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1 **Forest ecosystem changes from annual methane source to sink depending on late**
2 **summer water balance**

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12

13 Key Points

14 Summer precipitation may moderate a methane source-sink transition at this site

15 Ecosystem-scale photosynthesis correlates with methane fluxes over short and long
16 timescales

17 Multiyear flux datasets are needed to build predictive understanding

18

18

19 **Abstract**

20 Forests dominate the global carbon cycle, but their role in methane (CH₄)
21 biogeochemistry remains uncertain. We analyzed whole-ecosystem CH₄ fluxes from two
22 years, obtained over a lowland evergreen forest in Maine, USA. Gross primary
23 productivity (GPP) provided the strongest correlation with the CH₄ flux in both years,
24 with an additional significant effect of soil moisture in the second, drier, year. This forest
25 was a neutral to net source of CH₄ in 2011 and a small net sink in 2012. Inter-annual
26 variability in the summer hydrologic cycle apparently shifts the ecosystem from being a
27 net source to a sink for CH₄. The small magnitude of the CH₄ fluxes and observed control
28 or CH₄ fluxes by forest productivity and summer precipitation provide novel insight into
29 the CH₄ cycle in this globally important forest ecosystem.

30 **Introduction**

31 Global forests remove CO₂ from the atmosphere at a rate of ~2.4 Pg C per year [*Pan et*
32 *al.*, 2011]. The role of forests in methane (CH₄) cycling, however, has not been well
33 constrained, in part because of difficulties in assessing CH₄ fluxes at the landscape scale.
34 Most of what is known about forest CH₄ fluxes is derived from chamber measurements at
35 the level of the soil surface, which show that many forest soils are net consumers of
36 atmospheric CH₄ [*Megonigal and Guenther*, 2008]. Globally, CH₄-consuming bacteria in
37 terrestrial soils are believed to account for approximately 5% of total CH₄ oxidation, the
38 second largest sink of atmospheric CH₄ while anaerobic (saturated) soils are strong
39 sources of CH₄ [*Forster et al.*, 2007]. The division between what constitutes a CH₄
40 producing vs consuming soil is murky with upland soils demonstrated to emit CH₄ under

41 certain circumstances [*Savage et al.*, 1997; *Whalen et al.*, 1991; *Yavitt et al.*, 1995; *Yavitt*
42 *et al.*, 1990] and localized (often discrete) soil flux measurements are difficult to scale up
43 due to their high spatial and temporal variability.

44 Forests with high water tables and organic-rich soils, such as many boreal forests,
45 provide an especially complex picture with dry and wet soil conditions intermixed due to
46 small-scale topographic variability. Such forests have the most potential to produce and
47 emit significant quantities of CH₄. In addition, direct interaction of trees with forest CH₄
48 emissions have also been posited, either aerobically [*Keppler et al.*, 2006], through
49 internal anaerobic rot [*Covey et al.*, 2012], or with the trees acting as conduits for soil-
50 produced CH₄ dissolved in the transpiration stream [*Nisbet et al.*, 2009; *Pangala et al.*,
51 2013]. Determining what controls the magnitude and seasonality of forest CH₄ fluxes
52 above the canopy will define the roles of forest soils and trees in the global CH₄ cycle.

53 Recent improvements in fast-response CH₄ analyzers have made it possible to measure
54 ecosystem-scale CH₄ fluxes by eddy covariance [*Peltola*, 2011; *Smeets et al.*, 2009;
55 *Wang et al.*, 2013]. Here we present and analyze the first multi-year eddy covariance time
56 series of CH₄ fluxes from a forested ecosystem. The results show that the site was a
57 neutral to small net source of CH₄ during 2011 but a net sink during 2012. Importantly,
58 no strong CH₄ sources, either from the soils or trees, are indicated by this study. The
59 strongest correlate for the 4-day averaged CH₄ flux dynamics was GPP during both years,
60 with soil moisture accounting for significant variance during dry periods. Our results
61 suggest that multi-year studies will be critical to developing model structures capable of
62 reproducing net fluxes and predicting changes in future CH₄ fluxes from forested
63 ecosystems.

64 **Methods**

65 *Site Description*

66 Research was conducted at the Howland Forest AmeriFlux site located about 35 miles
67 north of Bangor, Maine, USA (45°15' N, 68°44' W, 60 m asl) on forestland owned by
68 the Northeast Wilderness Trust. Howland Forest is a boreal-temperate transition forest,
69 with stands dominated by red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga*
70 *canadensis* (L.) Carr.) with lesser quantities of other conifers and hardwoods. The soils
71 have never been cultivated and the upland soils are classified as Skerry fine sandy loam,
72 Aquic Haplorthods. Peats have formed in the poorly drained positions dominated by
73 sphagnum. Fernandez et al. [1993], and Hollinger et al. [1999; 2004] have previously
74 described the climate, soils, and vegetation at the site.

75 *Flux measurements*

76 Fluxes were measured at a height of 29 m with systems consisting of a model SAT-
77 211/3K 3-axis sonic anemometer (Applied Technologies Inc., Longmont, CO, USA) and
78 a fast-response CH₄/CO₂/H₂O cavity ring down spectrometer (model G1301-f in 2011
79 and G2311-f in 2012; Picarro Inc., Santa Clara, CA) with data recorded at 5 Hz. The CO₂
80 flux measurements were also independently quantified with a co-deployed fast response
81 CO₂/H₂O infrared gas analyzer (model Li-7200, Li-Cor Inc., Lincoln, NE, USA). In 2011,
82 H₂O concentrations measured with the Li-7200 were used for density correction of CO₂
83 and CH₄ fluxes measured with the G1301-f because that instrument could not output all
84 three concentrations simultaneously. Fluxes were calculated and filtered according to
85 Hollinger et al. [1999; 2004]. In 2012, fluxes were calculated via the same equations and
86 assumptions (600 s time constant running mean filter, double rotation, etc.) using

87 commercially available software (EddyPro version 4, Li-Cor Inc., Lincoln, NE, USA). In
88 both years, the CO₂ fluxes were nearly identical between the Picarro and Licor analyzers
89 (Fig S1). The sign convention used is that flux to the ecosystem is defined as negative.
90 Further details on the filtering of the flux data are available in the SI.

91 *Environmental Data*

92 Profiles of soil temperature and soil moisture were measured hourly at 5, 10, 20, 50, and
93 100 cm using Hydra probes (Stevens Water Monitoring Systems Inc., Beaverton, OR,
94 USA) 20 near the base of the tower. Water table depth was measured using a
95 barometrically compensated pressure transducer (model WL400, Global Water, Gold
96 River, CA, USA) in a shallow well. Solar radiation (photosynthetic photon flux density,
97 PPF), air temperature, and precipitation were measured from the top of the flux tower
98 as described previously [Hollinger *et al.*, 2004]. We note that the measurement scale for
99 the soil data differs from that of the flux data.

100 *Statistical Analyses*

101 The half-hourly CH₄ flux data were low-pass filtered to give a set of mean fluxes, each
102 representing a 4-day window. This was combined with Monte-Carlo resampling in order
103 to obtain an estimate of the uncertainty on these mean fluxes. Details are available in the
104 SI.

105 We used an Artificial Neural Network (ANN) to characterize the climatic sensitivity of
106 ecosystem-atmosphere CH₄ exchange and to estimate annual CH₄ budgets. This
107 methodology choice is supported by a recent study showing the effectiveness of ANNs
108 for gap-filling CH₄ fluxes [Dengel *et al.*, 2013]. An ANN is an inductive approach based

109 on statistical multivariate modeling [Bishop, 1995; Rojas, 1996] by which one can map
110 drivers directly onto observations [Moffat *et al.*, 2010]. We used a feed-forward ANN
111 with a sigmoid activation function trained with a back propagation algorithm. An
112 ensemble of 100 ANNs was trained both on the hourly and running mean aggregated
113 eddy-covariance CH₄ fluxes independently. See SI for description of our 3-stage training
114 process.

115 **Results**

116 Many variables including GPP, air temperature, PPFD, CO₂ flux, and soil moisture and
117 soil temperature at 10 and 20 cm were significantly correlated (Kendall rank correlation,
118 $p \ll 0.01$) with the CH₄ flux signal in both years, but any combination of these variables
119 explains only a small fraction of the variation in the CH₄ fluxes (multiple $r^2 < 0.05$) at the
120 30 minute time step. The neural network approach was able to explain a maximum of 8-
121 10% of the total variability in the data for each year (Fig S3) using a combination of
122 environmental drivers (GPP, air temperature, wind direction, wind speed, relative
123 humidity, soil moisture, soil temperature, and water table depth). The individual driver
124 with the highest explanatory power in the ANN was air temperature in 2011 and GPP in
125 2012. These low correlations emerge because of the large random errors (noise) in the
126 measurement, which argues for the use of statistical approaches for time averaging of the
127 data to reduce uncertainties and permit elucidation of the trends.

128 Averaging the fluxes by time of day, we observed more CH₄ efflux during the daytime
129 and more CH₄ consumption at night. This pattern was only present during summer
130 months (Fig S4). We used a wavelet coherence analysis as an alternate approach for
131 examining the significance of this diurnal structure. Using this analysis we found

132 coherent periodic behavior in both the CH₄ and GPP signals at the 18-28 hour time scale
133 over the summer and early fall seasons, although the time periods when this relationship
134 was significant were intermittent. The coherence between the CH₄ flux and GPP signals
135 was stronger than between CH₄ flux and air temperature. Due in part to the intermittent
136 nature of the coherence, it was not possible to determine whether CH₄ flux lagged GPP,
137 which could potentially indicate a causal relationship.

138 The use of 4-day mean fluxes elucidated the seasonal pattern in the CH₄ flux data. CH₄
139 fluxes were mostly positive during the summer months, trending negative in the late
140 summer or fall, then remaining consistently negative through the winter months (Fig 1).
141 By comparison, the CO₂ fluxes (here processed as GPP) showed the opposite pattern with
142 the highest rates of CO₂ uptake during the midsummer, followed by decreasing uptake
143 through the fall into the winter.

144 The spring and summer precipitation patterns differed between 2011 and 2012. While the
145 total annual precipitation measured at the tower was lower in 2011 (870 mm) than in
146 2012 (940 mm), the precipitation during July and August was much greater during 2011
147 than 2012 (224 vs 76 mm). This precipitation change led to a large difference in
148 summer/fall soil moisture between the years (Fig 1). Historical precipitation data
149 (<http://www.ncdc.noaa.gov/cdo-web/>) from Millinocket station (located ~50 km north of
150 Howland forest) for July and August for 1970-2010 gives a mean (\pm 1sd) precipitation of
151 200 ± 73 mm for those months combined. In 2011 Millinocket recorded July-August
152 precipitation of 282 mm during 2011, compared with 127 mm for 2012, indicating that
153 2011 was wetter than the 40-yr average whereas 2012 was drier than average.

154 Using a wide selection of variables (air temperature, soil temperature, soil moisture, wind
155 direction, water table depth, relative humidity, and wind speed) the ANN produced a
156 model explaining nearly 65% and 90% of the variability in the 4-day CH₄ fluxes during
157 2011 and 2012. However, to reduce the redundancy due to correlations between many of
158 these drivers, we forced the ANN to use GPP and then tested for the additional
159 explanatory power (if any) attained by each remaining driver (Fig 2, S5). GPP was
160 chosen because it was the individual variable with the highest explanatory power in both
161 years. The importance of each driver using this reduced approach is shown in Fig 2. We
162 observe that, in 2011 and 2012 respectively, variation in GPP accounted for 60% and
163 50% of the variability in the 4-day CH₄ fluxes. Including soil moisture increases the
164 explanatory power of the model by >10% during 2012 (the drier year) but has negligible
165 influence in 2011 (the wetter year). Therefore, a model using only GPP and 10-cm soil
166 moisture was able to explain ~ 60 and 70% of the variability in 4-d mean CH₄ fluxes for
167 2011 and 2012. All other drivers provide negligible improvement to the model fit. This
168 order of importance of drivers was supported by separate linear regression analysis
169 (Table S1).

170 Despite the fact that the principal environmental drivers were the same in both years,
171 models derived from the 2011 fluxes did a poor job predicting CH₄ fluxes in 2012, and
172 vice versa (Fig. S6). We also trained the model on the 4-day means from both years
173 together and while the ANN produced a model that explained 40% of the variability in all
174 the data this represented a substantial decrease in goodness-of-fit compared to modeling
175 each year individually.

176 We estimated the annual CH₄ budgets for 2011 and 2012 for Howland forest in two
177 ways; using either the ANN or a linear model combined with Monte Carlo resampling.
178 Using the linear modeling approach (Fig S7) we estimate net efflux (mean ± 1sd) of 7 ±
179 4.6 mmol m⁻² yr⁻¹ for 2011 and consumption -18 ± 2.7 mmol m⁻² yr⁻¹ for 2012. Using the
180 ANN, annual fluxes were 6 ± 11 mmol m⁻² yr⁻¹ for 2011, and -9 ± 3.7 mmol m⁻² yr⁻¹ for
181 2012 (Fig 2). Larger uncertainties were contributed by the first few months of the year
182 due to the absence of measurements to constrain the model during these periods. This
183 increase in variance was particularly large in the ANN because of its inherently nonlinear
184 structure. Both approaches indicated that the annual CH₄ flux in 2011 was small but
185 likely positive while the forest was a net consumer of CH₄ in 2012.

186 **Discussion**

187 The lowland evergreen forest studied was an intermittent source of CH₄ to the
188 atmosphere, showing efflux from July through October during 2011, and from June
189 through July 2012 while recording net uptake for the remainder of each year (Fig 1).
190 Using an artificial neural network (ANN), we found that a combination of GPP and 10-
191 cm soil moisture was able to explain 60 and 70% of the variability in 4-d mean CH₄
192 emissions for 2011 and 2012 individually (Fig 2), while use of all the drivers resulted in a
193 model explaining nearly 90% of the variability during 2012 (the maximum explainable
194 variance in 2011 is just above 60%). Additionally, a diurnal cycle was present in the CH₄
195 flux signal during the summer and fall that was consistent with that observed in GPP. The
196 ANN, supported by linear modeling, consistently found GPP to be a stronger correlate of
197 the 4-day mean CH₄ fluxes than air temperature.

198 Gross primary production is highly correlated with a wide variety of other environmental
199 parameters, such as air temperature, PPFD, and soil temperature, and it could be argued
200 that GPP is driving CH₄ emissions only indirectly through cross-correlations. The a priori
201 assumption would be that CH₄ fluxes are controlled by soil moisture [*Adamsen and King,*
202 *1993; Castro et al., 1994; Castro et al., 1995*] due to the dependence of both CH₄
203 oxidation and CH₄ production on soil diffusivity (through O₂ availability) with
204 temperature being a secondary controlling variable [*Castro et al., 1995*] due to the
205 positive influence of temperatures on reaction rates (positive Q₁₀ values). However, both
206 the neural network and linear modeling approaches found GPP to be the stronger
207 predictor of CH₄ emissions when treating each year individually, or together, with soil
208 moisture only important during 2012.

209 There are several mechanistic reasons why changes in GPP may lead to changes in CH₄
210 emissions. First, CH₄ production rates have been linked to photosynthesis through root
211 exudation in some wetlands [*King and Reeburgh, 2002*]. Carbon isotope studies have
212 shown that most CH₄ released from wetlands is derived from “new carbon” rather than
213 from dissolved soil organic matter [*Chanton et al., 1995*]. In a rice paddy, wavelet
214 coherence analysis found the diurnal cycle in CH₄ emissions to be driven by GPP [*Hatala*
215 *et al., 2012*]. However, trees may also be influencing the seasonal and diurnal cycle if
216 dissolved CH₄ is emitted through transpired soil water [*Nisbet et al., 2009*], such that
217 GPP could be more proxy than mechanism. It is more difficult to directly connect CH₄
218 oxidation and GPP, although microbial priming could link these processes. In this case,
219 carbon leakage from the roots of trees and other plants increases total microbial activity;
220 because many CH₄ oxidizing bacteria are capable of consuming a wide variety of

221 methylated substrates their population dynamics could respond to overall soil carbon
222 degradation rates, leading to higher rates of CH₄ oxidation linked to increased soil
223 respiration activity. We interpret these results as indicating a significant role for GPP in
224 influencing CH₄ flux, both in its high frequency and low frequency variability although
225 we acknowledge that the mechanism is not yet clear.

226 The role of soil moisture in forest CH₄ flux may involve a threshold: once volumetric soil
227 moisture exceeds some level (here ~0.1 WFV), there are sufficient anoxic pore spaces to
228 support CH₄ production near the surface and correlations become weak, while below this
229 threshold, soil moisture is an important factor controlling the balance between CH₄
230 production and CH₄ oxidation. It is also possible that the lower correlations are a result of
231 spatial variability in soil moisture over the tower footprint related to the small-scale
232 topography that was not captured by this study. However, the trends of drying and
233 wetting, also observed in the precipitation data, would be expected to be felt to some
234 degree throughout the landscape. Overall, we found soil moisture had a smaller overall
235 influence than GPP but remains important under drier conditions.

236 Despite the high correlations of a model using GPP and soil moisture to the data in each
237 year, the explanatory power of these models diminished almost to zero when applied to
238 data on which the model was not trained (Fig S6). Similar challenges have been observed
239 with modeling CH₄ fluxes [*Mastepanov et al.*, 2012; *Moore et al.*, 2011; *Treat et al.*,
240 2007], as well as CO₂ fluxes [*Richardson et al.*, 2007] from a variety of environments.

241 Net CH₄ emission is the result of two processes acting in opposition – CH₄ production
242 and CH₄ oxidation, and it appears that a correlative model based on emissions may lack
243 the appropriate structure needed to extrapolate fluxes over longer timescales, despite

244 success over shorter timescales. Achieving an appropriate model structure and
245 complexity is necessary for improving the CH₄ components of larger earth-system
246 models and predicting natural CH₄ emissions from forests under changing environmental
247 conditions. Multiple years of flux measurements under a range of conditions will be
248 needed to accurately characterize the climatic and physiological dependence of forest
249 CH₄ fluxes. Experimental methods combining ecosystem-scale flux measurements, soil
250 chamber flux measurements, and soil-gas profiles may also provide needed insight into
251 the mechanistic controls driving both the sign and magnitude of CH₄ flux.

252 In the context of the overall climate impact of greenhouse gas fluxes at this site, the CH₄
253 fluxes are small contributors (see SI) relative to the total CO₂ uptake. This contrasts with
254 other ecosystems, such as boreal wetlands where the climate impact of CH₄ fluxes can be
255 larger than the climate benefit of their CO₂ uptake [*Whiting and Chanton, 2001*].

256 **Conclusions**

257 We provide the first multi-year set of CH₄ fluxes measured by eddy-covariance over a
258 forested ecosystem. Multi-year data sets of CH₄ fluxes capturing a wide variety of
259 environmental conditions are critical to developing model structures that are capable of
260 adequately predicting future CH₄ fluxes. GPP provided the strongest correlation with the
261 calculated 4-day mean CH₄ fluxes during each year. Including soil moisture as a driver
262 for CH₄ production improved the fit of the model only during 2012, which had a drier
263 than average summer. Despite the potential for CH₄ efflux from this temperate-boreal
264 transition site, our observations suggest that neither the soils nor trees are large sources of
265 CH₄ from the forest to the atmosphere. This study finds evidence for a link between GPP

266 and CH₄ flux, and a small sink/source transition controlled by summer hydrologic
267 conditions.

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364 **Figure Legends**

365 Figure 1: The 4-day running mean CH₄ fluxes (open circles) with 4-day mean GPP (grey
366 stars) and volumetric soil moisture at 10 cm (black squares). Data from 2011 is shown in
367 the top panel against data from 2012 in the lower panel. The dotted black line highlights
368 the line of 0 flux, above which the forest is a net source of CH₄ to the atmosphere and
369 below which the forest is a net sink for CH₄.

370 Figure 2: Results from the ANN for both years, with the top panels indicating the
371 importance of various environmental drivers contributing to the model. Each
372 environmental driver is shown separately with the black portion of the column indicating
373 the additional predictive power this driver gives the model when combined with GPP (the
374 grey portion of the column). The horizontal dotted lines indicate the maximum attainable
375 predictive capacity if all drivers are used simultaneously. The bottom panels show the
376 ANN modeled fluxes for the entire year (black lines) \pm 1 sd (vertical bars).