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REVIEW

Global Change Impacts on Forest Elementomes and Insights for Improved Management Practices

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Abstract

Purpose of Review The elemental composition of organisms (the elementome) strongly determines their functional traits and their functioning. Global change presents significant potential impacts on forest elementomes of trees, soils, and soil microbes, influencing primary production, nutrient cycling, and food-web dynamics in forest ecosystems. This review aims to summarize recent advancements in understanding the response of forest elementomes to global change and how we can help them adapt to new conditions through improved management practices.

Recent Findings Atmospheric CO_2 enrichment, increased nitrogen (N) deposition, climate warming and droughts strongly influence the elemental composition of trees, microbes and soils of forest ecosystems. Accounting for the composition and availability of essential elements such as N, phosphorus (P) and potassium (K) in the plant-soil system can largely improve projections of forest carbon(C) cycle, especially when simulating the capacity of globally increasing C fixation by the rising atmospheric CO_2 concentration and N deposition.

Summary Global change influences forest elementomes across various scales, with diverse spatiotemporal variation and underlying mechanisms. Future research should integrate multi-source information to enhance the monitoring of elementomes and facilitate the adaptation of forests to the new environmental conditions through forest management, particularly focusing on the interaction effects of the multiple facets of global change.

Keywords Climate change · Biogeochemistry · eCO_2 · Nitrogen deposition · Droughts · Warming · Forest management

Introduction

Global forests contain 861 ± 66 Pg C (mean ± standard deviation) in plant biomass, soil (including soil microbial biomass), deadwood and litter, which have a profound effect on the global carbon (C) cycle and the mitigation of climate change [1]. Forest elementomes, defined as the concentration of elements within organisms of trees, soils, and soil microbes, influence primary production, nutrient cycling, and food-web dynamics in forest ecosystems [2–4]. Even though some trees exhibit a very strong stoichiometric

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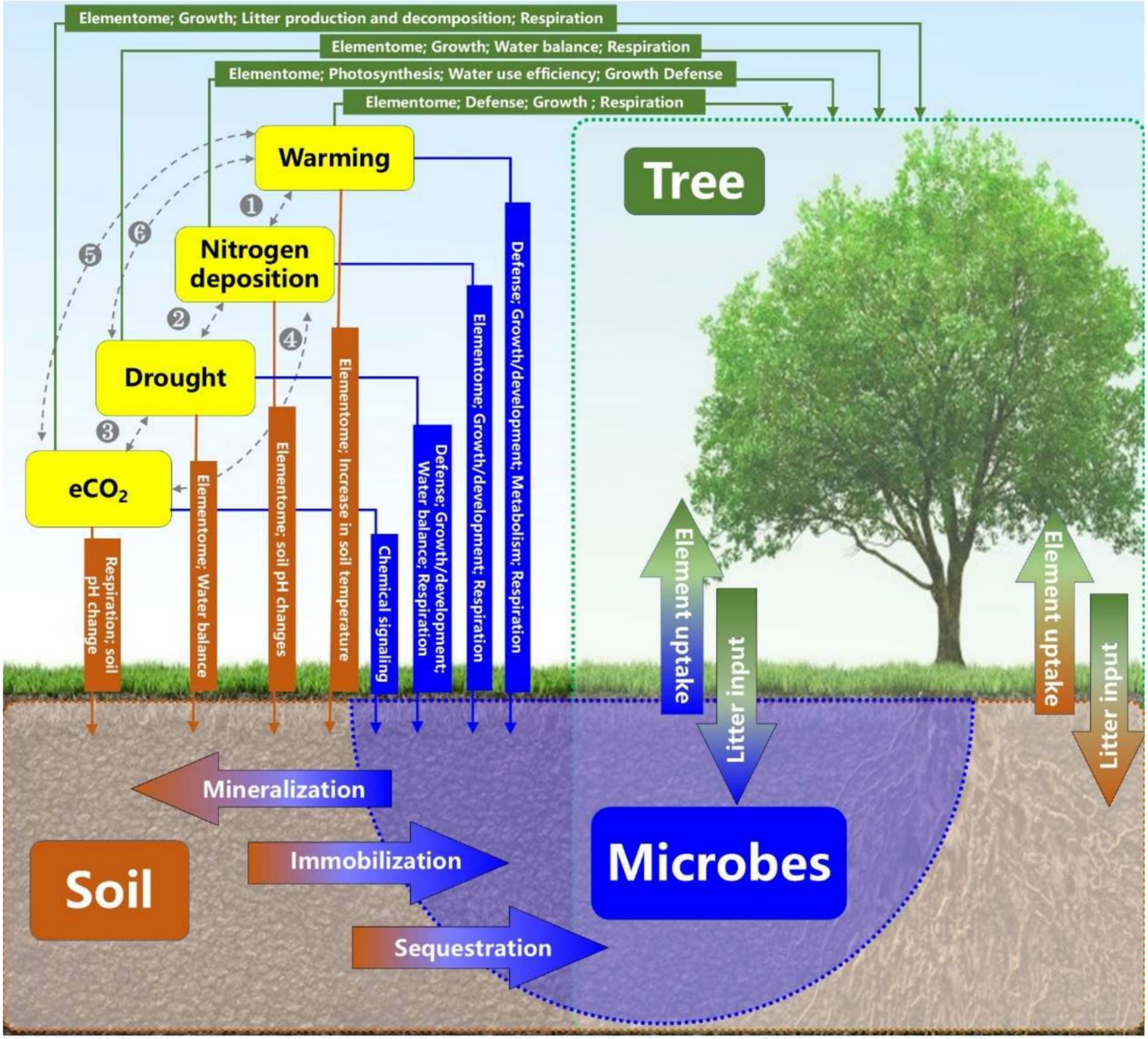
homeostasis, most trees present some degree of stoichiometric flexibility in response to global changes [5, 6].

Under global change, atmospheric CO_2 enrichment, nitrogen (N) deposition, and climate warming could stimulate tree growth and promote a more efficient photosynthesis in many parts of the world [7–12]. These increases in C availability for plants have generally diluted leaf-level nutrient concentrations and then soil- and microbe-level nutrient concentrations. While other global changes, such as drought, may inhibit tree growth and decrease photosynthetic efficiency and may condense their nutrient concentrations [13, 14]. In addition, different elements present different levels of homeostatic control depending on the environmental availability, and on whether they are macronutrients, essential micronutrients or trace elements [4, 5]. A less explored, but equally important, research front is how global change, and in particular, climate change alters the elemental composition through shifts in tree growth, soil microbial metabolism and soil nutrient supplies (Fig. 1). This will have important implications for developing forest management practices that help forests adapt to new environmental conditions.



The grey dashed lines represent the interactions between different global change types:❶ Warming and N deposition can interact to alter effects on forest elementomes. ❷ Drought can decrease the effects of N deposition on tree and microbial growth. ❸eCO_2 can alleviate water stress in forests, while drought can limit CO_2 effects on photosynthesis. ❹N deposition and eCO_2 may have a positive interaction on tree and microbial growth. ❺ CO_2 and temperature can interact to alter effects on forest elementomes. ❻ Drought and warming may have a negative interaction on tree and microbial growth.

Fig. 1 Conceptual diagram of the influences of climate change on the processes that control forest elementomes of the tree, soil, and soil microbes

Recent studies have shown that forest tree species and soil microbial communities have flexible elementomes along their natural ranges of distribution in response to natural and anthropogenic gradients [15–18]. These studies indicate that accounting for stocks, fluxes, and availability of N, phosphorus (P), and potassium (K) as well as iron (Fe), zinc (Zn), and calcium (Ca) in the plant-soil system can largely improve the simulations of the C cycle in ecosystems, especially when simulating global change impacts. Micronutrients and trace elements are essential to regulate vital plant functions such as photosynthesis and chlorophyll production (magnesium [Mg], Fe), drought tolerance (K), defense (silicon (Si)), or reproduction (Zn) [19–22]. The decreases of the availability of these elements can limit the capacity of globally increasing C fixation by the rising concentration of atmospheric CO_2 and N deposition over time [7, 8]. These improvements in the performance of simulations should be translated into more accurate projections and scenarios from Earth system models [23]. Hence, investigating the degree to which tree species adjust their elementomes in response to environmental changes is necessary to obtain knowledge of stoichiometric flexibility and its ecological significance. This should allow us to understand the role of stoichiometric flexibility, as opposed to stoichiometric homeostasis, and its relationship with ecological characteristics of species, such as growth strategy, capacity to adapt to environmental changes and nutrient-use efficiency.

In this review, we systematically summarize the new progress of peer reviewed papers which were mostly published in the recent 5 years. Then we provide a comprehensive synthesis of the impact of global change on elementomes of trees (leaf, bark, stem, root), soils (mineral soil, humus layer, deadwood, litter) and soil microbes (microbial biomass, community composition, keystone microbes, and enzyme activities) in forest ecosystems with a particular focus on the impacts of elevated CO_2, N deposition, drought and warming. Later, we review the insights into how forest elementomes adapt to the new environmental conditions through forest management (e.g., tree species selection and tree biodiversity management). Finally, we hope this review can provide new insights for our understanding of global change impacts on forests structure, stability and functioning.

Elevated CO_2 Impacts on Forest Elementomes

Overview

Rising atmospheric CO_2 concentrations represent one of the most significant drivers of global change, profoundly influencing land and ocean biogeochemical cycles and directly affecting the entire climate system [24, 25]. Since the 1990s, atmospheric CO_2 levels have risen from approximately 350 ppm to 425 ppm as of 2024 [26]. This increase has led to complex alterations in the ecosystem elementome, affecting the elemental composition of multiple trophic levels, including plant tissues, animals, and soil microorganisms [27]. One of the key ecological hypotheses linked to elevated CO_2 (eCO_2) is the “CO_2 fertilization effect” or “greening effect”, which posits that anthropogenic CO_2 emissions enhance plant photosynthesis and the accumulation of carbohydrates [28]. Observational studies and eCO_2 experiments have provided substantial evidence supporting this hypothesis [29–33]. However, the ecosystem responses to eCO_2 extend beyond C, affecting over 20 essential elements critical to life. Emerging research reveals consistent declines in nutrient elements, ranging from N and P to boron (B) and Zn [27, 34, 35]. Evidence suggests that eCO_2 often leads to reductions in these nutrients, causing a ‘dilution effect’ produced by an increase in the concentration of C that cascades through ecosystems, affecting other trophic levels and biogeochemical cycles [27, 35]. This decline in micronutrients and trace elements could eventually lead to nutrient deficiencies propagating through the food web, entailing potential changes in the functioning of these organisms and the entire ecosystem [27]. Empirical evidence of these effects on the composition of elements beyond C, N, and P and their stoichiometry remains, however, elusive.

Observational Evidence: Nutrient Declines in Plants

Observational studies have consistently demonstrated a decline in the nutrient status of ecosystems under eCO_2 conditions [7, 36–39]. For instance, research from Europe forests highlights significant decreases in forest foliar concentrations of key nutrients, including N, P, K, sulfur (S), and defined before (I changed it) Mg, with reductions of 5%, 11%, 8%, 6%, and 7%, respectively, over the past three decades [17]. These declines are particularly pronounced in Mediterranean and temperate forests, where rising atmospheric CO_2 levels are strongly correlated with decreases in foliar N, P, K, Mg, and S concentrations, alongside an increase in the N:P ratio [7]. Similarly, studies from the United States reveal that soil N availability has generally decreased since at least the 1850s, with the most significant reductions occurring in cool, wet forests [36]. In China, analyses of 1,811 herbarium specimens collected from 1920–2010 in subtropical forests revealed a 23.1% decrease in foliar P concentrations and a 21.2% increase in foliar N:P ratios, with evergreen species exhibiting larger increases in N:P than deciduous species [39]. The underlying drivers of these changes differ by functional type: for evergreens, eCO_2 and related factors such as N deposition and rising mean annual temperatures contributed to the increase in leaf N:P, while for deciduous species, mean annual temperature and vapor pressure deficit played a key role in driving the observed N:P increases [39]. In order to uptake soil nutrients, plants could increase root exudation of organic acids under eCO_2 and finally facilitated P uptake from soil in the *Eucalyptus* woodlands with seedlings [40]. While in a mature, P-limited *Eucalyptus* forest, eCO_2 increase roots associated-C gains and -C losses but decreased P availability and specific enzymatic activity [41].

The Value of eCO_2 Experiments: Insights from FACE Studies

Unlike targeted experiments, observational studies often integrate multiple confounding factors beyond eCO_2, such as N and S deposition, as well as climate warming. This highlights the critical value of controlled experiments, like Free-Air CO_2 Enrichment (FACE) studies, in isolating the specific effects of eCO_2. The FACE technology, initially developed by Brookhaven National Laboratory for agricultural systems, has been adapted to study the effects of elevated CO_2 on natural ecosystems. A notable prototype forest FACE system was tested at Duke University in 1994–1995, followed by the first fully operational FACE experiment in a loblolly pine (*Pinus taeda*) forest in 1996. Over time, FACE experiments have been implemented in diverse ecosystems worldwide, providing critical insights into CO_2-driven changes in ecosystem elementomes.

In line with observational findings, elevated atmospheric CO_2 levels reduce plant N and P concentrations yet simultaneously increase total N and P pools across all plant tissues—aboveground, belowground, and entire plant biomass—and in diverse ecosystems, including forests [42]. This pattern is consistent with the CO_2 fertilization hypothesis, which suggests that anthropogenic CO_2 emissions enhance photosynthesis and foster the accumulation of carbohydrate-rich compounds (CHOs) in plants. However, this shift toward CHO enrichment relative to other essential elements—ranging from N and P to micronutrients like B and Zn—highlights a significant global drawback: as plant biomass expands during the Anthropocene, its nutritional quality becomes increasingly diluted. Interestingly, elevated CO_2 concentrations have also been shown to profoundly alter soil P cycling. For example, under eCO_2 conditions, soil phosphatase activity increased by 19.3%, labile P rose by 4.2%, and total soil P declined by 10.1% [42]. These patterns underscore the intricate interplay between plant growth and nutrient cycling in eCO_2 environments, where phosphorus availability emerges as a key regulator of ecosystem responses. Notably, these results align with a recent meta-analysis of 97 published studies, which revealed overall positive response ratios of soil phosphatase activity under rising atmospheric CO_2 levels [43]. In mature temperate forests in the UK, elevated CO_2 conditions (+ 150 ppm above ambient) led to increased litterfall but a decline in the N concentration of that litter. This pattern suggests that plants conserve N through enhanced resorption before leaf senescence [44]. A recent global synthesis of forest FACE experiments provides further evidence of significant shifts in ecosystem stoichiometry and nutrient dynamics under elevated CO_2 [45]. For instance, leaf and soil C:N ratios increased by 26% and 4%, respectively, reflecting an overall imbalance in C–N stoichiometry. More specifically, leaf N concentrations declined by 12%, while stem N concentrations decreased by 7%. Concurrently, soil organic C rose by 5%, dissolved organic C by 15%, and soil microbial biomass C by 21% [45]. Collectively, these findings suggest that elevated CO_2 not only stimulates C cycling—enhancing forest productivity and increasing living biomass stocks—but also promotes N cycling [45]. This dual enhancement of carbon and nitrogen processes supports the CO_2 fertilization effect on forest growth and productivity, albeit accompanied by altered elemental balances.

Gaps and Challenges in Current Research

While eCO_2 promotes plant growth, the accompanying declines in nutrient concentrations underscore the need for holistic approaches to ecosystem management. Existing research heavily focuses on plants, often neglecting other trophic levels (e.g., soil animals and microorganisms) and plant-soil system, and prioritizes macronutrients like C, N, and P over trace elements. However, ecosystems function as integrated units, and nutrient reductions in vegetation could trigger dilution effects that cascade through food webs, reducing biodiversity at higher trophic levels. Such changes pose challenges for sustainable forest management and disrupt biogeochemical cycles, ultimately threatening ecosystem stability and resilience. Further, accounting for the strength of homeostatic control, how eCO_2 affects elementomes of coexisting individuals and species and individuals and species that do not coexist is still scarce. Such efforts are critical for understanding and mitigating the cascading effects of eCO_2 on ecosystem functioning under global change.

Nitrogen Deposition Impacts on Forest Elementomes

Overview

N deposition can indirectly influence elementomes of trees by altering soil N availability and modifying soil microbial nutrient demand for various functions, thereby causing shifts in stoichiometric relationships in forest ecosystems [35, 46, 47]. During the past decades, the much faster increase of reactive N to the biosphere than inputs of P has led to increases in plant N:P ratios [48]. These results show the importance of considering the stoichiometric ratios between N and other nutrients when testing the effect of N deposition on forest C cycling [49, 50]. For example, the N addition increases fungal colonization in deadwood through decreasing the wood C:N ratio in a subtropical forest, potentially increasing its decomposition rates [51, 52]. Thus, assessing the effects of N deposition on multiple elements holds ecological significance for understanding tree growth [53], soil microbial metabolism [51], species coexistence [54, 55], and nutrient cycling [18, 56].

Differences in Responses Among Forest Types

The response of foliar elementomes to N addition varies among plant families and functional groups [57–60]. For instance, a short-term N addition experiment in the Mediterranean found no changes in macro-element concentrations in the leaves of *Quercus ilex*, *Phillyrea latifolia*, and *Arbutus unedo* but change the ratio of N/P and C/P in *Arbutus unedo* and N/P ratio in *Phillyrea latifolia* [59]. In herbaceous plants, N addition significantly increased K, Mg, S, manganese (Mn), copper (Cu), and Zn concentrations but had minimal effects on woody plants [61]. Moreover, nutrient availability under N addition also explains distinct soil fungal colonization of angiosperm versus gymnosperm wood, as fungal colonization was more sensitive to N availability in angiosperms, and it change to P availability in gymnosperms [52]. Meanwhile, N enrichment has a higher acceleration effect on wood microbial respiration and soil nutrient inputs in gymnosperms than in angiosperms [51, 62]. These differential responses among plant functional groups could contribute to shifts in plant community composition and aboveground net primary productivity [57, 63, 64].

N-Deposition Effects Depend on Environmental Conditions

The extent of N input effects could vary across ecosystem types, soil nutrient conditions and experiment times [65–67]. A meta-analysis indicated that N addition reduces foliar concentrations of P, K, Ca, Mg, and the Ca:Al ratio while increasing foliar N, Al, and the ratios of N:K, N:Ca, and N:Mg [61]. However, another study has been shown to increase plant concentrations of Mg, Mn, Cu, and Zn [49]. The difference may be attributed to the contribution of European plots that were more extensively represented in the database of Sardans et al. [68]. A 30-year series study on European beech (*Fagus sylvatica*) in Europe revealed that the relationship between foliar element concentrations and N deposition partially depends on the content of soil organic matter [69]. Zheng et al. [70] found that the pattern of soil C flux changed in tropical forests under long-term N deposition (insignificant changes–dramatic decline–insignificant changes). However, several studies have indicated that long-term N addition decreased tree growth, soil microbial metabolism and soil C storage or insignificant changes depending on plant group, climate condition and experimental duration [66, 69, 71, 72]. Although N input could increase tree biomass production and soil C sequestration in the northern forests [9], the effects of decade-long experimental N additions decreased with increasing N loads [10].

Effects on Plant Physiology and Microbial Metabolism

N enhancement can significantly alter nutrient concentrations and physiological processes in plants [54, 58, 65, 73]. There is a reduction in foliar concentrations of Ca, Mg, Zn, and Mn due to increased N loads [59]. It has also been suggested that cation-deficient plants might partially compensate for nutrient deficiencies by increasing transpiration [16]. A two-year N addition experiment in subtropical forests revealed increased foliar N concentration but decreased concentrations of K, Ca, and Mg, but P and Na concentrations were unaffected [74]. In contrast, in a decade-long N addition experiment in a N-rich tropical forest, there was no long-term effect on foliar N or cation concentrations (e.g., Ca, Mg), photosynthesis, litterfall production, or annual plant growth rates [71]. This adaptation could enhance nutrient uptake while reducing leaching of soil nutrients beyond the root zone, helping plants maintain nutrient balance and physiological processes under N enrichment [71]. For example, N deposition would increase acid phosphatase activity for the uptake of soil P, but the increase was more for the arbuscular mycorrhizae trees than for the ectomycorrhizae trees [75]. On the other hand, N addition has also been shown to decrease the C:N ratio of litter and accelerate plant C input into soil through fast microbial decomposition [50, 51, 62]. While anthropogenic N enrichment enhances soil C accumulation by decreasing saprotrophs rather than ectomycorrhizal fungal activity and then impedes mass loss of litter [76]. Thus, N deposition may influence forest elementomes through its effects on plant physiology and microbial metabolism, ultimately impacting ecosystem functions.

Directions for Future Research

Numerous studies have examined the variation and allocation of multiple elements in plants, however, how these elements co-vary to adapt to the interaction of N enhancement and other environmental changes remain unclear. For example, the long-term N deposition could reduce water use efficiency in subtropical forests with low P availability [77]. Meanwhile, based on the biogeochemical niche hypothesis, Fernández-Martínez [22] integrated elementome diversity with traditional species diversity to investigate changes in ecosystem function and stability, presenting a promising research avenue to study the impacts of ecosystem diversity and function under N deposition. Understanding how leaf elemental composition under reduced N deposition affects photosynthetic rate, root growth, root exudation, and consequence soil microbial metabolism and C sequestration will be a critical direction for future research [78]. Further, research on N addition effects in forests has mostly involved direct understory addition of N and has ignored canopy interception and processing of N. The foliar N content of *Q. variabilis* and *Q. acutissima* was significantly higher with canopy addition of N than with understory addition of N for two years and promoted a higher root production [79]. These insights will provide a more comprehensive understanding of forest elements dynamics and ecosystem resilience in a changing world.

Drought Impacts on Forest Elementomes

Overview

Drought, as a major environmental stressor, disrupts biotic activity and nutrient mineralization, and thus nutrient availability, uptake, and distribution, which directly influence key physiological processes such as photosynthesis rate, stomatal conductance, and biomass allocation [13]. These disruptions often exacerbate the adverse effects of nutrient deficiencies, impairing water-use efficiency and reducing the adaptive capacity of trees [14, 80]. Understanding how drought affects forest elementomes is essential for predicting tree growth responses to future climatic conditions and informing forest management strategies.

Drought-Induced Changes in Forest Elementomes

Drought stresses lead to significant redistributions of nutrients within trees, soils and soil microorganisms. This water stress results in decreased N and elevated C:N and C:P ratios in plants and microbial biomass, altering nutrient availability and biogeochemical cycling [81, 82]. For example, in temperate forests, drought promotes the inorganic transformation of P, reducing its bioavailability, which in turn limits C assimilation and protein synthesis in trees [83, 84]. Compared with mild drought, the responses of plant and soil C:N:P stoichiometry were more sensitive to moderate and extreme droughts, particularly in humid areas [82]. Similarly, drought-induced reductions in K concentrations are widely observed in trees that are physiologically declining or approaching death, reflecting the negative effects of water scarcity on nutrient uptake and transport [13]. However, there is also a slight increase in N resorption efficiency during drought years [85], which may represent an immediate adaptation of trees to drought events. Such an adaptation could partially compensate for the reduced N uptake by roots during drought [86], thereby preventing N starvation and deficiency in the subsequent growing season. These nutrient imbalances are further compounded by inhibiting microbial activity and reducing fine root turnover, which collectively diminishes nutrient mobilization in the soil [87, 88].

Growth-Stage-Specific Responses

The response of the elementome to drought differs significantly across tree growth stages. Mature trees, with their extensive root systems, are often better equipped to access soil resources than saplings, enabling them to mitigate nutrient deficiencies more effectively [89, 90]. Although root exudates typically decrease in situations such as drought, inoculations of bacteria could increase root exudation rates on *Cupressus sempervirens* saplings grown and mitigate drought-induced decrease in leaf P and Fe through increasing soil phosphorous bioavailability [91]. However, the deeper roots of mature trees encounter nutrient limitations due to reduced availability of essential elements like P and K at greater soil depths [92]. Additionally, mature trees employ hydraulic lift mechanisms to draw water from deeper layers, supported by mycorrhizal networks that facilitate nutrient uptake under drought conditions [93, 94]. These adaptive strategies highlight the nuanced interactions between tree growth stages, water availability, and nutrient dynamics during water stress. Interestingly, during drought, the concentrations of some elements decline, while others increase or remain stable, e.g. Mn often accumulates in trees prior to their death, while P, Fe, and Cu concentrations typically decrease [95, 96]. These patterns vary with species traits, growth stages, and environmental conditions, underscoring the complexity of forest elementome in response to drought [97].

Impact of Drought Frequency and Intensity

The frequency and intensity of drought significantly influence nutrient dynamics within trees, particularly during leaf senescence. Reduced resorption efficiency of elements like K and P during drought can limit nutrient reserves, impairing growth potential and stress tolerance in subsequent seasons [85]. A five-year drought experiment, involving 0 mm of precipitation during each growing season for 3.5 months, revealed that prolonged water shortages led to potassium deficiency in green leaves and a tree mortality rate of 33% [98]. Similarly, in the Mediterranean Basin, long-term drought manipulation experiments highlighted a significant risk of nutrient leaching loss in forests, driven by severe and prolonged water scarcity [20]. Moreover, the responses of other elements, such as Ca and N, exhibit complex patterns depending on species characteristics and environmental conditions. For example, Ca absorption may increase or decrease under drought depending on the soil Ca condition [85]. In Ca-rich soils, the abundant Ca supply in the soil reduces the plant's need for Ca retrieval during drought [99]. Compensatory effects from Ca in the soil or the green leaf pool ensure that this reduction has no significant subsequent impact on the ecosystem [85]. These intricate responses emphasize the diverse roles of elementomes in forest structural and metabolic functions.

Future Directions

Future research should prioritize a deeper understanding of the multifaceted effects of drought on forest elementome dynamics. Investigating the synergistic interactions between elements and their relationship with water-use efficiency under drought conditions is particularly critical, especially when combined with the effects of elevated CO_2 on plant water and carbon metabolism [100]. Further, detailed studies on nutrient dynamics across tree organs, such as leaves, bark, and roots, are also essential, as their elemental composition may have different response to global changes. For instance, leaf elementomes (e.g., K and P) are highly sensitive to drought intensity, while root responses to drought often buffer these effects, playing a crucial role in maintaining overall tree health [13]. Lastly, water availability varies in a short period, but elemental composition was normally measured once a year. This miss-match in time might be a cause of misinformation around elemental composition responses under drought, especially with more mobile elements such as N and K [81, 82]. Thus, a finer temporal resolution of the samples should be paid more attention to in future studies. Based on the above discussion, related insights are vital not only for advancing theoretical knowledge of plant responses to drought but also for developing adaptive forest management and conservation strategies in the face of global change.

Warming Impacts on Forest Elementomes

Overview

Global warming, with an expected temperature increase of 1.5–4 ℃ by the end of the twenty-first century [101], poses significant challenges for element cycling in terrestrial ecosystems [102]. Nutrient dynamics, including essential elements such as C, N, P, K, Ca, Mg, Fe, and Zn, are influenced by warming through changes in plant metabolic rates, photosynthesis, soil microbial activity, and nutrient availability [103, 104]. This section discusses how warming affects the forest elementomes, focusing on its short- and long-term consequences, stoichiometric balances, spatial patterns, and knowledge gaps in understanding forest functioning of global-scale responses.

Short- and Long-Term Effects of Warming

Warming can enhance nutrient cycling by increasing the decomposition of organic matter and microbial activity when water is available, leading to short-term increases in the availability of nutrients such as N and P [11, 105]. For instance, warming accelerates the release of available N (NH_4^+ and NO_3^-) and promotes plant N uptake [106, 107]. Similarly, microbial activity stimulated by warming can enhance organic P mineralization, increasing plant P demand and potentially depleting soil P over time [108].

In the long term, warming may reduce nutrient pools due to organic matter depletion and changes in microbial community structure [102]. Elements such as K, Ca, and Zn are influenced by complex interactions between plant metabolic demand and soil nutrient availability. While warming generally promotes photosynthesis and tree growth rate, especially in cold regions, increasing the demand for K, and prolonged warming can exacerbate K depletion by accelerating soil K mineralization rates [109]. Warming promotes decomposition of organic matter, releasing more acids (e.g., organic acids), and may lead to increased oxygen depletion, which puts the soil in a reducing state and affects the solubility and availability of Ca and Fe availability [46]. The effects of short- and long-term warming on forest elementomes may be similar but may vary with different intensities. Short-term warming leads to more rapid and immediate changes, while long-term warming may trigger more complex feedback mechanisms that affect soil nutrient cycling, plant growth, and ecosystem stability and resilience. However, few studies paid attention to the temporal dynamic's effects of warming on the elementomes. Thus, the long- and short-term impacts of climate change need to be analyzed in depth in relation to specific ecosystem types and coping strategies.

Stoichiometric Balance and Ecosystem Stability

The stoichiometric homeostasis hypothesis suggests that organisms maintain stable element ratios for optimal growth, a mechanism critical for ecosystem structure and function under changing environments [110]. Warming alters element stoichiometry, often increasing plant N:P and C:P ratios due to enhanced N mineralization rates [102, 105]. Conversely, warming has been shown to reduce the ratios of N and P to alkaline cations, such as N:K, N:Ca, N:Mg, P:K, P:Ca and P:Mg ratio, which may depend on the warming intensity and duration across different ecosystem types [46]. These stoichiometric shifts vary across ecosystems due to differences in vegetation physiology, nutrient uptake, and utilization efficiency, underscoring the complexity of warming effects on nutrient cycling processes [103, 104].

Spatial Patterns of Elementome Responses to Warming

Across large spatial scales, the concentration of certain elements in organisms tends to decrease with increasing temperature and decreasing precipitation [110, 111]. In colder environments, higher concentrations of N, Ca, Mg, S, Fe, and Zn (excluding Mn and aluminium (Al)) serve as an adaptive response to freezing stress, promoting metabolic rate and reducing freezing damage [11, 112]. Conversely, in warmer ecosystems, warming can significantly reduce the concentrations of N, P, K, Cu, Fe, and Zn and soil fertility due to enhanced nutrient loss [113, 114].

In arid and semi-arid regions, warming may lead to a reduction in soil moisture and an increase in nutrient loss, and the effects of warming on elementomes are more pronounced [111]. In humid regions (e.g., tropical rainforests and temperate forests), warming may promote nutrient release, but the effects of warming on elemental cycling may be more complex due to denser biological communities and stronger nutrient return mechanisms [101]. Thus, the effects of warming on elementomes are not globally uniform, but strongly dependent on geographic location, ecosystem type, and specific climate-soil-vegetation interactions [46]. Manipulative warming studies in temperate and boreal forests revealed that warming effects on nutrient uptake are often small and species-specific, while warmer forests experience more pronounced shifts in nutrient availability and nutrient dynamics [115]. These findings indicate a critical need for global-scale analyses to assess the effects of warming intensity, duration, and ecosystem type on element cycling processes. With a global meta-analysis, fine-root N increased by 13.3% on average under warmer conditions, whereas fine-root C:N ratio was decreased by 16.4%, and root C and P concentrations showed no significant responses to warming [116]. Meanwhile, the effect size for fine-root N increased while that for fine-root C:N ratio decreased with an increasing magnitude of warming. The effect size for fine-root N did not vary with warming duration, while the negative effects of warming on fine-root C:N ratio increased with increasing warming duration.

The Interaction of Warming and other Global Changes

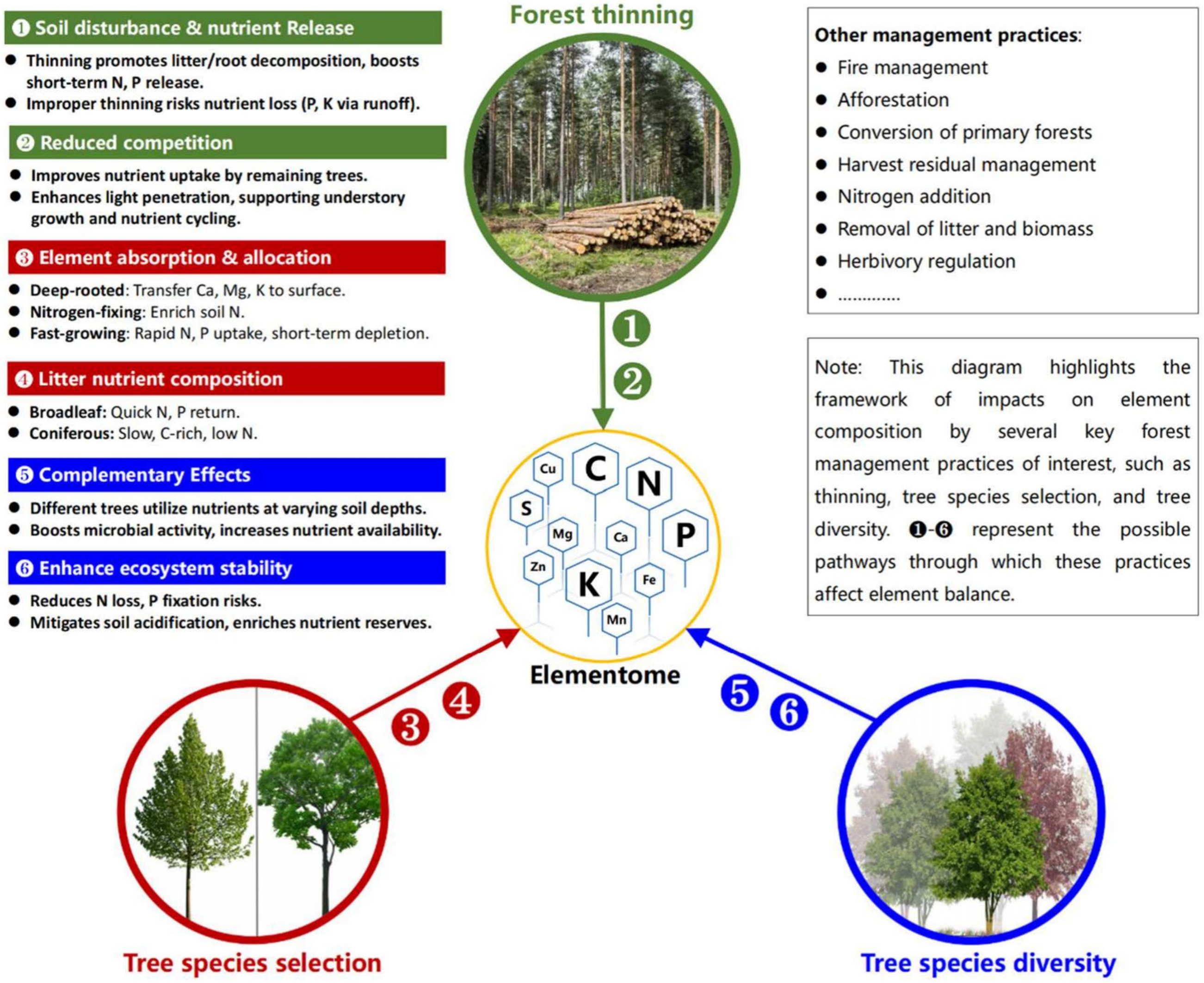
Although significant progress has been made in understanding the dynamics of warming on forest elementomes at local and short-term scales, there remains a pressing need to unravel the broader implications of warming across ecosystems, climate regimes, seasons, and varying levels of climate change intensity. Further, the effects of warming in interaction with other climate change drivers (e.g., CO_2, N addition, and drought) on the elementome of forest ecosystems are complex and multidimensional, with a poor understanding. The fertilization effects of N addition and CO_2 may be further amplified under warming conditions, leading to increased plant demand for these elements, which may trigger shortages or imbalances in the supply of elements in forest ecosystems [105]. Warming is usually accompanied by increased drought, which can limit water uptake by plants, and water limitation may lead to a decrease in the solubility of elements, affecting their availability in the soil and thus the partitioning of the elemental groups [46].

Future Directions

Future research should aim to integrate experimental data with large-scale observational studies to capture the multifaceted impacts of warming on forest elementomes. This includes exploring how warming-induced changes in element cycling affect ecosystem productivity, biodiversity, and resilience, as well as identifying thresholds where ecosystems transition to new functional states. Developing predictive models that link the dynamics of elements with ecosystem stability and services will be essential for forecasting responses to global warming and informing sustainable management practices. By advancing our understanding of these processes, we can better anticipate the ecological consequences of warming and design strategies to maintain ecosystem function and stability in an increasingly uncertain climate.

Improving Forest Management Practices under Global Change

Improving forest management practices to cope with global change involve monitoring and anticipating those changes that are going to happen in the following decades and undertaking actions to avoid their negative consequences or taking advantage of potential benefits of future changes in forest soil fertility [117, 118]. Adopting the principles and practices of sustainable forest management can provide a sound basis for addressing the challenges of climate change on forest elementomes (Fig. 2). However, our failure to implement the multi-faceted components of sustainable forest management in many forests around the world is likely to limit their capacity to adapt to climate change [119, 120]. As fertilizer practices are not common in forest ecosystems, recent studies mostly focus on the impact of tree species and tree biodiversity on forest elementomes.



❶ Soil disturbance & nutrient Release

- Thinning promotes litter/root decomposition, boosts short-term N, P release.
- Improper thinning risks nutrient loss (P, K via runoff).

❷ Reduced competition

- Improves nutrient uptake by remaining trees.
- Enhances light penetration, supporting understory growth and nutrient cycling.

❸ Element absorption & allocation

- **Deep-rooted**: Transfer Ca, Mg, K to surface.
- **Nitrogen-fixing**: Enrich soil N.
- **Fast-growing**: Rapid N, P uptake, short-term depletion.

❹ Litter nutrient composition

- **Broadleaf:** Quick N, P return.
- **Coniferous:** Slow, C-rich, low N.

❺ Complementary Effects

- Different trees utilize nutrients at varying soil depths.
- Boosts microbial activity, increases nutrient availability.

❻ Enhance ecosystem stability

- Reduces N loss, P fixation risks.
- Mitigates soil acidification, enriches nutrient reserves.

Other management practices:

- Fire management
- Afforestation
- Conversion of primary forests
- Harvest residual management
- Nitrogen addition
- Removal of litter and biomass
- Herbivory regulation
- ....

Note: This diagram highlights the framework of impacts on element composition by several key forest management practices of interest, such as thinning, tree species selection, and tree diversity. ❶-❻ represent the possible pathways through which these practices affect element balance.

Fig. 2 Conceptual diagram of the insights of how forest elementomes adapt to new environmental conditions through forest management

Tree Species Selection

Tree species significantly influence the elementomes of forest soils and soil microbes through various mechanisms [121–125]. Different trees produce plant residues (including leaves, fine root, branch, stem, etc.) with different elementomes and different productions, especially when they coexist with similar plant biogeochemical niches [4, 68, 126]. This further significantly influences element inputs into soil and microbial metabolism [51, 52]. In broad-leaved forests, litter generally contains higher nutrient concentration and less lignin compounds and results in a faster decomposition rate compared with litter in coniferous [51, 127]. As for the root nutrients, deciduous species exhibited higher root N concentration compared with evergreen species, resulting in a higher root turnover for deciduous species [128]. This is because acquisition of nutrients should be coupled with aboveground C fixation to optimize plant growth [129]. Hence, this could increase nutrient concentrations and decrease C: nutrient ratios under broad-leaved forests [121]. This could consequently accelerate microbial metallic rate in broadleaved forests, because microbes should release less C when they get a unit of N, resulting in a higher microbial C use efficiency compared with coniferous forests [130, 131]. Meanwhile, there is a positive correlation between microbial C use efficiency and forest soil carbon storage [132]. Additionally, tree root exudates can also increase soil organic matter input, which are different among tree species [133].

The impact of tree species composition on soil elementomes may depend on the geographical location, and the selection of some species over others should respond to the purpose of the forest management [125, 134]. Combined with the climate condition and soil type, each species has its own unique characteristics that can affect the soil elementomes in different ways [122, 123]. These impacts would depend on physiological properties, root types, and litter quality of trees and interactions with soil microorganisms [131]. For example, the growth of coniferous trees is generally more limited by N, while that of broadleaved trees appears to be more limited by P [135]. In the case of deciduous species, birch trees (*Betula* species) are becoming interesting due to their rapid growth rate and benefits on soil nutrient concentrations, especially on post-agricultural or reclaimed land. The results suggest that when planning to reduce CO_2 emissions by increasing use of wood biomass for bioenergy, it is crucial that nutrient limitations for tree growth are considered when selecting the tree species for replanting forests [123, 136].

Tree Biodiversity Management

Currently, tree biodiversity has declined in ecosystems worldwide, mostly due to global changes and land use changes [137, 138]. Compared with monocultures, plants growing in diverse communities change their elemental compositions, to either reduce or increase N and P concentrations depending on the species is coexistence [139–141]. This indicates that competition for resources is an important driver of elementome plasticity especially when plants have a similar biogeochemical niche. Although there are inconsistent results on biodiversity effect of tree elementomes, tree biodiversity generally promotes biomass production associated with the relaxation of interspecific competition due to niche complementarity [137, 142–144]. Moreover, this therefore increases litter and root inputs in diverse plant communities and then increases soil C and N stocks [143]. However, how this affects forest elementomes is uneven, especially accounting for elements in plant-soil system beyond the C, N, and P [145]. The tree diversity effects on plant elementomes could translate into soil and microbes through litter and root inputs [43, 146–148]. Compared with monocultures, concentrations of soil N, P, K, Ca, Mg, and microbial biomass N and C were significantly higher under mixed stands [146–148]. However, it is also possible that soil microorganisms maintain stoichiometric homeostasis by either compensatory regulation of their extracellular enzyme production or by adjustments in microbial nutrient use efficiencies to cope with excess C or imbalanced nutrient concentrations in their energy source [149].

The study of tree diversity on forest elementomes could be very useful to understand and predict ecosystem functioning [22]. Elementomes have been proven to be very useful to understand both plant ecological niches and their growth. Elementome diversity correlates well with plant ecological niches and functional diversity, and so it could be expected as a universal metric to compare ecosystems and investigate diversity–ecosystem functioning relationships [22, 150]. Meanwhile, elementome distance is a good proxy to measure the competition between organisms and temporal changes in plant and ecosystem functioning [32]. The lower elementome distance presents the stronger the competition, as species occupy the same niche [22]. It could also be used to monitor shifts in elementomes related to biodiversity changes under global changes (e.g. N deposition, climate warming or drought). For example, Fernández-Martínez [151] suggest that differences in elementomes could be used to understand community assemblages and functional diversity with different environmental conditions. As higher tree biodiversity broadens the biogeochemical niches, it could be possible to facilitate the adaptation of forests to the new environmental conditions through managing the balance between elementome plasticity and homeostatic regulation. Chen & Chen [145] indicate that plant biodiversity increased the C:nutrient ratios of plants and soils when background soil C:nutrient ratios were low but decreased them when the respective background ratios were high. Thus, forest management should pay attention to tree diversity to achieve the desired effects on forest elementomes and promote function diversity and sustainability.

Direction of Future Research

So far, there is less knowledge about the influence of forest management on the stoichiometry of elements beyond C, N and P, and how it is influenced by multiple global changes [145, 152]. In the future, we should study how taxonomic, phylogenetic, and functional richness affects the concentration, composition and stoichiometry of elements in plants and herbivores to understand the management-induced changes in forest functioning and their potential resilience to anthropogenic impacts [22, 153, 154]. Further, managing canopy structure of plantation and its tree density could also increase biodiversity and resources use efficiency (e.g., light, water and nutrients) through balancing nutrient allocation and use efficiency between the overstory and understory vegetation [155–157]. There is strong evidence that competition between species decreases with the distance between their elementomes could lead to new research and methodologies for studying community assemblages and functional diversity under global change. Although the niche theory, neutral theory, and metacommunity theory have made great progress in explaining the community assemblages of natural forest, the related research of community construction in planted forests is still scarce. In the future, more studies are needed to explore community assemblages, competitive and mutualistic interactions between species with different biogeochemical niches and the relationships between biodiversity, nutrient availability and productivity in ecosystems. This will help forest managers use practices to balance the elemental composition of forests, especially the essential elements of N, P, K, and improve ecosystem functioning and stability under global changes.

Conclusion

This review highlights the strong influence of global changes (i.e., eCO_2, N deposition, climate warming and droughts) on the elemental composition of trees, soils and soil microbes across various scales, with diverse spatiotemporal variation and underlying mechanisms. Forest elementomes not only potentially define how ecosystems work but also provide information regarding how they change their structure, stability and functioning as a response to global change. Accounting for the elemental composition, especially essential elements such as N, P and K, in the plant-soil system can largely improve projections of forest C cycle and help us facilitate the adaptation of forests to the new environmental conditions through forest management. Future research should integrate multi-source information to enhance the monitoring of forest elementomes and encourage the incorporation of their dynamics in future models of forest C cycling. In particular, we consider of vital importance to measure the elemental composition of trees, soils and soil microbes simultaneously at the ecosystem level and focus on the interactive effects of the multiple facets of global change on those elementomes in order to understand how forests will evolve in the future.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing Interests The authors declare no competing interests.

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