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- 1 Influence of species and stand position on isotopic and molecular composition
- 2 of leaf litter during degradation in an urban mangrove forest
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- 9 Abstract

10 Understanding the diagenetic processes of organic matter (OM) within mangrove forests is essential to grasp ecosystem dynamics and exchanges with adjacent ecosystems. This study investigated 11 12 the influence of urban runoff on leaf litter degradation in a New Caledonian mangrove forest, subjected to urban rainwater for over 50 years. Focusing on Avicennia marina and Rhizophora 13 14 stylosa, our objectives were to determine factors affecting leaf litter degradation, assess urban runoff effects on decay rates and element concentrations, and understand OM changes at the molecular 15 level. Litterbags containing senescent leaves placed on the mangrove floor were collected after 7, 16 17 14, 28, 56, and 72 days. C and N along with their stable isotopes were evaluated during degradation 18 as well as lignin and neutral carbohydrates contents. Despite lower initial N content, R. stylosa 19 exhibited faster degradation ($t_{1/2}$ of 36±3 and 28±2 days) than A. marina ($t_{1/2}$ of 43±9 and 33±4 days), 20 emphasizing the critical role of species position within the mangrove forest regarding tidal immersion. Urban runoff, submerging the urban site, intensified leaf litter degradation, influencing 21 both mass loss and molecular changes in OM. After 72 days of leaf litter degradation, the loss of 22 rhamnose and glucose was more pronounced at the control site (13% and 75% for rhamnose and 23 24 46% and 53% for glucose for A. marina and R. stylosa, respectively) compared to the urban site. The study also exposed molecular tendencies during mangrove leaf litter degradation. The content 25 of ferulic acid in the leaf litter decreased at all stands after 72 days of degradation (between -25%) 26 and -58%), while total syringyl phenols increased (between +64% and +232%). This research 27 exposed the global implications of urban runoff, indicating accelerated leaf litter degradation in 28

mangrove forests, potentially disrupting C sequestration dynamics and threatening ecosystem
 services.

31 <u>Keywords:</u> mangrove, litterbag, stable isotopes, lignin, neutral carbohydrates

32 **1. Introduction**

Mangrove forests are coastal ecosystems established in tropical and sub-tropical areas 33 34 around the world, with some species present in temperate regions (e.g. Auckland, NZ). These forests have a very large organic carbon (OC) stock, much larger than any marine and terrestrial 35 ecosystems within the same latitudes (Alongi, 2014). Most of this OC is stored in the soil, but about 36 15% is in the aboveground biomass (Alongi, 2020). 31% of the total net primary production of 37 mangrove forests comes from the production of litter (Bouillon et al., 2008). Once this biomass turns 38 39 into litter, it becomes a crucial part of the trophic chain of the mangrove forest and adjacent 40 ecosystems. Litterfall degradation actively contributes to the energy and material flow in the forest 41 and is considered an energy source for coastal productivity (Lugo and Snedaker, 1974; Twilley et 42 al., 1986). The litterfall organic matter (OM) can be consumed in the forest floor by autochthonous fauna and microorganisms, dissolved during decomposition, and exported to adjacent ecosystems 43 at ebb tide as debris, dissolved OM, or dissolved inorganic matter, which also has a key role in the 44 45 trophic chain (Fleming and Lin, 1990; Rezende et al., 1990; Wafar et al., 1997; Kristensen et al., 46 2017; Kida et al., 2019).

Mangrove leaves account for the major part of the litterfall (Twilley et al., 1986; Day et al., 47 48 1987), varying between 40 and 90% (Mackey and Smail, 1996). Fruits, flowers, and the woody 49 tissues account for the remaining litterfall. Therefore, most studies on litterfall degradation focused on leaf litter, using the litterbag experiment for comparison with literature (Nordhaus et al., 2017; 50 51 Yang et al., 2018; Vinh et al., 2020). Leaf litter degradation occurs in three main stages: 1) the initial leaching of soluble compounds, 2) the colonization by microorganisms (i.e., fungi, bacteria, and 52 53 protozoa) and decomposition via litter breakdown (Fell et al., 1975; Cundell et al., 1979; Fell and 54 Master, 1980), and 3) the slow refractory phase where the least labile molecules are consumed (Valiela et al., 1984; Wilson et al., 1986; Tam et al., 1990). The rate of degradation of the leaf litter 55 56 depends on multiple parameters, with varying significance depending on the context. The initial

chemical composition of the leaves, especially C/N ratio, tannin, and lignin content, is one of the key
parameters influencing the decay rates (Robertson, 1988; Tam et al., 1990; Mfilinge et al., 2002;
Vinh et al., 2020). The leaf-consuming fauna and microbial communities of the forest floor also
impact degradation rates (Fell and Master, 1980; Robertson, 1986; Imgraben and Dittmann, 2008).
Many abiotic factors can influence litterfall degradation such as particle size of the forest soils, redox
conditions, temperature, available oxygen, and the degree and frequency of tidal inundation (Lugo
and Snedaker, 1974; Steinke and Ward, 1987; Chale, 1993; Vinh et al., 2020).

64 Leaf litter degradation in mangrove forests is a source of nutrients; therefore, the change in element contents such as C, N, macronutrients, and neutral carbohydrates during degradation is of 65 interest. The capacity of elements to be mobilised from degrading litter depends on the 66 concentrations of these elements in the soil and incoming water, as well as on their role for litter 67 feeders and whether they form complexes with leachable or refractory compounds (Mfilinge et al., 68 69 2002; Hossain et al., 2014; Gautam et al., 2016; Nordhaus et al., 2017). Neutral carbohydrates and organic N-rich compounds are easily degraded from the plant material, while lignin-rich litter resists 70 71 decay (Fell et al., 1975; Cundell et al., 1979; Twilley et al., 1986; Chale, 1993). The depletion of 72 elements during leaf litter degradation indicates leaching to the surroundings, or breakdown and consumption by microorganisms (Fell and Master, 1980; Fourgurean and Schrlau, 2003; Gautam et 73 al., 2016; Nordhaus et al., 2017). The enrichment of elements and macronutrients in leaf litter during 74 the degradation process is attributed to the production of these elements from microorganisms 75 76 during decomposition such as the polysaccharides exudates from bacteria (Fell et al., 1975; 77 Robertson, 1988; Mfilinge et al., 2002; Yang et al., 2018), or inputs from the water column (Rice and 78 Windom, 1982; Lacerda et al., 1988; Tam et al., 1990; Vinh et al., 2020). The study of these various elements and molecular compounds such as neutral carbohydrates and lignin give essential 79 80 information on the litterfall degradation and preservations processes, which directly affect the soil OM and exported OM quality. 81

One of the major worldwide threats to mangrove ecosystems is the urbanization of the littoral zone. Almost half of the world's mangrove forests are located in only 4 countries: Indonesia (28.4%), Brazil (9.4%), Malaysia (5.8%), and Papua New Guinea (5.1%) (Hamilton and Casey, 2016). On 85 average, a third of the population of these countries lives on the coastline (CIESIN, 2012). Consequently, there is competition for space between mangrove ecosystems and economic and 86 87 urban development. Urbanization can inhibit mangrove landward migration, prevent the water flow into the mangrove forest, and be a source of urban water runoffs, which may contain contaminants 88 89 (Friess et al., 2019). The inputs of urban runoff can modify the immersion conditions of the mangrove 90 trees, change the physico-chemical parameters of the mangrove soil such as pH, redox conditions, and salinity, and be a source of dissolved nutrients, OM, and multiple contaminants (Cavalcante et 91 al., 2009; Bastakoti et al., 2019; Robin et al., 2022; Fiard et al., 2022). Therefore, urban runoff in 92 mangrove forests may influence the decay rates of the litterfall on the soil surface as well as the 93 94 quality of this litterfall during degradation. To our knowledge, only one study looked at the effect of 95 anthropogenic sewage on mangrove litterfall degradation and concluded that the discharge had no effect on the degradation processes (Tam et al., 1998). It is therefore essential to collect data and 96 97 gain knowledge on which mangrove characteristic changes driven by the urbanization of the coasts influence the litterfall degradation processes. 98

99 New Caledonia is a French archipelago located in the South Pacific Ocean between 20°S and 23°S. Semi-arid mangrove forests cover 80% of the West coast of the main island, which has 100 semi-diurnal tidal cycles (Douillet, 2001). 24 mangrove species develop mainly in monospecific 101 stands, but two are dominant, Rhizophora spp., which are present on the seaward side of the forests 102 and represent more than 50% of mangrove plants, and Avicennia marina, which are established at 103 104 higher elevation and on saltier soil, representing about 15% of mangrove plants in the archipelago 105 (Deborde et al., 2015). The population density in New Caledonia is low (16 people per km²), but 60% of the population is concentrated in the capital and the four cities nearby, that are all located 106 on the littoral zone where mangrove forests develop (Insee, 2020). Urbanization in New Caledonia 107 108 has caused the destruction of mangrove forests, but only few studies have been conducted on the influence of urbanization on mangrove forests dynamics (Robin et al., 2022). 109

110 The study of change in element concentrations during litterfall degradation in a mangrove 111 forest is crucial to understand the OM diagenetic and preservation processes within the forest and 112 exchanges with adjacent ecosystems. The aim of this paper is to evaluate leaf litter degradation

dynamics in an urban semi-arid mangrove forest (New Caledonia), receiving urban rainwater for 113 more than 50 years. The objectives of this study are 1) to determine factors influencing the 114 115 differences in leaf litter degradation between mangrove species (i.e., initial composition of the leaves or position of the stand in the mangrove forest), 2) to assess the effects of urban rainwater runoff on 116 leaf litter decay rates and leaf litter changes in element concentrations, and 3) to understand OM 117 litterfall changes with degradation at the molecular level (neutral carbohydrates and lignin content). 118 We hypothesize that the main factors affecting leaf litter decay rates are the stands position in the 119 120 intertidal zone and the urban rainwater runoff as higher stands immersion times enhance leaching 121 and urban runoff modifies microbial communities. We also hypothesize that the change in 122 composition of leaf litter during degradation will be mainly influenced by the initial composition of the litter and the redox conditions, both factors dependent on the mangrove species and the urban 123 runoff. To this aim, a litterbag experiment has been undertaken for 72 days in a control and an urban 124 mangrove forest for the two main mangrove species present in New Caledonia, Avicennia marina 125 and *Rhizophora stylosa*. Decay rates have been calculated from the mass loss, while total C, total 126 127 N, and their stable isotopes have been determined for each sample, as well as their neutral carbohydrates and lignin contents. 128

129 2. Materials and Methods

130 2.1. Study sites

One of the main cities of New Caledonia, Dumbea, has seen its population increase by 33% 131 132 this last decade resulting in the development of urban infrastructures in the littoral zone (Insee, 133 2020). Two mangrove forests in Dumbea have been chosen as study sites in order to compare forests that share a common geological unit as the source of their watersheds and the same 134 135 vegetation type. The first site is the control mangrove forest (22°12'08"S, 166°26'20"E), located in the Apogoti Bay. Even though housing lots have developed recently around the mangrove, no direct 136 anthropogenic inputs are discharged in the mangrove forest. The second site is the urban mangrove 137 138 forest (22°12'39"S, 166°27'19"E). Urban rainwater runoff from the upper allotment (mainly housing lots for 10 000 inhabitants) flows into the mangrove forest and has done so for more than 50 years 139 140 (Fig. 1). At both sites, the two main mangrove species observed, developing in monospecific stands,

are *R. stylosa* and *A. marina*. Visible impacts of urban runoff in the urban mangrove forest are the
position of *R. stylosa* stand landward of *A. marina* at the entrance of the runoff, with much higher *R. stylosa* trees (about 8-10 m high compared to 2 m high at the control site).

144 2.2. Sampling and processing

145 Yellow senescent leaves about to fall on A. marina and R. stylosa trees were collected at the 146 control site. To limit factors other than the urban runoff, potentially affecting leaf litter degradation such as the senescent leaves initial composition, it was chosen to use the same senescent leaves 147 samples at both sites. This is why senescent leaves were only collected at the control site. Fresh 148 green leaves were also collected from the trees in triplicates, but at both sites, to determine whether 149 the composition of the leaves change significantly between the fresh and senescing stage. One 150 151 sample of fresh leaves correspond to 30 leaves picked from 5 different adjacent trees. The leaves were carefully washed and air-dried for 24h at the laboratory. Three random samples of about 50 g 152 of whole senescent leaves per species were frozen, freeze-dried, and ground with a cutting mill, 153 corresponding to the samples at t0 "senescent leaves". Samples of about 6 g of dried A. marina 154 whole leaves and 15 g of dried R. stylosa whole leaves were prepared and precisely weighed. Each 155 samples were placed into individual nylon litterbags (2 mm mesh size) for the litterbag experiment. 156 The 2 mm mesh size allowed for soil contact enabling bacterial activity while limiting the physical 157 158 actions of large detritivores such as crabs. A total of 90 bags were attached to the roots of the corresponding tree species, on the surface of the soil, and in three different spots within the same 159 species stand in both the control and urban mangrove sites. Triplicates of litterbags were collected 160 161 at the three spots, for each species, after 7, 14, 28, 56, and 72 days (a total of 36 bags per day of 162 collection). The experiment was stopped after 72 days because the degradation was already very 163 advanced, and samples further degraded would be too hard to analyse properly. The litterbags were 164 immediately opened at the laboratory, the leaves were carefully washed and air-dried for 24h prior 165 to weighing. Samples were then frozen, freeze-dried, and ground with a cutting mill. Fresh green leaves were also collected immediately from the trees at both sites in triplicates, washed, freeze-166 dried, and ground. 167

168 2.3. Mass loss and half-life

The percentage mass loss or percentage mass remaining after 7, 14, 28, 56, and 72 days of degradation were obtained with the initial mass (± 0.001 g) of the air-dried leaves prior to placing in the litterbags and the mass of the same air-dried leaves after collection (± 0.001 g) in the mangrove site. For comparison with literature, single exponential trends were plotted for each species:

$$W_t = W_0 e^{-kt}$$
(1)

with W_t the mean mass remaining in g, W_0 the initial mass in g, k the exponential factor, and t the time in days. The half-lives ($t_{1/2}$) in days were obtained with the following equation and the uncertainties calculated with R from the decay rates and their standard deviations:

177

$t_{1/2} = \ln(2)/k$ (2)

178 2.4. Carbon, nitrogen, and stable isotopes analysis

179 Total C, total N, and their stable isotopes were measured on an isotope ratio mass spectrometer Sercon Integra 2 at the LAMA laboratory of the Institute of Research and Development 180 of New Caledonia. About 30 mg of samples were weighed in tin cups and folded into tightly closed 181 spheres. The samples were transported in a combustion column with helium gas where they were 182 heated at 1 000 °C and oxidized with Cu and Cr oxides, while silver wool trapped sulphur and 183 halogens. The samples were then transferred to the reduction column at 600 °C where the Cu 184 185 interacts with excess oxygen so that the NOx is reduced to N₂. The water in the samples was trapped with $Mg(CIO_4)_2$ and N_2 and CO_2 of the samples were separated by gas chromatography. The 186 separated molecules were quantified by mass spectrometry in positive ESI mode. The mass 187 188 spectrometer measures the relative abundances of isotopes in the sample gas. For carbon, it measures the ratio of ¹³C to ¹²C (expressed as δ^{13} C), while for nitrogen, it measures the ratio of ¹⁵N 189 to ¹⁴N (expressed as δ^{15} N). To calculate the δ values, the measured isotopic ratio is compared to a 190 known standard. The standard used is the Vienna Pee Dee Belemnite (VPDB) standard for C, and 191 192 the atmospheric nitrogen standard for N. For quality control, duplicate of samples were passed through the spectrometer (1 every 10 samples) (Table S1). 193

194 2.5. Neutral carbohydrates

195 Neutral carbohydrates were analysed at the Earth Sciences Institute of Orleans (ISTO). About 50 mg of samples were hydrolysed 4h at 105 °C in pyrex tubes with 5 mL of 4M of 196 197 trifluoroacetic acid (TFA). After cooling in an ice bath, 500 µL of internal standard (2-deoxyglucose at 8 mg L⁻¹) were added and the sample was centrifuged for 30 min at 5 600 rpm. The extract was 198 199 evaporated, and the dried samples were kept frozen. Prior to analysis, neutral carbohydrates were derivatized with the addition of 500 µL of ethoxy ammonium chloride solution in pyridine (40 mg mL⁻ 200 ¹) heated for 1h at 70 °C. 250 µL of BSTFA were added and the sample was once again heated at 201 70 °C for 1h. After evaporation, the residue was dissolved in 2 mL of heptane, and the solution 202 203 passed through a 45 µm filter prior to injection in the GC-MS. The GC is a Trace 1 300 (Thermo 204 Scientific) coupled to a MS ISQ7000 (Thermo Scientific). The GC is equipped with at Restek Rxi-5Sil MS column (60 m x 0.25 mm, 0.25 µm diameter) with 5 m of pre-column. Helium gas is used 205 as vector and the analysis is carried out at constant 1 mL min⁻¹ flow rate. The injector was heated 206 at 280 °C and the transfer line at 300 °C. 1 µL of sample was injected in splitless mode and passed 207 through the column with a temperature program (Table S2). For the MS analysis the source was 208 209 heated at 240 °C and the ions obtained via electronic impact (70 eV). The spectra were obtained between 50 and 750 Da with a scan time of 0.4 s scan⁻¹. Quality control consisted of duplicate 210 211 technical samples (≤11% standard deviation) and measurement of the internal standard (Table S3).

212 2.6. Lignin-derived phenols

200 mg of samples were hydrolysed for 3 h at 170 °C in 8 mL of 2N NaOH with 100 mg of 213 $Fe(NH_4)_2(SO_4)_2$ under N₂. After cooling, the extract was collected once the sample was centrifuged 214 at 3 000 rpm for 10 min. The extract was acidified at pH 1 with HCl and lignin-derived phenols were 215 extracted twice with 3 mL of anhydrous diethyl ether. After complete evaporation, lignin-derived 216 217 phenols were diluted in 1 mL of 50:50 methanol:H₂O, filtered at 45 µm and analysed via UPLC-MS. Chromatographic separation was achieved using a Vanquish Flex system (Thermo Fisher Scientific, 218 219 France) consisting of a binary pump, an autosampler and a heated column compartment. Samples were separated on a Hypersil GOLD column (1.9 µm particle size), 50 x 2.1 mm (Thermo Scientific). 220 For elution, a binary gradient program was used (Table S4), the mobile phase was a mixture of 221 222 ultrapure water containing 0.1% of formic acid (Carlo Erba) (eluent A) and methanol OPTIMA LC/MS

(Fischer) with 0.1% of formic acid (eluent B). The flow rate was set to 0.5 mL min⁻¹ and injection (2 223 µL) was made automatically by the autosampler. UV detection was carried out at 280 nm. MS 224 225 detection was performed using an Orbitrap Exploris 120 (Thermo Fisher Scientific, France) and operated with the heated electrospray ionization source in negative ion mode with a vaporizer 226 227 temperature of 300 °C. Scan modes were both full MS – ddMS² and SRM. The full MS mode had a resolution of 30 000 and a scan range of 50 - 250 m/z with HCD Collision energies specified for 228 each molecule. The SRM mode had a resolution of 120 000 at 20% HCD collision energy. The full 229 UPLC-MS optimized parameters are displayed in Table S4. The quantification was performed with 230 an external calibration curve (Table S5) and laboratory reference materials spiked with the analytes. 231 232 For quality control, a blank solution was passed at the beginning and end of every series in the same conditions as the samples and values were all below detection limits (Table S6). A quality control 233 solution (QC) consisting of a point of the calibration curve was passed every 10 samples in the same 234 conditions as the samples and the values obtained were all below 15% difference with the expected 235 value (Table S6). 236

237 2.7. Statistical analyses

Statistical analyses were performed using R studio software (version 1.2.5001). For comparison between species or study sites the Mann-Whitney test was performed. All other statistical analyses with more than two variables were tested with a Kruskal-Wallis test followed by a Wilcoxon test. All tests were performed with a 95% confidence interval and $n \ge 3$. Kendall correlation analysis was performed to obtain correlation matrices.

243 3. Results

244 3.1. Sources characteristics

All measured variables for the fresh and senescent leaves of *A. marina* and *R. stylosa* at both sites are displayed in Table 1. The fresh leaves of both species have significantly higher $\delta^{15}N$ values (p< 0.01) and lower $\delta^{13}C$ values (p< 0.05) at the urban site (5.8‰ and -27.7‰, and 2.6‰ and -30.7‰, for *A. marina* and *R. stylosa*, respectively) than those collected at the control site (1.1‰ and -25.8‰, and -1.3‰ and -27.5‰, for *A. marina* and *R. stylosa*, respectively). At the control site, fresh leaves are more enriched in ¹³C than senescent leaves for both species, but for *R. stylosa* they are less enriched in ¹⁵N (-1.3‰ vs -0.2‰). Both fresh and senescent leaves of *A. marina* have significantly higher N contents (p< 0.01), δ^{13} C (p< 0.05), and δ^{15} N values (p< 0.05) than *R. stylosa* but lower C/N ratios (p< 0.01) (39 for *A. marina* and 166 for *R. stylosa*).

254 In Table 1 it is shown that the total lignin contents (Σ 11 phenols) of the fresh and senescent leaves of *A. marina* are significantly higher than those of *R. stylosa* (p< 0.05), which is also the case 255 for the 4 phenol groups (p-hydroxyl or P, vanillyl or V, syringyl or S, and cinnamyl or C). The 256 257 senescent leaves at the control site have significantly higher total lignin concentrations than the fresh leaves (p< 0.01) by a factor of 10 for *A. marina* and a factor of 6 for *R. stylosa* due to higher 258 vanillyl and cinnamyl contents. Therefore, the ratios P/(V+S), P/V, and S/V are much lower in the 259 senescent leaves than in the fresh leaves for both species. The acid over aldehyde ratios (Ad/Al) in 260 261 senescent leaves are also much higher than in the fresh leaves (Table 1).

Fresh leaves of A. marina are more enriched in neutral carbohydrates than R. stylosa but 262 the leaves of *R. stylosa* have higher concentrations of hexoses (mannose and galactose) and deoxy 263 sugars (fucose and rhamnose), especially fucose and galactose than A. marina (Table 1). Total 264 265 carbohydrates content is significantly higher in the senescent leaves than the fresh leaves at the 266 control site (p < 0.05) (Table 1). Neutral carbohydrates represent 45.2% and 49.9% of the total mass 267 for the senescent leaves of A. marina and R. stylosa, respectively (Table 1). Xylose, arabinose, and glucose are the most concentrated neutral carbohydrates measured representing up to 33%, 34%, 268 and 42 % of the total neutral carbohydrates, respectively. Ribose and fucose are the least 269 270 concentrated neutral carbohydrates measured in both fresh and senescent leaves with values as low as 0.48 mg g^{-1} , and 0.71 mg g^{-1} , respectively (Table 1). 271

3.2. Decay rates

The decay rates of *A. marina* and *R. stylosa* leaf litter degradation at both sites are displayed in Figure 2. The calculated half-lives are 43 ± 9 days and 36 ± 3 days for *A. marina* and *R. stylosa* at the control site, respectively, and 33 ± 4 days and 28 ± 2 days at the urban site, respectively. At both sites, in the first 7 days, *A. marina* leaves lost 41% of their initial mass and *R. stylosa* leaves lost

61% of their initial mass. After 72 days, on average, 26% and 19% of the initial mass of *A. marina*leaves remained at the control and urban sites, respectively, while 17% and 11% were remaining
for *R. stylosa*, respectively.

Leaf litter mass loss is significantly more important after 56 and 72 days at the urban site than at the control site (p< 0.01). Through the entire degradation experiment, the leaf litter mass loss of *R. stylosa* is more important than that of *A. marina* (p< 0.001).

3.3. Carbon and nitrogen content, and respective stable isotope composition

The C and N content generally increased at both sites over time and for both species. At the control site, the C content for both species and N content for *A. marina* increased the first 28 days, and after 56 days. The N content of *R. stylosa* continuously increased during the 72 days of degradation. At the urban site, the *R. stylosa* litterfall constantly increased in N and C contents. C and N contents increased for *A. marina* until day 56 and 28, respectively, prior to a loss (Fig. 3A & B). The C/N ratios for *A. marina* were stable the whole 72 days of degradation, while *R. stylosa* C/N ratios continuously decreased with time (Fig. 3C).

The stable isotope ratios showed an initial enrichment for 7 days for δ^{15} N and 14 days for δ^{13} C at both sites and for both species. Overall, after 72 days of degradation, the δ^{15} N of the litterfall significantly decreased compared to the initial values (p< 0.05) except for *A. marina* at the urban site where it increased (Fig. 3D). The δ^{13} C values significantly decreased for *R. stylosa* (p< 0.001) while they were similar for *A. marina* at both sites after 72 days of degradation (Fig. 3E).

296 3.4. Molecular analyses

297 3.4.1. Neutral carbohydrates

After 72 days of litterfall degradation, total neutral carbohydrates content decreased from 452 to 380 mg g⁻¹ (-16%) and to 385 mg g⁻¹ (-15%) for *A. marina* at the control and urban sites, respectively, and from 498 to 250 mg g⁻¹ (-50%) and to 388 mg g⁻¹ (-22%) for *R. stylosa* at the control and urban sites, respectively (Fig. 4A). The most labile neutral carbohydrates after 72 days of degradation were arabinose, rhamnose, galactose, and glucose with loss ranges of 23% to 80%,

2% to 76%, 31% to 50%, and 33% to 53%, respectively (Table 2). Xylose, ribose, fucose, and mannose all increased their concentrations in the leaf litter after 72 days of degradation for most stands reaching up to 152 mg g^{-1} , 1.2 mg g^{-1} , 10 mg g^{-1} , and 16 mg g^{-1} , respectively (Table 2).

For *A. marina*, the concentrations of pentoses (xylose + arabinose) and deoxy sugars (rhamnose + fucose) in the senescent leaves (212 and 54 mg g⁻¹, respectively) are similar to the concentrations in the 72 days-degraded leaves. For *R. stylosa*, the concentrations in the degraded leaves are lower by 9% to 67% than the senescent leaves (235 mg g⁻¹ of pentoses and 66 mg g⁻¹ of deoxy sugars). After 72 days of degradation, the concentrations of hexoses (mannose + galactose) significantly decreased (p< 0.001) for the four stands by a range of 20% to 39% (Table 2).

312 3.4.2. Lignin-derived phenols

313 During the whole decay process, the sum of the lignin-derived phenols is significantly larger in the A. marina litter than in R. stylosa litter (p< 0.01), whatever the site (Fig. 4B). This is also the case 314 for the four phenol groups (Table 3). After 7 days of degradation, the lignin content increased for *R*. 315 stylosa but decreased for A. marina. The total lignin content after 72 days of degradation also 316 increased for *R. stylosa* and decreased for *A. marina* compared to the lignin content in the senescent 317 318 leaves (Fig. 4B). This is only the case for the vanilly phenols, while after 72 days of degradation the syringyl phenols increased all between 71% and 231% (Table 3). In contrast to the total lignin 319 content, the ratios p-hydroxyl/vanillyl (P/V), syringyl/vanillyl (S/V), and cinnamyl/vanillyl (C/V) 320 increased after 7 and 72 days of degradation for A. marina, but decreased for R. stylosa, and 321 322 followed similar patterns with degradation at the two sites (Table 3). In the first days of degradation, 323 there was a decrease in the p-hydroxybenzoic acid/p-hydroxybenzaldehyde ratio ((Ad/Al)) at both sites and a decrease in the vanillic acid/vanillin ratio $((Ad/AI)_v)$ at the urban site only. After 72 days 324 of degradation, the three acid/aldehyde ratios (Ad/Al) decreased at both sites and for both species 325 (Table 3). 326

327 4. Discussion

4.1. Variability of organic matter quality of the fresh and senescent leaves of A. marina and R. stylosa

329 Our investigation into the OM quality of leaves from A. marina and R. stylosa in urban and control sites presented findings that connect with broader scientific contexts. Fresh leaves from the 330 331 urban site revealed high N and δ^{15} N values, aligning with expectations given the anthropogenic influence in urban runoff. This is consistent with previous studies indicating elevated δ^{15} N values in 332 333 urban environments (Rumolo et al., 2011). Our study expanded upon this understanding by demonstrating the species-specific nature of ¹⁵N discrimination during N uptake, evident in the 334 greater δ^{15} N values observed in *A. marina* compared to *R. stylosa*, which was previously observed 335 336 for the same two genus in other studies (Herbon and Nordhaus, 2013; Regina Hershey et al., 2021).

The isotopic values, particularly δ^{13} C mean values of fresh leaves, provided valuable insights 337 into the adaptive responses of mangrove trees. Coastal plants, including mangrove trees, often 338 exhibit enhanced water-use efficiency under salinity stress. Our findings, showing lower δ^{13} C values 339 in the urban site and in *R. stylosa*, contributed to the understanding of these adaptive mechanisms 340 341 (Medina and Francisco, 1997). Plants have a decarboxylating enzyme that discriminates ${}^{13}CO_2$ when assimilating atmospheric CO₂ (O'Leary, 1981). The salinity of the soil and the position of the 342 mangrove stand in the mangrove forest may impact the mangrove species efficiency to assimilate 343 CO₂ or discriminate ¹³CO₂ (Farquhar et al., 1982; Lin and Sternberg, 1992). In New Caledonia, A. 344 marina grows on saltier soil than R. stylosa (26 and 37 psu, respectively at the control site) (Robin 345 et al., 2022) and therefore, has less ${}^{13}CO_2$ discrimination and higher $\delta^{13}C$ values. Moreover, the 346 upper soil at the urban site had a salinity of 0 psu for the first 10 cm (Robin et al., 2022), which may 347 348 explain the lower values measured.

As we explore the changes from fresh to senescent leaves at the control site we observed a decline in N content, δ^{13} C values, and a notable rise in C/N ratios, especially in *R. stylosa* (up to 150%). These senescence-related shifts are connected with biochemical changes before leaf falling, linking to established knowledge in mangrove ecology (Garten and Taylor, 1992; Rao et al., 1994; Nordhaus et al., 2011). Prior to leaf falling, the mangrove trees can relocate the N from the leaves to other tissues of the plant to limit N loss explaining the decline in N content. A general decrease in C content during senescing can be expected due to the loss of photosynthetic activity, but the

relative increase in carbohydrates as a signal for senescing may induce the increase in C content
in some mangrove species as observed in this study for *A. marina* (Wingler et al., 2006).

358 Examining lignin-derived phenols and neutral carbohydrates content, our study contextualized findings within the existing literature on mangrove leaf composition and degradation 359 dynamics (Marchand et al., 2005; Lallier-Vergès et al., 2008; Bala Krishna Prasad and Ramanathan, 360 2009). Higher lignin and neutral carbohydrate content in the fresh leaves of A. marina compared to 361 R. stylosa agree with previous studies (Dittmar and Lara, 2001). However, the higher proportions of 362 363 hexoses and deoxy sugars in the leaves of *R. stylosa*, especially fucose and galactose, underscored the need for a comprehensive insight of initial leaf compositions. The production or loss of neutral 364 carbohydrates and lignin-derived phenols during senescence contribute to our knowledge of the 365 intricate senescence process in mangrove leaves (Benner et al., 1990b; Opsahl and Benner, 1995, 366 367 1999).

368 4.2. Factors influencing leaf litter degradation between mangrove species

The leaf litter of *R. stylosa* was degraded more rapidly on the soil surface than the leaf litter 369 370 of A. marina at both sites; a trend opposite to conventional findings where species with higher initial 371 N content, and consequently lower C/N ratios, typically undergo faster degradation (Mfilinge et al., 2002; Yang et al., 2018; Vinh et al., 2020). Notably, A. marina, initially possessed five times more N 372 in its senescent leaves than *R. stylosa*. The higher N content in plant material is known to attract 373 leaf-degrading organisms due to the nutritional value of N compounds (Wafar et al., 1997; Nordhaus 374 375 et al., 2011). We propose that the species' position within the mangrove forest is a crucial 376 determinant of litterfall decay rates. Generally, species the most submerged experience faster degradation rates (Twilley et al., 1986; Steinke and Ward, 1987; Silva et al., 1998; Bosire et al., 377 378 2005). The physical impact of tides facilitates plant material breakdown (Vinh et al., 2020), and submersion by seawater or runoff promotes microbial development and leaching of soluble 379 380 compounds from litterfall (Robertson, 1988; Tam et al., 1990; Ashton et al., 1999). In the mangrove 381 forests of New Caledonia, R. stylosa is found on the seaward side of the mangrove forest, while A. 382 marina is present at higher elevations with higher soil salinity (Deborde et al., 2015). However, in 383 the urban mangrove forest, continuous runoff from urban rainwater altered soil physico-chemical

parameters, particularly pH and salinity (0 psu in the upper 10 cm) (Robin et al., 2022). Consequently, *R. stylosa* trees are established on the landside and at the entrance of the runoff in the mangrove, providing a subtidal context unique to the urban site. Therefore, submersion of the *R. stylosa* stand by seawater at the control site and submersion by the urban runoff at the urban site may contribute to enhanced litterfall degradation for *R. stylosa*, by favoring leaching and microbial development on the leaf litter compared to *A. marina* (Robertson, 1988; Molnar et al., 2014).

390 Despite the unexpected degradation trend observed in the leaf litter of *R. stylosa* compared 391 to A. marina, further insights into the isotopic dynamics shed light on unique microbial processes driving the decomposition of litterfall of *R. stylosa*. The statistically significant decrease in $\delta^{15}N$ 392 values with leaf litter degradation was only observed for R. stylosa. Bacteria dominating 393 decomposition processes have low δ^{15} N values as bacteria favour the immobilization of 15 N-depleted 394 nitrate (Bragazza et al., 2010; Nordhaus et al., 2011). The results therefore suggest that microbial 395 development beneath the R. stylosa stands at both sites was enhanced, possibly due to their 396 position compared to the water sources, and can therefore ultimately lead to the lowering of 397 398 degrading leaf litter δ^{15} N values (Leopold et al., 2013; Molnar et al., 2014).

399 Leaf litter composition changes during degradation, specifically the N content, C/N ratio, and isotopic values (δ^{13} C and δ^{15} N), were investigated. Degradation of the leaf litter of *R. stylosa* resulted 400 in a decrease in the C/N ratio not observed for the leaf litter of A. marina. The decreasing ratio for 401 R. stylosa may be associated with the immobilization of N by bacteria as observed in a variety of 402 tropical environments (Gotto and Taylor, 1976; Rice and Tenore, 1981; Twilley et al., 1986; Benner 403 et al., 1990a). As suggested in the previous paragraph, the decreasing ratio may only be observed 404 405 for R. stylosa as microbial development beneath the R. stylosa stands at both sites was possibly 406 enhanced. The decrease in the C/N ratio may also be partly linked to the degradation of hydrolysable 407 components, particularly neutral sugars, rather than refractory N-rich components like lignin (Chale, 408 1993; Yang et al., 2018). Indeed, the neutral carbohydrate content of the leaf litter of R. stylosa decreased during degradation by 22% and 50% at the urban and control sites, respectively, while 409 the lignin content increased after 7 and 72 days of degradation. Therefore, bulk leaf decayed more 410 rapidly than lignin, as reported in the literature for anaerobic and sulphate reducing environments 411

(Benner et al., 1984, 1991; Dittmar and Lara, 2001). Conversely, the lignin content decreased in the 412 leaf litter of A. marina. The upper soil beneath A. marina was less reducing than R. stylosa (Robin 413 et al., 2022), which can favour lignin degradation (Benner et al., 1991; Opsahl and Benner, 1995). 414 A. marina also had a higher percentage of lignin content in its senescent leaves than R. stylosa, 415 suggesting that the initial molecular composition of the leaves influenced the lability of the molecules 416 during degradation. Higher lignin content may enhance lignin degradation by favouring microbial 417 access to lignin polymers. This phenomenon, where the concentrations of the molecules in 418 419 senescent leaves influence their decays, aligns with findings in terrestrial plants (Talbot et al., 2012).

420 4.3. Urban runoff effects on leaf litter degradation

Urban runoff and associated modified conditions at the urban site seemed to affect leaf litter 421 422 degradation rates as the mass loss was faster in the urban mangrove forest compared to the control mangrove forest. This discrepancy in mass loss can be attributed to the continuous flooding of the 423 forest floor by urban rainwater runoff, which could enhance the early leaching process of the leaf 424 litter. While previous studies have reported faster mass loss in subtidal stands compared to intertidal 425 stands (Robertson et al., 1992), our findings reveal that, after 7 days of degradation, there is no 426 significant difference in leaf litter mass loss between the urban and control sites. However, it is after 427 56 days of leaf litter degradation that statistical differences in mass loss emerge between the urban 428 and control sites. This suggests that the second phase of degradation, involving the breakdown of 429 430 litter by microorganisms, becomes more prominent at the urban site. Therefore, we suggest that urban runoff likely favors microbial activity on the soil surface, leading to the observed divergence 431 432 in mass loss between the two sites during the later stages of leaf litter degradation. The runoff gives a more stable, nutritious, and humid environment for microbial development (Robertson, 1988; 433 434 Leopold et al., 2013; Molnar et al., 2014). Mineralization of OC in coastal wetland soils is significantly influenced by temperature and soil water content, which regulate microbial metabolism (Marchand 435 436 et al., 2022a). Additionally, it is impacted by the rate of electron acceptor renewal, varying with immersion. As the duration of immersion increases, the mineralization process may be enhanced or 437 reduced, depending on soil permeability (Marchand et al., 2022b). 438

The influence of urban runoff on leaf litter degradation was also evident in the larger increase in N content during degradation at the urban site than the control site. Urban rainwater runoff may have acted as an additional source of N to the forest floor and litter (Tam et al., 1998). Nitrogen can also be produced by microorganisms during leaf litter degradation (Tam et al., 1990; Mfilinge et al., 2002). The higher degradation rates associated with the higher enrichment of fucose and ribose at the urban site, characteristic of microbial production (Cowie and Hedges, 1984), indicated stronger microbial activity on the soil surface at the urban site.

446 The modified soil conditions created by the submerging urban runoff may also have influenced molecular degradation processes of the leaf litter. After 72 days of degradation rhamnose 447 and glucose loss was more important at the control site than at the urban site. With a lower soil 448 surface salinity (Robin et al., 2022), the urban mangrove forest was a less suitable environment for 449 the secretion of some enzymes such as cellulases, which enhance cellulose and hemicellulose 450 451 hydrolysis (Arfi et al., 2013; Ivaldi et al., 2021). Also, the more anoxic environment of the urban forest's upper soil (Robin et al., 2022) limited the hydrolysis of neutral carbohydrates including 452 453 rhamnose and glucose. The more reducing conditions may also have favoured lignin conservation over bulk OC during the early phase of degradation (Benner et al., 1984, 1991), explaining the higher 454 relative lignin enrichment in the leaf litter of *R. stylosa* at the urban site than at the control site after 455 7 days of degradation. 456

457 4.4. Leaf litter molecular composition during degradation

458 The molecular-level changes of OM during leaf litter degradation revealed species-specific 459 and site-dependent influences on the stability of some molecules. In this study, we observed that the most abundant sugars, that is glucose, arabinose, galactose, and rhamnose, were the most 460 461 labile, and the least abundant, that is sugars fucose, ribose, and mannose, were the most refractory ones. Trends like this one were observed in neutral carbohydrates and lignin-derived phenols during 462 463 degradation, suggesting a potential end for compositional uniformity (Opsahl and Benner, 1999). 464 The hypothesis of compositional uniformity suggests that the most abundant sugars would be more labile than the least abundant in order to end up with a uniform composition of neutral carbohydrates 465 466 in the most degraded leaves (Opsahl and Benner, 1999). Except for xylose in this study, results

seem to agree with this hypothesis. We suggest that xylose may be associated to more refractory components of the litter such as lignin, which enhanced protection from enzymatic degradation (Opsahl and Benner, 1999), as suggested by the correlation between xylose and p-hydroxyl phenols (r = 0.61) and cinnamyl phenols (r = 0.50) (Table S7).

The order of lability of the 11 lignin-derived phenols differed between mangrove species and 471 sites but observations agreed with previous work. In the literature, syringyl phenols were classified 472 as the most stable phenols and ferulic acid the least (Benner et al., 1990b). In the present study, 473 474 ferulic acid content per g of TOC decreased in the leaf litter at the four stands after 72 days of degradation (Table S8), while total syringyl phenols increased. The hypothesis of compositional 475 476 uniformity may also work here as for both species, the most abundant phenol group in the senescent leaves was also the most labile during degradation; that is vanilly phenols for A. marina and 477 478 cinnamyl phenols for R. stylosa.

479 4.5. Limitations of the experiment and models

480 The litterbag experiment was conducted using senescent leaves from the control site only 481 for both species. This design of experiment aimed to evaluate the changes in leaf litter mass and 482 composition over 72 days of degradation with a focus on the influence of urban runoff on these changes. The choice of having the same senescent leaves at both sites enabled to limit the factors 483 potentially affecting these changes other than runoff such as initial senescent leaves composition. 484 The influence of initial composition was evaluated between species but not between sites. This 485 486 experiment design was therefore not a limitation regarding the general processes investigated in 487 this study. However, it is not possible from this experiment to quantify the elements or molecules released, stored, or gained by the leaf litter at the urban site. Furthermore, the experiment ended 488 489 after 72 days of degradation as the mass remaining was the lower limit to conduct all the analyses. A longer experiment could have given further information relative to the refractory degradation stage. 490

In this study, single exponential models were computed on the mass loss of the leaf litter
with degradation. Single exponential models were used to calculate the half-lives of the litter and
are frequently used in similar works using the litterbag experiment (Flores-Verdugo et al., 1987;

494 Ashton et al., 1999; Bosire et al., 2005; Nordhaus et al., 2017; Vinh et al., 2020). However, double exponential models seemed more suitable for the degradation rate in this study as shown by the 495 496 regression coefficients (R²) of the exponential regression lines (Figure S1), as previously suggested in the literature (Wider and Lang, 1982). Two phases of degradation stood out in the double 497 498 exponential model with a first stage from 0 to 14 days for *R. stylosa* or to 28 days for *A. marina*, and a second to 72 days (Figure S1). The double exponential model indicated that the mass loss of the 499 leaf litter was faster for the four stands during the first days of degradation as soluble compounds 500 501 were leached. Still, the use of the single exponential model is preferential as comparison with 502 literature is possible and the differences between species and sites were noticeable as much as with 503 the double exponential model.

504 **5. Summary and conclusions**

505 In this study, changes in mangrove leaf litter OM quality during degradation was analysed in relation to mangrove species (A. marina and R. stylosa) and to mangrove forests (urban and control) 506 with a focus on the potential influence of urban runoff. Considering mangrove species, we were 507 surprised to observe that despite lower initial N content, degradation of R. stylosa leaf litter was 508 faster than the one of *A. marina* at both sites. We suggest that species position in the intertidal zone 509 is crucial and that length of immersion, either tidal or runoff, are key factors controlling degradation 510 rates. The immersion not only influences the leaching but also enhances the microbial development, 511 as evidenced by $\delta^{15}N$ values variations beneath both *R. stylosa* stands. Regarding mangrove 512 forests, the urban runoff submerging the mangrove soil amplified leaf litter degradation as shown by 513 the lower half-lives (about ten days) for both species compared to the control site. We suggest that 514 515 the runoff enhanced both leaching and microbial activity. Further experiments in mesocosms with 516 controlled parameters should be undertaken to better understand the decay processes generated 517 by the runoff. The physico-chemical conditions (more reducing, lower salinity, ...) at the urban site 518 not only influenced mass loss but also shaped the molecular composition of the OM during leaf litter degradation. The lower soil surface salinity may have limited enzyme secretion and hydrolysis of 519 neutral carbohydrates. While urban runoff and site conditions impact leaf litter degradation, this 520 study highlights that the initial molecular composition of the litter also plays a crucial role in 521

controlling its molecular evolution during degradation. The observed leaf litter composition in neutral
 carbohydrates and lignin-derived phenols during degradation underscored the intricate interplay
 between environmental factors and OM stability in mangrove ecosystems.

525 These findings have broader implications for understanding the global impacts of urban 526 runoff on mangrove ecosystems, including potential reductions in carbon sequestration capacity and 527 threats to ecosystem services such as habitat provision, fisheries support, and coastal erosion 528 mitigation.

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535 Data Availability

536 Data are available through Mendeley Data, V2 at https://doi:10.17632/hh48m5g37v.2.

537 Appendix A. Supplementary Material

- 538 Supplementary data referred in the text are available as supplementary material. Information on the
- 539 instrument methods and quality control is available (GC-MS and UPLC-MS).

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 decomposition to regional excessive nitrogen input and global warming between two mangrove
 species. *Estuar. Coast. Shelf Sci.* 214, 141–148.
- 734 Tables
- Table 1. Fresh and senescent leaves characteristics (mean value ±SD).

Species		A. marina		R. stylosa			
Site	Site Contro		Urban	Control		Urban	
Leaf	Fresh	Senescent	Fresh	Fresh	Senescent	Fresh	
C (g kg ⁻¹)	404±22	441±3	416±23	407±23	374±3	422±24	
N (g kg⁻¹)	19±2	11±1	24±2	7.6±1.5	2.3±0.4	15±2	
C/N	21±4	39±2	17±3	54±14	166±30	28±5	

δ ¹³ C (‰vsVPDB)	-25.8±0.3	-27.7±0.0	-27.7±0.7	-27.5±0.1	-28.3±0.3	-30.7±1.0
δ ¹⁵ N (‰vsAir)	1.1±0.6	0.9±0.7	5.8±1.7	-1.3±0.5	-0.2±0.2	2.6±0.1
Σ11 phenols (mg g ⁻¹)	4.1±1.2	43±11	5.0±1.3	1.3±0.3	6.6±2.2	1.4±0.5
p-hydroxyl (mg g ⁻¹)	0.62±0.10	0.27±0.03	0.56±0.11	0.21±0.02	0.15±0.00	0.14±0.04
Vanillyl (mg g⁻¹)	2.0±0.6	33±10	2.0±0.4	0.56±0.27	0.90±0.17	0.58±0.16
Syringyl (mg g ⁻¹)	0.33±0.07	0.22±0.00	0.26±0.04	0.22±0.02	0.14±0.06	0.20±0.04
Cinnamyl (mg g ⁻¹)	1.1±0.1	9.2±1.1	2.1±0.9	0.34±0.06	5.4±2.3	0.48±0.24
P/V	0.31	0.01	0.28	0.38	0.17	0.24
S/V	0.17	0.01	0.13	0.39	0.16	0.34
P/(V+S)	0.27	0.01	0.25	0.27	0.14	0.18
(Ad/Al)p	0.2	2.57	0.2	0.3	4.58	0.3
(Ad/Al)v	0.8	10.98	3.3	1.1	20.88	2.1
(Ad/Al)s	1.2	2.99	1	3.2	1.36	1.7
Neutral carbohydrates (mg g ⁻¹)	384	452±52	322	228	499±14	304
Xylose (mg g ⁻¹)	128	122±23	61	49	104±7	66
Arabinose (mg g ⁻¹)	97	90±14	62	62	131±6	102
Ribose (mg g ⁻¹)	1.9	1.0±0.1	1.6	0.48	0.76±0.07	1.4
Rhamnose (mg g ⁻¹)	41	52±6	29	27	58±1	37
Fucose (mg g ⁻¹)	1.4	1.9±0.5	0.71	3.8	8.0±0.2	4.5
Mannose (mg g ⁻¹)	10	11±2	5.1	4.1	11±1	5.6
Galactose (mg g ⁻¹)	38	42±6	28	34	69±3	61
Glucose (mg g ⁻¹)	66	133±1	135	48	118±3	27

11 phenols = p-hydroxybenzoic acid, p-hydroxybenzaldehyde, p-hydroxyacetophenone, vanillic acid, vanillin,
acetovanillone, syringic acid, syringaldehyde, acetosyringone, coumaric acid, and ferulic acid; p-hydroxyl = phydroxybenzoic acid, p-hydroxybenzaldehyde, and p-hydroxyacetophenone; vanillyl = vanillic acid, vanillin, and
acetovanillone; syringyl = syringic acid, syringaldehyde, and acetosyringone; cinnamyl = coumaric acid and ferulic acid;
P/V = ratio of p-hydroxyl over vanillyl; S/V = ratio of syringyl over vanillyl; P/(V+S) = ratio of p-hydroxyl over the sum of
vanillyl and syringyl; (Ad/Al) = acid/aldehyde.

Table 2. Mean neutral carbohydrate concentrations (\pm SD) in mg g⁻¹ in leaf litter with degradation at the control and urban sites for both *A. marina* and *R. stylosa*.

Control A. marina	senescent	7 days	14 days	28 days	56 days	72 days
Xylose	122±23	127±11	97±2	122±1	167±1	152±0
Arabinose	90±14	85±4	57±5	55±1	76±3	70±6
Ribose	1.0±0.1	1.0±0.3	0.71±0.01	0.52±0.20	0.94±0.02	0.83±0.22
Rhamnose	52±6	52±5	37±2	36±1	47±1	45±5
Fucose	1.9±0.5	2.0±0.5	1.7±0.0	1.8±0.1	2.3±0.5	2.5±0.9
Mannose	11±2	18±3	11±0	9.3±2.2	14±5	15±8
Galactose	42±6	41±3	21±2	16±2	24±5	25±9
Glucose	133±1	103±5	70±0	58±0	74±3	71±9
Control R. stylosa	senescent	7 days	14 days	28 days	56 days	72 days
Xylose	104±7	73±1	83±17	85±12	86±4	78±5
Arabinose	131±6	76±2	73±10	63±4	50±3	46±2
Ribose	0.76±0.07	0.39±0.07	0.46±0.05	0.48±0.06	0.40±0.02	0.41±0.05
Rhamnose	58±0	33±1	33±6	25±4	15±2	14±1
Fucose	8.0±0.2	6.0±0.7	6.3±1.5	6.9±0.2	7.5±0.3	8.0±0.9
Mannose	11±0	8.6±0.4	8.3±3.5	11±0	11±2	14±4
Galactose	69±3	48±2	47±11	42±2	34±5	34±6
Glucose	117±3	61±11	62±22	56±2	50±10	55±9
Urban <i>A. marina</i>	senescent	7 days	14 days	28 days	56 days	72 days
Xylose	122±23	150±6	108±10	134±4	157±14	145±22
Arabinose	90±14	100±2	59±4	67±5	76±9	72±9
Ribose	1.0±0.1	1.3±0.3	1.0±0.0	1.5±0.0	1.2±0.1	1.2±0.1

_	Rhamnose	52±6	64±5	38±1	52±0	50±14	50±0
	Fucose	1.9±0.5	2.8±0.8	1.5±0.0	2.6±0.5	2.2±0.1	2.1±0.0
	Mannose	11±2	20±5	11±2	21±3	16±1	13±1
	Galactose	42±6	47±9	21±1	30±1	26±2	22±1
	Glucose	133±1	118±2	67±6	87±4	79±21	80±3
	Urban <i>R. stylosa</i>	senescent	7 days	14 days	28 days	56 days	72 days
	Xylose	104±7	113±11	96±3	127±4	111±10	135±6
	Arabinose	131±6	115±9	83±10	71±17	58±13	78±10
	Ribose	0.76±0.07	0.75±0.03	0.70±0.07	1.1±0.0	0.96±0.21	1.2±0.4
	Rhamnose	58±0	51±8	36± 0	21±15	19 ± 2	21±4
	Fucose	8.0±0.2	9.3±0.3	10±0	14±3	7.5±1.0	10±1
	Mannose	11±0	13±1	12±1	33±29	15±3	16±3
	Galactose	69±3	72±8	55±0	66±14	38±4	47±3
	Glucose	117±3	91±10	76±1	30±40	64±8	79±9

Table 3. Lignin-derived phenols parameters in leaf litter with degradation at the control and urban
sites for both *A. marina* and *R. stylosa* (mean values ± SD).

Control A. marina	senescent	7 days	14 days	28 days	56 days	72 days
p-hydroxyl (mg g ⁻¹)	0.27±0.03	0.15±0.03	0.20±0.02	0.22±0.04	0.26±0.07	0.26±0.04
Vanillyl (mg g ⁻¹)	33±10	18±14	15±2	10 ±2	4.4±0.9	14±3
Syringyl (mg g ⁻¹)	0.22±0.001	0.14±0.05	0.31±0.21	0.42±0.10	0.47±0.26	0.50±0.05
Cinnamyl (mg g ⁻¹)	9.2±1.1	6.8±0.7	6.8±0.5	11±2	12±2	12±2
P/(V+S)	0.029	0.022	0.028	0.020	0.021	0.022
P/V	0.008	0.008	0.013	0.021	0.058	0.019
S/V	0.007	0.008	0.021	0.041	0.106	0.037
C/V	0.27	0.38	0.45	1.00	2.68	0.86
(Ad/Al)p	2.57	2.01	1.50	0.54	0.49	0.52
(Ad/Al)v	10.98	11.62	5.57	0.89	0.70	1.10
(Ad/AI)s	2.99	2.53	0.52	0.39	0.45	0.47
Control R. stylosa	senescent	7 days	14 days	28 days	56 days	72 days
p-hydroxyl (mg g ⁻¹)	0.15±0.001	0.12±0.02	0.13±0.01	0.11±0.004	0.14±0.01	0.13±0.004
Vanillyl (mg g ⁻¹)	0.90±0.17	5.7±4.1	2.6±1.5	2.2±0.9	3.3±1.2	3.4±0.4
Syringyl (mg g ⁻¹)	0.14±0.06	0.12±0.01	0.14±0.03	0.16±0.04	0.20±0.03	0.24±0.02
Cinnamyl (mg g ⁻¹)	5.4±2.3	4.2±0.5	3.8±0.3	3.0±0.3	4.7±0.9	4.9±0.7
P/(V+S)	0.026	0.027	0.034	0.033	0.029	0.025
P/V	0.160	0.021	0.051	0.048	0.042	0.039
S/V	0.152	0.021	0.054	0.073	0.061	0.073
C/V	5.99	0.75	1.45	1.36	1.42	1.45
(Ad/Al)p	4.58	3.71	2.32	2.38	1.82	1.78
(Ad/Al)v	20.88	19.53	34.32	26.32	19.50	13.59
(Ad/Al)s	1.36	1.08	1.12	1.38	1.40	1.10
Urban A. marina	senescent	7 days	14 days	28 days	56 days	72 days
p-hydroxyl (mg g ⁻¹)	0.27±0.03	0.23±0.005	0.23±0.08	0.21±0.02	0.28±0.03	0.30±0.16
Vanillyl (mg g ⁻¹)	33±10	7.5±6.0	15±9	11±5	16±6	23±16
Syringyl (mg g ⁻¹)	0.22±0.001	0.39±0.01	0.68±0.22	0.53±0.19	0.61±0.15	0.73±0.35

_	Cinnamyl (mg g ⁻¹)	9.2±1.1	9.1±4.1	10±4	9.1±2.1	14±1	9.7±4.4
	P/(V+S)	0.029	0.024	0.021	0.021	0.020	0.029
	P/V	0.008	0.030	0.015	0.019	0.017	0.013
	S/V	0.007	0.051	0.045	0.049	0.038	0.031
	C/V	0.27	1.21	0.68	0.85	0.85	0.42
	(Ad/Al)p	2.57	0.56	1.00	0.66	0.86	0.61
	(Ad/Al)v	10.98	2.58	3.21	1.83	4.09	2.46
	(Ad/Al)s	2.99	0.48	0.43	0.62	0.64	0.60
	Urban <i>R. stylosa</i>	senescent	7 days	14 days	28 days	56 days	72 days
-	p-hydroxyl (mg g ⁻¹)	0.15±0.001	0.20±0.05	0.12±0.02	0.17±0.03	0.23±0.07	0.18±0.07
	Vanillyl (mg g ⁻¹)	0.90±0.17	11±15	3.5±3.2	2.6±0.9	6.8±3.5	2.6±1.2
	Vanillyl (mg g ⁻¹) Syringyl (mg g ⁻¹)	0.90±0.17 0.14±0.06	11±15 0.17±0.02	3.5±3.2 0.12±0.09	2.6±0.9 0.22±0.17	6.8±3.5 0.11±0.03	2.6±1.2 0.23±0.08
	Vanillyl (mg g ⁻¹) Syringyl (mg g ⁻¹) Cinnamyl (mg g ⁻¹)	0.90±0.17 0.14±0.06 5.4±2.3	11±15 0.17±0.02 3.8±0.6	3.5±3.2 0.12±0.09 2.4±0.3	2.6±0.9 0.22±0.17 3.5±1.6	6.8±3.5 0.11±0.03 4.6±1.6	2.6±1.2 0.23±0.08 6.0±1.7
	Vanillyl (mg g ⁻¹) Syringyl (mg g ⁻¹) Cinnamyl (mg g ⁻¹) P/(V+S)	0.90±0.17 0.14±0.06 5.4±2.3 0.026	11±15 0.17±0.02 3.8±0.6 0.051	3.5±3.2 0.12±0.09 2.4±0.3 0.049	2.6±0.9 0.22±0.17 3.5±1.6 0.045	6.8±3.5 0.11±0.03 4.6±1.6 0.050	2.6±1.2 0.23±0.08 6.0±1.7 0.029
	Vanillyl (mg g ⁻¹) Syringyl (mg g ⁻¹) Cinnamyl (mg g ⁻¹) P/(V+S) P/V	0.90±0.17 0.14±0.06 5.4±2.3 0.026 0.160	11±15 0.17±0.02 3.8±0.6 0.051 0.018	3.5±3.2 0.12±0.09 2.4±0.3 0.049 0.035	2.6±0.9 0.22±0.17 3.5±1.6 0.045 0.064	6.8±3.5 0.11±0.03 4.6±1.6 0.050 0.034	2.6±1.2 0.23±0.08 6.0±1.7 0.029 0.071
	Vanillyl (mg g ⁻¹) Syringyl (mg g ⁻¹) Cinnamyl (mg g ⁻¹) P/(V+S) P/V S/V	0.90±0.17 0.14±0.06 5.4±2.3 0.026 0.160 0.152	11±15 0.17±0.02 3.8±0.6 0.051 0.018 0.015	3.5±3.2 0.12±0.09 2.4±0.3 0.049 0.035 0.036	2.6±0.9 0.22±0.17 3.5±1.6 0.045 0.064 0.085	6.8±3.5 0.11±0.03 4.6±1.6 0.050 0.034 0.017	2.6±1.2 0.23±0.08 6.0±1.7 0.029 0.071 0.091
	Vanillyl (mg g ⁻¹) Syringyl (mg g ⁻¹) Cinnamyl (mg g ⁻¹) P/(V+S) P/V S/V C/V	0.90±0.17 0.14±0.06 5.4±2.3 0.026 0.160 0.152 5.99	11±15 0.17±0.02 3.8±0.6 0.051 0.018 0.015 0.34	3.5±3.2 0.12±0.09 2.4±0.3 0.049 0.035 0.036 0.69	2.6±0.9 0.22±0.17 3.5±1.6 0.045 0.064 0.085 1.34	6.8±3.5 0.11±0.03 4.6±1.6 0.050 0.034 0.017 0.67	2.6±1.2 0.23±0.08 6.0±1.7 0.029 0.071 0.091 2.34
	Vanillyl (mg g ⁻¹) Syringyl (mg g ⁻¹) Cinnamyl (mg g ⁻¹) P/(V+S) P/V S/V C/V (Ad/Al)p	0.90±0.17 0.14±0.06 5.4±2.3 0.026 0.160 0.152 5.99 4.58	11±15 0.17±0.02 3.8±0.6 0.051 0.018 0.015 0.34 1.86	3.5±3.2 0.12±0.09 2.4±0.3 0.049 0.035 0.036 0.69 1.90	2.6±0.9 0.22±0.17 3.5±1.6 0.045 0.064 0.085 1.34 1.37	6.8±3.5 0.11±0.03 4.6±1.6 0.050 0.034 0.017 0.67 1.60	2.6±1.2 0.23±0.08 6.0±1.7 0.029 0.071 0.091 2.34 1.49
	Vanillyl (mg g ⁻¹) Syringyl (mg g ⁻¹) Cinnamyl (mg g ⁻¹) P/(V+S) P/V S/V C/V (Ad/Al)p (Ad/Al)v	0.90±0.17 0.14±0.06 5.4±2.3 0.026 0.160 0.152 5.99 4.58 20.88	11±15 0.17±0.02 3.8±0.6 0.051 0.018 0.015 0.34 1.86 6.25	3.5±3.2 0.12±0.09 2.4±0.3 0.049 0.035 0.036 0.69 1.90 10.69	2.6±0.9 0.22±0.17 3.5±1.6 0.045 0.064 0.085 1.34 1.37 4.63	6.8±3.5 0.11±0.03 4.6±1.6 0.050 0.034 0.017 0.67 1.60 2.55	2.6±1.2 0.23±0.08 6.0±1.7 0.029 0.071 0.091 2.34 1.49 6.25
	Vanillyl (mg g ⁻¹) Syringyl (mg g ⁻¹) Cinnamyl (mg g ⁻¹) P/(V+S) P/V S/V C/V (Ad/Al)p (Ad/Al)v (Ad/Al)s	0.90±0.17 0.14±0.06 5.4±2.3 0.026 0.160 0.152 5.99 4.58 20.88 1.36	11±15 0.17±0.02 3.8±0.6 0.051 0.018 0.015 0.34 1.86 6.25 2.31	3.5 ± 3.2 0.12 ± 0.09 2.4 ± 0.3 0.049 0.035 0.036 0.69 1.90 10.69 1.36	2.6±0.9 0.22±0.17 3.5±1.6 0.045 0.064 0.085 1.34 1.37 4.63 1.47	6.8±3.5 0.11±0.03 4.6±1.6 0.050 0.034 0.017 0.67 1.60 2.55 1.09	2.6±1.2 0.23±0.08 6.0±1.7 0.029 0.071 0.091 2.34 1.49 6.25 0.56

747 P = p-hydroxyl, V = Vanillyl, S = Syringyl, C = cinnamyl, Ad = acid, Al = aldehyde.

748 Figure captions

Figure 1. Control mangrove forest and urban mangrove forest in Dumbea city in New Caledonia with
 delimitation of the new allotments and the old allotment and the entrance of the urban rainwater
 runoff.

Figure 2. Decay rates of leaf litter degradation represented by the mean mass remaining of the leaf litter in the litterbags during degradation at the control site for (A) *A. marina* and (B) *R. stylosa* and at the urban site for (C) *A. marina* and (D) *R. stylosa*. The error bars represent the standard deviations.

Figure 3. Mean values (±SD) of (A) C in g kg⁻¹, (B) N in g kg⁻¹, (C) C/N ratio, (D) δ^{15} N (‰vsAir) and (E) δ^{13} C (‰vsVPDB) during leaf litter degradation for *A. marina* and *R. stylosa* at the control and urban sites.

Figure 4. (A) Mean (\pm SD) total neutral carbohydrate content in mg g⁻¹ in leaf litter with degradation at the control and urban sites and for *A. marina* and *R. stylosa* and (B) mean (\pm SD) sum of the 11 lignin-derived phenols in mg g⁻¹.

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