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1 **Standing dead trees are a conduit for the atmospheric flux of CH<sub>4</sub> and CO<sub>2</sub> from wetlands**

2

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24 **Abstract**

25 In vegetated wetland ecosystems, plants can be a dominant pathway in the atmospheric  
26 flux of methane, a potent greenhouse gas. Although the roles of herbaceous vegetation and live  
27 woody vegetation in this flux have been established, the role of dead woody vegetation is not yet  
28 known. In a restored wetland of North Carolina's coastal plain, static flux chambers were  
29 deployed at two heights on standing dead trees to determine if these structures acted as a conduit  
30 for methane emissions. Methane fluxes to the atmosphere were measured in five of the  
31 chambers, with a mean flux of  $0.4 \pm 0.1 \text{ mg m}^{-2} \text{ h}^{-1}$ . Methane consumption was also measured in  
32 three of the chambers, with a mean flux of  $-0.6 \pm 0.3 \text{ mg m}^{-2} \text{ h}^{-1}$ . Standing dead trees were also a  
33 source of the flux of  $\text{CO}_2$  ( $114.6 \pm 23.8 \text{ mg m}^{-2} \text{ h}^{-1}$ ) to the atmosphere. Results confirm that  
34 standing dead trees represent a conduit for the atmospheric flux of carbon gases from wetlands.  
35 However, several questions remain regarding the ultimate source of these carbon gases, the  
36 controls on the magnitude and direction of this flux, the mechanisms that induce this flux, and  
37 the importance of this pathway relative to other sources at the landscape level.

38

39 **Keywords**

40 Carbon cycle, carbon dioxide, dead vegetation, decomposition, gas transport, methane, wetlands

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42 **Data Availability**

43 The datasets analyzed during the current study are available from the corresponding author on  
44 reasonable request.

45

46

47 **Introduction**

48 Carbon dioxide (CO<sub>2</sub>) and methane (CH<sub>4</sub>) are widely recognized as two of the most  
49 important greenhouse gases due to their abundance in the atmosphere and strength as an agent of  
50 global warming, respectively (Shindell et al. 2009; Hansen et al. 2013; Myhre et al. 2013).  
51 Methane is recognized as a potent greenhouse gas, with a global warming potential ca. 28-34×  
52 that of CO<sub>2</sub> over a 100 year period (Myhre et al. 2013). Atmospheric CH<sub>4</sub> concentrations are  
53 once again on the rise (Saunois et al. 2016) after an almost two-decade period of oscillation  
54 between stabilization and increase (Kirschke et al. 2013). The cause for this current increase is  
55 currently unknown, but is likely attributed to increases in both anthropogenic (e.g. agriculture  
56 and the fossil fuel industry) and natural (e.g. wetlands) sources (Saunois et al. 2016).

57 Quantitatively, wetlands represent the single largest source in the annual flux of CH<sub>4</sub> to  
58 the atmosphere (Myhre et al. 2013; Schlesinger and Bernhardt 2013). In wetland ecosystems,  
59 CH<sub>4</sub> is produced by methanogenesis, the terminal step in the anaerobic degradation of carbon,  
60 which occurs in nutrient-depleted, anoxic microsites within sediments. Once CH<sub>4</sub> is produced, it  
61 has a variety of fates in wetland systems, including escaping as a flux across the soil/sediment-  
62 (Chanton et al. 1989; Morse et al. 2012), water- (Helton et al. 2014; Poindexter et al. 2016), or  
63 plant-atmosphere (Schütz et al. 1991; Rusch and Rennenberg 1998) interface. Of these three  
64 pathways, the plant-based pathway is arguably the least well understood, despite mounting  
65 evidence that it may be a dominant pathway for CH<sub>4</sub> flux from vegetated wetland ecosystems  
66 [see Carmichael et al. (2014) and references therein].

67 From a historical perspective, the role of both live and dead herbaceous vegetation as a  
68 conduit for wetland CH<sub>4</sub> emissions has long been established (Dacey and Klug 1979; Sebacher et  
69 al. 1985; Brix 1990; Smith and Lewis Jr. 1992). Schütz et al. (1991) first proposed that woody

70 vegetation (i.e. tree stems) might also be a source of CH<sub>4</sub> flux from wetlands, a pathway that was  
71 confirmed in 1998 by Rusch and Rennenberg. A handful of studies have expanded on this initial  
72 research, confirming live trees as a pathway for CH<sub>4</sub> emissions in both upland and wetland  
73 systems [see review by Carmichael et al. (2014) and references therein, in addition to more  
74 recent papers by Pangala et al. (2015), Terazawa et al. (2015), Machacova et al. (2016), Wang et  
75 al. (2016), Wang et al. (2017), and Warner et al. (2017)]. In these studies, CH<sub>4</sub> flux occurred  
76 across all possible exchanging surfaces at the plant-atmosphere interface, including the leaf,  
77 stem, and trunk. In some cases, specialized wetland adaptations for tissue aeration (e.g.  
78 aerenchyma, lenticels, and pneumatophores) have also been implicated as pathways for CH<sub>4</sub>  
79 flux; but, that is not universally the case, as stomata on leaf surfaces may also contribute to CH<sub>4</sub>  
80 flux (Garnet et al. 2005).

81         Dead vegetation is an important component of forest carbon budgets (Litton et al. 2007)  
82 that represents a substantial, dynamic carbon stock (Cornelissen et al. 2012). Deadwood and  
83 litter represent a substantial aboveground C sink (Pacala et al. 2001), accounting for ca. 15% of  
84 the global forest carbon storage (Pan et al. 2011). However, the role of standing dead trees in  
85 wetland carbon dynamics has been largely ignored, despite the fact that ca. 15-30% of the  
86 estimated total global wetland extent consists of forested ecosystems (Matthews and Fung 1987;  
87 Lehner and Döll 2004). After tree death, water is evacuated from cavities and hydraulic elements  
88 in the trunk, leaving an intricate network of open conduits within the plant tissue that provide a  
89 continuum of connectivity, from soil/sediment to the atmosphere. In wetland systems, dead trees  
90 likely possess a suite of structural adaptations already honed for gas transport from the  
91 atmosphere to above- and belowground tissues (Hook 1984a). Barriers to diffusion in the inner  
92 bark and xylem are generally viewed as resistors to gas exchange in woody tissue; however, as

93 the decay process begins, microbial and insect activity could lead to increased wood porosity via  
94 the formation of additional channels within plant tissue that may facilitate gas exchange with the  
95 atmosphere (Teskey et al. 2008). Interestingly, Hook and Brown (1972) observed that  
96 microscopic pores as small as 2-5  $\mu\text{m}$  in diameter were large enough to permit gas exchange  
97 across the cambium in *Nyssa aquatica* L. (water tupelo) and *Fraxinus pennsylvanica* Marshall  
98 (green ash), two common wetland species. Thus, it is possible that the open conduit systems in  
99 dead trees may provide a pathway for the atmospheric flux of sediment-borne greenhouse gases  
100 from wetland systems [as suggested previously by Carmichael et al. (2014) and Oberle et al.  
101 (2017)].

102 In order for standing dead trees (hereafter snags) to act as a source of the atmospheric  
103 flux of greenhouse gases, two conditions must occur: (1) gas evolution and/or accumulation  
104 within the trunk airspace of a dead tree and (2) flux of this gas across the plant atmosphere  
105 interface (Carmichael and Smith 2016b). A recent study described the potential for snags to act  
106 as conduits for  $\text{CH}_4$  and  $\text{CO}_2$  emissions from wetland ecosystems (Carmichael and Smith 2016b),  
107 providing evidence that snags accumulate carbon-based greenhouse gases within trunk airspace  
108 at significantly higher concentrations than the atmospheric samples taken immediately outside of  
109 the trunk, thus establishing a concentration gradient that would be expected for a plant-  
110 atmosphere flux to occur. But, several questions remained, namely the ultimate source of these  
111 carbon gases (i.e. sediment- or plant-based decomposition pathways) and whether the gases  
112 actually escape from snags as a flux to the atmosphere. Therefore, we conducted a study in the  
113 summer of 2016 to determine if snags represent a conduit for the flux of  $\text{CH}_4$  and  $\text{CO}_2$  to the  
114 atmosphere from wetland ecosystems.

## 115 **Materials and Methods**

116 *Site Description*

117           Due to the potential for highly productive croplands, much of North Carolina's  
118 Albemarle-Pamlico peninsula was converted from wetland habitat to farmland in the 1970's  
119 (Carter 1975). However, land in the region drains poorly (Titus and Richman 2001; Sallenger Jr.  
120 et al. 2012; Hauer et al. 2016) and farmlands must be intensively managed, often through the  
121 installation of drainage canals and pump stations, to prevent soil waterlogging and declines in  
122 crop productivity. In the late 1990's, the Great Dismal Swamp Mitigation Bank, LLC purchased  
123 the former Timberlake Farms to restore the site as a compensatory mitigation bank. The  
124 Timberlake Observatory for Wetland Restoration (hereafter TOWeR) is a 1,700 ha site located  
125 on the Albemarle-Pamlico peninsula (35°54'22"N, 76°09'25"W, Fig. 1). Detailed descriptions of  
126 the region, site, and restoration practices and management can be found in Needham (2006),  
127 Ardón et al. (2010a), and Ardón et al. (2010b).

128           Restoration was completed at TOWeR in 2007 when the pump station at the northern end  
129 of the site was disabled, hydrologically reconnecting the site to surrounding waters. With the  
130 restoration of historical hydrology, several areas within the site that were not previously farmed  
131 converted into ghost forest landscapes (Fig. 2a and b), as flood-intolerant species (e.g. *Acer*  
132 *rubrum* L.) succumbed most likely to the stress associated with living in a permanently  
133 inundated environment (Hook 1984b; Kozłowski 1997). To date, living trees persist, but are  
134 restricted to either flood-tolerant species such as *Taxodium distichum* (L.) Rich., *Nyssa aquatica*  
135 L., *Nyssa sylvatica* Marshall var. *biflora* (Walter) Sarg. or raised hummock microsites. The  
136 selected research sites for the present study consisted of two ghost forest landscapes (Fig. 1a),  
137 one located in the northwestern quadrant of the TOWeR property, and the second within a  
138 permanently inundated section of the restored wetland.

139 *Site mesoclimate and additional environmental measurements*

140 Environmental variables were continuously measured at each sampling location (Fig. 1a)  
141 in July 2016 and compared to historical data from the State Climate Office of North Carolina's  
142 Climate Retrieval and Observations Network of the Southeast (CRONOS) Database monitoring  
143 station #311949 located within 2 km of TOWeR in the Gum Neck Community of Tyrrell  
144 County, North Carolina. Air temperature and relative humidity were measured continuously at 2  
145 m above ground using a HOBO Pro V2 sensor and data logger (Model U23-001, Onset, Bourne,  
146 MA) shielded from direct sunlight and the nighttime sky.

147 Daily water quality measurements were taken in each ghost forest landscape at three  
148 representative locations as described in Carmichael and Smith (2016a). Salinity was monitored  
149 using a YSI EcoSense EC300A portable conductivity, salinity, and temperature meter (YSI,  
150 Yellow Springs, OH). Surface water pH was monitored using a YSI EcoSense pH100A portable  
151 pH, mV, and temperature meter. All instruments were calibrated in the field prior to  
152 measurements. In addition to mesoclimate and water quality measurements, tree diameter at  
153 breast height (DBH, 1.37 m) and the water depth next to each tree and each floating static flux  
154 chamber (see below) were measured.

155 *Plant-Atmosphere greenhouse gas fluxes*

156 We used a static chamber approach (Livingston and Hutchinson 2009) to measure plant-  
157 atmosphere greenhouse gas fluxes on ten trees in the northwest quadrant of the TOWeR property  
158 (Fig. 1a). Snags were systematically selected to ensure that each tree was located in standing  
159 water (mean water depth  $0.23 \pm 0.03$  m, range 0.10–0.38 m) and was structurally sound enough to  
160 support static flux chambers and withstand drilling. An effort was made to repeat measurements  
161 on as many trees as possible from a 2014 study (Carmichael and Smith 2016b).



162 Chambers (Fig. 2c) were constructed based on a modified version of the chamber design  
163 described in Pangala et al. (2012). The description and dimensions of the chambers matched  
164 those described in Pangala et al. (2012) with the following exceptions: chambers were  
165 constructed of 3 mm clear Lexan and gas-impermeable closed cell foam (MD Building Products,  
166 Oklahoma City, OK) was used to provide a seal between the two halves of the chambers. Each  
167 chamber contained two gas sampling ports [8 mm Suba Seal stoppers (Sigma-Aldrich, St. Louis,  
168 MO) sealed in place with 100% Silicone caulk (General Electric, Fairfield, CT)] and an internal  
169 fan (Jameco Electronics, Belmont, CA), which was used to ensure that the air in each chamber  
170 was well-mixed during incubations and sampling. Central chamber openings were custom fit to  
171 the diameter of each tree using 5 mm closed cell resilient sealing tape (Advanced Acoustics,  
172 Mansfield, UK). After each chamber was mounted and secured in place, gas-impermeable PTFE  
173 tape (3M, St. Paul, MN) was used as a secondary sealant over each joint. Two chambers were  
174 deployed on each tree, one chamber located at 10-50 cm above water level and a second at 60-  
175 100 cm, as studies from living trees indicate an inverse relationship between CH<sub>4</sub> flux and  
176 distance above the soil surface (Pangala et al. 2012).

177 At the beginning of each sampling interval, air temperature, barometric pressure, and  
178 wind speed were recorded using a Kestrel 4000 weather and environmental meter (Kestrel  
179 Instruments, Boothwyn, PA). Ten mL gas samples were collected from each chamber in  
180 triplicate at seven time points over an 80 minute incubation: 0, 5, 10, 20, 50, 60, and 80 minutes.  
181 Gas samples were injected into pre-evacuated 9 mL glass vials (Teledyne Tekmar, Mason, OH),  
182 providing an overpressure to prevent atmospheric gas from leaking into the sample vial.

183 *Greenhouse gas sampling from trunk airspace*

184 To confirm the presence of greenhouse gases in trunk airspace, a protocol inspired by  
185 Covey et al. (2012) and described in detail in Carmichael and Smith (2016b) was utilized on the  
186 ten trees selected for greenhouse gas flux measurements. Sampling occurred immediately after  
187 the static flux chambers were removed from the trees. Three holes were drilled to center of each  
188 tree using a 5/16 in drill bit: one at 30 cm and a second at 80 cm above water level (the mid-point  
189 height of each static flux chamber), with a third hole at breast height (1.37 m) to have a  
190 standardized height on each tree. Immediately after drilling, each hole was plugged with an 8  
191 mm SubaSeal stopper (Sigma-Aldrich, St. Louis, MO) and a gas-tight syringe was used to  
192 extract a single 10 mL sample of gas from the trunk airspace at 30 cm above water level. The  
193 sample was injected into a pre-evacuated 9 mL glass vial (Teledyne Tekmar, Mason, OH),  
194 providing an overpressure to prevent atmospheric gas from leaking into the sample vial.  
195 Immediately after sampling the trunk airspace, a second sample was taken as described above  
196 from the atmosphere directly next to the trunk at 30 cm above water level. This procedure was  
197 then repeated at 80 cm above water level and at breast height. After trunk greenhouse gas  
198 sampling was completed, samples of ambient air (n= 3 daily) were taken at a TOWeR location  
199 away from any obvious CH<sub>4</sub> sources to obtain background concentrations for atmospheric  
200 greenhouse gases for the site.

#### 201 *Water-Atmosphere greenhouse gas fluxes*

202 To compare the relative importance of greenhouse gas flux pathways, water-atmosphere  
203 greenhouse gas fluxes were also measured using a static chamber approach following a protocol  
204 that had been used successfully at TOWeR (Helton et al. 2014). Floating static flux chambers  
205 (Fig. 2d) were constructed from 10 L gas sampling bags as described in detail in Helton et al.  
206 (2014). Static flux chambers (n=8) were deployed at three locations within a ghost forest

207 landscape in the restored wetland (Fig. 1a). At the beginning of each sampling interval, air  
208 temperature, barometric pressure, and wind speed were recorded using a Kestrel 4000 weather  
209 and environmental meter (Kestrel Instruments, Boothwyn, PA). Triplicate 10 mL gas samples  
210 were collected from each chamber as described in Helton et al. (2014) at three time points over  
211 24 hour incubation: 0, 8, and 24 hours.

#### 212 *Gas analyses*

213 All gas samples were stored at room temperature for less than one week before analysis  
214 via gas chromatography at the Duke River Center. Gas samples were analyzed for CH<sub>4</sub> and CO<sub>2</sub>  
215 concentrations at the Duke River Center following protocol outlined in Morse et al. (2012),  
216 Helton et al. (2014), and Carmichael and Smith (2016b). Samples were injected by a Tekmar  
217 7050 Headspace Autosampler into a Shimadzu 17A gas chromatograph with electron capture  
218 detector and flame ionization detector (Shimadzu Scientific Instruments, Columbia, MD)  
219 retrofitted with sixport valves and a methanizer to allow the determination of the three gases  
220 from the same sample. Ultra-high purity N<sub>2</sub> was used as the carrier gas, and a P5 mixture served  
221 as the make-up gas for the electron capture detector. A Nafion tube (Perma Pure, Toms River,  
222 NJ) and counter-current medical breathing air were used to remove water vapor from the sample  
223 stream. Gas concentrations were determined by comparing the peak areas of samples and  
224 certified primary standards (range of standards 0.3–5,000 μL L<sup>-1</sup> for CH<sub>4</sub> and 100–10,000 μL L<sup>-1</sup>  
225 for CO<sub>2</sub>; Airgas, Morrisville, NC) using GCsolution software (Shimadzu Scientific Instruments).

#### 226 *Plant-Atmosphere and Water-Atmosphere greenhouse gas flux calculations*

227 Under ideal conditions in static chamber incubations, gases either accumulate or are  
228 consumed linearly over time (Livingston and Hutchinson, 2009); gas fluxes are determined by  
229 regression analysis of the change in gas concentration over time in the chamber. Static flux

230 chambers are sensitive to disturbance, so rigorous quality control measures (see description  
231 below) must be applied. Measured gas concentrations were initially converted using the ideal gas  
232 law and field measurements of air temperature and barometric pressure from ppmv to  $\mu\text{g m}^{-3}$ .  
233 Quality control measures, as described in detail in Helton et al. (2014) and McInerney and  
234 Helton (2016), were then applied to the data set.

235 For gas flux calculations, we began by calculating the average of all sample replicates  
236 that were within 10% of one another (McInerney and Helton 2016). Next, we used these values  
237 to calculate the minimum detectable concentration difference (MDCD) for each sampling date  
238 (Yates et al. 2006): incubations that did not exceed the MDCD were excluded from the analysis.  
239 Gas fluxes are reported as a flux per unit exchanging surface area. Therefore, some additional  
240 transformations were required before regression analyses could be completed. For plant-  
241 atmosphere gas fluxes, the volume of each static flux chamber was obtained by subtracting the  
242 volume of each stem in a chamber (approximated as a truncated cone) from the total chamber  
243 volume. The exchanging surface area of the trunk was approximated as a truncated cone. These  
244 two numbers were used to calculate the volume to surface area ratio, which was then used to  
245 report flux rates by surface area. For water-atmosphere fluxes, the volume to surface area ratio  
246 for the static flux chambers obtained by Helton et al. (2014) was used for conversions. Once  
247 these conversions were completed, linear regression was used to calculate gas fluxes. An  
248 incubation met the assumption of linearity when  $r^2 > 0.85$ ; all incubations below this value were  
249 discarded from analysis.

#### 250 *Statistical analyses*

251 For gas samples obtained from trunk airspace, paired t-tests were used to evaluate  
252 measured differences in greenhouse gas concentrations between trunk airspace and the air next to

253 the trunk at a given height. A one-way analysis of variance was used to evaluate both the  
254 comparison between trunk airspace greenhouse gas concentrations at all heights above water  
255 level and the comparison between greenhouse gas concentrations in the air next to the trunk at all  
256 heights above water level.

257 To test for the effect of height above water level on plant-atmosphere greenhouse gas  
258 fluxes, t-tests were used to compare plant-atmosphere flux measurements from the two static flux  
259 chambers on each tree. T-tests were also used to compare the magnitude of plant-atmosphere  
260 fluxes to the flux associated with the water-atmosphere interface and to compare the magnitude  
261 of carbon (CO<sub>2</sub> and CH<sub>4</sub>) fluxes across the water-atmosphere interface.

262 In all cases described above, a Shapiro-Wilk test was used to test for normality. If  
263 normality assumptions were violated, a non-parametric equivalent (i.e. Wilcoxon Signed Rank  
264 Test, Kruskal-Wallis one-way ANOVA on ranks with a Tukey test for multiple comparisons,  
265 or Mann-Whitney Rank Sum Test) was utilized. Statistical analyses were conducted using Sigma  
266 Plot v.12 (Systat Software, San Jose, CA) and R 3.0.1 (R Core Team).

## 267 **Results**

### 268 *Site mesoclimate and additional environmental measurements*

269 Mesoclimate data indicate that the daily temperature profile in July 2016 was similar to  
270 both the 10 year weather averages and the 30 year climate normal for Tyrrell County, North  
271 Carolina. Fresh surface water conditions (salinity =  $0.1 \pm 0.0$  ppt) and relatively constant surface  
272 water pH (pH =  $4.69 \pm 0.07$ ) were maintained throughout the study period: these observations are  
273 consistent with long-term observations (unpublished site monitoring data). The mean water depth  
274 at standing dead tree locations was  $0.23 \pm 0.03$  m (range, 0.0–0.5 m). DBH ranged from 2.0–16.0

275 cm, with an average value of  $7.9\pm 0.6$  cm. The mean water depth at water-atmosphere static flux  
276 chamber locations was  $0.31\pm 0.03$  m (range, 0.19–0.45 m).

### 277 *Greenhouse gas sampling from trunk airspace*

278 The trunk airspace  $\text{CH}_4$  and  $\text{CO}_2$  concentrations were significantly elevated ( $P<0.01$ ) at  
279 30 and 80 cm compared to the air immediately outside of the trunk (Fig. 3). Trunk airspace  $\text{CH}_4$   
280 and  $\text{CO}_2$  concentrations were also significantly elevated ( $P<0.05$ ) at 30 cm compared to breast  
281 height. There were no significant differences in trunk airspace greenhouse gas concentrations  
282 between either 30 cm and 80 cm or 80 cm and breast height, possibly due to high variability in  
283 the dataset.

284 Mean concentrations of  $\text{CH}_4$  and  $\text{CO}_2$  in the air immediately outside of the trunk (Fig. 3)  
285 fell within the 95% confidence intervals for  $\text{CH}_4$  and  $\text{CO}_2$  measured in the ambient air at the site,  
286 indicating that atmospheric greenhouse gas concentrations near the trunk were not significantly  
287 elevated as compared to background concentrations reported on the sample date. The single  
288 exception was the concentration of  $\text{CH}_4$  in the air outside of the trunk at 30 cm ( $5.1\pm 1.1$   $\mu\text{L L}^{-1}$ ),  
289 which was slightly elevated compared to the background concentration in ambient air on sample  
290 days ( $2.7\pm 0.1$   $\mu\text{L L}^{-1}$ ). There were no significant differences in the concentrations of either  $\text{CH}_4$   
291 or  $\text{CO}_2$  in the air immediately outside of the trunk at the base of the trunk (30 cm) compared to  
292 80 cm and 1.37 m, which is indicative of atmospheric mixing.

### 293 *Plant-Atmosphere greenhouse gas fluxes*

294 Of the twenty static flux chambers that were used to measure greenhouse gas fluxes  
295 across the plant-atmosphere interface, eight (40%) passed quality control standards (Table 1).  
296 Methane production was measured in five (62%) of the chambers, with an average flux of  
297  $0.4\pm 0.1$   $\text{mg m}^{-2} \text{h}^{-1}$  (range, 0.1–0.7  $\text{mg m}^{-2} \text{h}^{-1}$ ). Methane consumption was measured in three

298 (38%) of the chambers, with an average flux of  $-0.6 \pm 0.3 \text{ mg m}^{-2} \text{ h}^{-1}$  (range,  $-0.3$ – $-1.2 \text{ mg m}^{-2} \text{ h}^{-1}$ )  
299 <sup>1</sup>). For CO<sub>2</sub>, seven (88%) of the chambers were a source of carbon flux to the atmosphere (mean  
300  $114.6 \pm 23.8 \text{ mg m}^{-2} \text{ h}^{-1}$ , range  $42.1$ – $224.9 \text{ mg m}^{-2} \text{ h}^{-1}$ ). A single chamber provided evidence of  
301 CO<sub>2</sub> consumption at a rate of  $-29.6 \text{ mg m}^{-2} \text{ h}^{-1}$ . For both CH<sub>4</sub> and CO<sub>2</sub>, there were no significant  
302 differences in fluxes based on location of chamber placement (i.e. bottom vs. top) ( $P > 0.05$ ).

### 303 *Water-Atmosphere greenhouse gas fluxes*

304 All eight floating static flux chambers passed quality control standards for water-  
305 atmosphere fluxes of CH<sub>4</sub> and CO<sub>2</sub>. The mean water-atmosphere flux of CO<sub>2</sub> ( $343.9 \pm 16.1 \text{ mg m}^{-2} \text{ h}^{-1}$ )  
306 was an order of magnitude greater than the mean water-atmosphere flux of CH<sub>4</sub> ( $30.9 \pm 6.1$   
307  $\text{mg m}^{-2} \text{ h}^{-1}$ , Table 1). For CH<sub>4</sub>, water-atmosphere fluxes demonstrated some spatial  
308 heterogeneity, ranging from  $10.2$ – $63.3 \text{ mg m}^{-2} \text{ h}^{-1}$ . This was also the case for CO<sub>2</sub>, but fluxes  
309 were much less variable (range,  $274.2$ – $417.9 \text{ mg m}^{-2} \text{ h}^{-1}$ ). Water-atmosphere CO<sub>2</sub> fluxes were  
310 significantly higher ( $P < 0.001$ ) than those associated with CH<sub>4</sub>. In addition, water-atmosphere  
311 CH<sub>4</sub> and CO<sub>2</sub> fluxes were significantly higher than those across the plant-atmosphere interface  
312 ( $P < 0.001$ ). The water-atmosphere flux of CH<sub>4</sub> was roughly two orders of magnitude greater than  
313 that of the plant-atmosphere flux, whereas the water-atmosphere flux of CO<sub>2</sub> was ca.  $4 \times$  greater  
314 than the flux associated with snags.

### 315 **Discussion**

316 Our results identify standing dead trees as a pathway for the flux of CH<sub>4</sub> and CO<sub>2</sub> from  
317 wetland ecosystems providing an increased resolution to the pathways responsible for the  
318 atmospheric flux of greenhouse gases from wetlands. Snags were sources of the atmospheric  
319 flux of CO<sub>2</sub>, but were both sources and sinks of the more potent greenhouse gas, CH<sub>4</sub>, with  
320 measured CH<sub>4</sub> fluxes quantitatively offsetting one another in the present study.

321 *Greenhouse gas sampling from trunk airspace*

322           Results from trunk airspace greenhouse gas sampling confirmed the development of a  
323 concentration gradient across the snag-atmosphere interface, a necessary first step for snags to  
324 act as a source of carbon flux to the atmosphere. These data are consistent with results from a  
325 2014 pilot project at TOWeR (Carmichael and Smith 2016b) that demonstrated both the  
326 accumulation of carbon-based greenhouse gases within the trunk airspace of snags and the  
327 establishment of a concentration gradient within trunk airspace. However, as in Pitz and  
328 Megonigal (2017), methodological limitations in our study did not allow for the determination of  
329 the source of the accumulated gases. Potential sources of gas production include chemically-  
330 driven degradation of methoxyl groups in plant tissue (Keppler et al. 2006; McLeod et al. 2008;  
331 Vigano et al. 2008), microbial decomposition of woody tissue in the snag (Zeikus and Ward  
332 1974; Covey et al. 2012; Lenhart et al. 2012; Hietala et al. 2015; Wang et al. 2017), and/or plant-  
333 mediated transport from the sediment (Gauci et al. 2010; Pangala et al. 2012; Terazawa et al.  
334 2015).

335           As a result of internal barriers to diffusion in the inner bark and xylem, it is not unusual  
336 to observe high gas concentrations in trunks and stems relative to atmospheric air (Teskey et al.  
337 2008), a pattern that has been observed in both living trees (Teskey et al. 2008; Covey et al.  
338 2012; Wang et al. 2017) and deadwood stocks (Covey et al. 2016; Warner et al. 2017). Several  
339 studies, as reviewed in Teskey et al. (2008) and as observed in Wang et al. 2017, have noted a  
340 positive correlation between internal concentrations of stem gases and measured efflux across the  
341 plant-atmosphere interface. Therefore, chamber-based work was necessary to 1) confirm if the  
342 high internal gas concentrations observed in this study escaped the plant-atmosphere interface as



343 a flux and 2) more finely resolve if deadwood stocks, such as snags, represent a source or a sink  
344 of carbon flux to the atmosphere.

#### 345 *Plant-Atmosphere greenhouse gas fluxes*

346 Snags were confirmed here as a conduit for the flux of carbon gases from wetlands. In the  
347 present study, there were no clear spatial patterns in the data that were collected and many of the  
348 chambers did not meet quality control standards, indicating either the absence of fluxes from an  
349 individual snag or that some fluxes may be too small to be detected due to instrumentation limits.  
350 However, among detectable fluxes, there was evidence of both CH<sub>4</sub> and CO<sub>2</sub> production and  
351 consumption across the plant-atmosphere interface. For both CH<sub>4</sub> and CO<sub>2</sub>, plant-atmosphere  
352 fluxes were lower in magnitude than those measured across both the water- (this study) and soil-  
353 atmosphere interfaces (Morse et al. 2012) at TOWeR. Plant-atmosphere fluxes of CH<sub>4</sub> in this  
354 study were similar in magnitude to those measured from both live trees and coarse woody debris  
355 in other studies of both wetland (Pangala et al. 2012) and upland (Wang et al. 2016; Wang et al.  
356 2017; Warner et al. 2017) systems. However, fluxes of CH<sub>4</sub> in this study exceeded those  
357 measured in other studies from live trees in both wetland (Gauci et al. 2010; Machacova et al.  
358 2013) and upland (Machacova et al. 2016; Pitz and Megonigal 2017) systems by up to 3 orders  
359 of magnitude. It is not uncommon to observe high spatial and temporal variation in studies that  
360 measure plant-atmosphere greenhouse gas fluxes. Although CO<sub>2</sub> fluxes from woody vegetation  
361 are rarely reported in the literature related to the role of vegetation in the flux of greenhouse  
362 gases from wetland systems, the values in our study largely agree with those measured in live  
363 trees and coarse woody debris in upland systems by Warner et al. (2017).

364 Despite the growing body of literature on the role of plants in the flux of carbon gases  
365 from wetland systems, much is yet to be learned about this pathway, a statement that is

366 especially relevant for the newly recognized pathway of snags. First, it is still unclear whether  
367 the ultimate source of the carbon gases in this study was decomposition of woody tissue, plant-  
368 mediated transport of sediment-borne gases, or a combination of both. Future experiments  
369 focused on measuring the potential for CH<sub>4</sub> production and oxidation in tissue harvested from  
370 snags could help to clarify this unknown. In addition, stable isotopic studies of gases trapped in a  
371 flux chamber might also be a useful approach [similar to Schwietzke et al. (2016)], though  
372 identifying sources of CH<sub>4</sub> using this technique can be somewhat complicated (Newton 2016).

373         Second, the abiotic and biotic controls on the magnitude and direction of carbon fluxes  
374 from snags are currently unknown. A variety of abiotic factors have been shown to impact decay  
375 rates in deadwood: surface area exposed to ground contact and/or physical position (Harmon  
376 1982; Oberle et al. 2017), exposure to radiation and wind (Harmon 1982), the chemical  
377 composition of wood (Zanne et al. 2015), the water content of wood (Wang et al. 2017), and the  
378 availability of carbon substrates (Covey et al. 2016). In addition, any factor that impacts  
379 properties associated with diffusion in deadwood would likely also affect gas fluxes across the  
380 plant-atmosphere interface (Covey et al. 2016). For example, the state of decay (Warner et al.  
381 2017), wood density (Pangala et al. 2012), woody porosity (Visser and Bögemann 2003), and the  
382 diameter of stems or trunks (Covey et al. 2016) are all factors that likely influence fluxes from  
383 snags. Plant-microbe interactions may also act as a control on the strength and direction of  
384 fluxes. Negative CH<sub>4</sub> fluxes were measured in this study, and a comparison of gas concentration  
385 values in dead trunk airspace to those in experimental models of biologically inert trunks (2"  
386 PVC columns, unpublished data) provides evidence that dead trunks, as biologically active  
387 structures, may actually play a role in mediating CH<sub>4</sub> flux. Methanotrophic symbionts are known  
388 to colonize wetland plant tissue (Raghoebarsing et al. 2005), and it is possible this relationship

389 could turn an individual plant from a source of CH<sub>4</sub> to a sink if rates of CH<sub>4</sub> consumption were  
390 high enough.

391 Third, the mechanisms that induce the flux of carbon gases across the plant-atmosphere  
392 interface are yet to be elucidated. A flux could purely be diffusive, but it is also likely that  
393 environmental conditions such as wind exposure may drive and/or enhance fluxes across the  
394 plant-atmosphere interface. During one sampling event, a storm system was moving through the  
395 area. When having difficulty extracting a gas sample from a packed column at water level, a gust  
396 of wind pulsed through the site and the sample was easily extracted. According to Bernoulli's  
397 principle, as fluid speed increases, fluid pressure drops. Therefore, fast moving air generates a  
398 lower pressure than still air. It is possible that this burst of wind could create a vacuum,  
399 suctioning accumulated gases out of the column airspace, and pointing towards a potential  
400 mechanism for the induction of fluxes across the plant-atmosphere interface in snags. In fact,  
401 Bernoulli's principle has been demonstrated to induce gas flows in other non-living structures  
402 built from biological activity (Vogel et al. 1973), and low-air-pressure events, such as those  
403 associated with storm systems, can induce CH<sub>4</sub> fluxes across both the soil- (Clements and  
404 Wilkening 1974) and water-atmosphere (Mattson and Likens 1990) interface.

405 Finally, from a source-strength perspective, little is known about 1) diurnal and/or  
406 seasonal fluctuations in the magnitude of CH<sub>4</sub> and CO<sub>2</sub> fluxes across the plant-atmosphere  
407 interface in snags and 2) the current spatial extent of ghost forests within coastal landscapes.  
408 However, it is clear that ghost forest landscapes will become increasingly common in the future,  
409 as stressors associated with global climate change represent a present and imminent threat to  
410 coastal wetlands. This is particularly true for wetlands of the United States' Atlantic and Gulf

411 coasts, where an estimated 58,000 km<sup>2</sup> of land lies less than 1.5 m above sea level (Titus and  
412 Richman 2001).

### 413 *Water-Atmosphere greenhouse gas fluxes*

414         These data also provided supporting evidence for the quantitative importance of water-  
415 atmosphere carbon fluxes from wetland ecosystems, an often overlooked component of gas  
416 transport processes in lentic and lotic freshwater systems (Bastviken et al. 2011; Poindexter et al.  
417 2016; Stanley et al. 2016). Recent experimental evidence indicates that carbon fluxes across the  
418 water-atmosphere interface are likely a dominant transport pathway in wetland systems,  
419 especially during ebullition events (Walter et al. 2006; DelSontro et al. 2014) and over nighttime  
420 hours (Poindexter et al. 2016), a window in which greenhouse gas flux measurements are rarely  
421 completed. In the present study, water-atmosphere fluxes of CH<sub>4</sub> and CO<sub>2</sub> were significantly  
422 higher (ca. two orders of magnitude and 4× respectively) than fluxes across the plant-atmosphere  
423 interface. For CH<sub>4</sub>, water-atmosphere fluxes were consistently higher than those measured at  
424 similar sites in TOWeR in July 2012 [Helton et al. (2014), CO<sub>2</sub> fluxes were not reported in this  
425 study]. In addition, water-atmosphere fluxes of CH<sub>4</sub> were an order of magnitude higher than  
426 mean soil-atmosphere fluxes measured in a multi-year study at TOWeR; for CO<sub>2</sub>, the ranges of  
427 water- and soil- atmosphere fluxes were within the same order of magnitude and overlapped  
428 Morse et al. (2012). Though the focus of the present study was not necessarily hydrodynamic  
429 transport processes, our data indicate that water-atmosphere flux of CH<sub>4</sub> and CO<sub>2</sub> may be a  
430 quantitatively important pathway in the atmospheric flux of greenhouse gases from wetland  
431 ecosystems.

### 432 *Conclusions*

433 Results from this study have identified standing dead trees as a previously unrecognized  
434 pathway in the flux of CH<sub>4</sub> and CO<sub>2</sub> from wetland ecosystems. However, several key questions  
435 remain regarding 1) the ultimate source of these carbon gases, 2) the abiotic and biotic controls  
436 on the magnitude and direction of this flux, 3) the mechanisms that induce this flux, and 4) the  
437 importance of this pathway relative to other sources at the landscape level. Over time, knowledge  
438 regarding the mechanisms that induce and control carbon fluxes from snags could lead to the  
439 development of management strategies for decreasing greenhouse gas emissions from wetlands,  
440 as suggested in McNerney and Helton (2016). Though stocks of deadwood in forests are  
441 notoriously difficult to estimate (Woodall et al. 2012), globally stressors associated with global  
442 climate change (i.e. sea level rise, saltwater incursion, and extreme episodic events such as  
443 intense drought or hurricanes) are already leading to the conversion of large swaths of coastal  
444 forested wetlands to ghost forest landscapes, increasing the spatial footprint of snags in coastal  
445 landscapes (Gilbert et al. 2012; Melillo et al. 2014) and the quantitative importance of standing  
446 dead trees in wetland carbon dynamics.

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659 **Table 1** Plant-atmosphere and water-atmosphere carbon fluxes at TOWeR in July 2016. Values are reported as mean±standard error  
 660 and only represent chambers that met quality control criteria as outlined in the methods. Sample sizes are given in parentheses  
 661

	<b>CH<sub>4</sub> (mg m<sup>-2</sup> h<sup>-1</sup>)</b>		<b>CO<sub>2</sub> (mg m<sup>-2</sup> h<sup>-1</sup>)</b>	
	<b>Plant-Atmosphere</b>	<b>Water-Atmosphere</b>	<b>Plant-Atmosphere</b>	<b>Water-Atmosphere</b>
Production	0.4±0.1 ( <i>n</i> =5)	30.9±6.1 ( <i>n</i> =8)	114.6±23.8 ( <i>n</i> =7)	343.9±16.1 ( <i>n</i> =8)
Consumption	-0.6±0.3 ( <i>n</i> =3)	–	-29.6 ( <i>n</i> =1)	–

662



663 **Figure Captions**

664 **Fig. 1** Site map of the Timberlake Observatory for Wetland Restoration (a) in relation to the state  
665 of North Carolina and the Albemarle-Pamlico Peninsula (b). The circle in panel 1a marks the  
666 location of the ghost forest stand where plant-atmosphere greenhouse gas fluxes were measured.  
667 The white square denotes the location of the chambers used to measure water-atmosphere  
668 greenhouse gas fluxes. Both panels were created using Google Earth; image is copyrighted by  
669 DigitalGlobe (2016)

670 **Fig. 2** Representative ghost forest landscapes at the Timberlake Observatory for Wetland  
671 Restoration in Tyrrell County, North Carolina and field equipment used to measure trace  
672 greenhouse gases: a) deepwater site for the measurement of plant-atmosphere fluxes, b) ghost  
673 forest where water-atmosphere flux chambers were deployed, c) static flux chambers for plant-  
674 atmosphere gas fluxes, and d) static flux chambers for water-atmosphere gas fluxes

675 **Fig. 3** CH<sub>4</sub> (a) and CO<sub>2</sub> (b) concentrations in trunk airspace compared to the ambient air  
676 immediately outside of the trunk at 30 cm, 80 cm, and breast height (1.37 m). Values given as  
677 mean±standard error. Asterisks indicate significantly elevated greenhouse gas concentrations  
678 within the trunk airspace compared to the ambient air immediately outside of the trunk at a given  
679 height. The solid line represents the mean greenhouse gas concentration in ambient air at the site,  
680 whereas the dotted lines indicate the 95% confidence interval of the mean





