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Revisiting the role of nutrient availability on global forest carbon balance

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Global forests dominate the capacity of carbon (C) sequestration in terrestrial ecosystems and have strong feedbacks to changes in atmospheric CO_2 concentrations and climate factors. The role of nutrient availability is becoming crucial with growing evidence that it can regulate the response of ecosystem C sequestration to increased CO_2 concentrations, elevated temperature and changed water availability (Oren *et al.*, 2001; Wamelink *et al.*, 2009). Fernández-Martínez *et al.* (2014) recently concluded that nutrient availability was the chief determinant of net ecosystem production (NEP) and ecosystem carbon-use efficiency (CUEe, the ratio of NEP to gross primary production, (GPP)) in global forests.

However, De Vries (2014) seriously concerned that their analysis of global observational datasets can be subject to bias due to the inclusion of outliers (three very young nutrient-rich forests with extremely high NEPs) and assumed linearity in relationships. Using the same datasets retrieved by digitalizing figures from Fernández-Martínez *et al.* (2014), here I have performed statistical analysis regarding the concerns of De Vries (2014) and found that nutrient-rich and nutrient-poor forests have no

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difference in their allocation of GPP to NEP and ecosystems respiration (Re).

The datasets showed a non-linear relationship of NEP against GPP (100~ 3800 g C m^{-2} yr^{-1}) for nutrient-poor forests (Fig. 1a), which indicates that same GPP ranges should be used for nutrient-rich and nutrient-poor forests when comparing their differences. Unfortunately, the datasets of GPP (1000~ 2400 g C m^{-2} yr^{-1}) for the nutrient-rich forests did not cover the whole range for the non-linear curve. In addition, three very young forests (age < 5 years) with extremely high GPP (2000~2400 g C m^{-2} yr^{-1}) and NEP(1100~ 1500 g C m^{-2} yr^{-1}) are actually outliers, because youngest forests commonly have lowest GPPs and NEPs (Odum, 1969; Goulden et al., 2011).

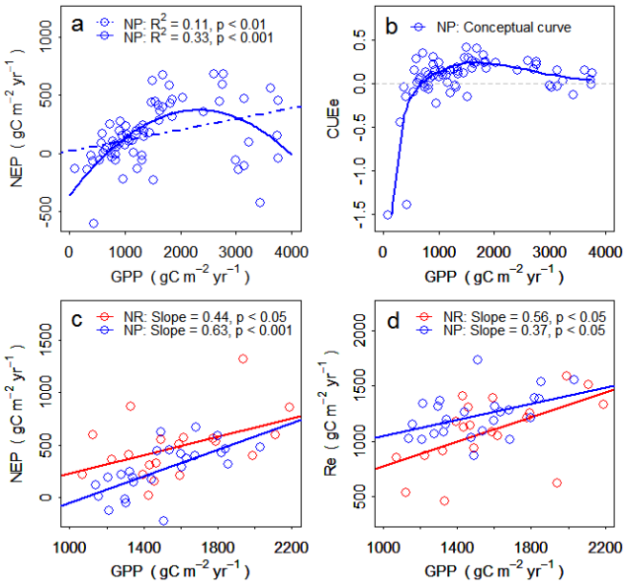

Figure 1. NEP (g C m^{-2} yr^{-1}), CUEe, and Re (g C m^{-2} yr^{-1}) against GPP (g C m^{-2} yr^{-1}) in nutrient-rich (NR) and nutrient-poor (NP) forests. (a) Change in NEP against GPP within whole data range of GPP in nutrient-poor forests, (b) Non-linear conceptual model of the relationship between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

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When excluding the three outliers and using the common GPP ranges (1000 ~ 2200 g C m^{-2} yr^{-1}), NEP and Re both showed significant positive relationship against GPP in either nutrient-rich forests or nutrient-poor forests (Fig 1c and Fig 1d). The slope of NEP against GPP for the nutrient-rich forests (slope = 0.44, $p<0.05$) was not statistically different from that (slope = 0.63, $p < 0.001$) for nutrient-poor forests (COANOVA, $p = 0.49$) (Fig 1c). Accordingly, the slope of Re against GPP for the nutrient-rich forests (slope = 0.56, $p<0.05$) was not significantly different from that (slope = 0.37, $p < 0.05$) for nutrient-poor forests (COANOVA, $p = 0.85$) (Fig 1d). These results indicate that nutrient-poor forests and nutrient-rich forests have no significant difference in their allocation of GPP to NEP and Re.

Moreover, a generalized linear model (GLM) analysis (NEP ~ GPP+ Nutrients + Nutrients*GPP) further 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 1). This further challenges the conclusions of Fernández-Martínez et al. (2014) that nutrient availability is the chief determinant of global forest carbon balance.

Forest ecosystems sequester C both in trees and soil, the sum of which is the NEP. Woody biomass production, with long turnover times, determines the C sequestration by forest trees. Non-woody biomass production, with shorter turnover times, dominates the C inputs to soil and thereby soil C sequestration after a large loss of the C inputs via decomposition. Therefore, higher allocation to woody versus non-woody biomass can lead to higher efficiency of the ecosystem C sequestration and therefore the CUEe. Experimental evidence suggests that nutrient (e.g. N) fertilization can result in larger,

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developmentally advanced trees with allometry inherently different from the allometry of trees grown without nutrient enrichment (Coyle and Coleman, 2005). Therefore, nutrient availability might only accelerate the development of trees without changing their inherent parameters of allometric relationships, resulting in no difference in the allocation of GPP to NEP and Re between nutrient-poor and nutrient-rich forests. Accordingly, no significant effect of nutrient availability on NEP was found when using common GPP range for the nutrient-poor and nutrient-rich forests.

Here, I further propose a non-linear conceptual model of CUEe against GPP (Fig. 1b), which implies the characteristics of C allocation of GPP to NEP in forest ecosystems. Youngest forests commonly show very low GPP and negative CUEe because of higher Re than GPP (Goulden *et al.*, 2011), and then 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). The non-linear model of CUEe against GPP would improve our understanding of forest carbon balance and should be considered in forest carbon cycle modelling.

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