Biodiversity-ecosystem functioning relationships in forests

Do the same processes drive biodiversity-ecosystem functioning relationships above- and belowground in forests?

Abstract

Climate change and deforestation are presenting huge threats to forest biodiversity. This decline poses a risk to the ecosystem functioning of forests. The processes determining how biodiversity impacts ecosystem services in forests can differ between above- and belowground communities. This literature review provides an overview of the different processes driving the above- and belowground biodiversity-ecosystem functioning relationships in forests. Evidence for both the complementarity effect hypothesis and the selection effect hypothesis was evaluated. Among the complementarity causes (i.e. spatial partitioning, temporal partitioning, partitioning across the chemical form of nitrogen, resource enrichment, physical stress buffering, negative and positive biotic feedback) that enhance ecosystem functioning, spatial partitioning is predominant above- and belowground in forests. In addition, temporal partitioning and physical stress buffering were also widely found to drive the aboveground positive biodiversity-ecosystem functioning relationship. Whereas partitioning across the chemical form of nitrogen together with the overlap between resource enrichment and positive biotic feedback, via nitrogen fixing species and mycorrhizae, enhances belowground ecosystem functioning. Furthermore, the selection effect hypothesis can also act as a driver of the biodiversity-ecosystem functioning relationship above- and belowground in forests. Compared to aboveground studies, belowground processes are poorly studied. Therefore, future research should focus on providing a more detailed picture of the belowground processes driving biodiversity and their effect on ecosystem functioning. Which could increase the efficiency of management and conservation of ecosystem functioning in forest.

Layman's summary

Currently, biodiversity is declining in forests through climate change and deforestation. Biodiversity has a positive effect on the functioning of ecosystems. Therefore, the loss of forest biodiversity can severely impact humans, as forest sequester large amounts of carbon. There are different hypotheses on how the positive relationship between biodiversity and ecosystem functioning is driven. It could be that forests with a higher biodiversity have a higher chance of containing a species that has a large impact on ecosystem functioning (selection effect hypothesis). Or it could be because a higher biodiversity results in more species complementing each other (complementarity effect hypothesis). Species can complement each other through several complementarity causes: through partitioning in resource use (by different spatial, temporal of chemical partitioning), through facilitation each other with abiotic factors (by making resources more available or reduce physical stress) and through biotic feedback (reducing enemies or increasing mutualists). In forests, the drivers of the biodiversity-ecosystem functioning relationship have similarities and differences between aboveground and belowground. For both above- and belowground, spatial partitioning is a strong driver. In addition, temporal partitioning and the reduction of physical stress were also widely found to drive the aboveground positive biodiversity-ecosystem functioning relationship. Whereas partitioning across the chemical form of nitrogen together with the overlap between making resource more available and positive biotic feedback, via e.g. nitrogen fixing species, enhances ecosystem functioning. Furthermore, the selection effect hypothesis can also act as a driver of the biodiversity-ecosystem functioning relationship above- and belowground in forests. However, as literature on this subject (especially belowground) is limited, the processes driving the relationship could differ in reality. Therefore, future research is needed to paint a more detailed belowground picture of the biodiversity-ecosystem functioning relationship in forests. This could increase the efficiency of management and conservation of ecosystem functioning in forest.

Introduction

Climate change has impacted the world in many ways. Due to greenhouse gas emissions, the world is facing global warming, rising sea levels and more extreme weather events (IPCC, 2022). Not only does this affect human populations, the current biodiversity loss of flora and fauna has been unprecedented. The presence of biodiversity is important to humans for cultural services, but it also affects ecosystem functioning. Thereby providing humans with food provisioning, carbon sequestration, etc. This biodiversity-ecosystem functioning relationship has been an important topic in ecological research since a few decades (Jochum *et al*., 2020). Most of the research is performed in grasslands (Nadrowski *et al*., 2010), but the relationship in forests also provide an interesting research field.

Forests provide several ecosystem services, such as sequestration of carbon and production of oxygen. Through these mechanisms, forests could mitigate the effects of climate change (Mengist & Soromessa, 2019). However, forest ecosystems are also facing an alarming decrease in biodiversity through deforestation (IPCC, 2022). Therefore, it is important to research the effect of biodiversity on ecosystem functioning in forests, since the decline of biodiversity could have a more detrimental effect than expected. Most studies on the biodiversity-ecosystem functioning relationship has been focused on the community aboveground. However, different processes could be driving this relationship.

Therefore, this review aims to answer the question: *Do the same processes drive biodiversity ecosystem functioning relationships belowground as aboveground in forests?* First, an overview is provided for biodiversity-ecosystem functioning research. This is followed by presenting evidence supporting the different processes as drivers above- and belowground. At the end, the research question is answered, suggestions for future research are made and a conclusion is drawn.

Biodiversity-ecosystem functioning research

Biodiversity-ecosystem functioning relationships have been suggested in the 1990s (Schulze & Mooney, 1993) and have been an important topic in ecological research ever since (Jochum et al., 2020). Ecosystem functioning, as measured in this type of research, is a term that consists of the sizes of pools of material (carbon, biomass, etc.) and the rates of processes (fluxes of energy or material between pools) (Hooper *et al*., 2005). In biodiversity-ecosystem functioning research, biomass, carbon storage and productivity are often used as measures of ecosystem functioning.

Within biodiversity-ecosystem functioning research, two hypotheses are commonly used: the complementarity effect hypothesis and the selection effect hypothesis. The complementarity effect hypothesis states that biodiversity enhances ecosystem functioning through complementarity in species (Loreau & Hector, 2001). Three complementarity causes have been identified, namely resource partitioning, abiotic facilitation and biotic feedback. Resource partitioning is the complementary use of resources (Jesch *et al*., 2018). One form of resource partitioning is spatial partitioning, in which species differentiate between their uses of the available space. This could be horizontally or vertically and can increase the efficiency of resource uptake, since species gather their resources from different places. Another form of resource partitioning is temporal partitioning. This complementarity cause can act as a driver of the biodiversity -ecosystem functioning relationship when species use the same resources at different times. Thereby making more efficient use of the available resources. The last form of resource partitioning is resource partitioning across the chemical form of nitrogen. Within ecosystems, nitrogen is available in different chemical forms, such as NO_3^- and NH_4^+. When species differentiate between their form of nitrogen uptake, it leads to complementary use of this resource and a more efficient resource uptake (Barry *et al*., 2019).

The second complementarity cause is abiotic facilitation, in which species facilitate a more favourable environment for other species (Wright *et al*. 2017). One way for this to occur is through resource enrichment. This complementarity cause take place when a species makes a previously unavailable resource available for other species. This increases the amount of resource in a community and thereby creates a more favourable environment. Another form of abiotic facilitation is physical stress buffering. With this complementarity cause, species protect another species form physical stress, thereby creating a more favourable environment (Barry *et al*., 2019).

The third and final complementarity cause is biotic feedback (Barry *et al*., 2019). When negative biotic feedback occurs, species-specific enemies have less effect because biodiversity decreases the concentration of that species. This decrease in damage by enemies leads to enhanced ecosystem functioning. Positive biotic feedback, on the other hand, occurs when mutualistic relationships increase with increased biodiversity. These relationships can enhance ecosystem functioning through positive rewards obtained by plants (Barry *et al*., 2019).

The selection effect hypothesis implies that through increased biodiversity, the chance increases that one or a few species occur with favourable traits. These species become dominant in a community and have a strong influence on ecosystem functioning (Loreau & Hector, 2001). Often, these species perform better in monocultures than in mixtures. The hypothesis suggests that if the dominant species were to disappear from the community, the ecosystem functioning would severely diminish.

Most research on the biodiversity-ecosystem functioning relationship in controlled experiments show an positive relationship. However, some studies in natural systems obtain neutral or negative relationships. Several explanations can be given for these results. For example, a negative selection effect can occur, in which one species has a large negative effect on ecosystem functioning (Jiang *et al*., 2008). Another reason for negative or neutral relationships could be that environmental conditions are driving ecosystem functioning (Sandau *et al*., 2018).

Table 1. The number of articles found that support a complementarity cause or the selection effect hypothesis. Blue indicates complementarity causes labelled as resource partitioning, red indicates complementarity causes indicated as abiotic facilitation and green indicates complementarity causes labelled as biotic feedback.

	Complementarity effect		Selection effect
Aboveground	Spatial partitioning	15	30
	Temporal partitioning	1	
	Partitioning across the chemical form of nitrogen	0	
	Resource enrichment	1	
	Physical stress buffering	1	
	Negative biotic feedback	1	
	Positive biotic feedback	0	
	No complementarity cause presented	10	
Belowground	Spatial partitioning	7	6
	Temporal partitioning	0	
	Partitioning across the chemical form of nitrogen	1	
	Resource enrichment	1	
	Physical stress buffering	0	
	Negative biotic feedback	0	
	Positive biotic feedback	1	
	No complementarity cause presented	1	

For this literature review, an online search was performed to gather evidence on different processes driving biodiversity-ecosystem functioning relationships above- and belowground in forests. This resulted in a total number of 76 studies found (table 1). Of these studies, the majority (59) was focussed on aboveground biodiversity-ecosystem functioning relationships. Furthermore, some studies (11) did not mention a complementarity cause, but did contribute enhanced ecosystem functioning to the complementarity effect. These studies are included in the table as evidence for the complementarity effect, but are not included as evidence for a particular complementarity cause. Since the search terms included "biodiversity ecosystem function", there was no evidence found for some complementarity causes as the link between the increased biodiversity and enhancement of ecosystem functioning was not made. Therefore, evidence for these complementarity effects was found using more loose search terms or via references in other articles.

Aboveground biodiversity-ecosystem functioning relationships

Most biodiversity-ecosystem functioning research has been focused on the aboveground relationships. Both the selection effect hypothesis and the complementarity effect hypothesis have been found to drive this relationship. Below, the evidence that supports those hypotheses is discussed.

Complementarity effect hypothesis

Resource partitioning

As mentioned above, there are three complementarity causes that enhance ecosystem functioning. The first one is resource partitioning, that can occur in different forms. One of these is spatial partitioning. In forests, spatial partitioning can most easily be found in forest stratification. Experiments show that a higher species diversity causes the height of trees to be more distributed in the canopy space. This leads to overyielding, thus an increase in ecosystem functioning, through less competition for space (Tatsumi, 2020; Williams, *et* al., 2017). Furthermore, spatial partitioning can also increase the resource uptake in forests. As the available space is more densely packed, the light capture increases (Sapijankas *et al*., 2014). Through the more efficient use of this resource, the productivity of the ecosystem increases (Ali *et al.*, 2019). In addition, biodiversity increases litterfall through spatial partitioning of the canopy (Zheng *et al*., 2019), which causes resource partitioning. This creates intertwining of multiple causes of the complementarity effect, namely spatial partitioning (resource partitioning) and resource enrichment (abiotic facilitation). However, the spatial partitioning can also have negative impact on ecosystem functioning. The increased biodiversity of overstory layers can reduce the biodiversity and productivity of understory layers, as less light reaches this layer (Zhang *et* al., 2017; Zheng *et al*., 2022). This indicates that all forest strata should be taken into account during biodiversity-ecosystem functioning relationship research (Ali & Yan, 2017).

The temporal partitioning in aboveground forests is less studied than the spatial partitioning, but there is evidence that temporal partitioning plays a role in the complementarity of species. For instance, temporal niche complementarity due to difference in phenology can enhance light capture in mixtures (Sapijanskas *et al*., 2014) The uptake of water is also an example of temporal partitioning. Research shows that water use of has seasonal differences between species. These differences are caused by different growing periods of their leaves, flowers, fruits, etc. (Meinzer *et* al., 1999; Stratton *et al*., 2000). Furthermore, the different growing periods of flowers and fruits also causes temporal partitioning for reproduction. The timing of reproduction determines which species interact with the new individuals during their growth (Usinowicz *et al.*, 2017). This not only includes competition from other individuals, but also includes the mutualistic relationships with others during seed dispersal and germination (Usinowicz *et al*., 2012). Temporal partitioning can also affect ecosystem functioning over a longer time than seasonality. Complementarity between species in their successional rates, i.e. early and late successional species, can increase the ecosystem functioning of a growing forest (Yuan *et al*., 2019).

Despite aboveground research being more prominent in the research on biodiversity-ecosystem functioning relationships, the resource partitioning across the chemical form of nitrogen is better studied belowground. However, the canopy nitrogen uptake in forests also shows evidence for resource partitioning. For example, conifers mostly filter out NH_4^+, leaving mostly NO_3^- for understory species to take up. This results in complementary N use strategies among different forest strata (Schwarz *et al*., 2014).

Resource partitioning is the best documented process of complementarity as a driver of the aboveground biodiversity-ecosystem functioning relationship in forests. Especially the spatial partitioning is well researched and provides clear evidence that this process enhances ecosystem functioning. However, resource partitioning across the chemical form of nitrogen aboveground is less studied, as this current evidence does not link it to ecosystem functioning aboveground.

Abiotic facilitation

The second complementarity cause that enhances ecosystem functioning is abiotic facilitation. There are two ways in which abiotic facilitation can affect ecosystem functioning. The first is resource enrichment, in which neighbouring species make resource accessible. There has been little evidence found for this aboveground in forests, since most resource uptake of plants happens belowground. However, litterfall of trees provides other trees with nutrients. The litterfall of neighbouring trees can increase the yield of mixtures due to improved site quality (Sapijanskas *et al*., 2013), providing abiotic facilitation.

The process of physical stress buffering has been more widely shown in literature, for example in microclimates. Microclimates, like the rest of the planet, are warming, but the forest canopy can mitigate the effects (Zellweger *et al*., 2020). This provides the lower parts of the forest with less evaporation and lower temperatures. Mixtures, compared to monocultures, amplify these mitigating effects on microclimates (Fichtner *et* al., 2017; Montgomery *et al*., 2010; Zhang *et al*., 2022).

Overall, the process of abiotic facilitation is a driver of the aboveground biodiversity-ecosystem functioning relationship. However, there is more evidence for physical stress buffering than for resource enrichment.

Biotic feedback

The third and final cause that enhances ecosystem functioning is biotic feedback. Negative biotic feedback occurs when the damage done by antagonists, such as herbivores and pathogens, decreases with a higher biodiversity. This can best be seen with species specific herbivores. In monocultures, the specific species is highly available, whereas the availability of the specific species is less in mixtures. The spatial barrier might be too big to overcome for some herbivores, such as small insects, therefore causing less damage (Jactel & Brockerhoff, 2007). For aboveground pathogens, similar effects can be seen. A higher richness can reduce the pathogen load, as some species may not be afflicted by the pathogen. This results in less carriers and therefore less pathogens (Hantsch *et al*., 2013).

Positive biotic feedback has been less studied as a cause for the complementarity effect than negative biotic feedback. Aboveground mutualistic relationships in forests have mostly been studied in the context of habitat fragmentation. Habitat fragments are known to be less biodiverse than non-fragmented forests. Studies show that habitat fragments also are less diverse than non-fragmented forests when it comes to seed dispersers. Due to specific mutualistic plant-disperser relationships, the disappearance of one means the disappearance of the other. If the disperser were to disappear, for example, seedlings would occur closer to parental trees and would be less likely to survive this competition (Cordeiro & Howe, 2003). In theory, this situation could be reversed. Then, one could argue that higher plant diversity would lead to higher disperser diversity. However, these studies have not been performed and situation is only theoretical.

Overall, the aboveground biotic feedback in forests is not well studied, especially in regards to ecosystem functioning. Studies often looked at the relationship between biodiversity of trees/plants and their mutualists or antagonists, but failed to include the effect on ecosystem functioning. Furthermore, there was no evidence for the aboveground positive biotic feedback, either determining that there is a knowledge gap or that this process does not drive the aboveground biodiversity-ecosystem functioning relationship.

Selection effect hypothesis

The selection effect hypothesis states that ecosystem functioning enhances with increasing biodiversity through increased chance of the community containing a highly productive species (Loreau & Hector, 2001). Most studies performed on the selection effect find that one or a few dominant species are responsible for a great amount of aboveground biomass (e.g. Finegan *et* al., 2014; Villa *et al*., 2020; Xu *et al*., 2020), carbon storage (e.g. Balvanera *et al*., 2005; Lin *et al*., 2016; Yuan *et al*, 2018) and/or productivity (e.g. Finegan *et* al., 2014; Ayma-Romay *et al*., 2021). However, the selection effect can also enhance ecosystem functions such as nutrient cycling and regeneration (Rosenfield & Müller, 2020).

Which species is dominant in an ecosystem is determined by its traits. Which traits are of importance, are determined by the environment in which the community stands. For example, traits of the dominant species in young deciduous tree communities included smaller seeds (Tobner *et al*., 2016). Whereas larger seeds were one of the traits associated with dominant species in a temperate deciduous forest (Fotis *et al*., 2017). A similar controversy is found in tree communities experiencing drought stress. In semi-arid Mediterranean forests, dominant species exhibiting acquisitive traits (such as greater maximum height and lower wood density) drive productivity (Ayma-Romay *et al*., 2021). On the contrary, the dominant species driving productivity in tropical dry forests contain conservative traits (Prado-Junior *et al*., 2016).

Despite the traits of dominant species differing between communities, the same species can exhibit dominance in different ecosystem functions. A study in a tropical forest show that between 2.5% and 12% of species were responsible for half of the wood decomposition, standing biomass, litter production and productivity. Many of the species important for one of these ecosystem functions were also of high importance for other functions (Lohbeck *et al*., 2016). Another study also showed that some species in the Amazonian forest contribute disproportionately much to aboveground biomass compared to stem abundance. The contribution of these “hyperdominant” species to aboveground biomass are explained by mismatched traits, such as extreme maximum size and wood density (Fauset *et al*., 2015). An example of hyperdominance is invasive species dominating an ecosystem. These species have an advantage over native species through their traits, such as faster growth rate, greater shade tolerance, etc. This leads to more aboveground biomass in areas that include invasive species (Flombaum *et al*., 2017).

All in all, the selection effect is relatively well studied in forests, including its links to ecosystem functioning. However, the traits that make a species dominant provide an interesting topic for future research. The required traits are not uniform over forests ecosystems and in some cases contradictory.

Belowground biodiversity-ecosystem functioning relationships

As previously stated, less studies have focused on the belowground biodiversity-ecosystem functioning relationships compared to these relationships aboveground. Despite the smaller amount of studies, there is evidence that similar processes drive the relationship. Below, evidence on the driving processes is discussed.

Complementarity effect hypothesis

Resource partitioning

Resource partitioning is the first complementarity cause that will be discussed. Belowground, a few studies have focussed on spatial partitioning. Diversity promotes the filling of soil volume by fine roots and thereby increasing its productivity (Brassard *et al*., 2012). Furthermore, some species adapt their root distribution and grow more roots in deeper soil layers (Brassard *et* al., 2012; Sun *et al*., 2017). This spatial partitioning is even more evident when some species have more abundant roots at shallower levels, increasing the complementarity (Ewel *et al*., 2015). The stratification of roots increases productivity through the more efficient uptake of resources. Communities with more diverse root lengths can obtain resources like water (Stratton *et al*., 2000) and nitrogen (Moreno-Chacón & Lusk, 2004) from different soil depths.

Research on belowground temporal partitioning has been limited. Few studies has been performed on this complementarity cause, none of which linked it with ecosystem functioning. However, there is evidence that there are seasonal patterns of nitrogen uptake. The fluctuation of nitrogen uptake between seasons is higher for some species than others (Trogisch *et al*., 2012). Furthermore, due to the temporal partitioning of leaf and fruit production (see above for aboveground temporal partitioning), the utilization and uptake of water can differ between species (Stratton *et al*., 2000). This indicates that aboveground temporal partitioning can lead to belowground partitioning.

Resource partitioning across the chemical form of nitrogen is better studied belowground than aboveground. Within the soil, NH_4^+ and NO_3^- are two of the most common forms of nitrogen. Both have their advantages, as NH_4^+ requires less energy for assimilation and NO_3^- is more mobile and can therefore be more easily captured by roots (Gurevitch *et al*., 2020). Research shows that taller plants with more leaves prefer NO_3^- and smaller plants prefer NH_4^+, which can lead to enhanced biomass production (Liu *et al*., 2022). This partitioning therefore can lead to enhanced ecosystem functioning. Other studies however do not regard these nitrogen preferences as complementarity, because species are flexible in their nitrogen form use. Species can revert to other forms of nitrogen if their preferred form is used by other species (Jacob & Lueschner, 2014). Therefore, ecosystem functioning would be enhanced by the flexibility of species, not complementarity of their preferred nitrogen form.

Overall, there is evidence found that spatial partitioning and partitioning across the chemical form of nitrogen drive the biodiversity-ecosystem functioning relationship. However, this evidence is not consistent across all literature. Furthermore, the evidence found on temporal partitioning did not link this to enhanced ecosystem functioning.

Abiotic facilitation

Another complementarity cause that enhances ecosystem functioning is abiotic facilitation. One form of this facilitation is resource enrichment. As many resources are taken up belowground in forests, there is relatively good evidence found for resource enrichment belowground in forests. An example of this is the hydraulic lift. This occurs when a species takes up water from deep soils and redeposits it in shallower soil layers (Dawson, 1993). This makes water from deeper soil layers available for species with shallower roots (Pretzsch *et al*., 2013). Other resources can also be taken from deeper soils by one species and made available for other species. An example of this is phosphorus, which species with deep roots can take up and enrich the shallower soils with it through litterfall (Ewel *et al*., 2014). The same principle can be found for calcium, which beech trees for example can redistribute in shallower soils. However, studies on mixtures of beech and spruce show that the acidification caused by spruce had a stronger effect on the availability of calcium in shallower soil layers (Berger *et al*., 2006). Similar results have been found for phosphorus, as acidic organic exudates may also be responsible for its facilitation in shallower soils (Ewel *et al*., 2015).

There is little evidence for belowground physical stress buffering in forests. In grasslands, a higher diversity increases the resilience of microclimates against drought stress. This is due to higher levels of soil moisture in the upper soil layers in more diverse communities (Wright *et al*., 2020). As previously mentioned, hydraulic lifting in forests increases the water content of shallower soil layers (Dawson, 1993). Therefore, a similar effect as in grasslands could occur, where the hydraulic lifting of species causes better drought resilience. However, there is no evidence for this in forests.

Overall, there is evidence found that resource enrichment occurs belowground in forests. For physical stress buffering, no evidence can be found. However, both of these forms of abiotic facilitation are not linked to ecosystem enhancement in literature.

Biotic feedback

The final complementarity cause that enhances ecosystem functioning is biotic feedback. Evidence for belowground negative biotic feedback in forests is scarce in literature. In grasslands, there is evidence that mixtures perform better than monocultures, because species-specific soil enemies have less effect (Barry *et al*., 2019). Evidence for this in forest is lacking. However, there is evidence that species are less susceptible to enemies when they share a mycorrhizae network (Germain & Lutz, 2021). Furthermore, mycorrhizal fungi can improve nutrition, tolerance and defences against enemies (Bennet *et al*., 2006). However, the effect of mycorrhizae interactions with plants and their enemies is a better suited as evidence for positive biotic feedback.

The effect of mycorrhizae on soil enemies is not the only positive biotic feedback of these fungi. They also improve the nitrogen availability in soil through their mutualistic relationship with plants (Ferlian *et al*., 2018). The increased availability of nitrogen through mycorrhizae leads to a higher diversity and enhances ecosystem functioning in forests (Soudzilovskaia *et al*., 2019) Furthermore, other soil biota, such as bacteria, also engage in mutualistic relationships with plants though nitrogen fixation (Lladó *et al*., 2017). Another example of positive biotic feedbacks is the presence of nitrogen fixing species, which cause nitrogen enrichment effects on non-nitrogen fixing species (Wang *et al*., 2019). Furthermore, introducing nitrogen fixing species in mixtures can lead to higher productivity (Forrester *et al*., 2006). This enrichment of nitrogen through biotic feedback could also be considered abiotic facilitation through resource enrichment (Barry *et al*., 2019). No evidence is present on non-resource belowground positive biotic feedback in forests.

Overall, there is evidence that belowground biotic feedback can increase biodiversity in forests. However, the overlap between positive and negative biotic feedback, as well as the overlap between biotic feedback and abiotic facilitation makes it difficult to differentiate between these complementarity causes.

Selection effect hypothesis

As stated by the selection effect hypothesis, ecosystem functioning can be enhanced through the presence of dominant species. Research shows that the selection effect plays a role belowground in forests. Functional identity can be more important than functional diversity on belowground biomass (Xu *et al*., 2019). For example, studies show that the presence or absence of *C. glauca* influences fine root biomass (Zeng *et al*., 2020). Mixtures containing this species have higher fine root biomass and productivity (Liu *et al*., 2021). Furthermore, specific traits of species can significantly enhance ecosystem functioning through their presence. An example of this is the presence of nitrogen fixating species. As mentioned above, nitrogen fixating species can enhance ecosystem functioning though the increase of nitrogen availability (Forrester *et al*., 2006). This suggests positive biotic feedback/resource enrichment. However, the absence or presence of nitrogen fixating species has a significant effect on ecosystem functioning (Luo *et al*., 2016). Therefore, it could be argued that the effect of nitrogen fixating species is evidence for the selection effect hypothesis belowground in forests.

Furthermore, there is also evidence for the selection effect hypothesis in the usage of different forms of nitrogen by tree species. For example, a study on Chinese firs shows that mixtures of this species with other species can either increase or decrease their biomass. This was dependent on the flexibility of nitrogen form uptake in different soil layers by the other species (Zhou *et al*., 2021). Therefore, the presence or absence of species with compatible flexibility determined the biomass production of the community, thereby providing evidence for the selection effect hypothesis. The effect of conifers in general provides evidence for the selection effect hypothesis belowground in forests. These species are a strong driver of belowground carbon stocks (Dawud *et al*., 2016). Furthermore, evergreen species, to which most conifers belong, increase belowground biomass as they allocate relatively more biomass to belowground parts compared to deciduous species. (Archambault *et al*., 2019). Even when species diversity in general has a negative effect on fine root biomass, conifers can dampen these negative effects (Wambganss *et al*., 2021).

All in all, there is strong evidence for the selection effect hypothesis as a driver of the belowground biodiversity-ecosystem functioning relationship. Compared to evidence for the complementarity effect hypothesis, relatively many studies linked the presence of dominant species to ecosystem functioning. However, some evidence is contradictory to evidence found for the complementarity effect hypothesis.

Which processes drive the above- and belowground biodiversity-ecosystem relationship?

This review aims to answer the question: *Do the same processes drive biodiversity ecosystem functioning relationships belowground as aboveground in forests?* Through literature research, the processes driving this relationship have been studied. Two main hypotheses arise in literature, the complementarity effect hypothesis and the selection effect hypothesis. For both hypotheses, there is evidence that shows these drivers impact ecosystem functioning. For the complementarity effect hypothesis, evidence supports the three complementarity causes differently above- and belowground.

Spatial partitioning, a complementarity cause classified as resource partitioning, is found above- and belowground. In both cases, vertical and horizontal stratification increases biodiversity above- and belowground by filling the canopy space (Sapijankas *et* al., 2014; Tatsumi, 2020) and filling the soil layers respectively (Brassard *et al*., 2012; Ewel *et al*., 2015). The evidence for temporal partitioning is more limited compared to spatial partitioning for both above- and belowground. Seasonal water uptake is a form of temporal partitioning that overlaps between above- and belowground, as the timing of leaves and fruits aboveground determines the water uptake belowground (Stratton *et al*., 2000). Resource partitioning across the chemical form of nitrogen was more evident in belowground literature than in aboveground literature. However, in both cases species diversity their uptake of nitrogen forms (Liu *et al*., 2022; Schwarz *et al*., 2014). Overall, it can be said that the process of resource partitioning drives both the above- and belowground biodiversity-ecosystem functioning relationship.

For resource enrichment, a complementarity cause classified as abiotic facilitation, there is more evidence for this belowground. There is evidence of several mechanisms providing neighbouring species with resources belowground (Dawson, 1993; Ewel *et al*., 2014, 2015) and some evidence for resource enrichment through increased litterfall (Sapijanskas *et al*., 2013). Evidence for physical stress buffering was more prominent in literature focussed on aboveground relationships. There, biodiversity mitigates the climate change effects on microclimates (Zellweger *et al*., 2020). Evidence of physical stress buffering belowground is only found in grasslands (Wright *et al*., 2020). All in all, abiotic facilitation drives biodiversity-ecosystem functioning relationships above- and belowground.

However, evidence for resource enrichment is more prominent belowground, where evidence for physical stress buffering is more evident aboveground.

Evidence for negative biotic feedback is more found for aboveground relationships than for belowground relationships. Enemies such as herbivores and pathogens have less effect on communities with a higher biodiversity (Hantsch *et al*., 2013; Jactel & Brockerhoff, 2007). For belowground they only evidence present links the better resistance of soil enemies to mycorrhizae (Bennet *et al*., 2006; Germain & Lutz, 2021). However, evidence for positive biotic feedback is more found for belowground relationships. There, the presence of mycorrhizae and nitrogen fixating plant species enhances ecosystem functioning (Soudzilovskaia *et al*., 2019; Forrester *et al*., 2006). Aboveground, evidence for positive biotic feedback is circumstantial (Cordeiro & Howe, 2003). Therefore, biotic feedback is driving both the above- and belowground biodiversity-ecosystem functioning relationships. However, more evidence for negative biotic feedback is available for aboveground relationships, where evidence for positive biotic feedback is more available for belowground relationships.

The selection effect hypothesis is supported by evidence both above- and belowground. The presence of species with traits that enhance ecosystem functioning are driving the biodiversity-ecosystem functioning relationship.

In summary, evidence for spatial partitioning as a driver the biodiversity-ecosystem functioning relationship is predominant for both above- and belowground. Furthermore, different complementarity causes are supported with strong evidence as driver of the above- and belowground relationships. Aboveground, temporal partitioning and physical stress buffering are widely found to drive the biodiversity-ecosystem functioning relationship. For this relationship belowground, partitioning across the chemical form of nitrogen is a strong driver. In addition, the overlap between resource enrichment and positive biotic feedback, via nitrogen fixing species and mycorrhizae, is also widely found to drive the biodiversity-ecosystem functioning relationship. Next to complementarity causes driving biodiversity-ecosystem functioning relationships above- and belowground, evidence is also widely present for the selection effect hypothesis as a driver.

Therefore, this review shows that different processes drive the biodiversity-ecosystem functioning relationship aboveground in belowground in forests. However, similarities do occur. This result could be due to research being skewed towards either above- or belowground biodiversity-ecosystem functioning research. Or due to different processes could in fact drive the above- and belowground biodiversity-ecosystem functioning relationships.

Furthermore, several processes driving the biodiversity-ecosystem functioning relationships are overlapping. An example of this is resource enrichment and positive biotic feedback belowground. The enhancing presence of mycorrhizae or nitrogen fixating species on ecosystem functioning could be considered biotic feedback, as it is an interaction between plants and their mutualists. However, since these interactions cause nitrogen to become more available in soils, they could be considered resource enrichment. Another example of this overlapping is spatial partitioning and resource enrichment aboveground. Spatial partitioning of the canopy increases litterfall. This increased litterfall enriches the soil with more nutrients. The overlapping of processes makes it harder to determine which process drives the biodiversity-ecosystem functioning relationship.

Future research

For future research on the processes driving the biodiversity-ecosystem functioning relationships above- and belowground, several suggestions can be taken into account. The first suggestion is to include more complementarity causes when enhanced ecosystem functioning is awarded to the complementarity effect. Several studies conclude that complementarity is the driver, but do not include which complementarity cause is responsible for that. An addition to this suggestion for future research would be to include that increased biodiversity leads to enhanced ecosystem functioning. Studies included in this revies often show that a complementarity cause increases biodiversity, but fail to mention the effect of this increased biodiversity on the ecosystem functioning. Linking complementarity causes to ecosystem functioning enhancement and vice versa could provide a more complete picture of the biodiversity-ecosystem functioning relationship, as previously suggested in another study (Barry *et al*., 2019).

Another suggestion is that more research should be dedicated to belowground biodiversity-ecosystem functioning relationships. The evidence for these relationships is being underrepresented in literature compared to these relationships aboveground. This review shows that dissimilarities occur between the processes driving the biodiversity-ecosystem functioning relationships above- and belowground. This could be because of a lack of studies being performed on these relationships belowground. Therefore, more research on belowground relationships could provide a different answer to the research question of this review.

Conclusion

Biodiversity-ecosystem functioning relationships in forest are driven by different processes above- and belowground. However, similarities in the driving processes also occur. Current evidence is not sufficient to draw hard conclusions on which processes drive the relationships above- and belowground in forests. Therefore, future research is needed to determine the importance of each process. With a better understanding of the processes driving biodiversity-ecosystem functioning relationships aboveground and belowground in forests, management and conservation can be applied in the most productive forms. As this would create the most suitable approach to maintain ecosystem functioning of forests in the face of global biodiversity declines.

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