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Living the street life: long-term carbon and nitrogen dynamics in parisian soil-tree systems

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**THÈSE DE DOCTORAT DE
L'UNIVERSITÉ PIERRE ET MARIE CURIE – PARIS VI**

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ALEKSANDAR RANKOVIC

POUR OBTENIR LE GRADE DE
DOCTEUR DE L'UNIVERSITÉ PIERRE ET MARIE CURIE – PARIS VI

**LIVING THE STREET LIFE:
LONG-TERM CARBON AND NITROGEN DYNAMICS IN
PARISIAN SOIL-TREE SYSTEMS**

**DYNAMIQUES DE LONG TERME DU CARBONE ET DE L'AZOTE
DANS DES SYSTÈMES SOL-ARBRE PARISIENS**

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“O chestnut-tree, great-rooted blossomer,
Are you the leaf, the blossom or the bole?
O body swayed to music, O brightening glance,
How can we know the dancer from the dance?”

William B. Yeats, “Among school children”, *The Tower*, 1928

“A lifetime can be spent in a Magellanic voyage around the trunk
of a single tree.”

Edward O. Wilson, *Naturalist*, 1994

“I play the street life
Because there’s no place I can go
Street life
It’s the only life I know”

The Crusaders, “Street life”, 1979.

“The weeds in a city lot convey the same lessons as the redwoods.”

Aldo Leopold, *A Sand County Almanac*, 1949.

Summary

Urban areas impose multiple and intense environmental changes on the ecosystems they contain or that surround them, and the ecosystem responses to urban environments are still poorly known, even on fundamental ecosystem processes such as carbon (C) and nitrogen (N) cycling. The dynamics of urban ecosystems, especially on the long-term, have received little attention. The present work uses a 75-year chronosequence of street soil-tree systems (plantations of *Tilia tomentosa* Moench) in Paris, France, as its main case study to detect long-term patterns in urban C and N cycling and infer potential underlying mechanisms.

This thesis describes age-related patterns of C and N accumulation in soils, and we hypothesize that tree root-derived C and deposited N from the atmosphere and animal waste accumulate in soils. Then, an analysis of soil particle-size fractions further points towards a recent accumulation of soil organic matter (SOM), and ^{13}C and ^{15}N analysis suggests that tree roots are a major contributor to the increase of SOM content and N retention. Potential nitrification and denitrification rates increase with street system age, which seems driven by an increase in ammonia-oxidising bacteria. The long-term dynamics of C seem characterized by increasing belowground inputs coupled with root-C stabilization mechanisms. For N, the losses are likely compensated by exogenous inputs, part of which is retained in plant biomass (roots) and SOM.

These results are then discussed in light of results obtained on Parisian black locust systems (*Robinia pseudoacacia* Linnæus), as well as other data, and management recommendations are proposed.

Résumé

Les régions urbaines imposent d'intenses et multiples changements environnementaux sur les écosystèmes qu'elles contiennent et qui les entourent, et les réponses des écosystèmes à ces environnements urbains est encore relativement peu connue, même pour des processus fondamentaux comme les cycles du carbone (C) et de l'azote (N). Ce travail utilise une chronoséquence de systèmes sol-arbre d'alignement (plantations de *Tilia tomentosa* Moench) de 75 ans, situés à Paris, comme étude de cas principale, afin de détecter des tendances de long terme dans les cycles urbain du C et du N et d'en inférer les potentiels mécanismes sous-jacents.

Un patron d'accumulation du C et du N dans les sols de rue est décrit, et nous faisons l'hypothèse que le C dérivé des racines, et le N issu des dépôts atmosphérique et apports animaux, s'accumulent dans ces sols. Ensuite, une analyse des fractions organo-minérales des sols suggère qu'il y a bien une accumulation de matière organique du sol (MOS) relativement récente. Les analyses ^{13}C et ^{15}N suggèrent que les racines sont un contributeur majeur à cette augmentation de la teneur en MOS et de la rétention du N exogène. Les taux de nitrification et de dénitrification potentielles augmentent avec l'âge des systèmes de rue, ce qui semble être déterminé par une augmentation des bactéries oxydant l'ammoniaque.

Les dynamiques de long terme pour le C semblent caractérisées by une augmentation des apport hypogés couplée à des mécanismes de stabilisation du C racinaire. Pour le N, les sorties de N semblent contrebalancées par d'importants apports exogènes et les racines, apports dont une partie est retenue dans la biomasse végétale (racines) et la MOS.

Ces résultats sont ensuite mis en perspective d'autres données, portant notamment sur des plantations parisiennes de robinier (*Robinia pseudoacacia* Linnæus), et des recommandations de gestion sont proposées.

Extended summary

Human influence on the biosphere is deep and pervasive, to the point that our geological epoch may soon be officially recognized as the Anthropocene. To better depict the ecology of contemporary Earth, ecologists must increase their research efforts on anthropized ecosystems, which now represent the majority of ice-free land on the planet. In particular, a major planetary shift occurred during the 20th century, when humans became a predominantly urban species, and it is a trend that will persist in the decades to come.

Urban areas impose multiple and intense environmental changes on the ecosystems they contain or that surround them, and the ecosystem responses to urban environments are still poorly known, even on fundamental ecosystem processes such as carbon (C) and nitrogen (N) cycling. A particularly neglected aspect of urban ecosystems is their dynamics, especially on the long-term. The knowledge base on which one could anticipate the trajectory of urban ecosystems, and thus the sustainability of urban ecological engineering projects, is thus rather weak.

This is particularly problematic in a context where calls to rely on “green infrastructure” to enhance urban sustainability are increasing, and where fast-pace greening initiatives are multiplying in many cities worldwide. The principal goal of this work is to increase our understanding of the long-term dynamics of urban ecosystems, as grasped through the C and N cycles, and thus also to increase knowledge on these central biogeochemical cycles in cities and infer recommendations for management. It thus wishes to describe parts of the ecology of some of the most anthropized ecosystems there is, in order to better understand and care after some of our closest non-human companions on Earth.

Urban environments have been shown to have profound, yet still poorly understood effects on C and N cycling in ecosystems. Patterns of increased cycling rates, coupled with long-term accumulations of both C and N, have been reported in numerous cities worldwide, but the involved mechanisms are still poorly known and require further investigation. The present work uses a 75-year chronosequence of street soil-tree systems (plantations of *Tilia tomentosa* Moench) in Paris, France, as its main case study. It combines approaches from stable isotope ecology (analyses of ¹³C and ¹⁵N natural abundances) and microbial ecology (qPCR and laboratory incubations to assess potential activities).

In Chapter 1, we detect age-related patterns of C and N accumulation in soils and we hypothesize that tree root-derived C and deposited N from the atmosphere and animal waste accumulate in soils. These hypotheses are supported, notably, by an enrichment of soil $\delta^{13}\text{C}$ along the chronosequence, possibly due to chronic water stress of trees in streets, leading to an enrichment of foliar $\delta^{13}\text{C}$ that could be subsequently transmitted to soil organic matter (SOM) through roots (*via* rhizodeposition and turn-over). For N, the exceptionally high soil and foliar $\delta^{15}\text{N}$ in streets, as well as increased contents in mineral N forms, suggest chronic inputs of ¹⁵N-enriched N sources and subsequent microbial cycling, through nitrification and denitrification in particular.

In Chapter 2, an analysis of soil particle-size fractions further points towards a recent accumulation of C and N in older street soils, and fine root $\delta^{13}\text{C}$ suggests that the enrichment in street foliar $\delta^{13}\text{C}$ is transmitted to SOM and to microbial respiration. Analysis of root N suggests that exogenous N inputs are assimilated by surface roots and then incorporated into SOM, but a very strong difference between foliar and root $\delta^{15}\text{N}$, suggests that, as trees age, they diversify their N sources, and that whole-tree N nutrition relatively less depends, with time, on the N assimilated from topsoil.

In Chapter 3, we show that both potential nitrification and denitrification rates increase with street system age, and are much higher than at arboretum sites. While both ammonia-oxidising archaea (AOA) and bacteria (AOB) are more abundant in street soils than at the arboretum, the abundance of AOB in surface soils shows consistent age-related trends and is positively correlated to potential nitrification, soil mineral N contents and both soil and foliar $\delta^{15}\text{N}$. We suggest that the increase in nitrification rates could be driven by the observed increase in AOB populations, which itself could be due to increasingly favorable conditions for AOB in street soils, namely increased ammonium content and circumneutral soil pH. Denitrification, in turn, could be favored by increased soil nitrite and nitrate content, as well as soil organic C.

In the general discussion, these results are discussed and interpreted in terms of the long-term trajectory they seem to depict for street systems. Results are also discussed in light of results obtained on Parisian black locust systems (plantation of *Robinia pseudoacacia* Linnæus), as well as other data (urban pollinators, soil trace metal content), to assess the possibility to generalize our interpretations and to refine our recommendations for management. The discussion ends on a reflection on the role of urban ecological research in helping to solve environmental issues.

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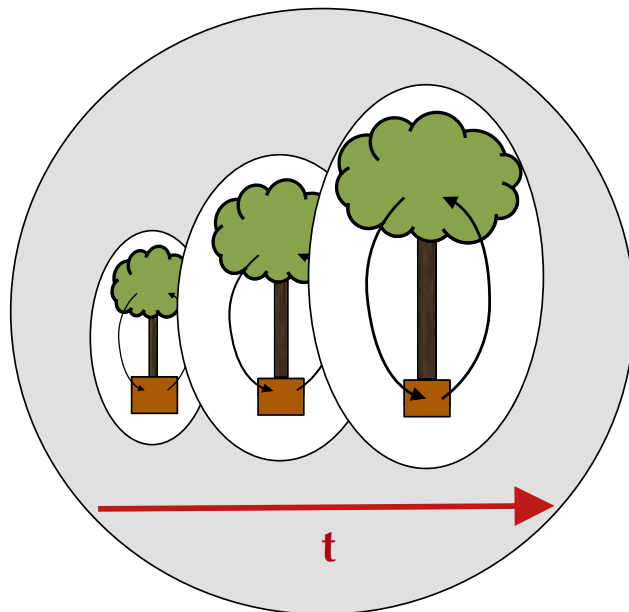
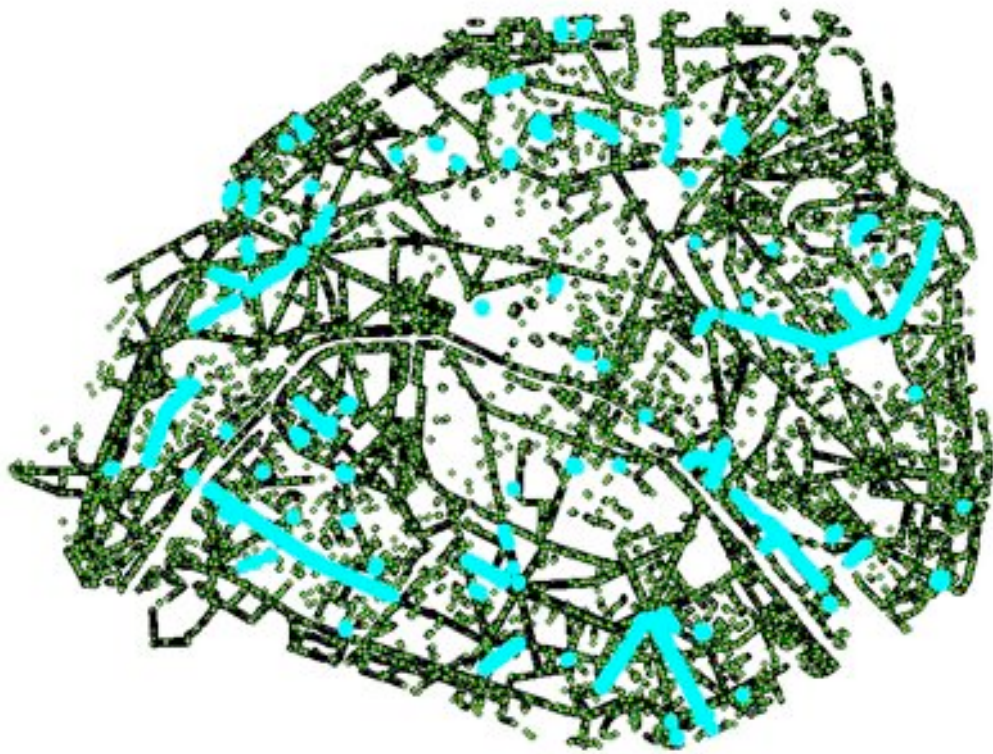
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General introduction

1. Ecology and the first urban century

Human influence on the biosphere is deep and pervasive (Vitousek et al., 1997a; Crutzen, 2002; Waters et al., 2016), to the point that our geological epoch may soon be officially recognized as the Anthropocene (Waters et al., 2016). When he proposed the ecosystem concept, Arthur Tansley already put forth the necessity for ecologists to fully and explicitly include the multifold influence of humans in their studies (Tansley, 1935). Yet, while this challenge has undoubtedly been acknowledged in ecological sciences, the associated research effort does not seem to be at scale. Martin et al. (2012), for instance, reviewed over 8000 studies published in ten leading ecological journals between 2004 and 2009, and showed that 63-84 % of studies had been conducted in protected areas (most often located in temperate, wealthy regions) even though they represent less than 13 % of Earth's ice-free land. On the other hand, agricultural areas, rangelands and densely settled areas were found to be strongly underrepresented (16.5 % of studies) relatively to their global extent (47 %). This suggests that anthropized ecosystems, even though they now represent the majority of the terrestrial biosphere (55 % in the year 2000: Ellis et al., 2010), are understudied in ecology's most influential research. As pointed by Martin et al. (2012), this fundamentally questions the ability of ecological research to properly depict the planetary ecology of contemporary Earth.

A major planetary shift occurred during the 20th century, when humans became a predominantly urban species. Urban areas now concentrate more than half of world population, and urban population will likely increase by between 2.5-3 billion people by 2050, representing about two thirds of the expected 9.7 billion world population (Seto et al., 2014; United Nations, 2015). Estimating

the extent of urban land cover area is not straightforward, and different global satellite mappings have yielded a range of between 0.28 and 3.5 million km², representing between 0.2 % and 2.7 % of ice-free land (Potere 2009; Schneider et al., 2009). When compared to 2000 estimates, urban land cover area worldwide will possibly triple in size by 2030 (Seto et al., 2012, 2014).

Even though they represent a relatively small fraction of Earth's surface, urban areas have a considerable influence on the rest of the planet, either indirectly through their "metabolism" and large "footprint" (Wolman, 1965; Folke et al., 1997; Rees, 1998; Seto et al., 2014), or more directly through the multiple and intense environmental changes they impose on the ecosystems they contain or that surround them (Gregg et al., 2003; Kaye et al., 2006; Grimm et al., 2008; Lorenz & Lal, 2009; Kaushal et al., 2014; Bai et al., 2015; Chambers et al., 2016). Urban areas are often characterized by high spatial heterogeneity, reduced connectivity, anthropized soils, surface sealing, high near-ground atmospheric CO₂ concentration, high levels of atmospheric nitrogen (N) deposition, increased surface temperatures and heat island effects, high levels of pollutant contamination, hydrologic changes, increased presence of non-native organisms, intense management practices, and so on (McDonnell & Pickett, 1990; McDonnell et al., 1997; Morel et al., 1999; Schwartz et al., 2001; Carreiro & Tripler, 2005; Kaye et al., 2006; Cheptou et al., 2008; Grimm et al., 2008; Lorenz & Lal, 2009; Hahs & Evans, 2015; Alberti, 2015; Chambers et al., 2016).

These urban features, because of their individual magnitude and/or because they can all occur simultaneously, constitute evolutionary novelties that make cities interesting "ecological theaters" (Hutchinson, 1965) that can present several interests for ecologists (McDonnell & Pickett, 1990; McDonnell & Hahs, 2014; Alberti, 2015). Over the last decades, it has thus been proposed that urban ecological research could enhance general ecological knowledge by describing the response of different ecological processes to the quite unique sets of

constraints and perturbation regimes that are found in cities (McDonnell & Pickett, 1990; Cheptou et al., 2008; McDonnell & Hahs, 2014; Hahs & Evans, 2015; Alberti, 2015; Groffman et al., 2016). Given the similarities between some urban features (*e.g.*, near-ground CO₂ concentrations that can be several hundreds of parts per million (ppm) higher than background levels, high amounts of N deposition, higher average temperature when compared to surrounding areas), urban ecosystems have also been considered as “sentinels of change”, foreshadowing what ecosystem responses to global changes, such as global warming and human inputs of N into the biosphere, could look like in the decades to come (Carreiro & Tripler, 2005; Grimm et al., 2008; Alberti, 2015).

Early on, urban ecology was also considered as an opportunity to provide some answers to the intellectual challenge of better including the influence of humans on ecosystems (*e.g.*, McDonnell & Pickett, 1993), as well as for ecologists to engage with the rest of society (*e.g.*, McDonnell & Pickett, 1990; Tanner et al., 2014; Pataki, 2015). In particular, urban ecologists have displayed a growing interest in participating to urban planning, for different purposes. For biodiversity conservation, ecological works have for instance contributed to the design of greenways to try and mitigate the fragmentation of ecosystems due to urbanization (Clergeau, 2007; Forman, 2008). Ecologists have also produced works on the design and management of urban ecosystems, such as urban forests or green roofs (Carreiro et al., 2008; Oberndorfer et al., 2007), both to increase understanding of, and increase the services provided by, the “green infrastructure” of cities (Pataki et al., 2011; Rankovic et al., 2012 – Appendix 1).

Calls to rely on green infrastructure to enhance urban sustainability are increasing (European Commission, 2013; FAO, 2016). “Fast-pace” greening initiatives are multiplying in many cities worldwide (Day & Amateis, 2011; Pincetl et al., 2012; Churkina et al., 2015), as is probably best illustrated by New York City’s “MillionTreesNYC” programme and its goal to plant one million

new trees across the city in a decade¹. In Paris, an increase of 20 000 trees by 2020 is planned under the current mandate, in addition to the 183 000 trees already planted in streets, parks, graveyards and other public areas, thus representing an increase of 11 % in less than 6 years². Justifications for such initiatives are usually based on embellishment purposes but also, increasingly, on a range of ecosystem services expected from tree plantings and other green spaces. These typically include pollution removal from air and water, local cooling, stormwater regulation, carbon (C) sequestration in soils and plants, or even food provision (*e.g.*, Bolund & Hunnamar, 1999; Nowak, 2003; Pataki et al., 2011; Rankovic et al., 2012; FAO, 2016). Despite a long-standing interest in these questions (Smith & Staskawicz, 1977; Meyer, 1991; Stewart et al., 2011), uncertainties and even controversies among authors are still lively, especially on the magnitude of said ecosystem services and their actual effects on the health of urbanites (Pataki et al., 2011; Rankovic et al., 2012; see for instance the recent sharp debates in *Environmental Pollution* on the magnitude of PM_{2.5} removal by trees in US cities: Whithlow et al., 2014a,b; Nowak et al., 2014).

These difficulties are not surprising, given the complexity of urban environments and the relatively recent structuring of the field of urban ecology. Thus, notwithstanding a steady development of urban ecology over the last three decades, many aspects of urban ecological processes remain unknown. A particularly neglected aspect of urban ecosystems is their dynamics, especially on the long-term. Besides remnant patches of “native” ecosystems, most ecosystems in cities are the product of landscaping activities, where human decisions and actions result in different types of “constructed ecosystems”, and where soils, plants, water and sometimes animals are assembled as part of urban design projects. Given the complexity of urban environments, once an ecosystem is constructed in a city, predicting its own dynamics and long-term

¹ <http://milliontreesnyc.org/>; last consulted 15 September 2016.

² <http://www.paris.fr/arbres>; last consulted 15 September 2016.

trajectory (changes in structure, in processes) is challenging. This question, furthermore, has seldom been explicitly investigated in urban ecological research, which has so far mostly relied on spatially-explicit studies (*e.g.*, urban-rural gradients or watershed-level analysis) and relatively less on temporally-explicit approaches (*e.g.*, chronosequences or long-term series of data). The knowledge base on which one could anticipate the trajectory of urban ecosystems, and thus the sustainability of urban ecological engineering projects, is thus rather weak.

Other key aspects of urban ecosystems remain understudied. Biogeochemical cycles, which underpin many of expected urban ecosystem services (Pataki et al., 2011), count among the least studied aspects of urban ecosystems. For instance, in a review covering 319 studies using urban-to-rural gradients, published over 17 years, McDonnell & Hahs (2008) found that 63 % of studies focused on the distribution of macroorganisms while only 17 % concerned biogeochemical aspects (“pollution/disturbance/nutrient fluxes” category in their review).

These considerations form the starting point of the present work. Its principal goals are to increase our understanding of the long-term dynamics of urban ecosystems, as grasped through the C and N cycles, and thus also to increase knowledge on these central biogeochemical cycles in cities and infer recommendations for management. It thus wishes to describe parts of the ecology of some of the most anthropized ecosystems there is, in order to better understand and care after some of our closest non-human companions on Earth.

In the following section, the importance of C and N cycling in ecosystems is addressed. Then, a synthesis of studies on urban C and N cycling is provided, with a particular attention to studies focusing on temporal dynamics. In the last section of this general introduction, the rationale for choosing Parisian street soil-tree systems as a case study will be outlined and the thesis structure will be

presented.

2. Carbon and nitrogen dynamics in urban ecosystems

2.1. Carbon and nitrogen cycles as ecological crossroads

The C and N cycles occupy a central role in ecosystem studies. In most ecosystems, the solar energy fixed in carbohydrates (assembled from CO₂ and water) by plants during photosynthesis forms the basis of most available energy that is used by organisms that feed on living or dead plant material and which then circulates through foodwebs. The C compounds produced by plants also make up important “structures” in terrestrial ecosystems, such as the living plants themselves, dead wood, soil litter and soil organic matter (Bormann & Likens, 1979). The amount of plant primary production partly determines the amount of microbes and animals that can be sustained in an ecosystem. The recycling of organic matter by soil microbes and animals is a key process controlling the availability of major nutrients for plants. N is considered to be the major limiting nutrient for primary production (Vitousek, 1982; Vitousek & Howarth, 1991; Gruber & Galloway, 2008), and the C and N cycles are tightly coupled. The availability of N strongly constrains primary production and thus C inputs into ecosystems, notably because important amounts of available N are required to synthesize the proteins that constitute the enzymatic apparatus of photosynthesis (*e.g.*, van Groenigen et al., 2006). N foraging strategies by plants, in turn, can have strong influences on C cycling, for instance by increasing belowground C allocation and providing fresh organic matter to soils, which can increase decomposition rates by soil biota and in turn lead to increased N availability (*e.g.*, Bardgett et al., 2014; Shahzad et al., 2015). C and N acquisition strategies both can differ among plant species and are the object of numerous cooperative and competitive interactions between plants, plants and soil microbes and between soil microbes. Herbivory, pollination and even feedbacks from predation can also interact with C and N cycling. Through the

production of greenhouse gases such as CO₂, CH₄ and N₂O, C and N dynamics are also of significant importance for global biogeochemistry and climate (*e.g.*, Schimel, 1995; Gruber & Galloway, 2008; Philippot et al., 2008; Ostle et al., 2009).

The C and N cycles are thus at the crossroads of numerous ecological interactions that link aboveground and belowground components of ecosystems (*e.g.*, Tateno & Chapin, 1997; Wardle et al., 2004) and they strongly constrain, and are shaped by, biotic processes. As such, they are also a precious focal point for the investigator, as changes in these dynamics can help detect ecosystem changes and infer some of their causes, *e.g.*, during ecosystem formation and development. Accordingly, they are at the heart of the core research areas of the US Long Term Ecological Research (LTER) network³ and have early on been proposed as key indicators of ecosystem development and stability (Odum, 1969) and as key attributes to monitor the success of ecological restoration projects (Aronson et al., 1993).

Furthermore, human influences on C and N cycles are major components of anthropogenic global environmental changes (Vitousek et al., 1997a; Ciais et al., 2013; Waters et al., 2016) and “markers” of the Anthropocene (Waters et al., 2016). Atmospheric CO₂ concentrations have increased by 40 % between 1750 and 2011 (from 278 ppm to 390.5), with the most part due to the burning of fossil fuels (Ciais et al., 2013). This increase in CO₂ can have several consequences at the individual plant level, as well as at the community and the ecosystem levels (Bazzaz, 1990), and many uncertainties remain as to how ecosystems will respond to rising CO₂ concentrations on the long-term, and how these responses will feed back to global C biogeochemistry. For instance, terrestrial biogeochemical models attribute a “fertilization effect” to increased CO₂ levels, in order to explain the magnitude of the terrestrial C sink (Ciais et

³ <https://lternet.edu/research/core-areas>; last consulted 15 September 2016.

al., 2013). However, potential nutrient and/or water limitation of primary production in the future make the long-term magnitude of this effect rather uncertain (Ciais et al., 2013).

The strong human influence on the N cycle also adds uncertainties about the future of Earth. Prior to the intensification of human activities, N could enter ecosystems through atmospheric deposition of “reactive” N species produced in the atmosphere by lightning, or through the microbial fixation of N₂ by free or symbiotic bacteria (Vitousek et al., 1997b). It is estimated that human activities, through industrial N fixation (Haber-Bosch process), combustion processes and legume crops, now inject an amount of reactive N into the biosphere that is equivalent to all natural atmospheric, terrestrial and marine sources combined (Gruber & Galloway, 2008; Ciais et al., 2013).

This added N, especially for ecosystems that were N-limited, can have profound effects on N cycling rates in ecosystems. The additional N can stimulate plant growth and be retained in plant biomass and soil organic matter, but an important body of research has shown, through observational, experimental and modeling works, that added N can lead to increased losses through leaching or through gaseous emissions after microbial transformation in soils (Aber et al., 1989, 1998; Pardo et al., 2006; Lovett & Goodale, 2011; Niu et al., 2016). This phenomenon, where additional N inputs lead to increased N losses, has been coined “N saturation” (Aber et al., 1989; Niu et al., 2016). It is assumed that it is due to N inputs exceeding the capacity of plants and soils to retain added N, leading to more N being available to enter N loss pathways such as nitrification and denitrification (Lovett & Goodale, 2011; Niu et al., 2016). Many unknowns remain concerning the response of ecosystem N cycling to added N, such as the proportion of N that is retained or lost, the dominating retention and loss processes, or the precise chain of mechanisms linking the deposition of N to a saturation syndrome (Niu et al., 2016).

2.2. Overview of urban studies on carbon and nutrient cycling

Urban environments have been shown to have profound, yet still poorly understood effects on C and N cycling in ecosystems (De Kimpe & Morel, 2000; Scharenbroch et al., 2005; Kaye et al., 2006; Lorenz & Lal, 2009; Pouyat et al., 2010). There are only few syntheses and meta-analyses covering the topic, and besides papers synthesizing specific research programmes (e.g., McDonnell et al., 1997; Pickett et al., 2011) there is, to my knowledge, no international synthesis covering urban C and N biogeochemistry.

Authors have suggested that the importance of urban drivers on ecosystem processes, and their similarities across cities, could surpass natural drivers and lead to similar ecosystem responses on key ecological variables in different cities, an assumption coined the “urban ecosystem convergence hypothesis” (Pouyat et al., 2003, 2010; see also Groffman et al., 2014). If studies have indeed reported patterns of urban soil C and N accumulation worldwide (e.g., McDonnell et al., 1997; Ochimaru & Fukuda, 2007; Chen et al., 2010; Raciti et al., 2011; Gough & Elliott, 2012; Vasenev et al., 2013; Huyler et al., 2016), important unknowns remain, however, on the mechanisms leading to such accumulation.

The body of research conducted in the Urban-Rural Gradient Ecology (URGE) programme provides a good illustration of the interactive effects of urban biotic and abiotic factors on C and N biogeochemistry. The studies conducted between 1989 and 1997 in the New York metropolitan area in the URGE programme probably constitute the first intensive research conducted on urbanization effects on C and N cycling. The programme used a transect of 9 unmanaged forest sites (dominated by *Quercus rubra* and *Quercus velutina*) spanning 140 km from the Bronx borough in New York City (NYC) to rural Litchfield County, Connecticut (McDonnell et al., 1997; Carreiro et al., 2009). The studies conducted in the URGE programme mainly focused on the

decomposition rates of leaf litter and N cycling. Initially, the underlying rationale was that these processes would integrate a possible urban influence, through changes in leaf litter chemistry (*e.g.*, response to ozone) and changes in microbial processes associated to temperature and pollutants (McDonnell et al., 1997; Carreiro et al., 2009).

Decomposition rates in urban stands were found higher than in the rural stands, despite a lower chemical quality (attributed to ozone exposure) for decomposers (Pouyat et al., 1997; Carreiro et al., 1999). Higher N mineralization and much higher nitrification rates were also found in the urban stands, and despite a faster turn-over rate of litter, urban stands contained a larger stable C pool (Zhu & Carreiro, 1999, 2004a, 2004b; Pouyat et al., 2002; Carreiro et al., 2009). Urban litter was also shown to contain less microbial biomass (both fungal and bacterial) than rural stands (Carreiro et al., 1999). These rather puzzling patterns were found to be best explained by an up to ten-fold higher abundance of earthworms in urban stands (Steinberg et al., 1997), with urban earthworm populations being mostly composed of two exotic epigeic species. Their activity was experimentally associated to faster litter decay, higher N mineralization and nitrification, and C sequestration in microaggregates inside casts was seen as a possible explanation for a larger stable C pool in urban stands (McDonnell et al., 1997; Pouyat et al., 2002; Carreiro et al., 2009). Other factors, such as higher temperatures in urban stands, higher heavy metal content in urban soils and long-term exposure to higher atmospheric N deposition rates (Lovett et al., 2000) are considered to possibly interact with the influence of earthworms (Pouyat & Turechek, 2001; Pouyat & Carreiro, 2003; Carreiro et al., 2009). For instance, the strong stimulation of nitrifiers by earthworms could make nitrifiers more prompt to nitrify the ammonium deposited from the atmosphere, thus leading to even higher nitrification rates (Carreiro et al., 2009). Other studies conducted on this

gradient have, for instance, shown a decrease in methane uptake by urban soils (Goldman et al., 2005) and reduced mycorrhization in urban sites when compared to rural sites (Baxter et al., 1999). Detailed summaries of the URGE programme results can be found in McDonnell et al. (1997), Cadenasso et al. (2007), Carreiro et al. (2009) and Pouyat et al. (2009).

Studies conducted in other cities have reported similar results. Koerner & Klopatek (2010) conducted a study in and around Phoenix (Arizona) on communities dominated by the bush *Larrea tridentata* and found higher levels of soil organic C, total N and nitrate levels in urban sites but found higher soil respiration rates in rural sites, possibly because of reduced soil moisture and litter quality in urban sites. Urban sites did not show the island of fertility effect observed in more natural communities dominated by *L. Tridentata*: urban interplant soils contained similar levels of total N and nitrate than soils under plant canopy. Higher N levels in urban sites were attributed to higher atmospheric N depositions in urban sites, which were also considered to cause the disappearance of the “fertility island” pattern in urban sites. Rao et al. (2013) studied N deposition levels and the fate of deposited N on an urban-rural gradient spanning 100 km westward from Boston (Massachusetts). They showed that urban sites received almost twice as much N, mostly in the form of ammonium, than rural sites. Dual isotope analysis of leached nitrate showed that, for 5 of their 9 studied sites, the leached nitrate came almost entirely from nitrification in soils, suggesting that deposited N is first microbially transformed before leaching. In France, Pellissier et al. (2008) report significantly higher nitrate concentration in urban soils than in soils from peri-urban and rural sites in and around Rennes, which was attributed to higher N deposition.

In a recent meta-analysis on N cycling rates in urban ecosystems (soils and water), covering 85 studies conducted in 9 different countries, Reisinger et al. (2016) report that urban forests and riparian areas show higher rates of N

mineralization and nitrification when compared to reference ecosystems.

When it comes to temporal dynamics, a limited number of studies have adopted an “age”-explicit approach. Scharenbroch et al. (2005) showed that for different types of systems (residential yards, mulch beds, street trees), soil organic C content, N content and microbial biomass all increased as a function of system age. Golubiewski (2006) showed that conversion of native grassland to residential yards increased belowground and aboveground (ornamental trees) stocks of C with time, and soil N stocks with time. Smetak et al. (2007) studied turfs from residential yards and public parks, and showed that older sites contained more C, more N and more earthworms than younger sites. Park et al. (2010) sampled roadside soils and lawn soils of different ages and showed that older soils of both types had higher C and N contents, with road-side soils of all ages containing more C and N than lawns. Raciti et al. (2011) and Lewis et al. (2014) found that residential lawn soils accumulated C and N over time. Similar results were reported for C by Gough & Elliott (2012) and by Huyler et al. (2014, 2016). Kargar et al. (2013, 2015) showed an increase in street tree pit C and N content with tree age. Setälä et al. (2016) report similar results for parks and show that the temporal trend in C and N accumulation differs according to different vegetation types, with the strongest effect observed for soils under evergreen trees.

From this overview, it appears that both spatially- and temporally-explicit studies suggest that urban environments can influence C and N cycling and that these changes at least partly persist on the long-term. The mechanisms that could lead to C and N accumulation are not well understood. For instance, urban aboveground litter is often exported and data on belowground litter inputs are scarce (Templer et al., 2015; Huyler et al., 2016), and urban soils are subjected to varying and sometimes substantial inputs of exogenous organic C depositions such as “black C” particles produced by incomplete combustion of fossil fuels

and biomass (Rawlins et al., 2008; Edmonson et al., 2015). The origin of accumulated organic C can thus be multifold and more data is required to assess, in systems where aboveground litter is exported, whether belowground C inputs are actually accumulated. Similarly, for N, the literature points towards either fertilizers or deposited N as the source of accumulated N. In addition, the mechanisms underlying the accumulation of N despite higher cycling rates require more investigation. Similarly, the changes in the structure and/or activity of microbial communities leading to changes in N cycling rates has received little attention, while they could help better explain the biotic responses leading to observed biogeochemical changes (Zhu & Carreiro, 1999; Zhu et al., 2004; Hall et al., 2009). On this point, a stronger attention to plant strategies for resource acquisition or use optimization (*e.g.*, changes in metabolism, changes in biomass allocation, changes in phenology etc.) is also necessary, as plants are far from passive organisms and their responses to urban environments, while still poorly known (Calfapietra et al., 2015), are very likely to influence C and N cycling. Finally, street tree plantations, surprisingly, have received relatively little attention, despite being the ecosystems that are the most directly exposed to the environment of cities.

3. The long-term carbon and nitrogen dynamics in “Haussmannian ecosystems” as a case study

In the first months of this research, I started to discuss with city managers in Paris, both to better understand green space management in Paris and, importantly, to obtain the authorization (see Appendix 2) to do fieldwork in Paris. These discussions proved very useful to identify the case study that I would work on, namely the tree plantations that populate Parisian sidewalks.

The establishment of street plantations in Paris rests on similar principles since the 19th century and the Haussmannian works that introduced street tree

plantations as part of the Parisian landscape (Pellegrini, 2012). When planting a new sapling (of age 7-9), a pit about 1 m 30 deep and 3 m wide is opened in the sidewalk and filled with a newly imported peri-urban agricultural soil (Paris Green Space and Environmental Division, pers. comm.). If soil is already in place for a previous tree, it is entirely excavated, disposed of and replaced by a newly imported agricultural soil from the surrounding region. Tree age thus provides a good proxy of soil-tree system age, *e.g.*, the time that a tree and soil have interacted in street conditions (Kargar et al., 2013, 2015). Aboveground litter is completely exported and no fertilizers are applied by city managers.

Thus, they were pretty appealing for someone interested in the dynamics of systems very much directly exposed (*e.g.*, Bettez et al., 2013) to a range of typical urban factors (traffic and domestic gaseous emissions, high amounts of impervious surface and thus a strong heat island effect, strong human density etc.). As systems dominated by trees, very long-lived organisms, they also seemed suited for studying the long-term response of soil-plant systems to the city (Calfapietra et al., 2015). They also seemed to constitute an interesting case study from a C and N cycling perspective. They were systems where the combination of aboveground litter exportation, exogenous N inputs (atmosphere, animals), uncertainties about root ecology, and more generally about soil ecology and long-term tree response to the street environment, made it particularly challenging – and interesting! – to try and predict the temporal trends that could be found in C and N cycling.

Furthermore, in the Parisian context, the potential existence of long-term trends in street plantation biogeochemistry is also of interest for city managers. It is currently assumed that soils get exhausted in nutrients with time and that when replacing a tree, existing soils must be replaced by a newly imported peri-urban soil. This “soil exhaustion” hypothesis has never been tested empirically, which implied that a study on long-term C and N cycling in Parisian street soil-

tree systems could also help assess whether the assumption of a time-related soil exhaustion, on which current practices are based, could be confirmed or not. For ecologists, contrary to the soil exhaustion hypothesis, the fact that plants (especially perennials), through the accumulation of dead and live plant material and microbial biomass in soils, can lead to an increase in soil organic matter and nutrients and have a “fertility island” effect in the landscape (*e.g.*, Jackson & Caldwell, 1993; Mordelet et al., 1993) is well established. However, as stressed above, whether this applies to street systems is a rather opened question.

Studying temporal dynamics of urban soil-plant systems might also help anticipate their future trajectories in a changing environment, which has received relatively little attention. For instance, current estimates of the cooling potential of urban soil-plant systems might not reflect their future potentials, if plant productivity and evapotranspiration come to be affected by water shortages imposed by climate change. The focus, currently, is so to speak more on how to use ecosystems for urban climate change adaptation, but how urban ecosystems will themselves adapt to climate change is highly uncertain and a relatively opened question (Rankovic et al., 2012). This has important consequences for projects of urban ecological engineering, because it can impede the long-term efficiency of projects. It is also important for adjusting the care provided to urban streets and soils, to improve their own living conditions.

On this point, some very basic features of street soil-tree systems are very poorly known. There is a rather widespread acknowledgement that urban trees have a shorter lifespan than their rural or forest conspecifics (Quigley, 2004; Roman et al., 2015). However, the causes of this decline seems nor well identified nor much hierarchized in the literature. In terms of design choices, some fundamental aspects can be in cause. For instance, tree pit size (surface, volume) seems to be a critical point for tree growth and lifespan, probably because of the constraints it imposes on water infiltration and overall available

water and nutrient quantities for trees (Kopinga, 1991; Day & Amateis, 2011). In Paris, because of space constraints on sidewalks, the current policy leads to numerous trees being planted in even smaller soil volumes, which could prove harmful to trees. A study of long-term C and N cycling could also bring information, for instance *via* the detection of signs of nutrient limitation or water stress, to the discussion of how trees fare under current practices and what could be done to improve their situation.

Finally, something that I somewhat had in mind early on, but that revealed itself even more clearly through fieldwork, is that a lot of people really interact on a day to day basis with street plantations and that they are very familiar ecosystems to many urbanites, especially children. They are systems on which it is relatively easy to start discussions even on rather “technical” aspects such as C and N cycling. I found them a particularly interesting occasion to illustrate that even the most apparently mundane urban “green infrastructure” can have unexplored long-term dynamics, and lot of stories to tell about its own “street life”. I found these systems to be a rather powerful example of how urban ecosystems can illustrate some important questions on C and N biogeochemistry and thus provide an interesting tool for discussion and education on (planetary) ecology.

In the research that follows, all of these aspects are to some respect “meshed” together. The core of the present work is based on a 75-year chronosequence of street plantations of the silver linden (*Tilia tomentosa* Moench), comprising 78 sites spread across Paris. For the sake of comparison, samples were also taken at the National Arboretum of Chèvreloup, near Paris, where trees live “in freedom”, without litter export, without spatial constraint for root exploration, without pruning etc. The silver linden is a species from Central Europe, considered well suited for street plantations because of its aesthetics and resistance to street conditions (Radoglou, 2009). It has been used in Paris since

at least the 19th century (Nanot, 1885; Lefevbre, 1897). A chronosequence of 15 street plantations of black locust (*Robinia pseudoacacia* Linnæus) was also analyzed and its results are presented in the general discussion.

The chronosequence approach, widely used in ecology and soil sciences (Strayer et al., 1986; Walker et al., 2010), is based on the assumption that similar systems of different ages, when put into a series of data, can actually depict a theoretical trajectory for the studied systems. Many factors, such as differences in initial conditions or historical events, can actually blur or even falsify the information that is reconstructed by the investigator. When using such approaches, special care must thus be paid during interpretation. Ideally, temporal patterns should be inferred on multiple variables, as independent from each other as possible, in the systems, and confounding factors addressed when possible (Walker et al., 2010). I tried to follow these principles as far as was possible in this work.

Street plantations will often be referred to as “street soil-tree systems”, “street ecosystems” or even by the nickname “Haussmannian ecosystems”, which I tend to affectionate because it explicitly refers to all the hybridity of these systems, stemming from a very centralized vision and planning of Paris, yet now completely embedded in the daily experience of Parisians, while at the same time still retaining their own agency (still mysterious, for the most part!), despite their very human origin. However, it must be noted that the boundaries of ecosystems are always partly a mental and practical construct (Tansley, 1935; Gignoux et al., 2011), and the boundaries chosen by the analyst always contain a part of arbitrary. Here, I tend to restrain my systems to the trees and the soils in the pit, in part because I expected these components to be the most tightly interacting ones (for instance, I expected to find more interactions between trees and the pit soils than between trees and the mineral matrix of the sidewalks), and also because of the practical constraints of this fieldwork which imposed to

restrict myself to the pit (top)soil (I could not dig further, nor break the concrete around trees etc.). Other interactions, with atmospheric processes or animals, or even with elements located outside the pit in the sidewalk, are considered to be interactions with external elements from the soil-tree systems. Hopefully, these distinctions and how they are used to describe and discuss the systems should be relatively obvious to the reader in the next chapters.

In terms of tools, I made use of C and N stable isotopes, molecular analyses on soil DNA and laboratory incubation to measure soil potential activities. While investigating C and N cycling, the study of natural abundances of C and N stable isotopes, ^{13}C and ^{15}N , can help infer mechanistic hypotheses on the involved processes. Stable isotopes can act as “ecological recorders” (West et al., 2006) and integrate information on the sources of elements, as well as the transformations and circulations they undergo while they cycle in ecosystems (Peterson & Fry, 1987; Mariotti, 1991; Högberg, 1997; Robinson, 2001; Craine et al., 2015). As such, they have been proven useful, albeit arguably still underused, tools in urban ecology (Pataki et al., 2005). The heavy isotopes of C and N, ^{13}C and ^{15}N , have one more neutron in their nucleus than the light isotopes (^{12}C and ^{14}N). They behave *almost* exactly as the light isotopes during chemical reactions, but because they are slightly heavier, they tend to be more discriminated against by enzymatic reactions, leading to isotope fractionation between the substrate and the product of a reaction (Fry, 2006). As a consequence, for instance, C3 photosynthesis leads to a production of organic matter that is more depleted in ^{13}C than ambient CO_2 , and nitrification produces nitrate that is more depleted in ^{15}N than the nitrified ammonium pool. Similar fractionation events occur in atmospheric chemical reactions that produce the deposited N, which tends to be ^{15}N enriched in urban environments (Pearson et al., 2000; Widory, 2007; Wang & Pataki, 2009; Hall et al., 2016). While investigating microbial N cycling, nitrification and denitrification are the most

widely studied loss pathways (Reisinger et al., 2016). In recent years, a previously unknown group of microorganisms, ammonia-oxidising archaea, was discovered to play a major role in nitrification besides ammonia-oxidising bacteria, and an important contemporary question concerns their niche partitioning and respective control on nitrification rates in ecosystems. Molecular tools (quantitative PCR) enable to quantify the number of respective gene copies for the two groups of ammonia-oxidisers and use it as a proxy for their abundances. Put in regard of other soil data, potential activities, as well as information on N cycling obtained through elemental and isotope analysis, this can help infer underlying biotic causes of observed trends in ecosystem N cycling.

In the following chapters, this research is presented in three chapters, corresponding to three papers in preparation. In Chapter 1, C and N age-related accumulation patterns in soils are detected and it is hypothesized that tree root-derived C and deposited N from the atmosphere and animal waste accumulate in soils. These hypotheses are supported, notably, by an enrichment of soil $\delta^{13}\text{C}$ along the chronosequence, possibly due to chronic water stress of trees in streets, leading to an enrichment of foliar $\delta^{13}\text{C}$ that could be subsequently transmitted to soil organic matter (SOM) through roots (*via* rhizodeposition and turn-over). For N, the exceptionally high soil and foliar $\delta^{15}\text{N}$ in streets, as well as increased contents in mineral N forms, suggest chronic inputs of ^{15}N -enriched N sources and subsequent microbial cycling, through nitrification and denitrification in particular. Uncertainties remain however, on potential legacy effects due to historical changes in the types of soils being imported in Paris. Indeed, expert knowledge suggests that soils imported around 1950, especially those used previously for market gardening agriculture, likely had higher SOM content than soils entering Paris today, and further evidence was thus needed to confirm the hypotheses of C and N accumulation, and investigate the mechanisms which

could underly such an accumulation.

In Chapter 2, the analysis of soil particle-size fractions shows that in older street soils, most C and almost half of N is contained in coarse fractions (sands). The proportion of C and N contained in coarse fractions increases along the soil chronosequence, as do the proportion of ^{13}C and ^{15}N . This suggests a long-term accumulation dynamics of organic C and N in street soils, with sources of both elements being enriched in their respective heavy isotope. The $\delta^{13}\text{C}$ of fine roots showed an increase with soil-tree system age, confirming the possibility that a ^{13}C signal is transferred from leaves to roots, and that root-C is accumulating in soils. The $\delta^{13}\text{C}\text{-CO}_2$ of soil respiration, assessed through laboratory incubations, shows a consistent increase with street system age, suggesting that root inputs imprint C cycling in street soils, and that the progressive ^{13}C -enrichment of roots is likely gradually transferred to SOM, *via* assimilation of root-C into microbial biomass and accumulation of humified root material. SOM mineralization rates show an age-related decrease in street soils, and are lower in all street soils when compared to the arboretum. On the other hand, root-C inputs are likely to increase with street system age (as fine root density increases with time). Taken together, these two trends – increased root-C inputs and decreased SOM mineralization with time – could lead to C accumulation in street soils. The decrease in SOM mineralization rates in street systems could have several causes, among which we suggested that the interplay between root chemical composition and higher N availability in street soils could lead to accumulated recalcitrant compounds (lignin-rich) becoming less interesting for soil microbes to degrade. In addition, specific physico-chemical and physical protection mechanisms could, compared to leaf litter, better protect root-C from microbial degradation.

Concerning N dynamics, Chapter 2 also shows that root N concentrations are higher in street systems than at the arboretum, and are higher closer to the

surface. This suggests a higher mineral N availability in street soils, and higher at the surface. Root $\delta^{15}\text{N}$ is exceptionally high and becomes progressively closer, with time, to soil $\delta^{15}\text{N}$. These results are interpreted as a sign of close dependence of root N uptake to N mineralization, which could be increased in the vicinity of live roots through rhizosphere priming effect. However, a very high difference is found between foliar and root $\delta^{15}\text{N}$, which could mean that, as trees age, they diversify their N sources, and that whole-tree N nutrition relatively less depends, with time, on the N assimilated from topsoil. This could be due to older tree N demand surpassing the available N stocks at soil surface, which would be consistent with the age-related decrease in foliar N content shown in Chapter 1. We propose that the possible other sources include the uptake of leached nitrate by deeper roots, N-foraging by tree roots outside the tree pit, and foliar N uptake of reactive gaseous N forms.

In Chapter 3, we show that both potential nitrification and denitrification rates increase with street system age, and are much higher than at the arboretum. While both ammonia-oxidising archaea (AOA) and bacteria (AOB) are more abundant in street soils than at the arboretum, the abundance of AOB in surface soils shows consistent age-related trends and is positively correlated to potential nitrification, soil mineral N contents and both soil and foliar $\delta^{15}\text{N}$. We suggest that the increase in nitrification rates could be driven by the observed increase in AOB populations, which itself could be due to increasingly favorable conditions for AOB in street soils, namely increased ammonium content and circumneutral soil pH. Denitrification, in turn, could be favored by increased soil nitrite and nitrate content, as well as soil organic C. Taken together, these results on N i) support the hypothesis that deposited N is assimilated by soil-tree systems, which leads to an accumulation of N in soils, ii) that deposited N increases the rates of N cycling and that N-loss pathways are stimulated by street conditions, which contributes to the observed high soil, root, and foliar $\delta^{15}\text{N}$ values. Even

though loss pathways are increased, the accumulation of N with time means that N inputs are higher than losses and/or that N stabilization mechanisms, possibly in microbial biomass and SOM, are involved.

In the general discussion, these results are recalled and discussed as to what long-term trajectory they seem to depict for street systems. Results on silver linden systems are also discussed in light of results obtained on black locust systems, as well as other data (urban pollinators, soil trace metal content), to assess the possibility to generalize our interpretations and to refine our recommendations for management. The discussion ends on a reflection on the role of urban ecological research in helping to solve environmental issues.



Chapter 1

Long-term trends in carbon and nitrogen cycling in Parisian street soil-tree systems⁴

1. Introduction

An increasing attention is being paid to the “green infrastructure” of cities, for its role in supporting urban biodiversity and providing ecosystem services such as urban heat island mitigation, stormwater runoff regulation, air pollution reduction or carbon storage (Nowak, 2006; Pataki et al., 2011; Oldfield et al., 2013; Livesley et al., 2016). However, the ecology of urban ecosystems, and their long-term dynamics especially, are still poorly known. Once an ecosystem is “constructed” in a city, its trajectory and future behavior are still difficult to predict (Pouyat et al., 2009; Alberti, 2015). This complicates the assessment of urban ecological engineering projects’ sustainability, especially under global environmental change (Grimm et al., 2008). More generally, despite significant progress in urban ecological research over the last decades, a mechanistic understanding of urban ecosystem processes is often lacking, and many unknowns remain as to how urban land-use influences key ecosystem processes such as carbon (C) and nitrogen (N) cycling (Carreiro & Tripler, 2005; Pickett et al., 2008; Pataki et al., 2011; McDonnell & MacGregor-Fors, 2016). In urban areas, C and N cycling can be influenced by numerous interacting factors including management practices, high atmospheric CO₂ concentration, high levels of atmospheric N deposition, increased surface temperatures, pollutants, surface sealing, hydrologic changes or increased presence of non-native

⁴ A research article based on this chapter’s results will be prepared for an international journal by authors (in alphabetic order after first author) Rankovic, A., Abbadie, L., Barot, S., David, A., Lata, J.-C., Leloup, J., Quenea, K., Sebilo, M., Vaury, V. & Zanella, A.

organisms (McDonnell & Pickett, 1990; McDonnell et al., 1997; Carreiro & Tripler, 2005; Kaye et al., 2006; Grimm et al., 2008; Lorenz & Lal, 2009; Hahs & Evans, 2015; Alberti, 2015).

Urban street tree plantations are one of the most widespread ecosystems that can be found in densely urbanized areas, and given the long lifespan of trees, street soil-tree systems can be a useful model to study long-term *in situ* responses of ecosystems to urban conditions (Calfapietra et al., 2015). For these systems, as for other types of urban ecosystems (Pickett et al., 2008; Pouyat et al., 2009), predicting the net effect of street conditions on C and N cycling over time is not straightforward. The exports of aerial litter and dead wood, for instance, remove an important part of organic matter and mineral nutrients (in their organic form) inputs to soil (Templer et al., 2015), which has usually been considered to disrupt C and N cycling and could decrease soil C and N content with time (Pufford, 1991; Craul, 1993). However, root inputs represent an important part of plant C input to soils and studies have shown that root derived-soil organic matter could constitute the major part of stabilized organic matter in soils (*e.g.*, Rasse et al., 2005; Xia et al., 2015). Similarly, important atmospheric N deposition could balance or even exceed N losses through aerial litter exports, especially in systems exposed to heavy traffic (Ammann et al., 1999; Lovett et al., 2000; Pearson et al., 2000; Rao et al., 2013).

The resulting effects of these antagonistic processes have potentially important consequences for our understanding of street soil-tree systems and their management. Urban C and N biogeochemistry is closely tied to practical issues such as the maintenance of urban soil fertility and tree survival (De Kimpe & Morel, 2000; Scharenbroch & Lloyd, 2006; Pouyat et al., 2010; Morel et al., 2015) or urban heat island mitigation through evapotranspiration, which is linked to root development and plant productivity (Rahman et al., 2011; Pataki et al., 2011). In Paris, France, for instance, it is currently assumed, though never

tested empirically, that tree-pit soils get exhausted in nutrients with time and that when a tree is replaced, existing soils must be replaced by a newly imported peri-urban soil (Paris Green Space and Environmental Division, pers. comm.). This hypothesis of soil exhaustion, which underlies current street soil management practices, could be questioned if opposing temporal trends were shown to be at play. Beyond the Parisian context, such knowledge would likely be of interest for the managers of other cities worldwide (James et al., 2009; Kargar et al., 2013; Oldfield et al., 2013).

Ornamental trees in parks and yards have been associated to increased soil C and N content with time (Scharenbroch & Lloyd, 2006; Park et al., 2010; Huyler et al., 2016), and Kargar et al. (2013, 2015) report an increase of soil organic matter and nutrient availability with tree age in Montreal street plantations. Previous studies on urban forest remnants have also shown that urban soils could contain larger C and N pools compared to their rural counterparts (McDonnell et al., 1997; Pouyat et al., 2002; Carreiro et al., 2009; Chen et al., 2010). Higher mineral N content, N mineralization, nitrification and denitrification rates, have also been reported for urban sites (Zhu & Carreiro, 1999, 2004a, 2004b; Hope et al., 2005; Groffman et al., 2006; Pellissier et al., 2008; Chen et al., 2010), suggesting symptoms of N saturation in urban ecosystems (Fang et al., 2011). Given the complexity of urban environments and the many anthropogenic influences that can simultaneously occur on C and N cycling (either direct through management practices for instance, or indirect through increased atmospheric CO₂ levels or N depositions), the mechanisms leading to such patterns, such as the sources and subsequent cycling of C and N, are still poorly known (Huyler et al., 2016).

While investigating C and N cycling, the study of natural abundances of C and N stable isotopes, ¹³C and ¹⁵N, can help infer mechanistic hypotheses on involved processes. Stable isotopes can act as "ecological recorders" (West et al.,

2006) and integrate information on the sources of elements, as well as the transformations and circulations they undergo while they cycle in ecosystems (Peterson & Fry, 1987; Mariotti, 1991; Högberg, 1997; Robinson, 2001; Craine et al., 2015). As such, they have been proven useful, albeit arguably still underused, tools in urban ecology (Pataki et al., 2005).

Stable isotope analyses have been used to trace the assimilation of fossil fuel CO₂, strongly depleted in ¹³C compared to background levels, to urban grasses in Paris and Los Angeles (Lichtfouse et al., 2003; Wang & Pataki, 2010). Using δ¹⁵N measurements, Ammann et al. (1999) estimated that about 25% of N in the needles of pines growing along a highway in Switzerland likely originated from direct stomatal uptake of gaseous NO_x from car exhausts. Similarly, Wang & Pataki (2010) showed strong spatial patterns in the δ¹⁵N of annual grasses sampled in the Los Angeles basin, with grasses in the mostly urbanized areas being strongly enriched in ¹⁵N when compared to the rest of the basin, a result consistent with several reports indicating enriched δ¹⁵N values for deposited N species (*e.g.*, Ammann et al., 1999; Pearson et al., 2000; Widory, 2007).

Besides “tracing” urban pollutants, stable isotope analyses can also help infer plant and soil responses to urban influences. For four tree species growing in parks of New York City, Falxa-Raymond et al. (2014) report higher foliar δ¹³C (*e.g.*, less depleted) values than in rural areas, likely reflecting reduced stomatal conductance in response to water stress (water-use efficiency – WUE – strategy). In Los Angeles, Wang & Pataki (2012) found a strong relation between soil moisture and grass δ¹³C, grasses were more depleted in ¹³C as soil moisture increased. A similar result was found for roadside trees in Kyoto by Kagotani et al. (2013), who suggest that isotopic effects linked to WUE could compensate the isotopic imprint of fossil fuel-derived CO₂ on the organic matter produced by trees. Wang & Pataki (2012) also found that soil processes such as nitrification interacted with N deposition in determining plant δ¹⁵N. As yet,

however, no study has jointly reported soil and foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for urban soil-tree systems.

We here present a study investigating the existence and trajectories of long-term trends in C and N cycling in street soil-tree systems. We studied a 76-year chronosequence of street plantations of silver lindens (*Tilia tomentosa* Moench) in Paris, France. On 78 street sites spread across Paris, we analyzed soil and foliar C and N content and ^{13}C and ^{15}N natural abundances. We also analyzed soil concentration of mineral N forms as a “snapshot” to provide additional indications of urban effects on N cycling (Hope et al., 2005). Fine root density was used as a proxy to compare potential belowground litter inputs. The same parameters were also measured on 7 silver linden stands at the National Arboretum of Chèvreloup, where trees grow in open ground and without aerial litter removal. Our specific objectives were:

- (i) To compare the values measured on soils and leaves of street soil-tree systems of increasing age;
- (ii) To compare different depths in the soil profile to seek for trends in stratification of C and N parameters;
- (iii) To compare values obtained in street systems with values obtained at the National Arboretum of Chèvreloup, taken as a point of contrast, to further help infer interpretations from the observed patterns in street systems.

We hypothesized that the soil exhaustion hypothesis could be contradicted if tree root inputs counterbalanced the lack of aerial litter return, which would result either in an absence of soil C content decrease along the chronosequence or even an increase if root C accumulated with time. Similarly, if urban N inputs (atmosphere, animal sources) compensated N losses through aerial litter export, no age-related decrease would be visible, and an increase could be possible if exogenous N inputs surpassed N losses. Concerning ^{13}C , as street plantations are

not irrigated, we hypothesized that street trees, more exposed to urban heat island effects, could have more enriched foliar $\delta^{13}\text{C}$ values compared to the arboretum, and possibly gradually transmit this signal to soils through belowground litter. On the other hand, urban CO_2 influences could lead the $\delta^{13}\text{C}$ signal in the other direction, leading to more depleted foliar $\delta^{13}\text{C}$ values and consequently soil $\delta^{13}\text{C}$ values over time. Finally, for $\delta^{15}\text{N}$ values, we expected to find trends similar as those reported in the literature, and see a progressive enrichment of street systems, in both soils and leaves, in ^{15}N with time. Concerning soils, we overall expected to find some vertical stratification in measured parameters, which would further indicate the existence of long-term dynamics in these systems and help in general interpretations.

2. Materials and methods

2.1. Site description and chronosequence design

The study was conducted in Paris, France (48°51'12.2"N; 2°20'55.7"E) and at the National Arboretum of Chèvreloup in Rocquencourt (48°49'49.9"N; 2°06'42.4"E), located about 20 km east of central Paris. The Parisian climate is temperate, sub-Atlantic (Crippa et al., 2013), and mean annual temperatures are on average 3°C warmer at night in the center of the agglomeration due to the urban heat island effect (Cantat, 2004). The studied sites comprised silver linden (*Tilia tomentosa* Moench) street plantations in Paris and silver linden stands at the National Arboretum of Chèvreloup. The establishment of street plantations rests on similar principles since the 19th century and the Haussmannian works that introduced street tree plantations as part of the Parisian landscape (Pellegrini, 2012). When planting a new sapling (of age 7-9), a pit about 1 m 30 deep and 3 m wide is opened in the sidewalk and filled with a newly imported peri-urban agricultural soil (Paris Green Space and Environmental Division, pers. comm.). If soil is already in place for a previous tree, it is entirely excavated, disposed of and replaced. During the three first post-implementation

years, plantations are irrigated with 250 l of water every two weeks (Paris Green Space and Environmental Division, pers. comm.). Subsequently, there is no management practice other than pruning, litter removal and the occasional cleansing of soil surfaces (*e.g.*, waste withdrawal). There is no fertilizer input during tree life (Pellegrini, 2012; Paris Green Space and Environmental Division, pers. comm.). Tree age thus provides a good proxy of soil-tree ecosystem age, *e.g.*, the time that a tree and soil have interacted in street conditions (Kargar et al., 2013, 2015).

The sampling design was based on 3 tree diameter at breast height (DBH) classes, used as a proxy for tree age. The three classes were designed to cover the DBH range of street silver lindens in Paris, which spans from approximately 6 to 76 cm, as retrieved in the databases provided by the Paris Green Space and Environmental Division. This was done so that the chronosequence ranged from about the youngest to the oldest silver lindens street plantations in Paris. Sites were also selected so as to be spread across the city (Figure 1). Only sites with either bare or drain-covered soils were selected to keep similar conditions of air and water circulation in soils, and thus avoid important differences in terms of rooting conditions (*e.g.*, Rahman et al., 2011). In total, 78 street plantations were sampled according to 3 DBH classes: Class 1 = [6.8; 14.6 cm] (n = 28), Class 2 = [32.5; 42.7 cm] (n = 29), Class 3 = [56.7; 73.2 cm] (n = 21). The sites were located in 18 different streets across Paris.

Tree-ring counts on wood cores subsequently helped determine tree age (David et al., submitted) and provide an estimation of “soil-tree system age”, by subtracting 7 years to every tree age to account for sapling age at their plantation in streets. A linear regression between street tree DBH and age yielded an R^2 of 0.88 ($p < 0.001$). This was considered satisfying and the initial repartition of sites in three DBH-based classes was kept. Overall, the street chronosequence spans from ecosystems of age 1 to age 76. Class 1 includes systems of an

average age of 4.3 ± 4.7 years, Class 2 includes systems of age 39.1 ± 13.0 years, and Class 3 includes systems of age 71.4 ± 9.6 years. Thereafter, these three classes will respectively be referred to as "younger systems", "intermediate systems" and "older systems" (Table 1). A Kruskal-Wallis test ($H = 59.1$, $df = 2$, $p < 0.001$) followed by a Wilcoxon-Mann-Whitney test confirmed that age was significantly different between each class (Younger-Intermediate: $p < 0.001$; Younger-Older: $p < 0.001$; Intermediate-Older: $p < 0.001$).

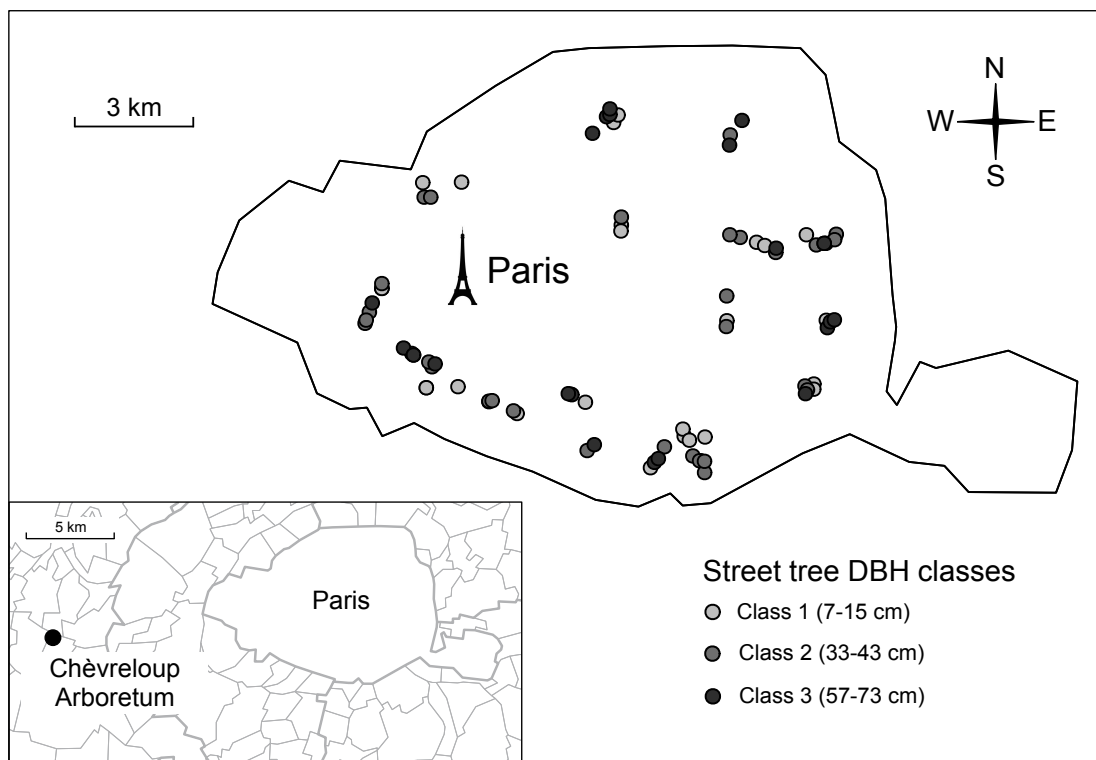


Figure 1. Location of sampled street plantations in Paris and the arboretum.

Table 1. Classes of tree DBH and ecosystem age. Tree DBH was measured in July 2011 for street trees and 2012 for arboretum trees. Trunk circumferences were tape-measured at 1.30 m from the ground and divided by π . Tree ages were estimated by counting tree rings on extracted wood cores (David et al., submitted). Ecosystem age was obtained by subtracting 7 years to every tree age to account for sapling age at plantation.

Paris street soil-tree ecosystems (n = 78)											
Younger systems (4.3 years \pm 4.7, n = 28)			Intermediate systems (39.1 years \pm 13.0, n = 29)			Older systems (71.4 years \pm 9.6, n = 21)			Arboretum stands (55.7 years \pm 25.1, n = 7)		
Sites	Tree DBH (cm)	Ecosystem age (years)	Sites	Tree DBH (cm)	Ecosystem age (years)	Sites	Tree DBH (cm)	Ecosystem age (years)	Sites	Tree DBH (cm)	Ecosystem age (years)
T01	6.8	1	T29	32.5	43	T58	56.7	71	CLT1	46.8	30
T02	7.6	2	T30	32.5	29	T59	57.3	71	CLT2	47.1	30
T03	8.0	1	T31	33.1	33	T60	57.3	NA	CLT3	38.2	30
T04	8.3	1	T32	33.1	63	T61	57.3	76	CLT4	73.8	70
T05	8.6	2	T33	33.7	32	T62	57.3	76	CLT5	111.1	90
T06	8.6	2	T34	34.1	40	T63	57.3	76	CLT6	68.4	70
T07	8.6	1	T35	34.1	35	T64	58.3	NA	CLT7	67.2	70
T08	8.9	2	T36	34.4	31	T65	58.9	43			
T09	9.2	1	T37	34.7	28	T66	60.5	76			
T10	9.2	NA	T38	34.7	19	T67	60.5	NA			
T11	9.5	1	T39	35.3	27	T68	60.5	51			
T12	9.5	1	T40	35.7	46	T69	60.5	74			
T13	9.9	3	T41	36.3	74	T70	60.8	76			
T14	9.9	8	T42	36.6	35	T71	61.4	76			
T15	10.8	6	T43	36.6	38	T72	63.0	NA			
T16	11.1	3	T44	37.9	41	T73	63.7	76			
T17	11.5	2	T45	38.2	41	T75	64.9	76			
T18	11.5	2	T46	39.2	44	T76	65.3	68			
T19	12.7	4	T47	39.5	37	T77	71.3	76			
T20	13.1	3	T48	39.5	NA	T78	72.6	76			
T21	13.1	14	T49	39.8	40	T79	73.2	76			
T22	13.7	NA	T50	39.8	14	-	-	-			
T23	14.0	21	T51	39.8	31	-	-	-			
T24	14.0	7	T52	40.4	57	-	-	-			
T25	14.3	4	T53	41.4	37	-	-	-			
T26	14.3	2	T54	41.7	40	-	-	-			
T27	14.6	7	T55	41.7	NA	-	-	-			
T28	14.3	9	T56	42.0	39	-	-	-			
-	-	-	T57	42.7	62	-	-	-			

The National Arboretum of Chèvreloup (<http://chevreloup.mnhn.fr>) is a 205-hectare arboretum adjacent to the Palace of Versailles complex and located in the municipality of Rocquencourt in the Yvelines department, region of Île-de-France (Figure 1). The current arboretum was created in 1927 and is the property of the French National Museum of Natural History. At the arboretum, trees are usually grown on site at the nursery and planted as saplings when about 10 years old. Trees are not submitted to pruning, not fertilized and aboveground litter is not removed. There is little to no competition for crown development space. Compared to street trees, there seem to be no space constraint for root system development⁵. At the arboretum, 7 silver linden stands were sampled. Their plantation date is known and was used to estimate soil-tree ecosystem age, giving an average age of 55.7 ± 25.1 years (Table 1). Arboretum soil-tree systems thus had an age comprised between intermediate and older street systems.

2.2. Sample collection and processing

Samples from street plantations were collected over July 2011. At each site, soil was sampled at 2 points around each tree trunk with a 3 cm diameter gouge auger. The sampling points were situated at 25-40 cm from the trunk, depending on accessibility (size of drain holes, obstruction by thick roots etc.). The 10-30 cm and 30-40 cm depths of both soil cores were respectively pooled. Samples from the arboretum were collected in July 2012. Four soil cores were extracted around the trunk at the same distance from the trunk as for the street sites. The four extracted soil cores were pooled at 0-10, 10-20, 20-30, 30-40 cm depths respectively. For the arboretum, the 10-30 cm data presented here are an average of values obtained for 10-20 and 20-30 cm depths. For street and arboretum soils, subsamples were frozen in liquid N₂ in the field for subsequent NH₄⁺, NO₂⁻ and NO₃⁻ analysis.

⁵ A good overview of the arboretum can be seen here: http://www.dailymotion.com/video/x18igt6_arboretum-de-chevreloup (video copyright of the French National Museum of Natural History).

Twigs were sampled on four opposite points of the external lower canopy. Leaves were either the antepenultimate or penultimate leaf of the cut twigs. Four leaves were sampled per tree.

Soil samples were air-dried and manually sieved at 2 mm. Representative subsamples were homogenized in an agate ball-mill for elemental and isotopic analyses. Leaves were washed with MilliQ water, gently brushed and again rinsed with MilliQ water to remove adsorbed particles (Freer-Smith et al., 1997). They were air-dried and pulverized at $< 80 \mu\text{m}$ with an ultracentrifugal grinding mill (ZM100, Retsch, Haan, Germany).

Fine roots (diameter $< 2 \text{ mm}$) were separated from soil samples with an electrostatic method, following the principle described by Kuzyakov et al. (2001). Additional purifying steps were added to separate the extracted roots from the co-extracted soil particles and plant debris. The extracts were immersed in a sonicating bath with MilliQ water and floating organic particles were retrieved while the mineral particles sank to the vessel bottom. The process was repeated until only the mineral fraction remained at the vessel bottom. If a few roots remained mixed with the mineral fraction at the bottom, they were recovered with tweezers. After oven-drying at 40°C , roots were weighed on a microbalance which provided the fine root biomass of each sample. Fine root biomass was then divided by the mass of dry $< 2 \text{ mm}$ soil samples from which they were extracted, to obtain the fine root gravimetric density (fine root density, thereafter; $\text{mg Root.g Soil}^{-1}$).

2.3. Soil characteristics

Soil texture after decarbonation, cationic exchange capacity (CEC), and total CaCO_3 were performed by a routine soil-testing laboratory (INRA-LAS, France) according to French and international (AFNOR and ISO) standard

procedures⁶.

Soil pH was measured in water (5:1 v/v water:soil) with a pH meter (SevenEasy™, Mettler Toledo, Viroflay, France) according to the norm NF ISO 10390 (AFNOR, 2005).

Bulk density ($\text{g}\cdot\text{cm}^{-3}$) was calculated by dividing the mass (g) of the fine soil (< 2 mm) by its volume. Total soil core volume was estimated by immersing a wax molding of the auger in a measuring cylinder filled with water and reading the volume change. The volume for a 10 cm sample was estimated to be 45 cm^3 . The mass and volume of roots and rocks retained by the 2 mm sieve were subtracted from the mass and volume of the total soil core. The volume of > 2 mm rocks and roots was obtained by immersing them in a measuring cylinder filled with water.

2.4. C and N contents and isotope ratios

Soils were analyzed for organic C content and $\delta^{13}\text{C}$ after carbonate removal with the HCl fumigation method (Harris, 2001). Briefly, 30 mg of homogenized sample were weighted in silver capsules, moisturized with 50 μl of milliQ water, and placed for 6 h in a vacuumed desiccator with a beaker containing 200 ml of 16 M HCl. Then, samples were double-folded in tin capsules for better combustion (Harris, 2001; Brodie et al., 2011) and analyzed at INRA-Nancy by EA-IRMS (NA 1500, Carlo Erba, Milano, Italy, coupled with a Delta S, Finnigan, Palo Alto, USA). For total N content and $\delta^{15}\text{N}$, soil samples were analyzed by EA-IRMS (vario Pyro cube, Elementar, Hanau, Germany, coupled with an IsoPrime, Gvi, Stockport, UK) without any pre-treatment to avoid unnecessary bias on N parameters (Komada et al., 2008; Brodie et al., 2011). Pulverized leaf samples were analyzed for C content, N content, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by EA-IRMS (vario Pyro cube, Elementar, Hanau,

⁶ List of norms: Texture: NF X 31-107 (AFNOR, 2003); CEC: NF ISO 23470 (AFNOR, 2011); Total CaCO_3 : NF ISO 10693 (AFNOR, 2014).

Germany coupled with an IsoPrime, Gvi, Stockport, UK).

For isotopic values, results are expressed using the usual delta notation that allows expressing the content in ^{13}C or ^{15}N as the relative difference between the isotopic ratio of the sample and a standard, calculated as:

$$\delta(\text{‰}) = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}]*1000$$

where R_{sample} is the isotope ratio ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ for C and N, respectively) of the sample and R_{standard} the isotope ratio of the standard. The international standard for C is the Pee Dee Belemnite standard, with a $^{13}\text{C}/^{12}\text{C}$ ratio of 0.0112372 (Craig, 1957). For N, the international standard is atmospheric dinitrogen for which the $^{15}\text{N}/^{14}\text{N}$ ratio is 0.003676 (Mariotti et al., 1983, 1984).

For measures of soil concentration in and NH_4^+ , NO_2^- and NO_3^- about 1 g of frozen subsample was mixed with a 0.5 M KCl solution with a 1:2 soil:solution ratio. Samples were then placed on a rotary shaker for 30 minutes and then centrifuged at 4000 rpm for 5 min. The supernatant was then analyzed by colorimetric methods using an autoanalyser (Gallery, Thermo Fisher Scientific, Cergy-Pontoise, France).

2.5. Statistical analyses

Statistical analyses were performed with the R-software (R Development Core Team, 2013). Four sample classes (three DBH classes and the arboretum) and two depths (10-30 and 30-40 cm) and their interaction were used as explanatory factors for soil variables. For foliar parameters, as well as for $\Delta^{15}\text{N}_{\text{leaf-soil}}$, linear models were used with class as an explanatory factor. For soil parameters, linear mixed-effects models with a “site” random effect were used for soil variables to account for non-independence of soil depths at each sampling site. R^2 values for linear mixed-effects models were calculated with the function `r.squared.lme` (version 0.2-4 (2014-07-10)) that follows the method

described in Nakagawa & Schielzeth (2013). Values for conditional R^2 , which describes the proportion of variance explained by both the fixed and random factors, are shown. Tukey post-hoc tests were performed for ANOVA models yielding significant results. For variables that did not satisfy ANOVA assumptions even after log transformation, non-parametric tests were used: a Kruskal-Wallis test was used for each depth to test for differences between classes, and a Wilcoxon-Mann-Whitney test was used for pairwise comparisons of means for different depths. For all tests, the null hypothesis was rejected for $p < 0.05$ and significance was represented as follows: *** when $p \leq 0.001$; ** for $0.001 < p \leq 0.01$ and * when $0.01 < p \leq 0.05$. Effects with $0.05 \leq p < 0.10$ are referred to as marginally significant.

3. Results

3.1. Soil characteristics

Clay, silt and sand contents significantly differed among classes for both depths (Table 2, Table 3). Soils from younger street systems and the arboretum had similar clay content that was significantly higher than soils from intermediate and older systems. Soils from intermediate systems contained more clay than soils from older systems. Overall, soils from younger systems and the arboretum were finer textured than soils from street intermediate and older systems and appeared as silt-loam soils. Soils from street intermediate systems were loam soils and soils from older street systems were sandy loam soils (Table 2, Table 3).

Bulk density at 10-30 cm showed no significant difference between street age classes. At 30-40 cm, soils from younger systems had a significantly lower bulk density than soils from intermediate and older systems. Soils from intermediate and older systems had higher bulk densities at 30-40 cm than in 10-30 cm. Soils from all street age classes had a significantly higher bulk density at both depths compared to arboretum soils (Table 2, Table 3). Soil pH did not

differ significantly between street age classes but was significantly different between street systems and soils in the arboretum (Table 2, Table 3). CEC showed no significant difference between street age classes and between street sites and the arboretum (Table 2, Table 3).

Total CaCO_3 was significantly higher in street soils compared to arboretum soils, at both depths. At 10-30 cm, it showed a significant increase with age classes. At 30-40 cm, soils from intermediate and older systems had significantly more CaCO_3 than soils from younger systems. A significant difference between both depths was observed for each street class, with more CaCO_3 contained in the 10-30 cm than in 30-40 cm. This difference among depths was not observed in the arboretum (Table 2, Table 3).

3.2. Soil C and N contents and isotope ratios

Soil organic C content was significantly different between street age classes at 10-30 cm (Table 4, Figure 2A). Soils from intermediate and older systems had higher organic C contents compared to soils from younger systems, with respective means of 2.3 and 2.6 % for intermediate and older systems and 1.4 % for younger systems. The difference in organic C content between younger and older systems was thus almost two-fold at 10-30 cm. At 30-40 cm, the mean organic C content for soils of younger, intermediate and older systems was respectively 1.5, 1.8 and 2.5 %. The difference between younger and intermediate systems was not significant, and soils of older systems were significantly above the other street systems. At 10-30 cm, mean organic C content in arboretum soils was of 1.8 %, not significantly different from soils of street young and intermediate systems but significantly lower than soils of older street systems.

Table 3. Kruskal-Wallis table. Reports the effect of class on soil clay, silt and sand content, bulk density, pH and CaCO₃ content, at both studied depths.

Variable	Soil depth	Factor: Class		
		H	df	p
Clay (< 2 μm)	10-30 cm	29.7	3	***
	30-40 cm	9.8	3	**
Silt (2-50 μm)	10-30 cm	51.7	3	***
	30-40 cm	16.9	3	***
Sand (50-2000 μm)	10-30 cm	44.3	3	***
	30-40 cm	11.8	3	**
Bulk density	10-30 cm	20.7	3	***
	30-40 cm	25.4	3	***
pH _{H2O}	10-30 cm	19.9	3	***
	30-40 cm	23.1	3	***
CaCO ₃	10-30 cm	51.0	3	***
	30-40 cm	17.5	3	***

At 30-40 cm, arboretum soils contained 1.1 % of organic C in average, which was significantly lower than soils from older street systems at both depths, significantly different from soils of intermediate systems at 10-30 but not at 30-40, and not significantly different soils of younger systems at both depths. Organic C content showed a much stronger stratification in arboretum soils than in street systems. Arboretum soils contained about 62 % more organic C at 10-30 cm than at 30-40 cm (significant difference), while in Paris only soils from intermediate systems displayed a significant difference between depths, but in a much lower magnitude (22 % more organic C at 10-30 cm) (Table 4, Figure 2A).

Table 2. Soil characteristics. For each parameter, the mean \pm standard deviation is indicated. Different lower case letters indicate a significant difference, among and between classes at different depths, with $\alpha = 0.05$. For CEC, differences were tested with a linear mixed-effect model (Table 4). For the other variables, differences were tested with Kruskal-Wallis tests and followed by Wilcoxon-Mann-Whitney tests for pairwise comparisons. For arboretum sites, and younger, intermediate and older street systems, respectively, at 10-30 cm/30-40 cm, $n = 7/7$, $n = 28/9$, $n = 29/10$ and $n = 21/10$ for soil clay, silt and sand content; $n = 7/7$, $n = 28/28$, $n = 28/28$, and $n = 21/21$ for bulk density; $n = 7/7$, $n = 27/28$, $n = 24/29$ and $n = 18/21$ for pH; $n = 7/7$, $n = 9/4$, $n = 10/8$, $n = 9/6$ for CEC; and $n = 7/7$, $n = 28/10$, $n = 29/10$ and $n = 21/10$ for CaCO_3 content.

Soil parameter	Soil depth (cm)	Paris street soil-tree ecosystems			Arboretum
		Younger systems	Intermediate systems	Older systems	
Clay (<2 μm) (g.kg^{-1})	10-30	193.6 \pm 37.8 ^a	157.3 \pm 34.1 ^b	131.2 \pm 58.9 ^c	219.5 \pm 18.32 ^a
	30-40	200.0 \pm 65.1 ^{ad}	210.4 \pm 56.6 ^a	157.0 \pm 74.5 ^{cbd}	250.43 \pm 40.87 ^a
Silt (2-50 μm) (g.kg^{-1})	10-30	534.8 \pm 104.9 ^a	274.9 \pm 139.0 ^{bf}	174.0 \pm 120.0 ^c	446.0 \pm 72.6 ^{dg}
	30-40	552.1 \pm 120.7 ^a	338.8 \pm 194.6 ^{bg}	212.2 \pm 168.1 ^{ef}	443.6 \pm 91.7 ^{dg}
Sand (50-2000 μm) (g.kg^{-1})	10-30	243.4 \pm 120.1 ^a	478.8 \pm 144.5 ^{be}	569.4 \pm 147.7 ^c	333.3 \pm 85.5 ^{af}
	30-40	234.3 \pm 186.1 ^{ad}	385.5 \pm 202.3 ^{bd}	548.0 \pm 193.1 ^{ce}	304.4 \pm 82.1 ^{bf}
Bulk density (g.cm^{-3})	10-30	2.5 \pm 0.4 ^a	2.7 \pm 0.6 ^a	2.5 \pm 0.3 ^a	1.5 \pm 0.2 ^c
	30-40	2.7 \pm 0.6 ^a	3.1 \pm 0.6 ^b	3.04 \pm 0.3 ^b	1.4 \pm 0.2 ^c
pH _{H2O}	10-30	7.6 \pm 0.4 ^{ab}	7.7 \pm 0.3 ^{ab}	7.6 \pm 0.3 ^{ab}	5.7 \pm 0.4 ^c
	30-40	7.6 \pm 0.3 ^a	7.7 \pm 0.5 ^b	7.7 \pm 0.5 ^{ab}	5.7 \pm 0.4 ^c
CEC (molc+)	10-30	12.1 \pm 3.2 ^a	13.0 \pm 2.8 ^a	12.8 \pm 4.3 ^a	10.7 \pm 2.9 ^a
	30-40	12.1 \pm 5.7 ^a	13.8 \pm 3.7 ^a	14.4 \pm 1.9 ^a	9.6 \pm 2.6 ^a
CaCO ₃ (g.kg^{-1})	10-30	29.1 \pm 33.0 ^a	88.5 \pm 54.7 ^b	120.3 \pm 50.0 ^c	0.5 \pm 0.5 ^e
	30-40	15.8 \pm 17.2 ^a	70.7 \pm 80.2 ^{ad}	81.6 \pm 67.2 ^{bd}	1.5 \pm 0.2 ^e

Table 4. ANOVA table of F values. Reports the effects of class and depth and their interaction on soil organic C content, soil total N content, soil C:N, soil $\delta^{13}\text{C}$, soil $\delta^{15}\text{N}$, soil NH_4^+ , NO_2^- and NO_3^- content, fine root density and CEC, as tested with a linear mixed-effect model with a site random effect. For foliar parameters, only the effect of class was tested with a a linear model, and only one depth (10-30 cm) was considered for $\Delta^{15}\text{N}_{\text{leaf-soil}}$. The reported values for significant terms and R^2 are the values obtained after removal of non-significant factors in the model.

Variables	Factors									Model R^2
	Class			Depth			Class x Depth			
	F	p	df	F	p	df	F	p	df	
log (Soil %C)	11.5	***	3	10.0	**	1	7.6	***	3	0.67
log (Soil %N)	8.9	***	3	3.6	***	1	12.0	***	3	0.74
log (Soil C:N)	7.9	***	3	2	ns	1	1.8	ns	3	0.12
Soil $\delta^{13}\text{C}$	37.0	***	3	28.2	***	1	1.1	ns	3	0.61
log (Soil $\delta^{15}\text{N}$)	73.4	***	3	42.2	***	1	16.5	***	3	0.82
log (NH_4^+)	8.3	***	3	12.9	***	1	1.35	ns	3	0.61
log (NO_2^-)	23.2	***	3	11.4	***	1	2	ns	3	0.69
log (NO_3^-)	12.7	***	3	17.1	***	1	1.51	ns	3	0.55
log (Fine root density)	3.5	*	3	6.8	*	1	0.8	ns	3	0.61
CEC	0.8	ns	3	2.0	ns	1	1.7	ns	3	-
Foliar $\delta^{13}\text{C}$	2.54	0.06	3	-	-	-	-	-	-	-
Foliar $\delta^{15}\text{N}$	32.1	***	3	-	-	-	-	-	-	0.53
Foliar %N	5.0	**	3	-	-	-	-	-	-	0.13
Foliar C:N	3.3	*	3	-	-	-	-	-	-	0.08
$\Delta^{15}\text{N}_{\text{leaf-soil}}$	13.6	***	3	-	-	-	-	-	-	0.31

At 30-40 cm, average soil $\delta^{13}\text{C}$ was -26.1 ‰ for young systems, -25.3 ‰ for intermediate systems and -25.0 for older systems with a significant difference between each class. At the arboretum, soil $\delta^{13}\text{C}$ was -26.6 ‰ at 10-30 cm and -26.2 ‰ at 30-40 cm. At both depths, soil $\delta^{13}\text{C}$ at the arboretum was not significantly different from street younger systems but was significantly lower than soil $\delta^{13}\text{C}$ of intermediate and older street systems. Depth had a significant effect on soil $\delta^{13}\text{C}$ values, with notably intermediate and older street systems showing a soil $\delta^{13}\text{C}$ about 0.5 ‰ unit higher at 30-40 cm. Soils from older street systems had about 1 ‰ unit more enriched $\delta^{13}\text{C}$ values compared to arboretum and young street system soils.

Soil total N content was significantly different between street age classes at 10-30 cm (Table 4, Figure 3A). Average soil N content was 0.12 % for younger street systems, 0.18 % for intermediate street systems and 0.21 % for older street systems, with significant difference between each class. The difference in soil N content between younger and older street systems was about two-fold. At 30-40 cm, soil N content in younger systems (0.13 %) was not significantly different from intermediate systems (0.13 %), but soils from older systems contained significantly more N (0.17 %) than soils from younger and intermediate systems. Soils from the arboretum contained more N (0.2 %) at 10-30 cm than soils from younger street systems but had similar N content with soils from intermediate and older street systems. Soil N content was different between depths for all classes except for younger street systems. As for organic C, the difference between depths was stronger for arboretum sites, with N content at 10-30 cm being 83 % higher than N content at 30-40 cm (0.11 %) (significant difference). In street systems, soil N content at 10-30 cm was 38 % higher than at 30-40 cm in intermediate systems (significant difference) and a similar trend was observed on older systems.

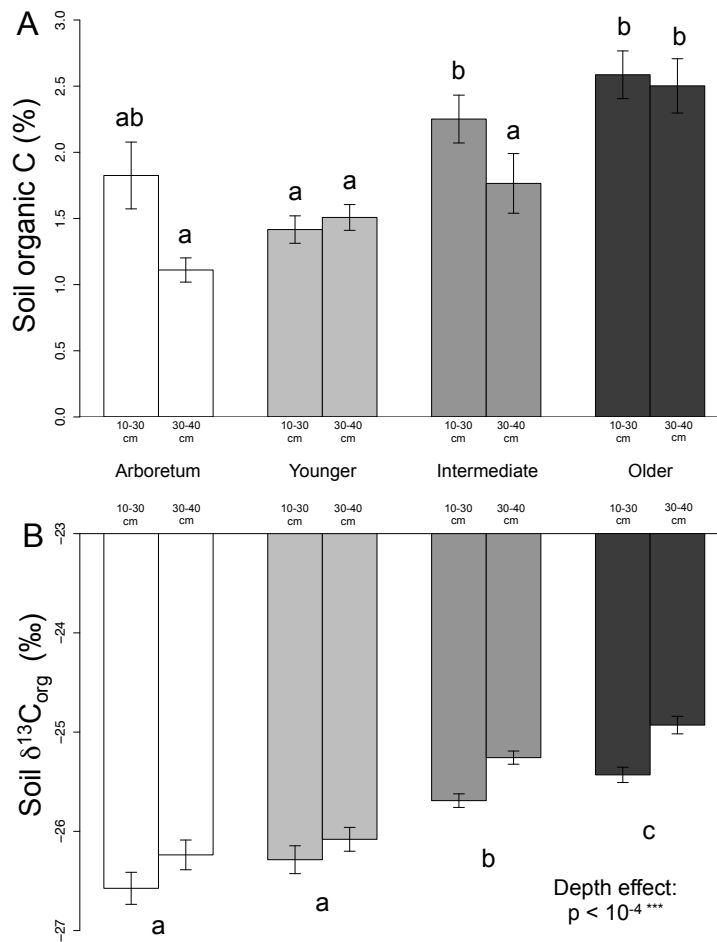


Figure 2. (A) Soil organic C content (%) and (B) Soil $\delta^{13}\text{C}$ at 10-30 cm and 30-40 cm in the different sample classes. Bars show means and error bars correspond to standard error. Different lower case letters indicate a significant difference between depths among and between classes for soil organic C content, and among classes for soil $\delta^{13}\text{C}$, following the results of linear mixed-effect models and Tukey post-hoc tests (see Table 4 and text). For arboretum sites, and younger, intermediate and older street systems, respectively, at 10-30 cm/30-40 cm, $n = 7/7$, $n = 28/28$, $n = 29/29$ and $n = 20/21$ for soil organic carbon content, and $n = 7/7$, $n = 28/27$, $n = 29/29$ and $n=19/20$ for soil $\delta^{13}\text{C}$.

Soil $\delta^{15}\text{N}$ at 10-30 cm was significantly different between street younger systems and intermediate and older systems (Table 4, Figure 3B). Average soil $\delta^{15}\text{N}$ at 10-30 cm was 10.4 ‰ for young systems, 13.2 ‰ for intermediate systems and 14.2 ‰ for older systems. At 30-40 cm, average soil $\delta^{15}\text{N}$ was 8.4 ‰ for young systems, 11.9 ‰ for intermediate systems and 13.3 ‰ for older systems with a significant difference between each class. At the arboretum, soil

$\delta^{15}\text{N}$ was 6.9 ‰ at 10-30 cm and 9.5 ‰ at 30-40 cm, with soils being significantly more enriched in ^{15}N at 30-40 cm than at 10-30 cm. For street systems in Paris, it was the opposite, with soils being significantly more enriched in ^{15}N at 10-30 cm than at 30-40 cm for younger and intermediate street systems. At 10-30 cm, soils of younger street systems were significantly more enriched in ^{15}N compared to arboretum soils at the same depth but not significantly different from arboretum soils at 30-40 cm. Soil $\delta^{15}\text{N}$ at both depths at the arboretum was significantly different from both depths in street intermediate and older systems. Overall, average soil $\delta^{15}\text{N}$ from older street systems was 3.8 ‰ units higher at 10-30 cm and 4.9 ‰ units higher at 30-40 cm when compared to soils from younger systems, and 7.4 ‰ units higher at 10-30 cm and 3.8 ‰ units higher at 30-40 cm when compared to soils from the arboretum.

Soil NH_4^+ content did not differ between arboretum soils and intermediate and older street soils (Table 4, Figure 4B). Soils from intermediate and older systems had higher NH_4^+ content than soils from younger systems. There was an observed trend in stratification between depths in all classes, with an overall significant depth effect on NH_4^+ content. At 10-30 cm, soils from intermediate and older street systems contained about twice the amount of NH_4^+ found in younger street systems.

Soil NO_2^- content was higher in all street sites at both depths compared to arboretum soils (Table 4, Figure 4C). Older street systems had higher soil NO_2^- at 10-30 cm than younger systems at both depths. At 10-30 cm, soils from older street systems contained almost ten times more NO_2^- when compared to arboretum soils, four times more when compared to younger street systems and 1.6 times more when compared to intermediate systems. There was an observed trend in stratification in intermediate and older street systems, with a significant depth effect (Table 4, Figure 4C).

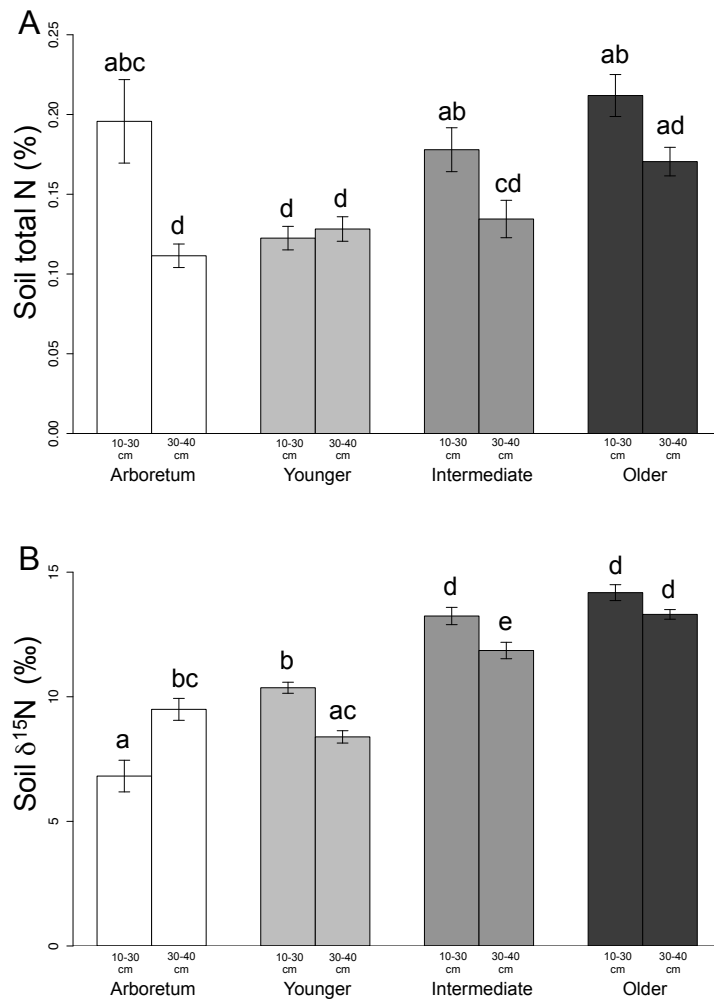


Figure 3. Figure 2. (A) Soil total N content (%) and (B) Soil $\delta^{15}\text{N}$ at 10-30 cm and 30-40 cm in the different sample classes. Bars show means and error bars correspond to standard error. Different lower case letters indicate a significant difference between depths among and between classes, following the results of linear mixed-effect models and Tukey post-hoc tests (see Table 4 and text). For arboretum sites, and younger, intermediate and older street systems, respectively, at both depths $n = 7$, $n = 28$, $n = 29$ and $n = 21$ for both variables.

Soil NO_3^- content was higher in street systems at 10-30 cm when compared to arboretum soils at both depths (Table 4, Figure 4D). Street soils had, on average, 22 times more soil NO_3^- than arboretum sites at 10-30 cm, and about 165 times more NO_3^- at 30-40 cm. There was an observed trend in stratification in intermediate and older street systems (Table 4, Figure 4D), with a significant effect of depth. Soil in intermediate systems contained 3 times

more NO_3^- at 10-30 cm than at 30-40 cm on average, and the observed difference was two-fold in older systems (Figure 4D).

3.3. Foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and N content

There was a marginally significant difference in foliar $\delta^{13}\text{C}$ between arboretum and street trees (Table 4, Figure 5C). Average foliar $\delta^{13}\text{C}$ was -29.0 ‰ in arboretum trees and -27.8 ‰, -28.0 ‰ and -28.1 ‰ in younger, intermediate and older street trees, respectively. Street tree leaves thus had an enrichment ^{13}C of about 1 ‰ unit when compared to arboretum trees.

Foliar $\delta^{15}\text{N}$ was significantly different between arboretum trees and street trees (Table 4, Figure 5A). Mean foliar $\delta^{15}\text{N}$ of arboretum trees was 2.3 ‰, while it was 7.0 ‰, 7.2 ‰ and 8.0 ‰ for younger, intermediate and older street trees, respectively. On average, street tree foliar $\delta^{15}\text{N}$ was about 5 ‰ units higher than arboretum tree foliar $\delta^{15}\text{N}$.

Foliar N content was different between younger street trees and intermediate and older street trees (Table 4, Figure 5B). Foliar C:N was significantly higher in older street trees when compared to younger street trees (Figure 5D).

3.4. Soil and plant coupling

Fine root density was significantly higher in older street systems than in younger street systems and the arboretum (Table 4, Figure 6A). A marginally significant difference was found between intermediate soil systems and the arboretum ($p = 0.08$). There was an observed trend in stratification in intermediate and older street systems, and an overall significant effect of depth (Table 4, Figure 6A). At 10-30 cm, fine root density was about three times higher in older and intermediate street systems compared to younger street systems and the arboretum (Figure 6A).

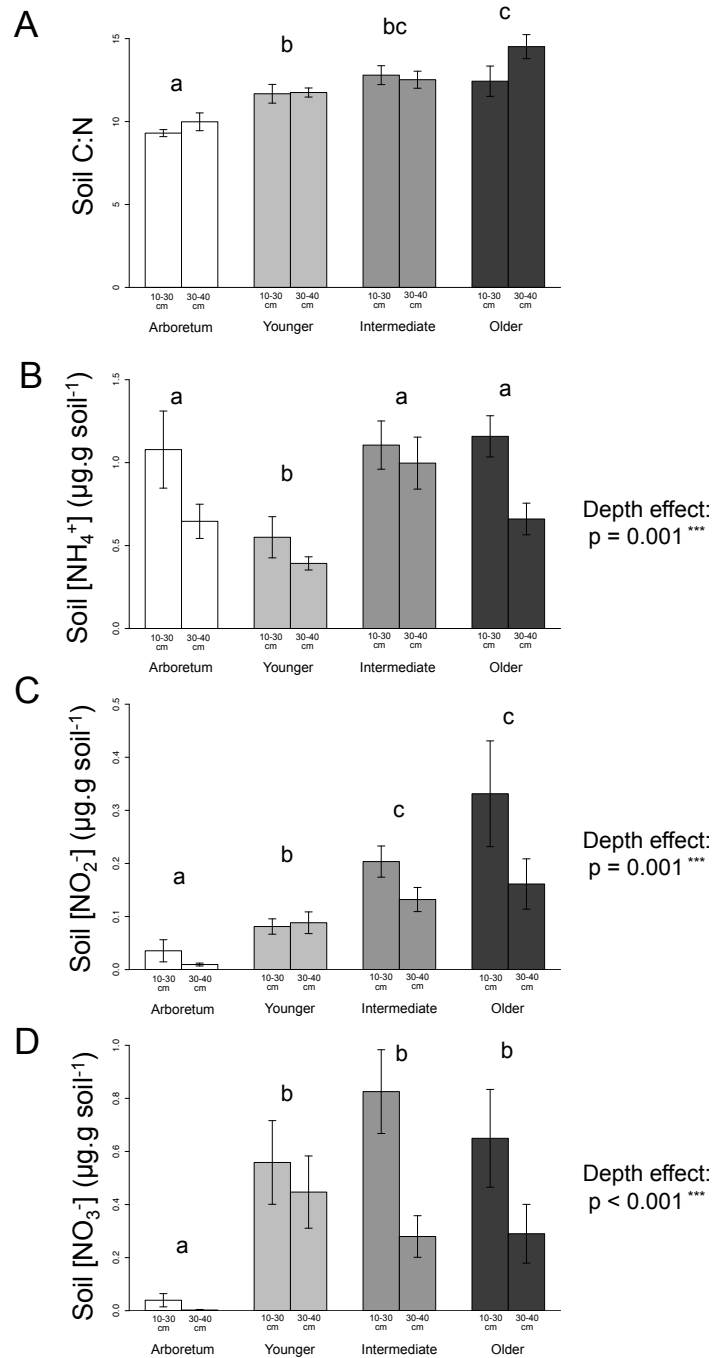


Figure 4. (A) Soil C:N, (B) Soil NH₄⁺ content, (C) Soil NO₂⁻ content and (D) Soil NO₃⁻ content at 10-30 cm and 30-40 cm in the different sample classes. Bars show means and error bars correspond to standard error. Different lower case letters indicate a significant difference between classes, following the results of linear mixed-effect models and Tukey post-hoc tests (see Table 4 and text). For arboretum sites, and younger, intermediate and older street systems, respectively, at 10-30 cm/30-40 cm, $n = 7/7$, $n = 28/28$, $n = 29/29$ and $n = 20/21$ for soil C:N; $n = 7/7$, $n = 10/10$, $n = 10/10$, and $n = 8/9$ for NH₄⁺ content; $n = 7/7$, $n = 10/10$, $n = 10/10$ and $n = 8/10$ for NO₂⁻ content; $n = 7/7$, $n = 9/9$, $n = 10/10$, $n = 9/9$ for NO₃⁻ content.

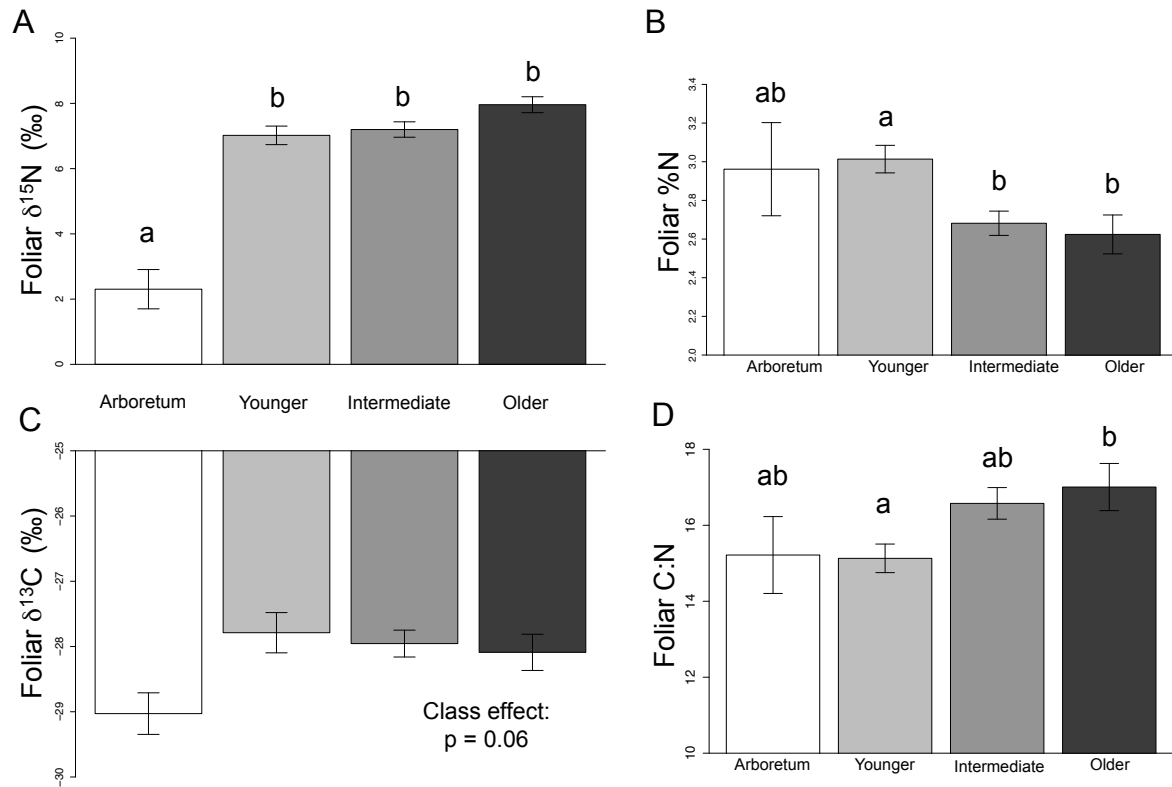


Figure 5. (A) Foliar $\delta^{15}\text{N}$, (B) Foliar %N, (C) Foliar $\delta^{13}\text{C}$ and (D) Foliar C:N, in the different sample classes. Bars show means and error bars correspond to standard error. Different lower case letters indicate a significant difference between classes, following the results of linear models and Tukey post-hoc tests (see Table 4 and text). For arboretum sites, and younger, intermediate and older street systems, respectively, $n = 7$, $n = 28$, $n = 29$ and $n = 20$ for all variables.

The difference between foliar $\delta^{15}\text{N}$ and soil $\delta^{15}\text{N}$, $\Delta^{15}\text{N}_{\text{leaf-soil}}$, was calculated by using the soil $\delta^{15}\text{N}$ at 10-30 cm. It was significantly lower in older and intermediate street systems when compared to younger street systems, and significantly lower than in the arboretum in older street systems (Table 4, Figure 6B). $\Delta^{15}\text{N}_{\text{leaf-soil}}$ in older street systems was about 3 ‰ units lower than in younger street systems (Figure 6B).

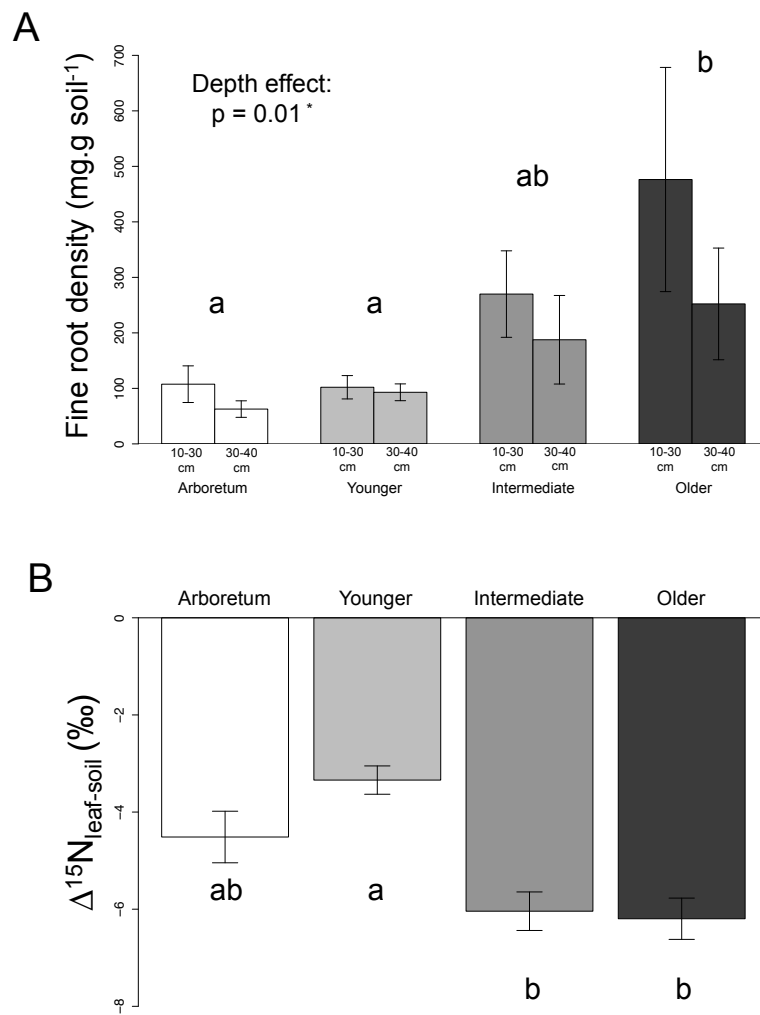


Figure 6. (A) Fine root density and (B) $\Delta^{15}\text{N}_{\text{leaf-soil}}$. Bars show means and error bars correspond to standard error. Different lower case letters indicate a significant difference between classes, following the results of a linear mixed-effect model for fine roots and of a linear model for $\Delta^{15}\text{N}_{\text{leaf-soil}}$, and Tukey post-hoc tests (see Table 4 and text). For arboretum sites, and younger, intermediate and older street systems, respectively, at 10-30 cm/30-40 cm, n = 7/6, n = 10/10, n = 9/9 and n = 10/10 for fine root density ; and n = 7, n = 28, n = 29 and n = 20 for $\Delta^{15}\text{N}_{\text{leaf-soil}}$.

4. Discussion

4.1. Age-related trends in soil organic C: Accumulation of root C?

Our results show that in Parisian street tree plantations, soil organic C content is higher in older plantations than in younger ones, which could suggest a dynamics of C accumulation over time. Compared to arboretum sites, foliar

$\delta^{13}\text{C}$ values in Parisian trees were higher, possibly indicating a tree response to water scarcity, leading to a foliar enrichment in ^{13}C through higher WUE (Farquhar et al., 1989). The important amount of impervious surface around street trees, impeding water infiltration, as well as the Parisian urban heat island effect imposing higher evaporation demand, could indeed expectedly lead to increased water scarcity in street conditions compared to the arboretum. This is confirmed by dendroclimatic works on the same chronosequence, which have shown that street silver linden growth in Paris is particularly sensitive to spring and autumn precipitation (David et al., submitted). Even slight changes in the $\delta^{13}\text{C}$ of organic matter produced through photosynthesis by trees can quickly be reflected in the C allocated belowground (Mariotti, 1991; Ekblad & Högberg, 2001), and thus imprint this isotopic signal on soil organic matter (SOM). Soil $\delta^{13}\text{C}$ consistently showed a significant increase with soil-tree system age, which had the same order of magnitude between younger and older street soils (about 1 ‰ unit) than the difference observed in foliar $\delta^{13}\text{C}$ between street and arboretum trees. Even in a context where most aboveground litter is exported, this gradual ^{13}C signal transfer between trees and soils could thus occur through belowground C inputs (Ekblad & Högberg, 2001).

The trends we observed in fine root densities would tend to support such a scenario. At a depth of 10-30 cm, fine root densities in older street systems were more than four times higher than in younger street systems and the arboretum, suggesting a higher allocation of C belowground as street trees age, further imprinting a ^{13}C -enriched signal to SOM. Furthermore, a higher allocation of C belowground, in the form of fine roots, could also represent a drought response strategy by trees (Craine, 2009), and is theoretically expected as a possible water acquisition strategy for forest tree species (Gaul et al., 2008; Meier & Leuschner, 2008; Craine, 2009), which could be consistent with the trends discussed above. Another result that points towards an accumulation of organic C through

continuous belowground input is the trend in soil C:N, which gradually increases across street system age classes and is higher in older street systems than at the arboretum. This trend is, too, consistent with a scenario where street systems, as they age, experience an increased and sustained input of fresh organic matter through roots.

Another possible factor explaining age-related trends in soil $\delta^{13}\text{C}$ could be the influence of microbial biomass. Indeed, the microbial assimilation of C is known to cause a ^{13}C enrichment of microbial biomass compared to the original substrate (Lerch et al., 2011). The trend in stratification of soil $\delta^{13}\text{C}$ values that seem to occur in street soils with time, with more ^{13}C -enriched organic carbon at 30-40 cm than at 10-30 cm, would be consistent with a scenario where the $\delta^{13}\text{C}$ values at 10-30 cm would more reflect the fresh root inputs while the more enriched $\delta^{13}\text{C}$ values at 30-40 cm, where SOM would be relatively more humified, would bear a stronger microbial imprint.

Taken together, these converging trends and putative underlying mechanisms tend to support the hypothesis of a root-derived C accumulation in street soils.

4.2. Age-related trends in N cycling: Rapid N saturation of street systems?

Similarly to soil C, total soil N seemed to increase with street system age, reaching a similar level as found in the arboretum despite aboveground litter export. Furthermore, one of the most striking trends observed in this study was the exceptionally high average soil $\delta^{15}\text{N}$ value of intermediate and older street systems, with respective averages of 13.2 ‰ and 14.2 ‰. These values fall in the range of the 10 % of highest values measured worldwide, and three sites had a $\delta^{15}\text{N}$ above 17 ‰, close to some of the highest soil $\delta^{15}\text{N}$ measured worldwide (Martinelli et al., 1999; Amundson et al., 2003; Craine et al., 2015). The $\delta^{15}\text{N}$ values measured at 10-30 cm at the arboretum, with an average of 6.9 ‰, were

close to typical values found for surface plain soils in the Île-de-France region (Billy et al., 2010). The stratification of soil $\delta^{15}\text{N}$ values in street systems, with $\delta^{15}\text{N}$ values higher in near-surface horizons than at higher depths, was opposite to the one found at the arboretum where soils showed higher $\delta^{15}\text{N}$ with depth, as is generally observed in soil profiles (Mariotti et al., 1980; Högberg, 1997; Hobbie & Ouimette, 2009). Street foliar $\delta^{15}\text{N}$ values also fall among the highest values measured in temperate forests (Martinelli, 1999; Pardo et al., 2006, 2013).

This firstly suggests that N inputs with enriched $\delta^{15}\text{N}$ values enter street soils from the surface. In Paris, Widory (2007) measured that atmospheric particulate N (ammonium and nitrate) had a $\delta^{15}\text{N}$ as high as 10 ‰ on a yearly average. Direct measures from vehicle exhaust yielded a $\delta^{15}\text{N}$ for particulate N of 3.9 to 5.6 ‰ (Widory, 2007). Depositions from such sources are likely to occur for street soils, as they are very closely exposed to traffic. Animal sources (humans, pets), in the form of urine or feces, are another likely source of N. The $\delta^{15}\text{N}$ of such sources would be highly dependent on animal diet. Kuhnle et al. (2013) report, for humans feeding on a diversified diet (red meat, fish, vegetables), $\delta^{15}\text{N}$ values of about 5.4 ‰ for feces and 6.7 ‰ for urine. Heaton (1986) considers a typical animal waste $\delta^{15}\text{N}$ of 5 ‰, which is consistent with the order of magnitude reported by Kuhnle et al. (2013). In contemporary human and pet hair samples, Bol & Pflieger (2002) report that $\delta^{15}\text{N}$ values were of the same order of magnitude for human and dog samples in England, suggesting a diet based on similar (mostly processed) food sources. Dog waste $\delta^{15}\text{N}$ could thus likely reflect the values found in human waste.

Both likely sources of exogenous N, atmospheric deposition and animal, are suspected to have high $\delta^{15}\text{N}$ values, which is consistent with the possibility of a gradual imprint by these sources of surface soil $\delta^{15}\text{N}$ with time. However, the $\delta^{15}\text{N}$ of potential sources cannot alone explain the massive shift that seems to take place with time towards extreme soil $\delta^{15}\text{N}$ values. Such a shift requires

further processing of deposited N, especially by microbial activity. As a matter of fact, the trends observed on N parameters in street systems match certain symptoms of N saturation, which refers to a process where N-limited forests chronically receive elevated N inputs, ultimately resulting in higher ecosystem N outflows by increased volatilization, nitrification and denitrification (Aber et al., 1998; Pardo et al., 2006; Lovett & Goodale, 2011).

The observed trends in street soil and foliar $\delta^{15}\text{N}$ closely match, for instance, the theoretical expectations of Högberg (1997) for a forest receiving high rates of N deposition. An important deposition of NH_4^+ can lead to increased nitrification, further enriching the substrate NH_4^+ pool in ^{15}N , thus leading to an increase in plant tissue $\delta^{15}\text{N}$. The recycling of plant biomass in the upper horizons would then lead to a relative ^{15}N enrichment of soil surface compared to deeper layers, where, furthermore, stabilized fractions of the relatively ^{15}N -depleted nitrate would have leached, further increasing the abnormal stratification in soil $\delta^{15}\text{N}$ values. Increased nitrification at the soil surface could also make more nitrate available for uptake by plants, leading to an increased difference between soil $\delta^{15}\text{N}$ (more enriched) and foliar $\delta^{15}\text{N}$ (relatively less enriched). But increased nitrate availability could also lead to increased denitrification, which would lead to a ^{15}N enrichment of residual nitrate. This nitrate, if absorbed by the plant and its ^{15}N -enriched N recycled in SOM, could too lead to an increase of surface soil $\delta^{15}\text{N}$. The difference between soil and foliar $\delta^{15}\text{N}$ would then depend on the equilibrium between nitrification and denitrification, and the relative proportions of ammonium and nitrate consumed by the tree.

The high values and inverse stratification of soil $\delta^{15}\text{N}$ in street soils, as well as the high foliar $\delta^{15}\text{N}$ for street trees, tend to support such a scenario. The mineral N content of street soils, especially in nitrite and nitrate, were much superior than the values found at the arboretum and could suggest increased

nitrification and denitrification. Nitrite, especially, is an intermediary in both nitrification and denitrification, and its accumulation in street soils could be seen as a proxy of increased nitrification and denitrification (Burns et al., 1996; Homyak et al., 2015). The decrease of $\Delta^{15}\text{N}_{\text{leaf-soil}}$ between younger street systems and older street systems suggests that trees in these systems have access, in part, to a source of N that is ^{15}N -depleted compared to SOM. This could, as discussed above, be explained by an increased reliance on nitrate produced through nitrification, which would be ^{15}N -depleted when compared to ammonium derived from the recycling of SOM, whose $\delta^{15}\text{N}$ would be close to the $\delta^{15}\text{N}$ of bulk soil, since little fractionation occurs during N mineralization (Högberg, 1997).

Taken together, these trends seem to point towards important N inputs to street systems, which rather quickly lead these systems to a state of N saturation. Younger street systems, for instance, with an average age of about 5 years, already present important symptoms of N saturation: high foliar $\delta^{15}\text{N}$ values, higher $\delta^{15}\text{N}$ values in soil surface, and high concentrations of mineral N forms suggesting an increased activity in N-loss pathways (*e.g.*, nitrification, denitrification).

An intriguing result in foliar N values concerns foliar N content and foliar C:N. In street systems, despite a likely increased soil N content with time, foliar N content was lower in intermediate and older trees compared to younger trees and, accordingly, younger trees had lower foliar C:N ratios. A first hypothesis could be that physiological changes related to tree aging are involved (Gilson et al., 2014). However, even though the differences between the arboretum trees and the street systems were not significant, the mean value of both foliar N content and foliar C:N were both closer to the values found in younger systems and systematically higher and lower, respectively, than the foliar N content and foliar C:N of intermediate and older street systems. This could thus also be

interpreted as a progressive N limitation for trees, portraying a paradoxical situation of simultaneous N saturation and limitation. However, even if soil N content increases in the upper part of the pit, and in the part that is unsealed, this does not mean that, as trees develop and their N needs increase, that the total soil pit N stock would be enough to meet their N needs, and trees might have to develop strategies to acquire N. An increased fine root density could, in this case too, be one of them, as it increases the fine root surface in contact with soil and susceptible to uptake N. It also enables living roots to be closer to decaying dead roots, thus increasing the chance of new roots to uptake N as it is being recycled from old roots (Abbadie, 1992; de Parseval et al., 2015). The fact that fine root density increases with street tree age, not only at the surface, but also in deeper layers (30-40 cm, here), would also fit such a scenario. It could, furthermore, also enable trees to uptake a higher proportion of the nitrate that leaches from the surfaces with rainfall.

Trees could also increase their direct foliar uptake of gaseous NO_x compounds (Ammann et al., 1999; Sparks, 2009), which has been experimentally shown to be a controlled process by plants, that can rely more on foliar nutrition when root nutrition is limited (Vallano & Sparks, 2008). The $\delta^{15}\text{N}$ value of gaseous NO_x compounds is usually lower than that of particulate N that derives from them (Widory, 2007), and Ammann et al. (1999) report values for traffic-derived NO₂ of 5.78 ‰. Compared to the potential $\delta^{15}\text{N}$ of deposited N on soil, as discussed above, this atmospheric source of N would be less enriched in ¹⁵N, and an increased reliance on foliar N uptake by trees would be, too, consistent with the trends observed in $\Delta^{15}\text{N}_{\text{leaf-soil}}$ in street systems.

The apparent tension between of saturation and limitation could thus be released by distinguishing between soil N content (a percentage) and the actual available N stock (a mass) in the pit soil. Comparing the latter to tree N demand could further answer the question of whether nutrient supply in Parisian street

plantation is sufficient to sustain healthy trees on the long run. This would have important practical interest, since it would shift the question from a “substrate” perspective (“Is my soil chemically fertile enough?”) to a perspective where the whole pit design and management (its volume, its irrigation, its greening etc.) as a whole would be questioned regarding its performance to sustain healthy trees.

4.3. Uncertainties linked to potential legacy effects

As urban areas develop over natural or agricultural land, the potential influence of past land-uses on current soil properties often constitutes an important source of uncertainty when trying to interpret contemporary patterns (Raciti et al., 2011; Lewis et al., 2014). Less often mentioned, however, are the uncertainties due to varying characteristics of soils that are imported for landscaping purposes. In the context of this study, such legacy effects of initial soil conditions must be considered.

Soil texture differed among street age classes and probably reflects historical differences in imported soil types. Indeed, the geographical origins of imported soils are historically tightly linked to the development of urbanization in the Parisian region during the 20th century. Prior to 1950, soils were coming from areas closer to Paris, most likely from market gardening cultures that had more sandy soils (Nold, 2011; Paris Green Space and Environmental Division, pers. comm.). As the agglomeration spread across Île-de-France, imported soils gradually came from further areas in the region, and now tend to come from more peripheral plains and plateaux and are probably soils that were formerly under cereal crops (Nold, 2011; Paris Green Space and Environmental Division, pers. comm.). Such difference among imported soil types could also be reflected in initial SOM content. Expert knowledge tends to confirm that soils imported around 1950, especially those used previously for market gardening agriculture, likely had higher organic matter content than soils entering Paris today (Nold, 2011; Paris Green Space and Environmental Division, pers. comm.). Different

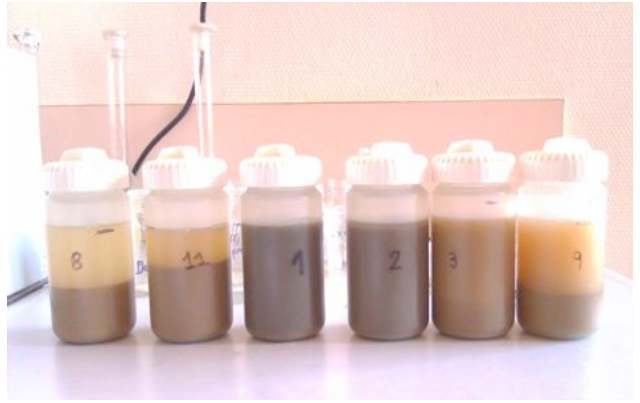
agricultural practices between historical periods could also affect the $\delta^{15}\text{N}$ of imported soils, since the majority of recently imported soils likely have received synthetic fertilizers while older soils likely received organic fertilizers (different types of manure and compost). Synthetic fertilizers generally have low $\delta^{15}\text{N}$ values, while organic fertilizers usually have high $\delta^{15}\text{N}$ values: for the former, Bateman & Kelly (2007) report an average $\delta^{15}\text{N}$ of 0.2 ‰, and an average of 8.2 ‰ for the latter. Soils that have received chronic applications of one or the other type of fertilizers would likely have contrasted $\delta^{15}\text{N}$ when arriving to Paris.

While these uncertainties are important and would require further investigation to discriminate between legacy effects and actual dynamics in C and N cycling, it seems difficult to attribute an overriding effect to potential legacies in light of all the converging patterns described in previous sections. The different stratification patterns, in particular, that were observed in street systems, (*e.g.*, fine root densities, soil $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, and mineral N) rather suggest an imprint from biological activity of trees and soil microbes and point towards the existence of long-term dynamics in C and N cycling after street soil-tree systems are “constructed” in streets.

Concerning the hypothesis of soil exhaustion that drives current management practices of street soils in Paris, by taking SOM content, soil C:N, soil total N and soil mineral N as proxies for fertility, the present work does not confirm the hypothesis that older soils are less fertile than newly imported soils, and even suggests the opposite trend. This means that reflections could be engaged on the potential recycling of old street soils. Further investigations are needed, however, on the question of whether current tree-pit design (volume etc.) is appropriate to ensure a proper nutrient supply to trees. Signs of water stress, confirming other studies on the same systems (David et al., submitted), also suggest that irrigation might be considered to enhance tree health.

5. Conclusion

The combination of a long-term approach and stable isotope analysis enabled the observation of age-related patterns in C and N cycling in Paris street plantations. Even though the studied systems were spread across the city, the variance of several key variables was strongly explained by system age and soil depth alone. As most studies in urban ecosystem ecology have so far adopted a spatial approach to study ecosystem response to urban environments, this study suggests that the age of ecosystems, *e.g.*, the time they have spent in a city, can be a key explanatory variable for several ecosystem features, and help us better understand ecosystem trajectory on a mechanistic basis. Here, we make the hypothesis of a root-derived C accumulation, and the hypothesis of a fast occurring, and amplifying with time, state of N saturation for street soil-tree systems. Further works on this chronosequence should, in particular, focus on SOM dynamics to confirm the root source of accumulating SOM, as well as investigate the causes of SOM accumulation, and look at microbial N processing to confirm whether a higher activity in N-loss pathways is detected. The existence of these temporal trends is of interest for city managers, and opens the questions of whether old street soils should be recycled and tree pit design and management adjusted to enhance the health of trees.



Chapter 2

Legacy or accumulation? A study of long-term soil organic matter dynamics in Haussmannian tree plantations in Paris⁷

1. Introduction

Urban environments have been shown to have profound, yet still poorly understood effects on carbon (C) and nitrogen (N) cycling in ecosystems (De Kimpe & Morel, 2000; Scharenbroch et al., 2005; Kaye et al., 2006; Lorenz & Lal, 2009; Pouyat et al., 2010). Authors have suggested that the importance of urban drivers on ecosystem processes, and their similarities across cities, could surpass natural drivers and lead to similar ecosystem responses on key ecological variables in different cities, an assumption coined the “urban convergence hypothesis” (Pouyat et al., 2003, 2010; see also Groffman et al., 2014). If studies have indeed reported patterns of urban soil C and N accumulation worldwide (*e.g.*, McDonnell et al., 1997; Ochimaru & Fukuda, 2007; Chen et al., 2010; Raciti et al., 2011; Gough & Elliott, 2012; Vasenev et al., 2013; Huyler et al., 2016), important uncertainties remain, however, on the mechanisms leading to such accumulation.

The effects of past land-uses on current soil C and N content (*e.g.*, Raciti et al., 2011; Vasenev et al., 2013; Lewis et al., 2014), or uncertainties on the origin of soils, can add difficulties in interpreting patterns in urban C and N cycling. Identifying the sources of the accumulated organic C is not straightforward either, as urban aboveground litter is often exported and data on

⁷ A research article presenting this chapter’s results will be prepared for an international journal by authors (in alphabetic order after first author) Rankovic, A., Abbadie, L., Barot, S., Barré, P., Camin, F., Cardénas, V., David, A., Lata, J.-C., Lerch, T. Z., Scattolin, L., Sebiló, M., Vaury, V. & Zanella, A.

belowground litter inputs are scarce (Templer et al., 2015; Huyler et al., 2016). Furthermore, urban soils are subjected to varying and sometimes substantial inputs of exogenous organic C depositions such as “black C” particles produced by incomplete combustion of fossil fuels and biomass (Rawlins et al., 2008; Edmonson et al., 2015). For N, similar uncertainties are found concerning fertilization due to landscaping practices, or on the amount, origin and fate of atmospheric N deposition to urban soils (*e.g.*, Raciti et al., 2011; Bettez et al., 2013; Rao et al., 2013). Various types of littering, especially animal dejections, could also contribute to C and N inputs to urban soils.

Furthermore, after C and N inputs, the mechanisms leading to their subsequent accumulation are not clearly elucidated either. Soil organic matter (SOM) is the main source of energy and nutrients for soil organisms, and without mechanisms of relative stabilization, organic C has a spontaneous tendency to be mineralized as CO₂ by soil microorganisms. Research on soil organic C dynamics has identified several factors explaining how soil organic C could escape from microbial degradation. These factors include the chemical properties of SOM, making it more or less recalcitrant to microbial biodegradation, the interaction with soil minerals that can for instance shield SOM from microbial catabolic activity through its occlusion in soil aggregates or its sorption to clay surfaces, and the abiotic environmental constraints to microbial activity (temperature, nutrient availability, pH, soil water potential etc.) (*e.g.*, Six et al., 2002; Fontaine et al., 2003, 2007; von Lützow et al., 2006; Schmidt et al., 2011; Feller & Chenu, 2012; Janzen, 2015; Paradelo et al., 2016). How these factors, and their interactions, influence the fate of SOM in urban soils is still poorly understood.

Here, we report on a study investigating the long-term dynamics of SOM on a 75-year chronosequence of street soil-tree systems in Paris, France. The establishment of street plantations in Paris rests on similar principles since the

19th century and the Haussmannian works that introduced street tree plantations as part of the Parisian landscape (Pellegrini, 2012). When planting a new sapling (of age 7-9), a pit about 1 m 30 deep and 3 m wide is opened in the sidewalk and filled with a newly imported peri-urban agricultural soil (Paris Green Space and Environmental Division, pers. comm.). If soil is already in place for a previous tree, it is entirely excavated, disposed of and replaced by a newly imported agricultural soil from the surrounding region. Tree age thus provides a good proxy of soil-tree system age, *e.g.*, the time that a tree and soil have interacted in street conditions (Kargar et al., 2013, 2015). Aboveground litter is completely exported and no fertilizers are applied by city managers. We also took soil samples under 7 silver linden individuals at the National Arboretum of Chèvreloup, where trees grow in open ground and without aerial litter removal.

Previous works on these systems have shown strong C and N age-related accumulation patterns in soils and it was hypothesized that tree root-derived C and deposited N from the atmosphere and animal waste accumulated in soils (Rankovic et al., Chapter 1). These hypotheses were supported, notably, by an enrichment of soil $\delta^{13}\text{C}$ along the chronosequence, possibly due to chronic water stress of trees in streets, leading to an enrichment of foliar $\delta^{13}\text{C}$ subsequently transmitted to SOM through roots (*via* rhizodeposition and turn-over). For N, the exceptionally high soil and foliar $\delta^{15}\text{N}$ in streets, as well as increased contents in mineral N forms, suggested chronic inputs of ^{15}N -enriched N sources and subsequent microbial cycling, through nitrification and denitrification in particular. Uncertainties remained however, on potential legacy effects due to historical changes in the types of soils being imported in Paris. Indeed, expert knowledge suggests that soils imported around 1950, especially those used previously for market gardening agriculture, likely had higher SOM content than soils entering Paris today, and further evidence is thus needed to confirm the

hypotheses of C and N accumulation, and investigate the mechanisms which could underly such an accumulation.

While investigating C and N cycling, the study of natural abundances of C and N stable isotopes, ^{13}C and ^{15}N , can help infer mechanistic hypotheses on involved processes. Stable isotopes can act as "ecological recorders" (West et al., 2006) and integrate information on the sources of elements, as well as the transformations and circulations they undergo while they cycle in ecosystems (Peterson & Fry, 1987; Mariotti, 1991; Högberg, 1997; Robinson, 2001; Craine et al., 2015). Furthermore, the fractionation of soils into size classes of organo-mineral particles is useful to study SOM dynamics, as SOM is distributed across organo-mineral particles which range in size from coarse sands to clay, and which have different chemical properties: SOM contained in coarser particle-size fractions is, on average, younger and composed of relatively large fragments of plant material, while SOM contained in finer fractions is on average older and composed of more humified material (*e.g.*, Christensen, 1987, 2001; Balesdent et al., 1991, 1998; Nacro et al., 1996; von Lützow et al., 2007; Feller & Chenu, 2012; Yonekura et al., 2013; Feng et al., 2016).

In the present work, we combined a soil physical fractionation procedure, ^{13}C and ^{15}N abundance analysis and soil incubations. We assessed how C and N and their isotopes were distributed among soil fractions, and we hypothesized that if C and N accumulated from chronic inputs, respectively from roots and urban N depositions, with both sources being enriched in the respective stable isotope, then coarser soil fractions should contain an increasing proportion of C, N, ^{13}C and ^{15}N along the chronosequence. We also measured the $\delta^{13}\text{C}$ of tree fine roots, to further assess the plausibility of a ^{13}C signal transfer to soil from roots. Soil incubations were performed to estimate the $\delta^{13}\text{C}$ of respired CO_2 and see whether the hypothesized root ^{13}C imprint on SOM would be further detectable in soil C cycling (*e.g.*, Ekblad & Högberg, 2001). During incubations,

soil respiration rates were also measured and used to calculate C mineralization rates (Dommergues, 1960), to inform on potential changes in microbial activity on the chronosequence and to help infer mechanisms of C and N accumulation. Fine root N content and $\delta^{15}\text{N}$ were measured to gain knowledge on soil N cycling and accumulation (Pardo et al., 2006) and improve our understanding of N nutrition in street trees.

2. Materials and methods

2.1. Site description and chronosequence design

The study was conducted in Paris, France (48°51'12.2"N; 2°20'55.7"E) and at the National Arboretum of Chèvreloup in Rocquencourt (48°49'49.9"N; 2°06'42.4"E), located about 20 km east of central Paris. The Parisian climate is temperate, sub-Atlantic (Crippa et al., 2013), and mean annual temperatures are on average 3°C warmer at night in the center of the agglomeration due to the urban heat island effect (Cantat, 2004). The studied sites comprised silver linden (*Tilia tomentosa* Moench) street plantations in Paris and soils under individual silver lindens at the National Arboretum of Chèvreloup.

The sampling design was based on 3 tree diameter at breast height (DBH) classes, used as a proxy for tree age. The three classes were designed to cover the DBH range of street silver lindens in Paris, which spans from approximately 6 to 76 cm, as retrieved in the databases provided by the Paris Green Space and Environmental Division. This was done so that the chronosequence ranged from about the youngest to the oldest silver lindens street plantations in Paris. Sites were also selected so as to be spread across the city (Figure 1). Only sites with either bare or drain-covered soils were selected to keep similar conditions of air and water circulation in soils, and thus avoid important differences in terms of rooting conditions (e.g., Rahman et al., 2011). In total, for this study, 15 street plantations were sampled according to 3 DBH classes: Class 1 = [7; 15 cm] (n =

5), Class 2 = [33; 40 cm] (n = 5), Class 3 = [57; 71 cm] (n = 5). The sites were located in 9 different streets across Paris (Figure 1).

Tree-ring counts on wood cores subsequently helped determine tree age (David et al., submitted) and provide an estimation of “soil-tree system age”, by subtracting 7 years to every tree age to account for sapling age at their plantation in streets. Overall, the sampling comprised ecosystems of age 1 to age 77. Class 1 sites included ecosystems of an average age of 3.4 ± 2.6 years, Class 2 sites included ecosystems of age 47 ± 13.5 years, and Class 3 sites included ecosystems of age 77 ± 0 years. A Kruskal-Wallis test ($H = 10.8$, $df = 2$, $p < 0.01$) followed by a Wilcoxon-Mann-Whitney test confirmed that age was significantly different between each class (Younger-Intermediate: $p < 0.05$; Younger-Older: $p < 0.05$; Intermediate-Older: $p < 0.05$). Thereafter, these three classes will respectively be referred to as “younger systems”, “intermediate systems” and “older systems” (Table 1).

The National Arboretum of Chèvreloup (<http://chevreloup.mnhn.fr>) is a 205-hectare arboretum adjacent to the Palace of Versailles complex and located in the municipality of Rocquencourt in the Yvelines department, region of Île-de-France (Figure 1). The current arboretum was created in 1927 and is the property of the French National Museum of Natural History. At the arboretum, trees are usually grown on site at the nursery and planted as saplings when about 10 years old. Trees are not submitted to pruning, not fertilized and aboveground litter is not removed. There is little to no competition for crown development space. Compared to street trees, there seem to be no space constraint for root system development. At the arboretum, 5 silver linden stands were sampled. Their plantation date is known and was used to estimate tree age, giving an average age of 54.0 ± 22 years (Table 1). Arboretum soil-tree systems thus had an age comprised between intermediate and older street systems.

2.2. Sample collection and processing

Samples were collected in July 2012 over one week. At each site, soil was sampled at four points around the tree trunk with a 2 cm diameter gouge auger. The sampling points were situated at 25-40 cm from the trunk, depending on accessibility (size of drain holes, obstruction by thick roots etc.). The four extracted soil cores were pooled at 0-10, 10-20, 20-30, 30-40 cm depths respectively. The 0-10 cm depth being more submitted to potential short-term perturbations (littering, animal dejections, surface scraping for cleaning etc.) and the 20-30 cm depths being intermediary, the 10-20 cm and 30-40 cm samples were preferred for this study.

Soils were air-dried and manually sieved at 2 mm. Representative subsamples were homogenized in an agate ball-mill for elemental and isotopic analyses. Fresh soil subsamples were processed at the University of Padova to retrieve fine roots (diameter < 2 mm) which were carefully cleaned in tap water. Roots were then air-dried and manually grinded.

2.3. Soil characteristics

Soil texture after decarbonation was analyzed at a routine soil-testing laboratory (INRA-LAS, France) according to the norm NF X 31-107 (AFNOR, 2003), involving destruction of organic matter with H₂O₂.

Water holding capacity (WHC) was determined by saturating 5 g of soil samples with water during 24 h. Samples were then suspended for 24 h at 15 °C to allow the excess water to be drained away by gravity. Samples were then weighed a first time. After drying for 48 °C at 105 °C, samples were weighed again and WHC was then calculated as $WHC = [(wet\ weight - dry\ weight) / dry\ weight] * 100$. Each soil was analyzed in triplicate.

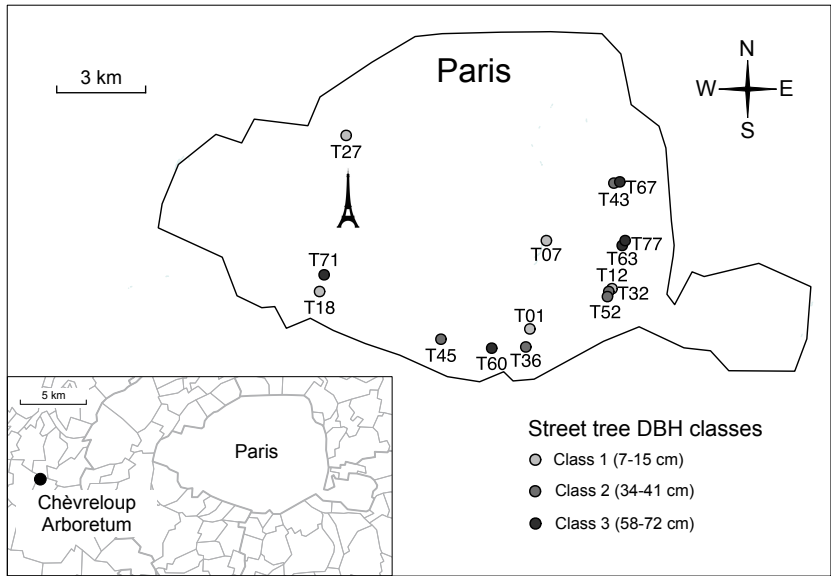


Figure 7. Location of sampled street plantations in Paris and the arboretum.

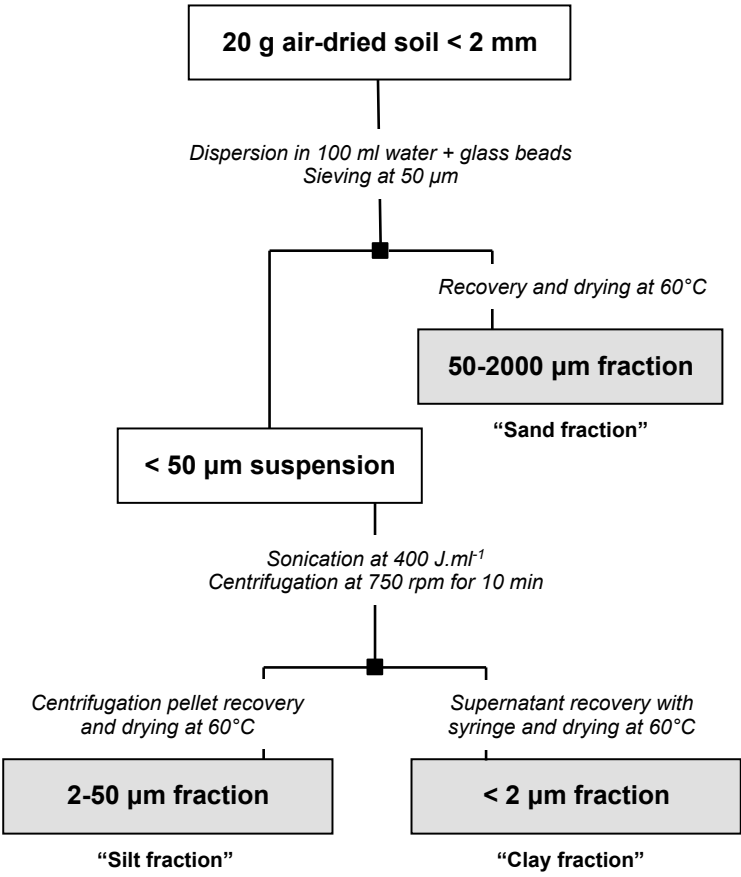


Figure 2. Summary of the physical fractionation procedure used to separate soil organo-mineral fractions. The procedure was applied to 40 samples.

Table 1. Classes of tree DBH and ecosystem age. Tree DBH was measured in July 2011 for street trees and 2012 for arboretum trees. Trunk circumferences were tape-measured at 1.30 m from the ground and divided by π . Tree ages were estimated by counting tree rings on extracted wood cores (David et al., submitted). Ecosystem age was obtained by subtracting 7 years to every tree age to account for sapling age at plantation.

		Sites	Tree DBH (cm)	Ecosystem age (years)
Paris street soil-tree ecosystems (n = 15)	Younger systems (3.4 years \pm 2.6, n = 5)	T01	7	2
		T07	9	2
		T12	10	2
		T18	12	3
		T27	14.8	8
	Intermed. systems (47 years \pm 13.5, n = 5)	T32	33.5	64
		T36	35	32
		T43	37	39
		T45	38.5	42
		T52	41	58
	Older systems (77 years \pm 0, n = 5)	T60	58	NA
		T63	57.5	77
		T67	61	NA
		T71	61.5	77
		T77	71.5	77
Arboretum (54 years \pm 21.9, n = 5)	CLT1	46.8	30	
	CLT3	38.2	30	
	CLT4	73.8	70	
	CLT6	68.4	70	
	CLT7	67.2	70	

2.4. Physical fractionation procedure

Soil subsamples were physically fractionned following a procedure similar as the one described in Balesdent et al. (1991). No chemical dispersant or other reagents were used in order to avoid chemical SOM alteration. The fractionation procedure was conducted in four steps and is summarized on Figure 2. For each of the four sample classes, and for both depths, the procedure was applied to five soils. The total number of fractionated samples was thus 40.

- Step 1: Dispersion in water with glass beads.

20 g of dry soil were placed in a plastic bottle and volume was completed to 100 ml with distilled water. 15 glass beads (5 mm diameter) were added and bottles were horizontally shaken during 16 h. This process allowed physical dispersion of macroaggregates without significant alteration of particulate organic matter (Balesdent et al. 1991).

- Step 2: Sieving at 50 μm to separate the sand fraction.

The suspension obtained in Step 1 was then sieved at 50 μm . Particles of diameter 50-2000 μm were recovered and oven-dried at 60 °C. They correspond to what will be subsequently referred to as the “sand fraction”. The rest of the initial suspension was carefully recovered and placed back in the plastic bottle.

- Step 3: Ultrasound dispersion of the < 50 μm suspension

Ultrasound dispersion was then used to disperse microaggregates and separate elementary particules. An ultrasonic probe was immersed in the < 50 μm suspension and the protocol was set so that samples received between 400-425 $\text{J}\cdot\text{ml}^{-1}$. The bottle containing the suspension was immersed in ice during sonication, to avoid excessive temperature rise that could alter SOM and its distribution.

- Step 4: Separation of silt and clay fractions by centrifugation

The suspension was then horizontally centrifuged at 750 rpm during 10 minutes (parameters set by using Stokes' law). After centrifugation, the pellet was considered to correspond to particles of size 2-50 μm , referred to as the “silt fraction” here. The supernatant was considered to correspond to particles of size < 2 μm , referred to as the “clay fraction” here. The supernatant was carefully recovered with a 100 ml syringe and oven-dried at 60 °C. The pellet was recovered and oven-dried at 60 °C.

In summary, the following three fractions were obtained:

1. The sand fraction, corresponding to particles of size 50-2000 μm ;
2. The silt fraction, corresponding to particles of size 2-50 μm ;
3. The clay fraction, corresponding to particles of size $< 2 \mu\text{m}$.

Once dried, the fractions were weighed to obtain their mass and the percentage of initial soil mass that they represented.

The distribution of C and N across soil fractions was evaluated by calculating the contribution of each fraction to total C and N pools (Nacro et al., 1996; Nacro, 1998), *i.e.* the percentage of total retrieved C and N pools contained in each fraction, calculated by mass balance. For each fraction i and element X, the percentage PX_i was calculated as:

$$PX_i = m_i \cdot \%X_i / (m_i \cdot \%X_i + m_j \cdot \%X_j + m_k \cdot \%X_k)$$

with m_i being the mass of the fraction i retrieved through physical fractionation, $\%X_i$ the element X content (%) of the fraction i and m_j , $\%X_j$, m_k , $\%X_k$ being respectively the retrieved masses and element X contents (%) of the two other fractions j and k .

For the distribution of ^{13}C and ^{15}N pools across fractions, the δ value was considered as an approximation of heavy isotope content in a given sample (Fry, 2006) and the contribution of each fraction to total ^{13}C and ^{15}N pool was calculated as:

$$P_{\text{iso}X_i} = m_i \cdot \%X_i \cdot \delta X_i / (m_i \cdot \%X_i \cdot \delta X_i + m_j \cdot \%X_j \cdot \delta X_j + m_k \cdot \%X_k \cdot \delta X_k)$$

with δX_i , δX_j and δX_k being the δ value for the heavy isotope of element X measured in the fraction i , j , and k respectively.

2.5. Mineralogical analysis of clay fractions by X-ray diffraction

X-ray diffraction analysis on "oriented" deposits was used to identify the types of clay minerals present in the samples. Around 100 mg of clay fraction were suspended in 3 ml of distilled water, and deposited on a glass slide. Once dried, the preparation was analyzed with an X-ray diffractometer (PANalytical Xpert Pro Diffractometer, Rigaku, Tokyo, Japan) equipped with a copper anode. The diffraction measurement enables to obtain the distance between the sheets of a crystalline structure following Bragg's law: $2d\sin\theta = n\lambda$, where d is the distance between two crystallographic planes, θ the scattering angle (half the angle between the incident beam and the detector direction), n the order of the reflection and λ the X-ray wavelength. On the obtained diffractograms, each peak corresponded to a different type of clay mineral. In the soils studied here, the clay minerals were principally composed of illite-smectite, illite and kaolinite. A qualitative analysis of each diffractogram was performed and the height of each peak was compared to the other peaks. A scale from 0 to 3 was then applied to score each mineral: 0 for an absent peak; 1 for a weak peak; 2 for a moderate peak; 3 for a strong peak. This enabled a qualitative analysis of clay mineral composition for each soil.

2.6. C and N contents and isotope ratios

Complete soils and soil fractions were analyzed for organic C content and $\delta^{13}\text{C}$ after carbonate removal with the HCl fumigation method (Harris, 2001). Briefly, 30 mg of homogenized sample were weighted in silver capsules, moisturized with 50 μl of milliQ water, and placed for 6 h in a vacuumed desiccator with a beaker containing 200 ml of 16 M HCl. Then, samples were double-folded in tin capsules for better combustion (Harris, 2001; Brodie et al., 2011) and analyzed at INRA-Nancy by EA-IRMS (NA 1500, Carlo Erba, Milano, Italy, coupled with a Delta S, Finnigan, Palo Alto, USA). For total N content and $\delta^{15}\text{N}$, samples were analyzed by EA-IRMS (vario Pyro cube,

Elementar, Hanau, Germany, coupled with an IsoPrime, Gvi, Stockport, UK) without any pre-treatment to avoid unnecessary bias on N parameters (Komada et al., 2008; Brodie et al., 2011).

Root samples were analyzed for C content, N content, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at the Piattaforma Analisi Isotopiche, Fondazione E. Mach (Italy) by EA-IRMS (Flash EA 1112, ThermoFinnigan coupled with a Delta Plus V, ThermoFinnigan).

For isotopic values, results are expressed using the usual delta notation that allows expressing the content in ^{13}C or ^{15}N as the relative difference between the isotopic ratio of the sample and a standard, calculated as:

$$\delta(\text{‰}) = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}]*1000$$

where *R_{sample}* is the isotope ratio ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ for C and N, respectively) of the sample and *R_{standard}* the isotope ratio of the standard. The international standard for C is the Pee Dee Belemnite standard, with a $^{13}\text{C}/^{12}\text{C}$ ratio of 0.0112372 (Craig, 1957). For N, the international standard is atmospheric dinitrogen for which the $^{15}\text{N}/^{14}\text{N}$ ratio is 0.003676 (Mariotti et al., 1983, 1984).

2.7. Soil incubation, CO₂ and ^{13}C -CO₂ analysis

Soil sub-samples (6 g dry weight) were pre-incubated for a month at 40 % WHC. They were brought to 80 % WHC at the beginning of the incubation. Immediately after adding the water, the sample bottles were flushed with CO₂ free air (19 % O₂, 81 % N₂). The bottles (100 ml) were closed with Teflon[®] rubber stoppers crimped on with aluminium seals and the samples were incubated at 25 °C in the dark for 2 months. Headspace CO₂ concentration was measured after 7, 15, 22, 29, 42 and 62 days of incubation. Measurements were carried out with a micro-gas chromatograph (490 Micro GC, Agilent, Paris, France). For each date, mineralization rates were expressed both in cumulated

mineralized carbon per gram of soil (soil respiration, mg C-CO₂.g soil⁻¹) and as the ratio of mineralized soil organic carbon (% Soil C_{org}). The daily rate of mineralization was calculated by dividing the final date by length of incubation (62 days) (data expressed as mg C-CO₂.g soil⁻¹.day⁻¹ and % C_{soil}.day⁻¹). At each sampling date, 1 ml of headspace gas was manually extracted with a gas syringe and introduced in an evacuated 12 ml Exetainer[®] vial. The isotopic composition (expressed in δ¹³C-CO₂, ‰, calculated as above) of the CO₂-C was measured at INRA Nancy using the gas-bench inlet of an IRMS (Delta S, Finnigan, Palo Alto, USA).

2.8. Statistical analyses

Statistical analyses were performed with the R-software (R Development Core Team, 2013). Four sample classes (three DBH classes and the arboretum) and two depths (10-20 cm and 30-40 cm) and their interaction were used as explanatory factors for bulk soil, root and soil incubation data. For particle-size data, four classes, two depths and three fractions and their interactions were used as explanatory factors. Linear mixed-effects models with a "site" random effect were used for soil variables to account for non-independence of soil depths at each sampling site. R² values for linear mixed-effects models were calculated with the function `r.squared.lme` (version 0.2-4 (2014-07-10)) that follows the method described in Nakagawa & Schielzeth (2013). Values for conditional R², which describes the proportion of variance explained by both the fixed and random factors, are shown. For Δ¹⁵N_{root-soil} and Δ¹⁵N_{leaf-root}, only the four classes were used as explanatory factors in a linear model. Tukey post-hoc tests were used as explanatory factors in a linear model. Tukey post-hoc tests were performed for ANOVA models yielding significant results. For variables that did not satisfy ANOVA assumptions even after log transformation, non-parametric tests were used: a Kruskal-Wallis test was used for each depth to test for differences between classes, and a Wilcoxon-Mann-Whitney test was used for pairwise comparisons of means. Simple linear regressions were performed

between soil, root and incubation data. For all tests, the null hypothesis was rejected for $p < 0.05$ and significance was represented as follows: *** when $p \leq 0.001$; ** for $0.001 < p \leq 0.01$ and * when $0.01 < p \leq 0.05$. Effects with $0.05 \leq p < 0.10$ are referred to as marginally significant. Data on foliar $\delta^{15}\text{N}$, root density and soil ammonium content are used from previous works (Rankovic et al., Chapter 1)

3. Results

3.1. Soil texture, quality of fractionation and clay minerals

As already discussed in Chapter 1, soils from younger street systems and the arboretum had a finer texture than soils from street intermediate and older systems and appeared as silt-loam soils. Soils from street intermediate systems were loamy soils and soils from older street systems were sandy loam soils.

The particle-size distribution obtained by the physical fractionation procedure was compared to the particle-size distribution obtained by textural analysis after H_2O_2 destruction of organic matter and decarbonation (Table 2). A Kruskal-Wallis test showed that there was no significant difference between the two particle-size distributions for the silt and sand fractions, but a significant difference for the clay fraction ($H = 23.6$, $df = 1$, $p < 0.001$). A pairwise comparison through a Wilcoxon-Mann-Whitney test showed that the difference was significant for the soils from younger systems and from the arboretum. Overall, the clay fraction appeared to be underestimated by the physical fractionation procedure (about 60 % of the clay content obtained through textural analysis) and the silt fraction appeared to be overestimated (130 % when compared to textural data). The sand fraction yielded similar results with both methods (ratio of about 100 %). This is similar to the results obtained by Nacro et al. (1996) on a savanna soil when comparing particle-size distributions obtained by textural analysis after H_2O_2 destruction of SOM and a physical fractionation procedure similar to the one employed here. In their study, the clay

fraction retrieved by physical fractionation represented about 77 % of the clay fraction retrieved by textural analysis, and the silt fraction about 130 %, a result similar to ours.

This means that silt and clay fractions were not optimally separated during steps 3 and 4 of the fractionation procedure, and that part of the clay fraction was retrieved with the silt fraction. This difference between the physical fractionation and textural analysis could be explained by the fact that organic matter was not destroyed by H_2O_2 during physical fractionation, and that part of the clay-size particles may have remained binded together, forming silt-size microaggregates that were retrieved with the silt fraction, thus leading to its overestimation. When added together, silt and clay fractions retrieved by physical fractionation represented about 100 % of the sum of silt and clay contents measured by textural data, which tends to confirm this hypothesis. This also indicates that the fractionation procedure adequately separated the finer fractions (silt and clay, $< 50 \mu m$) from the coarse fraction (sand, $> 50 \mu m$) when compared to textural data. A linear regression of physical fractionation results against textural data confirmed that physical fractionation yielded similar results across the 40 fractionned soils for the sand fraction ($R^2 = 0.98$, ***) and the sum of silt and clay ($R^2 = 0.97$, ***), which indicates that the coarse and finer fractions were well separated for all samples. As the present study is especially interested in comparing SOM distribution between coarse fractions and finer fractions, this result is satisfying and validates the physical fractionation procedure that was used for the present study.

The qualitative analysis of X-ray diffractograms (Figure 3) obtained for clay minerals suggested that soils from younger systems had a higher proportion of smectite than soils from intermediate and older street systems. Soils from older street systems, in particular, seemed to have a lower proportion of smectite.

Table 2. Comparison of particle-size distributions between textural analysis and physical fractionation. Different Greek letters mean that a significant difference ($p < 0.05$) was indicated by a Kruskal-Wallis test followed by Wilcoxon-Mann-Whitney tests. For each reported mean, $n = 5$.

System class	Method	% Clay ($< 2 \mu\text{m}$)		% Silt ($2-50 \mu\text{m}$)		% Sand ($50-2000 \mu\text{m}$)	
		10-20 cm	30-40 cm	10-20 cm	30-40 cm	10-20 cm	30-40 cm
Younger systems	Textural analysis	19.3 (5.7) ^a	23.8 (6.9) ^a	57.0 (11.9) ^a	54.6 (11.7) ^a	23.7 (16.9) ^a	21.6 (16.8) ^a
	Physical fractionation	6.8 (6.2) ^b	8.0 (6.1) ^b	69.0 (18.9) ^a	71.3 (13.0) ^a	24.3 (17.1) ^a	20.8 (10.5) ^a
Intermediate systems	Textural analysis	16.6 (5.0) ^a	21.7 (10.2) ^a	25.0 (7.7) ^a	33.3 (21.8) ^a	58.3 (9.5) ^a	45.1 (26.1) ^a
	Physical fractionation	12.0 (3.6) ^a	12.8 (7.2) ^a	31.0 (7.6) ^{b,a}	42.6 (21.8) ^a	57.1 (9.9) ^a	44.6 (27.9) ^a
Older systems	Textural analysis	10.5 (5.0) ^a	15.0 (4.9) ^a	18.5 (19.6) ^a	19.1 (17.3) ^a	71.0 (24.5) ^a	66.0(21.2) ^a
	Physical fractionation	6.1(4.8) ^a	13.4 (9.5) ^a	24.9 (17.0) ^a	25.1 (17.4) ^a	69.0 (21.4) ^a	61.5 (20.5) ^a
Arboretum	Textural analysis	21.4 (1.2) ^a	24.4 (4.7) ^a	42.6 (8.0) ^a	42.0 (9.9) ^a	35.9 (8.8) ^a	33.7 (7.3) ^a
	Physical fractionation	12.4 (2.3) ^b	13.5 (4.4) ^b	49.6 (9.4) ^a	51.9 (11.7) ^a	38.0 (8.0) ^a	34.7 (7.6) ^a

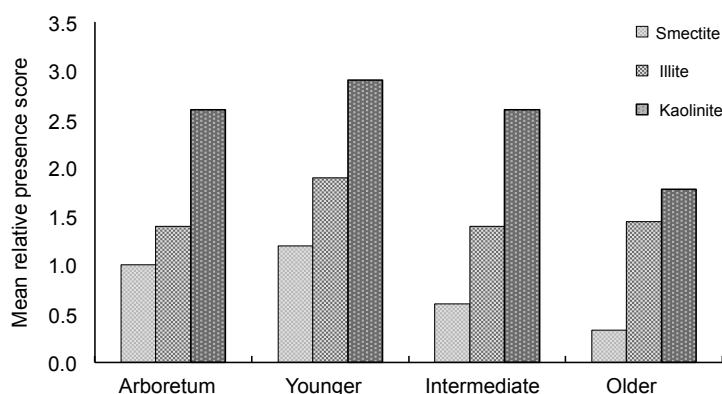


Figure 3. Mean relative presence scores for clay minerals. Scores obtained by a qualitative analysis of X-ray diffractograms. For each bar, $n = 5$.

3.2. Soil C and N contents and isotope ratios

Soil organic C increased with system age in street systems at both depths. Soils from older systems contained significantly more organic C at both depths when compared to arboretum soils and soils from younger and intermediate street systems (Table 3, Figure 4A). At 10-20 cm, average soil organic C content was 1.8 % for arboretum soils, and 1.2 %, 2.1 % and 4.1 % in soils from younger, intermediate and older systems respectively. In street systems, there

was thus about a two-fold increase in soil organic C among age classes. At 30-40 cm, soils contained 1.1 % at the arboretum and 1.5 %, 1.4 % and 2.7 % in younger, intermediate and older systems, respectively. Soils from older systems contained significantly more organic C than soils from the arboretum and younger and intermediate street systems (Table 3, Figure 4A).

Soil $\delta^{13}\text{C}$ at 10-20 cm was significantly higher in soils from intermediate and older street systems when compared to soils from younger street systems and arboretum soils (Table 3, Figure 4B). At the arboretum, soil $\delta^{13}\text{C}$ was -26.6 ‰ at 10-20 cm. In street systems at the same depth, average soil $\delta^{13}\text{C}$ was -26.3 ‰, -25.4 ‰ and -24.9 ‰ for younger, intermediate and older systems, respectively. The same trend was observed at 30-40 cm, with soils from older systems being significantly more enriched than arboretum soils and soils from younger street systems (Table 3, Figure 4B). Average soil $\delta^{13}\text{C}$ at 30-40 cm was -26.2 ‰ at the arboretum and -26.1 ‰, -25.7 ‰ and -25 ‰ in younger, intermediate and older systems, respectively. At 10-20 cm, average soil $\delta^{13}\text{C}$ was 1.4 ‰ units higher in older street systems than in younger street systems, and 1.7 ‰ higher in older street systems when compared to the arboretum. At 30-40 cm, soil $\delta^{13}\text{C}$ was 1.1 ‰ units higher in older street systems when compared to younger systems, and 1.2 ‰ units higher in older street systems when compared to the arboretum (Figure 4B).

Soil total N content at 10-20 cm was significantly higher in older street systems than in younger street systems (Table 3, Figure 4C). At 30-40 cm, soils from older street systems contained significantly more N than soils from younger and intermediate systems and soils from the arboretum (Table 3, Figure 4C).

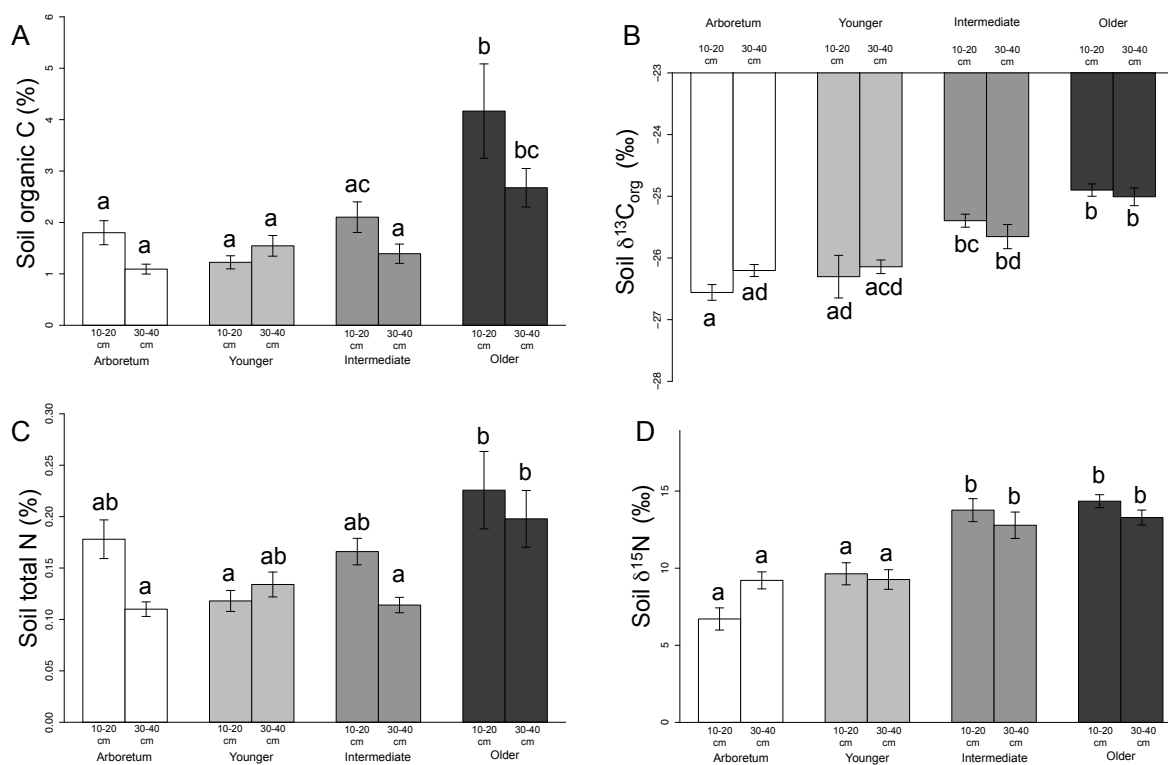


Figure 4. (A) Soil organic C content, (B) Soil $\delta^{13}C$, (C) Soil total N content and (D) Soil $\delta^{15}N$ at 10-20 cm and 30-40 cm in the different sample classes. Bars show means and error bars correspond to standard error. Different letters mean that a significant difference ($p < 0.05$) was indicated by a linear mixed-effect model and Tukey post-hoc tests (see Table 3 and text). For each bar, $n = 5$.

Average soil total N content at 10-20 cm was 0.18 % at the arboretum, and 0.12 %, 0.17 % and 0.23 % for younger, intermediate and older street systems, respectively. At 10-20 cm, soils from older street systems thus contained about twice more total N than soils from young street systems, and about 1.3 times more than soils from the arboretum (Figure 4C). At 30-40 cm, soils from older street systems contained significantly more total N than soils from the arboretum and intermediate street systems. Average total N content at 30-40 cm was 0.1 % for the arboretum, and 0.13 %, 0.11 % and 0.2 % in younger, intermediate and older street systems respectively. Soils from older street systems contained about twice more N than the other soils.

Soil $\delta^{15}N$ was significantly higher at both depths in intermediate and older street systems than in younger street systems and the arboretum, which did not

differ significantly (Table 3, Figure 4D). At 10-20 cm, average soil $\delta^{15}\text{N}$ was 6.7 ‰ at the arboretum, and 9.6 ‰, 13.8 ‰ and 14.3 ‰ in younger, intermediate and older systems, respectively (Figure 4D). At 30-40 cm, average soil $\delta^{15}\text{N}$ was 9.2 ‰ at the arboretum, and 9.3 ‰, 12.8 ‰ and 13.3 ‰ in younger, intermediate and older systems, respectively (Figure 4D). At 10-20 cm, soil $\delta^{15}\text{N}$ in older street systems was thus 7.6 ‰ units higher than at the arboretum, and 4.7 ‰ units higher when compared to younger street systems. At 30-40 cm, soil $\delta^{15}\text{N}$ in older street systems was 4.1 ‰ units higher than at the arboretum, and 4 ‰ units higher when compared to younger street systems.

Soil C:N was significantly higher in older street systems than in other street systems and the arboretum (Table 3). Older soils had a C:N of 17.7 at 10-20 cm and of 13.5 at 30-40 cm. This was significantly higher ($p = 0.01$) than values for intermediate street systems, which had an average soil C:N of 12.5 at 10-20 cm and 12.1 at 30-40 cm. Soil C:N in intermediate and older street systems both differed significantly from arboretum soils ($p < 0.05$ and $p < 0.0001$, respectively).

Table 3. ANOVA table of F values. Reports the effects of class and depth and their interaction on soil organic C, soil total N content, soil C:N, soil $\delta^{13}\text{C}$, soil $\delta^{15}\text{N}$, root N content, root C:N, root $\delta^{15}\text{N}$, root $\delta^{13}\text{C}$, soil respiration, soil organic C mineralization coefficient, $\delta^{13}\text{C}\text{-CO}_2$, as tested with a linear mixed-effect model. For $\Delta^{15}\text{N}_{\text{leaf-root}}$ and $\Delta^{15}\text{N}_{\text{root-soil}}$, a linear model was used and only included the class factor since the values were measured at only one depth. The reported values for significant terms and R^2 are the values obtained after removal of non-significant factors in the model. For all soil, root and incubation variable, $n = 5$ for each class and each depth. For $\Delta^{15}\text{N}_{\text{leaf-root}}$ and $\Delta^{15}\text{N}_{\text{root-soil}}$, $n = 5$ for each class.

Variables	Factors									Model R^2
	Class			Depth			Class x Depth			
	F	p	df	F	p	df	F	p	df	
log (Soil %C)	8.0	**	3	11.8	**	1	4.24	*	3	0.78
log (Soil %N)	4.8	*	3	15.6	**	1	6.3	**	3	0.77
log (Soil C:N)	13.1	***	3	1.5	ns	1	2.5	ns	3	0.51
Soil $\delta^{13}\text{C}$	27.1	***	3	0.1	ns	1	1.4	ns	3	0.72
Soil $\delta^{15}\text{N}$	22.3	***	3	0.008	ns	1	11.6	**	3	0.93
Root %N	7.7	**	3	10.40	**	1	0.7	ns	3	0.80
Root C:N	10.0	***	3	3.3	ns	1	2.44	0.1	3	0.53
Root $\delta^{15}\text{N}$	21.12	***	3	0.06	ns	1	1.3	ns	3	0.93
Root $\delta^{13}\text{C}$	5.01	*	3	0.9	ns	1	1.1	ns	3	0.79
$\Delta^{15}\text{N}_{\text{leaf-root}}$	19.8	***	3	-	-	-	-	-	-	0.77
$\Delta^{15}\text{N}_{\text{root-soil}}$	3.6	0.06	3	-	-	-	-	-	-	-
Soil respiration day ⁻¹	4.2	*	3	7.8	*	1	2.5	0.1	3	0.36
log (% Soil C mineralised day ⁻¹)	8.7	**	3	0.0	ns	1	1.24	ns	3	0.69
$\delta^{13}\text{C}\text{-CO}_2$	6.5	**	3	0.1	ns	1	0.7	ns	3	0.70

Table 4. ANOVA table of F values. Reports the effects of class, depth and fraction and their interaction on the distribution of the pool of soil organic C, the pool of soil total N content, the pool of ^{13}C , and the pool of ^{15}N , as tested with a linear mixed-effect model. The reported values for significant terms and R^2 are the values obtained after removal of non-significant factors in the model. For each class x depth x fraction, $n = 5$.

Factors		Variables			
		C pool	N pool	^{13}C pool	^{15}N pool
Class	F	0	0	0	0
	p	ns	ns	ns	ns
	df	3	3	3	3
Depth	F	0	0	0	0
	p	ns	ns	ns	ns
	df	1	1	2	1
Fraction	F	37.7	8.3	40.0	5.0
	p	***	***	***	**
	df	2	2	3	2
Class x Depth	F	0	0	0	0
	p	ns	ns	ns	ns
	df	3	3	3	3
Class x Fraction	F	11.5	13.2	11.8	13.7
	p	***	***	***	***
	df	6	6	6	6
Depth x Fraction	F	2.7	0.6	2.71	0.43
	p	0.07	ns	0.07	ns
	df	2	2	2	2
Class x Depth x Fraction	F	2.0	0.5	1.9	0.55
	p	0.08	ns	0.09	ns
	df	6	6	6	6
Model R^2		0.54	0.46	0.55	0.46

3.3. Distribution of SOM across particle-size fractions

For soil organic C, the distribution was significantly different across fractions and the distribution among fractions significantly varied between soil-tree system classes (significant interaction between fraction and system class, Table 4, Figure 5A). In younger street systems at 10-20 cm, the mean percentage of soil C pool contained in the sand fraction was 27.4 %, significantly lower than in the silt fraction (61.1 %) and higher than the clay fraction (11.5 %). The finer fractions together accounted for about 72.6 %. Though the difference between fractions were not significant, in soils from intermediate street systems the distribution of C across fractions had a mean of 46.7 % for the sand fraction, 31.6 % for the silt fraction and 21.8 % for the clay fraction. The finer fraction accounted for about 53.4 % of the C pool in intermediate street systems. In older street systems, the sand fraction contained a significantly higher proportion (57.9 %) of the soil C pool than both the silt (32.3 %) and clay (9.8 %) fractions, and contained a higher proportion of the soil C pool than the finer fractions combined (42.1 %) (Figure 5A). The proportion of soil C contained in the sand fraction in intermediate street systems did not differ significantly from the proportion contained in the sand fraction in younger and older street systems, but this proportion was higher in older systems when compared to younger systems (Tukey post-hoc test, $p < 0.05$). The mean proportion of soil C contained in the sand fraction did not differ between street younger and intermediate systems and the arboretum (32.1 %), but was significantly higher in older street systems when compared to the arboretum (Tukey post-hoc test, $p > 0.0001$).

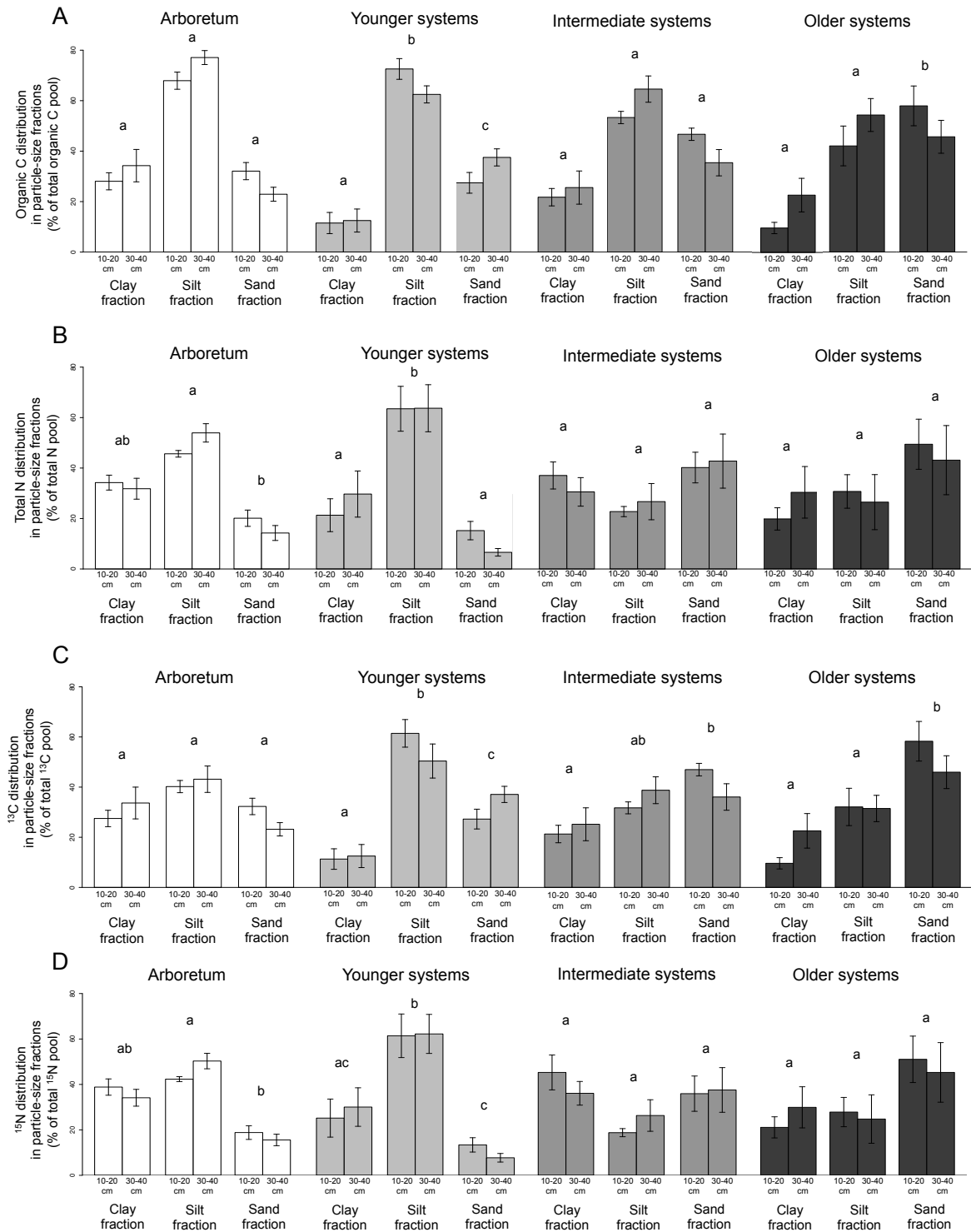


Figure 5. Distribution across particle-size fractions of (A) organic C, (B) total N, (C) ¹³C and (D) ¹⁵N at 10-20 cm and 30-40 cm in the different sample classes. Bars show means and error bars correspond to standard error. Different letters mean that a significant difference ($p < 0.05$) was indicated by a linear mixed-effect model and Tukey post-hoc tests (see Table 4 and text). Letters only refer to differences among fractions inside of a given class, and differences among classes are discussed in text. For each bar, $n = 5$.

The proportion of soil C contained in the sand fraction at 10-20 cm was thus of 32.1 % at the arboretum, 27.4 % in younger street systems, 46.7 % in intermediate street systems and 57.9% in street older systems, with soils from older systems containing a significantly higher proportion of their C in their sand fraction than the other studied soils. The proportion of C contained in the sand fraction in older street systems was 1.8 higher than in the arboretum, 2.1 times higher than in younger street systems and 1.2 times higher than in intermediate systems (Figure 5A).

For soil total N, the distribution was significantly different across fractions and the distribution among fractions significantly varied between soil-tree system classes (significant interaction between fraction and system class, Table 4 and Figure 5B). In younger street systems at 10-20 cm, the mean percentage of the soil N pool contained in the sand fraction was 15.2 %, significantly lower than for the silt fraction (63.5 %) and not significantly different than for the clay fraction (21.3 %). On average, the finer fractions together accounted for about 84.8 % of the soil N pool in younger street systems. Though the difference between fractions were not significant, in soils from intermediate street systems the distribution of N across fractions had a mean of 40.2 % for the sand fraction, 22.7 % for the silt fraction and 37.1 % for the clay fraction. The clay and silt fraction together accounted for about 59.8 % of the soil N pool in intermediate systems. In older street systems, the sand fraction on average contained 49.4 % of the soil N pool, with a marginally significant difference (Tukey post-hoc test, $p < 0.1$) with the soil N pool proportion contained in clay (19.8 %) and had a higher but not significantly different soil N pool proportion than the silt fraction (30.7 %). The sand fraction in intermediate street systems contained a significantly higher proportion of the soil N pool than the sand fraction of younger street systems, as did the sand fraction of older street systems (Tukey post-hoc test, $p = 0.001$ and $p < 0.0001$, respectively). The

mean proportion of soil N contained in the sand fraction did not differ between street younger systems and the arboretum (20.1 %), but was significantly higher in intermediate and older street systems when compared to the arboretum (Tukey post-hoc test, $p < 0.05$ and $p < 0.01$, respectively). The proportion of soil N contained in the sand fraction at 10-20 cm was thus of 20.1 % at the arboretum, 15.2 % in younger street systems, 40.2 % in intermediate street systems and 49.4 % in street older systems, with soils from intermediate and older street systems containing a significantly higher proportion of their N in their sand fraction than soils from younger street systems and the arboretum. The proportion of N contained in the sand fraction in older street systems was 2.5 times higher than in the arboretum, 3.3 higher than in younger street systems and 1.3 times higher than in intermediate systems.

For ^{13}C (Table 4, Figure 5C), the distribution was significantly different across fractions and the distribution among fractions significantly varied between soil-tree system classes (significant interaction between fraction and system class). In younger street systems at 10-20 cm, the mean percentage of the soil ^{13}C pool contained in the sand fraction was 27.3 %, significantly lower than for the silt fraction (61.4 %) and significantly higher than for the clay fraction (11.3 %). In intermediate street systems, the sand fraction on average contained 47.0 % of the soil ^{13}C pool, significantly higher than the clay fraction (21.3 %) and not significantly different than for the silt fraction (31.8 %). In older street systems, the sand fraction contained 58.3 % of the soil ^{13}C pool, significantly higher than both the silt (32.1 %) and clay (9.6 %) fractions. In older systems at 10-20 cm, the sand fraction contained a higher proportion of the soil ^{13}C pool than both finer fractions combined (41.7 %). The mean proportion of soil ^{13}C contained in the sand fraction was significantly higher in older street systems than in younger street systems (Tukey post-hoc test, $p < 0.001$). The mean proportion of soil ^{13}C contained in the sand fraction did not differ between street

younger and intermediate systems and the arboretum (32.3 %), but was significantly higher in intermediate and older street systems when compared to the arboretum (Tukey post-hoc test, $p < 0.05$, $p < 0.05$ and $p < 0.001$, respectively). The proportion of soil ^{13}C contained in the sand fraction at 10-20 cm was thus of 32.3 % at the arboretum, 27.3 % in younger street systems, 47.0 % in intermediate street systems and 58.3 % in street older systems, with soils from older street systems containing a significantly higher proportion of their ^{13}C in their sand fraction than soils from younger and intermediate street systems and the arboretum. The proportion of ^{13}C contained in the sand fraction in older street systems was 1.8 times higher than in the arboretum, 2.1 times higher than in younger street systems and 1.2 times higher than in intermediate systems.

For ^{15}N (Table 4, Figure 5D), the distribution was significantly different across fractions and the distribution among fractions significantly varied between soil-tree system classes (significant interaction between fraction and system class). In younger street systems at 10-20 cm, the mean percentage of the soil ^{15}N pool contained in the sand fraction was 13.4 %, significantly lower than for the silt fraction (61.4 %) and not significantly different than for the clay fraction (25.2 %). On average, the finer fractions together accounted for about 86.6 % of the soil ^{15}N pool in younger street systems. Though the difference between fractions were not significant, in soils from intermediate street systems the distribution of ^{15}N across fractions had a mean of 35.9 % for the sand fraction, 18.8 % for the silt fraction and 45.3 % for the clay fraction. The clay and silt fraction together accounted for about 64.1 % of the soil ^{15}N pool in intermediate systems. In older street systems, the sand fraction on average contained 51.0 % of the soil ^{15}N pool, with a marginally significant difference (Tukey post-hoc test, $p = 0.05$) with the proportion of soil ^{15}N contained in clay

(21.1 %) marginally significant difference (Tukey post-hoc test, $p = 0.07$) with the silt fraction (27.8 %).

The mean proportion of soil ^{15}N contained in the sand fraction was not significantly different between street intermediate and older street systems, but the sand fraction in intermediate street systems contained a significantly higher proportion of the soil ^{15}N pool than the sand fraction of younger street systems (Tukey post-hoc test, $p = 0.01$), as did the sand fraction of older street systems ($p < 0.0001$). The mean proportion of soil ^{15}N contained in the sand fraction did not differ between street younger and intermediate systems and the arboretum (18.8 %), but was significantly higher in older street systems when compared to the arboretum (Tukey post-hoc test, $p < 0.001$). The proportion of soil ^{15}N contained in the sand fraction at 10-20 cm was thus of 18.8 % at the arboretum, 13.4 % in younger street systems, 35.9 % in intermediate street systems and 51.0 % in street older systems, with soils from older street systems containing a significantly higher proportion of their ^{15}N in their sand fraction than soils from younger street systems and the arboretum. The proportion of ^{15}N contained in the sand fraction in older street systems was 2.7 times higher than in the arboretum, 3.8 higher than in younger street systems and 1.4 times higher than in intermediate systems.

Overall, there was no significant effect of depth was found in the distribution of pools among fractions. However, a marginally significant effect was found for the interaction of depth and fraction factors ($p = 0.07$) for both C and ^{13}C . The sand fraction of intermediate and older street systems contained a higher mean proportion of C and ^{13}C at 10-20 cm than at 30-40 cm (Figure 5A and 5C). The sand fraction of older street systems on average contained a higher proportion of N and ^{15}N at 10-20 cm when compared to 30-40 cm, but the difference was not significant (Figure 5B and 5D).

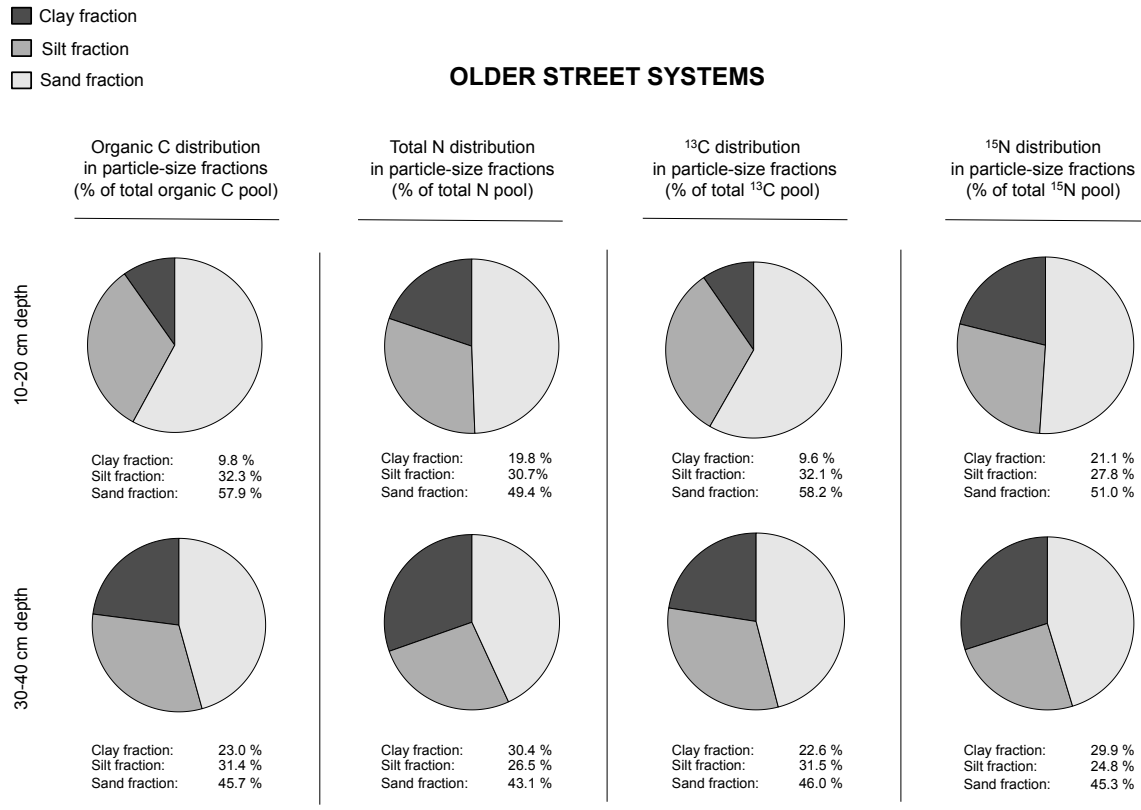


Figure 6. Summarized view of the distributions of organic C, total N, ¹³C and ¹⁵N in particle-size fractions in older street systems.

Overall, for older street systems, at 10-20 cm the sand fraction contained on average of 57.9 % of soil organic C, 49.4 % of soil total N, 58.2 % of soil ¹³C and 51.0 % of soil ¹⁵N. At 30-40 cm, these values were of 45.7 %, 43.1 %, 46.0 % and 45.3 %. Although no significant depth effect was found (only marginally significant interaction between fraction and depth factors, Table 4), the mean proportion of C, N, ¹³C and ¹⁵N was consistently higher for the sand fraction at 10-20 cm than at 30-40 cm. Figure 6 provides a summarized view of these distributions for older street systems.

3.3. Root C and N contents and isotope ratios

Fine root N content was significantly different between arboretum and street systems (Table 3, Figure 7A). At 10-20 cm, mean root % N was 0.9 % at the arboretum and 1.66 %, 1.66 % and 1.7 % for younger, intermediate and

older street systems, respectively. At 30-40 cm, mean root % N was 0.8 % at the arboretum and 1.5 %, 1.3 % and 1.6 % for younger, intermediate and older street systems, respectively.

Fine root C:N was significantly higher at the arboretum at both depths when compared to street systems (Table 3, Figure 7B). At 10-20 cm, root C:N was 44.7 at the arboretum and 26.0, 21.7 and 23.7 for younger, intermediate and older street systems. At 30-40 cm, average root C:N was 40.3 for the arboretum and 28.5, 33.5 and 25.3 in younger, intermediate and older street systems.

Fine root $\delta^{13}\text{C}$ was significantly different between older street systems and the arboretum and younger street systems (Table 3, Figure 7C). Roots from intermediate street systems did not differ significantly from younger and older street systems. At 10-20 cm, mean fine root $\delta^{13}\text{C}$ at the arboretum was -27.7 ‰ and was -27.1 ‰, -26.4 ‰ and -25.7 ‰ for younger, intermediate and older street systems, respectively. At 30-40 cm, mean fine root $\delta^{13}\text{C}$ at the arboretum was -27.4 ‰ and -27.1 ‰, -26.9 ‰ and -26 ‰ for younger, intermediate and older street systems. At 10-20 cm, mean fine root $\delta^{13}\text{C}$ in older street systems was 2 ‰ units higher when compared to the arboretum, and 1.4 ‰ units higher when compared to younger street systems. At 30-40 cm, mean fine root $\delta^{13}\text{C}$ in older street systems was 1.4 ‰ units higher when compared to the arboretum, and 1.1 ‰ units higher when compared to younger street systems.

Fine root $\delta^{15}\text{N}$ was significantly different between intermediate and older street systems and the arboretum and younger street systems, respectively (Table 3, Figure 7D). At 10-20 cm, mean fine root $\delta^{15}\text{N}$ was 3.1 ‰ at the arboretum and 6.8 ‰, 14.7 ‰ and 13.9 ‰ in younger, intermediate and older street systems, respectively. At 30-40 cm, mean fine root $\delta^{15}\text{N}$ was 4.9 ‰ at the arboretum and 6.1 ‰, 14.5 ‰ and 13.3 ‰ in younger, intermediate and older street systems, respectively. The difference between intermediate and older

street systems and the arboretum was thus of about 10 ‰ units at both depths, and of about 7 ‰ units at both depth when compared to younger street systems.

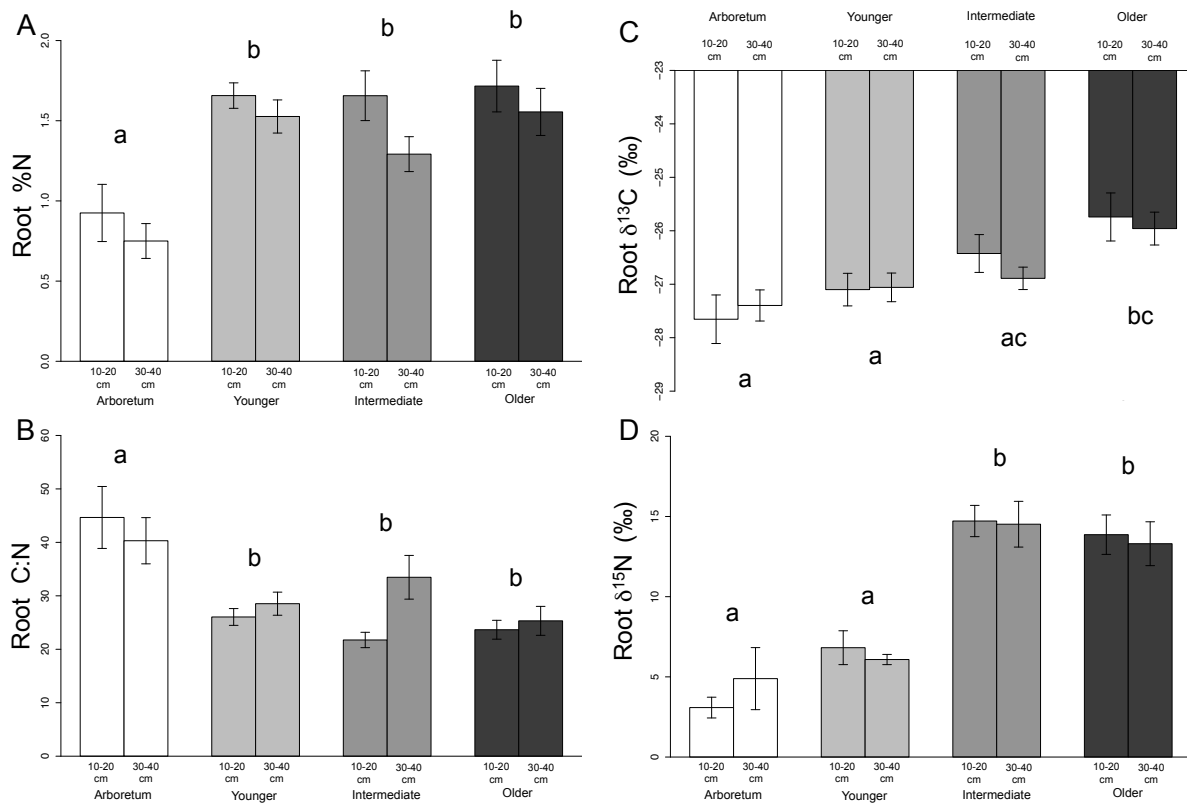


Figure 7. Fine root (A) N content, (B) C:N, (C) $\delta^{13}\text{C}$ and (D) $\delta^{15}\text{N}$ at 10-20 cm and 30-40 cm in the different sample classes. Bars show means and error bars correspond to standard error. Different letters mean that a significant difference ($p < 0.05$) was indicated by a linear mixed-effect model and Tukey post-hoc tests (see Table 3 and text). For each bar, $n = 5$.

3.4. C mineralization and $\delta^{13}\text{C}\text{-CO}_2$

The mean daily respiration rate measured at the end of incubation was significantly different between the arboretum and younger street systems (Table 3, Figure 9A), but not significantly different between street system classes, and intermediate and older street systems did not differ significantly from the arboretum. Mean respiration rates at 10-20 cm were $8.2 \mu\text{g C-CO}_2\cdot\text{g soil}^{-1}\cdot\text{day}^{-1}$ at the arboretum, and 3.1, 4.9 and $6.0 \mu\text{g C-CO}_2\cdot\text{g soil}^{-1}\cdot\text{day}^{-1}$ for the younger, intermediate and older systems, respectively. At 30-40 cm, mean respiration rates were $4.4 \mu\text{g C-CO}_2\cdot\text{g soil}^{-1}\cdot\text{day}^{-1}$ at the arboretum and 3.4, 4.0 and $4.4 \mu\text{g C-CO}_2\cdot\text{g soil}^{-1}\cdot\text{day}^{-1}$ in younger, intermediate and older street systems,

respectively. Older street systems thus had a two times higher soil respiration rate compared to younger street systems at 10-20 cm, and 1.3 times higher at 30-40 cm. Stratification increased with street system age, with respiration rates being 1.4 times higher at 10-20 cm than at 30-40 cm in older street systems. At the arboretum, respiration rates at 10-20 cm were 1.9 times higher than at 30-40 cm (Figure 9A).

The coefficient of soil organic C mineralization was obtained by calculating the percentage of soil organic C represented by soil respiration (Dommergues, 1960), *e.g.*, by dividing soil respiration rates by the mass of organic C initially contained in the sample and multiplying it by 100. It thus corresponds to the mineralization rate of C per mass unit of soil organic C. Soil organic C mineralization rate (cumulated, Figure 8; daily rate, Figure 9B) was significantly different between the arboretum and all street system classes, and was significantly lower in older street systems when compared to younger and intermediate street systems (Table 3). The mean daily soil organic C mineralization rate at 10-20 cm was of 0.045 % at the arboretum and 0.026 %, 0.024 % and 0.017 % in younger, intermediate and older street systems, respectively.

At 30-40 cm, the mean daily soil organic C mineralization rate was 0.039 % at the arboretum and 0.024 %, 0.032 % and 0.016 % in younger, intermediate and older street systems, respectively. Overall, the observed trend in street systems was a decreased soil organic C mineralization rate with increasing average system age, the rate being 1.5 times higher in younger systems when compared to older systems and 2.6 times higher at the arboretum when compared to older street systems at 10-20 cm. The trend was similar for both depths, apart from a higher rate for intermediate systems at 30-40 cm.

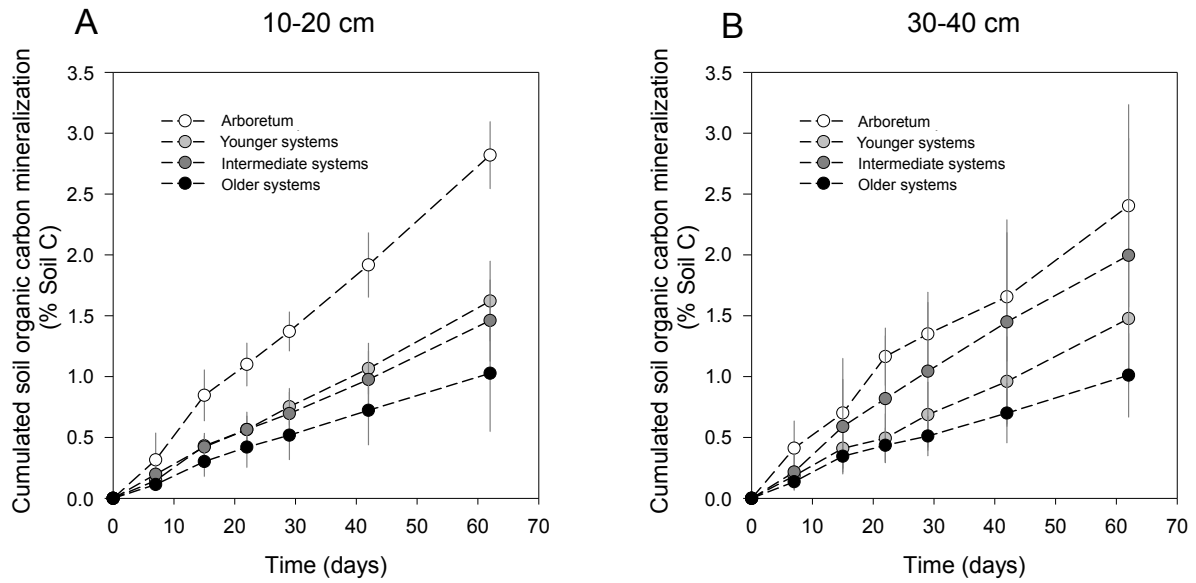


Figure 8. Cumulated soil organic C mineralization over the incubation period at (A) 10-20 cm and (B) 30-40 cm.

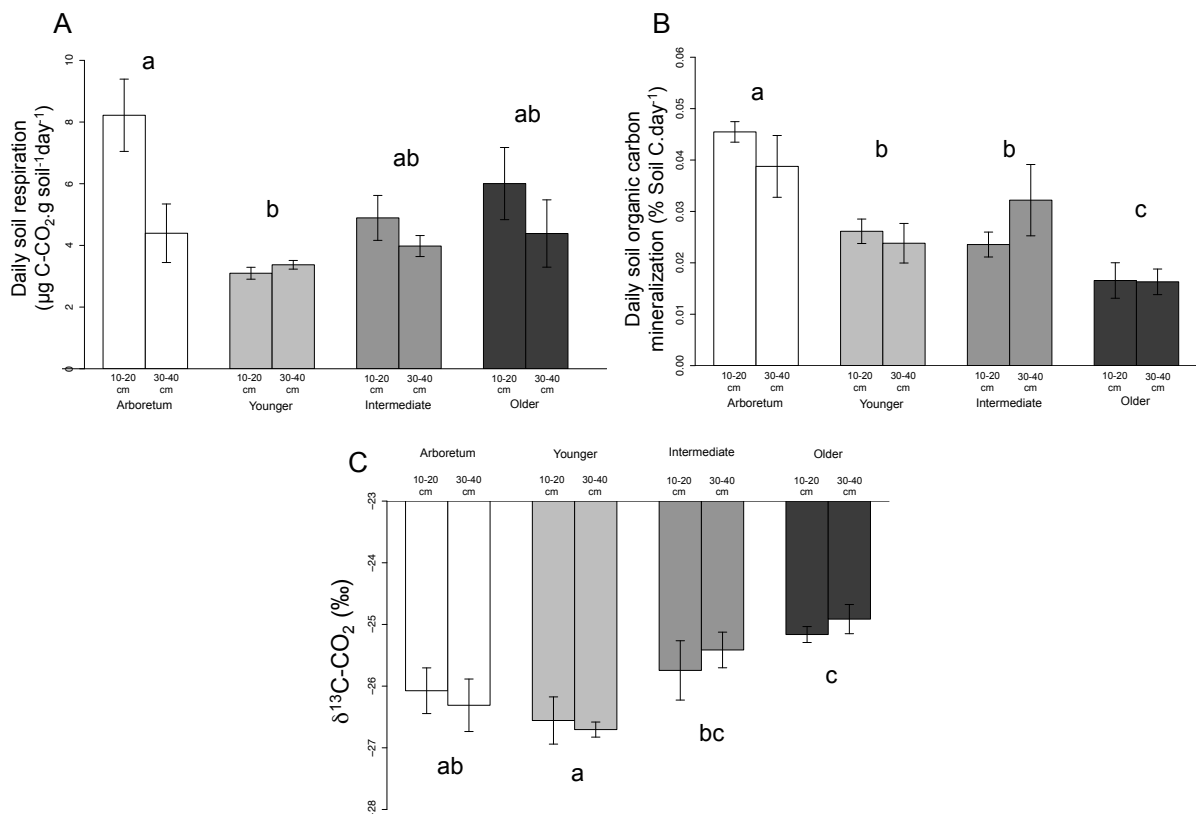


Figure 9. Mean (A) Daily soil respiration, (B) Daily soil organic carbon mineralization and (C) $\delta^{13}\text{C-CO}_2$ at 62 days, at 10-20 cm and 30-40 cm in the different sample classes. Bars show means and error bars correspond to standard error. Different letters mean that a significant difference ($p < 0.05$) was indicated by a linear mixed-effect model and Tukey post-hoc tests (see Table 3 and text). For each bar, $n = 5$.

The $\delta^{13}\text{C-CO}_2$ measured at the end of incubation was significantly higher for intermediate and older systems when compared to younger systems, and was significantly higher for older street systems than for the arboretum (Table 3, Figure 9C). $\delta^{13}\text{C-CO}_2$. Mean $\delta^{13}\text{C-CO}_2$ at 10-20 cm was -26.1 ‰ at the arboretum, -26.6 ‰ for younger street systems, -25.7 ‰ for intermediate systems and -25.2 ‰ for older street systems (Figure 9C). At 30-40 cm, mean $\delta^{13}\text{C-CO}_2$ was -26.3 ‰ at the arboretum and -26.7 ‰, -25.4 ‰ and -24.9 ‰ in younger, intermediate and older street systems, respectively. At 10-20 cm, mean $\delta^{13}\text{C-CO}_2$ was thus 0.9 ‰ unit higher in older systems when compared to the arboretum and 1.4 ‰ units higher when compared to younger street systems. Similar differences were found for 30-40 cm.

3.5. Soil and plant coupling

Simple linear regressions indicated that bulk soil $\delta^{13}\text{C}$ was significantly predicted by fine root $\delta^{13}\text{C}$ ($R^2 = 0.32$, ***; Figure 10A), that $\delta^{13}\text{C-CO}_2$ was significantly predicted by bulk soil $\delta^{13}\text{C}$ ($R^2 = 0.51$, ***; Figure 10B) and that $\delta^{13}\text{C-CO}_2$ was significantly predicted by fine root $\delta^{13}\text{C}$ ($R^2 = 0.23$, ***; Figure 10C). The difference between leaf and root $\delta^{15}\text{N}$ at 10-20 cm, $\Delta^{15}\text{N}_{\text{leaf-root}}$, was significantly different between the arboretum and younger street systems on the one side and intermediate and older street systems on the other side (Table 3, Figure 11).

At the arboretum, mean $\Delta^{15}\text{N}_{\text{leaf-root}}$ was 0.3 ‰, and it was 0.5 ‰, -7.3 ‰ and -5.8 ‰ in younger, intermediate and older street systems, respectively. The difference between root and soil $\delta^{15}\text{N}$ at 10-20 cm, $\Delta^{15}\text{N}_{\text{root-soil}}$, was marginally different ($p = 0.06$, Table 3) between classes. Mean value for $\Delta^{15}\text{N}_{\text{root-soil}}$ was -4 ‰ at the arboretum, -2.8 ‰, +1 ‰ and -0.5 ‰ in younger, intermediate and older street systems, respectively.

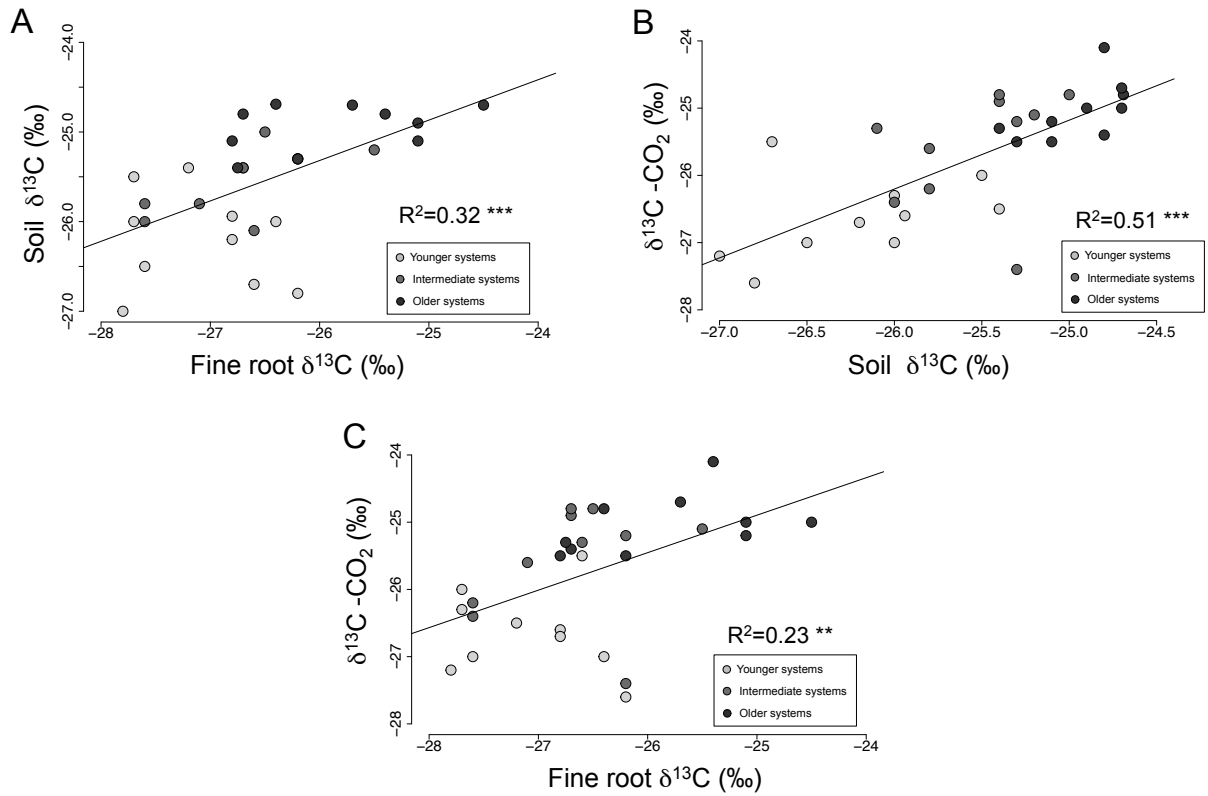


Figure 10. Plot of the linear regression of (A) soil $\delta^{13}\text{C}$ by fine root $\delta^{13}\text{C}$, (B) $\delta^{13}\text{C}-\text{CO}_2$ at 62 days of incubation by soil $\delta^{13}\text{C}$ and (C) $\delta^{13}\text{C}-\text{CO}_2$ at 62 days of incubation by fine root $\delta^{13}\text{C}$. For each age class, both depths are represented, $n = 5$ for each depth.

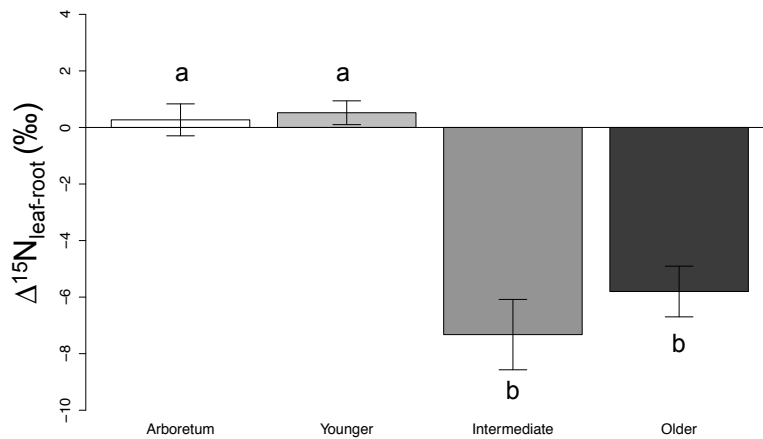


Figure 11. $\Delta^{15}\text{N}_{\text{leaf-root}}$ for the different sample classes for the 10-20 cm depth. Bars show means and error bars correspond to standard error. Different letters mean that a significant difference ($p < 0.05$) was indicated by a linear mixed-effect model and Tukey post-hoc tests (see Table 3 and text). For each bar, $n = 5$.

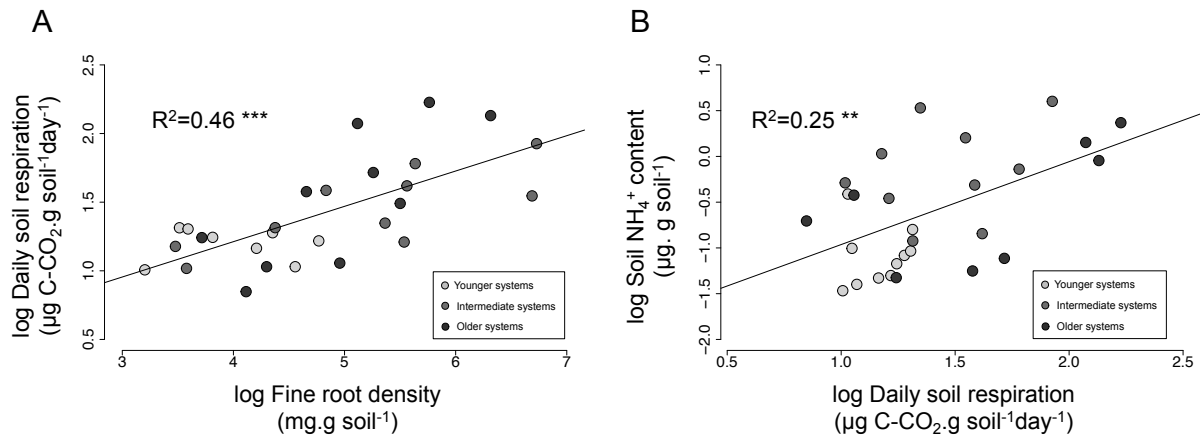


Figure 12. Plot of the linear regression of (A) the log of daily soil respiration by the log of fine root density in street systems, (B) the log of soil NH₄⁺ content and the log of daily soil respiration in street systems. For each class, n = 5 per depth.

A simple linear regression of soil respiration by fine root density indicated that root density significantly predicted soil respiration in street systems ($R^2 = 0.46$, ***; Figure 12A). A simple linear regression showed that soil NH₄⁺ content was significantly predicted by soil respiration in street systems ($R^2 = 0.25$, **; Figure 12B).

4. Discussion

4.1. Evidence of recent C and N accumulation in street soils

Results on bulk soils showed higher C and N contents and higher ¹³C and ¹⁵N enrichment in older street soils. In previous works (Rankovic et al., Chapter 1), we discussed the possibility of an accumulation of root C in street soils, with a gradual ¹³C-enrichment with time due to increased water stress in street trees. For N, we hypothesized an accumulation from exogenous sources, namely atmospheric N deposition and animal waste, both likely ¹⁵N-enriched, and a subsequent microbial cycling of N leading to exceptionally high values of soil δ¹⁵N. An important uncertainty in this accumulation scenario stemmed from potential historical differences between imported soils used for older and younger street soil-tree systems, as suggested by expert knowledge and our own data (e.g., differences in soil texture). Further evidence was needed to confirm

the hypothesized C and N accumulation processes and that the observed age-related patterns were not solely due to legacy effects.

In the present study, the analysis of particle-size fractions first shows that in older street soils, more than half of C and almost half of N are contained in the coarser SOM fractions. Even though the estimates of C mean residence time differ among fractionation methods and C turnover assessment methods (*e.g.*, laboratory incubation, C3/C4 chronosequences, ^{14}C analyses), the mean residence time of soil C associated with the sand fraction is reported to be of a few years to a couple of decades at most, while it is in the range of centuries to millennia for the C associated to the silt and clay fractions (Wattel-Koekkoek et al., 2003; Fontaine et al., 2007; von Lützow et al., 2007; Feng et al., 2016). For our older street systems, of which the oldest are 77 years old, this suggests that an important proportion of their C and N stocks are composed of C and N that accumulated after trees and soils were assembled in streets.

This assumption is supported by our results. C and N distribution differed among street age classes, with the coarse fraction containing an increasing proportion of C and N as systems age, which too could mean that recently added C and N represent an increasing proportion of soil C and N stocks with time in street soils. The observed trends in stratification, where surface horizons (10-20 cm) tended to contain a higher proportion of C and N, in their coarse fraction when compared to deeper layers (30-40 cm), also suggest chronic inputs of ^{13}C -enriched C and ^{15}N -enriched N from the soil surface. Such trends were also observed for both ^{13}C and ^{15}N , suggesting that recent C and N inputs are characterized by enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

For the potential sources of N, we have previously discussed that atmospheric N depositions and animal waste could contribute to exogenous ^{15}N -enriched inputs in street systems, that could be assimilated by roots and soil microbial biomass (Rankovic et al., Chapter 1). Concerning the sources of C, root $\delta^{13}\text{C}$ increased

with tree age and was significantly higher in older street soils than in younger and arboretum soils. This could be due to increasing water stress as street trees grow and thus higher water-use efficiency in older trees, leading to lower stomatal conductance and less discrimination towards ^{13}C during C3 photosynthesis, resulting in more ^{13}C -enriched organic matter produced by trees (e.g., Farquhar et al., 1989; Kagotani et al., 2013; Falxa-Raymond et al., 2014). The urban CO_2 , because of ^{13}C -depleted fossil fuels, tends to be depleted in ^{13}C compared to background CO_2 (Lichtfouse, 2003; Widory & Javoy, 2003), and rather than confounding this effect, it is probably weakening the observed pattern.

As fine roots can have a lifespan of several years (Gill & Jackson, 2000; Gaudinski et al., 2001; McCormack et al. 2012), root $\delta^{13}\text{C}$ might thus integrate over several growing seasons the ^{13}C signal of the chronic water stress that is suggested for street silver lindens in Paris (David et al., submitted). Root $\delta^{13}\text{C}$, alone, predicted more than 30 % of bulk soil $\delta^{13}\text{C}$. As shown in a previous study (Rankovic et al., Chapter 1), fine root density in older and intermediate street systems was respectively five and three times higher when compared to younger street systems and the arboretum. Taken together, these results suggest that as street systems age, there is an increasing input of root C, itself increasingly ^{13}C -enriched. This is consistent with the age-related trends observed in coarse fractions (discussed above) and tends to further confirm the likelihood of a scenario of important root C input and accumulation. The progressive increase of soil C:N (average of about 17 for oldest street soils), getting closer to root C:N (≈ 20), is also consistent with such a scenario.

Furthermore, data on $\delta^{13}\text{C}$ - CO_2 showed an age-related ^{13}C -enrichment of respired CO_2 by soils, with the same order of magnitude than age-related enrichment of root $\delta^{13}\text{C}$ (an increase of 1.4 ‰ units in older systems compared to younger systems). Root $\delta^{13}\text{C}$ significantly predicted $\delta^{13}\text{C}$ - CO_2 by (23 % of

explained variance by root $\delta^{13}\text{C}$ alone). These results indicate that besides imprinting C stocks with time, root-C seems to imprint the whole C cycling in soils. This can be seen as further evidence that a dynamics in C cycling takes place in street systems and is strongly shaped by tree influence on soils, which is consistent with contemporary views of a close and dynamic interdependence of the plant–microbe–soil system and the imprint of plant physiology on C cycling (Ekblad & Högberg, 2001; Ekblad et al., 2005; Högberg & Read, 2006; Shahzad et al., 2015).

Even though inherited C and N can contribute to current street soil C and N stocks, the results discussed above form, together, a body of converging evidence which strongly suggests that a long-term soil C and N accumulation dynamics indeed takes place in street systems, and that accumulated C and N constitute an increasing proportion, and perhaps the majority in the oldest systems, of C and N stocks in street soils.

4.2. Possible mechanisms for root-C accumulation in street soils

As root C inputs increase, several mechanisms could lead to C accumulation in street soils. Firstly, additional C can be incorporated into a growing microbial biomass, which could be responsible for increased soil respiration.

We also found that soil C mineralization decreased with street system age, which means that as root inputs increase, an increasing portion of inputs is more slowly mineralized in street soils. This could be due to several factors. A first hypothesis could be that older street soils offer higher levels of physical protection to SOM. However, textural data showed that older street soils were sandy loam soils and contained less clay than the other street soils. Furthermore, the qualitative analysis of X-ray diffractograms obtained for clay minerals suggested that, overall, clay mineralogy was dominated by kaolinite, and

especially in older street soils. Textural and mineralogical properties thus did not confer an increased SOM physical protection potential to older soils.

A second hypothesis would involve the higher bulk density found in street soils (Rankovic et al., Chapter 1), which had an almost two-fold bulk density (about 2.5 g.cm^{-3}) when compared to arboretum soils. Such high bulk density could impede air and water circulation and negatively influence microbial aerobic activities. However, bulk density was similar between street soils, and thus could not explain why older street soils present lower C mineralization rates compared to younger street systems. In addition, as soils were disturbed prior incubation (sieving at $< 2 \text{ mm}$) and incubated at similar water potential (80 % of WHC), it appears unlikely that differences in soil physical properties could alone explain the important differences in C mineralization rates that were observed (2.6 times higher rates in arboretum and 1.5 higher rates in younger street soils, when compared to older street soils).

A third hypothesis would involve the chemical composition of root inputs. Compared to the arboretum, a major difference in street soils is the export of aboveground litter and the three-fold higher fine root density in intermediate and older street soils (fine root density was similar between arboretum and younger street soils) (Rankovic et al., Chapter 1). As they age, street soils thus probably receive a much higher amount of root litter than younger street soils and arboretum soils. Root litter has been shown to have slower decomposition rates than leaf litter: in a global synthesis, Freschet et al. (2013) report that root litter decomposes about 2.8 times slower than leaf litter derived from the same plant species. This is attributed to a higher content of recalcitrant compounds, such as lignin and tannins, in roots compared to leaves (Rasse et al., 2005; Xia et al., 2015). For street soils, which are deprived of relatively more labile leaf litter inputs, this means that they receive higher inputs of relatively more recalcitrant C, of which, when compared to arboretum soils, a higher part could accumulate

in soils as chemically recalcitrant, leading to the lower C mineralization rates observed in street soils.

However, “intrinsic” chemical recalcitrance alone cannot control SOM stabilization, notably because soil microorganisms can degrade most organic molecules produced by plants (Schmidt et al., 2011). Another mechanism, involving the mediation of soil microbes is thus needed to explain the reduced C mineralization rates in street soils despite increased root-C inputs. Compared to arboretum soils, another major difference for street soils is their exposure to potentially high and chronic exogenous N inputs, which are likely to occur in street soils. High N depositions have been shown to decrease SOM mineralization in a wide range of soils (Bowden et al., 2004; Craine et al., 2007; Zak et al., 2008; Ramirez et al., 2012; Xia et al., 2015) and this has been predicted by theoretical works (*e.g.*, Ågren et al., 2001; Fontaine & Barot, 2005; Perveen et al., 2014). The literature suggests that the underlying mechanisms involve shifts in heterotrophic microbial physiologies and/or community composition associated to increased soil N availability. As N depositions increase soil N availability, soil microbial communities could reduce their N-mining on more recalcitrant SOM and shift towards a decomposition of more labile C when available, overall leading to a decreased soil C mineralization (Fontaine et al., 2003; Craine et al., 2007; Fontaine et al., 2011; Fierer et al., 2011; Ramirez et al., 2012). The lower C mineralization rates observed in street soils, and their decrease with system age, could then be due to a reduction in the mining of more recalcitrant root-C (*e.g.*, lignin). Accordingly, several studies report a decrease in activity of lignin-degrading enzymes in N enriched soils (Carreiro et al., 2000; DeForest et al., 2004; Edwards et al., 2011).

Finally, Rasse et al. (2005) proposed that root-C could benefit from specific physico-chemical and physical protection compared to leaf litter. Given its closer proximity to soil minerals which could facilitate its sorption, root-C

could be less accessible to microbial degradation. In addition, as very fine roots, root hair and mycorrhizal hyphae feeding on root exudates, can grow inside soil pores of just a few micrometers across, a higher proportion of root-derived C than leaf-derived C could be physically shielded from microbial degradation.

4.3. Street trees diversify their N sources

We previously hypothesized that N inputs, potentially ^{15}N -enriched, could be assimilated by roots and microbial biomass and contribute to the increase of soil N content. Here, we found that fine root N content presented sharply higher values, and root C:N lower values, in street systems when compared to the arboretum. This suggests that in street soils, a higher amount of N is available for root uptake than in the arboretum, especially at the surface. This is consistent with previously reported results showing an increase in soil mineral N content with soil age, especially at the surface of street soils (Rankovic et al., Chapter 1). Root $\delta^{15}\text{N}$ was on average 7 to 10 ‰ units higher in street systems than in the arboretum, and reached exceptionally high $\delta^{15}\text{N}$ values (≈ 14 ‰) in intermediate and older street systems, which range among the highest values measured worldwide in roots (Pardo et al., 2006, 2013).

We were not able to measure N mineralization rates in this study, however it could be expected that N mineralization rates increase with fine root density, as roots, especially through exudates, can stimulate the mineralization of SOM and release of ammonium into the soil solution through rhizosphere priming effect (*e.g.*, Kuzyakov, 2002; Raynaud et al., 2006; Cheng et al., 2014; Shahzad et al., 2012, 2015). In street soils, we found that fine root density significantly predicted soil microbial respiration rates, which significantly predicted soil ammonium content. This could mean that as soil-tree systems age, N mineralization rates increase. This is not contradictory with the above discussion on SOM stabilization and accumulation: we saw a relative decrease in SOM mineralization in street systems, not its suppression.

To explain the observed patterns in soil and root $\delta^{15}\text{N}$, we thus propose the following scenario. As ^{15}N -enriched exogenous N enters street soils, part of it is directly assimilated by roots and microbial biomass. Besides likely having high initial $\delta^{15}\text{N}$ values (Rankovic et al., Chapter 1), both deposited ammonium and nitrate pools can become further ^{15}N -enriched if volatilization, nitrification and denitrification take place in street soils before they are assimilated by roots and microbes. After being assimilated by roots and microbial biomass, the ammonium released as roots and microbial biomass are recycled could be partly nitrified as well, further ^{15}N -enriching the ammonium pool that is available for uptake, and further ^{15}N -enriching the next generation of roots and microbes. Retention and recycling of the added N can last over decades (Sebilo et al., 2013). Such a $\delta^{15}\text{N}$ “amplifying loop”, repeated over time, could explain the very high $\delta^{15}\text{N}$ values found in street soils. The various losses (leaching, gaseous losses, belowground litter exports) could be compensated and even surpassed by continuous inputs.

N mineralization induces little ^{15}N fractionation (Högberg, 1997; Dawson et al., 2002), so that the $\delta^{15}\text{N}$ of the produced ammonium is very close to soil $\delta^{15}\text{N}$ (N in SOM), and an ammonium uptake (which, too, induces little fractionation) by roots leads to root $\delta^{15}\text{N}$ closely matching soil $\delta^{15}\text{N}$. $\Delta^{15}\text{N}_{\text{root-soil}}$ values tended to get closer to 0 ‰ with increasing system age, which would be consistent with a root uptake of ammonium originating from SOM recycling. This is consistent with the soil $\delta^{15}\text{N}$ amplifying loop hypothesized above, and suggests that in street soils a tighter coupling takes place, over time, between dead root- and microbial biomass-N recycling, on one side, and live root N uptake on the other side (Abbadie et al., 1992; de Parseval et al., 2015).

How significant this tight coupling is for whole tree N nutrition, however, is uncertain. Contrary to root data, foliar data suggested the possibility that street trees become N limited as they age, possibly because tree pits, of relatively

limited volume, do not contain sufficient N stocks to match older tree N demand (Rankovic et al., Chapter 1). Contrary to $\Delta^{15}\text{N}_{\text{root-soil}}$, $\Delta^{15}\text{N}_{\text{leaf-soil}}$ was found highly negative in intermediate and older street systems (Rankovic et al., Chapter 1). $\Delta^{15}\text{N}_{\text{leaf-root}}$ was close to 0 ‰ in arboretum and younger street systems, suggesting a very tight coupling between root and foliar N nutrition. However, $\Delta^{15}\text{N}_{\text{leaf-root}}$ had much more negative values in intermediate and older street systems (-7.3 ‰ and -5.8 ‰, respectively). These are the highest differences reported in the literature between topsoil roots and leaves (Pardo et al., 2006, 2013), and suggest that street trees, as they age, access less ^{15}N -enriched N sources. This would mean that trees, as they age, probably diversify their N sources and that their N nutrition becomes less coupled to N available at the soil surface (here, the first 40 cm of soil; we found similar values at 10-20 cm and 30-40 cm, both for soil and roots). Possible sources include leached nitrate, that roots could uptake deeper in the soil pit. Foliar uptake of gaseous NO_x forms, that are likely to be less ^{15}N -enriched than dry deposited forms (Widory, 2007), could also substantially contribute to foliar N nutrition. It was shown to contribute to up to 25 % of needle N in Norway spruce along a highway in Switzerland (Ammann et al., 1999). Finally, there is considerable uncertainty as to the extent of street tree root systems, and even though their pits are surrounded by a mostly mineral matrix, there is a possibility that tree roots explore important underground volumes and possibly acquire N outside of their pits.

5. Conclusion

Current street soil management in Paris is based on the hypothesis that soils get exhausted with time. We previously reported that long-term age-related patterns in C and N cycling suggested an accumulation of root-C and exogenous N in Parisian street soil-tree systems. Further work was needed, however, to lift uncertainties about potentially overriding legacy effects. In the present study,

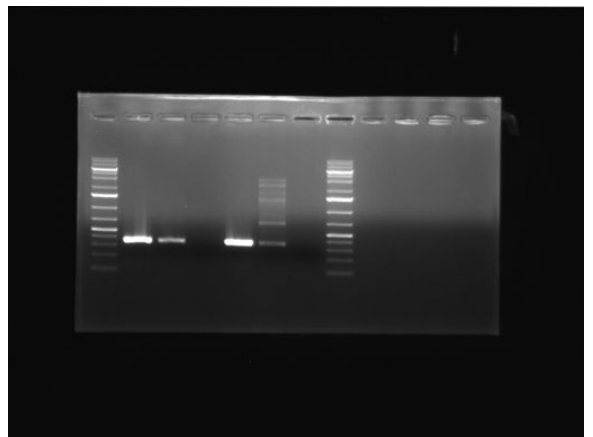
the strongly converging results in soil particle-size analysis, root $\delta^{13}\text{C}$, $\delta^{13}\text{C}$ of CO_2 respired during soil incubations, and SOM mineralization rates, further suggest an important accumulation of root-derived C in street soils. For N, particle-size analysis, root N content and $\delta^{15}\text{N}$ also further suggested an accumulation of exogenous N in street systems.

We propose several mechanisms that can lead to the joint accumulation of C and N in street systems. In particular, we suggest that important inputs of relatively more recalcitrant root litter and N-induced changes in soil microbial communities, where increased N availability in street systems would reduce microbial N-mining on recalcitrant SOM, can lead to reduced SOM mineralization rates in street soils and thus gradual accumulation of root-C. On the other hand, it is likely that high levels of fresh organic matter inputs through roots stimulate the mineralization of part of the SOM, at least in the vicinity of live roots. A growing body of research suggests that SOM dynamics are mediated by the complex interactions of C, N and energy foraging strategies of soil decomposers, and involve mechanisms named priming effects (PE) (Kuzyakov et al., 2000; Fontaine et al., 2003, 2007, 2011; Guenet et al., 2010a). PE involve an increase (positive PE) or a decrease (negative PE) of SOM mineralization rates following the addition of labile forms of C, N or both (Kuzyakov et al., 2000; Guenet et al., 2010a,b). Different PE can co-occur in soils (*e.g.*, Guenet et al., 2010b) and involve different substrates and microbial guilds. A possibility, in street soils, is that both a positive (rhizosphere PE) and a negative PE (interaction of recalcitrant root compounds and increased available N) co-occur in street soils, and that the balance between both mechanisms is favorable to the accumulation of root-C.

Removal of aerial litter is arguably a widespread practice across cities (Templer et al., 2015), and increase in root density following water stress, nutrient stress or as a response to increased urban CO_2 concentration is likely to

occur in other cities. Similarly, important levels of N deposition in urban environments are documented worldwide. Therefore, the mechanisms that we propose, if confirmed by future works, could likely occur in other cities and could in part explain the urban convergence in ecosystem processes that is mentioned in urban ecological literature.

In future works, ^{14}C dating could provide the absolute age of C in street soils, and definitely confirm the accumulation hypothesis. Furthermore, data on the chemical composition of SOM could further confirm the root-origin of accumulated C in street soils and its degree of transformation into microbial biomass. The microbial ecology – community structure and catabolic activity – of these soils could provide further information on the mechanisms underlying SOM accumulation, especially in relation to N dynamics. Finally, our results suggest that street trees present a surprising N-nutrition behavior. Future works should develop an integrated perspective on street tree N nutrition, documenting all potential N sources, including the different atmospheric and underground sources.



Chapter 3

Structure and activity of microbial N-cycling communities along a 75-year urban soil-tree chronosequence⁸

1. Introduction

Urban environments have numerous specific features that distinguish them from other environments met in the biosphere. One of these features is a highly anthropogenically influenced nitrogen (N) biogeochemistry (*e.g.*, Kaye et al., 2006; Lorenz & Lal, 2009), with abundant sources of biologically reactive N emitted into the atmosphere by combustion processes, that can enter soil-plant systems and modify N cycling.

Increased levels of soil N mineralization, nitrification and/or denitrification have been observed in urban soils (*e.g.*, Zhu & Carreiro, 2004; Groffman et al., 2009; Fang et al., 2011). In previous works on an urban chronosequence of street soil-tree systems in Paris (Rankovic et al., Chapters 1 & 2), we showed an age-related increase in soil total N content, as well as of mineral N content, coupled with exceptionally high topsoil, root and foliar $\delta^{15}\text{N}$ values, that were all among the highest measured worldwide (Martinelli et al., 1999; Amundson et al., 2003; Pardo et al., 2006, 2013; Craine et al., 2015). We hypothesized that these trends could be due to important N exogenous inputs from traffic-related emissions and animal waste, as well as increased microbial

⁸ A research article presenting this chapter's results will be prepared for an international journal by authors (in alphabetic order after first author) Rankovic, A., Abbadie, L., Barot, S., Changey, F., Fernandez, M., Lata, J.-C., Leloup, J., Lerch, T. Z., Robardet, J., Wolff, A.

processing of N, leading to increased rates in N-loss pathways (volatilization, nitrification, denitrification) leading to further ^{15}N -enrichment in street systems.

In the present study, we studied soils from 30 different street tree pits in Paris, as well as soils from an arboretum under the same tree species, *Tilia tomentosa* Moench. We tested whether age-related trends could be found in microbial N-cycling on the street soil chronosequence, and whether differences with arboretum soils could be observed. We used quantitative polymerase chain reactions (PCR) to quantify the abundances of ammonia oxidizers, both bacterial (AOB) and archaeal (AOA), as well as denitrifying bacteria and we measured potential nitrification and denitrification rates.

2. Materials and methods

2.1. Site description and chronosequence design

The study was conducted in Paris, France (48°51'12.2"N; 2°20'55.7"E) and at the National Arboretum of Chèvreloup in Rocquencourt (48°49'49.9"N; 2°06'42.4"E), located about 20 km east of central Paris. The Parisian climate is temperate, sub-Atlantic (Crippa et al., 2013), and mean annual temperatures are on average 3°C warmer at night in the center of the agglomeration due to the urban heat island effect (Cantat, 2004). The studied sites comprised silver linden (*Tilia tomentosa* Moench) street plantations in Paris and soils under individual silver lindens at the National Arboretum of Chèvreloup.

The sampling design was based on 3 tree diameter at breast height (DBH) classes, used as a proxy for tree age. The three classes were designed to cover the DBH range of street silver lindens in Paris, which spans from approximately 6 to 76 cm, as retrieved in the databases provided by the Paris Green Space and Environmental Division. This was done so that the chronosequence ranged from about the youngest to the oldest silver lindens street plantations in Paris. Sites were also selected so as to be spread across the city (Figure 1). Only sites with

either bare or drain-covered soils were selected to keep similar conditions of air and water circulation in soils, and thus avoid important differences in terms of rooting conditions (*e.g.*, Rahman et al., 2011). In total, for this study, 30 street plantations were sampled according to 3 DBH classes: Class 1 = [6.8; 14.6 cm] ($n = 10$), Class 2 = [33.1; 42.7 cm] ($n = 10$), Class 3 = [57.3; 72.6 cm] ($n = 10$). The sites were located in 18 different streets across Paris (Figure 1). Tree-ring counts on wood cores subsequently helped determine tree age (David et al., submitted) and provide an estimation of “soil-tree system age”, by subtracting 7 years to every tree age to account for sapling age at their plantation in streets.

Overall, the sampling comprised ecosystems of age 1 to age 76. Class 1 sites included soil-tree systems of an average age of 4 ± 4.2 years, Class 2 sites included ecosystems of age 43.9 ± 12.5 years, and Class 3 sites included ecosystems of age 67.7 ± 14.3 years. A Kruskal-Wallis test ($H = 44.2$, $df = 2$, $p < 0.001$) followed by a Wilcoxon-Mann-Whitney test confirmed that age was significantly different between each class (Younger-Intermediate: $p < 0.001$; Younger-Older: $p < 0.001$; Intermediate-Older: $p < 0.001$). Thereafter, these three classes will respectively be referred to as “younger systems”, “intermediate systems” and “older systems” (Table 1).

The National Arboretum of Chèvreloup (<http://chevreloup.mnhn.fr>) is a 205-hectare arboretum adjacent to the Palace of Versailles complex and located in the municipality of Rocquencourt in the Yvelines department, region of Île-de-France (Figure 1). The current arboretum was created in 1927 and is the property of the French National Museum of Natural History. At the arboretum, trees are usually grown on site at the nursery and planted as saplings when about 10 years old. Trees are not submitted to pruning, not fertilized and aboveground litter is not removed. There is little to no competition for crown development space. Compared to street trees, there seem to be no space constraint for root system development. At the arboretum, 7 silver linden stands were sampled.

Their plantation date is known and was used to estimate tree age, giving an average age of 54.0 ± 22 years (Table 1). Arboretum soil-tree systems thus had an age comprised between intermediate and older street systems.

2.2. Sample collection and processing

Samples from street plantations were collected over July 2011. At each site, soil was sampled at 2 points around the tree trunk with a 3 cm diameter gouge auger. The sampling points were situated at 25-40 cm from the trunk, depending on accessibility (size of drain holes, obstruction by thick roots etc.). The two extracted soil cores were pooled at 10-30 and 30-40 cm depths respectively. Samples from the arboretum were collected in July 2012. Four soil cores were extracted around the trunk at a similar distance than for street sites. The four extracted soil cores were pooled at 0-10, 10-20, 20-30, 30-40 cm depths respectively. For the arboretum, the 10-30 cm data presented here are an average of values obtained for 10-20 and 20-30 cm depths.

For each street and arboretum soil, samples were handled in three different ways: (1) subsamples were placed in Falcon tubes in the field, transported at $-20\text{ }^{\circ}\text{C}$ then stored at $-80\text{ }^{\circ}\text{C}$ for DNA analyses; (2) subsamples were frozen in liquid N_2 in the field and later used for mineral nitrogen extractions; (3) most of the sample was air-dried for 72h, sieved at 2 mm and then stored in the dark at ambient temperature and used for physico-chemical analyses and measurement of enzymatic activities.

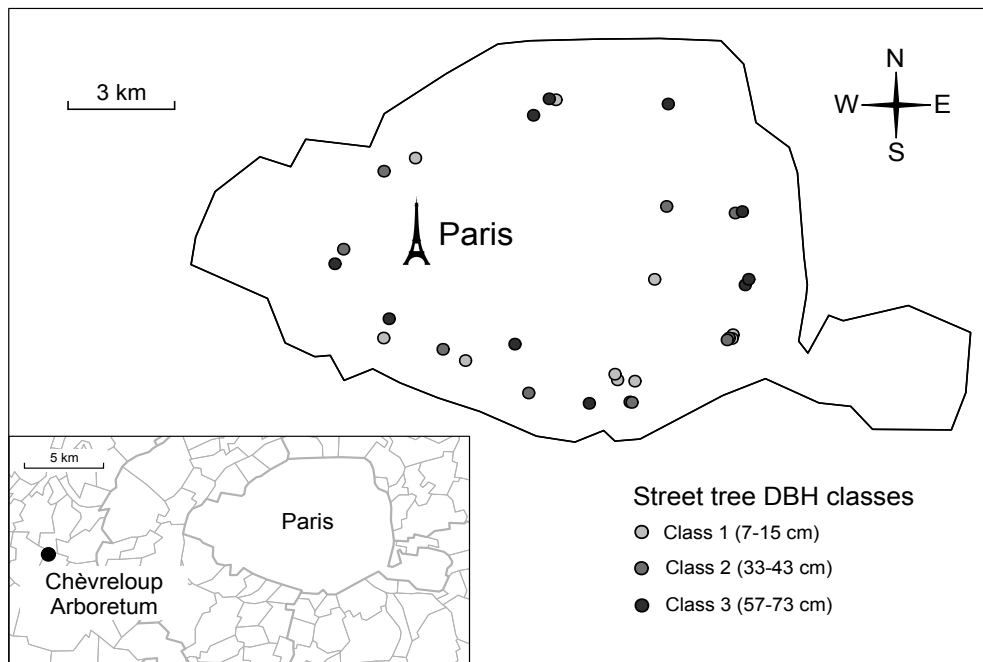


Figure 1. Location of sampled street plantations in Paris and the arboretum

2.3. Real-time quantitative PCR

Crenarchaeotal (*amoA*-AOA) and bacterial (*amoA*-AOB) nitrifying and bacterial denitrifying (*nirK* and *nirS*) communities abundances were determined by real-time quantitative PCR (qPCR) with specific primer sets (Table 2), carried out in an a CFX96 Real-Time System (Bio-Rad, France). Quantification was based on the increasing fluorescence intensity of SYBR Green dye during amplification. The real-time PCR assay was carried out in a 20 μ l reaction volume containing the Ssoadvanced™ SYBR® Green Supermix (2X, Bio-Rad), 1.25 μ l of bovine serum albumin (2 mg/ml) and two serial dilutions of DNA (2 and 0.2 ng). Two independent quantitative PCR assays were performed for each gene. Standard curves were obtained using serial dilutions of linearized plasmids containing the studied genes. PCR efficiency for the different assays ranged between 90 and 99 %.

Table 1. Classes of tree DBH and ecosystem age. Tree DBH (1.30 m) were measured in July 2011 for street trees and 2012 for arboretum trees. Tree ages were estimated by counting tree rings on extracted wood cores (David et al., submitted). Ecosystem age was obtained by subtracting 7 years to every tree age to account for sapling age at plantation.

Paris street soil-tree ecosystems (n = 30)											
Younger systems (4 years ± 4.2, n = 10)			Intermediate systems (43.9 years ± 12.5, n = 10)			Older systems (67.7 years ± 14.3, n = 5)			Arboretum stands (55.7 years ± 25.1, n = 7)		
Sites	Tree DBH (cm)	Ecosystem age (years)	Sites	Tree DBH (cm)	Ecosystem age (years)	Sites	Tree DBH (cm)	Ecosystem age (years)	Sites	Tree DBH (cm)	Ecosystem age (years)
T01	6.8	1	T32	33.1	63	T60	57.3	NA	CLT1	46.8	30
T03	8.0	1	T34	34.1	40	T63	57.3	76	CLT2	47.1	30
T07	8.6	1	T36	34.4	31	T65	58.9	43	CLT3	38.2	30
T12	9.5	1	T39	35.3	27	T67	60.5	NA	CLT4	73.8	70
T16	11.1	3	T43	36.3	38	T68	60.5	51	CLT5	111.1	90
T18	11.5	2	T45	38.2	41	T71	61.4	76	CLT6	68.4	70
T20	13.1	3	T49	39.8	40	T72	63.0	NA	CLT7	67.2	70
T21	13.1	14	T52	40.4	57	T75	64.9	76			
T24	14.0	7	T54	41.7	40	T77	71.3	76			
T27	14.6	7	T57	42.7	62	T78	72.6	76			

Target population	Target gene	Primers (ref)	[Primers] (μM)	Thermal conditions
Ammonia-oxidizing bacteria	<i>amoA</i> -AOB	AmoA1F – AmoA2R (Rotthauwe et al., 1997)	1	40 x [95 °C, 15 s ; 55 °C, 30 s ; 72 °C, 30 s]
Ammonia-oxidizing archaea	<i>amoA</i> -AOA	CrenamoA23F – CrenamoA616R (Tourna et al., 2008)	0.5	35 x [95 °C, 15 s ; 56 °C, 30 s ; 72 °C, 30 s]
Denitrifying bacteria	<i>nirS</i>	Cd3aF – Cd3R (Throbäck et al., 2004)	1	Touchdown: [95 °C, 15 s; 63 to 58 °C (1 °C/cycle), 30 s; 72 °C, 30 s], 30 x [95 °C, 15 s; 58 °C, 30 s; 72 °C, 30 s]
	<i>nirK</i>	NirK876F – NirK1040R (Henry et al. 2004)	0.5	Touchdown: [95 °C, 15 s; 63 to 58 °C (1 °C/cycle), 30 s; 72 °C, 30 s], 34 x [95 °C, 15 s; 58 °C, 30 s; 72 °C, 30 s]

Table 2. Details of qPCR protocols used for targeted genes.

2.4. Potential nitrifying and denitrifying activities

Soil nitrification potential was assessed through the Nitrification Enzyme Activity (NEA) method (Lensi et al., 1986; Lata et al., 1999, 2004; Patra et al. 2005, 2006). It is considered that NEA measurements are not affected by short-term environmental variations (Lensi et al., 1986) or by drying and storage (Abbadie & Lensi, 1990; Lensi et al., 1992). From each soil sample, 5 g subsamples ($n = 6$) were placed in 150 ml plasma flasks. Three subsamples were used to estimate the initial soil NO_3^- content. These subsamples were supplied with 6 ml of a suspension of a denitrifying *Pseudomonas fluorescens* ($\text{OD}_{580} = 2$) in a solution containing glucose and glutamic acid (for each: 0.5 mg C.g^{-1} dry soil). This procedure ensures high denitrifying potential and electron donors in excess. The flasks were sealed with rubber stoppers and the atmosphere of each flask was replaced by a $\text{He-C}_2\text{H}_2$ mixture (90–10) to ensure anaerobic conditions and N_2O -reductase inhibition. The flasks were incubated at 28 °C and N_2O accumulation was followed on a gas chromatographer (R-3000, Agilent) until a constant value (*i.e.* a total conversion of soil NO_3^- to N_2O) was reached (samples were followed over a week for verification).

The other three subsamples were used to determine potential NO_3^- accumulation. For these subsamples, 4 ml of a $(\text{NH}_4)_2\text{SO}_4$ solution was added ($200 \mu\text{g N.g}^{-1}$ dry soil) in order to ensure a moisture content equivalent to 80% WHC, and no limitation by ammonium. Flasks were then sealed with parafilm, which prevents soil from drying but allows gas exchange, and incubated at 28°C for 7 h in a horizontal position to ensure optimal, homogeneous aeration of the soil. After this aerobic incubation, which allows nitrate to accumulate, the soil samples were enriched with *Pseudomonas fluorescens* and incubated as described above for the other three subsamples. Nitrification potential was computed by subtracting the nitrate initially present in the soil from that present after aerobic incubation ($\text{g N.h}^{-1}.\text{g}^{-1}$ dry soil).

Soil denitrification potential was assessed through the Denitrification Enzyme Activity (DEA) as described in Patra et al. (2005, 2006). For each soil, 10 g of dry soil were placed in a 150 ml plasma flask. 6 ml of distilled water containing KNO_3 ($200 \mu\text{g NO}_3^-.\text{N.g}^{-1}$ dry soil), glucose (0.5 mg C.g^{-1} dry soil) and glutamic acid (0.5 mg C.g^{-1} dry soil) were added. Additional water was added to achieve 100% WHC. Flasks were then sealed with rubber stoppers and the atmosphere of each flask was evacuated and replaced by a 90:10 $\text{He}:\text{C}_2\text{H}_2$ mixture to provide anaerobic conditions and inhibit N_2O -reductase activity. The flasks were incubated at 28°C and N_2O accumulation was followed on a gas chromatographer (R-3000, Agilent) at 2, 4, 6 and 8 h of incubation. Denitrification potential was computed as $\text{g N.h}^{-1}.\text{g}^{-1}$ dry soil.

2.5. Statistical analyses

Statistical analyses were performed with the R-software (R Development Core Team, 2013). Four sample classes (three DBH classes and the arboretum) and two depths (10-30 cm and 30-40 cm) and their interaction were used as explanatory factors. Linear mixed-effects models with a "site" random effect were used for soil variables to account for non-independence of soil depths at

each sampling site. R^2 values for linear mixed-effects models were calculated with the function `r.squared.lme` (version 0.2-4 (2014-07-10)) that follows the method described in Nakagawa & Schielzeth (2013). Values for conditional R^2 , which describes the proportion of variance explained by both the fixed and random factors, are shown. Tukey post-hoc tests were performed for ANOVA models yielding significant results. For variables that did not satisfy ANOVA assumptions even after log transformation, non-parametric tests were used: a Kruskal-Wallis test was used for each depth to test for differences between classes, and a Wilcoxon-Mann-Whitney test was used for pairwise comparisons of means. Pearson's moment correlation tests were used to test for correlations among microbial, soil and plant variables. For all tests, the null hypothesis was rejected for $p < 0.05$ and significance was represented as follows: *** when $p \leq 0.001$; ** for $0.001 < p \leq 0.01$ and * when $0.01 < p \leq 0.05$. Effects with $0.05 \leq p < 0.10$ are referred to as marginally significant. Data on soil, root and foliar $\delta^{15}\text{N}$, root density, and soil physico-chemical parameters are used from previous works (Rankovic et al., Chapter 1).

3. Results

3.1. Abundances of soil AOB and AOA

On average, at 10-30 cm arboretum soils contained 1.6×10^7 *amoA*-AOB gene copies per gram of soil and the mean copy number was 2.0×10^7 , 4.1×10^7 and 5.1×10^7 in younger, intermediate and older street systems, respectively. At 30-40 cm, arboretum soils contained 5.1×10^6 gene copies and the average was 1.9×10^7 , 1.5×10^7 and 2.2×10^7 in younger, intermediate and older street systems, respectively. Soils from older street systems on average contained significantly more *amoA*-AOB gene copies than arboretum soils and younger street systems (Table 3, Figure 2A). Soils from intermediate street systems contained significantly more *amoA*-AOB gene copies than arboretum soils. At 10-30 cm, soils from older street systems contained about 3.2 times more *amoA*-

AOB gene copies than in arboretum soils, and about 2.6 times and 1.2 times more copy numbers than in younger and intermediate systems, respectively. At 30-40 cm, soils from older street systems contained about 4.3 times more *amoA*-AOB gene copies than in arboretum soils, and about 1.2 times and 1.5 times more copy numbers than in younger and intermediate systems, respectively. Depth effect was significant and a stratification in gene copy number was observed in arboretum soils and intermediate and older street systems. At 10-30 cm, soils from the arboretum contained 3.1 times more gene copies than at 30-40 cm, and soils from intermediate and older street systems had respectively 2.7 times and 2.3 times more gene copies at 10-30 cm than at 30-40 cm (Figure 2A). On average, soils from intermediate and older street systems contained about 2.9 times more *amoA*-AOB gene copies at 10-30 cm and 3.6 times more at 30-40 cm than arboretum soils.

Table 3. ANOVA table of F values for the effects of class and depth and their interaction on total AOB, AOA, *nirS* and *nirK* abundances and the AOA/AOB ratio. The reported values for significant terms and R^2 are the values obtained after removal of non-significant factors in the model. For each (depth x class) for street soils, n = 10; n=7 for the arboretum.

Variables	Factors									Model R^2
	Class			Depth			Class x Depth			
	F	p	df	F	p	df	F	p	df	
log(AOB)	6.8	***	3	17.8	***	1	0.95	ns	3	0.42
log(AOA)	7.0	***	3	0.3	ns	1	1.9	ns	3	0.66
log(AOA/AOB)	2.5	0.08	3	8.0	**	1	0.47	ns	3	0.54
<i>nirS</i>	2.2	ns	3	5.4	*	1	1.8	ns	3	0.68
<i>nirK</i>	3.1	*	3	5.50	*	1	1.4	ns	3	0.68

The abundance of ammonia-oxidizing archaea (AOA) in soils varied significantly across classes but there was no effect of depth (Table 3, Figure 2B). On average, at 10-30 cm arboretum soils contained 6.8×10^7 *amoA*-AOA gene copies per gram of soil and the mean copy number was 1.4×10^8 , 1.5×10^8 and 1.7×10^8 in younger, intermediate and older street systems, respectively. At 30-40 cm, arboretum soils contained 5.4×10^7 gene copies and the average was 1.7×10^8 , 1.4×10^8 and 1.7×10^8 in younger, intermediate and older street systems, respectively. Soils from street systems contained significantly more *amoA*-AOA

gene copies than arboretum soils, with average abundance for street systems being 2.6 times higher than the average abundance in arboretum soils (Figure 2B).

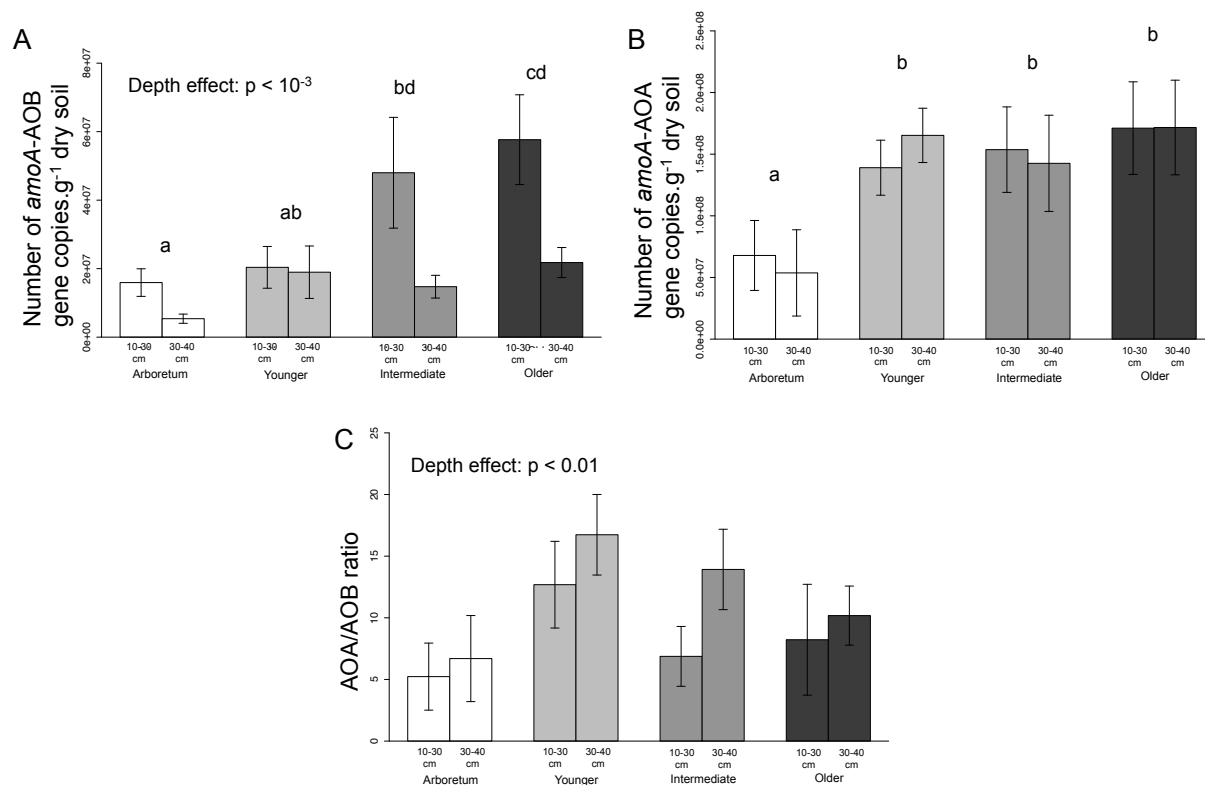


Figure 2. (A) Abundance of amoA-AOB, (B) Abundance of amoA-AOA and (C) AOA/AOB ratio at 10-30 cm and 30-40 cm in the different sample classes. Bars show means and error bars correspond to standard error. Different letters mean that a significant difference ($p < 0.05$) was indicated by a Tukey post-hoc test performed after an ANOVA. For each bar, $n = 10$ for street soils, $n = 7$ for the arboretum.

There was a marginally significant effect ($p = 0.08$) of system class on the AOA/AOB ratio and a significant effect of depth (Table 3, Figure 2C). At 10-30 cm, AOA/AOB averaged 5.2 at the arboretum and 12.7, 6.9 and 8.2 in younger, intermediate and street systems, respectively (Figure 2C). At 30-40 cm, AOA/AOB averaged 6.7 at the arboretum and 16.7, 13.9 and 10.2 in younger, intermediate and older systems, respectively (Figure 2C). AOA/AOB was 1.3 times higher at 10-30 cm than at 30-40 cm in arboretum soils and 1.3, 2.0, 1.2 times higher at 10-30 cm than at 30-40 cm in younger, intermediate and older

street systems, respectively (Figure 2C). At 10-30 cm, AOA/AOB was 1.8 times higher and 1.5 times higher in younger street systems when compared to intermediate and older street systems, respectively. At 30-40 cm, AOA/AOB was 1.2 times higher and 1.6 times higher in younger street systems when compared to intermediate and older street systems.

3.2. Abundances of soil bacterial denitrifiers

The abundance of *nirK* differed across classes and depths but there was no significant interaction between class and depth factors (Table 3, Figure 3A). On average, at 10-30 cm arboretum soils contained 1.4×10^8 *nirK* gene copies per gram of soil and the mean copy number was 2.3×10^8 , 1.7×10^8 and 3.1×10^8 in younger, intermediate and older street systems, respectively. At 30-40 cm, arboretum soils contained 1.2×10^8 gene copies and the average was 2.7×10^8 , 1.4×10^8 and 1.8×10^8 in younger, intermediate and older street systems, respectively. Soils from younger and older street systems contained significantly more *nirK* gene copies than arboretum soils. At 10-30 cm, street systems on average contained 1.7 times more *nirK* gene copies than arboretum soils. At 30-40 cm, they contained 1.6 times more *nirK* gene copies than arboretum soils (Figure 3A). Soils from older street systems contained 1.7 times more *nirK* gene copies at 10-30 cm than at 30-40 cm.

There was a significant effect of depth on the abundance of *nirS* (Table 3, Figure 3B). On average, at 10-30 cm arboretum soils contained 2.9×10^8 *nirS* gene copies per gram of soil and the mean copy number was 2.4×10^8 , 1.8×10^8 and 2.8×10^8 in younger, intermediate and older street systems, respectively. At 30-40 cm, arboretum soils contained 2.3×10^8 gene copies and the average was 3.6×10^8 , 1.3×10^8 and 2.1×10^8 in younger, intermediate and older street systems, respectively (Figure 3B). Arboretum soils contained 1.3 times more *nirS* copies at 10-30 cm than at 30-40 cm, and intermediate and older street systems respectively contained 1.4 times and 2.2 more copies at 10-30 cm than

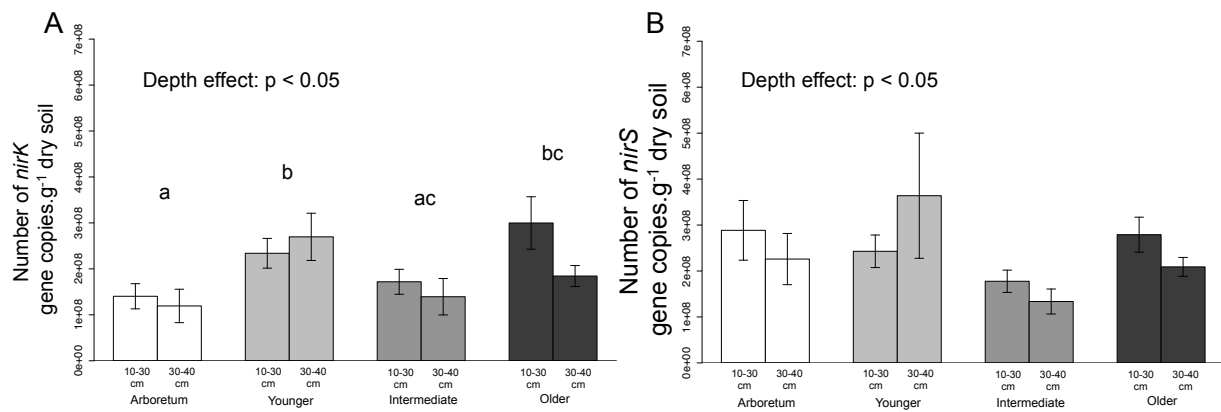


Figure 3. (A) Abundance of *nirK* and (B) Abundance of *nirS* at 10-30 cm and 30-40 cm soil depth in the different sample classes. Bars show means and error bars correspond to standard error. Different letters mean that a significant difference ($p < 0.05$) was indicated by a Tukey post-hoc test performed after an ANOVA. For each bar, $n = 10$ for street soils, $n = 7$ for the arboretum.

at 30-40 cm. The observed trend was opposite for younger street systems, with soils containing on average 1.5 times more copies of *nirS* at 30-40 cm than at 10-30 cm (Figure 3B).

3.3. Potential nitrification and denitrification

Potential nitrification (NEA) was significantly different between classes for both depths (Table 4, Figure 4A). NEA rates at 10-30 cm were $0.03 \mu\text{g N.h}^{-1}.\text{g}^{-1}$ dry soil at the arboretum and 0.59 , 0.63 and $0.90 \mu\text{g N.h}^{-1}.\text{g}^{-1}$ dry soil in younger, intermediate and older street systems, respectively. At 30-40 cm, measured nitrification rates were $0.004 \mu\text{g N.h}^{-1}.\text{g}^{-1}$ dry soil at the arboretum and 0.76 , 0.12 and $0.31 \mu\text{g N.h}^{-1}.\text{g}^{-1}$ dry soil in younger, intermediate and older street systems, respectively (Figure 4A). NEA rates at 10-30 cm were significantly higher in street systems when compared to arboretum soils and were respectively 19.7, 21 and 30 times higher in younger, intermediate and older street systems when compared to the arboretum. At 30-40 cm, NEA rate in younger street systems was significantly higher than in arboretum soils, with a mean rate 190 times higher in younger street systems than at the arboretum. At

30-40 cm, NEA rates were not significantly different between intermediate and older street systems and the arboretum, however the observed trend was that NEA rates were respectively 30 times and 77.5 times higher in intermediate and older street systems than at the arboretum. There was no significant difference among depths for younger street systems. However a significant stratification was observed in arboretum soils, with rates at 10-30 cm being 7.5 times higher than at 30-40 cm. A significant difference between depths was also observed for intermediate and older street systems, with rates at 10-30 cm being respectively 5.25 and 2.9 higher than at 30-40 cm.

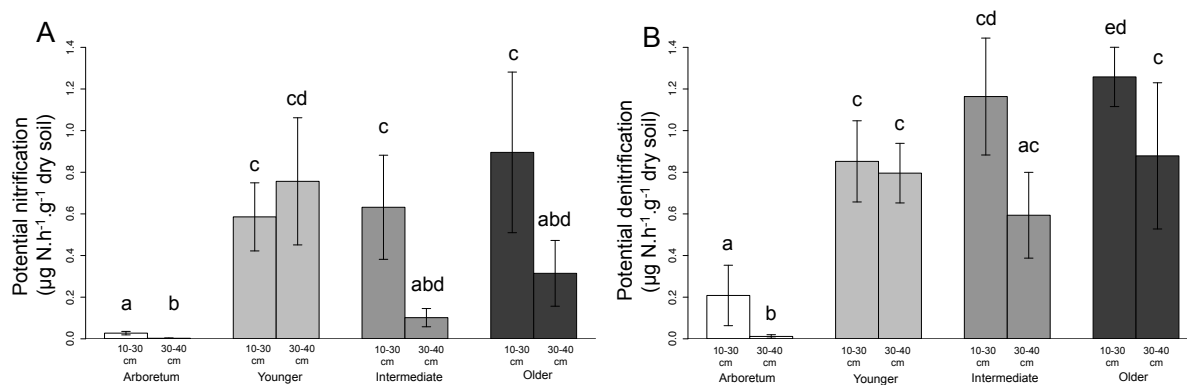


Figure 4. (A) Potential nitrification and (B) Potential denitrification at 10-30 cm and 30-40 cm soil depth in the different sample classes. Bars show means and error bars correspond to standard error. Different letters mean that a significant difference ($p < 0.05$) was indicated by a Wilcoxon-Mann-Whitney test. For each bar, $n = 10$ for street soils, $n = 7$ for the arboretum.

Potential denitrification (DEA) was significantly different between classes for both depths (Table 4, Figure 4B). DEA rates at 10-30 cm were $0.2 \mu\text{g N}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$ dry soil at the arboretum and 0.9 , 1.2 and $1.3 \mu\text{g N}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$ dry soil in younger, intermediate and older street systems, respectively. At 30-40 cm, measured denitrification rates were $0.01 \mu\text{g N}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$ dry soil at the arboretum and 0.80 , 0.60 and $0.88 \mu\text{g N}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$ dry soil in younger, intermediate and older street systems, respectively (Figure 4B). DEA rates were significantly higher in street systems than in the arboretum at both depths (Figure 4B). When compared to arboretum soils, younger, intermediate and older street systems showed

respectively 4.5, 6, and 6.5 higher DEA rates at 10-30 cm, and 80, 60 and 88 times higher rates at 30-40 cm. Soils from older street systems showed significantly 1.4 higher DEA rates than younger street systems at 10-30 cm (Figure 4B). An observed stratification trend was observed in arboretum soils and in intermediate and older street systems, with a significant difference between depths at the arboretum and in intermediate and older street systems (Figure 4B). Arboretum soils showed 20 times higher DEA rates at 10-30 cm when compared to 30-40 cm and soils from older street systems had about 1.5 higher rates at 10-30 cm when compared to 30-40 cm (Figure 4B). Although not found significant, a similar trend was observed in intermediate soils, with rates at 10-30 cm being 2 times higher than at 30-40 cm.

Table 4. Summary of Kruskal-Wallis tests for potential nitrification (NEA) and denitrification (DEA).

		Factor: Class		
	Depth	H	df	p
NEA	10-30 cm	12.9	3	**
	30-40 cm	8.7	3	*
DEA	10-30 cm	12.7	3	**
	30-40 cm	14.6	3	**

3.4. Correlations among microbial parameters and between microbial, soil and plant parameters in street systems

The results presented below concern Parisian street soil-tree systems only, *i.e.* they do not include the arboretum sites.

NEA was positively correlated to AOA abundance, and a marginally significant positive correlation was found between NEA and AOB abundance (Table 5). No significant correlation was found between NEA and AOA/AOB ratio.

The abundances of *nirS* and *nirK* genes were found to be positively correlated and DEA was found to be positively correlated with the abundances of both genes (Table 5).

The abundances of *nirS* were positively correlated to AOA and AOB abundances. The abundances of *nirK* and *nirS* were found to be positively correlated with NEA, as was DEA. DEA was positively correlated with AOA and AOB abundances. NEA and DEA were positively correlated (Table 5).

AOB abundances were positively correlated to soil total N content. AOA/AOB was negatively correlated to soil total N content (Table 6). Marginally significant positive correlations were found between total soil N and *nirS* abundance, *nirK* abundance and DEA.

Table 5. Correlations between soil microbial parameters. When the correlation is significant (bold) or marginally significant Pearson's correlation coefficient (r) is given.

	AOA		AOB		AOA/AOB		NEA		<i>nirS</i>		<i>nirK</i>	
	r	p	r	p	r	p	r	p	r	p	r	p
AOA	-	-	-	-	-	-	-	-	-	-	-	-
AOB		0.26	-	-	-	-	-	-	-	-	-	-
AOA/AOB	0.60^{log}	10⁻⁷	-0.52	10⁻⁵	-	-	-	-	-	-	-	-
NEA	0.36^{log}	0.012	0.27	0.06		0.374	-	-	-	-	-	-
<i>nirS</i>	0.41^{log}	0.002	0.31^{log}	0.015		0.7	0.32^{log}	0.02	-	-	-	-
<i>nirK</i>		0.35		0.17		0.42	0.50	0.003	0.56^{log}	10⁻⁶	-	-
DEA	0.30	0.03	0.31	0.015		0.9	0.50^{log}	0.003	0.34^{log}	0.009	0.28	0.027

Soil NH₄⁺ content was positively correlated to AOB abundance and negatively correlated with the AOA/AOB ratio. Soil NO₂⁻ content was positively correlated to AOB abundance and positively correlated to NEA. It was also positively correlated to DEA. A marginally significant (p = 0.07) negative correlation was found between soil NO₂⁻ content and the AOA/AOB ratio. Soil NO₃⁻ content was positively correlated with AOB abundance, NEA, *nirK*

abundance and DEA. Soil NO_3^- content was negatively correlated with the AOA/AOB ratio (Table 6).

The abundance of AOB was negatively correlated to soil pH, as was NEA. The AOA/AOB ratio was positively correlated to soil pH (Table 6). Water holding capacity (WHC) was positively correlated with DEA (Table 6).

Table 6. Correlations between soil microbial parameters and soil physico-chemical parameters. When the correlation is significant (in bold) or marginally significant Pearson's correlation coefficient (r) is given.

	C_{org}		N_{tot}		NH_4^+		NO_2^-		NO_3^-		pH		WHC		Soil $\delta^{15}\text{N}$	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p
AOA		0.19		0.15		0.8		0.56		0.222		0.67		0.95		0.8
AOB	0.36	0.005	0.28	0.03	0.34^{ns}	0.009	0.35	0.006	0.51	10⁻⁶	-0.28^{ns}	0.02		0.95	0.29	0.025
AOA/AOB	-0.37	0.005	-0.35	0.007	-0.32	0.02	-0.25	0.07	-0.34^{ns}	0.0161	0.27^{ns}	0.045		0.8	-0.23	0.09
NEA		0.74		0.95		0.335	0.33	0.02	0.71	10⁻⁴	-0.37^{ns}	0.008		0.16		0.58
<i>nirS</i>		0.66	0.23	0.07		0.47		0.7		0.43		0.7		0.43		0.9
<i>nirK</i>		0.66	0.31	0.085		0.72		0.62	0.29	0.04		0.22		0.55	-0.25	0.06
DEA		0.16	0.24	0.064		0.29	0.29	0.03	0.28	0.04		0.58	0.30	0.018		0.4

Soil $\delta^{15}\text{N}$ was positively correlated with AOB abundance. A marginally significant negative correlation was found between soil $\delta^{15}\text{N}$ and the AOA/AOB ratio ($p = 0.09$) and *nirK* abundance ($p = 0.06$) (Table 6).

Fine root density was positively correlated to AOB abundance and negatively correlated to the AOA/AOB ratio. A marginally significant negative correlation was found between fine root density and AOA (Table 7). Fine root C:N was negatively correlated with AOB abundance and positively correlated with the AOA/AOB ratio. A marginally significant correlation was found between fine root C:N and *nirS* abundance ($p = 0.09$) (Table 7).

A positive correlation was found between leaf $\delta^{15}\text{N}$ and AOB abundance, and a negative correlation was found between AOA/AOB and leaf $\delta^{15}\text{N}$.

Table 7. Correlations between soil microbial parameters plant parameters. When the correlation is significant (in bold) or marginally significant Pearson's correlation coefficient (r) is given.

	Fine root density		Root %N		Root C:N		Leaf %N		Leaf C:N		Root $\delta^{15}\text{N}$		Leaf $\delta^{15}\text{N}$	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p
AOA	-0.23	0.09		0.47		0.48		0.42		0.61		0.96		0.95
AOB	0.26	0.049	0.31	0.10	-0.43^{ns}	0.02		0.68		0.83		0.14	0.26	0.048
AOA/AOB	-0.31^{ns}	0.02	-0.30	0.10	0.49	0.006		0.9		0.9		0.37	-0.27	0.04
NEA		0.38		0.63		0.63		0.71		0.74		0.7		0.98
<i>nirS</i>		0.65		0.94	0.075	0.09		0.6		0.8	-0.38	0.03		0.22
<i>nirK</i>		0.779	0.41^{ns}	0.02		0.5	-0.21	0.10	0.27	0.03		0.4		0.9
DEA		0.93		0.79		0.9		0.9		0.92		0.64		0.13

4. Discussion

NEA showed considerably higher rates in street soils than in arboretum soils. For nitrification, more AOB were found in intermediate and older street soils compared to the arboretum, and more AOA were found in all classes of street soils compared to arboretum soils, which suggests an increase of soil nitrifying populations in response to the street environment. This increase is likely behind the higher nitrification rates, as suggested by the positive correlations between both AOA and AOB abundances and NEA rates. Nitrification parameters also presented age-related trends in street soils, with significantly higher AOB numbers in older street soils when compared to younger street soils. NEA rates in surface soils also tended to increase with system age, with an important stratification of NEA rates in intermediate and older street soils. These results suggest that street soils present more favorable conditions for nitrification than arboretum soils under the same tree species, and that these conditions are increasingly favorable with time at the surface of street soils. In a previous study, we showed that soil ammonium content was higher in intermediate and older street systems than in younger systems, and that nitrite and nitrate contents were considerably higher in street soils than in arboretum soils, and were increasing with street soil age (Rankovic et al., Chapter 1). This

could mean that as street systems age, an increasing amount of ammonium is available for ammonia oxidizers, and is oxidized to nitrite and then to nitrate.

Here, several results suggest that AOB are responsible for the age-related increase in nitrification in street soils. The age-related patterns found in AOB, of which the abundance increases with soil age at the surface, closely match the trends observed in NEA rates and previously observed in soil nitrite and nitrate content (Rankovic et al., Chapter 1). A positive correlation between AOB, soil ammonium content, nitrite content and nitrate content was found, while no correlation was found between AOA and these parameters. Furthermore, AOA/AOB showed a marginally significant decrease with street soil age, and was negatively correlated with soil ammonium content. AOB was positively correlated to NEA (marginally significant), while the correlation found between AOA and NEA was due to two outliers, and disappeared when they were removed.

These results are consistent with recent research on niche differentiation among AOA and AOB, which suggests that AOA are more competitive in low-nutrient conditions while AOB are more adapted to nutrient-rich environments (Martens-Habbena et al., 2009; Di et al., 2009; Simonin et al., 2015; Carey et al., 2016). In a recent meta-analysis of 33 studies on the effects of N-enrichment on soil AOA, AOB and nitrification rates, Carey et al. (2016) found that N additions increased both AOA and AOB abundances, but with an average increase of 27 % for AOA and 326 % for AOB. Furthermore, they found a positive correlation between the increase response of AOB and NEA rates across studies, while no correlation was found between AOA response and nitrification rates.

The increase of ammonia oxidizers, and especially of AOB, in street soils, is likely due, at least in part, to increased ammonium content. This higher mineral N content could be due to higher N deposition, likely to occur in such

roadside systems (Bettez et al., 2013), and to animal waste (especially urine). The added N could directly stimulate nitrification by increasing substrate availability. An increase in N mineralization with soil age could also lead to more ammonium being available to nitrifiers. We previously reported an almost five-fold increase in fine root density in older street systems when compared to arboretum and younger street systems (Rankovic et al., Chapter 1), and that fine root density was found to predict almost 50 % of the variance of soil respiration rates measured through soil incubations (Rankovic et al., Chapter 2). Soil respiration rates, in turn, significantly predicted 25 % of soil ammonium content. This suggests that in street soils, at least part of the age-related increase in ammonium content could come from higher N mineralization, stimulated by fine roots. The positive correlation between fine root density and AOB, negative correlation between fine root density and AOA, and negative correlation between fine root density and AOA/AOB, indeed suggest that the increase in fine root density might be, at least indirectly through an increase in N mineralization, involved in favoring AOB versus AOA.

Compared to arboretum soils, another feature of street soils that is likely to favor AOB nitrification is pH, which averages around 7.5 in street soils and 5.7 at the arboretum (Rankovic et al., Chapter 1). AOA are thought to dominate nitrification in acidic soils, while AOB are favored at circumneutral pH (Nicol et al., 2008; Prosser & Nicol, 2012; Carey et al., 2016). Nicol et al. (2008) found that AOB transcriptional activity was highest around a pH of 6.9 but then decreased at pH values of 7.3 and 7.5. In the present study, we found a negative correlation between pH and AOB abundance in street soils. AOB abundance seemed to slightly decrease in soils with pH higher than 7.5, as did NEA (data not shown). This result, firstly, further suggests that the increase in NEA in street soils is indeed driven by an increase in the abundance of AOB. Then, it

also suggests that the response of AOB to street conditions can, quite expectedly, be partly modulated by other soil properties besides ammonium content.

In the case of pH, street conditions could, too, have an influence and lead to the observed differences with arboretum soils. A first factor influencing street soil pH is the criteria employed by the city of Paris for its imported soils, for which the city requires a pH comprised between 6.5 and 7.5 (Paris Green Space and Environmental Division, pers. comm.), thus falling in the range of pH values likely to favor AOB. Then, the tendency of urban environments to alkalinize soil pH is a commonly observed feature and is usually explained, among other causes, by the weathering of calcium from building materials (concrete, cement, plaster etc.), the application of deicing salts on streets or the use of calcium enriched water for irrigation (Craul, 1982, 1999; De Kimpe & Morel, 2000), which could all occur in the Parisian context (irrigation during the first three years following soil-tree system establishment in streets). With initial pH values already higher than those measured at the arboretum, and subsequent potential alkalinization due to street conditions, street soils could thus reach pH values suitable for AOB activity. With the increase of ammonium availability in street soils, this could lead to much increased nitrification rates when compared to the arboretum, and an increase with time as ammonium becomes increasingly available. This increase of nitrification with time seems to be slightly offset by some pH values higher than 7.5, which could also be due to alkalinizing street conditions.

For denitrification, the abundance of denitrifiers, as assessed by the copy numbers of *nirS* and *nirK*, showed no significant trend between the arboretum and street soils, while being positively correlated with denitrification rates that showed an increase with mean street system age in surface soils. This suggests a partial decoupling between the responses of the number of *nirS*- and *nirK*-bearing populations and DEA rates. As most microorganisms are dormant in

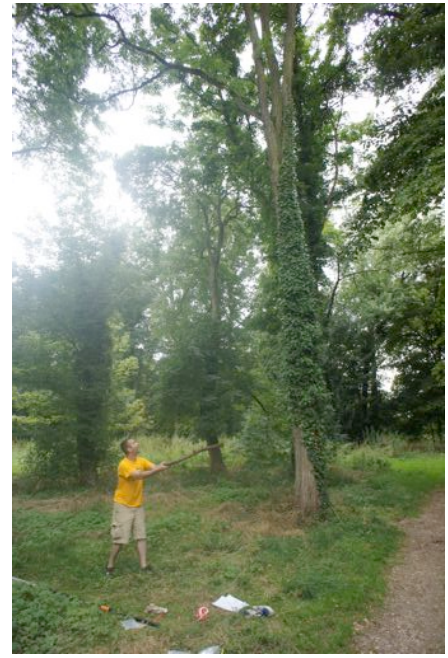
soils (*e.g.*, Fierer & Lennon, 2011) and awaiting favorable conditions to become active, this could be due to denitrifiers increasing their activity, and not necessarily multiplying, as conditions become more favorable to denitrification in street soils. In street soils, as nitrification increases, and as organic C increases with system age, more denitrification might become possible with time.

5. Conclusion

In previous works, we reported that street soils presented an age-related increase in $\delta^{15}\text{N}$, to the point of reaching exceptionally enriched values, and that root and foliar $\delta^{15}\text{N}$ also reached high values (Rankovic et al., Chapter 1 and 2). We hypothesized that, on top of ^{15}N -enriched exogenous N inputs, microbial N-cycling, especially in N-loss pathways, might further lead to an enrichment of soil $\delta^{15}\text{N}$. Here, we found that potential nitrification and denitrification rates in street soils were much higher than in the arboretum, and showed an increase with street system age. The increase of nitrification in street systems may be caused by street conditions, namely high ammonium content and circumneutral pH, favoring the growth of AOB abundance and activity. Denitrification, in turn, might be increased by increasingly favorable conditions for denitrifier activity with time, namely higher soil nitrate and organic C content. AOB abundance was positively correlated to both soil and foliar $\delta^{15}\text{N}$. Taken together, the present study suggests that increased levels of nitrification and denitrification in street soils could indeed be involved in the age-related trends found in $\delta^{15}\text{N}$ in street soil-tree systems.

In the context of a broader research on long-term C and N dynamics in street soil-tree systems in Paris, these results have several other implications. Firstly, the age-related trends observed in nitrification and denitrification parameters further reinforces the likeliness that a long-term dynamics is taking place in these systems. For N, these results suggest that high amounts of exogenous inputs enter soil-tree systems and are assimilated by trees and

microbes, and lead to increased N cycling, with likely increased rates of N losses (leaching losses, gaseous losses). Despite these losses, to which the loss of N through aboveground litter export must be added, the fact that soil N content increases with age further points towards important N inputs (higher than losses) and suggests an important N retention capacity in street soils. Finally, as increasing attention is being paid to the environmental quality of urban soils, this study confirms results reported for urban soils across the world of increased risks of nitrate leaching and emissions of N₂O, a potent greenhouse gas. To our knowledge, it is the first study, however, to provide evidence that these trends might be driven by an increase in AOB abundance and activity in non-acidic urban soils, opening the way to mitigation strategies targeting AOB in urban soils, such as pH manipulation.



General discussion

1. The long-term dynamics of Haussmannian ecosystems: a scenario

The long-term trajectory of urban ecosystems has received relatively little attention from urban ecological research. I have argued, in the general introduction, that focusing on long-term trends in C and N cycling in urban ecosystems could help improve our understanding of the effects of urban environments on ecosystems and provide useful information for their management, and that a chronosequence of street soil-tree systems could constitute an appropriate model for such investigations. Here, I will first recall the main results presented in the three chapters of this manuscript, and then use them to infer a scenario depicting the potential long-term trajectory of soil-tree systems as they experience the Parisian street life. Then, I will present data gathered on black locust plantations and pollinators, to discuss whether the observed trends in silver linden plantations are representative of more general trends in Paris ecosystems.

1.1. Summary of chapters

In Chapter 1, we saw that street soil-tree systems presented an age-related increase in soil C and N contents, as well as an increase of soil $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Foliar $\delta^{13}\text{C}$ were higher in street trees when compared to trees growing in an arboretum, and fine root densities were found to strongly increase with soil-tree system age. It was thus hypothesized that root-C could be the source of accumulated C in street soils, if the foliar ^{13}C -enrichment was transmitted to roots. For N, the exceptionally high soil and foliar $\delta^{15}\text{N}$ values in street systems suggested the deposition and assimilation of ^{15}N -enriched compounds in soil-tree systems, as well as increased rates of N cycling that would further ^{15}N -

enrich the soil-tree system N pool. This increase in N-cycling was considered to be likely because of an increase in soil mineral N content (ammonium, nitrite, nitrate) with system age. Uncertainties remained however, on potential legacy effects due to historical changes in the types of soils being imported in Paris, and further evidence was needed to confirm the hypothesis of C and N accumulation.

In Chapter 2, the analysis of soil particle-size fractions showed that in older street soils, most C and almost half of N was contained in coarse fractions (sands). The proportion of C and N contained in coarse fractions increased along the soil chronosequence, and so did the proportion of ^{13}C and ^{15}N . This suggested a long-term accumulation dynamics of organic C and N in street soils, with sources of both elements being enriched in their respective heavy isotope. The $\delta^{13}\text{C}$ of fine roots showed an increase with soil-tree system age, confirming the possibility that a ^{13}C signal is transferred from leaves to roots, and that root-C is accumulating in soils. The $\delta^{13}\text{C}\text{-CO}_2$ of soil respiration, assessed through laboratory incubations, showed a consistent increase with street system age, suggesting that root inputs imprint C cycling in street soils, and that the progressive ^{13}C -enrichment of roots is likely gradually transferred to soil organic matter (SOM), *via* assimilation of root-C into microbial biomass and accumulation of humified root material.

SOM mineralization rates showed an age-related decrease in street soils, and was lower in all street soils when compared to the arboretum. On the other hand, root-C inputs are likely to increase with street system age (as fine root density increases with time). Taken together, these two trends – increased root-C inputs and decreased SOM mineralization with time – could lead to C accumulation in street soils. The decrease in SOM mineralization rates in street systems could have several causes, among which we suggested that the interplay between root chemical composition and higher N availability in street soils

could lead to accumulated recalcitrant compounds (lignin-rich) becoming less interesting for soil microbes to degrade. In addition, specific physico-chemical and physical protection mechanisms could, compared to leaf litter, better protect root-C from microbial degradation.

Concerning N dynamics, in Chapter 2 we saw that root N concentrations were higher in street systems than at the arboretum, and were higher closer to the surface. This suggested a higher mineral N availability in street soils, and higher at the surface. Root $\delta^{15}\text{N}$ was exceptionally high and became progressively closer, with time, to soil $\delta^{15}\text{N}$. We interpreted these results as a sign of close dependence of root N uptake to N mineralization, which could be increased in the vicinity of live roots through rhizosphere priming effect. However, we found a very high difference between foliar and root $\delta^{15}\text{N}$, which could mean that, as trees age, they diversify their N sources, and that whole-tree N nutrition relatively less depends, with time, on the N assimilated from topsoil. This could be due to older tree N demand surpassing the available N stocks at soil surface, which would be consistent with the age-related decrease in foliar N content shown in Chapter 1. We proposed that the possible other sources included the uptake of leached nitrate by deeper roots, N-foraging by tree roots outside the tree pit, and foliar N uptake of reactive gaseous N forms.

In Chapter 3, we found out that both potential nitrification and denitrification rates increased with street system age, and were much higher than at the arboretum. While both ammonia-oxidising archaea (AOA) and bacteria (AOB) were more abundant in street soils than at the arboretum, the abundance of AOB in surface soils showed consistent age-related trends and was positively correlated to potential nitrification, soil mineral N contents and both soil and foliar $\delta^{15}\text{N}$. We suggested that the increase in nitrification rates could be driven by the observed increase in AOB populations, which itself could be due to increasingly favorable conditions for AOB in street soils, namely increased

ammonium content and circumneutral soil pH. Denitrification, in turn, could be favored by increased soil nitrite and nitrate content, as well as soil organic C. Taken together, these results on N i) support the hypothesis that deposited N is assimilated by soil-tree systems, which leads to an accumulation of N in soils, ii) that deposited N increases the rates of N cycling and that N-loss pathways are stimulated by street conditions, which contributes to the observed high soil, root, and foliar $\delta^{15}\text{N}$ values. Even though loss pathways are increased, the accumulation of N with time means that N inputs are higher than losses and/or that N stabilization mechanisms, possibly in microbial biomass and SOM, are involved.

1.2. Possible interpretations for long-term C and N dynamics in street systems

Concerning the possibility of long-term dynamics in C and N cycling taking place in Parisian street soil-tree systems, these results suggest several things. Firstly, age-related patterns were repeatedly found in multiple soil and tree parameters. These parameters were, moreover, measured with different and independent analytical techniques, that ranged from mass spectrometry to gas chromatography and molecular analysis. Rather simple and straightforward statistical models showed, overall, a high explanatory power of system age on these variables. This suggests that, in Paris, system age strongly influences C and N cycling parameters. In other words, based on these results on *T. tomentosa* plantations, it can be said that it is very likely that when sampling soil-tree systems in Paris, one can expect to find important differences in C and N parameters between younger and older systems. A corollary to this conclusion is that, if not controlled for, system age can induce an important variability in data. A spatial, random and non-age explicit sampling of *T. tomentosa* street plantations across Paris may have produced useful information too, but given the observed explanatory power of system age, it is probable that such an approach would have yielded rather idiosyncratic results, especially on soil data.

Most urban ecological studies, to date, have adopted a spatially explicit approach (especially the use of urban-rural-gradients, or sampling designs based on spatial grids), but relatively few have adopted a temporally explicit approach. The results presented here, as well as the studies reviewed in the general introduction, suggest that systematically controlling for system age may help detecting clearer patterns and improve our understanding of urban ecosystem processes. Of course, the spatial context of a given system is obviously important to consider too, and it is thus the development of spatio-temporally explicit approaches to urban ecosystem functioning that could prove most useful. In the context of this study, this would mean addressing how the local spatial context of street soil-tree systems may change across Paris (*e.g.*, street- or neighborhood-specific levels of N deposition, atmospheric CO₂, microclimate etc.) and modulate the effect of age on C and N cycling parameters.

Secondly, even though the age-related patterns were quite clear, in this work we have tried to be cautious in inferring their underlying causes. Early and repeated discussions with city managers made us better aware of the past and present complexity of greenspace management in Paris, and especially with respect to historical changes in the origin of greenspace soils. We have already discussed some of the uncertainties posed by potential legacy effects. Another type of uncertainty, that we have not mentioned yet, is linked to the fact that the urban context probably changes as well with time. How the atmospheric chemistry of Paris, its climate, its sidewalk structure etc., have changed over the 20th century might have an influence on the age-related patterns that we observe today, as systems of different ages might not have been exposed to the same past environmental conditions. Besides differences in imported soils, other changes in management practices could also occur over time and influence contemporary patterns. Thus, inferring a long-term dynamics based on contemporary patterns bears the risk of taking an observation artefact for an actual temporal trend – an

issue quite common in chronosequence studies in ecology (*e.g.*, Walker et al., 2010). With all this in mind, the recurring age-related trends that were found in this work, their magnitude, their convergence, and the several “stairway-like” patterns that we observed among classes, lead us to propose that the age-related trends in C and N cycling are indeed linked to long-term dynamics in street systems. How all the other factors (historical, etc.) might influence this dynamics should be addressed in future works, through multivariate analyses for example.

From the data presented here, the long-term dynamics that seems to take place is one where street trees, possibly in response to limited access to water and small soil volume to explore, increase their belowground C allocation for resource-foraging purposes (water, N and possibly other nutrients). In parallel, soil-tree systems are subjected to high amounts of deposited N, due to combustion processes occurring in the city or to animal waste. In topsoils, this N is rapidly taken up by roots and soil microbial biomass. The increased belowground C inputs through roots, as well as the increased N availability in soil-tree systems, induce important changes in soil microbial communities. They can favor the growth of microbial biomass, increasing soil activity. In the direct vicinity of living roots, the availability of labile organic compounds can increase microbial activity and potentially lead to an increase in N mineralization rates as previous generations of roots are degraded. The availability of N could make it less interesting for microorganisms to N-mine the more recalcitrant root compounds, reducing their degradation. The assimilation and retention of N in roots and microbes, and the assimilation of root-C into microbial biomass and plant and microbial necromass, can lead to a long-term accumulation of C and N.

Why would more N be available in soils? A possibility is that, in topsoils, because of deposition and increased mineralization, N is becoming available faster than maximum uptake rates by roots and microorganisms. A consequence

is that the “excess” ammonium can then stimulate the growth and activity of ammonia-oxidizing organisms, and especially bacteria, who gain advantage over archaea at high ammonium availability and who can be favored by the circumneutral pH found in urban soils. This leads to an increase in nitrification in street soils. Higher nitrate content and organic C in soils also increase denitrification, further enhancing N-loss pathways in soil-tree systems. However, if the annual amounts of chronic N inputs are higher than the amounts of losses, a net long-term N accumulation over time takes place.

All these processes, together, can lead to visible patterns in stable isotope abundances. For C, ^{13}C -enriched root inputs lead to an enrichment of SOM $\delta^{13}\text{C}$, which can be further enriched by microbial processing of SOM. For N, a $\delta^{15}\text{N}$ amplifying loop (schematized on Figure 1) could take place and lead to a very strong ^{15}N -enrichment of SOM over time. As ^{15}N -enriched compounds are deposited on soils, they are assimilated by roots and microbes. Part of deposited ammonium can be nitrified, and part of the resulting nitrate, as well as part of the directly deposited nitrate, can be denitrified. These processes lead to a ^{15}N -enrichment of the ammonium and nitrate that are available for plant and microbial assimilation. The ammonium released by SOM mineralization (root and microbial necromass) enters the same process, making the recycled available N even further ^{15}N -enriched when compared to initial inputs. As multiple iterations of this loop occur on the long term, SOM $\delta^{15}\text{N}$ values reach exceptionally high values over time.

Multiple iterations on the long-term

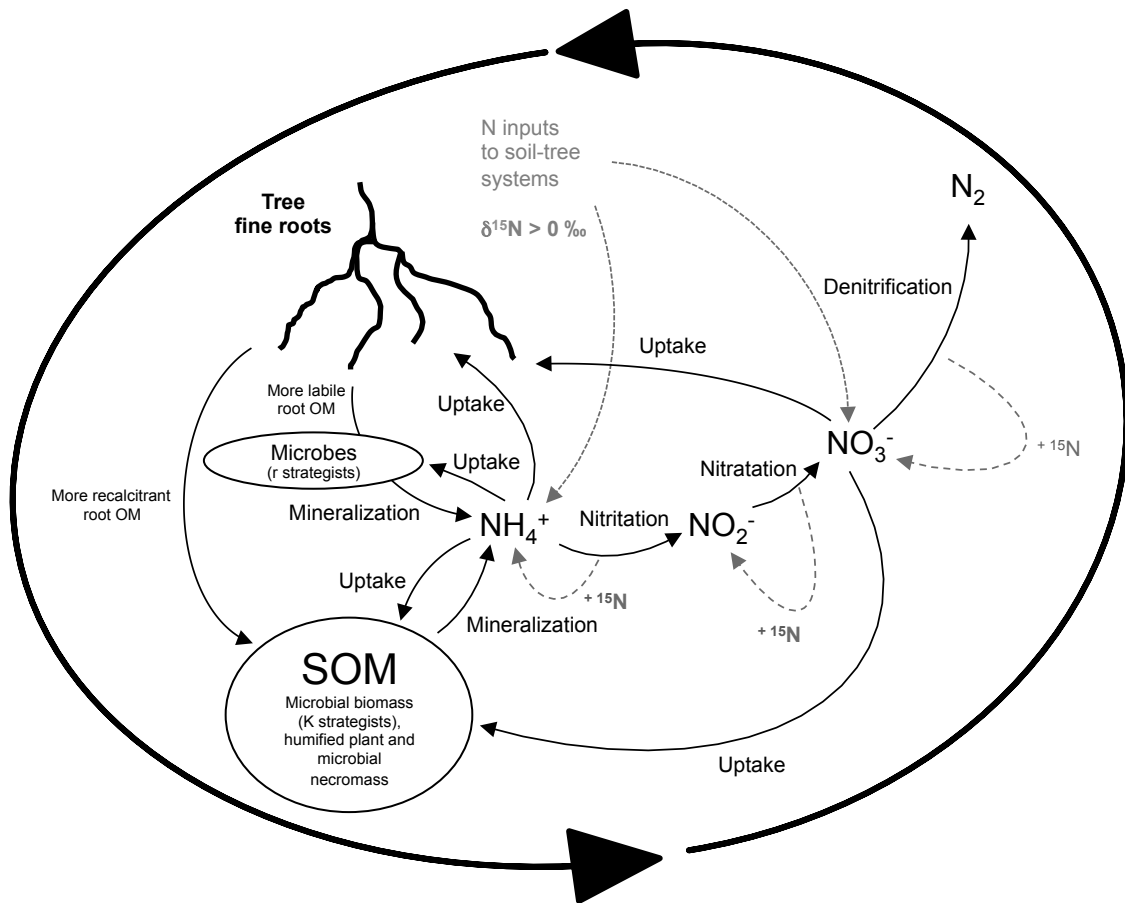


Figure 8. (Very) Schematic view of the hypothesized $\delta^{15}\text{N}$ amplifying loop in street soils. Full lines represent N movements inside soils. Dotted gray lines represent exogenous N inputs. Broken lines highlight major ^{15}N -enriching processes during soil N cycling. The view is not exhaustive nor on N cycling processes nor on isotope fractionation events.

Overall, these long-term dynamics depict systems where trees seem to be under water and nutrient stress, and where they develop strategies to alleviate these stresses. These strategies (*e.g.*, the increase in belowground C allocation), in addition to street features such as increased N deposition or soil pH, induce changes in soil microbial communities, leading to both more retention of C and N and a higher rate of N cycling, possibly involving different SOM pools and microbial communities. Where does this take the systems? Actually, the older soil-tree systems that we studied here are among the oldest in Paris, where the maximum life expectancy of trees is about 80 years. Several of the oldest trees

that I sampled have already been cut as I write these lines... The reasons for cutting trees are, in most cases, related to safety issues, because trees start to show signs of (more or less) advanced cavitation, often due to lignivorous fungi. How the water, nutrient, and the several other potential stresses that we have not addressed here, interact to make trees more vulnerable to parasites, should be addressed in future works.

1.3. Beyond silver lindens? Insights from black locust plantations and pollinators

Besides silver linden plantations, can we expect to find these patterns in other Parisian ecosystems? During this research, fifteen street plantations of black locust (*Robinia pseudoacacia* Linnæus) were sampled in Paris, based on three DBH classes, and at the Chèvreloup Arboretum. The black locust was chosen because, as an N-fixating tree (Fabaceae family), it provided a functional contrast to silver lindens with respect to N cycling. Given the C cost of symbiotic fixation for trees, we hypothesized that if reactive N depositions were abundant in street conditions, black locusts would less rely on symbiotic N-fixation in streets than at the arboretum. Since symbiotic fixation provides trees with an N whose $\delta^{15}\text{N}$ is close to 0 ‰, we expected that such changes in the rates of N fixation would be visible on $\delta^{15}\text{N}$ values found in these soil-tree systems.

On Figure 2, soil organic C content, soil total N content, and soil, foliar and root $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for black locust systems are displayed. The age-related patterns very closely matched those found for silver lindens, with an age-related increase in soil organic C and total N content. For C, street leaves, roots and soils were enriched in ^{13}C when compared to the arboretum, suggesting the same mechanisms as described for lindens. For N, soil, root and foliar $\delta^{15}\text{N}$ were higher in street systems, possibly due to the same $\delta^{15}\text{N}$ amplifying loop hypothesized above. Root $\delta^{15}\text{N}$ was expectedly close to 0 ‰ at the arboretum, but strongly

increased in street systems, and increased with street system age. However, we can see that the magnitude of root $\delta^{15}\text{N}$ increase for street black locusts is lower than for lindens, which could be due to street locusts still relying on some symbiotic N-fixation, and/or to lower rates of N cycling under locusts than under lindens. These changes could be reflected on soil $\delta^{15}\text{N}$, which also showed a lower response than soils under lindens.

Overall, these data on black locust plantations suggest three conclusions. Firstly, that the suggested long-term trends in C and N cycling in Parisian street soil-tree systems are not limited to silver linden plantations but can be found with other tree species, even with very contrasted functional traits concerning soil-tree relations. Secondly, these results suggest that the species type modulates the long-term trends, which opens the way to future, comparative works among species which could even further enhance our mechanistic understanding of C and N cycling in urban environments. In Paris, this might not be restricted to tree systems, but could also apply to grassy systems such as lawns. Finally, although they followed very similar age-related trends when compared to linden plantations, the $\delta^{15}\text{N}$ values found in black locust plantations were quite lower in magnitude. This suggests that the age-related patterns observed in street systems may indeed be the product of soil-plant interactions, and not an artefact due to legacy effects.

Robinia pseudoacacia plantations

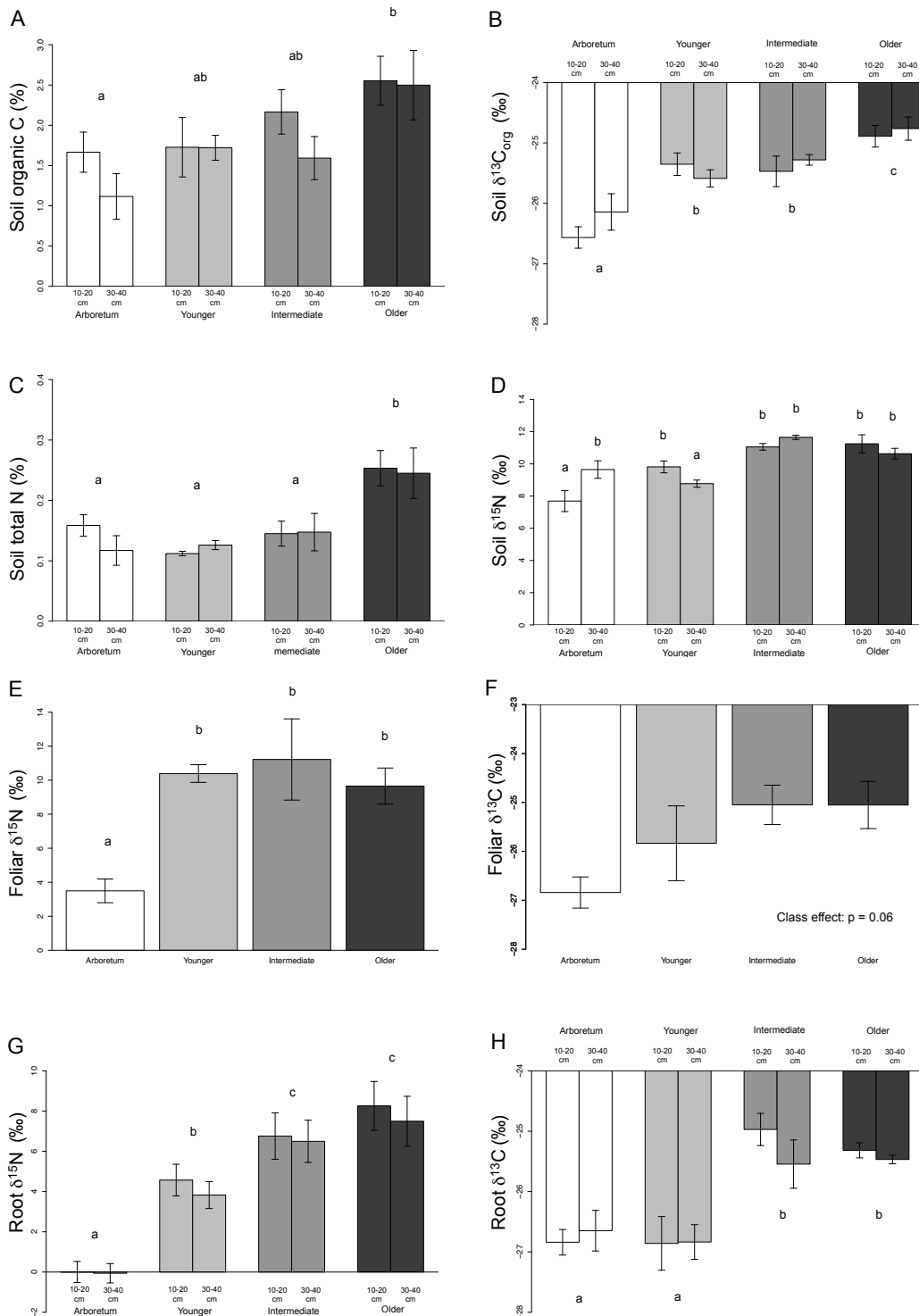


Figure 2. Summary of data on black locust (*Robinia pseudoacacia*) systems. A) Soil organic C content, B) Soil $\delta^{13}\text{C}$, C) Soil total N, D) Soil $\delta^{15}\text{N}$, E) Foliar $\delta^{15}\text{N}$, F) Foliar $\delta^{13}\text{C}$, G) Root $\delta^{15}\text{N}$ and H) Root $\delta^{13}\text{C}$. Bars show means and error bars correspond to standard error. Different letters mean that a significant difference ($p < 0.05$) was indicated by a linear mixed-effect model and Tukey post-hoc tests (not shown). For each bar, $n = 5$.

Beyond soil-tree systems, I also wanted to know whether the mechanisms of ^{13}C - and ^{15}N -enrichment that are proposed here are more widely generalizable to Parisian ecosystems. With colleagues Benoît Geslin Geslin and Isabelle Dajoz, both pollination ecologists, we hypothesized that if such trends were widespread across the city, the “urban isotopic signal” of an enrichment for both ^{13}C and ^{15}N should be transferred, through trophic relationships, to pollinating insects who solely feed on plant nectar and pollen. We took advantage of a collection of pollinating insects gathered on an urbanization gradient in Île-de-France (Geslin et al., 2013), and analyzed the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of three species of wild bees (*Lasioglossum laticeps*, *Lasioglossum morio* and *Lasioglossum nitidulum*) collected on the gradient. The bees were captured on 12 sites in the region (Figure 3), surrounded by four landuse types: semi-natural, agricultural, suburban and urban (Paris).

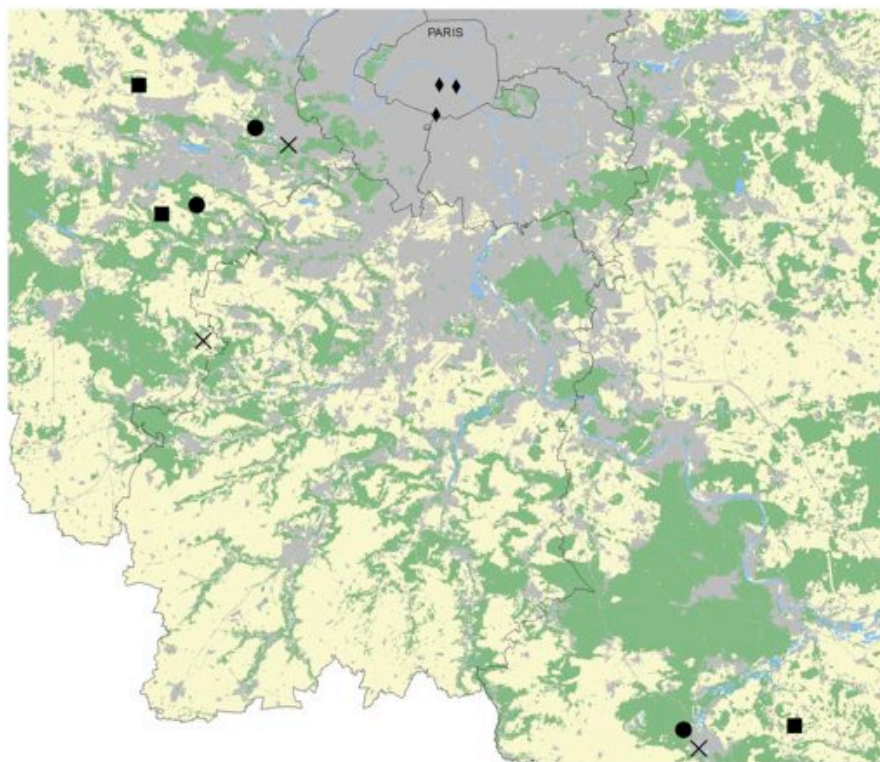


Figure 3. Distribution of agricultural (squares), semi-natural (dots), suburban (crosses) and urban (diamonds) sites where pollinators were captured. Reproduced from Geslin et al., (2013).

As shown on Figure 4, in urban sites an enrichment for both ^{13}C and ^{15}N was found in all three species (except for the $\delta^{13}\text{C}$ of *L. nitidulum*), suggesting (i) that the diverse plants on which insects forage in Paris are enriched in ^{13}C and ^{15}N , (ii) that this signal is transmitted from primary producers to their animal consumers, and can thus further imprint urban trophic networks.

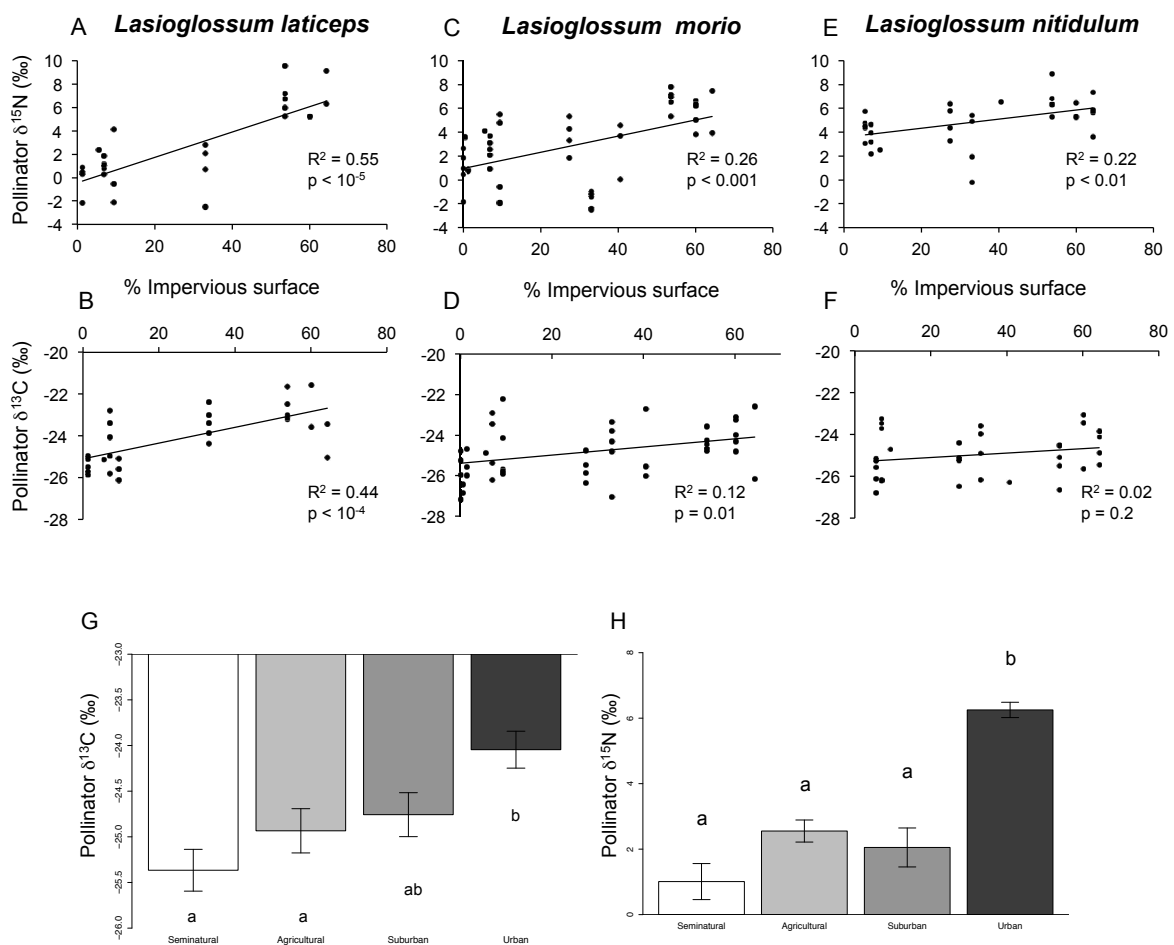


Figure 4. Summary of pollinator data on the urbanization gradient. A) to E): Regression of pollinator $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values by the percentage of impervious surface in a 500 m radius around capture sites, shown for each species separately. G) and H): Mean pollinator $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all three species averaged for each type of landscape. Different letters mean that a significant difference ($p < 0.05$) was indicated by a linear mixed-effect model and Tukey post-hoc tests (not shown).

Taken together, the results on silver linden systems, black locust systems and pollinators suggest that the ^{13}C - and ^{15}N -enrichment of plants might be a widespread phenomenon in the Parisian context, found in several types of systems. These results also highlight the fact that isotopic effects stemming from rather localized biological strategies and processes (^{13}C enrichment for water use efficiency, ^{15}N enrichment because of deposited N assimilation and microbial cycling) can feed back to, and imprint, biogeochemical cycles in whole ecosystems, from soils to animals.

2. Perspectives for future works and street plantation management

These results contribute to urban ecological research in several ways.

- (i) This study, to my knowledge, is the first to try and describe C and N cycling in street soil-tree systems, an ubiquitous type of ecosystem that can be found in most cities worldwide.
- (ii) It contributes to research on urban C and N cycling by showing strong age-related patterns and suggesting a long-term C and N accumulation in street soils, and proposes mechanisms that could potentially explain these patterns and that could occur in many other urban areas.
- (iii) It contributes to the rather small corpus of urban stable isotope studies, and reports the first values ever measured of urban root $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. It is also the first urban study to report such record-breaking soil and plant $\delta^{15}\text{N}$ values and to propose a long-term “loop” that could lead to the observed $\delta^{15}\text{N}$ values.
- (iv) The study provides the first molecular evidence that in urban soils of circumneutral pH, AOB might be a key group of organisms responsible for triggering an increase in the rates of N-loss pathways in urban ecosystems.

(v) The results on silver linden and black locust plantations, as well as on wild pollinators, suggest a widespread enrichment of soil-plant systems in ^{13}C and ^{15}N in Paris. These results are the first, to my knowledge, to show such isotopic transfers in the urban soil-plant-animal continuum, and this suggests that urban environmental features (*e.g.*, urban heat islands, depositions of reactive N) can influence all compartments of ecosystems at the elemental level and leave an “urban isotopic imprint.”

Future works on these systems will help enhance our mechanistic understanding of C and N cycling. Concerning C dynamics, more work is needed to elucidate the underlying mechanisms of C accumulation, and we can identify some avenues for future research. Firstly, ^{14}C measurements could provide definitive evidence of accumulation and estimates of the proportion of inherited C from accumulated C. Chemical analyses of SOM (on the different soil fractions for instance) could also shed light on the form of accumulated C, and whether it is stored as non-degraded plant (root) material or in microbially processed forms. Opening the microbial ecology black-box of SOM degradation in street soils could also help better understand the potential long-term microbial dynamics that lead to C accumulation. On this last point, more data have been acquired on soil microbial communities on the chronosequence: total bacterial, fungal and archaeal populations have been quantified by quantitative PCR, their respective structure has been assessed through molecular fingerprinting (T-RFLP), and a community-level physiological profiling technique (MicroRespTM)⁹ has been applied to seek for differences in their potential catabolic activities. This dataset, when analyzed, will help investigate for long-term changes in microbial communities and further infer potential microbial mechanisms involved in the accumulation of C in street systems.

⁹ For T-RFLP and MicroRespTM, in particular, I am very much indebted to Thomas "Z" Lerch for his friendly guidance and close collaboration.

Concerning N dynamics, we have mentioned that quantitative assessments of N stocks and fluxes would be needed. A clearer understanding of how much N is available in tree pits, how much N is lost (leaf litter export, N-loss pathways), how much N is needed by trees, will help better understand the street N cycle and whether trees are N limited or not. The reality and magnitude of foliar N uptake in Parisian streets should be assessed, as well as the fate of this assimilated N and where it is allocated. Other tree physiological processes pertaining to N (*e.g.*, translocation) could be studied, too. In soils, we have only analyzed parts of the N cycle, and the other steps (*e.g.*, nitrification) could be further analyzed. Data on N mineralization rates, in particular, would be important here, and help better link C and N cycling in street systems.

On this point, a study of mycorrhization in street systems may also provide important insights. Mycorrhizal symbiosis has been proposed as key mediator explaining soil-plant responses to increased N depositions (*e.g.*, Aber *et al.*, 1998) and a key component of soil C accumulation. As mycorrhizal fungi rely on root carbohydrates, and are highly competitive for mineral N uptake in soils, an increase in fine root density and N availability could lead to an increase in the biomass of mycorrhizal fungi, leading to less mineralization of SOM and retention of N in soils. A collaboration was established with the University of Padova (Italy) to assess the mycorrhizal status of the studied silver lindens, and its preliminary results showed a strong age-related increase in the number of mycorrhized root apices in street soils (Figure 5)¹⁰. Further work on street mycorrhization in Paris is undergoing in the MycoPolis (funded by Paris 2030 Programme) project led by Patricia Genet and its results could provide important insights to better interpret the long-term trends in C and N cycling in street systems, and better link them to tree N-foraging strategies. Finally, we solely

¹⁰ The study on mycorrhizal symbiosis was principally conducted by Linda Scattolin, Assistant Professor at the University of Padova. An accomplished triathlete, Linda deceased in a tragic accident while training in South Africa. We honour her memory.

focused on N in this, but other nutrients should be studied in the future, as carbon-nutrient and nutrient-nutrient interactions are key aspects of the coupling among biogeochemical cycles¹¹.

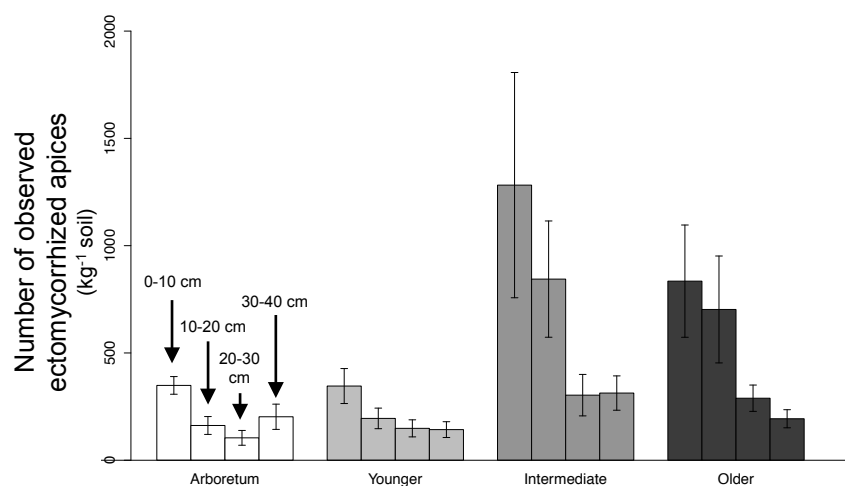


Figure 5. Estimated means of ectomycorrhizal apices per kg of soil at four depths in silver linden systems. Data acquired by L. Scattolin and collaborators.

Concerning the management of street plantations, we propose several perspectives based on this manuscript. At the moment, these are more speculative reflections than precise recommendations, and they require further discussion with city managers, and possibly experimentation.

- (i) **Questioning the hypothesis of soil exhaustion.** From the age-related trends in C and N content and microbial activity, we suggest that the current hypothesis of a temporal decrease of soil fertility is not verified. On this basis, the current practices of soil replacement and disposal could be questioned. On this point, it is important to note, however, that soil fertility is not only concern for city managers. With

¹¹ With the kind guidance and collaboration of Florence Maunoury-Danger and Michael Danger from the Université de Lorraine, silver linden foliar P concentrations were analyzed and will be put in regard of soil P concentrations in future works.

time, several urban pollutants can also accumulate in street soils, and might represent health hazards if, for instance soil particulates are ingested. With Katell Quenea and Maryse Castrec-Rouelle, we have found that several trace metals (Zn and Pb in particular) showed strong age-related increases in street soils (Figure 6). The consequences of these results for soil replacement will need to be further discussed with city managers. Furthermore, future works should analyze how pollutant accumulation influences soil-tree processes.

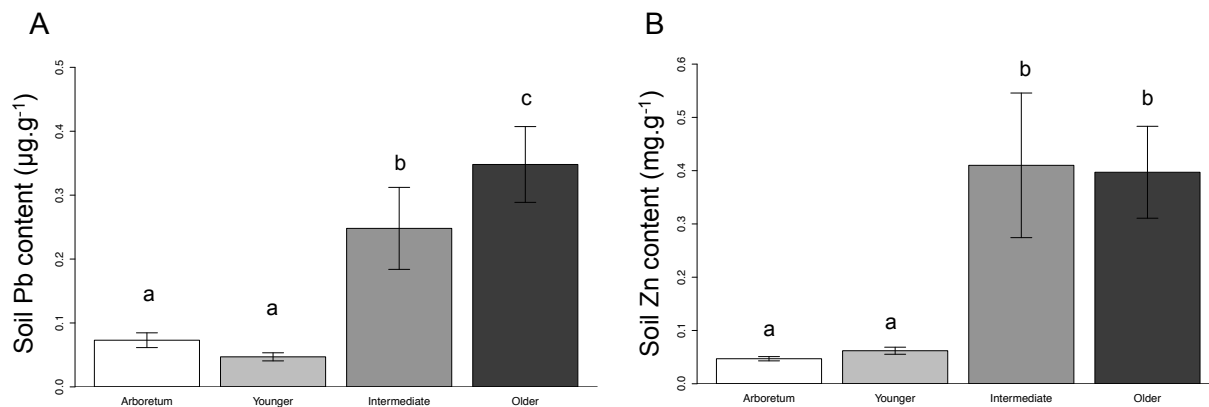


Figure 6. Mean soil concentration for A) Lead (Pb) and B) Zinc (Zn). Different letters mean that a significant difference ($p < 0.05$) was indicated by a Kruskal-Wallis test followed by Wilcoxon-Mann-Whitney tests (not shown). For each bar, $n = 10$.

(ii) **Increasing the volume of tree pits.** We have hypothesized that the limited soil volume of tree pits could participate to water and nutrient limitation of trees. It could be tested whether trees fare better with increased tree pit volumes, that could retain more water, have a higher N stock and offer more space for root exploration. The current trends in Paris, where elected officials are pushing for even more planted trees despite less available space on sidewalks, are currently the opposite, and we suggest that this could be questioned with respect tree health. For water, irrigation practices could also be tested.

- (iii) **Increasing N retention by planting understory plants.** In several cities worldwide, there is a trend of “greening” the soil surface surrounding tree trunks by planting ornamental plant species. We suggest that this practice might not only have aesthetic benefits, but could provide soil-tree systems with understory species that could uptake the “excess” N and increase its retention in plant biomass, thus potentially decreasing the rates of nitrification and denitrification. Species that could slightly acidify soil pH might also make soils less favorable to AOB.

3. “Global change in your street!”: Ecology *in* the first urban century

Despite lots of accumulated knowledge on the causes and consequences of environmental degradation worldwide, the environmental crisis is enduring and deepening on many levels. There is a tendency, especially in scientific audiences, to believe (or hope?) that the environment keeps degrading because evidence is lacking, or is not understood enough, or is not well communicated enough, or that we have yet to find the technical fix that would enable to solve the issue. The reality is probably much more complex, and there is a myriad of factors, rooted in human collective action, that can make a given environmental issue persist despite vast amounts of available knowledge on it (see for instance: Laurans et al., 2013; Rankovic & Billé, 2013 – Appendices 3 and 4). Fundamental inconsistencies in sectoral public policies, how international trade is organized and governed, or good old power asymmetries among actors are all components of what, in the biodiversity arena for instance, the international jargon calls “underlying causes” (Convention on Biological Diversity) or “indirect drivers” (IPBES) of biodiversity loss. These factors should receive acute attention if we wish to solve environmental issues (for more argumentation on this point, with the example of IPBES works, see Rankovic et

al., 2016 – Appendix 5).

However, I think that the importance of worldviews and imaginaries (Jasanoff, 2015) in shaping human collective action should not be underestimated. If the exclusion of non-human entities from human politics is indeed one of the anthropological roots of the environmental crisis (*e.g.*, Latour, 1999), then spreading the worldview of ecology might be a non-trivial contribution to environmental conservation (Descola, 2014). Here, I think that beyond the engineering aspects mentioned above, urban ecological research can be important precisely for this objective. As recently put by Janzen (2015), “[o]ur legacy as carbon scientists may be measured not only in tonnes of carbon stashed away, but in the restorative, hopeful images planted in human minds.”

Cities constitute the local environment of an increasing share of the world population, and urban ecosystems may be the most familiar ecosystems for a majority of people (Pickett, 2003). As Miller and Hobbs (2002) put it, many of the ecological processes seen in popular documentaries on television also occur in one’s own backyard, and this also applies to streets or urban parks. Quoting Aldo Leopold, they remind us that “the weeds in a city lot convey the same lessons as the redwoods”, and that an increased perception of ecological processes in urban areas could lead to a broader perception of ecological processes that occur in the rest of the planet (see also McKinney, 2002; Miller, 2005). Telling ecological stories about the environment where people “live and work” (Miller & Hobbs, 2002), and calling attention to entities with which people interact on a day-to-day basis thus appears to be of strategic importance.

This has important consequences for the engagement of the urban ecologist as a researcher and a teacher. As Pickett (2003) notes, conducting urban ecological research first requires to gain access to the sites to be studied, and this constitutes a first opportunity to exchange with other stakeholders, share the perspectives of ecologists and learn from other actors. Urban ecological

research is also “visible” to people, and discussions with curious pedestrians are privileged, serendipitous moments of sharing ecological research with people (Pickett, 2003). Moreover, an important part of city dwellers are children, and using urban ecosystems as learning tools can develop an early sensitivity to the subtle processes at play in the biosphere and an early sense of care (Chawla & Salvadori, 2003). This very much applies to biogeochemical cycles, probably amongst the least known features of the biosphere by the “general public,” but at the heart of some of the most important challenges of our time such as climate change, biodiversity loss, and food production – to name just a few...

Taken together, these considerations give urban ecology an important potential to contribute to the contemporary challenge of paying a greater attention to non-humans’ own agency and how it is meshed with human actions (Latour, 2014). Case-studies in urban ecology can constitute powerful illustrations of complex ecological dynamics by showing that even the most “man-made” entities, those whose essence is the most taken for granted, actually have their own dynamics and are full of surprises, and that there is a lot to be told on their history and its links with our own (Cronon, 1993). Here, even though more work is needed to obtain a clearer understanding of the processes occurring in street systems, I hope that I was able to show that even such apparently mundane systems like street soils and trees can illustrate some of the questions that haunt the ecologists trying to understand the biosphere and its future.



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Appendix 1

Rankovic et al. (2012)

Rankovic, A., Pacteau, C., Abbadie, L. (2012). Ecosystem services and cross-scale urban adaptation to climate change: An articulation essay, *Vertigo*, Special Issue 12, <http://vertigo.revues.org/11851> (in French)

CHAPITRE 1

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	<p>42 4 (83 / 52 33 . 4%83 : . : X 83- j- 8&. , A 3& 8%&) . (& & 4 , - 415&&4&, 836 3& 4&. 0 2& 82 85 %83 02/ ; :- 83 45&30/56 . 4j4& ((2 6: 30 2 &5 , 3A(2 40 2&U& 0, 8%8% - . 582%; 3h0 2 3& 4 832 315&3 , : 3h, A/ 4%&) , 852h, 0 / ,, 54/ . 4 / 30) : 2 15& 5 & / 2& 53 4&833) 8%2 15&B- 3 / 530 / 522 / . 3 4&2 15 3- & 44/53 832 315&3 34 3&. . / 4&C 1 5 3/ . 4%: Th 02/ ; :- 415&3 57 52% 4 5 & 41 5 0 / 522 & 4j 4& ((2 6: 3 0 2 , &) . (& & 4 , - 415&</p>
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4	<p>A7 54%& 2(83% . 3 / . 804/ . %A 2 3425 452&3Bo 2 &U& 0, &, 6 ,, 8%& / 0&) (5& / . 3425 43/ . 3 834 - 8%& %2 . (8%83& 5U%80 , 5 8&. 3 & 3 . 43 52%83) 283%& ?3 50: 2 8523 525 33&, & & 4 45&6 82 845 . & %0 4 4/ . h- / . %2& / 04 5 & 4 54 3h5 . / 04- / . %2& 15& 3 , A%04 4/ . % 43& 2&5, 4 2 852& & 4=V D F 84 - 0, 158%&) . (824/ 54, 83 834 - 8%8%2 . (&C</p>
	<p>833/ , 54/ . 34&) . 15&3 83/ . 40 3, 833 85, 3 / 8& 3h %30/34/ . 0 / 52, A%04 4/ . 83/ 54, 3 . 34 454/ . . &3 / 5%83 . 3425- & 43X. . 8230 856& 4&. 4&2&. T&5 0 2 &U& 0, &, A 34 454/ . . , 3 4/ . %A / 29/ . 3%&0, . X 4/ . h , / . (4&2- 8B& , / 2 80 2&U& 0, &4/ 53, 83 / 52 33&523 %& 5 8 . 40, 53%& , & 43% / 6& 44/ 53 83 . 30 2/ : %2h 5 . &U&2 80 2/ 30& 4 352, % 30/ . , 4 & & 5h . 3C & j- &%83) . (& & 43/ 2/ . 3 4/ . . &3% . 3 A- : . (& & 4%54&22 4 2&0 856& 4 (, & & 4 j 4& / - 023 / - - 8%833 424 (83% / 5 83B- j- 83 A, 3 52/ . 4&. 35 4&%83 / . 3: 15& 83&. 4&2- 83%83 42 4 (83 W52&3 352 830 , . 3%& / . 3425 4/ . 0 2&U& 0, &C</p>
C	<p>5 315& A 8245%& , - 415& 5(- & 4&2 0 %& & 4 6& , A/ (. & & 4%& A / 29/ . 4& 0 / 2& 5 . 83/ , 54/ . &34%& 2 %5 2& %52 8%86 8%83 . 6834 33& & 43&. 0 26, ; (. 4 , 83 . 6834 33& & 43h 2 / 4 4/ . 4& 0 / 2&, 80 , 532 0 %8B% . 3 , / 2834&2 80 2&U& 0, &, &34%: Th 2 & / - - . %% 54, 3&2 %83&33& 83h0 , 53 / 524&2 / 4 4/ . C</p>

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 /- o: 446 4 %A. &4&, & oo2/) & & 5U 542&g 342 4 (&g %A%o4 4/ .
 o,53 , 33 15&g G . . &o&54 15& 4 - &2 , A. ,83& - 3: 45 %&2 &g

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 - 3 . : . - / . 3 . : &33 2& / . 3425 2& %&3 342 4 (&3 %A%04 4/ .
 52 . &3& 3 . 4& o 24&352 ,&3 : /3834- &3 3& ,&o/33 ,&- 3
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 . Y5& & ,&3 / . & 4/ . 3 & 4&2: /3834;-& 3 & (3 3 4 352 ,&3 45U &4
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 / . 4/ . . & & 4 %& &3 %&2 &23 G 5&, &3 - /%X 4/ . 3 44& %2& &
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 2 o/. %2& 5A4& %/. %&3 : /3834;-& 3 % 3 ,& % 2&%&,A%o 44/ .
 52 . & % 3 15&, &3424: (& ,&3. 4:(2&2 G &5U o/522/ . 4,3 2 o/. %2&
 h. /3 44& 4&3 G H4 &- j- & 3A,3 3/ . 4 &5U- j- &3 /24& & 4 - o 4 3
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 5) . (& & 4 , - 4 15& 52 . &/ . 52 402/ ,& & 44/24 %& / .
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A45%&%&3 3&26 &3: /3834:- 15&3 52 . 3 &34 & /2&0&5 %6&/00: & /- - &3/5, (. : & . 42/ %5 4/. %&. /- 2&5U42 6 5U&U34& 4352, &3 2 ,&3 %&3 &30 &3 6&243&4%&, 6:(: 44 / . 52 . && (: . : 2& -3 0&5 %&42 6 5U /2%& 4, 15&34/. %&- . ; 2& . 4 (2 46& &3 42 6 5U3/ . 4 %&0,53 %30&23; 3 % . 3 %&3 2&65&3 %A /, / (& %&0) 83/, / (&6: (: 4 , & %& - : 4 / 2/, / (& %A 8%2/, / (& %A 2 / 2 5,45 2& %A- : . (& & 4 %& (&34/ . & 62/.. && . 4, & / 5 & / 2&%A / . / - & %&, & 62/.. && . 4 & . &34 03 35202& . 4:4. 4% . . : , %6 &234: &4, /-0 ,&U4: %&3 15&34/ . 3 0/3 &3 - 3 &34 . : - / . 3 5 .) . % 0 15 & 42 6& /24& & 4 , &3 42 6 5U %& 2&65& & 15 &Ub, 15&0&54j 42&, &- . 15& %&0&230& 46&3 . 4:(2: &33 52,1 5&34/ .

2 „& 523 ,&3 4&24/ 2 &3 52 . 3 3/ . 4423 0&5 2&0z 3& 4:3 % . 3 , &3 2&)&2)&3 0/24. 4352, &3 3&26 &3: /3834:- 15&3 &, &3 / . &2 & 4 &33& 4&, & & 4%&3- , &5U. 452&3B/ 2j 43 9/ . &3) 5- %&3 &4 C&43& . 452&3 B 83 (&3 (2 / , &3CB) &26 2 &4 , C H 35 4& 3 , &3 46 5U %A /, / (& %&3 - , & 5U 52 . 3 3&3/ . 4- 5,40, : 3 &3 6. (4 %&2 . ; 2&3 . . : &3 , 3 2&34& 40/ 52 , 0,50 24 %&3 204 3 &40&5 / 2&. 4:3 6&23 %&3/ T 4 3/0: 24/ .. &3 / 524. 4, & / . &043& , &j 4& 5 & 4& %&3 02/ 504/ . 3 %&. /- 2&5U)&2)&523 &4024 &. 3 & H 57 0&H- & 3 &4 , C&4%&(&34/.. 2&3: 4 435. & 3B! / 5. (C

d . /4& / . . 3 3 . & , 3&5, &05 , 4/ . 02/0/3 45. & 2&65& %&3 3&26 &3 2& %53 02 , &3 % : 2& 43480&3 %A /3834;- & 352 . 3 &34 &, & %& / , 5. %&4 5.)-2 IC &- . ; 2&. 4:2&33. 4&, &3 54&23 %6& /, 00& 45. &0 02/)& 30: X1 5&& . 452 . &0/52 , 3 3&2, &3 3&26 &3 , &52 23 / . . && . 4 / . 33 4&%A / 2%h 3&%&. %&2 15&3 02/ ; - & 3 , &3 3&26 &3: /3834:-1 5&3 0&56& 4 / . 42 5&2 h 2 3/5%2&5 . 6 &5 %&, 6,, & 053 h %& 4X&2 , &3 480&3 %A /3834;- & 3 2& % 4 &3 3&26 &3 , 3 2&; 6& 4 . 3 3 U3&26 &3 2& %530 23&04480&3 %A /3834- &3B , & 5 C

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Z, x %5 4/. %5 25 4 ,&3 352 &3- /,,&3 B/,3./ . - o&2 : , 3: 3C&4,
6:(: 44/ . o &2 &44&4%&2: %5 2& & 6 &5% & 25 4 :h, 2 5, 4/. E

Z,&%2 (& %&3 & 5U%&o,5 & ,&3: / 3834;- &3 52 . 3o&2 &44&4%&2&4& 2
,&3 o2 o 44/ . 3 &4%&6 5&2,& 5 o2 :6o /42. 3o 2 4/. :6 4. 4 . 3 ,&3
o2/ ; -& 3%&o/,,54/ . %&3 / 523 %&5U ,&3 & 5U%&25 33&, & & 4&4%&3
352) 2 (&%&3 3834- &3 %&6 5 4/. %&3 & 5U53 &3,/ 23 %&3 / 24&3 o2 o 4
4/ . 3 B/ 2315&,&3 3834;- &3 %&6 54/ . %&3 & 5U53 &3 %/- &3 415&3 &4 %&3
&5U %&2 53 3 ,& & . 4. &3/ . 4o3 %: / 5o,: 3E

Z,&42& -& . 4 %&3 &5U 53: &3 ,&3 9/. &3)5-% &3 . 452&,&3 /5 24X &,&3
o&2-& 44&4%&o52&2,&3 &5U 53: &3 B/. 3/-4 / . %&, - 4; 2&/ 2/ . 15&
&43 3,4/ . %&3. 542& . 4 3 2 ,&3/ 2/ . 3-& 3%: o 43%&3o 24 5,&3E

Z,&3 6,& 523 5,452&,&3 &42 2 46 &3 ,&3 &3o &3 6&243 52 . 3 3/ . 45. :;:
- & 4- T&52 %&, 15 , 4 %5 %&2%&6 & , 3 / 52 33& 4 %&3 / o o / 245. 4 3
%&/ 3 23&4 %&3: 4& 4&

& 3 3&o4448o&3 %&A / 3834;-& 3 %& 4X: 3 o2 ,&3 54&523 3/ . 4 ,&3 2 2&3
%&A, (. & & 4 ,&3 o&/ 53&3 %&3 o 2 3 ,&3 o 2 & ,&3 / 2&34; 2&3 52 . &3 ,&3
4&2&3 5,46: &3 52 . &3 ,&3 39/ . &3)5-% &3 52 . &3 , &3 / 523 %& 5 , &3
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352 , &3 o 445 %&3 2&3o& 46 &3 %&3 % : 2& 4348o&3 %&A / 3834;- &3 h 2& %&2
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h , o2/ ; -4 15& %&, A%o 44/ . . 3 , & %2& %& & , & o 2 , &3
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15 o2 3& 4& 4, A 4: 2j 4 , &o, 53 %2 & 4 / - - & . / 53, A6/ . 3 3/ 5, (. : 5
%&3 353 , &3 2&65 &3 &U) 534 6&3 352 , &3 5 T&43& , & 4 . &U 34 . 4&3 o2; 3
/ 53o 2/ o / 3/ . 34/ 54&/ 31 5& 15&3 ; :- & 43 3353 %& , 44 2 452&

/ 53 . & 42 &2/ . 3 o3 %& , 15&34/ . -3 / . o&54 : (, &- & . 4 o& 3&2 5U
: / 3834;-& 3 4&23 15 o&56& 4% 35. & &24. &-& 352&% . 5&2 , 65, : 2 , 4: 5U
/ . %4/ . 3B6/ 2o 2&U& o, & / 34 . 9 &4 , C

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%A 6 o/ 42 . 30 2 4/. &4 h , A- 2 (& 00/ 24: o 2 , &3 2 2&3
A6 o/ 42 . 30 2 4/. &34, &o) : ./ - ; . &%&42 . 3 &24%& 5 6&23, A4 / 30); 2&
%&05 3, &3 3&34- &3 3/, o, . 4&3 , A6 o/ 2 4/. %&, & 5 %&3 3/, 3&4, 42 . 3
o 2 4/. %&3 o, . 4&3 H, &&345. - /%5, 4&52 - o/ 24. 4%5 - 2/ , - 4
) B C2 00/ 24&%&3 3/p, A6 o/ 42 . 30 2 4/. 52 . &o&54 2: &2
%&3 W 3 3 %& 2 l) &52 h, 4& o: 2 452& . : 2 &52&%& c h c o 2 2 o
o/ 24 5U& 6 2/. 3 & , &4 5U%A6 o/ 42 . 30 2 4/. &34, A. %&3 4&523
- T&523 %&, A5(- & 4 4/. %&3 4& o: 2 452&3 %52 &3 & 6 ,, & &4, &3 &30 &3
6&243 52 . 3 3/. 4 (: : 2 , & & 40, 53 2 3 h / 8/ , : 4 - &352 15&
, &3 9/. &3 h / 56&246: (: 4, : 4 & 4& - / 8& . & c o, 53 2 l) &3 15&, &3
9/. &3 3 . 3 / 56&246: (: 4, B 4 o 2) C&45. &% : 2& &%& c
: 4 - 3&& : 6 %& && 42&%&3 o 2 3 52 . 3 &4, &- , &5 f4 , & 4/ 52 h
/ . 42 , B (C . 3 15 A , & & H3o (. & CB /- &9 &4 , C . &2
B C 4& 45. &3- 5, 4/. . 5- : 2 15&o/ 24. 4 352, 6 ,, &%& &7 !/ 2
&4 / . , 5 . 4 15&, /- . 3/. %&o, . 4 4/. %A 2 2&3 &4 %&4/ 452&3 6: (:
4, 3: &3 o&2- &42 4 %&2 %5 2&, 4& o: 2 452&%&, A 2 52 . %& c &
- / 8& . & &4 T 3 15& c % . 3 &24 . 3 15 24 &23/p, &o/ 4& 4 &%&6: (:
4, 3 4/. &34, &o, 53: , &6: &3 3- 5, 4/. 3 . 5- : 2 15&3 o/ 52, 2 (/ . %&
.) &34&2 35 (; 2& 4 15&, 6: (: 4, 3 4/. %&4 53, &3 4/ 43 %&3 & 42&3
6 ,, &3 / 542 4 & 3 %&/ 242) 5 & & 4 , - 4 15& h 5. &%- . 54/ .
%& c o 2 2 o o/ 24 h 5. 3 : . 2/ 3 . 36: (: 4, 3 4/. B ,, &4 , C
/ 52 & 15 &34 %&, A- 2 (& , &3 4 5U %5) (/ L 2 . / 2&34
, - 4& 2 / T& 4 B C / . 4 &34: 15&, A5(- & . 44/ . %& ? %&
, / 56&2452 %&3 2 2&3 B/ 4 & 62/. 47 3 2 2&3 o 2 f4- & . 4 Co/ 52
24 2: %5 2 &, %o& 3& 4/ 4, & : . &2 (& %&) 5 (& &4 %& , - 43 4/ .
%& h ? B) & 23/ . &4, C / 52 5. &o, 53 (2. %& & X 4:
, %30/ 34/ . %&3 2 2&3 % 4 j 42&/ 2 & 4 && / . 4/ . %&3 6& 43 &4 %5
3/ , & / 5 T 523 o/ 52) (/ , : 4: &34: 15 A. , 2 (& 2 2&%& 47 4
4/ 2 345: h, A 5 &34 %5. &2 3 %& && 21 5& 48 o1 5& %&, 6 ,, & o/ 564
2 %5 2 &, %&. %&. . 5&, && : . &2 (& %& , - 43 4/ . %& h ? &4, &3
%&. %&3 %&o 3 %& h ? 2 / . 42 , &3 2 2&3 345 3 h, A&34 %&3 f4
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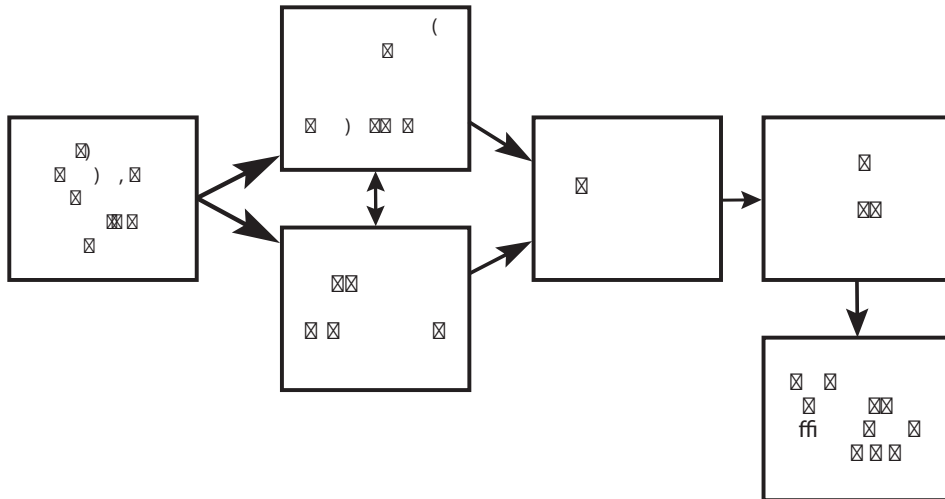
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B	<p>Z 5 . 44: & 415 , 4 %& & 5= Y5U%& & 24, 3 . 43 & 4%& 834 %&g Z 00/243%& & 24, 3 . 43= & 2452 4/. %&g 8 , &g %&g. 542- & 43 Z 2/ 33& & 4%&g%: o& 3&g: . & 2(: 415&g h 53& %& & 42& 4 Z /,, 54/. %& A 2 : & h, & 42& 4 & : - 33/. %& %/U8%& 2 / . & 4%& : 4) . & h 53& %& % /- o/ 34/. o /,, 5 . 43 4 / 30) : 215&g Z- 33/. %& /- o/ 3/ 2 (. 15&g 6 /, 4, 3 & 4%A: 2/ 3/, 33 & / . % 2&g Z & 42 4%&g; &g. 46&g Z 47% 5 4/. %&g; &g . 6 3 6&g</p>

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Appendix 2
Authorization to do fieldwork in Paris

ATTESTATION

Je soussignée Patricia ORSINI, Directrice Adjointe de la DEVE, autorise Monsieur Aleksandar RANKOVIC à procéder à des prélèvements de sol urbain au pied des arbres d'alignement à Paris.
Ces prélèvements sont réalisés en 2011/2012 dans le cadre de sa thèse pour l'étude de l'évolution des microorganismes des sols urbains et de leur composition.

Paris, le 30/10/2011

La Directrice Adjointe
des Espaces Verts et de l'Environnement


Patricia ORSINI

Copie : Christophe BALLOZ

Appendix 3

Laurans et al. (2013)

Laurans, Y., Rankovic, A., Billé, R., Pirard, R., Mermet, L. (2013). Use of ecosystem services economic valuation for decision making: Questioning a literature blindspot, *Journal of Environmental Management*, 119, 208-219



Review

Use of ecosystem services economic valuation for decision making: Questioning a literature blindspot

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ABSTRACT

Ecosystem Services economic Valuation (ESV) is often seen as a tool that can potentially enhance our collective choices regarding ecosystem services as it factors in the costs and benefits of their degradation. Yet, to achieve this, the social processes leading to decisions need to use ESV effectively. This makes it necessary to understand if and how ESV is or is not used by decision-makers. However, there appears to be a literature blindspot as to the issue of the Use of Ecosystem Services economic Valuation (UESV). This paper proposes a systematic review on UESV in peer-reviewed scientific literature. It shows that this literature gives little attention to this issue and rarely reports cases where ESV has been put to actual use, even though such use is frequently referred to as founding the goal and justification of ESV. The review identifies three categories of potential UESV: decisive, technical and informative, which are usually mentioned as prospects for the valuations published. Two sets of hypotheses are examined to explain this result: either the use of ESV is a common practice, but is absent from the literature reviewed here; or the use of ESV is effectively rare. These hypotheses are discussed and open up further avenues of research which should make the actual use of ESV their core concern.

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1. Introduction

High hopes have been placed on economic valuations to influence policy for coping with the accelerating degradation of ecosystem services and biodiversity (NRC, 2005). This was reaffirmed by the release of *The Economics of Ecosystems and Biodiversity* (TEEB) report, during the Tenth Conference of the Parties (COP) to the Convention on Biological Diversity in Nagoya in 2010: economic valuation is expected to serve as a governance resource that could change our individual and collective choices. The COP report itself⁵ recognizes economic valuation as a key tool for a more effective mainstreaming of biodiversity. In many publications (e.g. Randall, 1988; Daily et al., 2009) the 'measurement' of monetary

values that reflect the social importance of ecosystem services is seen as a prerequisite for better management decisions. Heated debates have been ongoing for many years. In 1997, ecologists Myers and Reichert (1997) made the diagnosis that 'we don't protect what we don't value'. In 2008 the TEEB Interim Report argued that 'you cannot manage what you do not measure' (p. 8). On the contrary, economist Heal stated: 'Valuation is neither necessary nor sufficient for conservation. We conserve much that we do not value, and do not conserve much that we value' (Heal, 2000). Vatn and Bromley (1994) made a similar assertion, claiming that 'valuing (or pricing) of environmental goods and services is neither necessary nor sufficient for coherent and consistent choices about the environment'. Balmford et al. (2011) even made it a positive statement: '[T]here is validity in calling for societal choices, especially in the domain of environmental decision-making, to be made without recourse to valuation or with the results of a cost-benefit analysis being a single component in a larger body of evidence'. Though the debate is obviously still lively today, it is also undeniable that international talks and publications now often promote ESV (Ecosystem Services economic Valuation) as a tool susceptible to make key contributions to biodiversity and ecosystem services protection. Questioning the supposed pragmatism of ESV, while standing clear from ideological statements, is the overall objective of this paper.

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Ecosystem Services economic Valuation (ESV) methods have been the subject of a large and fast-growing literature since the beginning of the 1990s (e.g. Adamowicz, 2004; Eftec, 2005; SCBD, 2007; Liu et al., 2010). Yet, economic valuation is in any case not sufficient in itself: if it is to be more than just an intellectual exercise it needs to be considered as a resource for policies and projects design, as it has been acknowledged for a long time (Pearce and Barde, 1991; Pearce and Moran, 1994). The hope that it will become an efficient political lever to alleviate biodiversity and ecosystem services erosion supposes above all that it actually be used for decision-making (OECD, 2002).

For this reason, one of the key issues relating to the development of ESVs is understanding if and how they are used, or expected to be used. Fisher et al. (2008), Gowan et al. (2006), Navrud (in OECD, 2002), Pearce and Seccombe-Hett (2000) and Liu et al. (2010) have underlined the salience of this issue. Others have exposed pessimistic views on the use of cost benefit analysis for European environmental policy (Turner, 2007) or the World Bank (Warner, 2010). Navrud and Pruckner (1997) observe that Europe hardly ever uses ESV. Pearce and Seccombe-Hett (2000) deem that for green accounting indicators, 'while there has been a considerable international "push" for green accounts, it is not obvious that they have met the high expectations of their advocates' (p. 1423). OECD (2001) notes that 'although fairly common in the environmental economics literature, valuation techniques have remained somewhat peripheral to environmental policy-making on major issues' (p. 11). Turner et al. (2003) regret that the qualities required of economic studies for the purposes of informing decision-making are seldom found. The Secretariat of the Convention on Biological Diversity (SCBD, 2007) puts the paucity of ESV use down to its cost. Fisher et al. (2008) observe that 'the integration of ecosystem services analysis directly with agents and processes within decision-making arenas is largely absent' (p. 2063). Liu et al. (2010) point out with respect to technical guidance: 'Indeed, one would imagine that ESV, the process of assessing the benefits of environmental services, must have been applied widely to guide payments for ecosystem services. ... In practice, however, ESV results have rarely been applied in setting payment amounts' (p. 2068). This analysis had been preceded by similar observations when Landell-Mills and Porras (2002) surveyed almost 200 PES mechanisms. More recently, Pirard and Billé (2010) reached a similar conclusion. Such observations by authors having discussed some dimensions of the UESV issue suggest at the very least that use is difficult to observe. In fact, there may well be a gap between the ambitions of ESV and its concrete achievements in terms of influencing decision-making.

However, most of the few previous studies on the UESV issue are recollections of their authors' experiences or theoretical expectations regarding UESV (e.g. Navrud and Pruckner, 1997; Pearce and Seccombe-Hett, 2000; Liu et al., 2010). Turner et al. (2003) state that they are performing a 'literature review' but give no indication of the list of references that were used or the reviewing methods employed. Furthermore, although they claim that their aim is to assess the 'policy relevance' of existing ESV, the key question of UESV is actually not addressed by the authors. The article mainly addresses ESV methods, with UESV being kept as a rather abstract horizon. To our knowledge, the article by Fisher et al. (2008) is the one which most closely tries to document UESV cases. After they identified 34 ESV case studies that seemed policy-relevant following their criteria, Fisher et al. contacted the authors with a list of questions such as 'Was the work commissioned by agents within the policy process?', 'Was this research used to influence a policy decision? If so, how?' or 'Was there any form of post-study implementation review or ex-post analysis undertaken?' (Fisher et al., 2008; supplementary material). The researchers received

only 14 answers with contrasted perceptions on UESV and, to a large extent, no knowledge of any *ex post* UESV analysis.

This article hence intends to shed light on what we consider as a literature blindspot on UESV. It proposes a systematic review of how the peer-reviewed scientific literature addresses the question of UESV, driven by two questions: (i) What are the expected UESV? (ii) How is the UESV issue addressed by the literature? The extent to which results can be used as a proxy to measure the actual use of ESV is a subject of the ensuing discussion.

The focus of this article is on "ecosystem services economic valuation". It builds on the great interest the 'ecosystem services' concept generates among scientists working on environmental management in general and biodiversity conservation in particular. This follows seminal work by e.g. Daily (1997) and institutionalization with the 2005 Millennium Ecosystem Assessment (MEA, 2005) (Vihervaara et al., 2010). The MEA defined ecosystem services as the benefits people obtain from ecosystems, including provisioning, regulating, cultural and supporting services. The 'ecosystem services' concept clearly draws on a utilitarian approach and facilitates the development of economic valuations in the field of biodiversity conservation. Economic valuation is understood here as a process by which economic analysis is used to allocate a monetary figure to a given entity – hence no difference is made with monetary valuation. Nevertheless, while focussing on ESV, we do allow ourselves to look at literature dedicated to other environmental subjects of economic valuation as deemed relevant for our analysis. It is all the more necessary as many economic valuations regarding similar objects (e.g. nature, species, environment, biodiversity) have been undertaken and discussed before the ecosystem services concept was introduced and mainstreamed.

After a presentation of the material and methods in Section 2, Section 3 on results first provides a synthetic typology of expected uses of ESV (or categories of UESV, namely: decisive, technical and informative), and then analyses how peer-reviewed scientific literature addresses the use issue. Section 4 discusses two sets of hypotheses to explain the literature patterns observed in Section 3, and proposes associated research avenues. Section 5 concludes.

2. Material and methods

2.1. Structure of the study

A systematic review was performed in order to analyse how UESV is envisaged and addressed in the dedicated literature. There are many terms and no actual consensus (e.g. Hunt, 1997; Cooper and Hedges, 2009) to refer to the process of research synthesis, i.e. the 'attempt to integrate empirical research for the purpose of creating generalizations' (Cooper and Hedges, 2009). The term *systematic review* is used to highlight that, compared to a *standard review* (on our topic, e.g. Turner et al., 2003), it is a process through which one methodically chooses a sample of works, extracts the targeted information and reports the results with transparency on the methods that were used at each step (Hunt, 1997).

Three major analytical steps were followed in this study. The choices made in the design of each step are justified in the subsections below. Step 1 was designed to build a database of peer-reviewed scientific publications to analyse. In Step 2, based on the information found in the publications within our database complemented by some grey literature references, a typology of UESV categories was built. It provided an answer to the study's first question: What are the expected UESV that can be found in the literature? In Step 3 the most influential journal in the ESV sub-area was identified and served as a proxy to observe patterns in the way

the UESV issue is addressed by the peer-reviewed scientific literature. This allowed addressing the study's second question: How is the UESV issue addressed by the literature?

Step 1 was used to provide material for Step 2 and Step 3, and the results from Step 2 were used as a framework to assess a publication pattern in Step 3: thus, both Step 1 and Step 2 fuelled the work in Step 3. As explained below, an iterative checking process was used to validate the categories of UESV and sub-categories therein.

2.2. Step 1: data collection

2.2.1. Rationale

The first step of the study aimed at collecting publications from the ESV field in order to constitute a database. Due to the abundance of references concerning ESV, which seems to have hampered other review exercises on our topic (e.g. Fisher et al., 2008; Liu et al., 2010), it was first decided to study only peer-reviewed scientific literature.

As it was neither possible to study all the peer-reviewed works on ESV, the representative coverage (Cooper, 1988) approach was adopted. It consists in focussing the review efforts on a population of works that are considered as being 'broadly representative of many other works in a field' (Cooper and Hedges, 2009). Retrieving works that compose or are representative of a given research sub-area is not a straightforward task, as works are scattered among many journals of more or less general scope (e.g. Van Campenhout et al., 2008). This is typically the case for the ESV literature, and it is all the more true as it is a topic of multidisciplinary interest. ESV works can hence be found in journals spanning from very general scope in natural sciences such as *Nature* and *Science* to more specialized journals in environmental economics (e.g. *Ecological Economics*, *Environmental and Resources Economics* etc.) or conservation sciences for instance (e.g. *Conservation Biology*). Thus, deciding whether a given coverage is representative or not always contains a part of arbitrary from the review's authors (Cooper, 1988), and as highlighted above scientific transparency on the method used is hence essential for the reader to be able to discuss the author's results (Hunt, 1997).

For this study, the choice was made to conduct database searches with a selection of keywords judged sufficiently broad to capture a vast diversity of phrasings relative to ESV, and then to gather the output references in a database. By searching different databases with different keywords, it was possible to build a large database of pluridisciplinary scope, that was judged sufficiently large and diverse to provide a rather accurate picture of the variety of works on ESV (Supplement 1 provides access to the gathered references).

2.2.2. Databases

The three ISI citation databases (*Science Citation Index*, *Social Science Citation Index* and *Arts & Humanities Citation Index*) were accessed through the *Web of Science* portal (WoS, thereafter), and Elsevier's *Scopus* was also used because these databases do not have the same literature coverage, which can cause disparities in terms of citation counting (Meho and Yang, 2007). Using both therefore limited 'false negatives' (relevant sources that are not identified; Reed and Baxter, 2009).

2.2.3. Keywords selection

For the same reason, instead of using a sole query (e.g. "ecosystem service", valuation"), results of several queries were combined. It also enabled to capture different forms in which the logic behind ESV was materialized in the last decades and that were often used interchangeably, as underlined in introduction. Since it

was not possible to capture all the possible phrasings used in the literature, the database search was limited to five keyword combinations, still sufficiently broad in our experience to capture most of the terms usually associated with ESV. These combinations were: "'valuation' and 'ecosystem service'", "natural capital", "'environmental' and 'valuation'", "'biodiversity' and 'valuation'", and "total economic value".

2.2.4. Gathered material

On 31/01/2012, this yielded an aggregated list of 5028 unique references from 1419 sources, mostly composed of peer-reviewed scientific journals. The full list of references is reproduced in Supplement 1, and the top 25 sources in terms of number of articles and total number of citations for each keyword and each database are reported in Supplement 2. As expected, the different keyword combinations yielded different results in terms of journal rankings, the more naturalistic ("biodiversity" and 'valuation'); "ecosystem service" and 'valuation') yielding more articles in ecological and conservation journals. The query "'environmental' and 'valuation'" was the one which yielded the most results and with the highest number of articles from environmental economics journals.

We used this database to build categories and sub-categories in Step 2, and the selection of articles was refined in Step 3 to conduct a quantitative analysis on publication patterns concerning UESV.

2.3. Step 2: construction of UESV categories and sub-categories

This step analysed the various UESV expected by authors. The 5028 references gathered in Step 1 were examined in order to find references from peer-reviewed scientific journals in English that could be used as a framework to build UESV categories. The selection criterion was that the references had to propose a list of well-defined UESV categories. Only three matched this criterion: Liu et al. (2010) propose a history of ESV research and a UESV typology; Navrud and Pruckner (1997) study the context of UESV in the USA and Europe; Pearce and Seccombe-Hett (2000) examine UESV in Europe and offer a typology.

Given the paucity of peer-reviewed references that matched the selection criterion, an addition of references from the grey literature was made to help define comprehensive UESV categories. Grey literature is here defined in the broadest sense, i.e. literature from various origins that has not been subjected to the peer-review process common to academic journals. It thus spans, for instance, from NGO reports and government documents to academic working papers and books. As explained by Rothstein and Hopewell (2009), grey literature can contain a lot of information that is not captured by peer-reviewed scientific literature, and can be a rich complementary resource for reviews. With the same selection criterion, several online resources that aggregated references on ESV were explored (see Supplement 3 for the list of online sources). We selected five grey literature references that matched our criterion: Navrud (2001), Pearce (2001), an anonymous chapter in OECD (2002), NRC (2005) and SCBD (2007).

The definitions of UESV categories found in these eight references were sorted and synthesized in order to build a typology of categories and sub-categories. This process was iterative: at each step of the study, we double-checked that the UESV mentioned in the rest of the literature could be unambiguously classified in one of the categories, i.e. that no category was missing, that none was left empty and that there was no category overlap.

This process resulted in the design of eight sub-categories under three categories, all presented in the results section. Each represents a way in which ESV is expected to be used for decision-making by the examined literature.

2.4. Step 3: searching for publication patterns in selected journals

In order to investigate the second question of this paper (how is the UESV issue addressed by peer-reviewed scientific literature?), it was decided to quantitatively assess the publication patterns regarding UESV. Two patterns were considered. The first concerns the way in which UESV is referred to, and three such ways were identified:

- (1) Cursory reference to a potential UESV: in introduction and/or conclusion, the authors merely mention the fact that economic valuations (their own or others') could actually be used, without more precision.
- (2) Analysis of the use issue: the core of the paper is UESV, i.e. the focus is, once economic valuations are produced, on how their results are used by stakeholders: which stakeholders, in which context, for which purpose, with which results etc.
- (3) Documentation of use cases: case studies that follow the subsequent use of an economic valuation by some stakeholders.

The second pattern considered dealt with the types of UESV categories that were addressed, if any.

Since it was not possible to analyse all 5028 references of our database along these lines, a subset of articles had to be isolated for this step, with the underlying idea that the observed patterns in terms of UESV treatment and expected UESV categories in this subset would reflect the rest of peer-reviewed scientific literature. Influence was chosen as a criterion to select this subset. Since there is no straightforward and unambiguous way to measure an author's, an article's or a journal's influence in a given sub-area, influence was assessed using the number of articles and number of citations resulting from our keyword search as broad proxies.

Journals' rather than articles' influence was used because some papers published in natural science journals, such as Costanza et al.'s paper in *Nature* (Costanza et al., 1997), were susceptible to distort the results in favour of ecological or conservation journals. The number of articles per journal and sum of citations for each journal were then compared.

Table 1 shows the top 10 journals according to number of articles and number of citations for our search. The presence of the journal *Nature* in the list can be seen as a kind of anomaly: it is mostly due to Costanza et al.'s paper (Costanza et al., 1997) which was, alone, cited 2282 times according to WoS and 2847 times according to Scopus.

Ecological Economics ranked either first or second to *Nature* for each keyword and on each database (Table 1 and Supplement 2). Given the 'Costanza anomaly', we therefore considered *Ecological Economics* as the most influential journal in this field, having published the highest number of ESV articles and received the highest number of citations in our database. Its editorial line strengthened our choice: from the outset, this journal aims to publish research focused on actions that support ecosystem management. Thus for example, Costanza and King (1999), in a survey article on the journal's first decade, affirm: 'Solving important problems is the first priority. Specific methodologies should serve this goal. [...] Methods are judged by their ability to usefully address the problem at hand' (p. 2) (see also Castro e Silva and Teixeira, 2011; Shi, 2004). Furthermore, as the full title of the journal indicates, its goal is transdisciplinary: *The Transdisciplinary Journal of the International Society for Ecological Economics*, which is illustrated by the journal's position at the interface between ecology and economics (see Costanza, 1996; Costanza et al., 2004). These three reasons: (i) the strong influence of *Ecological Economics* in the ESV sub-area, (ii) its action-oriented editorial line and (iii) its transdisciplinary position, seemed to make it the best candidate for an assessment of patterns in the way the UESV issue is addressed by the ESV literature.

In order to ensure a thorough exploration of this particular journal, hand searching was used so as to minimize even more the risk of potentially missed articles (Rothstein and Hopewell, 2009). The whole range of papers published in *Ecological Economics*, from issue 1 to 74, and all the articles in press on 13/02/2012, were thus screened. A selection of 676 papers was identified on the basis of a read-through of the titles and abstracts to identify all articles related to economic valuation of the environment, of biodiversity and of ecosystem services. From these 676 papers, 313 were selected because they at least made a cursory reference to UESV. Based on a whole-paper reading, mentions of UESV were then sorted according to the way UESV was referred to and the UESV categories mentioned, in order to assess both publication patterns. Since 26 papers out of the 313 mention two different UESV (i.e. belonging to two different UESV categories as explained in Section 2.3) and one paper (Driml, 1997) mentions three UESV, there are 340 categorized UESV in the selection.

Out of precaution, the 544 papers of our database that were published in the other four journals of the top 5, *Nature* put apart (namely *Journal of Environmental Economics and Management*, *Environmental and Resource Economics*, *Land Economics*, *Journal of*

Table 1
Top 10 journals according to number of articles and number of citations.

Ranking in number of articles (WoS + Scopus)		Ranking in number of citations (WoS)		Ranking in number of citations (Scopus)	
All articles	5028	All articles	45,278	All articles	56,738
1. Ecological Economics	574	1. Ecological Economics	8267	1. Ecological Economics	9773
2. Environmental and Resource Economics	219	2. Nature	2347	2. Environmental and Resource Economics	3608
3. Journal of Environmental Management	133	3. Journal of Environmental Economics and Management	2022	3. Journal of Environmental Economics and Management	2921
4. Journal of Environmental Economics and Management	103	4. Environmental and Resource Economics	1781	4. Nature	2914
5. Land Economics	89	5. Journal of Environmental Management	1126	5. Land Economics	1836
6. Environmental Management	61	6. Land Economics	948	6. Journal of Environmental Management	1590
7. American Journal of Agricultural Economics	57	7. American Journal of Agricultural Economics	857	7. American Journal of Agricultural Economics	931
8. Journal of Environmental Planning and Management	57	8. Landscape and Urban Planning	647	8. Landscape and Urban Planning	848
9. Environmental Values	49	9. Management Science	597	9. Science	630
10. Energy Policy	45	10. Science	596	10. Management Science	623

Environmental Management) were screened (whole paper screening) for a qualitative assessment of the first pattern (the way in which UESV is referred to). The result of this screening is briefly discussed as well in Section 3.2.

3. Results

3.1. Expected uses of ESV: a synthetic typology

As explained in Section 2.3, a first result is the construction of categories of UESV based on three peer-reviewed articles (Navrud and Pruckner, 1997; Pearce and Seccombe-Hett, 2000; Liu et al., 2010) and five references from the grey literature (Navrud, 2001; Pearce, 2001; an anonymous chapter in OECD, 2002; NRC, 2005; SCBD, 2007). This typology is synthetic in that it synthesizes heterogeneous categories scattered in the literature. We distinguish between three main categories of UESV depending on whether ESV is considered as being primarily *decisive*, *technical*, or *informative*, and eight sub-categories.

3.1.1. Decisive UESV (for a specific decision)

This first category involves cases where the valuation is meant to inform a specific decision. Here ESV can be seen as contributing to a process in which a given choice is to be made, *ex ante*, by a decision-maker facing alternatives. These options may involve a project or a policy, such as a regulatory proposal to be examined. It is then up to the ESV, when incorporated into a cost-benefit analysis (CBA), to provide elements on the opportunity of the project/policy and its economic consequences with regard to ecosystem services, thus enabling an informed choice.

Within this category, three sub-categories of UESV can be distinguished.

3.1.1.1. ESV for trade-offs. By proposing a monetary value for ecosystem services, ESV can aim at helping to factor related concerns into the CBA that are underpinning decision-makers' trade-offs. The CBA process is formalized quite precisely: 'CBA is characterized by a fairly strict decision making structure that includes defining the project, identifying impacts that are economically relevant, physically quantifying impacts as benefits or costs, and then calculating a summary monetary valuation' (Liu et al., 2010). This analysis may then be applied to all types of trade-offs about, for instance, programmes, laws and investment projects. In this respect, the purpose of the ESV is to enable the decision-maker to optimize social well-being by making choices that balance out preference criteria.

3.1.1.2. Participative ESV. Another approach considers economic analysis as a 'negotiation language' (Henry, 1984, 1989). Here ESV is still potentially 'decisive', and still intervenes *ex ante* as a decision-making tool. However, instead of providing a comprehensive range of choices that reflect a socially optimal decision, it is rather seen as a basis for discussion: through an open debate on ESV parameters and assumptions, stakeholders negotiate and define a project that is adjusted and enhanced in terms of compromise and the sum of interests. OECD (2001) gives such an example with a disputed transfer of ecosystem values in Oregon (see also Pearce and Seccombe-Hett, 2000; SCBD, 2007). Of course, this does mean that such UESV is limited to ESVs based on benefit transfers.

3.1.1.3. ESV as a criterion for environmental management. Within limited budgets allocated to ecosystem services protection, ESV can also help prioritizing conservation efforts within an organization, in an optimal way. It can facilitate the identification of options most likely to maximize benefits, or of territories that

contribute most to ecosystem services. Investment priorities may then be defined in accordance. ESV as a management criterion, or 'management tool' (Pearce and Seccombe-Hett, 2000), differs from the 'trade-off' sub-category in that it concerns only a specific organisation, and does not entail a choice among wide policy and social priorities.

3.1.2. "Technical" UESV (for the design of an instrument)

This second category involves those cases where ESV is applied *after* the choice of a policy or project, to adjust the economic instrument that will implement the decision. It covers two possible types of UESV.

3.1.2.1. ESV for establishing levels of damage compensation. Agents responsible for ecosystem services degradation can be obliged to pay compensation for such damage. This compensation may be *a priori* (i.e. compensating the anticipated effect of an operation), or *a posteriori* (i.e. remediating damages caused by an accident) (Burlington, 2004). In this case, ESV provides guidance for administrative decisions or court rulings that determine the amounts to be paid out (see OECD, 2002).

3.1.2.2. ESV for price-setting. In cases where an economic instrument has been decided, ESV can be used to determine the amounts payable on the basis of a willingness-to-pay or willingness-to-receive logic: payments made by the beneficiaries of services in the case of Payments for Ecosystem Services, entrance fees to protected areas, etc. ESV can also help to set prices that allow externalities to be internalized, for example by factoring environmental costs into the price of a product (such as energy). This is the role discussed by Navrud and Pruckner (1997) when they mention ESV as 'environmental costing'.

3.1.3. Informative UESV (for decision-making in general)

Aside from its decisive and technical role, ESV can also be seen as a means to provide information intended to have an indirect influence on decision-making, considered in a very broad sense. For instance, this is the type of UESV formulated by Fisher et al. (2008) when they report some of the responses given by ESV authors whom they questioned on the expected uses of their works: '(1) distributing the research results to policy agents (...); (2) directly informing and engaging policy agents; (3) providing influential support for current conservation initiatives' (p. 2063). In this case, the expectation is not that ESV determine a choice with respect to a specific decision, but rather that it contribute to discussions, progressively modify viewpoints, demonstrate the interest of certain policy directions or, in other words, have some sway. OECD (2001) defines this role in the following way: 'Regardless of its shortcomings, economic valuation plays an important role in educating decision-makers about biodiversity benefits ...' (p. 20).

This category of UESV has three sub-categories.

3.1.3.1. ESV for awareness-raising. Informative ESV may be seen as the vector for a broad message concerning the preferences that should be mainstreamed into society, particularly to ensure that ecosystem services considerations are integrated into public and private choices. Pearce (2001) and Daily et al. (2009), for example, basically consider that any ESV is a form of 'advocacy'. Costanza et al. (1997) launch the debate on their findings by stating that 'what this study makes abundantly clear is that ecosystem services provide an important portion of the total contribution to human welfare on this planet. We must begin to give the natural capital stock that produces these services adequate weight in the decision-making process, otherwise current and continued future human welfare may drastically suffer' (p. 259). Gómez-Baggethun et al.

(2010) show that this is the primary function of the concept of ecosystem services, insofar as it provides economic arguments (by putting a monetary value on pollination, wastewater treatment, nutrient cycling services, etc.) to reinforce the biophysical arguments that appear insufficient when it comes to substantially influencing choices.

3.1.3.2. *ESV for justification and support.* Here informative ESV is used by a stakeholder to promote a given course of action, as opposed to ESV for trade-offs where valuations are deemed neutral and inform an optimal choice. Here, it is about showing that an already identified choice is justified:

- Either *a priori*, to demonstrate the economic rationality of the measures envisaged. For example, 'to increase the social welfare, policy makers would be wise to place more weight on the conservation of black-faced spoonbill by banning activities that degrade the quality of the natural habitat. Therefore, this study will help policy makers in resolving the conflict for development or conservation of the ecological zone' (Jin et al., 2008).
- Or *a posteriori*, in which case ESV serves as a tool for verification: 'while a preoccupation with process is understandable, one aim of valuation is to provide a check on the efficiency of decisions, however they are made' (Pearce and Seccombe-Hett, 2000, p. 1424). This may also involve showing the economic relevance of decisions taken for conservation. For example, regarding the combat against invasive species: 'These environmental gains [from combating invasive species] alone

appear to cover a substantial proportion of the control costs' (Sinden and Griffith, 2007).

3.1.3.3. *ESV for producing 'accounting indicators'.* This last sub-category of informative ESV involves situations where valuation is designed to allow decision-makers, or the public opinion, to remain informed of the state of the natural capital and to integrate this information into their decisions in general. This category encompasses natural heritage accounts as a potential use of ESV. All eight framework references identify this type of ESV ambition. In particular, OECD (2002) treats ESV as a means of revising national accounts, and SCBD (2007) sees it as a way of integrating environmental externalities into the assessment of economic growth.

This section took ESV as an analytical tool designed to weigh in decision-making in various ways. The targeted effect may be direct as in the 'decisive' ESV category, instrumental as in the 'technical' ESV category, or indirect as in the 'informative' ESV category. It remains to be investigated how peer-reviewed scientific literature on ESV addresses these various categories.

3.2. *The use of ESV for decision-making rarely appears in the literature on ESV*

The 313 articles sampled from *Ecological Economics* have been categorized according to the way UESV is treated (cursory reference to a potential UESV, analysis of the use issue, documentation of use cases; total: 340 UESV) and to the type of UESV envisaged (decisive, technical, informative, together with related sub-categories). The results are summarized in Fig. 1.

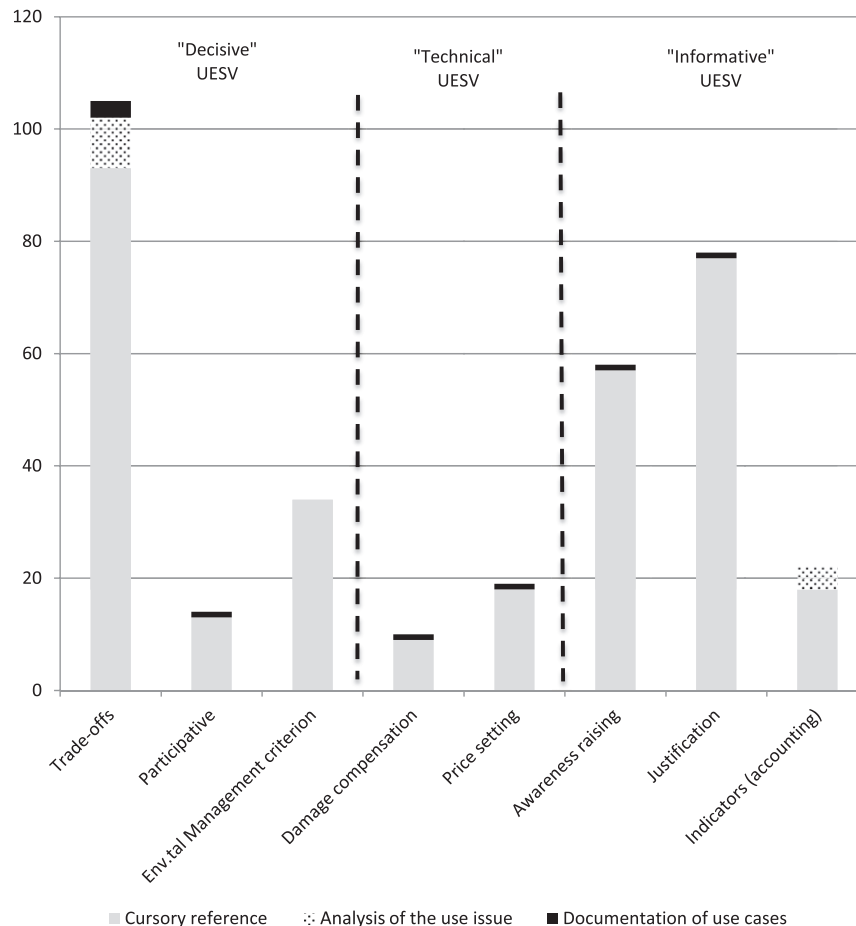


Fig. 1. Typology of UESV and treatment in the literature.

The main result of this analysis is the paucity of papers that describe, through a case study, how a specific ESV has played a role in a decision. Only eight such occurrences were identified, representing 2% of mentioned UESV in *Ecological Economics* (reported cases are numbered here, not papers). Among those eight occurrences of UESV, three are from papers specifically devoted to analysing how ESV was used (the other five are from papers that deal with the topic along with other subjects). Gowan et al. (2006) examine ‘the role and contribution of economic analysis, and specifically ecosystem valuation, in a precedent-setting dam removal case’ on the Elwha River in the state of Washington. They conclude that ‘ecosystem valuation played a minor role in the decision to remove the Elwha dams and participants in hydropower relicensing decisions in general do not rely on valuation studies to decide levels of ecosystem enhancements’. Henry (1989) reports the case of a harbour extension project in the Netherlands: after eliminating ‘from the beginning ecologically unacceptable proposals without any need of further examination’, authorities ‘judged each ecologically acceptable plan on the basis of an economic assessment of all the costs and benefits that could possibly be evaluated in monetary terms – including those damages to the natural environment which, without being drastic, should nevertheless be taken into account’. The result was that none of the extension options that did not seriously harm the natural environment was economically viable. Last, Rival (2010) explores the Ecuadorian Yasuni-ITT initiative and ‘the delight with which individuals and groups with little prior knowledge of economics are ready to crunch numbers. Such willingness to enter calculations usually associated with experts may be related to the fact that the proposal has opened a democratic space in which the country’s economic future may be debated and the calculations made by professional economists and government planners examined and challenged.’

In addition, the results of our review indicate that, for the most part, UESV receives no more than a cursory reference in the form of an expected, proposed or desired use (e.g. Brander et al., 2007 is archetypical of this treatment of UESV). These simple mentions of an expected use often envisage an *informative* use in the form of general advocacy to protect biodiversity and ecosystem services or to justify conservation choices (e.g. Amirnejad et al., 2006; Biao et al., 2010). Alternatively, they envisage the valuation as enabling decision-makers to decide on general trade-offs (but in this case without identifying a specific decision with its related context and criteria) and, more particularly, to give the preservation of ecosystem services some weight, overall, alongside other economic and social objectives (e.g. Barbier, 2000; Casey et al., 2006).

As indicated in Section 2.4, out of precaution we also screened (whole paper screening) the 544 ESV papers of our database that were published in the other four journals of the top 5, *Nature* put apart (namely *Journal of Environmental Economics and Management*, *Environmental and Resource Economics*, *Land Economics*, *Journal of Environmental Management*). Although a mere qualitative assessment of the first pattern (the way in which UESV is referred to), this screening confirms that the vast majority of studies that address UESV do so only in a cursory way. Based on the representativeness of *Ecological Economics* for the ESV sub-area, and on this complementary screening, we suggest that this pattern is likely to be widespread in the entire peer-reviewed scientific literature.

The following section examines possible explanations for the discrepancy between expectations and available information on UESV, and explores research avenues that such explanations open up.

4. Discussion: possible explanations to the literature patterns observed and avenues for research

Three preliminary remarks on the limits of our review are necessary:

- First, the keywords we used were unavoidably arbitrary. They match the authors’ culture in economy, ecology, management and political sciences, but it cannot be excluded that articles in other disciplines such as sociology, ethnology or psychology may deal with similar concerns (i.e. UESV) with different words. The only assumption that can be made is that such articles, if they exist, are probably few.
- Second, we did not consider grey literature in our systematic review – only was it taken into account to help build categories of UESV. It would be intuitive to assume that grey literature must be the ideal tool to report ESV use cases or address the use issue. However, exploring grey literature systematically was out of reach for our research. More importantly, the grey literature that was explored based on the six websites in Supplement 3 did not confirm this intuition, with still few – and often the same – cases reported. In any case a more systematic endeavour would be necessary here.
- Last, a literature review, however systematic, does not replace different kinds of research involving thorough analyses of specific decision processes to get a complementary perspective on if and how ESV are actually used (see e.g. Gowan et al., 2006; Laurans and Aoubid, 2012).

With this in mind, the results of our review still raise the question of why UESV issues are so rarely addressed by the ESV peer-reviewed scientific literature. The purpose here is not to conjecture on the most probable explanation for this result, but rather to examine a wide range of possible explanations. This is necessary to identify the different research avenues and lay the ground for subsequent work that we consider necessary. To this end, we divided the hypotheses into two main categories: either the use of ESV is a common practice, but is absent from the literature selected here (Section 4.1); or the use is effectively rare (Section 4.2).

4.1. A possible bias in the selected literature

Our observations mainly apply to peer-reviewed scientific literature. A first set of four hypotheses can thus be formulated, bearing in mind the general idea that such literature only paints a partial picture of actuality.

a. UESV may be difficult to observe

It is conceivable that UESV be seldom addressed by peer-reviewed scientific literature because the actual contexts for its use go unnoticed by ESV researchers. This is what Fisher et al. (2008) suggest: they note that by applying a ‘filter’ that selects ‘cases where ecosystem services analysis has been an integral part of the policy process (*ex ante*)’, the result turns out to be very selective, ‘since few studies in the literature make explicit policy linkages’ (p. 2062). UESV would then be more widely found in practice than peer-reviewed scientific literature indicates; it would generally go unnoticed in the targeted community of authors, and would not appear in the results of a keyword search, even were it to produce a vast number of titles. This could be reinforced by a potential time lag between economic valuations, their presentation in peer-reviewed scientific literature, and their use for decision making. Nevertheless, the time lag is unlikely to be a major source of

mismeasurement in our review since ESVs have been abundant in peer-reviewed scientific literature for over 15 years, not even mentioning environmental economic valuations produced before the ‘ecosystem services’ terminology emerged at the end of the 1990s, and included in our review.

In addition, observing and describing UESV in peer-reviewed scientific literature is certainly more difficult for an ‘informative’ type of use. Some actually argue that there is a sort of continuum between economic valuation for awareness-raising and economic valuation for trade-offs: ‘It appears that the specific valuation studies conducted for visibility impairments at the Grand Canyon had little *direct* effect on the decision. (...) I believe the early research published in *JEEM*, beginning in 1974, gave EPA staff the background necessary to be confident that it would be possible to estimate economic values for visibility improvements. (...) The valuation research helped to *frame the debate* over the standard even if the decision was not based on the net benefits of emission control’ (Smith, 2000). In that case tracing use cases takes a specific methodology based on decision-process analysis, examining the resources used by stakeholders, and considering ESV among other factors (as it is in Turner, 2007).

b. UESV may not yet be on the research agenda

It can be presumed that UESV has not been widely addressed by peer-reviewed scientific literature because, apart from a small minority of authors, specialists have not yet perceived the importance of working on this topic. This is what Gowan et al. (2006) suggest: ‘Acknowledgement of the social and discovery-oriented nature of the public policy debates might also prompt more professional and analytical attention to the study of the decision-process itself’ (p. 521).

c. UESV may not be an issue for economists

UESV relates to a social practice, as part of decision-making processes. It could thus be deemed that its scientific analysis has less to do with economics than with scientific disciplines that study decision-making practices (sociology, political sciences, management, psychology, anthropology, etc.), while our review showed that articles on ESV were published mostly in economics journals (4 of the top 5, with the exception of the *Journal of Environmental Management*).

d. UESV may not be a scientific question

Finally, it is also possible that, beyond economics, the use of valuation does not enjoy the same status as the valuation itself from a scientific point of view, insofar as it involves implementation in the real-world. The application of tools derived from a science does not necessarily constitute an object for research, and our analyses are primarily based on peer-reviewed scientific literature.

4.2. Use may fall short of expectations in practice

Aside from problems of selection that may explain why the literature examined makes scant references to uses that may nonetheless occur frequently in practice, it should also be conjectured that the use of valuations may be limited in reality, which would explain its relative absence in peer-reviewed scientific literature. Here six hypotheses can be investigated.

e. ESV may be too often inaccurate

It could be considered that valuation still has to be improved in terms of methods and techniques so as to yield more robust results that describe and distinguish the subject of its analysis more accurately. This hypothesis is often taken up by the authors of the ‘UESV analysis’ references mentioned earlier and, for example, by Navrud and Pruckner (1997), or Turner et al. (2003).

f. ESV may contain fundamental inadequacies

Some authors posit that the lack of UESV stems from the fact that the valuation is in most cases too incomplete (Toman, 1998) and not relevant enough to inform socially optimal decisions (Vatn and Bromley, 1994; O’Neill, 1997). Others argue that the objects measured by ESV do not represent the real issues at stake for decision-making. For example, while the parameters for a decision are primarily of a distributive nature – important decisions on environment-impacting policies and projects often create losers and winners – common practices for ESV often do not allow clear statements on distributional concerns (Turner, 2007). Even when they do, they may not be conclusive: knowing who loses and who wins does not tell which decision to make. ESV may also be considered as ill-adapted to certain types of ecosystem services: ‘Many would question whether monetary valuation alone adequately captures what decision makers need to know to confront irreversible ecosystem modification that could have serious long-term economic and social repercussions. Perhaps the most important task is to clarify where conventional economic values are sufficient for decisions and where broader human values – including non-monetary values – and criteria for decision making are more appropriate’ (Bingham et al., 1995, p. 75). Thus, for instance, a report commissioned by the French prime minister (Chevassus-au-Louis et al., 2009) proposed that ESV be reserved for ‘ordinary’ aspects of biodiversity, while ‘remarkable’ biodiversity should be seen as being beyond the scope of a usable economic valuation.

g. The cost of ESV may restrict their use

Another hypothesis is that the cost of ESV may be too high compared to the means that the contexts for their use would justify and/or allow to mobilize (this is notably one of the hypotheses put forward by SCBD, 2007; Navrud, 2001). This is reinforced by the fact that the situations associated with biodiversity and ecosystem services are very site- and problem-specific; they do not allow transferring values easily.

h. Decision-makers may not have sufficient training in economics

Many ESV authors consider that the scant use made of these valuations is partly due to the insufficient training of decision-makers in the language and axioms of economic analysis: they are unfamiliar with its logic or inexperienced and apprehensive at using poorly mastered tools. Thus, according to Driml (1997), the low level of UESV in Australia ‘is likely due in part to the lack of confidence, inside and outside the economics profession, in the techniques involved. Another likely factor is that many management agencies do not employ people with the necessary training to make the best use of the economic information that is available’ (p. 147).

i. Regulatory frameworks may not be conducive to UESV

Some authors consider that Europe, for example, resorts to ESV much less often than the United States, and explain this difference by the regulations in force (Liu et al., 2010). The degree of UESV would thus be tightly linked to the scope and precision of the regulations that require economic analyses, or that favour approaches and criteria far-removed from ESV. Navrud and Pruckner (1997), for instance, attribute the fact that economic valuation is little used in Europe to the vague and non-mandatory nature of European regulations. Likewise, Braüer (2003) considers: ‘One reason [why CBA is less used in Europe than in the US] is the different legislation which does neither offer the possibility of integrating non-use values into damage assessments nor the requirement of a CBA for new regulations’ (p. 485).

j. ESV, by enhancing transparency, may hamper political strategies that require a certain opacity or ambiguity

Finally for some, unintensive UESV may be due to the preference of certain decision-makers for processes that leave the distributive effects of their decisions in the dark, or that obscure arrangements which are indefensible with respect to the public interest: 'Politics affects the process in many ways that can block outcomes that would result in higher levels of economic welfare. Indeed, one of the primary lessons of the political economy of regulation is that economic efficiency is not likely to be a key objective in the design of policy. Policy ideas can affect interest group positions directly, which can then affect the positions of key decision makers (such as elected officials and civil servants), who then structure policies through the passage of laws and regulations that meet their political objectives' (Hahn, 2000, p. 18). In this perspective, limits on UESV mirrors political failures, and are inversely proportional to the quality of the institutions that support democratic accountability. Socio-cultural evolution and increasing pressures for better use of public funds would then slowly lead to more favourable conditions for UESV.

4.3. Avenues for research

The pivotal finding of this review is that the issue of ESV use for decision-making is rarely treated in peer-reviewed scientific literature beyond general statements and suggestions about possible uses. This holds true whether it involves an analysis of the use issue in itself, or reports of utilization cases. The most widespread practice is to present an economic valuation and then suggest that it could be useful for decision-making with no further precision or context. This finding is all the more striking as the literature examined often argues that valuations are highly useful for decisions.

We have put forward different hypotheses to explain this finding. They open up avenues of research to give greater weight to the

issue of UESV, provide deeper insight into the subject and step up efforts to find ways to improve use. Table 2 summarises these hypotheses and the three distinct though complementary research programmes that can be proposed in accordance.

4.3.1. Creating a specific field of research

The first three hypotheses (a, b, c) suggest the construction of a specific field of research focused on UESV. According to the first one, this field of research needs to be explored by researchers who are specialized in ESV, but who have not yet shown sufficient interest in this area and need to be encouraged to do so. In this respect, however, it should be noted that many ESV studied in this review were in fact 'applied' to a specific site and a precise environmental policy issue (conservation of a species or area, combating an invasive species, etc.). Moreover, experiments in which economic tools for environmental management such as PES were implemented seem to have been often carried out with active participation from economists (Liu et al., 2010).

Scientific work on ESV is not just theoretical or methodological but does appear to show an interest in environmental protection and related policies. On the other hand, to date, this work has often not been designed to fulfill specific needs of specific decision-makers. In addition, it is probably difficult, and not necessarily synergetic, to work simultaneously on refining an ESV technique and on ways in which it can be used for decision-making. Encouraging research from different disciplinary viewpoints and aimed at addressing social practices such as decision-making in environmental matters may be a response to this stumbling block.

As per Section 3.2, only three publications of *Ecological Economics* (Gowan et al., 2006; Henry, 1989; Rival, 2010) focus on the terms of an environmental policy debate, as well as on the analysis of the implications of ESV. Two of these (Gowan et al., 2006; Rival, 2010) mainly adopt an ethnological or sociological approach. However, the extensive bibliographic keyword search we conducted as a first step (Section 2.2), oriented us above all to

Table 2
Hypotheses and research avenues.

Categories of hypotheses	Hypotheses	Research avenues
A possible bias in the selected literature	a. UESV may be difficult to observe	Creating a specific field of research
	b. UESV may not yet be on the research agenda	
	c. UESV may not be an issue for economists	
	d. UESV may not be a scientific question	No relevant research avenue
Use may fall short of expectations in practice	e. ESV may be too often inaccurate	Refining ESV techniques
	f. ESV may contain fundamental inadequacies	
	g. The cost of ESV may restrict their use	
	h. Decision-makers may not have sufficient training in economics	Changing the context of use
	i. Regulatory frameworks may not be conducive to UESV	
	j. ESV may hamper political strategies that require a certain opacity or ambiguity	

economics journals and did not provide any clues as to whether the subject of UESV was substantially dealt with by other disciplinary fields or types of journals. Thus economic ethnology, for example, which observes people's economic behaviour, has not yet shown much interest in public decision-making, and even less in the environmental field (Weber, 2001; Strathern, 2000; Gudeman, 2009). It is thus by calling for collaboration with disciplines such as these that a deeper insight into UESV could be gained.

Hypothesis d (UESV is not a scientific question) is the only one that does not open up an avenue for research. It is certainly consistent with the scant attention given to the topic in peer-reviewed scientific literature, and with a proposal that would limit the subject to a purely operational and practical issue. Yet, it seems difficult to argue that a social practice could not be the subject of scientific investigation.

4.3.2. Refining ESV techniques

Hypotheses e, f and g assume that future developments of ESV methodology will help to substantially improve its use. In this perspective, research can engage in two opposite directions. One direction can target a certain 'standardization' of ESV techniques so as to generalize valuations and reduce their costs. 'Value transfer' is one of the responses envisaged by ESV authors (Loomis and Rosenberger, 2006). Yet value transfer renders the results less robust and less conclusive, as well as applicable only to issues that are not overly site-specific, which limits its scope (Brouwer, 2000). In other words, it is highly unlikely that standardizing the data underpinning valuations will allow them to be more frequently used for decision-making, since their conclusiveness for specific decisions would be impaired.

In the opposite direction, research could be oriented to broaden the ESV field, or ensure more precise studies, particularly in view of 'decisive' and 'technical' uses. It should however be noted that the few UESV cases reported do not evidence a greater precision of ESV than in other references. In all events, it is foreseeable that refining ESV studies would make the exercise more costly and thus more difficult to extend for 'decisive' and 'technical' use, which are both inherently topic- and scale-specific. We are thus faced with a tension between two strategies: either standardize ESV to make them more accessible, at the risk of also making them less usable for decisive purposes; or seek to refine ESV for decisive or technical use, at the risk of raising their cost.

4.3.3. Changing the context of use

The last three hypotheses (h, i, j) involve targeting, or at least hoping for, a change in users or in their operational context, rather than a change in valuations themselves. This implies for example training decision-makers to use ESV more effectively, adjusting laws and regulations to promote their use and reduce obstacles, or improving decision-makers' drive for transparency.

This prospect first seems at odds with one of the postulates underpinning the current enthusiasm for ESV, which assumes that decision-makers position themselves prioritarly on the basis of economic criteria. As one author advocating concrete application of ESV writes: 'Economics is there first, and all must speak its language seriously, at least some of the time, or be cut out of crucial parts of the debate' (Herendeen, 1998, p. 30). Secondly, when regulations provide for a CBA ahead of public decisions, as in the USA, the factoring in of ESV still seems to be far from satisfactory (Ruhl et al., 2007). Finally, it is indisputable that economic analysis can be assigned the role of revealing the inadequacies of a political or administrative decision-making process, as is shown in most democratic countries by the use of *ex-post* economic valuations conducted by auditing authorities. Yet, while auditing has existed for many years, economists' criticism of the reasoning behind public decisions has not abated (Hahn, 2000). All in all, changing

the context of use does not appear to be consistent with an approach that, as Liu et al. (2010) suggest, would rather aim to adapt the tools to the problems.

5. Conclusion

ESV are abundantly produced and disseminated within the current trend of a utilitarian view of the environment. These economic valuations are therefore promoted on the assumption that they respond to decision-makers' needs and/or that they help guiding decisions towards more and better conservation. The positive economic impacts of maintaining or increasing ecosystem services is demonstrated and taken into account; as are, conversely, the negative economic impacts of their degradation or destruction.

Our research aimed to explore the theoretical assumptions and empirical bases that underlay this hypothesis, and to examine to what extent there is evidence that UESV matches stated expectations. Our systematic literature review shows that the issue of use is overwhelmingly orphaned in peer-reviewed scientific literature on ESV, with few exceptions. The common rule is to present an economic valuation, then suggest that it be used for decision-making, but without this use being either explicited or contextualized, and without concrete examples being provided nor analysed.

The next step was to develop hypotheses resulting from this finding. They suggest multiple avenues for research. These hypotheses can be combined to explain the literature blindspot and/or the shortcomings of UESV to date. Evidence provided by the literature review leads to the conclusion that: (1) the vast majority of ESV are produced in a 'supply-side logic'; (2) it is thus uncertain that the type of tools offered to potential users are the best match for real decision-making needs; and (3) ESV is primarily geared towards an informative role for general influence and awareness-raising.

More broadly, and if all of the aforementioned hypotheses are taken into account to explain the relative absence of UESV in peer-reviewed scientific literature, it seems vital that the problem of using economic valuations be made a priority issue for research. To achieve this, many barriers must be overcome, existing research on this issue must be stepped up and new avenues of research opened up.

The paucity of UESV in peer-reviewed scientific literature is not only a puzzle that needs clarifying through further research but also a major concern for biodiversity and ecosystem services. Certainly, if decision-making processes fail to use ESV, economic valuation could lead to the type of disillusionment against which Redford and Adams (2009) give us due warning: 'conservation has a history of placing great faith in new ideas and approaches that appear to offer dramatic solutions to humanity's chronic disregard for nature ... only to become disillusioned with them a few years later' (p. 785). If ESV are supposed to be a decisive key for action, it hardly seems reasonable to sideline for much longer the question of the use of valuations that occupy a central place in today's discourse, thinking and debate around conservation.

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Appendix A. Supplementary material

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Appendix 4

Rankovic & Billé (2013)

Rankovic, A., Billé, R. (2013). Les utilisations de l'évaluation économique des services écosystémiques : un état des lieux. *Études et documents*, n°98. Commissariat général au développement durable, Ministère de l'Écologie, du Développement Durable et de l'Énergie.

Aleksandar RANKOVIC et Raphaël BILLE – Les utilisations de l'évaluation économique des services écosystémiques : un état des lieux

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L'utilisation des évaluations économiques comme problématique centrale

De grands espoirs semblent placés dans la monétarisation pour améliorer les décisions relatives à la biodiversité et aux écosystèmes, et ce de manière récurrente depuis de nombreuses années. Que ce soit par exemple chez l'économiste A. Randall, qui affirmait en 1988 que « la meilleure façon de protéger la biodiversité [était] de lui affecter une valeur économique » (Randall, 1988), chez les écologues J. Myers et J. Richert pour qui « l'on ne protège pas ce qu'on ne valorise pas » (« *we don't protect what we don't value* », la valeur étant entendue comme économique chez les deux auteurs ; Myers et Richert, 1997) ou plus récemment chez Pavan Sukhdev pour qui « l'économie des écosystèmes et de la biodiversité peut contribuer de façon décisive à la sauvegarde de la biodiversité » (The Economics of Ecosystems and Biodiversity, 2009), le constat semble unanime quant à l'utilité, voire l'obligation pragmatique, de recourir à l'étalon monétaire pour parvenir à stopper la dégradation des écosystèmes et l'érosion de la biodiversité.

Pourtant, le caractère évident de cette intégration effective de la monétarisation et de sa contribution, prépondérante et systématique, aux processus de décision suscite des réserves, notamment chez certains économistes. Claude Henry, par exemple, a mis en évidence, dès les années 80, la dimension négociée des évaluations économiques environnementales liées aux grands projets d'infrastructures (Henry, 1984, 1989). G. Heal, en 2000, souligne que « l'évaluation économique n'est ni nécessaire ni suffisante pour la conservation. Nous conservons beaucoup de choses que nous n'évaluons pas, et ne conservons pas de nombreuses choses que nous évaluons » (Heal, 2000). L'étude présentée ici, dont les résultats sont regroupés dans Laurans et al. (2013), part ainsi de l'hypothèse que la monétarisation, en ce qui concerne les prises de décision impactant les écosystèmes et la biodiversité, n'est pas suffisante en soi : pour apporter des « contributions décisives », elle doit être effectivement utilisée dans la prise de décision.

L'approche choisie a été la réalisation d'un état de l'art structuré autour de deux grandes questions :

1. Quelles sont les utilisations attendues des évaluations économiques des services écosystémiques dans la littérature ?
2. De quelle manière cette question est-elle traitée par la littérature ?

Le principal résultat a été la mise au jour d'un paradoxe : alors que de nombreuses utilisations sont attendues des résultats des exercices de monétarisation, au point qu'elles constituent leur raison d'être, cette question précise de l'utilisation est très peu abordée par la littérature : il semble exister un véritable point aveugle sur la question.



Une typologie synthétique des utilisations attendues par la littérature et un état des lieux du traitement de l'utilisation

La revue de littérature a été construite en trois étapes. En premier lieu, une base de données d'articles publiés dans des revues à comité de lecture a été constituée. Les articles ont été rassemblés à partir de recherches menées à l'aide d'une sélection de mots-clés sur *Web of Science* (sur ses trois indexes de citation) ainsi que *Scopus*. Plus de 5 000 articles ont été rassemblés au total. La seconde étape a consisté à rechercher, dans cette collection d'articles ainsi que dans une sélection d'articles issus de la littérature grise, les articles proposant des typologies d'usages attendus pour la monétarisation. Enfin, une analyse quantitative des tendances de la littérature concernant (i) la manière dont l'utilisation est abordée et (ii) les catégories d'utilisation envisagées, a été menée sur un sous-échantillon de 313 articles.

Une typologie des utilisations attendues par la littérature a été constituée à partir de l'analyse d'un ensemble d'articles de cadrage (Navrud et Pruckner, 1997 ; Pearce et Seccombe-Hett, 2000 ; OCDE, 2001 ; OCDE, 2002 ; NRC, 2005 ; SCBD, 2007 ; Liu et al., 2010). On y distingue trois grandes catégories d'utilisations.

L'évaluation décisive : cette première catégorie concerne les cas où l'évaluation permet *une* prise de décision en particulier. Dans ce cas, on peut la voir comme participant à un processus par lequel un choix est opéré, *ex ante*, par un décideur, qui fait face à des options alternatives. Ces options peuvent par exemple concerner une future infrastructure dont on procède à l'analyse coûts-bénéfices, ou bien une politique, sous la forme d'une proposition de réglementation à examiner.

L'évaluation technique : pour le réglage technique d'un instrument ou d'une politique (déjà décidée). Cette deuxième catégorie concerne les cas où l'évaluation s'applique *après* un choix de politique ou de projet, pour permettre le réglage de l'instrument économique qui mettra en œuvre la décision. Le cas des mécanismes de paiements pour services environnementaux, par lesquels les bénéficiaires des services rémunèrent leurs fournisseurs, en est en principe emblématique.

L'évaluation informative : l'évaluation peut aussi être considérée, non plus dans un rôle décisif, ni technique, mais comme un moyen d'information destiné à influencer de manière plus ou moins diffuse sur *la* décision, prise comme un ensemble indéterminé. Dans ce cas, l'évaluation n'est pas attendue pour déterminer un choix dans le cadre d'une décision particulière, mais pour alimenter la réflexion, modifier les points de vue, démontrer l'intérêt de certaines options politiques générales. Les fameux travaux de Costanza et al. (1997) évaluant la valeur des services écosystémiques à l'échelle de la planète illustrent parfaitement cette catégorie.

Ceci posé, comment la littérature traite-t-elle de la question de l'utilisation ? Nous avons distingué trois grands modes de traitement de la question de l'utilisation par la littérature : la simple évocation de l'utilisation, où les auteurs se contentent d'évoquer (souvent en introduction et/ou conclusion) que les évaluations monétaires (celles qu'ils présentent ou en général) pourraient avoir tel ou tel usage ; l'analyse, où les auteurs s'intéressent principalement à la question de l'utilisation des valeurs monétaires produites : par quelles parties prenantes, dans quels contextes, pour quel but et quels résultats, etc. ? ; enfin, la documentation des cas d'utilisation, ou des études de cas suivant précisément la manière dont les résultats d'évaluations monétaires sont utilisés par différentes parties prenantes. À partir des catégories d'utilisations évoquées plus haut et de ces modes de traitement, nous avons quantifié dans notre sous-échantillon de 313 articles le nombre d'articles pour chaque combinaison de catégorie et de traitement (Figure 1).

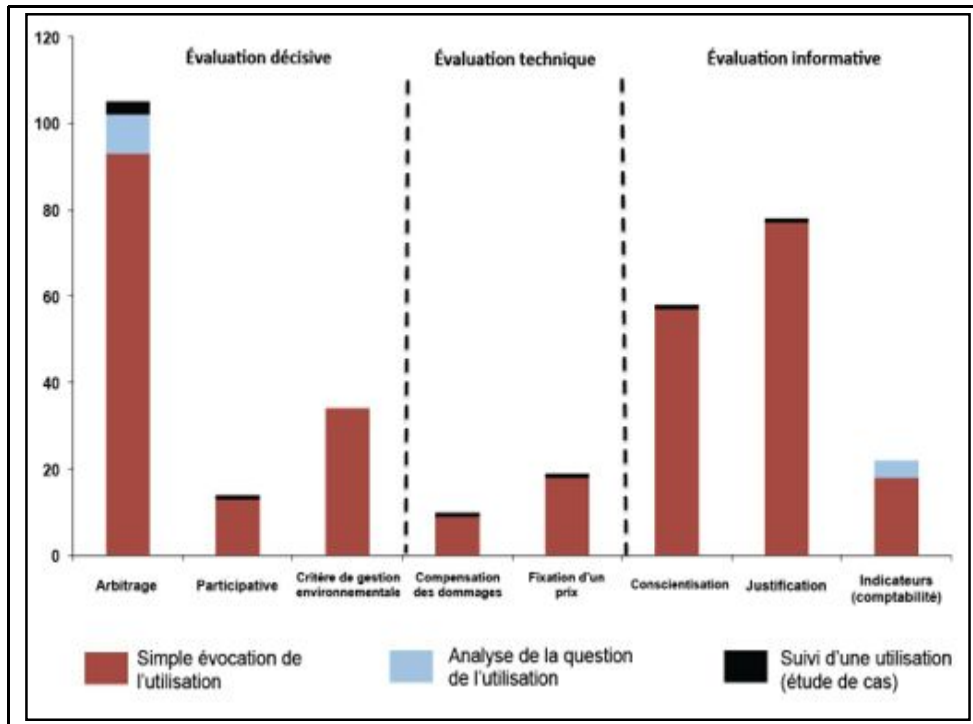


Figure 1 - Répartition du nombre d'articles du sous-échantillon en fonction des catégories d'utilisations envisagées et du mode de traitement de la question de l'utilisation (modifié d'après Laurans et al., 2013)

Le résultat principal de cette analyse est que le mode de traitement principal de la question de l'utilisation est la simple évocation. Seulement trois articles de notre sous-échantillon étaient centrés sur des études de cas, et seulement cinq autres cas d'utilisations ont été rapportés dans le reste des articles.

La question de l'utilisation est étonnamment peu présente dans la littérature sur la monétarisation des services écosystémiques et, lorsque présente, elle ne reçoit généralement pas plus d'attention qu'une simple évocation (référence des auteurs à une utilisation attendue, proposée ou souhaitée). Il semble donc exister un véritable point aveugle de la littérature sur la question, et ce alors même qu'une grande variété d'utilisations est envisagée et semble en tout cas plausible en théorie. Quelles explications avancer, et avec quelles conséquences ?

Origines possibles du point aveugle et conséquences en termes de recherche

Afin d'expliquer le point aveugle observé, nous nous sommes appuyés sur deux grandes familles d'hypothèse : soit il y a plus d'utilisation en pratique que rapporté dans la littérature étudiée, soit l'utilisation est effectivement rare. Ces deux familles et leurs conséquences en termes de recherche sont regroupées dans la Figure 2.

Catégories d'hypothèses	Hypothèses	Perspectives de recherche
Problème de littérature	Cas invisibles	Créer un champ de recherche
	Agenda de recherche	
	Inadéquation disciplinaire	
	Non scientifique	N/A
Peu d'utilisation	Imprécision	Perfectionner les méthodes
	Inadéquation	
	Coût	
	Manque de culture économique	Modifier le contexte
	Cadre légal	
	Stratégies politiques	

Figure 2 - Familles d'hypothèses expliquant le point aveugle et perspectives de recherche associées



Concernant la première famille d'hypothèses, une première possibilité concerne l'invisibilité potentielle des cas d'utilisation. Par exemple, il peut y avoir un décalage temporel entre le moment où la monétarisation est réalisée et le moment où son résultat est effectivement utilisé par des acteurs. Par ailleurs, dans le cas de l'utilisation informative, celle-ci étant plus diffuse, les cas d'utilisation avérée sont plus difficilement observables. Toutefois, étant donné l'ancienneté des pratiques de monétarisation dans le domaine de l'environnement (même dans le secteur des services écosystémiques, qui paraît émergent mais qui a déjà au moins quinze ans d'ancienneté), il apparaît peu probable que l'invisibilité aurait persisté si un effort de recherche s'y était consacré. Ceci amène au second point : il est fort vraisemblable que la question de l'utilisation n'ait en fait que très peu été portée à l'agenda de recherche. La plupart des travaux des économistes sur la question n'aborde que très peu la question de l'utilisation et il faut plutôt se tourner vers d'autres sciences humaines et sociales (sciences de gestion, sciences politiques, sociologie, anthropologie, psychologie etc.) qui étudient plus directement les processus de décision. Toutefois, même si nos références étaient majoritairement composées de travaux d'économistes, de nombreuses autres disciplines étaient représentées mais nous n'avons malgré tout pas trouvé plus de travaux traitant de la question de l'utilisation des évaluations économiques.

Concernant la seconde famille d'hypothèses, la littérature liste plusieurs facteurs qui pourraient expliquer qu'il y a moins d'utilisations en pratique qu'attendu. D'une manière générale, il s'agirait d'une part de perfectionner les méthodes d'évaluations, dont les imprécisions, l'inadéquation par rapport aux besoins des décideurs ou encore les coûts de réalisation seraient autant d'obstacles à leur utilisation dans la décision. L'attention est ici portée à l'ajustement des techniques d'évaluation : il s'agit de perfectionner l'outil et les méthodes. D'autre part, le manque de culture économique des décideurs (qui ne comprendraient donc pas les évaluations monétaires), le manque d'obligations légales à procéder à des évaluations économiques en matière d'environnement, ou encore un comportement stratégique des décideurs qui auraient des réticences face à la transparence apportée par les évaluations économiques, sont considérées comme des causes probables d'un déficit de prise en compte des évaluations économiques et invitent donc à modifier, non pas l'outil, mais le contexte de son utilisation (former les décideurs, changer les lois, exiger la transparence etc.).

Si une attention sur l'outil en lui-même et son contexte d'utilisation sont vraisemblablement souhaitables (et il existe, sur le premier aspect, de très nombreux travaux), il nous semble toutefois important d'insister sur le fait qu'une meilleure adéquation des évaluations économiques des services écosystémiques à ce à quoi elles sont censées servir en pratique – aider à améliorer les décisions impactant les écosystèmes et la biodiversité – doit d'abord passer par un suivi, sur les terrains où elle sont employées, de la manière dont elles s'intègrent dans les processus collectifs qui mènent à la décision. Or, c'est justement le point aveugle que nous avons identifié, et il nous semble donc urgent de mettre cette question encore trop ignorée au cœur de l'agenda de recherche.

Conclusion : Documenter, enfin, la vie sociale des évaluations économiques

Comme rappelé en introduction, beaucoup d'espairs semblent placés dans les évaluations économiques pour ralentir la dégradation des écosystèmes et l'érosion de la biodiversité. Néanmoins, pour qu'elles améliorent les décisions les impactant, ces monétarisations doivent dans les faits être utilisées.

Or, la littérature traite très peu de cette question, pourtant clé, alors même qu'une grande diversité d'utilisations y est envisagée. Que les évaluations soient véritablement utilisées ou non, qu'elles pèsent dans le sens de la conservation ou non, nous n'en savons collectivement que peu de choses. Il semble en tous cas urgent d'objectiver ces questions et d'insérer les retours du terrain dans les réflexions et débats. Cela passe par la multiplication des études de cas visant à documenter la « vie sociale » des évaluations économiques des services écosystémiques : qui participe à leur élaboration, par qui sont-elles utilisées, dans quel contexte, dans quel but et pour quels résultats ?

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Appendix 5

Rankovic et al. (2016)

Rankovic, A., Aubert, P.-M., Lapeyre, R., Laurans, Y., Treyer, S. (2016). IPBES after Kuala Lumpur: Assessing knowledge on underlying causes of biodiversity loss is needed. *Policy Brief n°05/16*, Institute for Sustainable Development and International Relations (IDDRI-Sciences Po), Paris, 4 p.

IPBES after Kuala Lumpur: Assessing knowledge on underlying causes of biodiversity loss is needed

Aleksandar Rankovic, Pierre-Marie Aubert, Renaud Lapeyre, Yann Laurans, Sébastien Treyer (IDDRI)

The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) recently released its first assessments during its fourth plenary meeting in Kuala Lumpur, Malaysia. How these first works will influence debates on biodiversity policies, and potentially support their implementation, will now be a point of attention for the conservation community. Thanks to its original structure and its desire to mobilize a vast diversity of knowledge, IPBES is a historic opportunity to synthesize available knowledge on the causes, rooted in human collective action, that are behind biodiversity loss. The release of the pollination assessment provides the occasion to identify challenges and opportunities to better integrate knowledge on public policies, economic processes and other underlying factors in future IPBES works. The released assessment, albeit identifying a series of direct drivers to pollinator decline, does not actually cover indirect drivers or underlying causes of biodiversity loss with the same depth of analysis. Addressing these topics will require the development of innovative interdisciplinary work among ecological and social sciences, and is crucial in order to find relevant policy options to halt biodiversity loss. There are several windows of opportunity, in the near future, to enhance the focus of IPBES on knowledge about the underlying causes of biodiversity loss.

RECOMMENDATIONS

1. While preparing the next IPBES work programme, governments should:

- a. Request and prioritize an *ad hoc* thematic assessment on existing policies and instruments having an effect on biodiversity worldwide;
- b. Emphasize the focus on “indirect drivers” in all their other assessment requests;
- c. Ensure that “indirect drivers”, and particularly policies and existing solutions for their implementation, are sufficiently covered in all scoping documents, with a dedicated chapter.

2. IPBES should actively reinforce the contribution of social sciences to its work:

- a. Works on biodiversity-impacting policies worldwide should not be considered as policy prescriptive on the basis that they synthesize research on on-going or past governmental action; they are necessary to support effective implementation of biodiversity policies;
- b. Governments and stakeholder organizations should nominate a higher number of social scientists so that they can be in a capacity to contribute to, and also coordinate, such interdisciplinary works;
- c. Similarly, the proportion of social scientists selected as IPBES experts and coordinating lead authors should be increased.

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1. IPBES AND THE IMPLEMENTATION CHALLENGE

IPBES has the overall objective of strengthening the science-policy interface for biodiversity and ecosystem services for the conservation and sustainable use of biodiversity, long-term human well-being and sustainable development. Compared to previous international assessment mechanisms on biodiversity,¹ IPBES innovates in its ambition to integrate a great diversity of academic and non-academic knowledge. Besides, its functions are not limited to producing assessments, as it possesses three other functions: *knowledge generation catalysis*, *policy support* and *capacity building*.² Taken together, these characteristics make IPBES a useful and innovative tool to build the necessary knowledge base to address the challenge of implementing biodiversity policies worldwide.

Indeed, almost twenty-five years after the Convention on Biological Diversity was signed, and with five other international conventions focusing on biodiversity issues,³ as well as numerous expertise mechanisms developed over the years, both the problem and the need to act seem well acknowledged internationally. The CBD's Strategic Plan 2011-2020 and its Aichi Targets, are another example of international commitment. Why then, despite this recognition, is biodiversity still eroding?

Synthesizing knowledge on this precise question would, actually, be a major contribution from IPBES to biodiversity governance. Alongside research on the state of biodiversity and its direct drivers, what is critically needed now is to understand what hampers the implementation of conservation policies and why given policies fail or succeed in halting biodiversity loss worldwide. Examples of questions that need an international synthesis effort include: What is the net effect on biodiversity of often contradictory sectoral domestic policies? How much does spending for conservation weigh compared to environmentally harmful incentives? What do studies tell us about the conservation efficacy of different types of instruments (legal, economic, technical) in the field?

1. For instance : the *Global Biodiversity Assessment*, the *Global Biodiversity Outlooks*, the *Millennium Ecosystem Assessment* and its declinations, *The Economics of Ecosystems and Biodiversity*.

2. Decision UNEP/IPBES.MI/2/9, Appendix 1.

3. Six international conventions focus on biodiversity issues: the CBD, the Convention on Conservation of Migratory Species, the Convention on International Trade in Endangered Species of Wild Fauna and Flora, the International Treaty on Plant Genetic Resources for Food and Agriculture, the Ramsar Convention on Wetlands, and the World Heritage Convention.

Answering such questions would require focusing on factors usually qualified as indirect drivers or underlying causes of biodiversity loss, which are typically the object of CBD's Aichi Targets 1-4. These underlying causes are linked to the functioning of human societies and refer to phenomena that are the traditional domains of investigation of social scientific research. IPBES could represent a historical occasion to develop innovative interdisciplinary work to synthesize available knowledge on policies and instruments having an effect on biodiversity worldwide.

2. CRITICAL BLINDSPOTS AND DISCIPLINARY GAPS IN THE IPBES POLLINATION ASSESSMENT

To achieve this vision, a series of obstacles would need to be overcome first, as revealed by IPBES first thematic assessment. The assessment on pollinators, pollination and food production provides a welcome synthesis on the state of world pollinators and what is known of their contribution to agriculture. It identifies a series of direct drivers threatening pollinators (land-use change, intensive agricultural management and pesticide use, environmental pollution, invasive alien species, pathogens and climate change), which is in itself an important progress in current policy debates. It leaves aside, however, knowledge on important underlying causes such as agricultural trade and policies that are only cursorily addressed in four short paragraphs at the end of Chapter 2. Even though contradictions among sectoral public policies and associated phenomena such as environmentally harmful subsidies are increasingly recognized as major causes behind continuous biodiversity loss,⁴ knowledge thereof is barely mentioned throughout the pollination assessment. In the summary for policymakers (SPM), the word *subsidy* does not even appear. International trade governance strongly influences the production of agricultural commodities, however evidence about this is neither mentioned. When it comes to the possible responses to halt pollinators decline (e.g. Table SPM.1 in the SPM), even though the assessment identifies categories such as transforming agricultural landscapes, it does not mention the contextual conditions that would enable such changes, nor the factors that are currently involved in blocking change.

4. James A. N., Kevin J., & Balmford A. (1999). Balancing the Earth's accounts. *Nature*, 401, 323-324; Centre d'analyse stratégique (2012). *Les aides publiques dommageables à la biodiversité*, rapport de la mission présidée par Guillaume Sainteny, Paris, La Documentation française, 418 p.

How could this be explained? The request to address indirect drivers was present in the scoping approved by governments: the chapter outline states that Chapter 2 will include an assessment of indirect drivers of change, including trade and policies in areas such as agriculture and spatial planning.⁵ There was, however, a lack of experts from social sciences able to tackle such research questions in the group of authors. An analysis of the disciplinary affiliation of the 85 authors: coordinating lead authors (CLAs), lead authors (LAs) and contributing authors (CAs) shows that less than 10% of authors were social scientists. Among them are three anthropologists, two economists, one ethnographer, one geographer and one scholar from education sciences, for a total of eight. Only 2 out of 17 CLAs come from social sciences. Chapter 2, on drivers, counted no social scientist among its authors. Chapter 6 on responses counted only one. The dearth of social sciences in the pollination assessment, and the fast track dimension of the assessment that likely urged to make quick progress in the drafting, plausibly explain that subsidies and other topics have not been considered as a priority for this thematic assessment.

3. CHALLENGES AND OPPORTUNITIES TO ENHANCE THE FOCUS ON UNDERLYING CAUSES OF BIODIVERSITY LOSS IN FUTURE IPBES WORKS

This analysis suggests three challenges to undertaking ambitious syntheses on underlying causes of biodiversity loss in IPBES works: (i) transition towards a solutions mindset; (ii) give more emphasis to underlying causes in IPBES work programme; and (iii) recruit a higher number of social scientists.

(i) Besides alerting on environmental issues, international environmental expertise is increasingly asked to thoroughly explore knowledge on available solutions.⁶ Here, policy relevance means, *inter alia*, synthesizing works that take current or past policies as objects for scrutiny, and pointing out to social contradictions and choices that lie behind the drivers of biodiversity loss. While such assessments might highlight the responsibilities of governments, assessments should not be considered as policy prescriptive on this basis. While moving towards the domain of solutions, the normative and potentially critical dimension of research (both from natural and social sciences)

should be acknowledged and openly debated to express results in a balanced way.⁷

(ii) In practice, given the number and complexity of direct and indirect drivers and their interactions, both families of drivers should systematically be addressed in a dedicated chapter in any thematic assessment. This would maximize chances to analyze the available literature and non-academic sources for each driver family, and also help identify and discuss knowns and unknowns on their interlinkages. In addition, given methodological developments required to produce exhaustive syntheses addressing indirect drivers or underlying causes, a dedicated thematic assessment during the next work programme would be appropriate. The general scope of such an assessment could be to synthesize knowledge on policies and instruments having an effect on biodiversity worldwide. This would constitute an important contribution from IPBES to advancing collective knowledge on these issues and making it available to policymakers, and would probably strengthen interdisciplinary work in IPBES and structure a core of expertise in social sciences.

(iii) To achieve its general objective, IPBES will need to recruit more experts from social sciences, in a capacity to contribute to or coordinate interdisciplinary work on the impact of policies and other indirect drivers on biodiversity. The current efforts undertaken by the governing bodies of IPBES to proactively reach out to social scientists⁸ is a promising trend. Answering challenges (i) and (ii) would also highlight topics covered by social sciences and would render IPBES assessments more attractive to social scientists. In assessing available knowledge on underlying causes of biodiversity loss, important knowledge gaps might be revealed. Here, one of the four functions of IPBES, i.e. *knowledge generation catalysis*, could help engage dialogues with key scientific organisations, policymakers and funding organisations and promote the development of new research to fill the identified knowledge gaps.

In the current IPBES work programme (2014-2018), there are windows of opportunity to further address the underlying causes of biodiversity loss and select relevant experts from social sciences. As for the next work programme, several windows of opportunity to answer the three challenges will open during its preparation. Taking the assessment

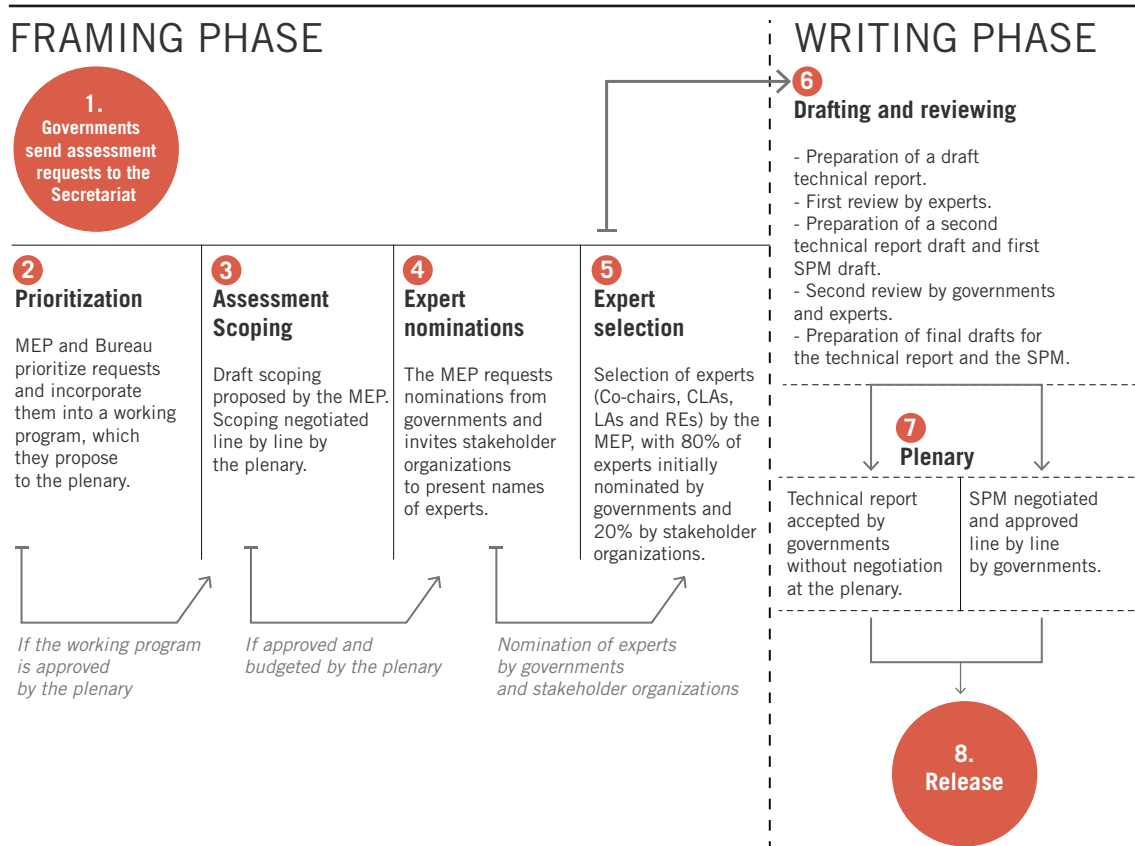
5. Decision IPBES-2/5: Work Programme for the period 2014-2018, p. 24.

6. Carraro, C., Edenhofer, O., & Flachsland, C. (2015). The IPCC at a crossroads: Opportunities for reform. *Science*, 96, 1-2.

7. Treyer, S., Bill, R., Chabason, L., & Magnan, A. (2012). Powerful International Science Policy Interfaces for Sustainable Development. *Policy Brief*, N 06/12, IDDRI, Paris, 4 p.

8. Larigauderie, A., Stenseke, A., Watson, R.T. (2016). IPBES reaches out to social scientists. *Nature*, 532, 313.

Figure 1. Schematic view of the IPBES assessment production process



Note: MEP - Multidisciplinary Expert Panel; CLA - Coordinating Lead Author; LA - Lead Author; RE - Review Editor; SPM - Summary for Policymakers

production process as a reference (see Figure 1), these opportunities are summarized as follows:

A. During the framing phase:

a. While preparing IPBES next work programme (post-2018), governments should put strong emphasis on underlying causes or indirect drivers in all their assessment requests. An ad hoc thematic assessment on existing policies and instruments having an effect on biodiversity should be requested and prioritized. While drafting the next work programme, the Multidisciplinary Expert Panel (MEP) and the Bureau should ensure ample space is given to indirect drivers. During negotiations on scoping documents, governments should ensure that indirect drivers are given enough attention and the object of a dedicated chapter (steps 1-3 on Figure 1).

b. During expert nominations and selections, IPBES governing bodies and partners should perform active outreach towards social scientists (individuals but also organizations, such as professional societies), and governments and stakeholder organizations should ensure to nominate a higher number of social scientists. Similarly,

there should be more CLAs coming from social sciences, especially in the most relevant chapters (steps 4-5).

B. During the writing phase: Authors should put more emphasis on the social scientific literature. All CLAs and LAs should mobilize CAs from social sciences when needed. If assessed works point towards governmental responsibility (e.g. harmful subsidies), such conclusions should not be considered as policy prescriptive, as the information is based on assessed literature. The same goes for the plenary during SPM approvals (steps 6-7).

To give biodiversity a chance, diagnostics are needed on what slows down or hampers the implementation of biodiversity policies. An ambitious knowledge synthesis effort by IPBES on the underlying causes of biodiversity loss would help find relevant policy options. A lot of knowledge on existing policies and instruments affecting biodiversity is available and waiting for IPBES to grasp it, and such effort should be supported by governments. ■

Appendix 6

Curriculum vitæ

ALEKSANDAR RANKOVIC

Born on 03.29.1986 in Paris, France
 French and Serbian citizenships
 Married

Professional contacts:
 IDDRI-Sciences Po
 Postal address: 27 rue Saint-Guillaume, 75007, Paris, France
 Office: 41, rue du Four, 75006, Paris, France
 + 33 6 33 49 64 00 (mobile)
 aleksandar.rankovic@iddri.org

POSITIONS

- January 2015 - Present** **Institute for Sustainable Development and International Relations (IDDRI-Sciences Po)**
 Research fellow on biodiversity and science-society interactions.
- January 2015 - May 2015** **Harvard University – John F. Kennedy School of Government**
 Fellow in the Program on Science, Technology and Society.
- January 2014 - July 2014** **Sorbonne Paris Cité program "Politics of the Earth in the Anthropocene"**
 Program led by Sciences Po (Prof. Bruno Latour). Scientific secretary, general coordination of the program.
- December 2010 - December 2013** **Centre National de la Recherche Scientifique (CNRS)**
 PhD fellow at the Lab of Biogeochemistry and Ecology of Continental Environments (BIOEMCO Lab – UMR 7618), Biodiversity and Ecosystem Functioning Team, Paris.

EDUCATION

- January 2011 - November 2016**
(expected) **PhD in Ecology**
 Université Pierre et Marie Curie-Paris VI, Doctoral School in "Sciences of Nature and Man: Ecology and Evolution" (ED 227)

 Dissertation title: *Living the street life: Long-term carbon and nitrogen dynamics in Parisian soil-tree systems*. Supervised by Luc Abbadie, Sébastien Barot, Jean-Christophe Lata and Julie Leloup. IEES-Paris, Integrative Ecology Team, Paris, France.
- 2008-2010** Dual degree program in Environmental Science and Policy
Master in International Affairs
 Paris Institute of Political Studies (Sciences Po Paris)
Master in Environmental Sciences
 Université Pierre et Marie Curie-Paris VI
- 2004-2008** **Bachelor in Life Sciences**
 Université Pierre et Marie Curie-Paris VI

EXPERIENCES

1. RESEARCH AND TEACHING**1.1. Grants and research contracts**

- 2016-17** **IUCN Centre for Mediterranean Cooperation**, "From nature-based solutions in INDCs to consistent adaptation and mitigation policy planning in the Mediterranean" (co-investigator).
- 2016-17** **French Ministry of the Environment, Energy and the Sea**, "Integrating nature-based solutions into climate change adaptation policies – dialogue and good practices" (principal co-investigator, project submitted).
- 2015-17** **Belmont Forum**, "Impacts of Human Drivers on Biodiversity in Savannas (IHDBS)", (co-investigator, axis leader).

- 2014-16** **University Sorbonne Paris Cité**, "Politics of the Earth in the Anthropocene" interdisciplinary programme (scientific secretary then co-investigator).
- 2014-16** **City of Paris**, Paris 2030, "Implication of mycorrhizal communities in street tree response to trace metal pollution in urban environments (MycoPolis)" (co-investigator).
- 2014-15** **Sorbonne Universités Alliance**, "Densification policies, biodiversity and quality of urban space: urban agriculture and greenways (Dens'City Project)" (co-investigator).
- 2011-13** **GIS « Climat, Environnement, Société »**, "Climate change and urban greenways" (co-investigator, axis leader).
- 2010-11** **PIR IngECotech (CNRS-IRSTEA)**, "Ecological engineering of urban soils in a megalopolis" (co-investigator).
- 2010-13** **Île-de-France region, R2DS**, « Fonctionnement des sols urbains (SOLURB) » (PhD grant).
- 2009-12** **Fondation d'entreprise Hermès - IDDRI**, "Place and role of economic valuations of biodiversity and ecosystem services in decision-making processes" (co-investigator).

1.2. Organization of scientific and multistakeholder events

- November 2016** **Side event at UNFCCC COP22**
 "From nature-based solutions in INDCs to consistent adaptation and mitigation policy planning in the Mediterranean. Feedback and perspectives from Morocco and Tunisia". Convened by the IUCN Centre for Mediterranean Cooperation and IDDRI, in partnership with the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification of Morocco and the Ministry of Environment and Sustainable Development of Tunisia. Co-organizer. 8 November, Marrakech, Morocco.
- October 2016** **Journées FRB 2016 & Troisièmes rencontres GIEC-IPBES : "L'influence du GIEC et de l'IPBES sur la prise de décision" (UNFCCC COP22 labeled event)**
 Co-organized by FRB and IDDRI. Main organizer on the side of IDDRI. 13-14 October 2016, Paris, France. Website: <http://www.fondationbiodiversite.fr/fr/fondation/evenements/evenements-frb/journeesfrb2016.html>
- June 2016** **CSaP-IDDRI workshop: "The works of and on IPBES: What research for what intervention?"**
 Main co-organizer with Alice Vadrot. Academic workshop co-organized by IDDRI and the Centre for Science and Policy, University of Cambridge. 27 June 2016, Cambridge, UK. Website: <http://www.iddri.org/Evenements/Ateliers/The-works-of-and-on-IPBES-What-research-for-what-intervention>
- April 2016** **Séminaire FRB-Idddri : « IPBES : Kuala Lumpur, et après ? »**
 Main co-organizer with Agnès Hallosserie (FRB). Multistakeholder workshop on the outcomes of IPBES' fourth plenary and how to address its influence on biodiversity policies. Institut des sciences de la communication, 28 avril 2016, Paris. Website: <http://www.iddri.org/Evenements/Conferences/IPBES-Kuala-Lumpur,et-apres>
- October 2015** **International conference « Des formes pour vivre l'environnement. Théorie, expérience, esthétique et critique politique »**
 Organized by the LADYSS (CNRS-Univ. Paris 1, 7, 8, 10) and the CRAL (CNRS-EHESS). Member of the scientific committee. 1-2 October 2015, Paris. Website : <http://cral.ehess.fr/index.php?2046>
- September 2015** **International conference "Ecology at the interface", symposium "Ecologists' strategies at science-policy interfaces: How can social sciences help?"**
 Main organizer, with Audrey Coreau, Laurent Mermet and Yann Laurans. Held at "Ecology at the interface", 13th European Ecological Federation (EEF) and 25th Italian Society of Ecology's (SIe) joint conference, 21-25 September, Rome, Italy.
- April 2015** **Harvard STS workshop "Science and its Publics: Conversations on accountability"**
 Organizer with Paulo Fonseca, Zara Mirmalek, Zoe Nyssa, Matthew Sample. Held on 28 April 2015 at Harvard University Center for the Environment. Website: <http://sts.hks.harvard.edu/events/workshops/science-and-its-publics/>

- April 2015** **Harvard STS special seminar on environmental migrations**
Organizer and discussant, seminar with François Gemenne on "Anthropocene and Its Victims: How We Name Those Displaced by Environmental Changes", 24 April at the John F. Kennedy School of Government.
Website: <http://sts.hks.harvard.edu/events/workshops/special-seminar-anthropocene-and-its-victims/>
- November 2014** **École thématique « Transition écologique et environnement urbain : cas de l'agglomération parisienne » of OSU Ecce Terra (UPMC-CNRS)**
Organizer and animator of the seminar «Vies de rue: Regards croisés sur les plantations d'alignements parisiennes» with presentations from researchers and practitioners. Held on 6 November 2014 at the National Museum of Natural History, Paris.
- January – July 2014** **Sorbonne Paris Cité "Politics of the Earth" programme**
Organizer of four interdisciplinary workshops and one conference evaluated by an international jury. Website: <http://politiquesdelaterre.fr>
- April 2012 – April 2014** **Seminar "History, Philosophy and Sociology of Ecology"**
Founder and organizer, with Alix Sauve and Henri de Parseval. Bimestrial sessions with invited speakers, held at IEES-Paris. Program (in French): <http://ieesparis.ufr918.upmc.fr/spip.php?article476>
- December 2012** **Symposium "Vegetation, Cities and Climate: Scientific approaches, political issues", organized by the CCTV2 project and Paris 2030 program**
Member of the scientific committee. Held on 3 December 2012, Auditorium de l'Hôtel de Ville, Paris.
- December 2011** **Sixth edition of the Regional Ecological Engineering Symposium, "Engineering the water continuum"**
Member of the scientific committee and co-chair of the final round table. Held on 13-14 December 2011, CIUP, Paris.
- December 2010** **Fifth edition of the Regional Ecological Engineering Symposium, "Biodiversity and ecological engineering: constraint or opportunity?"**
Member of the scientific committee. Held on 8-9 December 2010, CIUP, Paris.
- May 2010** **Symposium "A diverse but common world: Biodiversity and Cooperation between Peoples"**
Part of Sciences Po's "Politics of the Earth" research axis (POLEARTH). Main organizer, with Émilie Hache and Béatrice Cointe. Held on 6 May 2010, Sciences Po, Paris.
Website: <http://blogs.sciences-po.fr/recherche/files/2009/12/BiodiversityCooperation-Between-Peoples-2604.pdf>

1.3. Teaching:

- September 2016** **Summer school "Politics of the Earth" (Sciences Po & associate European universities)**
One-week programme, 5-9 September 2016. Member of the organizing committee, in charge of the day on "Politics of Biodiversity" (personal involvement in 6 hours of teaching). Funded by EDGE project (H2020).
- October 2012** **École Normale Supérieure, Paris**
Graduate program in biology, course unit "Insights in Life Sciences": Full development, teaching and evaluation of the course "Ecosystem ecology in urban environments: descriptive and practical challenges", three lectures of one hour.
- September - December 2011** **Université Pierre et Marie Curie-Paris VI**
Master "Sciences of the Universe, Environment, Ecology", course in "Great environmental issues" (10h teaching). Co-responsible and member of the final evaluation jury.

1.4. Mentoring:

• 2015-2016

- Stefanie Chan, M2 "International Public Management", Sciences Po. Five months, co-advised with Yann Laurans.

- Rémy Ruat, M1 "Environmental Science and Policy", Université Pierre et Marie Curie - Paris VI and Sciences Po. Six months, co-advised with Sébastien Treyer.

• **2013-2014**

- Iry Andrianjara, M2 "Ecology, Biodiversity, Evolution", Université Paris-Sud. Four months, co-advised with Katell Quenea and Jean-Christophe Lata.

- Anne Barbillon, M1 "Agronomic Engineering", SupAgro Montpellier. Five months, co-advised with Benoît Geslin, Éric Motard and Isabelle Dajoz.

• **2012-2013**

- Víctor Cárdenas Ortega, M2 "Ecology, Biodiversity, Evolution", Université Pierre et Marie Curie - Paris VI. Four and a half months, co-advised with Sébastien Barot and Pierre Barré.

- Quentin Guignard, M2 "Ecology, Biodiversity, Evolution", AgroParisTech. Six months, co-advised with Sébastien Barot.

- Marie Fernandez, M2 "Molecular and Cell Biology", École Normale Supérieure. Six months, co-advised with Julie Leloup.

- Christelle Leterme, M1 in Geography, major in environment, Université Paris 1-Panthéon-Sorbonne. Four months, co-advised with Anne Sourdril.

• **2011-2012**

- Ingrid Cheung Chin Tun, M2 "Environmental Science and Policy", Université Pierre et Marie Curie - Paris VI and Sciences Po. Six months, co-advised with Anne Sourdril.

- Anastasia Wolff, M2 "Ecology, Biodiversity, Evolution", École Normale Supérieure. Four months, co-advised with Julie Leloup.

- Zhanara Abikeyeva, dual degree in "Environmental Sciences", Université Paris-Sud and Tomsk Polytechnic University (Russia). Four months, co-advised with Jean-Christophe Lata.

- Anastasiya Stepanova, dual degree in "Environmental Sciences", Université Paris-Sud and Tomsk Polytechnic University (Russia), Four months, co-advised with Jean-Christophe Lata.

- Noémie Courtejoie, third year of the BSc in Biology, École Normale Supérieure. Two months, co-advised with Jean-Christophe Lata.

• **2010-2011**

- Benjamin Izac, M1 "Ecology, Biodiversity, Evolution", Université Paris-Sud. One month.

• **2009-2010**

- Ambre David, M1 "Ecology, Biodiversity, Evolution", Université Pierre et Marie Curie - Paris VI. Two months, co-advised with Luc Abbadie.

1.5. Service:

**April 2012 -
December 2013** **BIOEMCO Lab council**
PhD students representative.

**October 2011 -
December 2013** **Scientific committee of the Doctoral School in Diversity of Living Organisms,
Université Pierre et Marie Curie-Paris VI**
PhD students representative.

2. PARTICIPATION TO POLICY PROCESSES

November 2016 **UNFCCC COP 22, 7 November-18 November 2016, Marrakech, Morocco.**
Accredited observer (Pacific Community – SPC). Organization of a side event, interviews and observations.

February 2016 **Fourth plenary of IPBES, 22-28 February 2016, Kuala Lumpur, Malaysia.**
Accredited observer, representative of IDDRI. Observations and language proposal to the French delegation. Accepted language includes the ending sentence of the pollination assessment's summary for policymakers, as well as the ending sentence of its last key message.

December 2015 UNFCCC COP 21, 30 November-12 December 2015, Paris-Le Bourget, France.
Accredited observer (IDDRI). Interviews and observations.

3. CONSULTING, EXPERTISE

March 2014 **Institut de conseil et d'études en développement durable (ICEDD – Namur, Belgium)**
External reviewer for a study commissioned by the Walloon Region on the costs of climate change inaction. Chapter on biodiversity and ecosystem services.

March -
September 2010 **Veolia Environnement Recherche et Innovation (VERI)**
Project officer for the study "Ecosystem services in urban environments" (final Master internship). Final report: *Management of ecosystem services in urban environments: Research and application prospects*, 131 p.

September -
October 2009 **Chaire de Développement Durable de Sciences Po – European Commission**
Contribution to the European Union Development Days 2009 :
Redaction of a policy brief on the EU-Med cooperation for climate change adaptation, for the plenary session "The road to Copenhagen and beyond" held on 24 October. Attending to the event and on-site diffusion of the paper to international actors (22-24 October 2009, Stockholm, Sweden).

January -
June 2009 **Caisse des Dépôts et Consignations – Carbon Finance**
Student group work (Sciences Po's « projet collectif »):
Feasibility study for the implementation of an investment fund dedicated to "programmatic" joint implementation projects of greenhouse gas emissions reduction at the European level (Kyoto protocol framework). In charge of the methanization sector (agricultural and domestic waste).

OTHER EXPERIENCES

September 2008 -
June 2010 **Association Sciences Po Environnement (<https://sciencespoenvironnement.fr>)**
Association member and President from July to December 2009.

January 2005 -
July 2008 **Häagen-Dazs Saint-Honoré & Häagen-Dazs Rosny 2**
Staff then store manager.
Shops with respective annual turnovers of 700k€ and 450k€ in 2007. Staff management (10 et 5 employees), supervising the application of standards (hygiene and service quality), stock management, cash management.

SKILLS

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Languages

- French: Native speaker
- English: Fluent (TOEIC 990/990, TOEFL iBT 109/120)
- Serbo-Croatian: Native speaker, Cyrillic and Latin alphabets
- Spanish: Beginner
- Japanese: Notions

Analytical skills

- Fieldwork and experimental design
- Soil physico-chemistry (e.g. bulk density, texture, particle-size analysis, C and N contents, pH, etc.)
- Stable isotope (¹⁵N, ¹³C) analysis in ecology
- Microbial ecology (qPCR, T-RFLP, activity analysis by gas chromatography – CO₂, N₂O –, MicroResp™-CLPP)
- Univariate statistical modelling (R software)
- Qualitative research methods for the social sciences (semi-structured interviews, participant observations, direct observations)
- Research synthesis through systematic review methods

Soft skills

- Conduct of interdisciplinary research
- Research project development and management
- Experience in teaching and course development
- Mentoring students
- Scientific animation
- Outreach: oral communications and writings for local, national and European actors (City of Paris, French National Agency for Water and Aquatic Environments, French Ministry of the Environment, European Commission etc.) and the media (*Le Monde*, *Le Figaro*)

Others

- Black belt in karate (Shotokan-ryu)

PUBLICATIONS AND COMMUNICATIONS

1. EDITED VOLUMES

2016-2017. Principal guest editor for *Environmental Science & Policy*, special issue "A bridge for what? Discussing the politics of ecological sciences in biodiversity policy-making", co-edited with Audrey Coreau, Yann Laurans, Laurent Mermet and Sébastien Treyer. Forthcoming.

2. ARTICLES IN PEER-REVIEWED JOURNALS

David, A. A. J., Boura, A., Lata, J.-C., **Rankovic, A.**, Kraepiel, Y., Charlot, C., Barot, S., Abbadie, L., Ngao, J. (submitted). Street trees in Paris are sensitive to spring and autumn precipitation and recent climate changes.

Glatron, S., Blanc, N., Lamarche, T., **Rankovic, A.** (submitted). Urban vegetation as a means of mitigating the effects of global warming: what do city dwellers think?

Blanc, N., Glatron, S., Lamarche, T., **Rankovic, A.**, Sourdril, A. (submitted). A new hybrid governance of urban nature: French case-studies.

Natali, M., Zanella, A., **Rankovic, A.**, Banas, D., Cantaluppi, C., Abbadie, L., Lata, J.-C. (2016). Assessment of trace metal air pollution in the Paris area using TXRF-slurry analysis on cemetery mosses, *Environmental Science and Pollution Research*, doi:10.1007/s11356-016-7445-z

Gattuso, J.-P., Magnan, A., Billé, R., Cheung, W. W. L., Howes, E. L., Joos, F., Allemand, D., Bopp, L., Cooley, S., Eakin, C. M., Hoegh-Guldberg, O., Kelly, R. P., Pörtner, H.- O., Rogers, A.D., Baxter, J. M., Laffoley, D., Osborn, D., **Rankovic, A.**, Rochette, J., Sumaila, U. R., Treyer, S., Turley, C. (2015). Contrasting futures for ocean and society from different CO₂ emissions scenarios, *Science*, 349(6243), aac4722. DOI: 10.1126/science.aac4722

Laurans, Y., **Rankovic, A.**, Billé, R., Pirard, R., Mermet, L. (2013). Use of ecosystem services economic valuation for decision making: Questioning a litterature blindspot, *Journal of Environmental Management*, 119, 208-219

Rankovic, A., Pacteau, C., Abbadie, L. (2012). Ecosystem services and cross-scale urban adaptation to climate change: An articulation essay, *Vertigo*, Special Issue 12, <http://vertigo.revues.org/11851> (in French)

3. BOOK CHAPTERS

Chabason, L., **Rankovic, A.**, Bonnel, A. (2016). De l'expertise à l'expérimentation collective ? Les liens entre sciences et politiques à l'heure de la mise en œuvre du développement durable. *Regards sur la Terre 2016*, forthcoming.

4. WORKING PAPERS, POLICY BRIEFS, OUTREACH

Rankovic, A., Aubert, P.-M., Lapeyre, R., Laurans, Y., Treyer, S. (2016). IPBES after Kuala Lumpur: Assessing knowledge on underlying causes of biodiversity loss is needed. *Policy Brief n°05/16*, Institute for Sustainable Development and International Relations (IDDRI-Sciences Po), Paris, 4 p. <http://www.iddri.org/Publications/IPBES-after-Kuala-Lumpur-Assessing-knowledge-on-underlying-causes-of-biodiversity-loss-is-needed>

Aubert, P.-M., Ruat, R., **Rankovic, A.**, Treyer, S. (2016). Which accountability framework and transformational potential of a multi-stakeholder initiative? The case of the 4% Initiative. *Policy Brief n°01/16*, Institute for Sustainable Development and International Relations (IDDRI-Sciences Po), Paris, 4 p. <http://www.iddri.org/Publications/Cadre-de-redevabilite-et-potentiel-transformationnel-d-une-initiative-multi-acteurs-le-cas-du-4>

Aubert, P.-M., Ruat, R., **Rankovic, A.**, Treyer, S. (2016). Cadre de redevabilité et potentiel transformationnel d'une initiative multi-acteurs : le cas du 4 %. *Policy Brief n°01/16*, Institute for Sustainable Development and International Relations (IDDRI-Sciences Po), Paris, 4 p. <http://www.iddri.org/Publications/Cadre-de-redevabilite-et-potentiel-transformationnel-d-une-initiative-multi-acteurs-le-cas-du-4>

David, A., Boura, A., **Rankovic, A.**, Kraepiel, Y., Barot, S., Abbadie, L., Lata, J.-C., Ngao, J. (2015). Long term impact of climate on tree-growth patterns in Paris street trees and its consequences on tree cooling potential: A dendroclimatic approach. *Proceedings of ICUC9, 9th International Conference on Urban Climate jointly with the 12th Symposium on the Urban Environment (20-24 July, Toulouse, France)*, 5 p.

Rankovic, A., Billé, R. (2013). Les utilisations de l'évaluation économique des services écosystémiques : un état des lieux. *Études et documents*, n°98. Commissariat général au développement durable, Ministère de l'Écologie, du Développement Durable et de l'Énergie. http://www.developpement-durable.gouv.fr/IMG/pdf/E_D98_actes_seminaire_monetarisat_2012-2.pdf

Muller, Y., Nicolas, V., **Rankovic, A.**, Genet, P., Lacroix, G., Hulot, F. (2012). Engineering the water continuum. *ONEMA Meetings*, n°16, August 2012. <http://www.onema.fr/IMG/EV/meetings/Les-Rencontres-16UK.pdf>

Muller, Y., Nicolas, V., **Rankovic, A.**, Genet, P., Lacroix, G., Hulot, F. (2012). L'eau, ingénierie d'un continuum. *Les rencontres de l'ONEMA*, n°16, Août 2012. <http://www.onema.fr/IMG/pdf/rencontres/Onema-Les-Rencontres-16.pdf>

Billé, R., Laurans, Y., Mermet, L., Pirard, R., **Rankovic, A.** (2012). Valuation without action? On the use of economic valuations of ecosystem services. *Policy Brief n°07/12*, Institute for Sustainable Development and International Relations (IDDRI-Sciences Po), Paris, 6 p. <http://www.iddri.org/Publications/Collections/Syntheses/Valuation-without-action-On-the-use-of-economic-valuations-of-ecosystem-services>

Rankovic, A., Chancel, L., De Sahb, C. (2009). No-regret strategies in the Mediterranean: building sustainability through climate change adaptation. Reflexion paper for the European Union Development Days 2009, Stockholm, 22-24 October 2009, Stockholm, Sweden, 4 p.

5. OTHER ARTICLES, OPINIONS

Rankovic, A., Silvain, J.-F., Abbadie, L., Barot, S., Bœuf, G., Chenu, C., Dajoz, I., Frascaria-Lacoste, N., van den Hove, S., Jouzel, J., Laurans, Y., Lavorel, S., Le Treut, H., Leroux, X., Sarrazin, F., Treyer, S., Tubiana, L. (2016). Climat et biodiversité : les experts doivent évaluer réussites et échecs des politiques publiques. *Le Figaro*, 14 October 2016 (print). <http://www.lefigaro.fr/vox/societe/2016/10/13/31003-20161013ARTFIG00288-climat-les-experts-doivent-evaluer-reussites-et-echecs-des-politiques-publiques.php>

Silvain, J.-F. & **Rankovic, A.** (2016). Les premières évaluations de l'IPBES sont-elles à la hauteur des attentes des chercheurs ? *Fondation pour la Recherche sur la Biodiversité*, 4 p. http://www.fondationbiodiversite.fr/fr/images/documents/IPBES/Article_FRB_Iddri_formaté.pdf

Laurans, Y., **Rankovic, A.**, Lapeyre, R. (2016). L'IPBES pertinent politiquement : chiche ! *Blog Iddri*, <http://www.blog-iddri.org/fr/2016/05/23/l-ipbes-pertinent-politiquement-chiche/>

Rankovic, A. (2016). « Giec de la biodiversité » : l'étude globale sur la pollinisation fera-t-elle mouche ? *Le Monde* (web), 26 February 2016. http://www.lemonde.fr/idees/article/2016/02/26/giec-de-la-biodiversite-l-etude-globale-sur-la-pollinisation-fera-t-elle-mouche_4872468_3232.html

Collective (2015). Where Does France Go From Here? A Manifesto For Another Debate. *Harvard Kennedy School Review*, blog entry, 16 November 2015. <http://harvardkennedyschoolreview.com/where-does-france-go-from-here-a-manifesto-for-another-debate/>. French version: Et maintenant ? Manifeste pour un autre débat. <http://harvardkennedyschoolreview.com/et-maintenant-manifeste-pour-un-autre-debat/>

Billé, R., Laurans, Y., Mermet, L., Pirard, R., **Rankovic, A.** (2011). À quoi servent les évaluations économiques de la biodiversité ? *Ecorev' - Revue critique d'écologie politique*, n°32, 48-54

Rankovic, A. (2009). Chasse aux cétacés : coopération et conflits. *The Paris Globalist* Vol. III. n°2, p. 37 http://www.global21online.org/paris/pdf/Vol_III_Issue_2.pdf

6. ORAL COMMUNICATIONS AND POSTERS (*invited)

- Oral communications (O) and posters (P) presented at international scientific congresses

- Rankovic, A.** (2016). Long-term carbon and nitrogen dynamics in Parisian street soil-tree systems. First Open Science Meeting of the International Long-Term Ecological Research Network, 9-13 October, Kruger National Park, South Africa (P)
- Aubert, P.-M., Lapeyre, R., Laurans, Y., Vignes, R., **Rankovic, A.** (2016). The global value chains of commodities and the future of savannas: First results on soybean and the Brazilian cerrado. First Open Science Meeting of the International Long-Term Ecological Research Network, 9-13 October, Kruger National Park, South Africa (O, presenter)
- Charles-Dominique, T., Barot, S., Beckett, H., Blaum, N., Bond, W., Bustamante, M., Durigan, G., Kimuyu, D. M., Langan, L., Lata, J.-C., Laurans, Y., Murphy, B., Poux, X., **Rankovic, A.** (2016). Global and regional threats to savannas. First Open Science Meeting of the International Long-Term Ecological Research Network, 9-13 October, Kruger National Park, South Africa (O)
- Poux, X., **Rankovic, A.**, Bustamante, M., Coreau, A., Laurans, Y., Gignoux, J. (2016). How to ensure a long-term sustainability for world savannas? Insights from an international scenario-building initiative. First Open Science Meeting of the International Long-Term Ecological Research Network, 9-13 October, Kruger National Park, South Africa (O)
- Gignoux, J., Barot, S., Beckett, H., Blaum, N., Bond, W., Bustamante, M., Charles-Dominique, T., Durigan, G., Langan, L., Lata, J.-C., Laurans, Y., Poux, X., **Rankovic, A.** (2016). The interest of heuristic conceptual models to predict the future of biodiversity in different ecosystems. Application to savannas worldwide. First Open Science Meeting of the International Long-Term Ecological Research Network, 9-13 October, Kruger National Park, South Africa (O)
- Poux, X., **Rankovic, A.**, Bustamante, M., Coreau, A., Laurans, Y., Gignoux, J. (2016). The future of world savannas: a burning issue. EcoSummit 2016 - Ecological Sustainability: Engineering Change, 29 August - 1 September 2016, Montpellier, France (O)
- Rankovic, A.** (2016). The place to be? Questioning the ocean's quest for existence in the vast climate machine. Fifteenth Annual Meeting of the Science and Democracy Network, 23-25 June, London School of Economics and University College London, London, UK (O)
- Rankovic, A.**, Coreau, A., Laurans, Y., Mermet, L., Treyer, S. (2015). Ecologists' strategies at science-policy interfaces: How can social sciences help? Opening remarks. Symposium S25, "Ecologists' strategies at science-policy interfaces: How can social sciences help?", at "Ecology at the interface": 13th European Ecological Federation (EEF) and 25th Italian Society of Ecology's (SIe) joint conference, 21-25 September, Rome, Italy (O)
- Rankovic, A.**, Geslin, B., Barbillon, A., Vaury, V., Abbadie, L., Dajoz, I. (2015). The $\delta^{15}\text{N}$ signature of pollinating insects along an urbanization gradient in the Ile-de-France region. "Ecology at the interface": 13th European Ecological Federation (EEF) and 25th Italian Society of Ecology's (SIe) joint conference, 21-25 September, Rome, Italy (O)
- David, A., Boura, A., **Rankovic, A.**, Kraepiel, Y., Barot, S., Abbadie, L., Lata, J.-C., Ngao, J. (2015). Long term impact of climate on tree-growth patterns in Paris street trees and its consequences on tree cooling potential: A dendroclimatic approach. ICUC9, 9th International Conference on Urban Climate jointly with the 12th Symposium on the Urban Environment, 20-24 July, Toulouse, France (O)
- David, A., **Rankovic, A.**, Bariac, T., Richard, P., Bagard, M., Lata, J.-C., Barot, S., Abbadie, L. (2014). Street Ecohydrology: A project to study street tree water use strategies and their consequences for managing tree cooling effects. 17th International Conference of the European Forum on Urban Forestry, 3-7 June 2014, Lausanne, Switzerland (P)
- Blanc, N., Glatron, S., Lamarche, T., **Rankovic, A.**, Sourdril, A. (2014). Interdisciplinary perspectives on urban green infrastructure and climate change adaptation: The stakes of a governance reconfiguration (Paris case-study). Second Global Land Project Open Science Meeting, "Land Transformations: Between Global Challenges and Local Realities", 19-21 March, Berlin, Germany (O)
- Rankovic, A.**, Barot, S., Lata, J.-C., Leloup, J., Sebilo, M., Zanella, A., Abbadie, L. (2013). Urban ecosystem ecology at the soil-plant-atmosphere interface: Studies on a Parisian long-term chronosequence. INTECOL 2013, joint congress of the International Association for Ecology and the British Ecological Society, 18-23 August, London, United Kingdom (O)
- Rankovic, A.**, Fernandez, M., Wolff, A., Lerch, T., Lata, J.-C., Barot, S., Abbadie, L., Leloup, J. (2013). Patterns in urban soil nitrogen cycling communities from a soil-tree chronosequence in Paris: A case of long-term microbial succession? INTECOL 2013, joint congress of the International Association for Ecology and the British Ecological Society, 18-23 August, London, United Kingdom (P)

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Rankovic, A. (2016). Helping the bug bite? Explicit and implicit conceptions of "policy relevance" in the IPBES pollination assessment. CSaP-IDDRI joint workshop, "The works of and on IPBES: What research for what intervention?", 27 June, University of Cambridge, UK (O)

Rankovic, A., Geslin, B., Barbillon, A., Vaury, V., Abbadie, L., Dajoz, I. (2016). Biodiversité urbaine et pollinisateurs. Colloque de bilan du programme interdisciplinaire « Politiques de la Terre à l'épreuve de l'Anthropocène », 14 juin, Sciences Po, Paris (O)

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Rankovic, A. (2015). Discussant, with Claire Stockwell and Maximilian Mayer, of François Gemenne's seminar: "Anthropocene and Its Victims: How We Name Those Displaced by Environmental Changes", John F. Kennedy School of Government, Harvard University, 24 April 2015, Cambridge, MA, USA (O)

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***Rankovic, A.** (2013). Round table « Cultures et fonctionnalités de l'environnement », study days «Gouvernance des natures urbaines» organized by LADYSS, 5-6 December, Paris (O)

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***Rankovic, A.** (2013). Dynamique de long terme du carbone et de l'azote dans les écosystèmes urbains : cas des plantations d'alignement parisiennes. Communication to the first « Journée d'Écologie Urbaine », 9 July Université Pierre et Marie Curie, Paris (O)

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Blanc, N., Boudes, P., Glatron, S., **Rankovic, A.** & Sourdril, A. (2012). Greening, Climate and the City: the CCTV program. Communication to the Zones Ateliers - LTER meeting, 17 October, Paris (O)

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Billé, R., **Rankovic, A.** (2012). Actual use of ecosystem services valuation for decision making: Questioning a literature blindspot. Communication to the regular seminar of the Biodiversity and Ecosystem Functioning team, Lab of Biogeochemistry and Ecology of Continental thés, 30 January, École Normale Supérieure, Paris, France (O)

• Communications at multistakeholder symposia

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Lata, J.-C., **Rankovic, A.**, David, A., Dusza, Y., Kaisermann, A., Yusupov, D., Baranovskaya, N., Kim, J. (2014). Multifonctionnalité des écosystèmes urbains dans la lutte contre le changement climatique. Communication au colloque annuel du Groupe des Acteurs de l'Ingénierie Écologique, « L'ingénierie écologique : une option face au changement climatique ? », 15 December, Paris, France

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Andrianjara, I., **Rankovic, A.**, Lata, J.-C., Castrec Rouelle, M., Quenea, K. (2014). Estimation des concentrations en éléments traces métalliques dans les sols et feuilles d'une chronoséquence de plantations d'alignement parisiennes : conséquences pour le recyclage des sols et l'utilisation du compost de feuilles en agriculture urbaine. Communication aux « Ateliers d'été de l'agriculture urbaine et de la biodiversité » de Natureparif, 30 juin-2 juillet 2014, Paris, France

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***Rankovic, A.**, Billé, R. (2012). Les utilisations de l'évaluation économique des services écosystémiques : un état des lieux. Communication to the symposium « Monétarisation des biens et services environnementaux : Quelles utilisations pour les politiques publiques et les décisions privées ? » of the French Ministry of Ecology, Sustainable Development and Energy, 13 December, Paris, France
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7. AUDIOVISUAL AND OTHER PRODUCTIONS

Garrigou, A.-S., **Rankovic, A.** (2014). Videos summarizing the first year of the programme Politics of the Earth in the Anthropocene:

- Épreuve « *Geopolitique des dioxydes de carbone* » - *Résumé des travaux 2013-2014*. <https://www.youtube.com/watch?v=zW3o-vq-cfA>

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- Épreuve « *Dynamiques des zones critiques et conflits d'urbanisation* » - *Résumé des travaux 2013-2014*. <https://www.youtube.com/watch?v=T1wwrFLj0qQ>

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8. MENTIONS IN THE PRESS

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