Uncertain role of nutrient availability on forest carbon balance

Enzai Du

State Key Laboratory of Earth Surface Processes and Resource Ecology, and College of Resources Science & Technology, Beijing Normal University, Xinjiekouwai Street 19#, Beijing 100875, China. Email: enzaidu@bnu.edu.cn

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Fernández-Martínez et al. (2014) conclude that nutrient availability plays a crucial role in determining net ecosystem production (NEP) and ecosystem carbon-use efficiency (CUEe, the ratio of NEP to gross primary production, GPP) in global forests. However, their conclusions indeed solely depend on an improper treatment of differences in the GPP ranges of nutrient-rich and nutrient-poor forests (uneven sampling effect) and outliers. Using dataset retrieved by digitalizing figures in their paper, we have performed detailed statistical analysis and found that nutrient availability has no significant effect on NEP and CUEe.

NEP and CUEe both have a non-linear response to GPP (Fig. 1a and 1b) and this non-linear relationship indicates that the uneven sampling effect (differences in the GPP ranges) can result in misleading conclusions. Taking the nutrient-poor forests as an example, CUEe within the GPP range of 1000~2000 g C m^{-2} yr^{-1} (16 ± 3%; mean ± s.e.m.) can be significantly higher than CUEe within the whole data range (6 ± 4%) ($p < 0.05$). Results of generalized linear model analysis (GLM) (NEP ~ GPP+ GPP.class + GPP*GPP.class) clearly indicate a significant effect of uneven sampling (e.g. GPP ranges

of 1000 ~ 2000 g C m^{-2} yr^{-1} *vs.* whole GPP range), which means that the GPP ranges can exert significant effect on the variation in NEP (Table 1). Therefore, same data ranges of GPP should be used to avoid uneven sampling effect. Unfortunately, the GPP range for the nutrient-rich forests did not cover the whole range for the non-linear curve. Therefore, the main conclusions of Fernández-Martínez et al. (2014) should only be robust when based on data analysis using same data range of GPP.

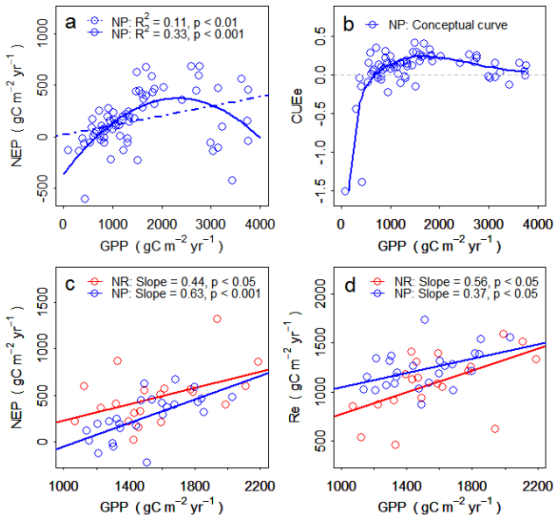

Figure 1. NEP (unit: g C m^{-2} yr^{-1}), CUEe, and Re (Unit: g C m^{-2} yr^{-1}) against GPP (Unit: g C m^{-2} yr^{-1}) in nutrient-rich and nutrient-poor forests. (a) Change in NEP against GPP within whole data range of GPP in nutrient-poor forests, (b) Non-linear conceptual model of the relationship between CUEe and GPP based on dataset in nutrient-poor forests, (c) comparison of the slope of NEP against GPP, and (d) comparison of the slope of Re against GPP in nutrient-rich and nutrient-poor forests.

Table 1. Results of GLM analysis indicate significant uneven sampling effect.

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	25.33916	52.44891	0.483	0.63012
GPP	0.09144	0.02896	3.157	0.00213 **
GPP.class#	-476.93935	223.14082	-2.137	0.03513 *
GPP:GPP.class	0.40034	0.15196	2.634	0.00984 **

 # GPP.class: GPP ranging between 1000 ~ 2000 g C m^{-2} yr^{-1} vs. whole data range of GPP

Three very young forests (age < 5 years) with extremely high GPP and NEP (Fernández-Martínez et al., 2014) are actually outliers and indeed dominate their statistical results. Obviously, these youngest forests are managed forests, but their high NEP and GPP are not likely caused solely by nutrient enrichment. Detailed information is needed to understand why these youngest forests have so high GPP and NEP. The authors argued that leverage tests showed that these three forests did not affect the statistical results, but unfortunately this is not true. We have found that the outliers indeed lead to misleading statistical results by significantly affecting the relationships of NEP versus GPP and ecosystems respiration (Re) versus GPP.

When excluding the three outliers and uneven sampling effect, NEP and Re both showed significant positive relationship against GPP in either nutrient-rich forests or nutrient-poor forests. The slope of NEP against GPP for the nutrient-rich forests (slope = 0.44, $p<0.05$) was lower than that for nutrient-poor forests (slope = 0.63, $p < 0.001$) (Fig 1c), but the difference was not significant ($p = 0.49$). Accordingly, the slope of ecosystems respiration (Re) against GPP for the nutrient-rich forests (slope = 0.56, $p<0.05$) was higher than that for nutrient-poor forests (slope = 0.37, $p < 0.05$) (Fig 1d) and the difference was also not significant ($p = 0.85$). Fernández-Martínez et al. (2014) conclude that a much larger proportion of GPP is allocated to NEP in nutrient-rich forests while a much larger proportion of GPP is released through Re in nutrient-poor forests. The statistical analysis above indicates that nutrient-poor forests and nutrient-rich forests have no difference in their allocation of GPP to NEP and Re, which is contrary to the conclusions of Fernández-Martínez et al. (2014) (also see Fig 1 and 2 in their paper). This

also indicates that the outliers significantly affect their results and should be excluded in the data analysis.

The authors mention that they also repeated all analyses excluding the three very young forests, but in this case they considered the whole GPP range again. It is tricky because they have never simultaneously considered the uneven sampling effect and outliers. Using the common data range of GPP for the two nutrient types (1000 ~ 2200 g C m^{-2} yr^{-1}) and excluding the three outliers in nutrient-rich forests, a GLM analysis (NEP ~ GPP+ Nutrients + Nutrients*GPP) showed that only GPP had strong control on NEP whereas the effects of nutrient availability ($p = 0.26$) and the nutrient*GPP interaction ($p = 0.49$) both were not significant (Table 2). This clearly indicates that nutrient availability does not exert a significant control on forest carbon balance. Our results conclude that the conclusions of Fernández-Martínez et al. (2014) solely depend on the uneven sampling effect and outliers.

Table 2. Results of GLMs analysis indicate the effect of nutrient class is not significant.

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	-211.8695	258.9502	-0.818	0.41787
GPP	0.4410	0.1621	2.720	0.00944**
Nutrient.class	-424.7619	368.2886	-1.153	0.25529
GPP:Nutrient.class	0.1648	0.2375	0.694	0.49154

We further propose a non-linear conceptual model of CUEe against GPP (Fig. 1b), which implies GPP and stand age may jointly determine C allocation of GPP to NEP. Young forests with low GPP commonly are C sources (Goulden et al., 2011), and CUEe increases rapidly with growing GPP to a critical point which is C neutral. Then CUEe

continues to increase but starts to slow down at a certain stage when nutrient limitation is intensified by biomass nutrient accumulation(Johnson, 2006), and further it reaches a maximum after which CUEe declines slowly due to increasing allocation of GPP to Re (Luyssaert et al., 2008).

References

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