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Dynamic carbon-nitrogen coupling under global change

Shuli Niu^{1,2*}, Lei Song^{1,2}, Jinsong Wang¹, Yiqi Luo³ & Guirui Yu^{1,2}

¹Key Laboratory of Ecosystem Network Observation and Modelling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China;

²College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China;

³Center for Ecosystem Science and Society, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA

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Carbon-nitrogen coupling is a fundamental principle in ecosystem ecology. However, how the coupling responds to global change has not yet been examined. Through a comprehensive and systematic literature review, we assessed how the dynamics of carbon processes change with increasing nitrogen input and how nitrogen processes change with increasing carbon input under global change. Our review shows that nitrogen input to the ecosystem mostly stimulates plant primary productivity but inconsistently decreases microbial activities or increases soil carbon sequestration, with nitrogen leaching and nitrogenous gas emission rapidly increasing. Nitrogen fixation increases and nitrogen leaching decreases to improve soil nitrogen availability and support plant growth and ecosystem carbon sequestration under elevated CO₂ and temperature or along ecosystem succession. We conclude that soil nitrogen cycle processes continually adjust to change in response to either overload under nitrogen addition or deficiency under CO₂ enrichment and ecosystem succession to couple with carbon cycling. Indeed, processes of both carbon and nitrogen cycles continually adjust under global change, leading to dynamic coupling in carbon and nitrogen cycles. The dynamic coupling framework reconciles previous debates on the “uncoupling” or “decoupling” of ecosystem carbon and nitrogen cycles under global change. Ecosystem models failing to simulate these dynamic adjustments cannot simulate carbon-nitrogen coupling nor predict ecosystem carbon sequestration well.

nitrogen limitation, carbon-nitrogen interaction, global change, carbon sequestration, soil nitrogen cycle

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Introduction

Nitrogen (N) is a life-supporting element in the earth system. It controls plant primary productivity, influences ecosystem carbon (C) sequestration, and regulates climate change (Fernández-Martínez et al., 2014; Hungate et al., 2003; Kicklighter et al., 2019). Nitrogen affects those processes mainly via its influence on C metabolism through processes such as photosynthesis, growth, and decomposition. Thus, how C and N cycles interact or couple with each other is crucial to predicting future

changes in plant production, ecosystem C sequestration, and climate.

One of the commonly held concepts about C-N coupling is the N limitation. The concept was originally established for plant productivity as plant growth generally increases with N availability either through N inputs or along natural gradients (Vitousek and Howarth, 1991). The N limitation of net primary productivity (NPP) has been widely observed from N addition experiments (LeBauer and Treseder, 2008). Once this N limitation of NPP is incorporated into C cycle models, simulated responses of global terrestrial C uptake to increasing CO₂ usually decrease (Goll et al., 2012). The inclusion of the N cycle in the land

*Corresponding author (email: sniu@igsnr.ac.cn)

models also dampens the net land C exchange in response to temperature and precipitation variation (Piao et al., 2013; Thornton et al., 2007). Those C-N coupled models simulate C sequestration with an assumption that N input drives the C cycle in a whole ecosystem. This assumption largely ignores microbial response and regulation (Wieder et al., 2013) and results in a poor agreement between modeled and observed C sequestration (Todd-Brown et al., 2013).

The soil N availability itself is highly dynamic in response to environmental change; long-term records especially demonstrate that N availability is declining in many regions of the world (Mason et al., 2022). For example, N leaching and gas emission usually increase soon after exotic N input (Fang et al., 2011; Niu et al., 2016), resulting in a temporal decrease in soil N availability. In contrast, soil N mineralization may persistently increase for years resulting in an increase in N availability and thus alleviating N limitation of plant growth under elevated CO₂ (Sun et al., 2018; Wu et al., 2020). As both C and N cycles have temporal dynamics, their coupling may shift if N processes do not synchronically change with the C cycle or vice versa. This shift in their coupling has recently been called “uncoupling”, “decoupling”, “imbalance”, or “unbalance” between C and N cycles in previous studies (Asner et al., 1997; Peñuelas et al., 2020; Peñuelas et al., 2012). These terms, such as “uncoupling” or “decoupling”, generally reflect changes in C and N stoichiometric relationships, shifted allocation in different pools, and altered relative amounts resulting from asynchrony in adjustment in C and N cycles. Thus, it is important to examine how the coupling of C and N processes dynamically adjusts in response to various global change factors.

This review aims to comprehensively evaluate dynamic C-N coupling by reviewing the responses of C processes to N overload and the responses of N processes to changes in C input under CO₂ enrichment and ecosystem succession or other regulatory environmental changes. Specifically, we addressed two questions in this study: (i) how do C processes dynamically change under N loading to shift their coupling? (ii) How do various N processes adjust their balance with changes in the C cycle under global change? To address these two questions, we reviewed the results of previously published studies. Our synthesis relies on results from studies of natural ecosystems and many meta-analyses, representing general patterns in C and N responses among different studies across ecosystems. We also examined how the coupling of C and N cycles shifts under global change, under which we reconcile recent new terms in the literature, such as “decoupling” and “uncoupling” between C and N cycles. Finally, we proposed future studies focusing on testing and applying dynamic C-N coupling in global change.

Dynamic changes of C processes with increasing N availability

Lots of N addition experiments, e.g., Nutrient Network, NITREX, NIPHYS and NitroEurope, have been conducted in the past three decades to investigate how N influences C cycling and associated ecosystem functions. We mainly reviewed three processes, plant growth and biomass accumulation, microbial biomass and decomposition, and soil C sequestration and net ecosystem exchange, to examine how different C processes change to dynamically couple with increasing N loading. Those processes represent key components of the terrestrial C cycle.

Pervasive increase of plant growth and biomass accumulation

There is ample evidence to support the notion that plant growth and NPP are pervasively increased in terrestrial ecosystems (Elser et al., 2007; Fay et al., 2015; Harpole et al., 2011; Vitousek and Howarth, 1991; Yang et al., 2022). This notion develops from three lines of evidence, namely, N addition experiments, N gradient observations, and stoichiometric ratios.

Hundreds of N addition experiments have shown increases in NPP under N addition (Figure 1). By synthesizing 257 experimental studies, Lu et al. (2011) showed an average increase of 35.7% in above-ground plant biomass. Another meta-analysis of 126 N addition experiments showed that N limitation constrains productivity in most ecosystems, although the degree of limitation varies with biomes over geographical regions (LeBauer and Treseder, 2008). However, with the continually increasing N input, the increase of NPP and plant N uptake will eventually plateau and perhaps even decline at high levels of N loading, forming a nonlinear response (Aber et al., 1998; Niu et al., 2016; Tian et al., 2016a; Tian et al., 2016b). These findings from N addition experiments advance our understanding of C-N coupling and indicate that N limitation on plant growth is pervasive.

In addition to experimental evidence, observations of NPP over large spatial scales indicate a strong coupling between NPP and N availability. In temperate forests in Western Europe and North America, NPP was higher at sites with more N deposition along a gradient of N deposition than at sites with less N deposition (Magnani et al., 2007). Other studies also suggest that ambient rates of N deposition likely increase forest growth (de Vries et al., 2008; Fang et al., 2014; Sutton et al., 2008). These observations are supported further by the results of temporal changes in N deposition and their consequences on NPP. Tree diameter measurements from 1984 to 2004 along an ambient N deposition gradient in the Adirondack Park, USA, indicate that N deposition leads to an increase in woody biomass, especially for the smaller

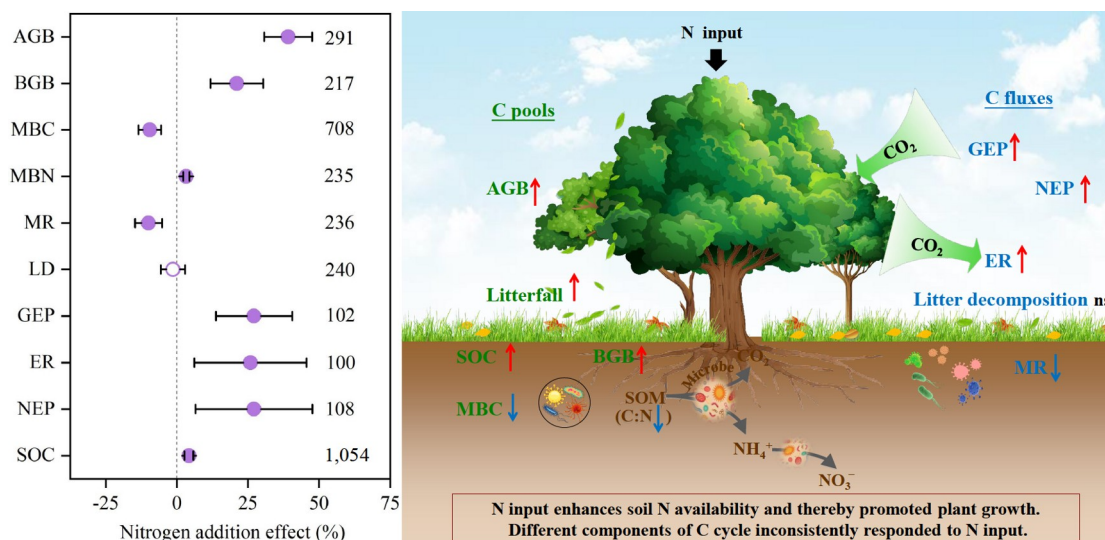


Figure 1 Conceptual diagram depicting the effects of N addition on C pools and fluxes. AGB, above-ground biomass; BGB, below-ground biomass; MBC, microbial biomass C; GEP, gross ecosystem productivity; ER, ecosystem respiration; MR, microbial respiration; SOC, soil organic C; SOM, soil organic matter. The red arrow indicates an increase, whereas the blue arrow indicates a decrease. ns means non-significant change. Numbers indicate the number of observations. We used the global meta-analysis dataset in Zhou et al. (2017), Zhang et al. (2018b), and Xu et al. (2021) to summarize the influence of N enrichment on ecosystem C cycling processes.

size groups of several species (Bedison and McNeil, 2009; Ibáñez et al., 2018).

Another approach to studying C-N coupling is based on stoichiometry, which provides valuable insights into potential element constraints of plant growth and activity. Nitrogen inputs always increase NPP and decrease C:N ratios substantially (Yang et al., 2011). The low C:N ratios and very high N:P ratios in lowland tropical forests suggest that N generally is less limiting in such systems. In contrast, tropical montane forests could be limited by N, as indicated by their higher C:N ratios (Cleveland et al., 2011).

Overall, the accumulated evidence from multiple studies over decades suggests that terrestrial plant C uptake and ecosystem NPP generally increase with increasing N availability (Figure 1), although there may be considerable heterogeneity in magnitude across ecosystems.

Decrease in soil microbial biomass and respiration under N enrichment

In coupling with increasing N availability, microbes do not have to decompose organic matter to obtain N. So, both microbial biomass C and respiration show significantly negative responses to N addition across experiments conducted in the world (Figure 1). A previous global meta-analysis also reported a 15% decrease in microbial biomass (Treseder, 2008). The microbial composition, such as fungi/bacteria ratio and gram-negative/gram-positive bacteria ratio, is impeded by N enrichment as well (Janssens et al., 2010; Zhang et al., 2018a). Those changes in microbial biomass and composition lead to lower microbial respiration, hindering the decomposition of soil organic matter (Zhang et al.,

2018a). A meta-analysis across litter decomposition experiments showed no significant response of microbial decomposition to N addition (Knorr et al., 2005). In regions with high N deposition, microbial decomposition rates either decrease or have no clear response. In contrast, other studies suggest that microbes are N-limited in natural soils where low soil N availability reduces microbial respiration (Hu et al., 2001). The apparent contradiction between the two perspectives can be reconciled by considering that the maximal rate of microbial decomposition only requires relatively little N to maintain (Schimel and Weintraub, 2003).

Microbes can mine N from the soil. Low N availability can increase litter decomposition because microbes usually use labile C substrates to acquire N from recalcitrant organic matter, which is called “microbial N mining” (Chen et al., 2014; Craine et al., 2007; Meyer et al., 2017; Moorhead and Sinsabaugh, 2006). Increasing mineral N input makes microbes reduce their breakdown of organic material to acquire N (Craine et al., 2007; Wild et al., 2019), leading to a reduction in microbial activity with the addition of N (Hartman and Richardson, 2013). Additionally, besides the higher availability of N, the increased mineral N input also results in soil acidification and accumulation of toxic metals, which hinders microbial growth and activity (Tian and Niu, 2015; Treseder, 2008).

Increase of soil C sequestration to long-term N enrichment

Nitrogen is thought to be a key parameter in regulating terrestrial C sequestration. It can be predicted that progressive N limitation would increasingly constrain C sequestration if the ecosystem N capital does not change over time (Luo et

al., 2004). However, N addition experiments show that net ecosystem C sequestration inconsistently responds to N enrichment, with either positive (Niu et al., 2010), negative (Bubier et al., 2007), or no change (Metcalf et al., 2013; Xing et al., 2022). Previous global synthesis studies also demonstrated that adding N into the ecosystem does not necessarily lead to increases in C sequestration in many N addition experiments (Crowther et al., 2019; Lu et al., 2011). In fact, some studies even revealed a decrease in soil C under N addition (Bubier et al., 2007; Mack et al., 2004). Nevertheless, a recent synthesis study including more observations on long-term N addition treatment reported an average of 4% increase in soil organic C under N addition globally (Xu et al., 2021). This implies that a detectable C sequestration under N addition requires a gradual accumulation over a long period.

Consistent with the increase in soil C storage, our recent global synthesis study also revealed an increase in net ecosystem productivity (NEP) under N enrichment (Figure 1). Although both ecosystem C uptake and release are stimulated by N addition, the increase in gross ecosystem productivity is relatively larger than that of ecosystem respiration, which leads to the increased NEP. This also contributed to the net accumulation of soil C pool over time.

Dynamic N processes and availability under global change

Section 2 examined how ecosystem C cycling changes to couple with changing N availability. This section examines how N processes can adjust to influence the dynamics of soil N availability in response to global change factors. Understanding the dynamics of soil N availability is crucial for evaluating C-N coupling.

Nitrogen leaching

Although plant N uptake increases under N enrichment, most of the added N can be rapidly lost through leaching within a few days (Hall and Matson, 1999; Niu et al., 2016). For example, in European forests, it was documented that when N deposition was above 25 kg N ha⁻¹ yr⁻¹, significant leaching occurred at all 65 surveyed sites (Dise and Wright, 1995). The slope of N input via deposition and N leaching was about 0.45 (Figure 2), indicating that almost half of N input leaches out from the ecosystem. It appears from the curvature of the leaching-deposition relationship that the leaching rate is much higher at high N input levels than at low N input levels (Figure 2A). Similarly, leaching from 69 forest ecosystems at 50 sites throughout China also shows that on average 32% of the throughfall dissolved inorganic N input leaches out (Figure 2B) (Fang et al., 2011).

A recent study in global forest ecosystems detected a saturation response of photosynthetic rate and large increases in N leaching once N deposition exceeded approximately 8 kg N ha⁻¹ yr⁻¹ (Fleischer et al., 2013). Nitrate leaching from the catchments varied between 2.8 and 100 kg N ha⁻¹ yr⁻¹ in Finland forests (Kortelainen et al., 1997) and from 0 to 85 kg N ha⁻¹ yr⁻¹ in German forests (Kiese et al., 2011). Using a mass balance approach, our global meta-analysis found that more than half of the added N is lost from the ecosystem, whereas the rest goes to above-ground plant N pool (~9%), litter N pool, and below-ground plant N pool (2%) and soil total N pool (25%) (Niu et al., 2016). The continually increasing N inputs to ecosystems lead to great N losses at the global scale (Braakhekke et al., 2017; Cheng et al., 2020). The great loss of the added N is a key mechanism that leads to a quick decrease of soil inorganic N concentrations to ambient levels within two years after cessation of a 12-year continuous addition of N (O'Sullivan et al., 2011).

On the other hand, elevated CO₂ levels result in decreased

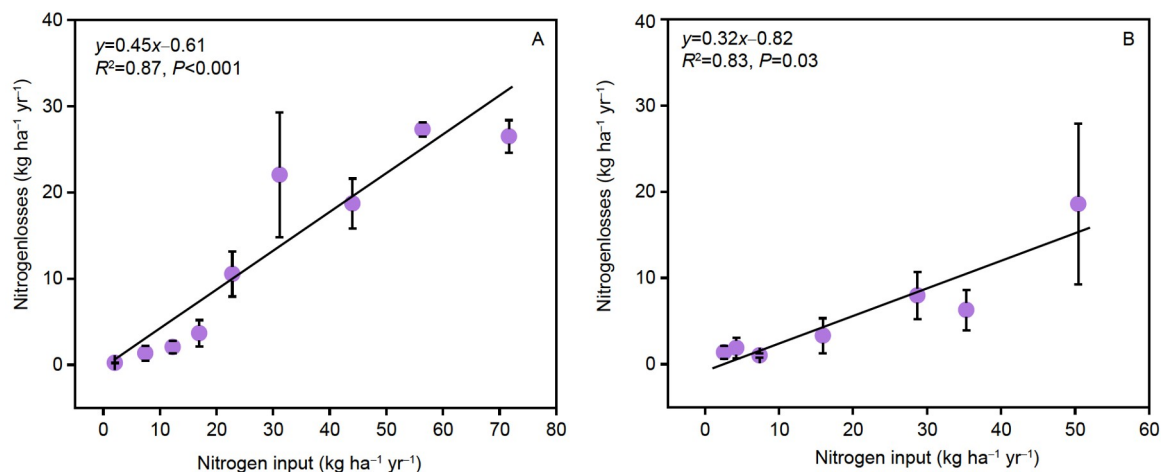


Figure 2 Nitrogen losses versus N input across 65 forested plots and catchments in Europe (A) (Date from Dise and Wright, 1995) and across 21 forest ecosystems in China (B) (Adopted from Fang et al., 2011).

N leaching (Figure 3A, Liang et al., 2016), primarily due to the increased plant N uptake and N sequestration in plant and soil pools (Finzi et al., 2006; Norby et al., 2010). Nitrogen leaching under climate warming is more uncertain (Figure 3B). Warming commonly stimulates leaching due to the increased N mineralization (Rustad et al., 2001). But no response of leaching to warming was reported from an experiment in four European shrubland ecosystems due to small changes in N mineralization under water limitation (Beier et al., 2008). Warming could also decrease leaching due to increased N uptake by vegetation in arable land in Denmark (Patil et al., 2010). Increased precipitation usually results in increases in N leaching due to the increased runoff (Braakhekke et al., 2017; Lewis et al., 1999). Therefore, soil N leaching can rapidly adjust to influence soil N availability and ecosystem C cycle under environmental change.

Nitrogenous gas emissions

N₂O emission exponentially increases with the amount of N deposition as N deposition provides an abundant substrate for N₂O production (Cheng et al., 2016; Shcherbak et al., 2014). High N₂O emission usually happens within days after N input into the soil (Hall and Matson, 1999). As time goes on, the higher nitrifier and denitrifier abundances after N input also contribute to the increased N₂O emission (Lour-enço et al., 2018). Although elevated CO₂ and warming may result in increased N₂O emission (Li et al., 2020a), it occurs only in N-fertilized ecosystems but not in unfertilized ecosystems (Figure 3, Liang et al., 2016). A recent meta-analysis showed that N₂O emission was not affected by elevated CO₂ with reduced soil inorganic N (Liu et al., 2018). This may be due to the deficient available N under elevated CO₂ could constrain the growth of microbes, especially for the group

containing functional genes of N₂O emission (Butterly et al., 2016). Similarly, the enhanced N₂O emission under warming treatment was accompanied by increased soil mineralization and inorganic N (Figure 3B, Bai et al., 2013; Dai et al., 2020). Decreased or unchanged N₂O emission with warming also happened in some N-limited ecosystems (Carter et al., 2012). The N₂O emission could be constrained by the lower denitrifier abundance with warming (Li et al., 2020a). Apparently, there is increasing N₂O emission with warming treatments when the ecosystem has enough N. In short, ecosystems can maintain N balance by controlling N₂O emission. They increase N₂O loss when N is abundant but have no or low gaseous N loss when there is N scarcity (Figure 3).

N fixation and gains

Biological N fixation is a major pathway through which atmospheric N₂ is converted into N available to plants (Cleveland et al., 2013). It is estimated that N inputs via symbiotic and free-living N fixation are roughly 70–140 Tg N yr⁻¹ in Vitousek et al. (2013), 100–290 Tg N yr⁻¹ in Cleveland et al. (1999), and 195.1 Tg N yr⁻¹ in Elbert et al. (2012), whereas the free-living N fixation may be as high as 10–15 kg N ha⁻¹ yr⁻¹ in some ecosystems (Reed et al., 2011). Global models forecasting C-N interaction generally assume that N fixation rates increase as a function of NPP (Wieder et al., 2015). Thus, N fixation is basically demand-driven. The increased plant growth and C storage under elevated CO₂ are often accompanied by N accumulation in ecosystems (Figure 3A). In fact, CO₂ enrichment significantly enhanced N influx to ecosystems by 44.3% through biological N fixation (Figure 3A) (Liang et al., 2016). In some ecosystems, this increase in N fixation is only realized in the first few years of

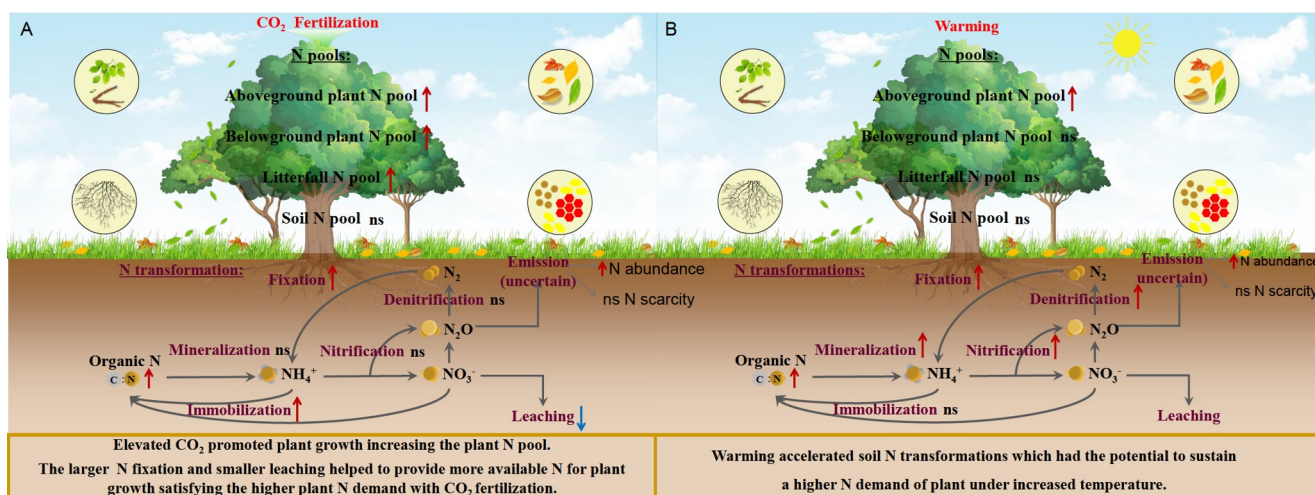


Figure 3 Conceptual diagram depicting the effects of elevated CO₂ (A) and climate warming (B) on nitrogen pools and transformation processes. The results are summarized mostly from a few meta-analyses (Bai et al., 2013; Dai et al., 2020; de Graaff et al., 2006; Liang et al., 2016; Sun et al., 2022; Yue et al., 2019; Zheng et al., 2020). The red arrow indicates an increase, whereas the blue arrow indicates a decrease.

CO₂ experiments because the availability of molybdenum, a key micronutrient of nitrogenase, gradually reduced as the number of treatment years increased (Hungate et al., 2004). The common increase in N fixation under elevated CO₂ is attributable to the stimulating activities of symbiotic and free-living heterotrophic N-fixing bacteria. These N-fixing organisms usually have an enormous competitive advantage over plants to fix N into the ecosystem (Vitousek and Howarth, 1991).

Besides, anthropogenic N fixation has doubled the total global flux of N to the biosphere during the 20th century. The increased N input via fixation and deposition coupled with the decreasing N losses through leaching lead to increased N retention under CO₂ enrichment, especially in plant and litter pools (Figure 3A). Increases in biological N fixation and decreases in N loss directly promote N availability for plant growth, and thus support the net accumulation of organic matter in ecosystems. The net C and N accumulation in plant and soil pools under elevated CO₂ indicate the adjustment of soil N cycling to meet N demand.

This adjustment of soil N cycling with changing C input is also reflected during primary or secondary forest succession (Figure 4) (Alexander and Mack, 2016; Kirschbaum et al., 2008; Vitousek, 2004). Plant N demand is generally higher during the active growth period before canopy closure (Chapin et al., 2011). If there is no sustainable N input, it is expected that the increasing N uptake and N accumulation in standing biomass will result in a decrease in soil N pools during forest succession. Nevertheless, soil N stock also increases with succession (Figure 4) (Li et al., 2012). The linear increase in the N stock associated with plant C stock indicates that there are long-term sources of N attributable to atmospheric N deposition and biological N fixation during forest succession (Morris et al., 2007; Yang et al., 2011). For example, Houlton et al. (2008) demonstrated that biological N fixation rates are 2.9, 4.9, and 2.2 g N m⁻² yr⁻¹ for tropical, temperate, and boreal forests, respectively. Atmospheric N deposition varies from <0.2 g N m⁻² yr⁻¹ in rural areas to >5 N m⁻² yr⁻¹ in industrial or intensive agriculture regions (Dentener et al., 2006). Around 40%–70% of the soil N increase can be attributed to N deposition and asymbiotic N fixation in southwest Michigan's afforested sites (Morris et al., 2007). Some other mechanisms, like N release by litterfall, N redistribution within soil profiles, and mining of deep soil N, are also thought to contribute to the increase in soil N during forest succession, especially at the later stage of succession (Knops and Tilman, 2000; Wang et al., 2019). Soil available N linearly increases with soil C stocks as succession progresses, whereas gaseous and leaching N losses generally decrease with succession (Figure 4) (Tian et al., 2018). The combination of those N sources is about 3–14 g N m⁻² yr⁻¹, which can roughly explain the observed N accrual during forest succession (9.5±4.5 g N m⁻² yr⁻¹

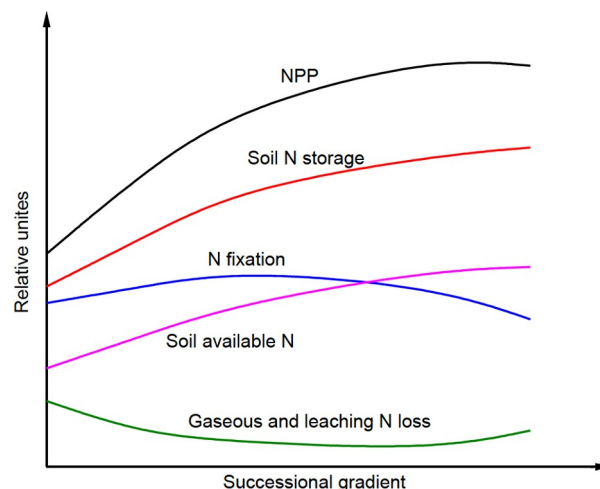


Figure 4 A conceptual figure on C and N cycle processes along forest succession, including NPP, plant N uptake, soil N storage and availability, N fixation, N leaching, and N gases emission. This conceptual figure was summarized according to Crews et al. (2016), Li et al. (2012) and Menge and Crews (2016).

when forest succession >50 years).

Besides elevated CO₂ and forest succession, other global change factors also modify N availability by rapidly adjusting N fixation and other processes. A meta-analysis revealed that N addition inhibits N fixation by 19.0% on average, regardless of biome type, due to decreased nitrogenase synthesis (Zheng et al., 2019). The decreased N fixation under N enrichment is also reported in other studies (Dynarski and Houlton, 2018; Hedin et al., 2009). This decrease in N fixation is partially eased by the addition of micronutrients, e.g., Mo and Fe, but not consistently by P addition (Zheng et al., 2019). Although the effects of global warming on N fixation remain inconclusive (e.g., Gundale et al., 2012; Hungate et al., 2004; Rousk and Michelsen, 2017), it has been reported that warmer climate can increase N fixation rates by a factor of 1.5–2 in the arctic regions due to increased metabolic processes in soil microorganisms (Figure 3B, Chapin and Bledsoe, 1992). However, this increase may be lowered by the light limitation and extreme temperature events (Gundale et al., 2012).

All these phenomena demonstrate the dynamic adjustment of N cycling with respect to plant growth and ecosystem N demand after disturbance. Nonetheless, pinpointing where the N originally comes from or how much each N process contributes to the total plant demand is still a major challenge. Closing this knowledge gap should be a priority for future research.

Other N processes: rock release, transformation, and N resorption

Apart from the above-mentioned dynamic changes in N losses and accumulations under environmental change, other

N cycling processes are also involved in influencing soil N availability and regulating C cycling. Ecosystems are expected to be N limited partly because N is considered largely absent in the parent rock. However, a recent study indicates that more than a quarter of the N available to plants comes from bedrock (Houlton et al., 2018). According to their estimation, bedrock weathering releases about 11.2–18.2 Tg N yr⁻¹, although it varies largely in different regions. This overlooked source of ecologically available N contributes largely to terrestrial C cycling. Forests associated with N-rich parent materials contain 42% more C in tree biomass and 60% more C in the top 30 cm soil than similar sites underlain by N-poor rocks (Morford et al., 2011; Morford et al., 2016). Unfortunately, how rock N release changes with global change factors has not been determined yet.

Soil microbial mineralization plays a more important role than the external N input (N fixation and deposition) in rapidly adjusting N availability. Recycled N from the soil N biogeochemical cycling accounts for 90% of the annual demand of terrestrial plants (Figure 5) (Cleveland et al., 2013). Model simulation suggests that the N input required to completely eliminate N limitation is 441 Tg N yr⁻¹ for each land grid cell on average, which is four times higher than the estimated N inputs from atmospheric deposition (6 Tg N yr⁻¹) plus biological N fixation (104 Tg N yr⁻¹) (Thornton et al., 2007). This further suggests that soil biogeochemical N cycling is important for meeting plant N demand. The global soil N transformation rates change largely with temperature and precipitation (Li et al., 2019; Li et

al., 2020b; Li et al., 2022), indicating that soil N transformation will adjust under global change. In fact, warming results in increased soil N mineralization, where the soil microbial biomass becomes larger (Dai et al., 2020; Xu and Yuan, 2017). Soil nitrification is also stimulated by warming, but the nitrifier abundance does not show a clear change (Dai et al., 2020). Furthermore, N resorption from leaves before senescence, which is less under N enrichment but more under N poor conditions and decreases with increasing mean annual temperature and mean annual precipitation, also adjusts to global change to regulate plant growth and C cycling (Vergutz et al., 2012; Yuan and Chen, 2009). Altogether, these N processes account for the substantial N regulations on C cycling under global change.

Dynamic C and N coupling and its implications for C sequestration

From the above illustrations, we demonstrate how ecosystem N and C processes are dynamically coupled with each other under global change. The N processes rapidly adjust to external changes, such as N deposition or fertilization, elevated CO₂, disturbances, and subsequent recovery to couple with the C process in a new balance. The shifts in C and N coupling are mainly reflected in three aspects, namely relative changes in total C and N amounts, changes in the allocation of C and N amounts among different pools, and changes in stoichiometric relationships (i.e., C:N ratios).

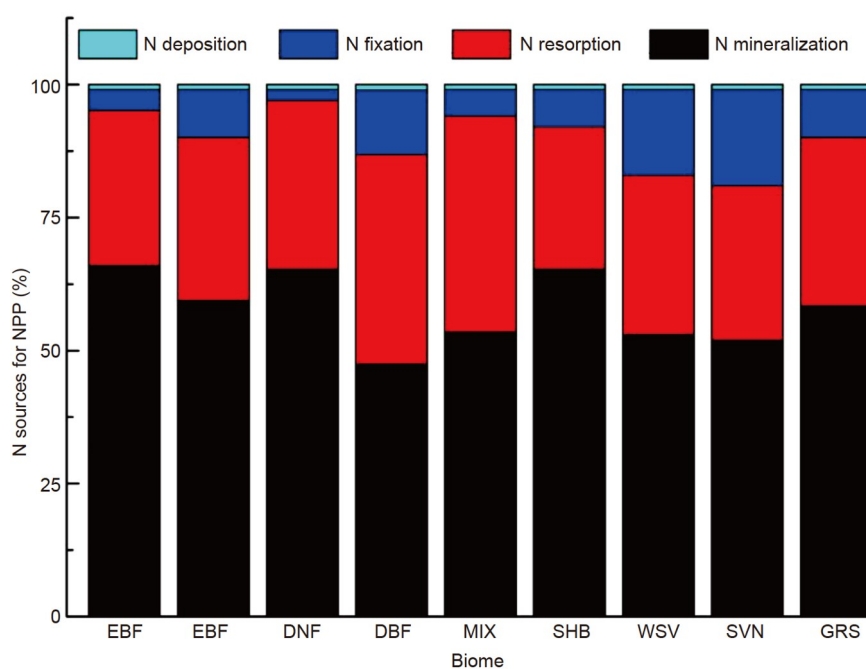


Figure 5 Different nitrogen sources and contributions of NPP in different biomes (adopted from Cleveland et al. (2013)). ENF, evergreen needle leaf forest; EBF, evergreen broad-leaf forest; DNF, deciduous needle leaf forest; DBF, deciduous broad-leaf forest; MIX, mixed forest; SHB, shrubland; WSV, wet savanna; SVN, savanna; GRS, grassland.

Nitrogen fertilization or deposition adds exotic N to an ecosystem, leading to shifts in coupling between C and N cycles. In response, a major fraction of the added N is lost by volatilization and denitrification to the atmosphere within days and weeks and by leaching to aquatic systems within months (Figure 6). The rest of the added N goes to the plant and soil as an ecosystem has no capacity for net mineral N retention (Mack et al., 2004; Niu et al., 2016). The N taken up by plants leads to lowered C:N ratios in plant tissues and stimulates photosynthesis and growth. Consequently, more N is allocated to plant pools than that without N fertilization or deposition. The N in plant pools resides in the ecosystem for months and years before transferring to litter pools and subsequent loss to the atmosphere, with a very small fraction going to the soil C pools via decomposition and microbial immobilization. Unless N fertilization or deposition recurs, the extra N from fertilization or deposition is eventually lost over time to maintain a balance with the C cycle (Sardans et al., 2016; Tian et al., 2019).

Similarly, changes occur in total C and N amounts, their allocation, and C:N ratios in response to additional C input under elevated CO₂ (Sun et al., 2018) and during forest succession (Li et al., 2012). Under these conditions, higher C availability shifts both C and N cycles. More C is allocated to roots to acquire N resources, resulting in more N allocation to the above-ground biomass. As N demand increases, N loss is reduced via decreased leaching and gaseous emission, whereas N fixation increases, resulting in an increase in the total N amount. When the increase in total N amount cannot match the increase in C input, C:N ratios increase in plant tissues, litter and soil pools, resulting in the downregulation of photosynthesis (Luo et al., 1994; Ruiz-Vera et al., 2017). Those processes, such as downregulation of photosynthesis, increase in N fixation, and more C allocation to root growth, help to shift C and N coupling to reach a new balance (Figure 6).

The shifts in C-N coupling have important implications for modeling ecosystem C sequestration under global change. The main motivation for developing coupled C-N models is to represent the constraints of N limitation on plant productivity (Zaehle and Dalmonech, 2011). Thus, those studies mainly focused on variables related to C uptake, like primary productivity and N use efficiency, rather than on various processes leading to shifts in C-N coupling. The dynamics of N leaching, gas emission, fixation, and other N cycling processes, and their regulation of the C cycle, are generally not well represented and/or constrained in the models (Davies-Barnard et al., 2020; Zaehle et al., 2014). Without realistic representation or data constraints on those processes, models cannot simulate the shifts in C-N coupling well and are deemed to cause large uncertainty in the prediction of C sequestration. For example, a model that is primarily based on the N limitation concept likely overestimates ecosystem C

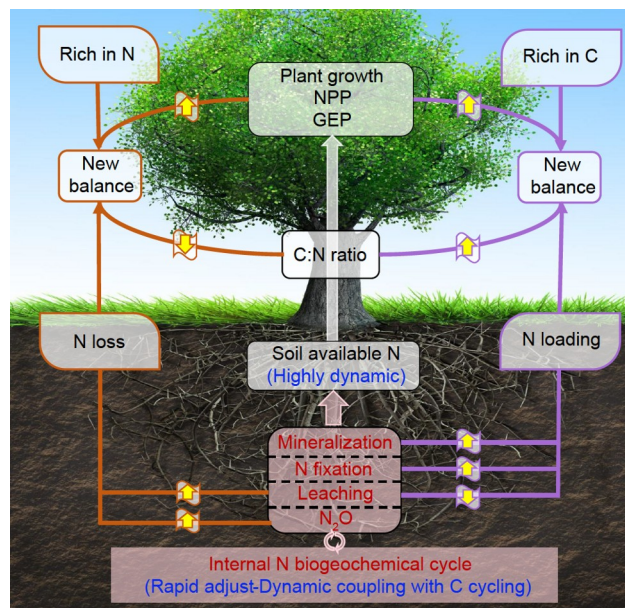


Figure 6 A conceptual framework of the dynamic C and N coupling under global change.

sequestration under N deposition because the model may not adequately represent N leaching and emissions and thus predict continuous increases in gross primary productivity and NEP with N addition (Sutton et al., 2008; Thomas et al., 2013).

In contrast, models that incorporate the N cycle usually overestimate N limitation under elevated CO₂, likely due to inadequate representation of adjustments in N processes. These models likely underestimate ecosystem C sequestration (Esser et al., 2011; Walker et al., 2015). Similarly, models that do not realistically consider adjustments in many C and N processes likely overestimate C loss under climate warming because they assume that the C cycle under warming is mainly determined by soil organic C decomposition. It is, therefore, critical to consider adjustments in various processes leading to shifts in C-N coupling in order to accurately predict ecosystem C sequestration under global change.

Concluding remarks

C-N coupling is among the most widely held concepts on interactions of C and N cycles. The concept has two components: regulation of C processes by N availability and dynamic changes of N availability itself over time. This review comprehensively evaluates the two components. Our review indicates that N input to the ecosystem mostly stimulates plant primary productivity but not microbial activities or inconsistently stimulates soil C sequestration. On the other hand, many N processes adjust to change soil N

availability and thus its coupling with the C cycle. Nitrogen leaching and N gas emission rapidly increase after N addition, whereas increases in N fixation and decreases in N leaching occur over the years to influence soil N availability and support plant growth and ecosystem C sequestration under elevated CO₂ and temperature or along ecosystem succession. In this review, we argue that many processes adjust to shift the coupling between C and N cycles in response to environmental change. This dynamic C-N coupling is fundamental for understanding and predicting ecosystem C sequestration under global change.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

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