata		
	Protaphorura paucisetosa		
Sminthurididae		*Sminthurides lepus*	
Sminthuridae	*Sminthurus* sp.1		
Tomoceridae		*Pogonognathellus*	
Tullbergiidae	*Ameritulla clavata*	*Mesaphorura*	*Mesaphorura macrochaeta*
	Mesaphorura macrochaeta	*Mesaphorura silvicola*	*Mesaphorura silvicola*
	Mesaphorura silvicola		

CHAPITRE II

MEASURING MANDIBULAR TRAITS OF COLLEMBOLA AND RESOURCE QUALITY TRAITS OF LITTER TO BETTER UNDERSTAND TROPHIC INTERACTIONS

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2.1 Abstract

The use of functional traits in community ecology has gained increasing popularity as it brings us closer to understanding mechanisms explaining community assembly or how communities influence ecosystem processes. Although its application to higher trophic levels (beyond plants) remains relatively recent, functional traits could be a valuable tool to assist in predictions of consumer-resource interactions of soil invertebrates given current limitations associated to traditional approaches like gut content analysis. The aim of this study was to (1) measure a new set of Collembola mandibular traits, (2) determine the relevance of Collembola body length and phylogeny as proxies for these traits and (3) establish if Collembola mandibular traits related to consumption covary with litter quality traits related to their resource. Collembola were sampled and extracted (Tullgren-Kempson) in summer 2015 under 12 single-species tree plots replicated at the Auclair and Cloquet IDENT sites (International Diversity Experiment Network with Trees). We successfully measured functional traits associated to Collembola feeding that included mandibular length, mandible/head ratio, molar plate length, mouth opening, apical morphology, mechanical advantage, deployment capacity of mandibles and the potential proxy trait of body length on a total of 52 species. Functional traits of the 12 leaf litter resources included N, cellulose, hemicellulose and lignin concentrations, C/N, leaf thickness, leaf toughness, water saturation capacity and microbial basal respiration. Despite some traits being proportional to body length (mandible length, mouth opening), our results demonstrated that neither body length or phylogeny were adequate proxies for mandibular traits given tremendous variation across closely related species. Collembola consumption traits covaried with resource traits of their litter at Cloquet (0.38). This covariation was similar when correlating Collembola species taxonomic composition with litter traits (0.40), suggesting that community structure was driven in part by available litter resources and associated microbes. Our findings suggest that these novel traits associated with the functionality of Collembola mouthparts could be a promising venue for predicting feeding interactions of Collembola and leaf litter resources as plant communities change globally.

Keywords : functional trait, consumer-resource interactions, trait-matching,
springtails, mouthparts, IDENT

2.2 Introduction

Soils are a major hub of biological diversity that contribute to the functioning of terrestrial ecosystems through determinant processes such as litter decomposition and nutrient cycling (Bardgett & van der Putten 2014, Handa *et al.* 2014). However, such functions depend on complex interactions among soil biota and with their abiotic environment and are often simplified as a "black box" (Cortois & De Deyn 2012). Indeed, trophic interactions of soil organisms are challenging to study given their small size (Gobat *et al.* 2010, Ball *et al.* 2014), their extreme diversity (Coleman 2008, Wurst *et al.* 2012) and opaque soil habitat (Cortois & De Deyn 2012). Common methods used to determine soil invertebrate diets (e.g. gut content and stable isotope analyses) have provided important advances in documenting interactions (Scheu 2002, Chahartaghi *et al.* 2005, Pollierer *et al.* 2009, Maraun *et al.* 2011), but do not reveal clear mechanisms driving consumer-resource interactions. Additionally, some oversimplified interpretations of species diet can occur; for example, gut content represents a brief snapshot of the full diet and is often difficult to determine (Hopkin 1997, Perdomo *et al.* 2012).

Collembola are a good case example of these limitations. Traditionally considered as fungivorous feeders, their diet has proven to be much more diverse than previously thought (e.g. dead and living leaves, lichens, mosses, microalgae, pollen, bacteria, faeces, roots, nematodes, mites, mineral particles; Hopkin 1997, Rusek 1998, Ponge 2000, Addison *et al.* 2003, Castaño-Meneses *et al.* 2004). Collembola are now considered as omnivorous opportunistic feeders with a preference for fungi (Hopkin 1997) and the capacity to switch diets depending on environmental conditions and resource availability (Filser 2002, Endlweber *et al.* 2009). Nonetheless, selective feeding can occur: for example, *Onychiurus armatus* (now *Protaphorura armata*) showed a definite preference for certain species of fungi depending on mycelial morphology, nutrient content and presence of secondary metabolites in laboratory experiments (Shaw 1988). However, feeding preference is not linked to the family of Collembola since taxonomically close species (Isotomidae) responded very differently to bacteria and fungal densities in a field study by Salamon *et al.* (2006), highlighting that even within one family, diversity of diets could be extensive. Curiously, the two main mouthpart types recognized for the Collembola ("piercing-sucking" and "chewing"; Christian 1989) do not adequately explain this diversity of diets within a family, as species from a same family are always characterized by the same mouthpart type (e.g. all Isotomidae have chewing mouthparts) (Christiansen & Bellinger 1998, Fjellberg 1998 & 2007, Hopkin 2007). Furthermore, the current mouthpart categories make it impossible to differentiate microbivore and litter consumers as both diets correspond to “chewing” mandibles (Malcicka *et al.* 2017). Santorufo *et al.* (2014) attempted to detail mandibles differently by being “strong” or “normal” depending on their morphology (lamellae, capitulum, fringe), but their classification remains limited to two categories. These examples suggest that to better predict feeding behaviour, we might consider incorporating new morphological traits associated to Collembola mouthparts. Currently, we cannot assign Collembola to a single trophic functional group or specific trophic position severely limiting our understanding of their role in the soil network and its emergent properties.

There is a current effort to extend the functional trait approach to invertebrates (Pey *et al.* 2014a, Pey *et al.* 2014b, Moretti *et al.* 2016) as it was initially developed for plants (e.g. Tilman *et al.* 1997, Lavorel and Garnier 2002, Wright *et al.* 2004, Pérez-Harguindeguy *et al.* 2013). The use of functional traits (i.e. every phenological, physiological, morphological or behavioural characteristics influencing species fitness) with invertebrates could lead to a better understanding of potential mechanisms governing soil food web interactions (Pey *et al.* 2014b, Brousseau *et al.* submitted). To determine how functional structures covary among trophic levels is key to understanding the emergent properties at the network level, but is still scarcely studied (McGill *et al.* 2006, de Bello *et al.* 2010, Gravel *et al.* 2016). Trait-matching studies between consumers and resources could increase the accuracy of prediction of interactions (Eklöf *et al.* 2013, Brousseau *et al.* 2017). For example, Le Provost *et al.* (2017) demonstrated that variation of resource-acquisition traits within grasshopper communities depended on plant traits. It was also demonstrated that correlation between traits of fruited plants and fruit-eating birds was stronger than between their strict abundances (Dehling *et al.* 2014). Although Salamon *et al.* (2006) showed that the abundance of microbivores, such as Collembola, did not necessarily correlate with that of microbes, this lack of relation between the abundance of consumers and that of their resource might have been due to abundances being less relevant than traits in terms of species covariation (Dehling *et al.* 2014). Additionally, spatial covariation may not only be driven by food availability, but also by time of reproduction and micro-climatic conditions for Collembola (Addison *et al.* 2003). Nonetheless, testing the covariation between Collembola mouthpart functional traits and litter traits could bring a more mechanistic understanding of Collembola community assembly and a first step towards formulating trait-matching hypotheses.

As observed in a previous experimental study, litter functional traits significantly explained the variation in Collembola community composition, suggesting a possible link to feeding traits of Collembola (Chapter 1). However, this correlation, driven mostly by the recalcitrant or labile traits of leaf litter, was not observed in both sites under study (Cloquet, but not Auclair), highlighting context-dependency (Table 1.2 in Chapter 1). Litter can indeed be consumed by Collembola (i.e. observed in gut content; Ponge 2000) but it is unclear whether it is for leaf nutrients or indirectly to consume microbes populating litter leaves. It is commonly assumed that recalcitrant litters will favor fungi while labile litters will favor bacteria (Scheu *et al.* 2005, De Deyn *et al.* 2008). Therefore, type of litter could be associated with Collembola mouthparts. For example, the molar plate is a mandibular structure associated with fungal consumption (Chen *et al.* 1997) that can be totally absent in some species (Christian 1989). It can be reasoned that species living in recalcitrant litters, where the main microbial resource should be fungi, should bear a more developed molar plate than species living in labile litters in order to consume available resources. However, bacterial and fungal carbon channels might not be as distinct as previously thought, given that recent work has shown that saprotrophic fungi also use labile C (de Vries & Caruso 2016). Therefore, using litter quality as a proxy for associated microbes should be done carefully given these varied energy channels for microbes.

Even though Collembola most likely consume microbes indirectly through litter, they still need mouthparts mechanically allowing such a consumption. Collembola species have potentially different feeding habits on litter (i.e. mechanically degrading and shredding, skeletonizing the leaves by consuming just between the veins and eating partially degraded pieces of organic matter; Rusek 1998) suggesting indeed that these specific habits could ensue from mouthpart morphology and/or litter quality. Surprisingly, beyond the classic feeding groups (Christian 1989, Rusek 1998), Collembola mouthpart morphology is yet to be described in detail in the literature (Manton & Harding 1964, Goto 1972). Attempts to better understand functionality of Collembola mouthpart morphology remain rare (Wetton 1988, Christian 1989, Chen *et al.* 1997) and the study of trait covariation between Collembola consumer traits and their resource traits could bring insight on the matter. Even more startling is the fact that maxillae are generally much more detailed in the literature than mandibles (e.g. Malcicka *et al.* 2017), yet are harder to observe on a binocular resulting in the taxonomic potential of mandibles for Collembola being often overlooked (Wetton 1988). Although Goto (1972) concluded that mandibles were unlikely to be useful in *Folsomia* species recognition, Wetton (1988) demonstrated, in contrast, that mandibular apical morphology differed greatly between *Folsomia* species differentiated taxonomically otherwise only by a setal character. Such results suggest that the three main Collembola taxonomic orders (Poduromorpha, Entomobryopmorpha and Symphypleona), which are characterized generally by body shape, are too coarse to be useful proxies for mandible functionality. For ground beetles, detailed mandible traits have been shown to be related to feeding interactions; for example prey cuticular toughness correlated with mandible strength (Brousseau *et al.* 2017). The study of detailed mandibles (as for beetles; Wheater & Evans 1989, Brousseau *et al.* 2017) could not only bring insight on consumer-resource relations, but also represents a simpler method than maxillae to assess mouthpart functions and infer Collembola trophic position in the soil network.

Here, our aim was to (1) measure a new set of Collembola mandibular traits, (2) determine if body length or phylogeny could be use as proxies for these traits and (3) to explore if there is a correlation between these newly described Collembola consumption traits and litter resource traits. Considering the great diversity in diet across Collembola species, we did not expect phylogeny to be a good proxy for mandibular traits. Additionally, we expected some dimension-related traits (e.g. mandible length) to correlate to body length as these are likely proportional. Finally, given our previous work showing a correlation between litter traits and Collembola species at the Cloquet site (Chapter 1), we hypothesized that with this dataset, a consumer trait-resource trait correlation would be also observed.

2.3 Material and methods

2.3.1 Experimental site and design

The study was conducted in the AuCl experiment of the International Diversity Experiment Network with Trees (IDENT), which is a network of Biodiversity – Ecosystem Function experiments in North America and Europe (Tobner *et al.* 2014). Samples came from two sites that were identically designed, one near Auclair (Au), Québec, Canada (47.7° N, 68.6° W) and the other in Cloquet (Cl), Minnesota, USA (46.7° N, 92.5° W). At each site, 12 single-species treatments were sampled (n=4): *Acer saccharum*, *A. platanoides*, *Betula papyrifera*, *B. pendula*, *Larix decidua*, *L. laricina*, *Quercus robur*, *Q. rubra*, *Picea abies*, *P. glauca*, *Pinus strobus* and *P. sylvestris*. For more details on the AuCl experiment, see Tobner *et al.* (2014).

2.3.2 Litter sampling and litter trait measurements

In October 2015, freshly senescent leaves of deciduous trees were collected on single-species plots at both sites and on at least five random trees per plot after gentle shaking of the trunks. Evergreen species senescent needles were collected throughout the field season in June, July and August 2015. All leaves per species per site were then pooled together and mixed homogeneously before trait measurements: leaf water saturation (% H_2O d.m.), leaf thickness (mm), leaf resistance to fracture (g $mm^{2\ -1}$), N concentration (% d.m.), cellulose, hemicellulose and lignin concentration (% o.m.), C/N and lignin/N ratios. For microbial basal respiration rate (µg CO_2-C $g^{-1}h^{-1}$), litter was manually collected directly on the forest floor at five random positions per plot during the field session and air-dried until MicroResp analyses (Campbell *et al.* 2003). Here we consider the mean litter microbial basal respiration rate per species (across four blocks per site) as a litter species functional trait. Details about trait measurements are in Annex 1.3 (Chapter 1).

2.3.3 Collembola sampling

Collembola were sampled in late July (Au) and early August (Cl) 2015. For each plot, two subsamples were randomly collected at its center to minimize any edge effect, yielding a total of 192 subsamples. Adequate sampling effort was determined by preliminary sampling tests at Auclair in June 2015. At each subsample site, litter was collected manually in a 15 x 15 cm quadrat. At the center of the quadrat, soil was extracted with a split soil core sampler (diameter 5.08 cm x depth 5 cm). Both litter and soil were transferred in hermetic containers and kept at 4 °C for transport to the laboratory for a maximum of 48 hrs. Litter and soil subsamples were then pooled together prior to Tullgren (Au) or Kempson (Cl) extraction during which the temperature was gradually increased during 7 days (20 °C to 50 °C) and fauna collected in 70 % ethanol. Collembola were cleared in lactic acid at 60 °C to better see structures needed for identification (e.g. chaetotaxy and post-antennal organ). Patterns and coloration were carefully noted before this step. Identification to the species level was done with a Leica DM1000 LED phase contrast microscope (800x) by using the keys of Christiansen & Bellinger (1998), Fjellberg (1998, 2007) and Hopkin (2007). Bellinger *et al.* (1996-2016) was used as complementary information to these keys. Cleared specimens were all slide-mounted in Hoyer's medium (50 ml distilled water – 30 g gum arabic – 200g chloral hydrate – 20 ml glycerol). Few damaged specimens were identified only to the family or the genus level (< 3 %) and were therefore excluded in further analyses along with three samples for which Collembola total abundance equaled zero (*B. pendula* (block A) in Auclair and *A. saccharum* (block A) and *P. abies* (block D) in Cloquet).

2.3.4 Collembola trait measurements

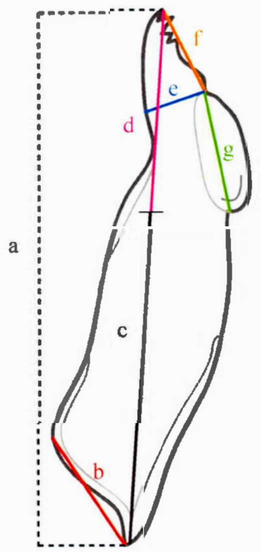
Once mounted, we proceeded to mandibular trait measurements with Leica LAS live measurement software (0.000 μm precision) on a phase contrast microscope with a maximum magnification of 800x and equipped with a Leica ICC50 W camera. For each species per site, the seven traits described in Table 2.1 were measured on at least six individuals (Fountain-Jones *et al.* 2015) along with body length (from the end of the abdomen to the top of the head, appendices excluded). When sampled individuals for a species per site were less than six, the replication was as high as possible. In total, measures were taken on 320 individuals. Mean value of replicates was then considered as the trait value for each trait per species per site. Only well mounted specimens in dorsal position were considered to avoid biases linked to mandible angle. Also, in order to avoid potential sexual, life stage (Chen *et al.* 1997) and mandibular side dimorphism (Goto 1972), measurements were done on left mandibles of female adults only. However, as sex was difficult to confirm on some Entomobryidae (genital plate hidden by furcula), we may have taken measurements on male or juveniles. In order to compensate for this possible bias, more replicates ($n \geq 10$; Annexes 2.1 & 2.2) were measured and marginally small individuals were not considered. Also collected Symphypleona were mostly juveniles, but given their very low abundance in our sampling, we still measured their traits. Two species were excluded from the analyses because their mandibles were too difficult to observe: *Neanura muscorum* (highly pigmented) and *Heteromurus nitidus* (damaged specimen). Given the small size of *Megalothorax minimus* (< 0.4 mm), this species was also excluded from the analyses due to possible sampling bias as some individuals may not have been detected. Further detail on trait measurements and hypothesized functions is provided in Table 2.1. Updated taxonomy was confirmed with Bellinger *et al.* (1996-2017).

2.3.5 Statistical analyses

Trait variation across Collembola and litter species was visualised with principal component analysis ordinations (PCA) after trait data standardization (Legendre & Legendre 2012). The relation between proxies and Collembola species mean mandibular traits was determined through PCA visualization, cluster analyses (phylogeny) as well as with correlations (body length). As mean trait data by species were not distributed normally (Shapiro Wilk test), non-parametric Spearman rank correlations between body length and mandibular traits were used (Legendre & Legendre 2012). Clustering was done with Ward's method on mandibular trait Euclidean distance (Legendre & Legendre 2012). Clustering uncertainty was assessed with approximately unbiased p-value via multiscale bootstrap resampling (bootstrap = 9999; Suzuki & Shimodaira 2006). Procruste analyses were executed to determine the association of standardized litter traits with Collembola species and traits (Peres-Neto & Jackson 2001). Prior to this, Collembola species abundances were Hellinger transformed for "species matrix" (Legendre & Legendre 2012) and a community weighted mean (CWM) for each trait was calculated for the "traits matrix" (Lavorel *et al.* 2008).

All statistical analyses were performed with R (v.3.2.1) (R Development Core Team, Vienna, Austria) and RStudio environment (v. 0.99.903) (RStudio Inc., Boston, USA). Vegan package (v. 2.4-0) by Oksanen *et al.* (2016) was used for Hellinger transformation (decostand/vegdist), trait standardization (decostand), PCAs (rda), clusters (hclust) and procrustes analyses (protest). FD package (v. 1.0-12) by Laliberté *et al.* (2015) was used to compute CWM matrices (dbFD), stats package (v. 3.2.1) by R Core Team was used for spearman correlations analyses (cor.test), and the pvclust package (v. 2.0-0) by Suzuki & Shimodaira (2015) was used to test clustering uncertainty (pvclust).

Table 2.1 Details on Collembola mandibular trait measurements and hypothesized functions associated to each trait

Schematic illustration	Trait	Measurement	Function	References
 a) Mandible length b) Mandible width c) Proximal portion length d) Distal portion length e) Distal portion width f) Toothed region length g) Molar plate length	Mandible length Mandible/Head ratio	= a = a / head length	Related to mechanical advantage, deployment capacity, size and type of ingested particles. Could be a proxy for other traits such as mandibular strength and body size.	Chen et al. 1997 Perdomo et al. 1972 (mites)
	Mechanical advantage	= b / a	If low, mandibles make short and fast movements (e.g. predator) but if high, mandibles make big and slow movements (e.g. litter consumers). Could also be a proxy for mandibular strength.	Perdomo et al. 2012 (mites) Wheater and Evans 1989 (beetles)
	Deployment capacity	= d / c	If high, bigger portion of the mandible can be protruded from the head capsule to collect resources (e.g. scraping scavengers). Also, the higher it is, the more the mandibles are conceived to transform their food (cut, grind, tear, etc.), and therefore should be adapted to eat more recalcitrant resources.	No reference
	Mouth opening	= labrum width – 2*(e)	Determines the size of the particles that can be manipulated and ingested.	Chen et al. 1997
	Apical development	= f / g, then classed in categories; 1 – < 0.75 2 – [0.75-0.95[3 – [0.95-1.05] 4 –]1.05-1.25] 5 – > 1.25 6 – no molar plate (g=0)	If high (6), related to piercing-sucking mouthparts. If intermediary (3-5) to cutting, grinding or scraping mouthparts. If low (1-2), rather related to consumption of fungi.	Christian 1989 Goto 1972
	Molar plate length	= g	Associated with consumption of fungi (brushing of hyphae), but probably not to grinding or chewing activity.	Chen et al. 1997 Hopkin 1997 Goto 1972

2.4 Results

2.4.1 A new set of mandibular traits for Collembola

The seven chosen traits (described in Table 2.1) were successfully measured on 52 sampled species without mandible extraction for a total of 2222 trait measures: mean trait values for each species per site are shown in Annexes 2.1 (Au) & 2.2 (Cl). These traits were either scarcely mentioned in the literature (mandible length, mouth opening), newly associated to Collembola (mechanical advantage, mandible/head ratio), revisited (molar plate length) or newly developed (deployment capacity, apical development). We described schematically how we measured the different traits on a given mandible and hypothesized specifically how we thought it would deepen our understanding of morphological functionality (Table 2.1). The only challenging factor encountered during trait measurements was dealing with individuals that had both dark body pigmentation and "sucking" mouthparts. For example, our protocol did not allow us to measure the mandibular traits of *Neanura muscorum*. Species richness of Collembola for which mandibular traits were measured were 29 species at Cloquet (n = 556) and 34 at Auclair (n = 959), for a total of 52 species. Subsequent analyses are based on 1509 individuals identified to species level across both sites.

2.4.2 The relation of newly measured Collembola mandibular traits and proxies such as body length and phylogeny

Collembola communities were well defined by their functional traits: the first two PCA axes explained 62.3. % of the variation in Collembola mandibular trait scores (Fig. 2.1). Dimension-related mandibular traits (i.e. mouth opening, mandible length and molar plate length), which were the only traits correlated to body length (0.7 to 0.8, Table 2.2), likely explained variation on the first axis (40.1%, Fig. 2.1). Variation on the second axis (22.2 %) was rather explained by apical development, mandible head ratio, deployment capacity and mechanical advantage (Fig. 2.1). Apical development and mechanical advantage were inversely correlated with mandible/head ratio and deployment capacity (Fig. 2.1), suggesting that mandibles with a well developed molar plate were 1) bigger in comparison to the head, 2) protruded further out of the head capsule and 3) could potentially make smaller and faster movements than mandibles without a molar plate. Additionally, taxonomic order did not present clear patterns of trait distribution (Fig. 2.1 & 2.2), although body length-related traits were partially related to it, with the largest sampled species being Entomobryomorpha (e.g. *Pogonognathellus flavescens*) and Poduromorpha being generally smaller (Fig. 2.1). In general, trait variation among genera and families was considerable, particularly for Isotomidae which were represented in 66 % of the significant clusters (light green in Fig. 2.2). Only Tullbergiidae (*Mesaphorura* and *Ameritulla* species) were all grouped together (red in Fig. 2.2). In summary, phylogeny was a poor proxy for mandibular traits; species taxonomically close could bear unsimilar mandibles and distant species, similar mandibles (Fig. 2.2).

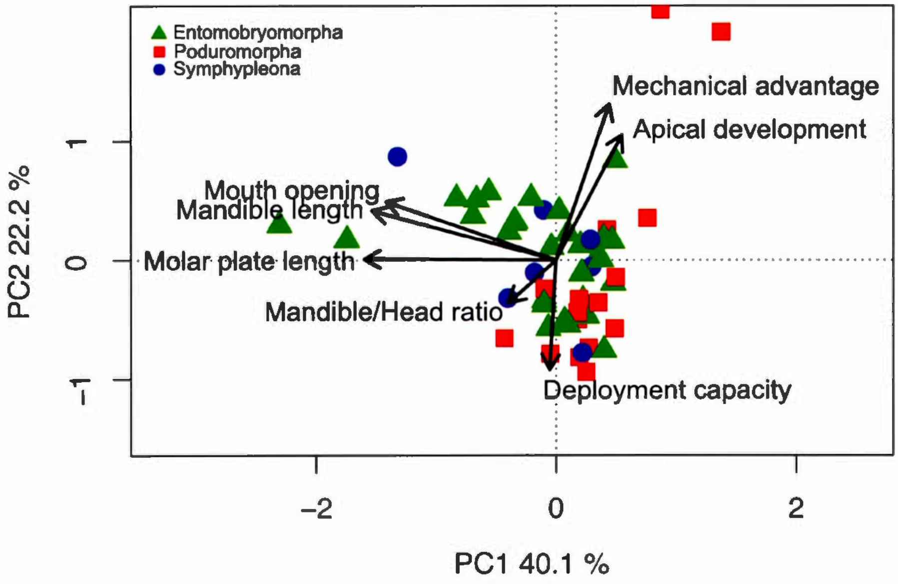


Figure 2.1 Principal component analysis (PCA) ordination of Collembola functional traits at both sites (AuCl) arranged by morphotype (shape). Data were standardized before analyses.

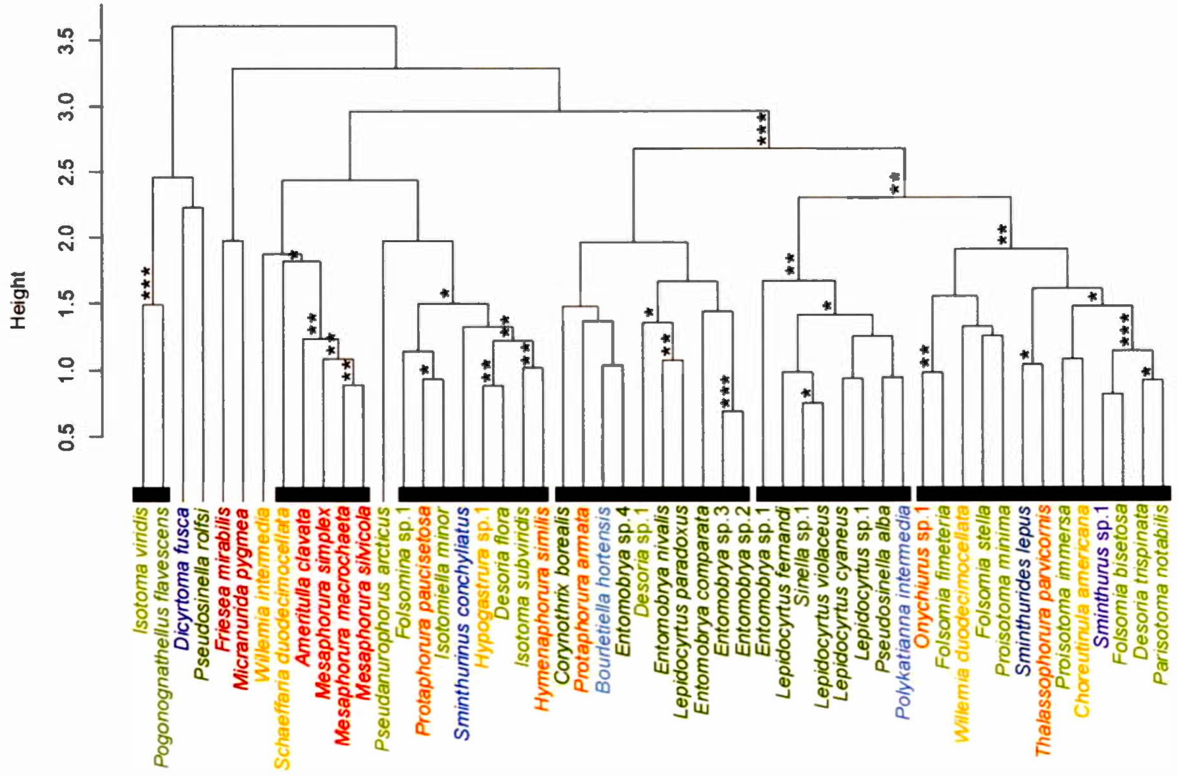


Figure 2.2 Auclair and Cloquet species clustered according to their standardized mandibular traits (Ward's method, Euclidean distance) and colored by family. Blues, greens and warm colours show the Symphypleona, Entomobryomorpha and Poduromorpha morphotypes respectively. Significant clusters (black rectangles) were determined by multiscale bootstrap resampling (bootstrap = 9999). Approximately unbiased p-value: * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Table 2.2 Spearman rank correlations (r_S) between mean mandibular traits and body length of 52 Collembola species (n = 52).

Mandibular trait	**Body length**	
	R_s	**P**
Apical development	-0.16	ns
Deployment capacity	-0.07	ns
Mandible length	0.82	***
Mechanical advantage	0.13	ns
Mandible/head ratio	0.12	ns
Molar plate length	0.79	***
Mouth opening	0.70	***

*** $P < 0.001$, ** $P < 0.01$, * < 0.05, ns = not significant

2.4.3 Litter as a resource for Collembola consumers

2.4.3.1 *Litter traits*

Litter from deciduous tree species (*Acer*, *Betula, Quercus* and *Larix* species) was characterized by labile characteristics such as high basal respiration, water saturation capacity, N and hemicellulose concentrations (Fig. 1.2 & Annex 1.4 in Chapter 1). On the other hand, litter from evergreen species (*Picea* and *Pinus* species) was rather recalcitrant and described by high foliar resistance, thickness, lignin and cellulose concentrations, lignin/N and C/N ratios (Fig. 1.2 & Annex 1.4 in Chapter 1).

2.4.3.2 *Spatial covariaton of Collembola mandibular traits and litter resource traits*

Procrustes analyses demonstrated a significant trait-trait correlation at Cloquet (0.38), but not Auclair (Table 2.3). Furthermore, our results demonstrated that both functional and taxonomic approaches gave similar results with comparable correlations (Table 2.3). Figure 2.3 illustrates in detail the significant trait-trait correlation observed at Cloquet. Traits correlated to body length (Table 2.2) were associated with recalcitrant litters. On the other hand, litter physical traits associated with recalcitrance (high resistance and thickness) were rather correlated to apical development, but weakly (Fig. 2.3). Deployment capacity along with mandible/head ratio correlated with labile litters, particularly those having high N concentration (Fig. 2.3). Finally, mechanical advantage was more of an in-between trait as it was both associated to high cellulose concentration and water saturation capacity (Fig. 2.3).

Table 2.3 Procrustes correlation between litter traits and AuCl Collembola community composition (species and traits) by site (9999 permutations). Here "species" refers to Hellinger transformed species abundances and "traits" to CWMs matrix.

Site	Species	Traits
Auclair	0.32 (ns)	0.28 (ns)
Cloquet	0.40 (**)	0.38 (**)

*** P < 0.001, ** P < 0.01, * P < 0.05, ns not significant

Sum of squares values → Species-Cl = 0.84 / Traits-Cl = 0.86 / Species-Au = 0.90 / Traits-Au = 0.92

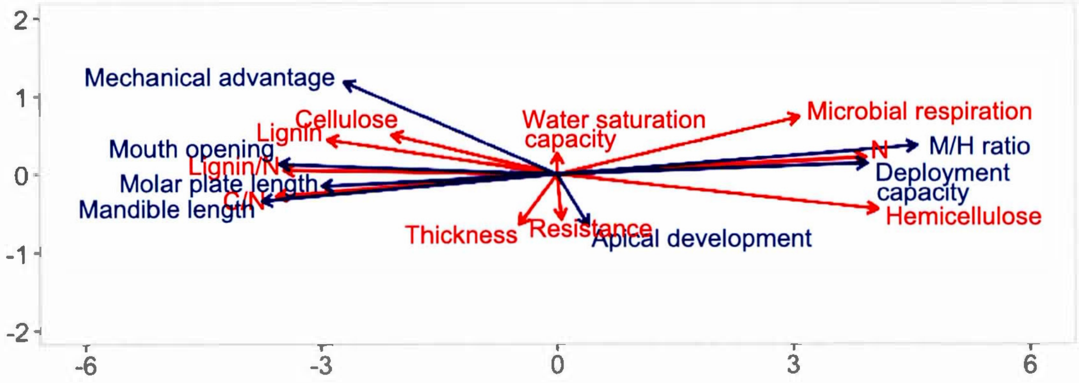


Figure 2.3 Procrustes correlation between standardized Collembola mandibular traits (blue) and litter traits (red) of Cloquet (9999 permutations, correlation = 0.4, $p < 0.05$). Prior to standardization, CWMs were calculated for each mandibular trait. M/H ratio is the Mandible/Head ratio.

2.5 Discussion

2.5.1 No strong proxy identified for mandibular traits

As hypothesized, phylogeny was not a good proxy for mandibular traits, but some traits were related to body length (Fig. 2.1 & 2.2). It is not surprising given that mandibular trait variation is neither considered as a taxonomic criteria to distinguish species from each other, except for the absence of a molar plate in Neanuridae (Christiansen and Bellinger 1998, Fjellberg 1998 & 2007, Hopkin 2007). We also demonstrated that mandibular morphology could vary greatly between similar species within a genus as observed by Wetton (1988) on *Folsomia.* Body length covaried with mouth opening, molar plate and mandible length suggesting that it was proportional to these mandibular traits (Fig. 2.1). This result is concordant with Chen *et al.* (1997) who showed that length and labrum width correlated with body size and ingested particle size for three Collembola species. However, the molar plate length-body length correlation (Table 2.2) was rather incoherent: while it can be assumed that longer mandibles could bear indeed longer molar plates, it seems harder to justify such a correlation for species without a molar plate given that they were under-represented (2 / 52 total species) and of small body length in our sampling (Annexes 2.1 & 2.2). For example, if we had successfully integrated in our analyses small species for which we were unable to measure mandibular traits, molar plate length correlation with other traits would have been likely different. We recognize that *N. muscorum* was a large species (1247.98 ± 202.56 μm) with no molar plate, while *M. minimus* was the smallest species sampled (367.86 μm) but had a molar plate (11.14 μm) (data not shown). So, these results add clear evidence that body length, mandible length and mouth opening (which was determined from labrum width) could be used to a certain extent as proxies for one another, but that molar plate length is tricky to relate to those traits across mouthparts types ("chewing" with molar plate and "piercing-sucking" without molar plate). Interestingly, PCA variation on the second axis was likely explained by mandible structure rather than dimension (Fig. 2.1); traits implied were not covarying with body length (Table 2.2). This lack of relation highlights the interest of studying mandibular traits such as apical development, deployment capacity and mechanical advantage as they can not be predicted by Collembola body length or phylogeny.

2.5.2 Do Collembola consumption traits covary with their resource traits ?

It was not surprising to observe a correlation between litter traits and Collembola consumption traits only at Cloquet (Table 2.3), given that site conditions differed considerably and a large intra-specific variation of litter traits between sites was observed (Fig. 1.2 in Chapter 1). It is plausible that the Auclair Collembola community might have been feeding on roots rather than on litter due to more favorable soil conditions (Chapter 1). What was however striking was that both taxonomic and functional approaches explained similarly the correlation between litter traits and the Collembola community (0.40 vs 0.38; Table 2.3), meaning that mandibular functional traits are particularly useful to understand mechanisms underlying consumer-resource feeding interactions. Furthermore, these equivalent correlations suggest that the relation between Collembola species and litter traits at the Cloquet site is completely driven by feeding interactions (Table 1.2 in Chapter 1), emphasizing that mandibular traits are indeed direct response traits to resource quality (results summarized in Table 2.4). The observed correlation was rather high considering that our hypothesis assumed a strictly bottom-up perspective of the resource influence on Collembola community structure. We did not consider other filters often shaping communities such as other trophic or non-trophic biotic interactions and environmental abiotic conditions (Brousseau *et al.* submitted). Understanding direct response traits is important to determine the extent of biotic responses to environmental change for ecosystem functioning (Luck *et al.* 2012) and these results definitely bring insight on Collembola trophic interactions.

2.5.2.1 *Body length-related mandibular traits*

Mandible length and mouth opening were correlated to recalcitrant litters (*Pinus* and *Picea* species), particularly through their chemical traits (high lignin/N and C/N values; Fig. 2.3). The energy channel resulting from recalcitrant litters is generally fungi-driven (Scheu *et al.* 2005, De Deyn *et al.* 2008, de Vries & Caruso 2016), thus it could be assumed that fungi are the main available microbial resource in evergreen treatments. Consequently, mandible length and mouth opening should be related to fungal consumption capacity. This hypothesis is supported by Chen *et al.* (1997) who suggested that the age specific food selection strategy (bacterivorous juveniles and fungivorous adults) described by Bakonyi (1989) was related to body size; they observed that larger species (*Orchesella hexfasciata*) could consume particles more than 30 times bigger than smaller species (*Isotoma notabilis*). In short, small species can mostly consume resources smaller than fungi such as bacteria. It is therefore not surprising to observe larger species in recalcitrant litters as their diet is likely fungi-centered. Additionally, the molar plate, a structure associated with hyphae consumption (Goto 1972, Chen *et al.* 1997, Hopkin 1997), was on average more developed in recalcitrant than labile litter treatments. Considering that labile litter most likely fueled both fungal and bacterial growth (de Vries & Caruso 2016), it is consistent to observe lower molar plate length community weighted means, hence a bigger range of species size in these treatments. Overall, these observations suggest that recalcitrant litters are dominated by fungal dominated microbial communities, which act as a filter for Collembola body length-related traits.

2.5.2.2 *Apical development*

One of the highlights of our results is that apical development did not correlate with chemical litter traits as body length-related mandibular traits, but rather with physical litter traits (Fig. 2.3), suggesting that this mandibular trait was not associated to consumption of fungi. Despite its weak correlations with litter traits, apical development is likely implied in direct consumption of the litter itself and feeding strategies, bringing a new dimension of mandible functionality. The distal portion of the mandible consists of the molar plate (if present) and apical teeth (Table 2.1). The molar plate is likely associated with fungal consumption and the teeth are likely to transform food before ingestion (e.g. recalcitrant resources) (Goto 1972, Chen *et al.* 1997). Our results showed that 1) apical tooth development correlated with litter thickness and recalcitrance, but that 2) species with piercing-sucking feeding strategies (i.e. no molar plate) were specifically correlated to more physically recalcitrant litter such as *Pinus* (Fig. 2.3). First, it could be interpreted that Collembola need more developed teeth than a molar plate to indeed break down thick and resistant litter particles before ingestion. Such an interpretation would be coherent with the molar plate being rather associated to a “brushing” function given its flexibles molar rods (Goto 1972, Chen *et al.* 1997) than a “grinding” function as traditionally perceived (Manton & Harding 1964). Yet, detailed apical portion morphology (e.g. number of teeth, tooth length, distance between the molar plate and the teeth, etc.) was not assessed in our study. Therefore it is impossible to say if species scraped material off litter surfaces or if they really broke down litter particles with their teeth as Wetton (1988) tried to assess with morphometric analyses. Although feeding behaviour is impossible to infer from our results, both scraping of microbes or breakdown of litter reflect the ability of consumers to feed on recalcitrant litter hence apical development is relevant to predicting litter-Collembola interactions. Finally, Neanuridae were mostly found in thicker litter treatments (as shown by apical development; Fig. 2.3). Our two neanurid species have strikingly different diets: *Friesea mirabilis* is considered as a hemiedaphic predator/scavenger while *Micranurida pygmaea*, as a eudaphic microbivore (Malcicka *et al.* 2017) with an apparent preference for ectomycorrhizal (EM) fungi (Malmström & Perrson 2011). These species could be linked to resistant and thick litters by an indirect effect on their resources (i.e. microbes and preys) rather then direct consumption of litter material.

2.5.2.3 *Deployment capacity, mandible/head ratio and mechanical advantage*

If fungi are indeed considered to consume both recalcitrant and labile C (de Vries & Caruso 2016), we could presume that fungi were also populating deciduous litter leaves. Consequently, mandibular traits specifically correlating with labile litters were not associated with fungi, otherwise we would not have observed such strong correlations (Fig. 2.3). Deployment capacity and mandible head/ratio were most likely related to bacterial abundance indirectly through labile litter traits (high N concentration and basal respiration values). These mandibular traits were thus not correlating with resource recalcitrance as expected (Table 2.1). Deployment capacity was thought to represent the ability to transform resources before ingestion, but given its probable relation to bacteria, it rather seems to be associated to a “scraping” feeding fonction (Table 2.1). Scraping could represent a more efficient method to forage bacteria than cutting, as bacteria probably need less transformation before ingestion than fungi. For its part, high mandible/head ratio might be associated to longer amplitude of movement which would be ideal to scrape resources. Contrary to what we expected (Table 2.1), this trait is unlikely a proxy for other traits. Finally, Wheater and Evans (1989) demonstrated that for beetles, mechanical advantage was related to mandibular strength, so it might be implied in recalcitrant resource consumption by Collembola (e.g. fungi and evergreen litters) as would suggest the observed correlation between body length-related traits and mechanical advantage (Fig. 2.3). That would be consistent with studies demonstrating a correlation of prey/leaf toughness with predator/herbivore mouthpart strength (Ibanez 2013, Brousseau *et al.* 2017, Le Provost *et al.* 2017). On the other hand, mechanical advantage correlation with foliar water saturation capacity suggest that this mandibular trait might also be linked to deciduous litter consumption (Fig. 2.3). Such contradictory interpretations imply that mechanical advantage is likely related to multiple mandibular mechanisms inducing a trade-off between mandible strength and movement speed (Table 2.1), thus its intermediate relation to labile and recalcitrant litters.

Table 2.4 Summary of results interpretations on mandibular traits

Trait	**Trait value**	**Potential resource**
Mandible length	high	Fungi
Mouth opening	high	Fungi
Molar plate length	high	Fungi
Apical development	high	Recalcitrant litter
	low	Labile litter
Deployment capacity	high	Bacteria
Mandible/Head ratio	high	Bacteria
Mechanical advantage	all	Unclear

2.6 Conclusion

Our study provided evidence of bottom-up effects of litter as a primary resource in the structuring of the Collembola community, which is clearly driven by feeding interactions; mandibles traits are responding to litter quality. Given the great inter-specific variability of mandibular traits and their covariation with litter traits, these results suggest that Collembola are not generalist feeders as commonly assumed (Hopkin 1997) and that their diet is not only resulting from food preference, but more likely limited by biomechanics. Still, to fully understand their feeding interactions, further efforts are needed to assess covariation of mandibular traits with a broader range of traits of consumed resources (e.g. roots, fungi, bacteria) given the great diversity in diet reported in the literature (Rusek 1998, Addison *et al.* 2003) and the context-dependency of how the litter resource affects the Collembola community (Endlweber *et al.* 2009, Chapter 1). Considering that the association of microbes (i.e. bacteria vs fungi) to litter type (i.e. labile vs recalcitrant) is not as dichotomous as previously thought (de Vries & Caruso 2016), these efforts are all the more important to interpret mechanisms underlying Collembola - litter feeding interactions. Furthermore, the study of mandibular functional traits could lead to the development of an efficient tool to predict the trophic position of Collembola species. A new categorization of mandible types based on more detailed traits and related resources moving beyond "chewing" and "piercing-sucking" types (Malcicka *et al.* 2017) will help us overcome the oversimplification of Collembola trophic interactions. Finally, our results are in line with current effort to demystify soil food webs through a functional approach (e.g. Pey *et al.* 2014a & 2014b, Moretti *et al.* 2016, Brousseau *et al.* 2017) and bring concrete evidence to better understand soil networks and their emergent properties.

2.7 Annexes

Annex 2.1 Mean trait values for each Collembola species at Auclair site.

Species (n)	**n**	**Mandible length (µm)**	**Mandible/Head ratio**	**Mechanical advantage**	**Deployment capacity**	**Mouth opening (µm)**	**Apical development [category]**	**Molar plate length (µm)**	**Body length (µm)**
Bourletiellidae									
Bourletiella hortensis	3	154.84 ± 19.33	0.67 ± 0.07	0.18 ± 0.02	0.51 ± 0.07	23.67 ± 0.49	0.83 ± 0.11 [2]	28.93 ± 1.74	619.01 ± 16.27
Entomobryidae									
Corynothrix borealis	1	192.46	0.59	0.23	0.56	26.03	0.89 [2]	38.69	1410.75
Entomobrya nivalis	7	195.37 ± 34.62	0.61 ± 0.07	0.25 ± 0.01	0.49 ± 0.06	34.17 ± 8.07	0.70 ± 0.05 [1]	35.20 ± 6.27	1543.00 ± 256.80
Entomobrya sp.1	5	96.43 ± 5.02	0.58 ±0.05	0.27 ± 0.03	0.37 ± 0.02	18.52 ± 3.09	0.83 ± 0.02 [2]	15.63 ± 1.01	621.16 ± 28.30
Entomobrya sp.2	13	173.79 ± 14.43	0.69 ± 0.02	0.24 ± 0.01	0.44 ± 0.04	37.43 ± 6.29	0.78 ± 0.04 [2]	31.50 ± 3.19	1251.45 ± 145.74
Entomobrya sp.3	7	166.99 ± 10.06	0.71 ± 0.02	0.21 ± 0.02	0.48 ± 0.04	33.81 ± 5.78	0.88 ± 0.03 [2]	29.94 ± 2.02	1148.41 ± 80.10
Entomobrya sp.4	8	165.88 ± 17.51	0.63 ± 0.03	0.21 ± 0.02	0.50 ± 0.05	17.11 ± 2.25	0.87 ± 0.05 [2]	29.02 ± 4.30	1196.53 ± 126.00
Lepidocyrtus cyaneus	8	88.55 ± 5.22	0.69 ± 0.05	0.26 ± 0.02	0.51 ± 0.03	13.72 ± 1.27	0.82 ± 0.06 [2]	15.80 ± 0.34	511.22 ± 24.33
Lepidoyrtus fernandi	15	131.15 ± 5.77	0.71 ± 0.02	0.25 ± 0.01	0.40 ± 0.02	21.63 ± 2.53	0.75 ± 0.04 [1]	23.71 ± 1.61	958.86 ± 60.26
Pseudosinella alba	5	125.84 ± 9.02	0.70 ± 0.02	0.22 ± 0.01	0.43 ± 0.02	14.00 ± 2.11	0.82 ± 0.03 [2]	21.44 ± 1.22	865.88 ± 58.06
Sinella sp.1	6	167.44 ± 14.83	0.69 ± 0.03	0.25 ± 0.02	0.46 ± 0.02	20.93 ± 3.54	0.91 ± 0.05 [2]	29.01 ± 3.55	1072.56 ± 103.37
Isotomidae									
Desoria flora	6	141.19 ± 26.25	0.71 ± 0.06	0.18 ± 0.02	0.67 ± 0.07	24.64 ± 6.09	0.81 ± 0.04 [2]	31.11 ± 7.16	923.84 ± 178.43
Desoria trispinata	3	106.58 ± 5.77	0.63 ± 0.01	0.19 ± 0.02	0.60 ± 0.12	16.50 ± 5.46	0.76 ± 0.01 [2]	22.11 ± 1.09	771.40 ± 28.67
Isotomiella minor	6	101.64 ± 4.58	0.70 ± 0.05	0.17 ± 0.01	0.67 ± 0.10	16.33 ± 2.44	0.85 ± 0.05 [2]	24.13 ± 1.15	716.13 ± 33.21
Isotomo subviridis	1	108.38	0.74	0.18	0.57	24.19	0.69 [1]	23.49	714.20
Isotoma viridis	6	359.49 ± 77.26	0.77 ± 0.04	0.20 ± 0.03	0.71 ± 0.07	65.92 ± 16.31	0.77 ± 0.06 [2]	99.63 ± 25.35	2810.30 ± 644.02
Folsomia stella	2	91.96 ± 14.41	0.60 ± 0.01	0.18 ± 0.00	0.55 ± 0.01	22.07 ± 7.93	0.99 ± 0.00 [3]	16.73 ± 2.08	837.87 ± 154.97
Folsomina sp.1	1	109.55	0.72	0.23	0.75	26.66	0.80 [2]	30.21	751.36
Parisotoma notabilis	10	87.87 ± 6.65	0.66 ± 0.04	0.17 ± 0.01	0.56 ± 0.02	16.19 ± 2.95	0.77 ± 0.07 [2]	20.55 ± 2.64	643.62 ± 62.03
Hypograstruridae									
Schaeffaria duodecimocellata	2	101.23 ± 7.46	0.82 ± 0.00	0.14 ± 0.00	0.70 ± 0.12	11.60	1.22 ± 0.06 [4]	18.84 ± 0.03	503.43 ± 59.70
Willemia intermedia	2	63.37 ± 3.43	0.77 ± 0.03	0.21 ± 0.04	0.38 ± 0.01	7.28 ± 1.48	1.08 ± 0.01 [4]	8.16 ± 0.66	513.96 ± 21.19
Katinannidae									
Sminthurinus conchyliatus	1	159.32	0.75	0.18	0.58	29.58	0.89 [2]	31.13	715.55
Neanuridae									
Friesea mirabilis	8	92.11 ± 8.98	0.63 ± 0.08	0.31 ± 0.03	0.32 ± 0.02	26.07 ± 3.31	[6]	0.00 ± 0.00	618.82 ± 73.41
Onychiuridae									
Hymenaphorura similis	9	129.82 ± 8.10	0.72 ± 0.03	0.15 ± 0.03	0.74 ± 0.16	16.89 ± 3.03	0.74 ± 0.11 [1]	29.13 ± 3.93	946.40 ± 56.18
Onychiurus sp.1	2	98.62 ± 1.81	0.68 ± 0.01	0.20 ± 0.01	0.55 ± 0.01	18.19 ± 0.60	1.06 [4]	15.60 ± 1.28	693.98 ± 7.22
Proisotoma immersa	7	109.73 ± 0.77	0.70 ± 0.03	0.17 ± 0.01	0.52 ± 0.02	22.54 ± 4.53	0.69 ± 0.05 [1]	24.23 ± 1.13	665.89 ± 18.08
Proisotoma minima	2	85.63	0.61	0.17	0.46	12.71	0.92 ± 0.03 [2]	13.90 ± 0.08	675.93 ± 97.21
Protaphorura armata	10	171.95 ± 14.29	0.67 ± 0.02	0.15 ± 0.02	0.58 ± 0.03	23.37 ± 1.84	0.75 ± 0.06 [1]	35.03 ± 2.39	1447.33 ± 108.94
Protaphorura paucisetosa	4	98.00 ± 0.62	0.75 ± 0.01	0.21 ± 0.02	0.69 ± 0.06	19.87 ± 0.15	0.96 ± 0.10 [2]	17.77 ± 1.27	617.60 ± 31.78
Sminthuridae									
Sminthurus sp.1	3	110.41 ± 4.35	0.66 ± 0.02	0.21 ± 0.02	0.50 ± 0.04	13.94 ± 2.55	0.87 ± 0.09 [2]	19.80 ± 0.95	432.71 ± 24.30
Tullbergiidae									
Ameritulla clavata	2	114.76 ± 20.54	0.78 ± 0.00	0.18 ± 0.03	0.60 ± 0.04	10.53	0.83 ± 0.04 [2]	23.94 ± 3.32	916.39 ± 172.31
Mesaphorura macrochaeta	7	65.30 ± 4.78	0.78 ± 0.02	0.17 ± 0.01	0.58 ± 0.05	9.46 ± 2.46	0.81 ± 0.06 [2]	13.39 ± 1.28	507.04 ± 51.45
Mesaphorura silvicola	6	89.49 ± 1.82	0.78 ± 0.01	0.21 ± 0.03	0.56 ± 0.04	12.84 ± 1.66	0.87 ± 0.01 [2]	18.44 ± 0.72	714.25 ± 47.19
Mesaphorura simplex	7	107.47 ± 7.53	0.76 ± 0.02	0.18 ± 0.01	0.51 ± 0.02	14.14 ± 1.74	0.90 ± 0.09 [2]	19.50 ± 1.65	865.85 ± 106.04

Annex 2.2 Mean trait values for each Collembola species at Cloquet site.

Species	n	Mandible length (µm)	Mandible/Head ratio	Mechanical advantage	Deployment capacity	Mouth opening (µm)	Apical development [category]	Molar plate length (µm)	Body length (µm)
Dicyrtomidae									
Dicyrtoma fusca	3	364.51 ± 53.79	0.76 ± 0.04	0.18 ± 0.02	0.51 ± 0.05	30.66 ± 3.34	1.35 ± 0.41 [5]	63.95 ± 11.69	1293.29 ± 266.67
Entomobryidae									
Entomobrya comparata	2	247.27 ± 26.02	0.719 ± 0.02	0.20 ± 0.01	0.35 ± 0.03	36.09 ± 0.84	0.84 ± 0.02 [2]	38.69 ± 1.63	1798.32 ± 111.17
Entomobrya nivalis	10	221.38 ± 19.71	0.65 ± 0.03	0.22 ± 0.02	0.41 ± 0.03	37.38 ± 4.75	0.90 ± 0.03 [2]	35.25 ± 3.36	1693.69 ± 162.64
Entomobrya sp.2	2	169.00 ± 43.38	0.74 ± 0.02	0.21 ± 0.03	0.46 ± 0.02	23.32 ± 1.61	0.86 ± 0.02 [2]	28.70 ± 7.81	1006.53 ± 230.78
Lepidocyrtus cyaneus	2	84.00 ± 3.49	0.59 ± 0.02	0.24 ± 0.00	0.42 ± 0.04	13.46 ± 1.37	0.68 ± 0.05 [1]	16.05 ± 0.40	664.04 ± 7.91
Lepidocyrtus fernandi	2	116.62 ± 11.00	0.63 ± 0.01	0.23 ± 0.01	0.50 ± 0.10	18.13 ± 5.71	0.79 ± 0.03 [2]	23.55 ± 1.43	899.09 ± 149.82
Lepidocyrtus paradoxus	15	188.28 ± 16.01	0.65 ± 0.01	0.22 ± 0.01	0.49 ± 0.03	44.58 ± 3.39	0.78 ± 0.03 [2]	35.78 ± 3.66	1461.66 ± 139.32
Lepidocyrtus violaceus	15	140.08 ± 10.30	0.70 ± 0.02	0.25 ± 0.01	0.45 ± 0.02	21.99 ± 1.54	0.82 ± 0.03 [2]	24.30 ± 2.05	995.00 ± 99.80
Lepidocyrtus sp.2	4	86.02 ± 3.02	0.68 ± 0.05	0.24 ± 0.02	0.48 ± 0.01	18.08 ± 1.06	0.82 ± 0.05 [2]	14.82 ± 0.58	526.60 ± 39.87
Pseudosinella rolfsi	2	210.61 ± 55.61	0.88 ± 0.03	0.22 ± 0.03	0.34 ± 0.01	32.63 ± 15.07	0.92 ± 0.00 [2]	33.51 ± 9.42	1438.56 ± 514.35
Isotomidae									
Desoria flora	2	116.32 ± 15.75	0.72 ± 0.01	0.27	0.66 ± 0.02	18.84 ± 1.96	0.74 ± 0.09 [1]	27.48 ± 4.94	736.43 ± 144.44
Desoria sp.1	8	131.87 ± 3.84	0.61 ± 0.04	0.21 ± 0.02	0.42 ± 0.04	40.99 ± 2.72	0.82 ± 0.05 [2]	22.62 ± 1.46	1130.18 ± 54.56
Folsomia bisetosa	1	99.17	0.67	0.20	0.53	19.89	0.89 [2]	20.12	748.48
Folsomia fimetaria	8	91.64 ± 8.84	0.68 ± 0.03	0.21 ± 0.01	0.57 ± 0.03	16.73 ± 2.74	1.00 ± 0.06 [3]	18.10 ± 1.53	713.14 ± 70.95
Isotoma subviridis	4	105.16 ± 5.00	0.73 ± 0.02	0.21 ± 0.01	0.63 ± 0.04	13.47 ± 1.12	0.89 ± 0.03 [2]	21.05 ±1.08	663.26 ± 44.86
Isotoma viridis	8	198.73 ± 26.52	0.74 ± 0.02	0.21 ± 0.02	0.59 ±0.05	41.33 ± 13.23	0.75 ± 0.02 [2]	45.97 ± 6.53	1355.54 ± 241.08
Isotomiella minor	2	101.45 ± 1.20	0.71 ± 0.00	0.24 ± 0.00	0.77 ± 0.01	23.62 ± 2.84	0.92 ± 0.05 [2]	24.70 ± 1.09	632.25 ± 10.84
Pseudanurophorus arcticus	1	81.43	0.59	0.20	0.82	13.76	0.83 [2]	20.37	597.64
Hypogastruridae									
Choreutinula americana	1	109.01	0.70	0.20	0.47	14.87	0.67 [1]	18.55	531.05
Hypogastrura sp.1	7	140.64 ± 12.86	0.74 ± 0.01	0.22 ± 0.00	0.62 ± 0.02	20.32 ± 3.87	0.92 ± 0.04 [2]	28.80 ± 3.78	754.57 ± 122.88
Willemia duodecimocellata	1	64.20	0.67	0.16	0.45	18.47	0.96 [3]	9.48	511.93
Katiannidae									
Polykatinna intermedia	2	120.07	0.65	0.22	0.43	11.34 ± 4.65	0.80 ± 0.05 [2]	23.05 ± 0.28	488.98 ± 17.35
Neanuridae									
Micranurida pygmaea	2	53.58	0.66	0.41	0.61	8.36	[6]	0.00 ± 0.00	436.96 ± 21.18
Onychiuridae									
Hymenaphorura similis	7	115.85 ± 10.64	0.70 ± 0.01	0.18 ± 0.01	0.58 ± 0.01	20.02 ± 2.60	0.92 ± 0.03 [2]	23.04 ± 2.12	783.80 ± 118.82
Thalassophorura parvicornis	1	86.01	0.66	0.14	0.57	12.90	0.75 [1]	18.15	599.16
Sminthurididae									
Sminthurides lepus	1	86.07	0.62	0.13	0.49	17.80	0.71 [1]	16.03	318.06
Tomoceridae									
Pogonognathellus flavescens	7	354.81 ± 26.42	0.70 ± 0.05	0.19 ± 0.01	0.57 ± 0.02	64.02 ± 4.44	0.75 ± 0.03 [1]	81.48 ± 6.47	2802.98 ± 329.45
Tullbergiidae									
Mesaphorura macrochaeta	7	67.62 ± 2.61	0.76 ± 0.03	0.20 ± 0.02	0.52 ± 0.03	8.45 ± 1.81	0.88 ± 0.03 [2]	12.89 ± 0.65	548.02 ± 58.42
Mesaphorura silvicola	8	80.43 ± 7.56	0.77 ± 0.05	0.22 ± 0.02	0.57 ± 0.02	10.98 ± 1.64	0.87 ± 0.07 [2]	16.20 ± 1.29	646.42 ± 66.04

CONCLUSION GÉNÉRALE

Le débat entourant la gestion des espèces exotiques, alimenté par le concept des nouveaux écosystèmes (Hobbs *et al.* 2006), est généralement ancré dans une vision très manichéenne (Sax *et al.* 2005). Toutefois, la littérature portant sur les espèces exotiques ne permet pas de cibler s'il existe un tel effet d'origine sur le fonctionnement de l'écosystème étant donné la présence de facteurs confondants tels que les traits des espèces comparées (p.ex. espèces envahissantes; Buckley et Catford 2016, Ricciardi *et al.* 2013, Van Kleunen *et al.* 2010). Étant donné ce manque d'évidence, le concept des nouveaux écosystèmes a pour prémisse que les décisions liées à l'aménagement devraient être basées sur les fonctions d'une espèce et non pas son origine (Hobbs *et al.* 2006, Miller et Bestelmeyer 2016). En ce sens, la présente étude visait à comprendre les potentielles répercussions des nouveaux assemblages d'espèces végétales sur le fonctionnement de l'écosystème, notamment sur le sol, en vérifiant l'influence de l'origine biogéographique et des traits fonctionnels de la litière forestière sur la composition des communautés de collemboles tant au niveau taxonomique que fonctionnel. Le dispositif expérimental à l'étude (Tobner *et al.* 2014) permettait non seulement de diminuer les effets confondants liés aux effets d'origine détectés via la comparaison d'espèces d'arbres congénères (6 genres; Fig 1.1), mais de comparer une variété de traits fonctionnels de la litière sur le gradient décidu-sempervirent (N, hémicellulose, capacité de saturation en eau, respiration microbienne, cellulose, C/N, lignine, lignine/N, résistance foliaire, épaisseur foliaire; Fig. 1.2).

Les résultats du premier chapitre ont démontré que, pour les deux sites à l'étude, l'origine de la litière n'avait pas d'influence sur la composition taxonomique de la communauté de collemboles, mais que les traits de la litière, le site et leur interaction expliquaient respectivement 7, 21 et 7 % de sa variance (Tableau 1.1). Cette influence du site s'explique probablement par les différences entre Auclair et Cloquet (p.ex. humidité et type de sol, Annexe 1.1) et la conséquente variance intraspécifique entre les traits de la litière (Fig. 1.2). Ceci souligne l'importance du contexte environnemental dans les études de diversité fonctionnelle, car cela aurait potentiellement influencé la nature même des filtres de la communauté de collemboles (Tableau 1.2). En effet, les résultats obtenus suggèrent une différenciation de l'utilisation des ressources liées aux arbres en fonction du contexte (litière vs racine; Endleweber *et al.* 2009) étant donné l'influence du genre de la litière aux deux sites (Tableau 1.1), mais la corrélation entre les traits de la litière et la communauté de collembole spécifique à Cloquet (0.40; Tableau 1.2). En somme, ces résultats ont confirmé nos hypothèses en fournissant une évidence empirique soutenant le concept des nouveaux écosystèmes: le débat de longue date opposant les espèces indigènes et exotiques aurait avantage à être orienté dans une perspective fonctionnelle.

Enfin, afin de mieux cerner les mécanismes impliqués dans la relation observée entre les traits de litière et la communauté de collemboles (Tableau 1.2), il est nécessaire d'approfondir nos connaissances sur la covariation de traits à travers différents niveaux trophiques (Gravel *et al.* 2016), d'où le deuxième chapitre de la présente étude qui visait explorer la relation consommateur-ressource dans une perspective fonctionnelle. À cet effet, des mesures de traits liés à la consommation des ressources ont été collectées sur les mandibules de 52 espèces, totalisant 320 individus (longueur de la mandibule, longueur de la plaque molaire, ouverture buccale, développement apical, avantage mécanique, capacité de déploiement, ratio mandibule/tête; Tableau 2.1). Cette approche innovante orientée vers les traits mandibulaires de collemboles avait également pour objectif de mieux cibler la position trophique de ces organismes étant donné les difficultés actuelles à différencier les différents régimes alimentaires (litière, bactéries, champignons) en fonction des deux types de mandibules établies dans la littérature (mâcheur vs perceur-suceur) (Malcicka *et al.* 2017).

Cet objectif a permis de mettre sur pied une nouvelle série de mesures mandibulaires pour les collemboles (Tableau 2.1). De plus, les hypothèses associées à ce deuxième chapitre ont été également confirmées. Tout d'abord, les associations entre la composition en espèces des communautés de collemboles et les traits de la litière (0.40) étaient bel et bien gouvernées par un appariement de traits relié à la capacité de consommation de la ressource (0.38; Fig. 2.3, Tableau 2.3). Cette covariation de traits a permis de déterminer certains mécanismes potentiels liés à l'alimentation des collemboles tels que résumés dans le Tableau 2.4, suggérant par le fait même une utilisation différentielle des ressources selon les espèces. Ces résultats, en plus du fait que les traits mandibulaires étaient difficilement généralisables à partir de la phylogénie et la longueur du corps (Fig. 2.1 et 2.2), ont confirmé la pertinence de considérer les traits mandibulaires des collemboles pour comprendre leurs interactions trophiques.

Cette étude a démontré un effet *bottom-up* de la ressource primaire sur la composition de la communauté de collemboles, contrairement à ce qui a été reporté avec des données d'abondance par Salamon *et al.* (2006). Ceci suggère que l'approche fonctionnelle peut en effet augmenter notre compréhension des interactions biotiques dans le sol et donc, la capacité de prédiction de l'assemblage des communautés (Brousseau *et al.* 2017). Toutefois, une part considérable de la variation de la composition de la communauté de collemboles n'était pas expliquée par le genre et les traits de la litière : ce qui n'est pas surprenant étant donné qu'un seul filtre (litière) était considéré dans la présente étude. Afin de mieux cerner les filtres biotiques influençant l'assemblage des communautés du sol, la covariation de traits sur trois niveaux trophiques (p.ex. : ressources primaires, consommateurs primaires et prédateurs) représenterait une avenue intéressante pour étudier simultanément les pressions *bottom-up*, *sideways* et *top-down*.

De plus, étant donné l'absence de donnée supportant un strict effet de l'origine biogéographique, les résultats font écho au fait que l'on devrait assumer au niveau sociétal que les décisions d'aménagement sont en partie gouvernées par des valeurs éthiques (Vellend 2017). Bien que cette étude n'avait pas pour but de se positionner sur l'inclusion de la valeur intrinsèque de la biodiversité dans les processus décisionnels, elle ouvre la porte à une telle discussion. La nature de nos résultats n'est pas réellement déterminante en contexte d'invasion, mais l'est pour les pratiques d'aménagements sylvicoles et urbains où certaines espèces végétales non indigènes y sont privilégiées pour leur performance ou leur adaptation aux environnements perturbés. Toutefois, comme il existe peu de données empiriques sur l'effet « isolé » de l'origine au sein de la littérature, de futurs efforts devraient être orientés vers l'étude des effets d'origine dans différents scénarios, mais dans un cadre expérimental similaire (p.ex.: étude à long terme, séquence temporelle, effet *top-down* vs *bottom-up* des espèces exotiques, polycultures diversifiées, etc.).

Finalement, il est également essentiel d'intégrer une plus grande variété de ressources (p.ex.: racines, bactéries, champignons) dans les futures analyses de covariation de traits mandibulaires de collemboles afin d'améliorer notre compréhension de la biomécanique y étant associée. De plus, un travail méthodologique devra être effectué pour améliorer ces mesures de traits, notamment pour les Neanuridae chez qui les pièces buccales sont parfois difficiles à observer selon le protocole établi dans cette étude. Afin de déterminer le nombre de réplicats suffisant pour chacun des traits mandibulaires, de futures recherches pourraient également porter sur la vérification de la variation intraspécifique selon le sexe, le stade de vie et le côté mandibulaire sur une multitude d'espèces. À la lumière de telles avancées, les traits mandibulaires des collemboles auraient le potentiel de s'insérer dans un éventuel guide de mesure de traits (Moretti *et al.* 2016), ce qui consisterait en un ajout intéressant aux outils fonctionnels reliés aux invertébrés et donc à la démystification de la « boîte noire » du sol.

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