Interactions between Climate and Nutrient Cycles on Forest Response to Global Change: The Role of Mixed Forests

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Abstract: Forest ecosystems are undergoing unprecedented changes in environmental conditions due to global change impacts. Modification of global biogeochemical cycles of carbon and nitrogen, and the subsequent climate change are affecting forest functions at different scales, from physiology and growth of individual trees to cycling of nutrients. This review summarizes the present knowledge regarding the impact of global change on forest functioning not only with respect to climate change, which is the focus of most studies, but also the influence of altered nitrogen cycle and the interactions among them. The carbon dioxide (CO_2) fertilization effect on tree growth is expected to be constrained by nutrient imbalances resulting from high N deposition rates and the counteractive effect of increasing water deficit, which interact in a complex way. At the community level, responses to global change are modified by species interactions that may lead to competition for resources and/or relaxation due to facilitation and resource partitioning processes. Thus, some species mixtures can be more resistant to drought than their respective pure forests, albeit it depends on environmental conditions and species' functional traits. Climate change and nitrogen deposition have additional impacts on litterfall dynamics, and subsequent decomposition and nutrient mineralization processes. Elemental ratios (i.e., stoichiometry) are associated with important ecosystem traits, including trees' adaptability to stress or decomposition rates. As stoichiometry of different ecosystem components are also influenced by global change, nutrient cycling in forests will be altered too. Therefore, a re-assessment of traditional forest management is needed in order to cope with global change. Proposed silvicultural systems emphasize the key role of diversity to assure multiple ecosystem services, and special attention has been paid to mixed-species forests. Finally, a summary of the patterns and underlying mechanisms governing the relationships between diversity and different ecosystems functions, such as productivity and stability, is provided.

Keywords: atmospheric carbon dioxide (CO_2) concentration; drought; N deposition; species interactions; ecosystem stoichiometry; adaptive management; diversity—functioning relationships

1. Introduction

Worldwide, forests cover 4.03 billion hectares, *Ca.* 30% of Earth's total land area. They account for 75% of terrestrial gross primary production, 80% of Earth's total plant biomass, and contain more carbon in biomass and soils than is stored in the atmosphere [1]. Globally, they support over half of all described species and provide a range of valuable goods and ecosystem services, including food, fiber, timber, medicine, clean water, aesthetic and spiritual values [2]. Forests play a particularly significant role in climate regulation, owing to their low albedo and high rates of evapotranspiration [3,4]. Forest ecosystems are associated with the regulation of 57% of total water runoff and about 4.6 billion people depend for all or some of their water on supplies from forests [5].

Human appropriation of land and water for agriculture and other purposes; emission of extraneous compounds to the atmosphere and water, extraction of food, fuel, and fiber from natural ecosystems; and transport of species around the globe, have pervasively influenced Earth's climate, hydrology, biogeochemistry, land cover, and species diversity [6,7]. The Earth and its ecosystems are undergoing rapid global change, driven by natural and human-induced factors, that is expected to influence plant species' dominance and distribution, primary productivity, and nutrient cycles worldwide [5,8]. Demographic, economic, socio-political, cultural, scientific, and technological factors (i.e., indirect drivers) cause physical and biological changes (i.e., direct drivers) in ecosystems. Global change involves the simultaneous and rapid alteration of several key environmental parameters that control the dynamics of forests [9,10]. Hence, forest ecosystems are currently facing unprecedented shifts in environmental conditions, with implications for biodiversity patterns, ecosystem functions, and services [4,11].

In this study, I first provide a brief description of the alteration of carbon (C) and nitrogen (N) cycles and the subsequent climate change that may affect forests. Second, a review of possible responses of forests to global change impacts is presented at three different scales: (i) individual tree level physiology and growth, (ii) influence of species' interactions at the community level, and (iii) nutrient cycling and stoichiometry of forests at the ecosystem level. Finally, bases for forest management in the face of global change are succinctly discussed with the focus on mixed-species forests as an adaptation strategy. In order to provide a comprehensive insight into the current state-of-the-art, an exhaustive review of existing bibliography has been conducted.

2. Alteration of Biogeochemical Cycles and Global Climate

The post-industrial planet has experienced a striking increase in atmospheric concentrations of the greenhouse gases carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), which have substantially exceeded the highest concentrations recorded in ice cores during the past 800,000 years. In 2014, atmospheric CO_2 concentration (*Ca*) surpassed the threshold of 400 p.p.m. and this concentration may double in the 21st century relative to concentrations recorded prior to 1850 [12]. From 1750 to 2011, anthropogenic CO_2 emissions released 555 Gt CO_2 year^{-1} (GtC) and are mainly attributed to fossil fuel combustion, cement production, and land use changes such as deforestation (Figure 1A) [13]. The steep rise in *Ca* and other greenhouse gases has been associated with ocean acidification and alteration of global climatic regimes. Mean global surface temperature has raisen on average by 0.85 °C since the late 19th century, and this warming has been particularly marked since the 1970s (Figure 1B). Furthermore, air temperatures are projected to continue increasing globally, possibly by as much as 4.8 °C by 2100 [12].

On the other hand, modification of the global hydrological cycle has been spatially heterogeneous, with precipitation increases in mid- and high-latitude land areas of the Northern hemisphere, while for other latitudinal zones precipitation trends have been less consistent [14]. Occurrence of extreme weather and climatic events has also increased since the middle of the 20th century, such as increases in either the frequency or intensity of heavy precipitation in North America and Europe, or drought events in the Mediterranean and West Africa [12,15]. Precipitation patterns are predicted to undergo further changes, with most arid and semiarid areas becoming drier and with an increase in heavy precipitation events, leading to an increased incidence in floods and droughts [12]. Furthermore, there is evidence that main large-scale atmospheric–oceanic circulation patterns, such as the North Atlantic Oscillation (NAO), which affects the severity of winter temperatures and precipitation in Europe and eastern North America, and the El Niño – Southern Oscillation (ENSO), which has large regional effects around the world, are behaving in unusual ways that appear to be linked to global warming [16].

Despite the growing concern for climate change impacts, global change is not restricted to climate since other drivers exert dramatic pressures on the ecosystems [8]. Burning fossil fuels, the advent of the Haber–Bosch process to create reactive N from atmospheric N_2 as fertilizer inputs, human-caused

biological fixation of atmospheric N_2 by cultivated leguminous crops and rice, as well as an increase in mass transportation and livestock numbers have drastically altered the global N cycle [6,17–19]. The consequent formation of nitrous oxides has resulted in a widespread increase in the N deposition, which has tripled since 1860 (Figure 1C) [6,20,21]. N deposition mostly impacts northern ecosystems, especially around densely populated areas, but will likely extend to the tropics during the 21st century [20,22,23]. Annual anthropogenic N deposition amounts to roughly 165–259 Mton N year^{-1}, and only ca. 22% of these inputs ends up accumulating in the soil and biomass [24]. Although in some regions, such as Europe and North America, N deposition levels are declining since the last decades [21] due to emission abatement policies and economic transformation [25]. N deposition from agricultural activities remain high and a large percentage of ecosystems are at risk of eutrophication [26]. Long-term N loading has been shown to alter soil nutrient cycling and promote soil acidification and leaching of nitrate and soil cations [27,28], and it is one of the greatest threats to global plant diversity [6,29].
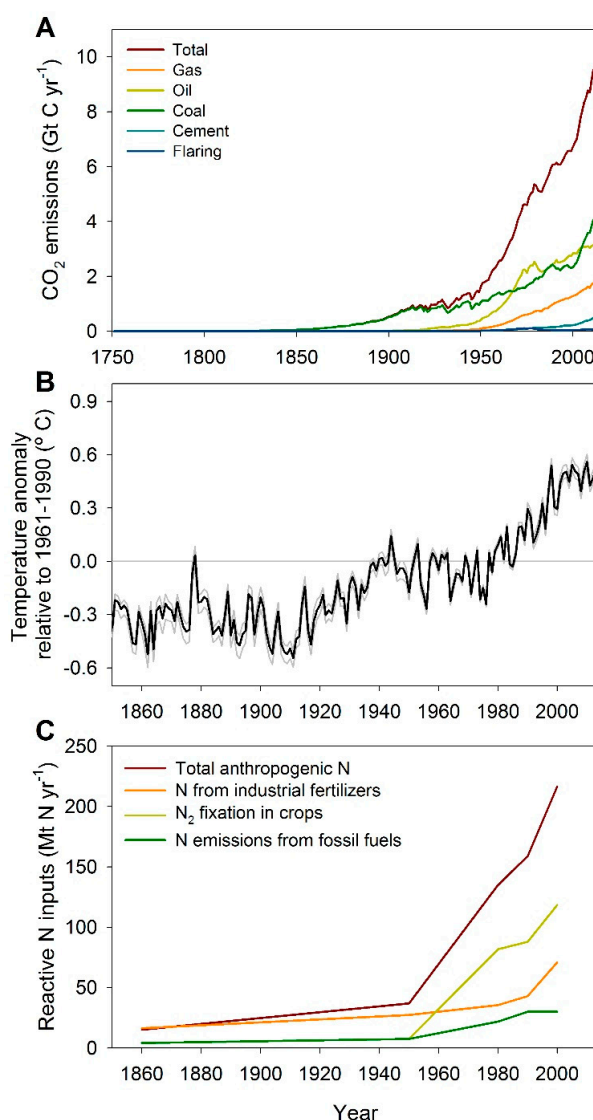

Figure 1. (**A**) Fossil fuel and cement CO_2 emissions by category, estimated by the Carbon Dioxide Information Analysis Center (CDIAC) based on UN energy statistics for fossil fuel combustion and US Geological Survey for cement production [30]. (**B**) Global average land-sea temperature anomaly relative to the 1961–1990 average temperature: grey lines represent upper and lower 95% confidence intervals [31]. (**C**) Anthropogenic reactive nitrogen inputs to the biosphere by sources [17].

The complex interactions among altered biogeochemical cycles, climate change, land-use changes, introduced species, and further global change drivers make it extremely difficult to forecast ecosystem changes [32], which can have both short-term or ecological and long-term or evolutionary consequences [13]. In addition, the interactions among different impacts of global change frequently generate non-additive effects on ecosystems that cannot be predicted based on single-factor studies [8,33–36]. The following section summarize the combined effect of C and N altered cycles and the consequent climate change at three levels of forest ecosystems' organization: (i) tree physiology and growth, (ii) tree-to-tree interactions, and (iii) nutrient cycles.

3. Impacts of Global Change on Forest Ecosystems

3.1. Tree Physiology and Growth

One of the main concerns is how elevated *Ca* could affect forests productivity [37]. Despite the significant rise in *Ca*, current levels do not suffice to saturate photosynthesis of unstressed C3 tree species [38,39]. Thus, increasing *Ca* will enhance the rate of carboxylation by the photosynthetic enzyme system and reduce photorespiration [40,41]. Increased *Ca* might also induce a partial closure of stomata, reducing water loss by transpiration, which results in an increase in the ratio of the carbon gain to water loss, i.e., water-use efficiency (WUE) [42–44]. In addition to direct leaf biochemical effects, indirect effects have been associated to rising *Ca*, such as soil moisture savings due to reduced transpiration and changes in leaf area index [45]. The combined direct and indirect effects have been commonly referred as CO_2 fertilization [46].

As a consequence of such fertilization effect, an enhancement of forest productivity is expected to occur [37]. Many tree-ring studies have reported either positive [47–51], or neutral to negative [52–58] growth responses to rising *Ca*. Such inconsistent results reveals the existence of other factors that may influence tree growth [37,40,59]. There are also concerns that CO_2 fertilization detected by tree-rings is an artifact of sampling bias [60].

On one hand, long-term elevated *Ca* exposure studies suggest that a reduction of photosynthetic capacity occurs over time [44,61]. Down-regulation has been associated with several processes such as a reduction in the capacity of dark reactions to process CO_2 due to the decrease in leaf N concentrations [62], or long-term anatomical and physiological adaptations for adjusting intercellular CO_2 concentration to rising *Ca*, including changes in stomatal density [63]. On the other hand, when trees are exposed to increased *Ca*, different co-occurring circumstances not related to CO_2 fertilization, such as temperature increase, drought events, or nutrient limitation, may become more important, thus modifying trees' ability to increase growth rates [9,64,65].

Nutrient limitation is hypothesized as a primary cause for the reduced or lacking CO_2 fertilization effect [66–68]. N constrains net primary production in terrestrial ecosystems. As a critical component of many important structural, genetic, and metabolic compounds in plant cells, N is required in relatively large quantities in connection to all growth processes [44]. Trees growing under rising *Ca* will increase the N demand and enhance N sequestration in long-lived biomass and soils, thus N availability will progressively decline [69]. As a consequence, long-term tree growth responses to increased *Ca* could be reduced due to N limitations, as predicted by the progressive N limitation hypothesis [66]. This hypothesis would be particularly important in temperate and boreal forests, whose young soils have been traditionally considered as N-limited and where N mineralization can be limited by low temperatures [70,71].

The synergistic effect of increased *Ca* and rising N deposition is expected to stimulate forest productivity [72], as has been reported in some boreal and temperate forests [73–79]. Such tree growth enhancement may be related to increases in foliar N content that can lead to improved photosynthetic capacity by enhanced photosynthetic enzyme activity and/or increasing leaf area [80,81]. Nevertheless, changes in C allocation from fine roots and mycorrhizal fungi to woody components rather than increasing photosynthesis have been also detected in long-term N-fertilization experiments [82].

Indeed, higher aboveground investments and increased shoot-root ratios have been found with increasing nutrient availability [83]. However, other studies report decreasing or negative growth responses, particularly at high N deposition rates [53,79,84–86], and even tree mortality under N saturation [77,87]. Such findings fit the N-saturation hypothesis [85,88], according to which tree growth responds unimodally to increasing N deposition (Figure 2A). Low to moderate levels of N deposition will relieve trees from growth limitation due to originally widespread N shortage. A critical threshold of N saturation is reached when N availability exceeds microbial and plant demands. Prolonged high N availability eventually leads to substantial leaching, growth decreases, and damage to forests due to nutrient imbalances, soil acidification, and increased susceptibility to biotic and abiotic stresses [9,17,84]. Thus, it is expected that high polluted forests may benefit from current declining trends in N deposition [19,89].
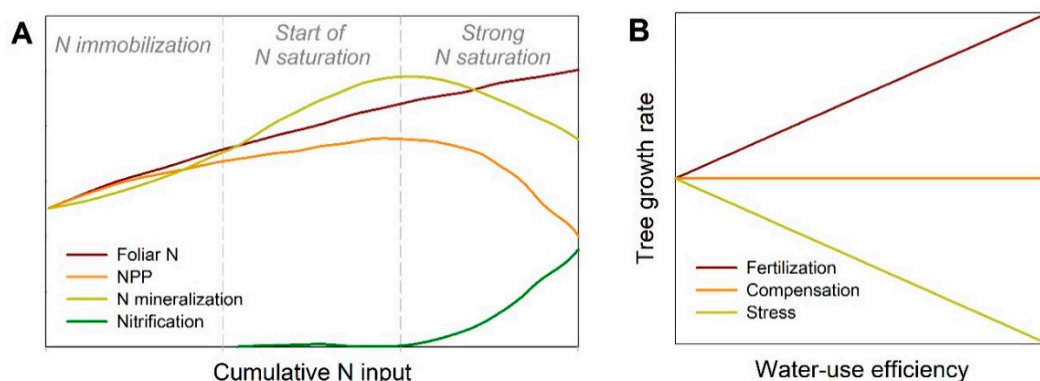

Figure 2. (**A**) Hypothetical responses of temperate forest ecosystems to long-term external N inputs in terms of foliar N, net primary production (NPP), and N biogeochemical processes, including N mineralization, nitrification, and leaching losses (adapted from [88]). (**B**) Expected relationships between water-use efficiency (WUE) and tree growth (adapted from [56]). When increased WUE, resulting from rising atmospheric CO_2 concentrations and/or water stress can override the physiological response to stress, a CO_2 fertilization effect on growth is expected (Fertilization). Conversely, if water, nutritional, or other type of stress is too strong, a negative growth-WUE would occur (Stress). No change is expected when CO_2 stimulation compensates for stress (Compensation).

Whereas boreal and temperate forests have been globally considered N-limited, older and highly leached tropical soils are usually phosphorus (P) depleted [70], as well as in Mediterranean areas due to the interaction with water availability [90]. Increases in P limitation and deterioration of tree P nutrition in temperate forests have been already observed [17,91–93], and may arise from nutrient imbalances related to high N deposition rates [17,19,88]. N surplus can induce P limitation through enhancement of nutrient requirements to maintain growth under N fertilization [24], and reduced investment in fine root biomass and mycorrhizal interactions [92,94]. This deterioration in the P nutritional status is expected to limit tree response to rising *Ca* and N deposition [79,95].

The fertilization effects of CO_2 and N on tree growth are also modulated by climatic conditions. Observed and projected increasing temperatures coupled with rising *Ca* are expected to enhance tree growth directly through the influence on xylogenesis activity [96], or lengthening of the growing season [97]. However, despite the concurrent effects of temperature and WUE improvement, resulting from rising *Ca* and reduced water availability [42,44,98], no clear evidence of positive tree growth response has been found in the last decades [53,56,99]. Instead, global growth response patterns in relation to temporal changes in WUE have been proposed to be dependent on water stress following a latitudinal gradient [56]. In cold regions, where water availability is usually not a limiting factor, the synergistic effect of warming and elevated *Ca* stimulates tree growth, as it has been observed in high altitude and high latitude regions [59,64,100]. The growth–WUE relationship becomes progressively more negative in Mediterranean, arid, subtropical, and tropical forests [52,54,58,99,101,102]. In warm

regions, higher temperatures often lead to increased leaf-to-air vapor pressure deficit, with the subsequent reduction of stomatal conductance [98,103]. Stomatal closure prolongs survival on limited water supply by reducing transpiration and the risk of hydraulic failure, but this situation also reduces photosynthesis and growth [104–106]. If water deficit is long and/or intense enough, drought-induced mortality may occur by means of hydraulic failure or hydraulically mediated C starvation, and subsequent predisposition to attack from biotic agents [105,107].

Hence, CO_2 fertilizer effect, and the subsequent beneficial influence of enhanced WUE, can be cancelled out by physiological stress (Figure 2B), including water deficit or nutritional interactions. Water availability has been found to modify tree growth responses to N deposition in boreal and temperate conifers and deciduous species [82,108,109]. This fact is supported by modeling and forest inventory-based studies, which stated that sensitivity of forest productivity to N input depends on climate variability and P nutrition [95,110]. High nutrient availability pre-disposes trees to experience greater water stress as they likely intensify water demand and reduce uptake capacity [35,82,108], and increases vulnerability to hydraulic failure under intensive water stress [111]. Meanwhile, trees growing under low nutrient availability will be more strongly affected by decreased nutrient availability and uptake during a drought event [112], thus increasing probabilities of C starvation under long-term water stress.

Furthermore, both situations may be modified by biotic agents. In fact, alterations in temperature and precipitation regimes have an impact on herbivore and pathogen survival, reproduction, dispersal, and distribution [32]. Wide areas of forests worldwide have been reported to have been affected by insect pests [113], which may cause regional mortality events [114]. Elevated nutrient availability results in low C:N ratios, thus increasing palatability to biotic agents [115]. On the contrary, low nutrient availability situations can lead to reduced production of N-based defense compounds [111], whose mobility may be limited by water stress [115].

Multiple interactions among *Ca*, N deposition, and climate over the physiological and growth responses of trees may occur. Interactions among different drivers introduce further complexity, because their effects can be synergistic or antagonistic, and not simply additive [36,116]. Understanding the dependencies among different impacts of global change is highly relevant in order to develop proper models that predict structure and functioning alterations of forest ecosystems in the face of global change [17,92]. Growth responses to environmental shifts are difficult to infer from tree responses to single factors [117]. However, observational or experimental multifactor studies in forests are still scarce (refer to [35,95,108,109,118]).

In addition, the nature of the combined effect of N deposition and drought on tree response to CO_2 fertilization is not only dependent on the physiological response of individual trees but is greatly modified by competing neighbors and stand structure [34,108,119,120]. The importance of species' interactions on the influence of global change is addressed in the following section.

3.2. Species Interactions

Tree-to-tree interactions can have greater influence on forest functioning than climate [102,121–123]. In forests, trees compete for light, water, and nutrients. When different tree species are present in a stand, forest performance can be modified from that expected from the performance of single-species forests by biodiversity effects. It has been found that trees exposed to intraspecific competition grew worse than trees in interspecific neighborhoods [102,122,124]. Two main processes contribute to positive biodiversity effects: facilitation (positive effect exerted by one species on the functioning of cohabiting species [125]), and resource partitioning (differences in functional traits that reduce competition for resources [126]). Both processes refer to biological mechanisms that modify the environment and the degree of stress experienced by trees [127], and generally are difficult to differentiate [128], so they are collectively named as relaxation (sensu [129]). Light, water, nutrient, and biotic related mechanisms underlie biodiversity effects (Figure 3). A thorough list of such mechanisms can be found in [128] and [129].

Changes in environmental conditions may lead to different situations regarding species interactions [129]. First, greater complementarity (variation of functional traits that enables a permanent association of species that enhances collective performance [130]) can develop as one or more species become less dominant. Second, changes in competitive balance among species can lead to a shift in species dominance and composition from an initial pool of species by means of selection effects [127,130]. Although tree biodiversity experiments support that positive mixing effects mostly result from selection effects [131,132], there is also empirical evidence that complementarities occur in tree mixtures that enhance productivity [133,134]. Finally, one or more species could migrate to a new area and establish novel interactions with species already established there.
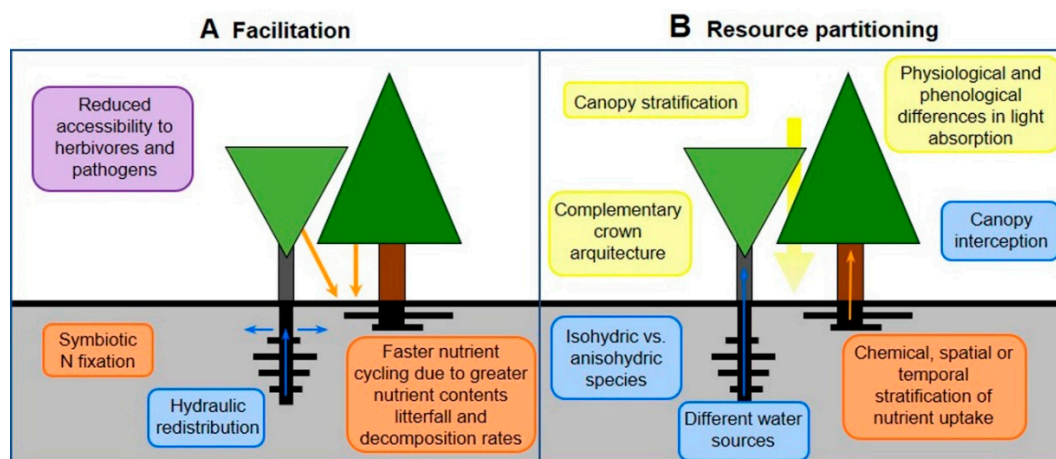

Figure 3. Illustration of underlying mechanisms that may lead to biodiversity effects divided into facilitation (**A**) and resource partitioning (**B**). Different colors represent processes related with nutrients (orange), water (blue), light (yellow), and biological agents (purple).

Some empirical studies indicate that more diverse forests tend to be less affected by droughts [135–138], although others did not find any beneficial effect [120,139,140]. After reviewing 28 studies that included 151 tree species, [141] stated that drought impacts on forests are modulated by tree diversity. However, the response is not necessarily positive, and it is dependent on multiple factors, including scale, environmental conditions, species identity, or management practices. Spatial changes in the interactions between a given combination of species have been found in many forests [142]. For instance, *Fagus sylvatica* L. underwent changing levels of stress in different regions of Europe with the same companion species [143]. Similarly, growth improvement of *Pinus sylvestris* L. with the admixture of *F. sylvatica* was dependent on site-specific conditions [102]. So environmental conditions in general, and climate in particular, play a key role determining the direction and magnitude of mixing effects on forest functioning [144–148]. Climate can modulate interactions among species directly by influencing the relative performance of each species [149], and indirectly through its effect on forest structure [150,151]. Among climatic factors, the study in [145] identified water availability as the most important factor modulating biodiversity effects.

It has been proposed that drought resistance is enhanced in mixed-species forests as long as net water-use partitioning or water-related facilitation processes take place [120], which depends on the functional traits of species involved in the mixture. The fact that responses to shifts in environmental conditions are mainly driven by species' identity effects rather than species diversity per se has been supported by recent studies [108,109,124,131,143,152–154]. Species-specific trade-offs between water conservation and C uptake [56,57,120,143,155], as well as responses to N deposition in terms of growth, succession, and mortality [77,87,108] have been broadly described.

In contrast to climate, studies assessing the influence of diversity on forest responses to N deposition are scarce. However, soil nutritional status has major influence on forests´ growth and mortality responses to climate [109,111]. Such response is species-specific [109], conferring different

competitive advantages and influencing species' interactions. From a grassland field experiment, the study in [156] shows that species-rich communities have greater growth response to the combined effect of rising *Ca* and N deposition than species-poor communities. However, whether such results can be extrapolated to forests' ecosystems is difficult to discern. For instance, the study in [108] identified different growth responses to N input as a function of the species' assemblages. Frequent shifts in understory and tree species composition has been also observed due to advantages for certain N-demanding species [29,77]. Hence, selection effects might be important in mixtures exposed to high N deposition rates.

In addition, changes in the ratio of elements of tree biomass and other ecosystem compartments resulting from high N external inputs likely affect competitive interactions [157]. Conversely: there is empirical evidence that biodiversity influences nutrient cycling [158]. Therefore, to understand and predict forest responses to global change is important to consider nutrient availability, which in turn is affected by global change. A review of the influence of global change drivers on different phases of cycle of nutrients in forests is introduced in the following section.

3.3. Nutrient Cycling

Biogeochemical cycles of key elements such as C, N, or P determine productivity, respiration, and decomposition in terrestrial ecosystems [17,71]. At the same time, C storage in forest ecosystems is controlled by the biogeochemical cycles of N and P. Living organisms require elements in strict proportions to catalyze metabolic reactions and synthesize essential compounds with specific element ratios: i.e., stoichiometry of organisms [159]. Thus, biogeochemical cycles are biologically coupled due to conserved elemental stoichiometry of plants and microorganisms that drive C, N, and P cycles [160]. Elemental stoichiometry can be associated with important ecological processes and ecosystem traits, such as ecosystem composition and diversity [161], the ability of trees to adapt to environmental stress [36,162], composition of decomposer communities and litter decomposition rates [163–166], or growth rate properties [159]. The latter are reflected in the growth rate hypothesis, which states that organisms must increase the relative allocation of P to P-rich ribosomal RNA to meet the demands for protein synthesis required for rapid growth, which is possible under low N:P ratios in the environment [159].

However, global change has drastically affected the biogeochemical cycles of C and nutrient elements of Earth's ecosystems [6]. Rapid environmental shifts have induced the imbalance among C, N, and P in ecosystems owing to different degrees of control by biological and geochemical processes [24,160]. Figure 4 summarizes possible mechanisms by which stoichiometry of trees can be modified as a consequence of increasing *Ca*, climate change and high N inputs. Forest disturbances derived from extreme events such as fires or droughts may also have strong impacts on nutrient cycling [32]. Forest fires are a global phenomenon and over 300 million ha of forested lands are annually burned [113]. Nutrient-related effects of fires include acceleration of nutrient cycling, soil erosion, and volatilization of soil nutrients [32]. Forest susceptibility to fire depends on forest composition and structure [167]. Furthermore, the structure of litter layer and its decomposition dynamics are related to their flammability, so affecting fire spread and intensity [34].

Litterfall constitutes a major proportion of nutrient cycling between plant and soils in forest ecosystems [168]. Climatic conditions are closely linked to variations in litterfall annual production [169–173], seasonal patterns [118,171,174–176], and nutrient composition [118,177–180]. Hence, projected increasing temperatures and alterations of precipitation regimes will have striking consequences on litterfall dynamics. Altered soil nutrient availability, due to impaired N and P deposition [17], has been also found to modify litterfall composition through the impact on nutrient uptake, allocation, and resorption processes [112,181–183].

Decomposition rates are driven by multiple factors, such as soils, climate, decomposer community, and litter quality [163,184]. Litter quality has been identified as the most important factor controlling decomposition in two global meta-analysis [185,186]. Stoichiometric relationships of leaf litter are

mainly the product of green leaves ratios and resorption [187,188], which undergo significant variations as a response to global change [157]. Under high *Ca* C:N and C:P ratios generally increase [189], and evidences of positive relationships between rising *Ca* and N:P ratios have been found [190]. High N deposition rates are clearly associated with foliar N:P increases [17], and with decreases in N resorption, thus boosting litter N:P ratios [191,192]. Warming and drought have been proposed to increase C:N and C:P ratios due to mechanisms associated with water conservation and increased nutrient use efficiencies [189], as well as, N:P ratios [157]. Globally, moist and warm conditions reduce and enhance N and P resorption efficiencies, respectively [178,193]. Furthermore, moisture conditions largely modulate the effect of rising *Ca* and N deposition on the stoichiometry of nutrient recycling [118,192].
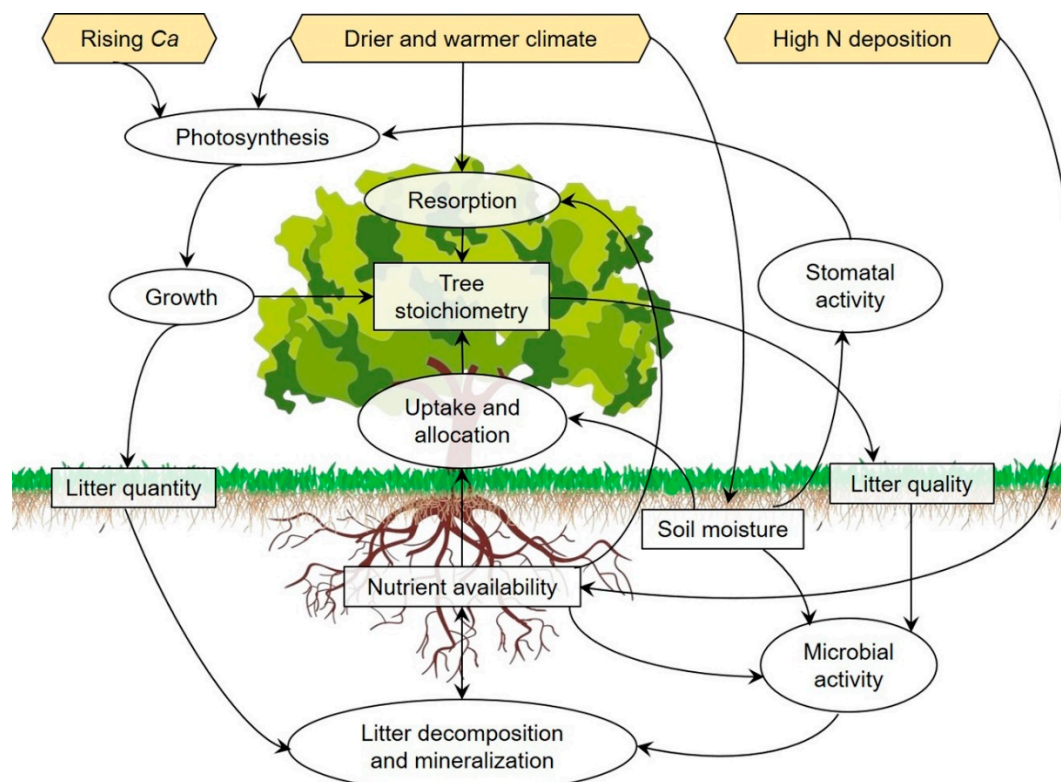

Figure 4. Conceptual diagram of the impacts of global change on processes controlling stoichiometry of trees. Yellow hexagons are global change drivers: increasing atmospheric CO_2 concentration (Rising *Ca*); climate change leading to drier and warmer conditions and high rates of atmospheric nitrogen (N) deposition; rectangles represent nutrient pools; and ellipses indicate biogeochemical processes.

The consumer-driven nutrient recycling theory predicts that the balance between litter stoichiometry and microbial element use efficiency directly determines nutrient recycling ratios [159]. Since soil microbes are largely homeostatic in terms of elemental stoichiometry, the stoichiometric imbalance between litterfall and microbial communities results in microbial activity limitation by a nutrient, and thus its immobilization in microbial biomass [192]. Decomposition rates have been negatively associated with high litter N:P ratios [194–196], hence the above-mentioned global change impacts on litter stoichiometry are expected to slow down nutrient return to soils. In fact, such phenomena has already been observed [197]. Furthermore, litterfall stoichiometry has been found to influence soil microorganism's diversity [164,166].

Nutrient mineralization is further affected by drought since reduced soil water availability decreases microbial activity in soils and ion mobility [112]. Water status also determines the CO_2 impact on mineralization [198]. Furthermore, warming increases net N mineralization and nitrification, and reduces soil P availability [199,200]. Finally, N deposition is known to impair litter decomposition, although the direction and degree of such response is dependent on interactions among deposition

rates and litter quality [201]. High external N inputs also contribute to acidification and eutrophication of forest soils, thus leading to increased mineral nutrient losses by leaching to surface and ground waters (Figure 2A) [88,202].

4. Forest Management under Global Change Scenarios

4.1. A Paradigm Shift

Historically, forest management has been focused on a single dominant objective, most commonly timber production. In addition, an emphasis on increasing management efficiency by simplifying and homogenizing forest structures and operations has prevailed [203]. However, global change drivers and their interactions have boosted variability and uncertainty regarding future environmental, biological, and social conditions [204], together with a likely increase in the frequency and severity of disturbances and the appearance of new combinations of disturbances (see previous sections) [11,32]. Increased concerns about the provision of an assortment of ecosystem goods and services have led to a shift in focus of the attention from timber towards a wide range of economic, social, and ecological objectives [5,205]. They include conservation of biological diversity, maintenance of the productive capacity of forest ecosystems, maintenance of ecosystem health, conservation and maintenance of soil and water resources, maintenance of forest contribution to global C cycles, or maintenance and enhancement of long-term multiple social and economic benefits [206]. Hence, forest management and silvicultural practices need to be re-evaluated as the record of historical conditions cannot provide a straightforward guide for future silvicultural practices [207].

Industrial plantations are managed for maximum productivity and profitability, therefore, mono-cultures are preferred due to the uniform nature of the trees, ease of harvesting, wood quality attributes, processing of timber, accurate yield estimates, and other industry-related reasons. Instead, forests have been proposed to be managed as complex adaptive systems, because they are heterogeneous, highly dynamic, and contain many biotic and abiotic elements which interact across different levels of organizations with various feedback loops [208,209]. Forests are non-linear systems, highly sensitive to initial conditions, which makes precise predictions about their future behavior very difficult. They also show a hierarchical organization: elements at different levels interact to form an architecture that characterizes the system [210]. Adaptation of forest management to deal with global change is a dynamic process which involves system resilience and adaptability, not only from the ecological point of view but also from that the social, political, and economic. Thus, it shifts the importance away from exclusively direct aspects of productivity [11,211]. As future uncertainty increases, as it has been predicted under global change, the increased emphasis on resilience and adaptation will become more important.

A range of silvicultural systems to adapt forest management to global change have been proposed [212,213]. One example is the systemic silviculture management, whose strategies are based on an adaptive approach and continuous monitoring of the natural responses of each forest stand to silvicultural interventions [214]. Another proposal is the 'close-to-nature' approach, which promotes diversity regarding species mixtures, age structure, spatial scales, and heterogeneous stand structures as opposed to even-aged intensive industrial plantations [204,215]. Such silvicultural developments are focused on diversity and heterogeneity, which are more likely to cope with new conditions when subject to unpredictable stress or disturbance, and thus have been proposed for dealing with global change [216]. They imply different stand level adaptation measurements regarding forest regeneration, thinning, or harvesting. Thinning has been shown to partially mitigate the negative impacts of more arid conditions [122,217–219]. Enrichment sowing and planting in naturally regenerated stands, tending, or small-scale harvesting are adaptation options that can promote genetic and structural diversity and mixed species forests [213]. Mixed forests have been proposed as an adaptation strategy to cope with global change [209,220] because they are considered more resistant to disturbances and extreme events [34,136,221], and may provide ecosystem goods and services

more effectively than pure stands [222,223]. Mechanisms leading to greater multifunctionality under higher unpredictability in environmental conditions, as well as, some management considerations, are reviewed in the following section.

4.2. Mixed-species Forests as Adaptation Strategy

There is increasing evidence supporting that biodiversity fosters forest productivity on both regional [224–229] and global scales [146,230,231]. This increased productivity in mixtures compared to the weighted contribution of each species in pure stands is commonly referred as overyielding. In a global meta-analysis, the study in [230] found that mixtures are 24% more productive than pure forests, although a later study reported a global growth increment of 15% based on a more conservative analysis [146]. The diversity–productivity relationship represents an asymptotic curve [226,231], and it has been found to be highly dependent on other factors such as climate, local conditions, stand density and evenness, stand age, functional traits involved in the mixtures, etc. [56,102,120,128,143,150,230,232–234].

Mixing effects vary along spatial gradients of resource availability [142] and over time due to environmental fluctuations [235] or changes in resource acquisition and species interactions with stand development [236]. Different responses to environmental shifting of the diversity–productivity relationships have been reported: increasing relaxation under more stressful conditions [135,145,237] and increasing relaxation with improved site quality or climate conditions [102,139,227]. However, such contrasting findings can be explained under the theoretical framework proposed by [128]. It is an extension of the stress gradient hypothesis [125], and states that when species interactions improve the availability, uptake or use efficiency of the resource that is becoming more limiting along a spatial or temporal gradient, relaxation also tends to increase along that gradient [142,238,239]. See Figure 3 for examples of mechanisms of relaxation regarding different resources.

Therefore, positive biodiversity effects on forest productivity arise only when relaxation processes occur in regard to the more limiting factor, which depends on the functional traits of species included in a mixture (see Section 3.2. for further discussion). In general, if underlying mechanisms of species interactions result in improved availability, uptake, or water (nutrient) use efficiency, biodiversity effects will become more positive along decreasing gradients of water (nutrients) availability. Otherwise, forests productivity will increase as soil properties or climate improve and denser canopy can develop if light interception is enhanced as a result of species interaction (Figure 5) [128,142]. As a case in point, the authors in [102] found in a tree-level study that although the admixture of *F. sylvatica* increased WUE of *P. sylvestris*, it only translated into growth improvements under mesic conditions. Growing together with *F. sylvatica* increased light absorption of *P. sylvestris* [240] as a result of enhanced morphological variability, crown extension, and canopy space filling [151,241]. It is likely that such beneficial light-related mixing effects on *P. sylvestris* were overridden by competition for water resources with *F. sylvatica* in drought-prone environments as faster depletion of soil water and higher canopy interception have been reported in mixtures [139,219]. Such results are in agreement with other studies [122,219,242] and they are supported by stand-level simulations at longer time scales [243].

Higher stability of mixed forests against environmental fluctuations than single-species forests has been reported in empirical [244–246] and modeling approaches [247,248]. Ecological stability involves several concepts, such as resilience, resistance, or persistence of ecosystem properties [249]. The diversity–stability relationship, which assess temporal stability of productivity, may arise from different mechanisms. Asynchrony in the species response to environmental fluctuations has been identified as a key factor in the stabilizing effect of diversity [250,251] and it is in accordance with the insurance hypothesis [252]. Species asynchrony generates asynchronous population dynamics that enables productivity compensation among species and promote productivity stability at community level [251]. Competitive reduction and facilitation resulting from species interactions also contribute to stability through the overyielding effect, because increased abundance or biomass reduced the risk of stochastic demographic dynamics [250].

Species' interactions may also promote resistance against natural disturbances such as drought [136,253,254], but see [120,139,143]; fire [255]; windstorms [256]; or insect herbivory [257]. Several mechanisms have been proposed to enhance the resistance of mixed forests. These include complementarity on resistance traits, reduction of fuel and food resources, or diminished accessibility to target trees [34]. Likewise, increased resilience to extreme events have been reported in more diverse forests [136,258]. Further forest functions and services that appear to improve under increasing diversity comprise C storage capacity [259], ecosystem health and vitality [220,221], or reduced economic risks [260].
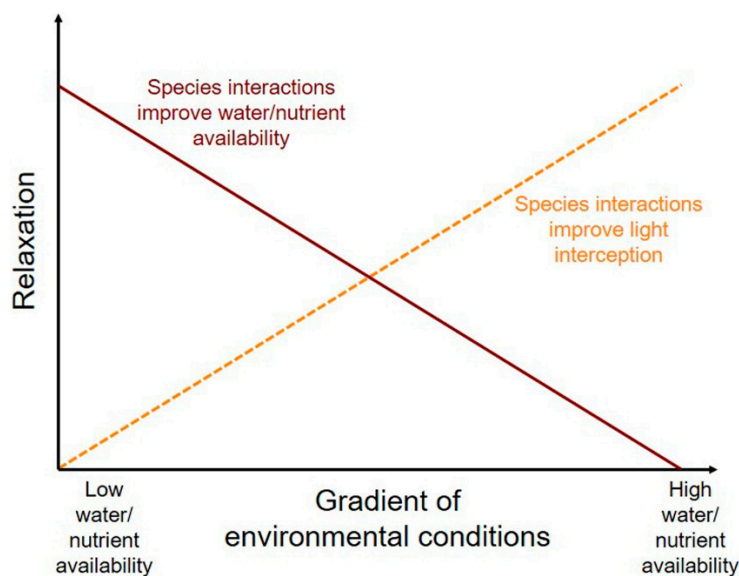

Figure 5. Conceptual framework for variation of mixing effects along spatial or temporal gradients of resource availability (based on [142] and [128]). If species' interactions enhance relaxation (sensu [129]) regarding water or nutrients, positive biodiversity effects will increase along decreasing gradients of water or nutrients availability (solid dark red line). On the contrary, light-related interactions will result in increased forest productivity as site quality and climate improve (dashed orange line).

However, despite the important benefits described above, managing mixed forests can be more complex than managing pure plantations because the provision of multiple services needs to be optimized, such as productivity, sustaining biodiversity, or climate change mitigation. Managing forests in a mixed condition requires more complicated operations, there are very few instructions for designing and managing mixtures, and the right combination of species and site conditions need to be achieved [261]. Indeed, the selection of the adequate species combination with different functional traits that enhance relaxation regarding the more limiting factor of a given site appears to be more important than increasing only the number of species in the stand [34,129,243,258]. Spatial scale is a further issue to be considered when planning mixed forest management. Positive biodiversity effects have been associated with local neighborhood species interactions rather than processes acting at stand level [229]. Hence, mixing configurations with close inter-specific intermingling can maximize benefits of species mixing, which has been supported in field studies [262] and modeling approaches [263], instead of mixing pure patches at the stand or landscape level. Moreover, planting schemes and/or thinning operations can control stand density in managed mixed stands. The degree and intensity of species interactions is modulated by stand density, so that at low densities interactions may not be strong enough to impact productivity, while at high densities competition can outweigh relaxation [128,150]. Designing management plans for mixtures may become even more complicated due to the lack of long-term field studies covering the whole lifespan of forest stands, the spatial and temporal changes in species interactions, and the uncertainty in changing environmental conditions. As a consequence, forest growth models represent a useful means of understanding and predicting forest functioning and

they are a valuable decision-support tool in forest management [264]. Hybrid models, which combine ecological processes and empirical data, are able to simulate the effect of species interactions of novel species combinations and proportions under novel environmental conditions, disturbances regimes, and/or management interventions [265].

5. Conclusions

Human-induced factors have led to the alteration of global biogeochemical cycles and climate. Increasing uncertainty is predicted regarding future environmental conditions with significant impacts on forests functioning and the range of services provided by forests. A multidisciplinary approach is needed to understand the complex effects of global change drivers on different levels of forests' organization. Studies downscaled to small levels of organization (i.e., organs, individuals) are important to elucidate mechanisms underlying community or landscape level patterns [129].

Nutritional status, C metabolism, and water balance of trees are affected by global change, so forest functions, such as productivity or drought resistance, will be likely modified. It is noteworthy that such tree and stand response is modulated by interactions among species. In general, enhanced performance of more diverse forests has been reported, although it depends on species combination, rather than on the number of species. Environmental conditions also impact species' interactions and the concomitant effect of rising CO_2 concentration, increasing drought frequency and intensity, and high N deposition rates, which alter population and community dynamics. Complex interactions among global change impacts have been also described on ecosystem processes that control the transfer of matter and cycling of nutrients. Thus, highlighting the importance of multi-factor studies using both empirical and modeling approaches.

Therefore, forest management must adapt to hardly predictable future environmental conditions, and so the emphasis shifts from productivity towards forests´ resistance and resilience. Encouragement of mixed forests, which enhance functional diversity and structural heterogeneity, has been proposed as an adaptation strategy to cope with global change. It is supported by the positive relationships found between diversity and productivity, stability, resistance, or resilience of forests. Nonetheless, there are important issues to consider when designing management plans of mixed forests, such species identity, mixing patterns, or stand density.

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