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Global evidence on nitrogen saturation of terrestrial ecosystem net primary productivity

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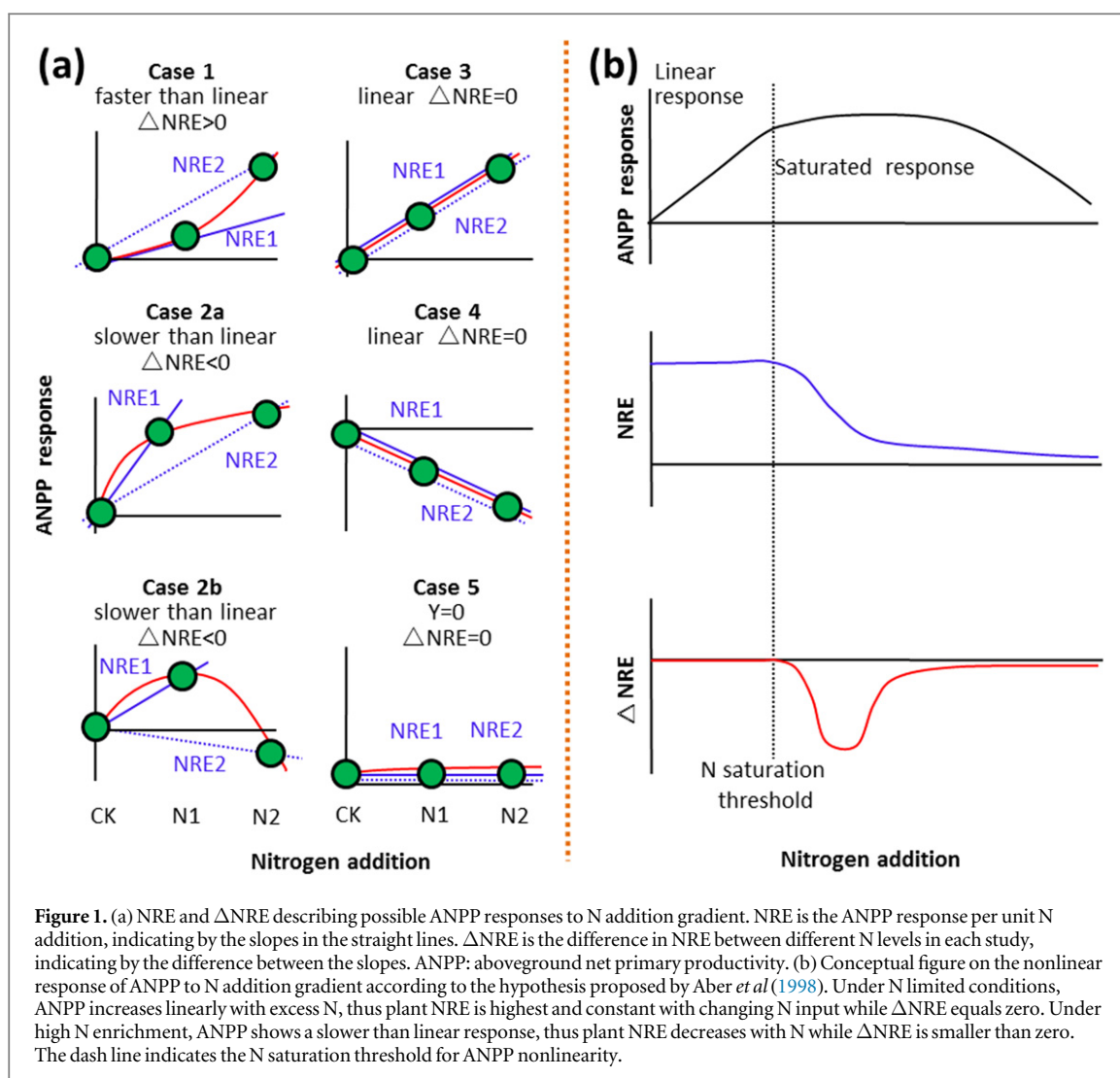
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Abstract

The continually increasing nitrogen (N) deposition is expected to increase ecosystem above-ground net primary production (ANPP) until it exceeds plant N demand, causing a nonlinear response and N saturation for ANPP. However, the nonlinear response of ANPP to N addition gradient and the N saturation threshold have not been comprehensively quantified yet for terrestrial ecosystems. In this study, we compiled a global dataset of 44 experimental studies with at least three levels of N treatment. Nitrogen response efficiency (NRE, ANPP response per unit N addition) and the difference in NRE between N levels (ΔNRE) were quantified to test the nonlinearity in ANPP response. We found a universal response pattern of N saturation for ANPP with N addition gradient across all the studies and in different ecosystems. An averaged N saturation threshold for ANPP nonlinearity was found at the N addition rates of 5–$6\,\mathrm{g\,m^{-2}\,yr^{-1}}$. The extent to which ANPP approaches N saturation varied with ecosystem type, N addition rate and environmental factors. ANPP in grasslands had lower NRE than those in forests and wetlands. Plant NRE decreased with reduced soil C:N ratio, and was the highest at intermediate levels of rainfall and temperature. These findings suggest that ANPP in grassland or the ecosystems with low soil C:N ratio (or low and high rainfall or temperature) is easier to be saturated with N enrichment. Overall, these results indicate that the beneficial effect of N deposition on plant productivity likely diminishes with continuous N enrichment when N loading surpasses the N saturation threshold for ANPP nonlinearity.

Introduction

Plant growth is generally limited by nitrogen (N) in terrestrial ecosystems (Elser *et al* 2007, Lebauer and Treseder 2008), but this limitation has been substantially alleviated by the continuous accumulation of N deposition (Lu *et al* 2011a, Yang *et al* 2012). Cumulative N input has the potential to cause N saturation for plant growth and induce a nonlinear response for aboveground net primary productivity (ANPP). The N saturation for ANPP has been conceptually discussed in previous studies (Aber *et al* 1998, Lovett & Goodale 2011, de Vries *et al* 2014). However, to our knowledge, there has been no global evidence to quantify plant N saturation along N addition gradient in terrestrial ecosystem.

The earliest hypothesis describing N saturation for NPP with N addition was proposed by Aber *et al* (1989) in temperate forests, which was then revised by Aber *et al* (1998). It is hypothesized that under N-limited condition, ANPP increases linearly with additional N at its low rate. When N availability exceeds plant N demand under continuous N enrichment, the increase in ANPP gradually levels off, leading to a nonlinear response (Aber *et al* 1989, Aber *et al* 1998). Even, ANPP shows a declined response under high N enrichment. Thus, this hypothesis implies that there is a saturation threshold of N input

Figure 1. (a) NRE and △NRE describing possible ANPP responses to N addition gradient. NRE is the ANPP response per unit N addition, indicating by the slopes in the straight lines. △NRE is the difference in NRE between different N levels in each study, indicating by the difference between the slopes. ANPP: aboveground net primary productivity. (b) Conceptual figure on the nonlinear response of ANPP to N addition gradient according to the hypothesis proposed by Aber *et al* (1998). Under N limited conditions, ANPP increases linearly with excess N, thus plant NRE is highest and constant with changing N input while △NRE equals zero. Under high N enrichment, ANPP shows a slower than linear response, thus plant NRE decreases with N while △NRE is smaller than zero. The dash line indicates the N saturation threshold for ANPP nonlinearity.

level, beyond which the responses of ANPP become slower than the linear, which indicates the initiation of plant N saturation. However, to our knowledge, this N saturation threshold for plant nonlinearity is not well-quantified yet in terrestrial ecosystems, except a case study conducted in a temperate steppe (Bai *et al* 2010). This will limit our ability to predict the risk of N saturation for terrestrial ecosystems.

Recently, Shcherbak *et al* (2014) proposed a new analysis method to identify the nonlinear response of soil N_2O flux to N fertilization rates. This method indicates that N response efficiency (NRE, ANPP response per unit N addition) (Iversen *et al* 2010) and the difference in NRE (△NRE) between different N addition rates can be used as two effective parameters to detect the nonlinearity in ANPP response to continuous N input. For example, when ANPP shows a linear response under low N availability, plant NRE is highest and does not change with N input while △NRE equals zero (figures 1(a), (b)). In contrast, when ANPP behaves a slower than linear response under high N, plant NRE will decrease with N input while △NRE is lower than zero. Hence, the negative △NRE

indicates a nonlinear response (less than linear), and a lower NRE suggests that plant growth is closer to being saturated with N enrichment. The N addition rate, at which plant response changes from linear to non-linear, is the N saturation threshold for ANPP nonlinearity.

NRE for ANPP may change with ecosystem type or environment factors. This is due to that plant response to N depends not only on the magnitude of N limitation, but also the likely co-limitations of other factors, such as temperature, precipitation and soil P availability (Aber *et al* 1989, Elser *et al* 2007, de Vries *et al* 2014). Plant NRE may decrease with increasing soil N availability due to less N limitation under higher soil N condition (Xia & Wan 2008), which likely makes plant growth closer to being saturated with external N addition. Soil C:N ratio is usually used to indicate relative N limitation (Agren 2008, Lu *et al* 2011b). With decreasing C:N ratio, soil N limitation will be lessened, likely reducing plant NRE. Similarly, an increase in ambient N deposition may also decrease plant NRE. Low soil pH has a potential to promote soil P availability (Galloway *et al* 2008, Stroia *et al* 2011) and

exacerbate N limitation, thus it is expected to increase NRE. Low precipitation and temperature likely limit plant responses to additional N (Del Grosso *et al* 2008, Bai *et al* 2010, Liang *et al* 2015), while high rainfall and temperature promote soil N mineralization (Rustad *et al* 2001, Melillo *et al* 2002, Lu *et al* 2011a). These suggest that low and high rainfall or temperature may result in a decrease in plant NRE. Therefore, we hypothesize that the N saturation threshold for ANPP nonlinearity may change with ecosystem types and environment factors.

In this study, we selected experimental studies with at least three levels of N treatment in terrestrial ecosystems, and compiled a global database (146 observations) of 44 studies that examined ANPP in response to N addition gradient. Using a new analysis method in a recent study (Shcherbak *et al* 2014), we test the N saturation for ANPP by analyzing NRE and ΔNRE in each study. In order to identify which ecosystems or areas are more likely to be saturated with N, we analyzed the variations of plant NRE with ecosystem types and environmental factors. Specifically, we address the following questions: (1) how terrestrial ANPP responds to N addition gradient at the global scale and in different ecosystems, linearly or nonlinearly? (2) If it shows a nonlinear response, what are the N saturation thresholds for ANPP nonlinearity in different ecosystems? (3) how ecosystem type, N addition rate and environmental factors influence the N saturation thresholds?

Methods

Data source

We searched literature on the response of ANPP to N addition that was published in journals included on the Web of Science from 1900 to 2015. Then, the studies used for analysis were selected according to the following criteria. First, the studies must be implemented in terrestrial ecosystems, not including agricultural systems. Second, the experiments include at least two levels of N addition plus a control treatment under the same condition. Third, the means and sample sizes for the response variables are explicitly shown.

To make the experimental studies statistically independent, we only gathered the data for the last time of measurement in each experiment (Liu & Greaver 2010, Lu *et al* 2011b, Lucas *et al* 2011). Furthermore, the data from different ecosystems, N-fertilizer forms and N addition levels in the same study were regarded as independent observations (Liu & Greaver 2009). The data presented in the figure-form was acquired by using the Engauge Digitizer software (Free Software Foundation, Inc., Boston, MA, USA). Finally, a global database (146 observations) was established with 44 independent studies from 33 papers (figure S1 and table S1). The database covers grassland, wetland,

temperate forest, boreal forest and tropical forest with precipitation ranging from 274 to 1650 mm and temperatures ranging from -1.4 to 19.6 °C. The N fertilizer used is in the form of NH_4NO_3, NH_4 and urea. Only one study applied urine in a temperate grassland (Xu *et al* 2015). Furthermore, we also collected the environmental data from the original papers, including soil total N, soil C:N ratio, soil pH, ambient N deposition, annual temperature and precipitation. Due to little data from tropical forest, our analysis did not include this ecosystem type. Thus, the forest ecosystem examined in this study represents temperate and boreal forest (most data are from temperate forest).

Meta-data analysis

In our analysis, we followed a new method in a recent study (Shcherbak *et al* 2014). Specifically, we first calculated nitrogen response efficiency (NRE), ANPP response per unit N addition, as follows: $100\% \times (ANPP_{treatment} - ANPP_{control})/ANPP_{control}/$ N addition amount. Then, ΔNRE was calculated as the difference between two close N rates in each study as follows: $(NRE2 - NRE1)/(N rate2 - N rate1)$. If there are three levels of N addition, two ΔNRE were respectively calculated by the difference in NRE between low and medium N levels and between medium and high N levels, and so on, for more than three N addition rates. If plant NRE2 is larger than NRE1 and the corresponding ΔNRE is positive, ANPP display a faster than linear response (case 1 in figure 1(a)). When plant NRE2 is smaller than NRE1 and the corresponding ΔNRE is negative, plants display a slower than linear response (case 2a in figure 1(a)). Notably, NRE2 may be negative (case 2b in figure 1(a)). In the case that plant NRE2 equals NRE1 and the corresponding ΔNRE is zero, three are three different cases as follows. First, if NRE1 and NRE2 are positive, plants show a linear response (case 3 in figure 1(a)). Second, if they are negative, plants behave a declined response (case 4 in figure 1(a)). Third, if they are zero, plants display no response (case 5 in figure 1(a)). However, the latter two cases do not exist in our dataset, thus ΔNRE equaling zero indicates a linear response in this study. Moreover, according to the hypothesis of Aber *et al* (1998), plant NRE is highest and constant with N input under N limited condition but decreases with continuous N enrichment after the initiation of N saturation. It is thus expected that the N saturation threshold for NPP nonlinearity occurs at the point that further N addition starts to decrease NRE (figure 1(b)). Similarly, plant ΔNRE is zero at the stage of linear N response but becomes negative at the stage of nonlinear N response (figure 1(b)). Therefore, the N saturation threshold for ANPP nonlinearity is also indicated when ΔNRE changes from zero to negative value.

Data were analyzed with the SPSS 21.0 software. First, we examined the distributions of NRE and ΔNRE and found they were not normally distributed ($p < 0.001$). Thus, we used a nonparametric analysis of bootstrap resampling (repeated $n = 5000$ times) to determine the means of NRE and ΔNRE and their 95% confidence internal (CI) at the global scale, across different ecosystem types (forest, grassland and wetland) and different ranges of N addition rates. Second, a bootstrapped t-test (repeated $n = 5000$ times) was conducted to compare the differences in NRE among ecosystem types or N addition rates (Shcherbak *et al* 2014). Third, to assess how environmental factors affect the N saturation threshold for ANPP nonlinearity, we employed a linear, logarithmic or quadratic function to analyze the relationships of plant NRE with soil total N, soil C:N ratio, ambient N deposition, soil pH, annual rainfall or temperature. In addition, when comparing the differences in NRE between different ecosystems, we only selected the data for the N addition rates of 4 to 22 g m^{-2} yr^{-1}, in order to ensure that the N addition amount was as consistent as possible among different ecosystems. The mean N addition rates were 11.06 g m^{-2} yr^{-1} for grasslands, 10.76 g m^{-2} yr^{-1} for forests and 12.36 g m^{-2} yr^{-1} for wetlands.

Results

Across all the studies at the global scale or in different ecosystems, our results consistently showed that ΔNRE was significantly lower than zero (figure 2). For plant NRE, it was relatively larger in wetlands (4.59% g^{-1} N) than in forests (3.75% g^{-1} N) and grasslands (2.94% g^{-1} N), although the differences between them were not significantly different.

N addition rate impacted plant NRE and ΔNRE. With the increase of N addition rate, plant NRE decreased quickly (figure 3). But, only when N inputs were greater than 6 g m^{-2} yr^{-1}, the reduction in NRE was statistically significant. Moreover, ΔNRE were also found to be significantly negative when N addition rates were larger than 5 g m^{-2} yr^{-1}, while they were not significantly different from zero below this N input level.
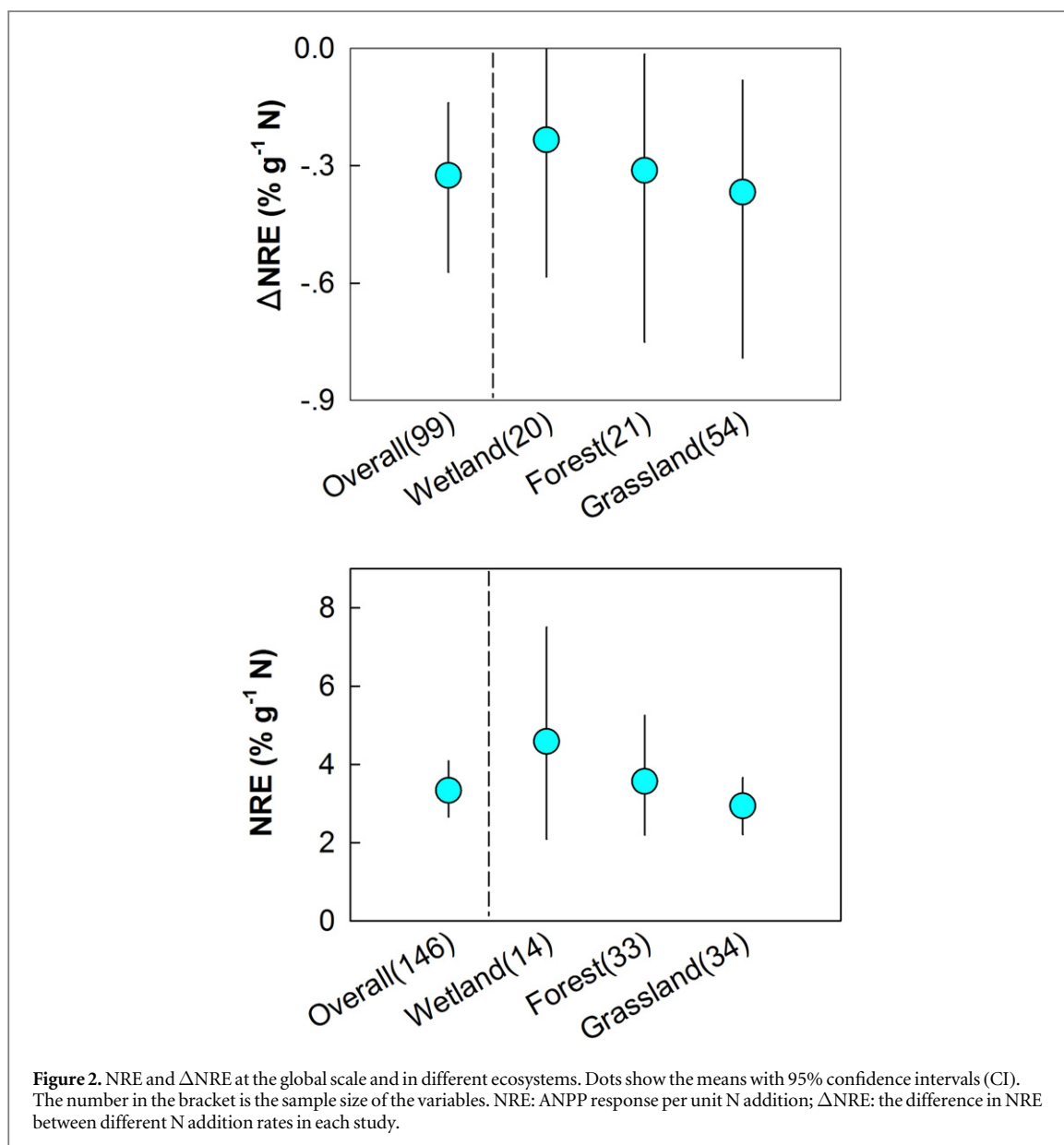
Plant NRE also changed with environmental factors. With increasing soil total N, plant NRE decreased significantly (figure 4(a)). In contrast, plant NRE increased linearly with soil C:N ratio (figure 4(b)). Changes in ambient N deposition did not have significant relationship with plant NRE (figure 4(c)). The reduction in soil pH enhanced plant NRE significantly (figure 4(d)). When precipitation was lower than 800 mm, plant NRE increased linearly with increasing precipitation, but decreased quickly with rainfall above 1100 mm (figure 4(e)). At about a temperature of 8 °C, plant NRE was highest, whereas it decreased with lower or higher temperatures (figure 4(f)).

Discussion

Nonlinear responses of ANPP with N addition gradient

Our results demonstrated that ΔNRE were significantly lower than zero at the global scale and in different ecosystems. The pattern detected using ΔNRE unequivocally indicates a nonlinear response of ANPP to continuous N enrichment. Although this nonlinearity in plant response to continuous N input is widely anticipated (Aber *et al* 1998, Burkett *et al* 2005, Arens *et al* 2008, de Vries *et al* 2014), our study is among the first to provide a global experiment evidence on the N saturation for ANPP across different terrestrial ecosystems. The result was supported by the decreased response of plant NRE with increasing N addition rates. These suggest that the beneficial effects of N deposition on plant productivity likely diminish with high continuous N enrichment in the future. Moreover, the excess N that can't be absorbed by plants will cause serious environmental problems, such as N leaching, N$_2$O emission and soil acidification (Lu *et al* 2011a, Shcherbak *et al* 2014, Tian & Niu 2015).
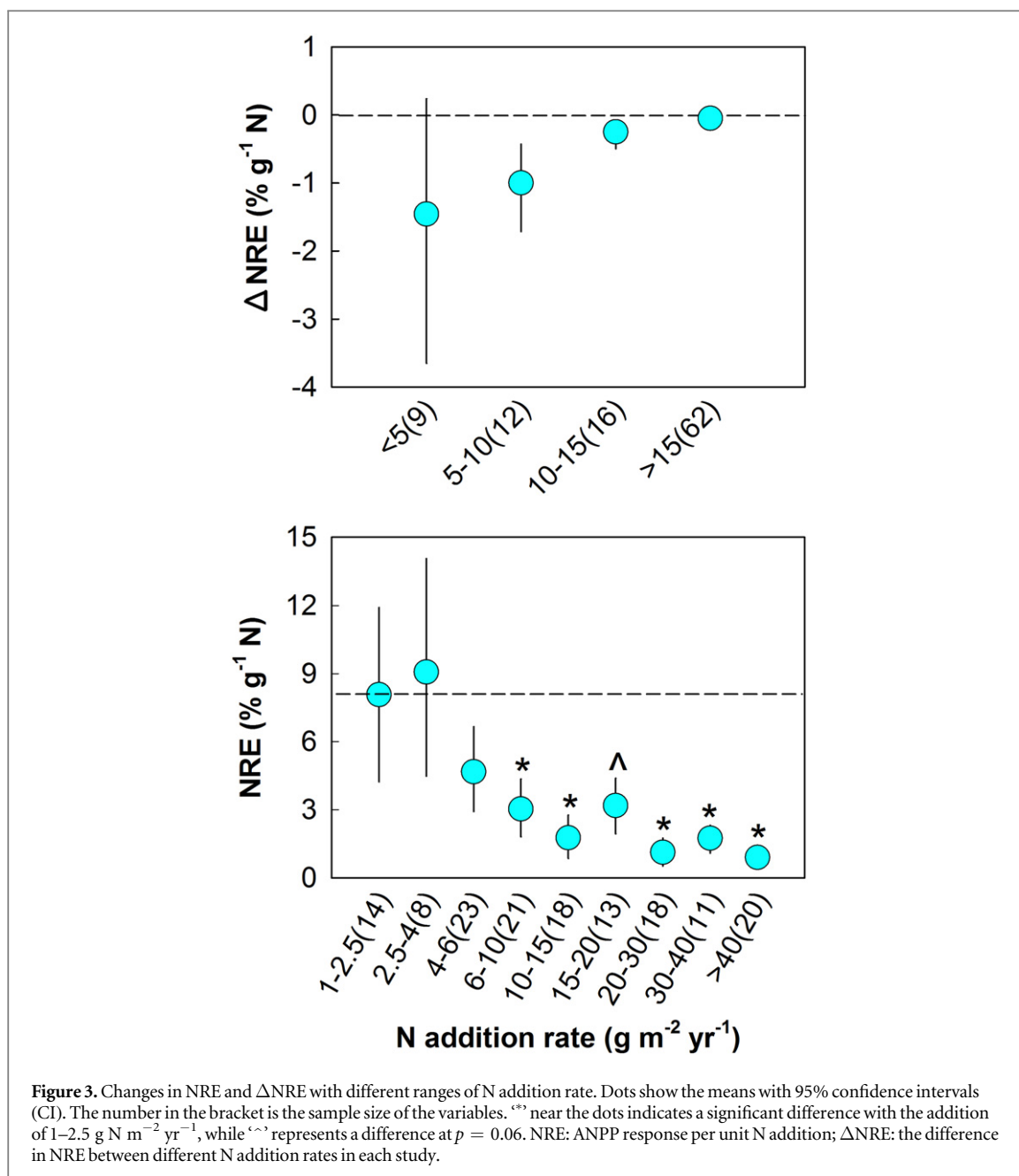
However, different ecosystems may have different patterns of N saturation. Plant NRE was 28% larger in forests than in grasslands, suggesting that grassland ANPP reaches a level to be less responsive to (or more easily saturated with) N addition than forest ANPP (most data from temperate forest). The difference in the responsiveness between these two ecosystems may be related to the environment factors. For example, grasslands have lower soil C:N ratio (12.47) than that (24.07) of forests, while low C:N ratio is associated with decreased plant NRE as indicated by our results (figure 4(b)). Furthermore, less rainfall (462 mm) in grasslands than that (858 mm) in forests also contributes to the decreased response in plant NRE (figure 4(e)). Wetlands had the highest plant NRE (56% larger than in grasslands), likely because this ecosystem generally has very low soil N availability with a high soil C:N ratio (Bragazza *et al* 2006, Min *et al* 2011, Song *et al* 2013, Zhang *et al* 2013). This result is partly supported by a previous study which revealed that soil acidification and NO$_3^-$ leaching (indicating ecosystem N saturation) in wetland ecosystems is less sensitive to N enrichment than in grasslands (Phoenix *et al* 2012). Although our analysis does not include tropical forest (due to the little data), ANPP in this forest ecosystem should be easier to be saturated with N, because it usually has a low soil C:N ratio with a very high rainfall and temperature (Lu *et al* 2011a, 2011b). Overall, this synthesis reveals an universal response pattern of N saturation for ANPP along N addition gradient in terrestrial ecosystems. The findings indicate that plant production in terrestrial ecosystems may have diminishing responses to cumulative N loading through deposition.

Figure 2. NRE and ∆NRE at the global scale and in different ecosystems. Dots show the means with 95% confidence intervals (CI). The number in the bracket is the sample size of the variables. NRE: ANPP response per unit N addition; ∆NRE: the difference in NRE between different N addition rates in each study.

Nitrogen saturation threshold for ANPP

Our results indicate that there exists a N saturation threshold (5–6 g m^{-2} yr^{-1}) for ANPP nonlinear response to N gradient. Three parallel lines of evidence all support this point. First, we found that ∆NRE were not significantly different from zero, which indicates a linear response for ANPP, when N additions were less than 5 g N m^{-2} yr^{-1}. But, above this N level, the ∆NRE was smaller than zero, implying a nonlinear response. It is thus expected that a threshold level of N addition for plant nonlinear response is around 5 g N m^{-2} yr^{-1}. Second, our results showed that there was no significant reduction in plant NRE until N inputs were above 6 g N m^{-2} yr^{-1}. This suggests that the threshold level of N input is around 6 g N m^{-2} yr^{-1}. Third, ambient N deposition (mostly below 2 g m^{-2} yr^{-1}) did not significantly reduce plant NRE (figure 4(c)), likely implying that the N saturation threshold should be above 2 g N m^{-2} yr^{-1}. Based on

all these lines of evidence, we conclude that the N saturation threshold for ANPP nonlinearity is between 5–6 g N m^{-2} yr^{-1}. Furthermore, we also analyzed the relationships of NRE with total N load (background N deposition + experimental N addition). The result showed that the N saturation threshold was around 6 g N m^{-2} yr^{-1} (figure S3), which is similar with the result above (5–6 g N m^{-2} yr^{-1}) calculated by experimental N addition alone. Our conclusion is supported by a recent literature review (de Vries *et al* 2014), which suggests that a threshold level at which forest ecosystem begins to saturate with N should be between 2 and 5 g N m^{-2} yr^{-1}. Furthermore, our result is also in accordance with the findings that critical N deposition loads at 1–5 g m^{-2} yr^{-1} can induce soil NO$_3^-$ leaching and increasing nitrification in terrestrial ecosystems of Europe and North American (Bobbink & Roelofs 1995, Bobbink *et al* 2010, Pardo *et al* 2011) and N addition causes soil acidification at 5 g m^{-2} yr^{-1} on average

Figure 3. Changes in NRE and ΔNRE with different ranges of N addition rate. Dots show the means with 95% confidence intervals (CI). The number in the bracket is the sample size of the variables. '*' near the dots indicates a significant difference with the addition of 1–2.5 g N m^{-2} yr^{-1}, while '^' represents a difference at $p = 0.06$. NRE: ANPP response per unit N addition; ΔNRE: the difference in NRE between different N addition rates in each study.
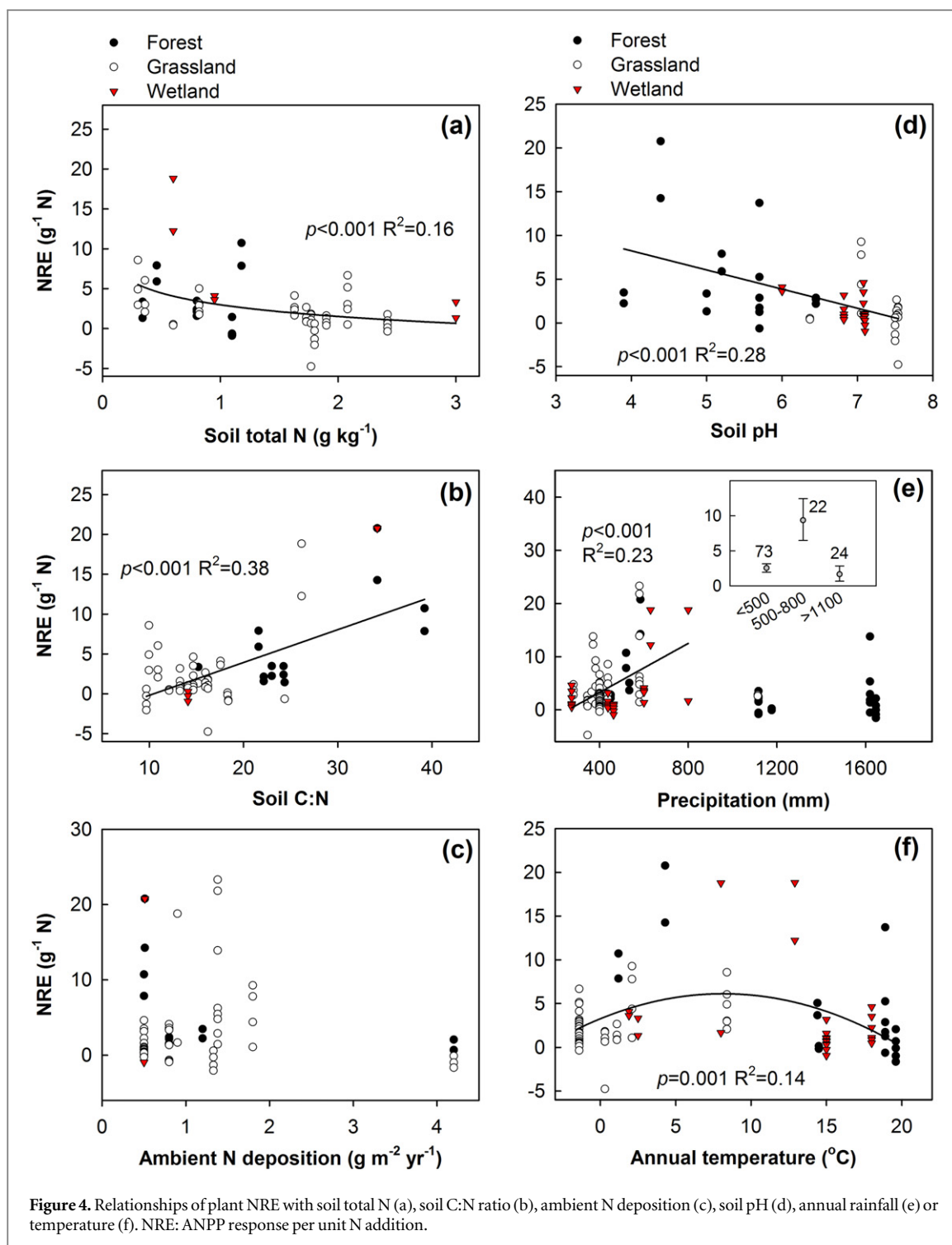
across all the terrestrial ecosystems (Tian & Niu 2015). As documented by a previous study (Penuelas *et al* 2013), most terrestrial ecosystems have received an accumulation of 2–5 g m^{-2} ambient N deposition from 2000–2010, which suggests that ANPP response in global terrestrial ecosystems may face the risk of N saturation in the near future.

Effects of environmental factors
This synthesis across all the experiments showed that NRE is influenced by soil and climate factors (figure 4). Consistent with our expectation, plant NRE declined with increasing soil total N content due to less N limitation (Lebauer and Treseder 2008). Thus, ANPP in ecosystems with high soil N likely has a lower N saturation threshold for additional N input, making it easier to be saturated with N enrichment. However, we

found that an increase in ambient N deposition did not significantly reduce plant NRE, likely because the current deposition rates (mostly below 2 g N m^{-2} yr^{-1}) do not surpass the N saturation threshold for ANPP (5-6 g N m^{-2} yr^{-1}). Moreover, our results revealed that soil C:N ratio was a powerful predictor of plant NRE ($R^2 = 0.38$). Plant NRE reduced linearly with the decreasing soil C:N ratio. As a consequence, the ecosystems with low soil C:N ratio are more likely to be saturated with N addition. Additionally, there was no significant relationship of soil C:N ratio with precipitation or annual temperature (figure S4). Thus, we suggest soil C:N ratio is an important parameter to be considered by global-C cycle model when evaluating the contribution of N deposition to plant productivity. As we expected, the decrease in soil pH enhanced plant NRE. This may be

Figure 4. Relationships of plant NRE with soil total N (a), soil C:N ratio (b), ambient N deposition (c), soil pH (d), annual rainfall (e) or temperature (f). NRE: ANPP response per unit N addition.

due to that low soil pH benefits soil P availability (Fujita *et al* 2010, Stevens *et al* 2010), further intensifying soil N limitation.

Besides soil variables, climate factors also influence NRE. When precipitation increased from 270 to 800 mm, plant NRE increased linearly, while it declined quickly with rainfall above 1100 mm. This implies that plant NRE should be highest at the rainfall of 800–1100 mm. Similarly, plant NRE was largest at 8 °C temperature, while it reduced with lower or

higher temperature. These are mainly due to that either cold or dry environments likely limit ANPP responses to additional N (Williams *et al* 1996, Curtis *et al* 2005, Del Grosso *et al* 2008, Bai *et al* 2010), while warm or wet conditions facilitate soil N mineralization (Rustad *et al* 2001, Lu *et al* 2011a). Furthermore, our result is similar with a previous study showed that *Sphagnum* production is more likely to be saturated with N deposition under warm and wet environments (Limpens *et al* 2011). These results suggest that

ecosystems with low and high rainfall or temperature have a lower N saturation threshold than those with medial rainfall and temperature.

The surrogates of N addition experiment for N deposition

Nitrogen addition experiments may not completely mimic N deposition in the real world. They differ in the amount, frequency, duration and chemical composition of added N. However, knowledge gained from this synthesis of N addition experiments offers insights into the responses of terrestrial ANPP to N gradient at least in the following three aspects. First, the accumulation of N deposition in most terrestrial ecosystems is already high (Penuelas *et al* 2013) and will eventually lead to plant N saturation as N deposition continues. However, it is difficult to detect the N saturation with N deposition from natural observations. Accumulation of ambient N deposition needs a long term to form a gradient of N amount. Even if a gradient is formed, there are confounding impacts of long-term ecosystem changes. A transect of natural N deposition at a spatial scale also have confounding factors of climate, soil properties and vegetation changes. In comparing with those natural N deposition gradients, multiple levels of N addition by manipulative experiment offer better opportunity to explore plant N saturation along N gradient. Second, through comparing the effects between different N fertilizer forms or application frequencies on plant NRE, we found that N addition frequency did not significantly change plant NRE (figure S2). The effects of fertilizer NH_4NO_3 and NH_4-form were not significantly different with each other, either. These suggest that N fertilizer form and applied frequency may have limited effects on the nonlinearity in plant responses to N addition, although they had a significant impact on other ecosystem properties, such as species diversity and soil carbon process (Du *et al* 2014, Zhang *et al* 2014). Third, the mean experimental duration in this meta-analysis is about five years. Though this time length is not as long as the duration of ambient deposition, it is relatively long to cause plant response. Overall, all these above indicate that N addition experiments should be a reasonable surrogate for ambient N deposition to examine plant nonlinear response.

Conclusion

Building upon the widely accepted concept of N saturation (Aber *et al* 1989, Aber *et al* 1998), we quantitatively detected the N saturation for ANPP with N addition gradients from 44 studies. We used a recently published method that calculates nitrogen response efficiency (NRE) and its changes from ANPP at three or more levels of N treatments as criteria of nonlinearity (Shcherbak *et al* 2014). This study provides a global evidence on the N saturation of ANPP along N addition gradient. We found an N saturation threshold of 5–6 g m^{-2} yr^{-1}, at which ANPP responses shift from linear to nonlinear phases as N addition rates increase across all the terrestrial ecosystems. This indicates that the contribution of N deposition on plant productivity will diminish with continuous N accumulation once the N inputs surpass the N saturation threshold in the future. The nonlinear response patterns change with ecosystem type, N addition rate and environmental factors like temperature, precipitation, soil N content, C:N ratios and soil pH. The patterns and relationships revealed in this synthesis could be used to benchmark global C-cycle models when examining the impacts of N deposition on plant-driven carbon sequestration. Future experimental studies with more N input levels are crucial to explore the mechanisms underlying the N saturation of ecosystem C cycle.

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