frontiers | Frontiers in Forests and Global Change

TYPE Opinion
PUBLISHED 21 January 2025
DOI 10.3389/ffgc.2024.1512518

EDITED BY
Verena C. Griess,
ETH Zürich, Switzerland

REVIEWED BY
Miranda Hart,
University of British Columbia, Canada

*CORRESPONDENCE
Suzanne W. Simard
✉ suzanne.simard@ubc.ca

RECEIVED 16 October 2024
ACCEPTED 24 December 2024
PUBLISHED 21 January 2025

CITATION
Simard SW, Ryan TSL and Perry DA (2025) Opinion: Response to questions about common mycorrhizal networks. *Front. For. Glob. Change* 7:1512518. doi: 10.3389/ffgc.2024.1512518

Opinion: Response to questions about common mycorrhizal networks

Suzanne W. Simard[1]*, Teresa (Sm'hayetsk) L. Ryan[1,2] and David A. Perry[3]

[1]Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, BC, Canada, [2]Ts'msyen Nation, Prince Rupert, BC, Canada, [3]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, United States

KEYWORDS

common mycorrhizal network, carbon transfer, regeneration, complex adaptive systems, temperate forests

Introduction

Common mycorrhizal networks (CMNs) are networks of mycorrhizal fungal hyphae held in common by at least two plants (Horton, 2015; Rillig et al., 2024) and were first discovered in the laboratory by Reid and Woods (1969) and later supported by Finlay and Read (1986) and Perry et al. (1989). Simard et al. (1997c) contributed to this knowledge by investigating underground transmission of carbon between ectomycorrhizal paper birch and Douglas-fir as well as arbuscular mycorrhizal western redcedar trees in the mixed temperate rainforests of western Canada. This body of pioneering work was followed by decades of creative peer-reviewed research by many scientists investigating the structure and function of CMNs in various forests around the world (see reviews including Newman, 1988; Simard et al., 2012; Horton, 2015; Tedersoo et al., 2020; Klein et al., 2023, and others). Research on the role of CMNs in the regenerative nature of forest ecosystems has recently come under targeted criticism by Karst et al. (2023), Henriksson et al. (2023), and Robinson et al. (2023). These criticism articles question the veracity and interpretations of the peer reviewed research. They were triggered by the memoir of Simard (2021), who told of how her experiences shaped her research, and what she thinks her findings about CMNs mean for forests in Canada. An important aspect of our roles as scientists is to ensure clarity of our research to support future informed thought and investigations. In the following paragraphs, we address some of the questions and perceptions about CMNs raised by these authors.

Context

A brief review of the four main questions scientifically investigated about CMNs in forests provide context for our response to the criticisms. Notably, the three criticism articles generally dismiss evidence for all four questions. The first question, whether CMNs exist in forest ecosystems, has been investigated over the past five decades using increasingly sophisticated tools, from microscopy to DNA sequencing, microsatellites, and isotopic tracing. These studies, in our view, have revealed that CMNs can connect the roots of trees with other trees (see Figure 1; Beiler et al., 2010), as well as with compatible seedlings, shrubs, or mycoheterotrophic herbs (Selosse et al., 2006; Tedersoo et al., 2020; Authier et al., 2022; Merckx et al., 2024). The second question investigated has been whether CMNs facilitate nutrient, carbon, water or infochemical transfer among trees. This has also been demonstrated, and most studies show multiple belowground pathways functioning simultaneously, including CMNs, mycorrhizal roots, and soil (Simard et al., 1997a,c; Song et al., 2015; Horton, 2015; Klein et al., 2016). The third question, how resource transfer between trees varies in forests, has been investigated using field and associated greenhouse and lab studies. These studies have demonstrated that transfer is

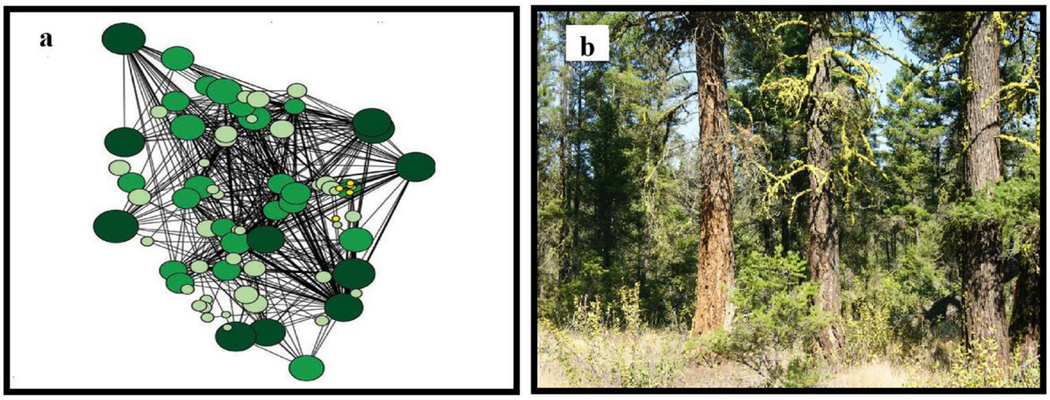

FIGURE 1
Temperate interior Douglas-fir forest in British Columbia with mutigenerational age and multilayered size structure. The panel includes: **(a)** map of CMN typology from Beiler et al. (2010), where interior Douglas-fir trees are connected through shared colonization of *Rhizopogon* spp. genets in a 30 m × 30 m plot (green circles = Douglas-fir, sized relative to stem diameter; black lines = genet linkages). **(b)** Interior Douglas-fir forest typical of where CMN mapping was conducted (photo credit: W. J. Roach).

affected by a range of factors in forests, including the light, water, nutrient and health status of donor and recipient trees (Simard et al., 1997c; Teste et al., 2010; Song et al., 2015; Klein et al., 2016), and the characteristics of the fungal species in the CMN (Teste et al., 2009; Merckx et al., 2024). A fourth question, whether membership in the CMN affects performance of trees, has also been investigated and results reveal this is also context dependent, as would be expected in complex systems like forests (Levin, 2005). Nevertheless, evidence exists that linking into CMNs in forests can affect establishment of seedlings (Booth and Hoeksema, 2010; Teste et al., 2009; Bingham and Simard, 2011), growth or carbon status of mature trees (Klein et al., 2016; Birch et al., 2021), and performance of mycoheterotrophic plants (Selosse et al., 2006).

This body of research investigating the structure and function of CMNs has fundamentally shifted how scientists understand forests (Perry et al., 2008), not only as collections of individual trees and plants competing for resources (Nyland, 2016), but as connected systems of multiple complex interactions (Simard et al., 2012; Beiler et al., 2015). Whenever there is such a fundamental shift in knowledge, however, there is resistance (Rowell, 2017), and the three critiques by Karst et al. (2023), Henriksson et al. (2023), and Robinson et al. (2023) generally conclude this body of research is inadequate to inform our understanding of forests. In the following paragraphs, we discuss the main points raised by these authors, with more detailed responses to select statements in Table 1.

Discussion

In the first paper, Karst et al. (2023) provide negative commentary against public media interpretations of the memoir of Simard (2021) to open their case that there is a positive citation bias regarding the role of CMNs in forests. They argue there is insufficient evidence that CMNs contribute to regeneration processes in forests. There are several weaknesses in their analysis as follows. First, their search of CMN research in the primary literature (Reporting Summary, https://www.nature.com/articles/s41559-023-01986-1#additional-information) is narrow and incomplete. As detailed in Table 1, they rely on subjective evaluations to determine which 18 studies to choose for their analysis, and then use unclear criteria to determine whether these papers have a positive bias. For example, they choose to exclude all studies investigating nurse tree facilitation of seedling establishment because they argue CMN effects cannot be disentangled from mycorrhizal colonization benefits (Table 1). However, scholars have argued facilitation of seedling establishment is likely the most important function of CMNs in natural ecosystems (Perry et al., 1989; Nara, 2006; Horton, 2015; Rillig et al., 2024). For each of the 18 selected papers, Karst et al. (2023) automatically counted the number of years in the paper's publication record, which augmented their sample size to 273 and increased the power of their tests. The rationale for this enhancement of sample size was vague and lacked evidence that each year was represented by a citation bias in the literature. In their analysis, they also failed to adjust their methods to account for the inherent growth of sample size over time as researchers increase numbers of investigations in an emergent field. Regardless, whether there is any citation bias in the literature, this does not override the fact that studies show all tree species are mycorrhizal dependent and CMN-dependent facilitation and transfer have been demonstrated (Klein et al., 2023; Rillig et al., 2024). It is unfortunate these key points were overlooked in the review process.

Karst et al. (2023) further imply that CMN-related field studies discount the role of alternative belowground resource transfer pathways to CMNs, such as through the soil or disconnected networks. Karst's criticism is echoed by Robinson et al. (2023) and Henriksson et al. (2023). However, as shown repeatedly by Simard et al. (1997a,c), Simard et al. (2012), and verified by others as detailed above, belowground transfer among trees occurs through multiple belowground transfer pathways simultaneously. All of these studies discussed alternative explanations to CMNs, contrary to the criticisms they did not. Regardless of this, Simard et al. (1997c) found that a fraction (18%) of carbon isotope was

TABLE 1 Issues raised in Karst et al. (2023), Henriksson et al. (2023), and Robinson et al. (2023).

Issue	Response
1. Hypotheses can be drawn up from popular media (Karst et al., 2023)	
The authors put weight on popular media to develop their hypotheses as follows: "Upon reviewing various sources of popular media, we identified three common claims: (1) CMNs are widespread in forests; (2) resources are transferred through CMNs, resulting in increased tree seedling performance, and (3) mature trees preferentially send resources and defense signals to offspring through CMNs."	Popular media and the scientific literature have divergent purposes and audiences. The former is designed to engage the public in otherwise inaccessible knowledge, but unlike scientific processes, it is not peer-reviewed. Popular media is thus being inappropriately used by Karst et al., as part of the scientific methodology, including hypothesis formulation.
2. CMN colonization of establishing plants can be ignored as evidence (Karst et al., 2023)	
The authors claim there is limited evidence that CMNs are widespread in forests, in opposition of their own research that supports CMN existence (e.g., Jones et al., 1997; Birch et al., 2021; Booth and Hoeksema, 2010). They exclude all research where CMNs formed between larger plants (or trees) and seedlings because, they say, these studies cannot separate CMN effects from fungal mediated effects, yet colonization of new seedlings is one of the most important functions of the CMN. Karst et al., nevertheless conclude that "as the roots of trees and seedlings intermingle closely, and many mycorrhizal fungi are host generalists, fungal links should be common." They also emphasize that fragmentation of hyphae and mycorrhizal root connections occurs due to quick turnover and grazing, and use this as an argument against the validity of evidence for CMN.	Excluding the body of research on nurse plants or trees ignores the broadly recognized vital role that CMNs of established plants play in colonizing new plants. Colonization is considered by many scholars to be the most important function of CMNs in forests (e.g., Perry et al., 1989; Nara, 2006). As such, the innovative studies of Beiler, Durall, Simard, Maxwell and Kretzer (2010) were conducted explicitly in uneven-aged Douglas-fir forests to investigate understory seedling dynamics within the CMNs of old trees. Additionally, fragmentation, regrowth and anastomosis are well known processes in CMNs and do not negate the evidence found in peer-reviewed research that CMNs exist.
3. Neither genet studies nor experiments using mesh barriers, hyphal severing, or trenching are sufficient to provide evidence for CMNs (Karst et al., 2023)	
The authors argue there is insufficient evidence from genet studies, or from experiments using mesh, isotopic labeling or any techniques, to establish that CMNs exist or facilitate flow of resources from one plant to another. However, they agree that "when conducted at fine scales, [genet] maps can provide strong evidence for a spatially continuous mycelium linking the roots of different trees in close proximity." They add, "Adjacent roots are often colonized by the same species of mycorrhizal fungi, suggesting that fungal links should be common."	There are multiple lines of evidence for the existence of CMNs, including from genet studies using microsatellites, as well as from DNA sequencing, microscopy and isotope labeling studies using mesh or natural mycorrhizal type differences. These studies have been conducted in arctic, boreal, temperate and tropical ecosystems, and have been documented in several reviews, including Simard et al. (2012), Horton (2015), Tedersoo et al. (2020), Authier et al. (2022), and Kuyper and Jansa (2023). In our own research, we have used a wide range of techniques in interior Douglas-fir ecosystems, including isotope tracing (Simard et al., 1997c,a,b; Philip et al., 2010; Teste et al., 2009, 2010; Bingham and Simard, 2011; Pickles et al., 2017); microsatellites (Beiler et al., 2010, 2012, 2015; Van Dorp et al., 2020; Teste et al., 2009), DNA sequencing (e.g., Twieg et al., 2007 and others), knowing that every experimental technique has its strengths and weaknesses. Each of these peer reviewed studies adds evidence that trees in interior Douglas-fir forests are involved in a CMN, and that these relationships among trees affect the forest. Most scientists working in this field similarly use multiple approaches when drawing inferences about CMNs in their ecosystems. Of particular importance, there are four studies of genet mapping of CMNs by Beiler et al. (2010, 2012, 2015) and Van Dorp et al. (2020) in interior Douglas-fir forests of Canada, and one in the in pine forests of Japan (Lian et al., 2006). Teste et al. (2009) also demonstrates carbon transmission is associated with shared genets in interior Douglas-fir forests.
4. Research is invalid unless continuously repeated (Karst et al., 2023)	
The authors argue that given there 73,300 tree species worldwide, any comment on the existence of CMNs in forests should wait until we study a multiplicity of these tree species and geographic areas.	More study is always welcome, and this literature is growing steadily around the world. It would be helpful to examine a majority of species and forests, and this field is rapidly expanding. However, detailed microsatellite studies that map CMNs in forests is arduous and time consuming, and will not happen quickly. The fact that these studies are taking time to complete, however, does not invalidate the peer review research that has been conducted. As well, top journals do not generally publish science that is an extension of previous discoveries, which de-incentivizes repeating publication of this intensive research multiple times.
5. Only field experiments, not those in labs, growth chambers or greenhouses, count as evidence for CMNs in forests (Karst et al., 2023)	
The authors narrowed their literature search to field experiments because they say "they are most relevant to making inferences on forest function, and because the role that adult trees play in forests can only be examined in the field" (Karst et al., 2023, p. 501)"	Karst et al. (2023) do not acknowledge the importance of combining field with greenhouse experiments and laboratory analysis to decipher the role of CMNs in forests. Researchers routinely and justifiably combine field with lab, greenhouse and/or growth chamber analysis to understand underlying mechanisms of in situ patterns (e.g., Jones et al., 1997). By ignoring accompanying ex situ experiments and analysis, Karst et al. (2023) have purposefully limited their ability to fully evaluate evidence for the existence and functioning of CMNs in forests.

(Continued)

TABLE 1 (Continued)

Issue	Response
	There are several examples of the value of including non-field studies in CMN research in forests. For example, Klein et al. (2016) applied stable isotope tracing methodologies developed in the lab to mature trees in the field. Orrego (2018) used lab-developed techniques to trace carbon flux from old growth hemlock trees to hemlock seedlings nearby. Pickles et al. (2017) overcame the difficulty of labeling large trees in the field by first establishing nurse trees in the greenhouse, then subsequently growing younger cohorts nearby to emulate forest conditions.
6. CMNs are the only pathway for resource transmission between trees that can be considered relevant in forests (Karst et al., 2023)	
The authors argue that CMNs are over-rated for resource transfer and that other transfer pathways are ignored.	Many peer reviewed studies examining belowground resource transmission among trees have found the existence for multiple belowground transfer pathways, not just CNMs (see review by Horton, 2015). In our articles, we consistently discuss evidence for multiple pathways (e.g., Simard et al., 1997c, p. 681) writes "Our study extends earlier laboratory results to the field, providing direct evidence for both bidirectional and net carbon transfer between plant species, for the occurrence of hyphal as well as soil pathways, and for source–sink regulation of net transfer in field conditions." Multiple belowground pathways for transmission of carbon, nitrogen and water have also been reported in the studies reviewed in Simard et al. (2012, 2015). Studies have shown that the magnitude and pathway of belowground resource transfer varies depending on the size, origin, water relations, phenology, and shade status of the trees, as well as the disturbance history and aridity of the forest.
7. CMN interpretations are a major departure from competitive frameworks (Karst et al., 2023)	
The authors state, "The results from this study (Simard et al., 1997c) have been interpreted as evidence that CMNs equalize resources within a plant community—a view that was a major departure from competitive frameworks" (Karst et al., 2023, p. 503).	Our work consistently shows there is a multiplicity of interaction types in forests, including competition and cooperation, and that resource transfers between individuals ought to affect these interactions. Simard et al. (1997c) states, "If our results reflect the magnitude of carbon transfer in natural systems, then the net competitive effect of one species on another cannot be predicted without a better understanding of interplant carbon transfer through shared mycorrhizal fungi and soil pathways. A more even distribution of carbon among plants as a result of below-ground transfer may have implications for local interspecific interactions, maintenance of biodiversity, and therefore for ecosystem productivity, stability and sustainability" (Simard et al., 1997c, p. 581). The critics own views on prioritizing competition in forests, as is done in forest policies and practices, support the simplification of plantations, diminishment of biodiversity, and enhancement of risks of fire, drought and other disturbances. Our work shows that a diversity of interaction types occurs in healthy forests (e.g., Simard and Vyse, 2006).
8. The potential to form a CMN has no effect on plant establishment, survival or growth (Karst et al., 2023)	
The authors conclude there are no forest experiments that demonstrate that the potential to form a CMN affects plant growth or survival.	This contradicts their own work, including Booth and Hoeksema (2010) and Birch et al. (2021), the latter who showed that growth, and the variability in growth, of adult Douglas-fir trees declined with decreasing numbers of connections. Other evidence for facilitation of plant establishment exists in temperate and subtropical ecosystems, where ectomycorrhizal seedlings tend to establish around parent trees or shrubs (McGuire et al., 2008; Nara, 2006; Teste et al., 2009; Beiler et al., 2010; Delavaux et al., 2023). Seedlings establishing in interior Douglas-fir forests are primarily colonized by tapping into the CMN that already exists among the adult trees (and less frequently by spores in the soil). We have found that seedlings that do not become colonized by CMNs do not survive beyond 3–4 months (Barker et al., 2013). Experiments examining CMN effects on seedling establishment, survival and growth in Douglas-fir forests have shown greater effects (especially on survival) where they had full access to CMN, mycorrhizal root and soil pathways. This was particularly pronounced when seedlings established from seed (rather than planted as nursery plugs), were within 2.5–5 meters of mature trees, or were growing in drier soils or more arid climates (Teste et al., 2009; Teste and Simard, 2008; Bingham and Simard, 2011).
9. There is no evidence trees preferentially communicate with offspring through CMNs (Karst et al., 2023)	
The authors assert there is no evidence that trees preferentially send resources or signals warning of insect damage to offspring through CMNs.	The recognition of relatives, or kin-recognition, has been well-studied in plants and found to involve signaling via roots and mycorrhizas (Dudley et al., 2013; Semchenko et al., 2014) as well as volatile organic compounds (Karban, 2015). We have added to this literature with evidence for kin recognition in interior Douglas-fir, and agree with previous studies that belowground it is mediated by roots and mycorrhizas (Pickles et al., 2017; Asay et al., 2020; Gorzelak et al., 2015). Adding to Song et al.'s (2015) evidence for defense signaling between trees, Gorzelak (2017) has also found that injured Douglas-fir preferentially signal defense information to kin over strangers. Evidence for kin recognition in forests elsewhere in the world continues to grow (Karban, 2015).

(Continued)

TABLE 1 (Continued)

Issue	Response
10. There is positive citation bias toward CMNs (Karst et al., 2023)	
The authors write, "We screened the resulting papers relevant to CMN function and structure, and from this list, we identified 'influential' field studies, defined as those having at least 50 citations, and evaluated citations of those studies" (Karst et al., 2023). "Citations outside common mycorrhizal network research were included in our evaluation" (Karst et al., 2023). "We assigned a citation as supported if the evidence was strong for the statement or unsupported if the evidence was weak or absent (Karst et al., 2023)."	The criteria for subjectively choosing the 18 "influential" papers while excluding other relevant studies is unclear. The search string for retrieving their sample, for example, was limited to CMN terms and then high graded by topic, presenting uncertainty for a complete search. This raises questions about objectivity, such as why certain field studies of their own were excluded, as well as other notable papers, including: any studies of CMN effects on regenerating seedlings, understory herbs, or understory shrubs; any studies of forest tree species in greenhouses; and other forest tree studies such as Bachelot et al. (2017), Sasaki et al. (2019), Peh et al. (2011), Avital et al. (2022), Cahanovitc et al. (2022), etc. How each study was evaluated for positive citation bias is unclear because the criteria were inadequately described. Out of the 18 "influential" studies included in their analysis, Karst et al. (2023; Figure 1) themselves are co-authors on 28% of the papers they say were subject to positive citation bias. The authors augmented the sample size by automatically counting every year since publication of a particular paper, expanding the sample size from 18 to 272. This would have increased the significance of their regression and would have automatically weighted older papers. In analyzing their positive citation bias, they fail to acknowledge that most CMN research has been conducted in the past 25 years, and the greater number of papers building on the foundational knowledge would naturally lead to statistically significant trends in citations, whether positive or negative.
11. "Mother tree hypothesis" (Henriksson et al., 2023)	
The authors claim that a "mother tree hypothesis" has been postulated by previous studies, citing eight scientific articles.	The authors have invented the "hypothesis" from the metaphor used in Simard (2021) memoir, meant to communicate how large, old trees are the hubs of CMNs in the temperate interior Douglas-fir forests of North America. They refer to the "hypothesis" as controversial, and falsely attribute it to scientific articles published years earlier. However, none of these publications mention this hypothesis.
The authors apply their "mother tree hypothesis" to nutrient poor Scandinavian boreal pine forests, then reject it using selected photos and results from trenching studies in pine forests.	After rejecting their hypothesis, they state that "the current formulation of the mother tree hypothesis is incongruent with patterns of forest regeneration in boreal forests." The "mother tree" metaphor applies to shade tolerant interior Douglas-fir trees in dry temperate forests and was never meant to apply to shade intolerant pine trees in boreal forests. Shade intolerant trees are well-known to establish best in the open, whereas shade tolerant trees often preferentially regenerate in the understory of adult trees. There is a rich literature (see reviews previously mentioned) demonstrating that any effects of CMNs in forests is highly context dependent on factors such as forest type, shade tolerance, light conditions, water relations, nitrogen status, disturbance severity, presence of pathogens or insects, or other environmental stresses.
12. Trees are altruistic, etc. Robinson et al. (2023)	
The authors rely upon Henriksson et al. (2023) and Karst et al. (2023) to make their claims.	The separate articles cite one another and some of the authors appear on two of the three papers.
The authors criticize that Simard's (2021) memoir "submits" trees behave altruistically.	The use of this "altruistic" term is "assumed" by the authors as stated in their Box 2. However, Simard has never stated that trees in CMNs behave altruistically or are not competitive.
The authors state the mother tree concept is incompatible with tree growth, citing a 1926 article (German language) on dry heath Scotch pine that mentions distance of seedlings to mother trees and suggests those seedlings are shade intolerant.	The phenomenon of CMN may be quite different in the forests of Scotland and Sweden than in the interior Douglas-fir forests of Canada where most of Simard's work was conducted. They are of different climates, biomes, species compositions, and have different ecologies.
The authors state, "Field observations often contradict the mother tree hypothesis, which predicts a higher growth rate of seedlings in the proximity of large trees [34]. In fact, emergence and growth of seedlings and saplings are in general negatively affected by proximity to large trees [34, 35]" (Robinson et al., 2023; Box 2).	Supporting citations used by the authors here are not independent primary field studies but rather the other two perspective articles by Karst et al. (2023) and Henriksson et al. (2023). Those familiar with the forests of British Columbia, particularly interior Douglas-fir forests, would readily see that seedlings of shade-tolerant species commonly establish near their parents.
13. Anthropomorphism is dangerous (Robinson et al., 2023)	
Robinson et al. (2023) state that anthropomorphism "clouds the issue at hand" and will cause harm to conservation.	Notwithstanding the confusion over Robinson et al.'s (2023) mixing of the terms personification, anthropomorphism, and humanization, we do not use such typologies in our research. With respect to Simard's memoir, it is well-documented that communicating science outside of the scientific literature is best done in ways that humans can relate to, and it results in better environmental conservation outcomes (Opermanis et al., 2015).
"What's at stake"	The authors assert that Simard is antagonistic to the forest industry in general. This is incorrect: Simard's applied research often involves forestry industry partners.

(Continued)

TABLE 1 (Continued)

Issue	Response
Society conceptions of forests are mentioned by the authors, with some brief history up to the present day, "…which partly views a forest as a social utopia where all trees support each other in harmony. Especially given the future uncertainties, we are most concerned that this kind of thinking will lead to restrictions on active forest management. Limited choices and options will likely leave us with forests that are ill-adapted and cannot provide essentially needed ecosystem services" (Robinson et al., 2023, p. 9).	Indeed, limited choices and options prevail in forest management practices world-wide, such as clearcutting, planting monocultures, and failing to manage woody debris, biodiversity or soils. These practices are leaving us an uncertain future, where forests are ill-adapted and unable to provide ecosystem services for generations to come. It is more logical to better understand how forests work, how they are connected above and below ground, and the role CMNs play in biogeochemical cycles, biodiversity, and forest regeneration. The peer reviewed and published work of Simard and colleagues are making contributions to expand the knowledge needed for conserving and managing forests for future generations.
The authors criticize the book publishing industry's policies as flawed, yet state, "This does not mean that books … should not appear in print and publishers should not be allowed to make profits from their sales. But the general public has a right to know what kind of book they are buying and the publishers should label them for what they are: tantalizing, but unsubstantiated hypotheses." (Robinson et al., 2023, p. 6)	Simard (2021) was peer reviewed for correctness and included references to peer reviewed scientific papers throughout. The memoir is based on the life of an accomplished scientist in the forests of interior British Columbia (not grasses as in Robinson and Fitter (1999)). Simard's work is published in hundreds of peer reviewed papers, and is supported by dozens of graduate student theses, with many students publishing their work. This includes the kin recognition research of Dr. Amanda Asay (*In memoriam,* 1988–2022). More of these publications are pending and in progress.

transmitted to arbuscular mycorrhizal western redcedar compared with that between ectomycorrhizal paper birch and Douglas-fir, providing experimental evidence for carbon transfer through the CMN and simultaneously and to a lesser degree through the soil. Here, all three species had comparably vigorous and overlapping mycorrhizal roots, as naturally occurred in the surrounding forest (Simard et al., 1997c; Twieg et al., 2007), rendering results that were realistic of the natural system. If, as Karst et al. (2023) imply, transfer patterns in Simard et al. (1997c) could be accounted for by differing root densities, and hence the gathering power of the different species, logic dictates that arbuscular mycorrhizal cedar growing among the two ectomycorrhizal trees would gather only one-fifth of the soil resources going to the ectomycorrhizal trees. Given the comparable health and vigor of the cedar roots and shoots to the other species of seedlings in the study, however, this is highly unlikely. Moreover, Karst's implication that the existence of one pathway rules out another, when they claim that transfer via mycorrhizal fungi had not been shown here in the field, misses the complexity of forest ecosystems.

The three criticism articles imply that the carbon transfer measured would be insignificant to plants because they say isotopes in these studies did not enter recipient shoots (Karst et al., 2023; Henriksson et al., 2023; Robinson et al., 2023). However, our studies have repeatedly demonstrated that significant amounts of carbon are transferred into both shoots and roots of recipient seedlings through CMNs and other pathways (e.g., Simard et al., 1997a,b,c; Teste et al., 2009; Philip et al., 2010; Song et al., 2015). In keeping with these findings, Klein et al. (2016) and Cahanovitc et al. (2022) have also found transfer into shoots of trees. This type of transfer has been associated with establishment of seedlings and mycoheterotrophic plants (see above; Van Der Heijden and Horton, 2009; Rillig et al., 2024; Merckx et al., 2024). Moreover, the requirement of transfer into shoots assumes that carbon supply is the limiting factor in the photosynthetic process, and dismisses the likelihood that carbon subsidies to roots and associated mycorrhizae enhance the gathering of soil nutrients essential for photosynthesis. Perry and Oetter (2024) found that growth of Douglas-fir in low light was limited by magnesium, not carbon supply, indicating the essential role of mycorrhizas in productivity. As with other issues, the critics are not looking at the bigger picture.

Karst et al. (2023) further argued that our research ignores the important role of competition in forest dynamics, possibly because CMN research in general has generated interpretations regarding cooperative relationships from trading of resources or infochemicals. However, none of our articles negate the process of competition in forests. Instead, we repeatedly discuss that multiple types of species interactions occur simultaneously, including competition, and that understanding forest dynamics must account for this complexity (Perry et al., 1989; Simard et al., 1997c, 2012; Simard and Vyse, 2006). This complexity is readily evident in the mature, multicohort, multi-storied temperate forests where these experiments were conducted, where seedlings readily establish in the understory of old trees following small scale natural disturbances (Figure 1). In younger plantation forests absent of old trees and where competition may be less intense, CMNs may play a lesser role in forest dynamics. Nevertheless, many of our experiments tracing resource transfer between trees through belowground pathways have been conducted in recently planted forests (e.g., Simard et al., 1997c; Teste et al., 2009), and we have also successfully mapped the architecture of CMNs in young Douglas-fir forests (Van Dorp et al., 2020), suggesting CMNs also exist in young temperate forests.

Our discovery of kin recognition in trees has also been discounted by Karst et al. (2023) because the precise belowground mechanism by which trees recognize their genetic relatives remains elusive (Gorzelak et al., 2015; Pickles et al., 2017; Asay et al., 2020). This dismissal is short-sighted because the novel discovery could, for example, lead to a greater diversity of reforestation practices in western Canada, which currently relies heavily on clearcutting with artificial regeneration (Simard and Vyse, 2006). By providing support for natural regenerative processes as an alternative or supplement to even-aged plantations, which are vulnerable to climate-related failures and wildfires (Clason et al., 2022), this finding could help in a transition toward more resilient regeneration methods, such as use of overstory retention (Franklin et al., 2018; Simard et al., 2020). In a large-scale experiment crossing a 900-km climate gradient in interior Douglas-fir forests (Simard et al., 2020; Roach et al., 2021), for example, Simard et al.

(2021) and Harris et al. (2025) have found that increasing levels of overstory retention facilitate regeneration success in increasingly arid regional climates.

Henriksson et al. (2023) mistakenly compare our work in interior Douglas-fir forests of Canada to boreal pine forests in Europe, which have not been part of our research. The individual papers we have published provide results applicable to the temperate forests where the studies occurred (e.g., Simard et al., 1997c; Teste et al., 2009; Beiler et al., 2010; Bingham and Simard, 2011). It is well-known that different species in specific ecosystems behave differently, and studies in the boreal pine forests of Scandinavia (Henriksson et al., 2023) may thus not find that CMNs play the same role as shade tolerant Douglas-firs in British Columbia (Beiler et al., 2015). Shade-intolerant pines in boreal forests, for example, require open conditions, whereas shade-tolerant Douglas-firs in dry temperate forests of Canada naturally regenerate in the shade and CMNs of parent trees. Our results are place-based and context dependent, and the absence or difference of a phenomenon in one forest does not negate its validity elsewhere (Zahra et al., 2021).

In the same vein as Henriksson et al. (2023), Karst et al. (2023), and Robinson et al. (2023) suggest our peer reviewed articles on belowground carbon transfer in temperate Douglas-fir forests of Canada inappropriately generalize to forests elsewhere in the world. This is incorrect; we have not made such statements in the literature. The evidence is clear, however, that mycorrhizas play a strong role in the nature of interactions among trees. For example, large analyses of global temperate and tropical forest biomes suggest there is strong positive feedback among conspecifics in ectomycorrhizal forests, but negative feedback in arbuscular mycorrhizal forests (Bennett et al., 2017; Pither et al., 2018; Delavaux et al., 2023). These authors suggest that mycorrhizal colonization by conspecifics (Bennett et al., 2017; Pither et al., 2018) or CMNs (Zahra et al., 2021; Delavaux et al., 2023) may play a role in structuring these disparate forest types. Further hypothesis testing is needed to clarify the role of CMNs in different forest biomes, disturbance histories, and stand structures. It is important to move forward in understanding these phenomena, which could be important in developing nature-based solutions to climate change (Drever et al., 2021).

Robinson et al. (2023) erroneously refer to "the mother tree hypothesis," and claim that it is harmful to forests of Europe. However, they have misused the metaphor of the mother tree in Simard's (2021) memoir meant for conveying scientific meaning to the public about the regenerative nature of interior Douglas-fir forests in Canada. Robinson et al. (2023) also refer to "recent reviews" to support their claims, but only cite those of Henriksson et al. (2023) and Karst et al. (2023). Robinson et al. (2023) further conflate two different types of mycorrhizas—arbuscular- and ecto-mycorrhizas—in comparing CMN carbon and nutrient transfer mechanisms to our work, which is specifically on ectomycorrhiza in Douglas-fir forests of Canada. These two types of mycorrhizal fungi are evolutionarily divergent with distinct hosts and ecological functions (Bennett et al., 2017; Haq et al., 2024).

Karst et al. (2023) suggest a strict set of requirements that must be met before any research on CMNs be considered valid in forests, but these are unrealistic to satisfy in the field given the relational, variable and dynamic nature of forests (Klein et al., 2023; Rillig et al., 2024). While it is not uncommon that lab tests or greenhouse experiments need reconciling with *ex-situ* methodologies, this is true for any scientific study of complex natural systems, and does not mean discarding valid investigation. Indeed, any researcher examining relationships in complex systems such as forests must confront the limitations of their experimentation and invoke a version of Occam's Razor to interpret their findings. It is the responsibility of anyone criticizing research to offer alternative explanations that have a probability greater than those interpreted from the published experiments. However, Karst et al. (2023) do not, nor do they provide new information that warrants discounting peer reviewed research. A more recent investigation proposes expanding terminology to identify mycorrhizal-dependent direct and indirect effects, but this does not diminish research investigating the role of CMNs in forest ecosystems (Rillig et al., 2024).

Finally, "*Finding the Mother Tree*" (Simard, 2021) was written in laypeople's terms so the public can critically assess whether industrial forest management, focused on timber extraction (Nyland, 2016; Ashton and Kelty, 2018), is serving the interests of our collective wellbeing (Mazzocchi, 2012). Forests are best understood through the multitude of relationships, connections, interdependencies and feedbacks that shape them, and CMNs are part of these processes (Perry et al., 1989; Simard et al., 2012; Beiler et al., 2015; Bennett et al., 2017). The intent of Simard (2021) was to engage people in how CMNs help shape temperate forests, and whether the unraveling of these connections and relationships through industrial forest management is worth the risks of biodiversity loss and climate change (Moomaw et al., 2019; IPCC, 2023; Ripple et al., 2024; Betts et al., 2024), or whether more holistic approaches are needed (Mazzocchi, 2012; Filotas et al., 2014; Sands et al., 2023; Robinson et al., 2021; Drever et al., 2021; Mina et al., 2022). Metaphors such as "mother tree" were used to help make these concepts more relatable to the public. Indeed, tree metaphors have been deeply understood in cultures worldwide for millennia (Blicharska and Mikusiński, 2014; Arnold, 2021), as well as in western scientific literature [e.g., the use of "family" in taxonomy; the translation, "mother," for the scientific genus name of hemlock, *Tsuga* (Pojar and MacKinnon, 1994; Farjon, 2010)]. Moreover, many Indigenous communities have place-based cultural practices that depict their ancient understanding of relationships in forests, including of elder trees or mother trees (Baumflek et al., 2021; Ryan, 2014; Turner, 2008; Turner et al., 2000; Wickham et al., 2022), and these could inform culturally revitalized land stewardship practices as climate changes (Charnley et al., 2007).

In summary, we argue that our peer-reviewed literature on CMNs stands up against the targeted criticisms of Karst et al. (2023), Henriksson et al. (2023), and Robinson et al. (2023), which appear to distort then undermine peer-reviewed findings. Their claims that our scientific articles (i) discount the role of alternative transfer pathways to CMNs, (ii) negate the importance of competition in forests, (iii) did not find carbon transfer to shoots, or (iv) that we extended our findings to all forests, are simply not true. These criticism articles fail to provide any new experimental evidence that would discount the peer reviewed literature. In our view, our research has contributed to a meaningful paradigm shift in how we view forests and this may be important for developing more holistic approaches for protecting, restoring and managing forests in our changing climate.

Author contributions

SS: Writing – original draft. TR: Writing – review & editing. DP: Writing – review & editing.

Funding

The author(s) declare that no financial support was received for the research, authorship, and/or publication of this article.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer MH declared a shared affiliation with the author(s) SS and TR to the handling editor at the time of review.

Generative AI statement

The author(s) declare that no Gen AI was used in the creation of this manuscript.

Publisher's note

References

Arnold, C. (2021). Reciprocal relationships with trees: rekindling indigenous wellbeing and identity through the Yuin ontology of oneness. *Aust. Geog.* 52, 131–147. doi: 10.1080/00049182.2021.1910111

Asay, A. K., Simard, S. W., and Dudley, S. A. (2020). Altering neighborhood relatedness and species composition affects interior Douglas-Fir size and morphological traits with context-dependent responses. *Front. Ecol. Evol.* 8:578524. doi: 10.3389/fevo.2020.578524

Ashton, M. S., and Kelty, M. J. (2018). *The Practice of Silviculture: Applied Forest Ecology*. Hoboken, NJ: John Wiley and Sons.

Authier, L., Violle, C., and Richard, F. (2022). Ectomycorrhizal networks in the anthropocene: from natural ecosystems to urban planning. *Front. Plant Sci.* 13:900231. doi: 10.3389/fpls.2022.900231

Avital, S., Rog, I., Livne-Luzon, S., Cahanovitc, R., and Klein, T. (2022). Asymmetric belowground carbon transfer in a diverse tree community. *Mol. Ecol.* 31, 3481–3495. doi: 10.1111/mec.16477

Bachelot, B., Uriarte, M., McGuire, K. L., Thompson, J., and Zimmerman, J. (2017). Arbuscular mycorrhizal fungal diversity and natural enemies promote coexistence of tropical tree species. *Ecology* 98, 712–720. doi: 10.1002/ecy.1683

Barker, J. S., Simard, S. W., Jones, M. D., and Durall, D. M. (2013). Ectomycorrhizal community fungal assembly on regenerating Douglas-fir after wildfire and clearcut harvesting. *Oecologia* 172, 1179–1189. doi: 10.1007/s00442-012-2562-y

Baumflek, M., Kassam, K. A., Ginger, C., and Emery, M. R. (2021). Incorporating biocultural approaches in forest management: insights from a case study of Indigenous plant stewardship in Maine, USA and New Brunswick, Canada. *Soc. Nat. Res.* 34, 1155–1173. doi: 10.1080/08941920.2021.1944411

Beiler, K. J., Durall, D. M., Simard, S. W., Maxwell, S. A., and Kretzer, A. M. (2010). Architecture of the wood-wide web: Rhizopogon spp. genets link multiple Douglas-fir cohorts. *New Phyt.* 185, 543–553. doi: 10.1111/j.1469-8137.2009.03069.x

Beiler, K. J., Simard, S. W., and Durall, D. M. (2015). Topology of *Rhizopogon* spp. mycorrhizal meta- networks in xeric and mesic old-growth interior Douglas-fir forests. *J. Ecol.* 103, 616–628. doi: 10.1111/1365-2745.12387

Beiler, K. J., Simard, S. W., Lemay, V., and Durall, D. M. (2012). Vertical partitioning between sister species of *Rhizopogon* fungi on mesic and xeric sites in an interior Douglas-fir forest. *Mol. Ecol.* 21, 6163–6174. doi: 10.1111/mec.12076

Bennett, J. A., Maherali, H., Reinhart, K. O., Lekberg, Y., Hart, M. M., Klironomos, J., et al. (2017). Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* 355, 181–184. doi: 10.1126/science.aai8212

Betts, M. G., Yang, Z., Gunn, J. S., and Healey, S. P. (2024). Congruent long-term declines in carbon and biodiversity are a signature of forest degradation. *Glob. Change Biol.* 30:e17541. doi: 10.1111/gcb.17541

Bingham, M. A., and Simard, S. W. (2011). Do mycorrhizal network benefits to survival and growth of interior Douglas-fir seedlings increase with soil moisture stress? *Ecol. Evol.* 1, 306–316. doi: 10.1002/ece3.24

Birch, J. D., Simard, S. W., Beiler, K. J., and Karst, J. (2021). Beyond seedlings: ectomycorrhizal fungal networks and growth of mature *Pseudotsuga menziesii*. *J. Ecol.* 109, 806–818. doi: 10.1111/1365-2745.13507

Blicharska, M., and Mikusiński, G. (2014). Incorporating social and cultural significance of large old trees in conservation policy. *Cons. Biol.* 28, 1558–1567. doi: 10.1111/cobi.12341

Booth, M. G., and Hoeksema, J. D. (2010). Mycorrhizal networks counteract competitive effects of canopy trees on seedling survival. *Ecology* 91, 2294–2302. doi: 10.1890/09-1139.1

Cahanovitc, R., Livne-Luzon, S., Angel, R., and Klein, T. (2022). Ectomycorrhizal fungi mediate belowground carbon transfer between pines and oaks. *ISME J.* 16:5. doi: 10.1038/s41396-022-01193-z

Charnley, S., Fischer, A. P., and Jones, E. T. (2007). Integrating traditional and local ecological knowledge into forest biodiversity conservation in the Pacific Northwest. *For. Ecol. Manage.* 246, 14–28. doi: 10.1016/j.foreco.2007.03.047

Clason, A. J., Farnell, I., and Lilles, E. B. (2022). Carbon 5–60 years after fire: planting trees does not compensate for losses in dead wood stores. *Front. For. Glob. Change* 5:868024. doi: 10.3389/ffgc.2022.868024

Delavaux, C. S., LaManna, J. A., Myers, J. A., Phillips, R. P., Aguilar, S., Allen, D., et al. (2023). Mycorrhizal feedbacks influence global forest structure and diversity. *Comm. Biol.* 6, 1–11. doi: 10.1038/s42003-023-05410-z

Drever, C. R., Cook-Patton, S. C., Akhter, F., Badiou, P. H., Chmura, G. L., Davidson, S. J., et al. (2021). Natural climate solutions for Canada. *Sci. Adv.* 7:eabd6034. doi: 10.1126/sciadv.abd6034

Dudley, S. A., Murphy, G. P., and File, A. L. (2013). Kin recognition and competition in plants. *Funct. Ecol.* 27, 898–906. doi: 10.1111/1365-2435.12121

Farjon, A. (2010). *A Handbook of the World's Conifers: Revised and Updated Edition*. Leiden: Brill.

Filotas, E., Parrott, L., Burton, P. J., Chazdon, R. L., Coates, K. D., Coll, L., et al. (2014). Viewing forests through the lens of complex systems science. *Ecosphere* 5, 1–23. doi: 10.1890/ES13-00182.1

Finlay, R., and Read, D. J. (1986). The structure and function of the vegetative mycelium of ectomycorrhizal plants. I. Translocation of 14C-labeled carbon between plants interconnected by a common mycelium. *New Phytol.* 103, 143–156. doi: 10.1111/j.1469-8137.1986.tb00603.x

Franklin, J. F., Johnson, K. N., and Johnson, D. L. (2018). *Ecological Forest Management*. Longrove, IL: Waveland Press.

Gorzelak, M. A. (2017). *Kin-selected signal transfer through mycorrhizal networks in Douglas-fir* (Doctoral dissertation). University of British Columbia.

Gorzelak, M. A., Asay, A. K., Pickles, B. J., and Simard, S. W. (2015). Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. *AoB Plants* 7:plv050. doi: 10.1093/aobpla/plv050

Haq, H., Hauer, A., Singavarapu, B., Christel, H., Cesarz, S., Eisenhauer, N., et al. (2024). The interactive effect of tree mycorrhizal type, mycorrhizal type mixture and tree diversity shapes rooting zone soil fungal communities in temperate forest ecosystems. *Funct. Ecol.* 1–14. doi: 10.1111/1365-2435.14651

Harris, T. C., Roach, J. W., Miller, E. M., and Simard, S. W. (2025). The interactive role of climatic transfer distance and overstory retention on Douglas-fir seedling survival and height growth in interior British Columbia. *Glob. Change Biol.* doi: 10.1111/gcb.70027

Henriksson, N., Marshall, J., Högberg, M. N., Högberg, P., Polle, A., Franklin, O., et al. (2023). Re-examining the evidence for the mother tree hypothesis – resource sharing among trees via ectomycorrhizal networks. *New Phyt.* 239, 19–28. doi: 10.1111/nph.18935

Horton, T. R. (ed.). (2015). *Mycorrhizal Networks, Vol. 224*. Dordrecht: Springer.

IPCC (2023). *Climate Change 2023: Synthesis Report*. Geneva: Sixth Assessment Report of the Intergovernmental Panel on Climate Change.

Jones, M. D., Durall, D. M., Harniman, S. M. K., Classen, D. C., Simard, S. W., et al. (1997). Ectomycorrhizal diversity on *Betula papyrifera* and *Pseudotsuga menziesii* seedlings grown in the greenhouse or outplanted in single-species and mixed plots in southern BC. *Can. J. For. Res.* 27, 1872–1889. doi: 10.1139/x97-160

Karban, R. (2015). *Plant Sensing and Communication*. Chicago, IL: Univ. Chicago Press.

Karst, J., Jones, M. D., and Hoeksema, J. D. (2023). Positive citation bias and overinterpreted results lead to misinformation on common mycorrhizal networks in forests. *Nat. Ecol. Evol.* 7:4. doi: 10.1038/s41559-023-01986-1

Klein, T., Rog, I., Livne-Luzon, S., van der Heijden, M. G. A., and Körner, C. (2023). Belowground carbon transfer across mycorrhizal networks among trees: Facts, not fantasy. *Open Res. Europe* 3:168doi: 10.12688/openreseurope.16594.1

Klein, T., Siegwolf, R. T. W., and Körner, C. (2016). Belowground carbon trade among tall trees in a temperate forest. *Science* 352, 342–344. doi: 10.1126/science.aad6188

Kuyper, T., and Jansa, J. (2023). Arbuscular mycorrhiza: advances and retreats in our understanding of the ecological functioning of the mother of all root symbioses. *Plant Soil* 489, 1–48. doi: 10.1007/s11104-023-06045-z

Levin, S. (2005). Self-organization and the emergence of complexity in ecological systems. *Bioscience* 55, 1075–1079. doi: 10.1641/0006-3568(2005)055[1075:SATEOC]2.0.CO;2

Lian, C., Narimatsu, M., Nara, K., and Hogetsu, T. (2006). *Tricholoma matsutake* in a natural *Pinus densiflora* forest. *New Phyt.* 171, 825–836. doi: 10.1111/j.1469-8137.2006.01801.x

Mazzocchi, F. (2012). Complexity and the reductionism–holism debate in systems biology. *WIREs Syst. Biol. Med.* 4, 413–427. doi: 10.1002/wsbm.1181

McGuire, K. L., Henkel, T. W., Cerda, I. G. D., Villa, G., Edmund, F., and Andrew, C. (2008). Dual mycorrhizal colonization of forest-dominating tropical trees and the mycorrhizal status of non-dominant tree and liana species. *Mycorrhiza* 18, 217–222. doi: 10.1007/s00572-008-0170-9

Merckx, V. S. F. T., Gomes, S. I. F., Wang, D., Verbeek, C., Jacquemyn, H., Zahn, F. E., et al. (2024). Mycoheterotrophy in the wood-wide web. *Nat. Plants* 10, 710–718. doi: 10.1038/s41477-024-01677-0

Mina, M., Messier, C., Duveneck, M. J., Fortin, M.-J., and Aquilué, N. (2022). Managing for the unexpected: building resilient forest landscapes to cope with global change. *Glob. Change Biol.* 28, 4323–4341. doi: 10.1111/gcb.16197

Moomaw, W. R., Masino, S. A., and Faison, E. K. (2019). Intact forests in the US: Proforestation mitigates climate change and serves the greatest good. *Front. For. Glob. Change* 2:27. doi: 10.3389/ffgc.2019.00027

Nara, K. (2006). Ectomycorrhizal networks and seedling establishment during early primary succession. *New Phyt.* 169, 169–178. doi: 10.1111/j.1469-8137.2005.01545.x

Newman, E. I. (1988). Mycorrhizal links between plants: their functioning and ecological significance. *Adv. Ecol. Res.* 18, 243–270. doi: 10.1016/S0065-2504(08)60182-8

Nyland, R. D. (2016). *Silviculture Concepts and Applications, 3rd Edn*. Long Grove, IL: Waveland Press, Inc.

Opermanis, O., Kalnins, S. N., and Aunins, A. (2015). Merging science and arts to communicate nature conservation. *J. Nat. Cons.* 28, 67–77. doi: 10.1016/j.jnc.2015.09.005

Orrego, G. (2018). *Western Hemlock Regeneration on Coarse Woody Debris Is Facilitated by Linkage Into a Mycorrhizal Network in an Old-Growth Forest* (M.Sc. thesis). UBC, Vancouver, BC.

Peh, K., Lewis, S. L., and Lloyd, J. (2011). Mechanisms of monodominance in diverse tropical tree-dominated systems. *J. Ecol.* 99, 891–898. doi: 10.1111/j.1365-2745.2011.01827.x

Perry, D. A., Amaranthus, M. P., Borchers, J. G., Borchers, S. L., and Brainerd, R. E. (1989). Bootstrapping in ecosystems: Internal interactions largely determine productivity and stability in biological systems with strong positive feedback. *Bioscience* 39, 230–237. doi: 10.2307/1311159

Perry, D. A., and Oetter, D. R. (2024). Thirty years of forest productivity in a mountainous landscape: The Yin and Yang of topography. *Ecosphere* 15:e4865. doi: 10.1002/ecs2.4865

Perry, D. A., Oren, R., and Hart, S. C. (2008). *Forest Ecosystems*. Baltimore, MD: The Johns Hopkins University Press.

Philip, L., Simard, S., and Jones, M. D. (2010). Pathways for below-ground carbon transfer between paper birch and Douglas-fir seedlings. *Plant Ecol. Divers.* 3, 221–233. doi: 10.1080/17550874.2010.502564

Pickles, B. J., Wilhelm, R., Asay, A. K., Hahn, A. S., Simard, S. W., and Mohn, W. W. (2017). Transfer of ^{13}C between paired Douglas-fir seedlings reveals plant kinship effects and uptake of exudates by ectomycorrhizas. *New Phyt.* 214, 400–411. doi: 10.1111/nph.14325

Pither, J., Pickles, B. J., Simard, S. W., Ordonez, A., and Williams, J. W. (2018). Below-ground biotic interactions moderated the postglacial range dynamics of trees. *New Phytol.* 220, 1148–1160. doi: 10.1111/nph.15203

Pojar, J., and MacKinnon, A. (1994). *Plants of Coastal British Columbia*. Vancouver, BC: Lone Pine Publishing.

Reid, C. P. P., and Woods, F. W. (1969). Translocation of ^{14}C-labeled compounds in mycorrhizae and its implications in interplant nutrient cycling. *Ecology* 50, 179–187. doi: 10.2307/1934844

Rillig, M. C., Lehmann, A., Lanfranco, L., Caruso, T., and Johnson, D. (2024). Clarifying the definition of common mycorrhizal networks. *Funct. Ecol.* 2024, 1–7. doi: 10.1111/1365-2435.14545

Ripple, W. J., Wolf, C., van Vuuren, D. P., Gregg, J. W., and Lenzen, M. (2024). An environmental and socially just climate mitigation pathway for a planet in peril. *Env. Res. Lett.* 19:021001. doi: 10.1088/1748-9326/ad059e

Roach, W. J., Simardm, S. W., Defrenne, C. E., Pickles, B. J., Lavkulich, L. M., and Ryan, T. L. (2021). Tree diversity, site index, and carbon storage decrease with aridity in Douglas-fir forests in western Canada. *Front. For. Glob. Change* 4:682076. doi: 10.3389/ffgc.2021.682076

Robinson, D. G., Ammer, C., Polle, A., Bauhus, J., Aloni, R., Annighöfer, P., et al. (2023). Mother trees, altruistic fungi, and the perils of plant personification. *Trends Plant Sci.* 29, 20–31. doi: 10.1016/j.tplants.2023.08.010

Robinson, D. G., and Fitter, A. (1999). The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. *J. Exp. Bot.* 50, 9–13. doi: 10.1093/jxb/50.330.9

Robinson, J. M., Gellie, N., MacCarthy, D., Mills, J. G., O'Donnell, K., and Redvers, N. (2021). Traditional ecological knowledge in restoration ecology: a call to listen deeply, to engage with, and respect Indigenous voices. *Rest. Ecol.* 29:e13381. doi: 10.1111/rec.13381

Rowell, A. (2017). *Green Backlash: Global Subversion of the Environmental Movement*. New York, NY: Routledge.

Ryan, T. L. (2014). *Territorial Jurisdiction: The Cultural and Economic Significance of Eulachon Thaleichthys pacificus in the North-Central Coast Region of British Columbia* (PhD Diss.). UBC, Vancouver, BC.

Sands, B., Machado, M. R., White, A., Zent, E., and Gould, R. (2023). Moving towards an anti-colonial definition for regenerative agriculture. *Agric. Hum. Values.* 40, 1697–1716. doi: 10.1007/s10460-023-10429-3

Sasaki, T., Konno, M., Hasegawa, Y., Imaji, A., Terabaru, M., Nakamura, R., et al. (2019). Role of mycorrhizal associations in tree spatial distribution patterns based on size class in an old-growth forest. *Oecologia* 189, 971–980. doi: 10.1007/s00442-019-04376-2

Selosse, M.-A., Richard, F., He, X., and Simard, S. W. (2006). Mycorrhizal networks: Des liaisons dangereuses? *Trends Ecol. Evol.* 21, 621–628. doi: 10.1016/j.tree.2006.07.003

Semchenko, M., Saar, S., and Lepik, A. (2014). Plant root exudates mediate neighbour recognition and trigger complex behavioural changes. *New Phyt.* 204, 631–637. doi: 10.1111/nph.12930

Simard, S., and Vyse, A. (2006). Trade-offs between competition and facilitation: a case study of vegetation management in the interior cedar–hemlock forests of southern British Columbia. *Can. J. For. Res.* 36, 2486–2496. doi: 10.1139/x06-150

Simard, S. W. (2021). *Finding the Mother Tree.* New York, NY: Penguin Random House.

Simard, S. W., Asay, A. K., Beiler, K. J., Bingham, M. A., Deslippe, J. R., He, X., et al. (2015). "Resource transfer between plants through ectomycorrhizal networks. *Ecol. Stud.* 224, 133–176. doi: 10.1007/978-94-017-7395-9_5

Simard, S. W., Beiler, K. J., Bingham, M. A., Deslippe, J. R., Philip, L. J., and Teste, F. P. (2012). Mycorrhizal networks: mechanisms, ecology and modelling. *Fung. Biol. Rev.* 26, 39–60. doi: 10.1016/j.fbr.2012.01.001

Simard, S. W., Durall, D. M., and Jones, M. D. (1997b). Carbon allocation and carbon transfer between *Betula papyrifera* and *Pseudotsuga menziesii* seedlings using a ^{13}C pulse-labeling method. *Plant Soil.* 191, 41–55.

Simard, S. W., Jones, M. D., Durall, D. M., Perry, D. A., Myrold, D. D., and Molina, R. (1997a). Reciprocal transfer of carbon isotopes between ectomycorrhizal *Betula papyrifera* and *Pseudotsuga menziesii*. *New Phytol.* 137, 529–542. doi: 10.1046/j.1469-8137.1997.00834.x

Simard, S. W., Perry, D. A., Jones, M. D., Myrold, D. D., Durall, D. M., and Molina, R. (1997c). Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388, 579–582. doi: 10.1038/41557

Simard, S. W., Roach, W. J., Beauregard, J., Burkart, J., Cook, D., Law, D., et al. (2021). Partial retention of legacy trees protects mycorrhizal inoculum potential, biodiversity, and soil resources while promoting natural regeneration of interior Douglas-fir. *Front. For. Glob. Change* 3:620436. doi: 10.3389/ffgc.2020.620436

Simard, S. W., Roach, W. J., Defrenne, C. E., Pickles, B. J., Snyder, E. N., Robinson, A., et al. (2020). Harvest intensity effects on carbon stocks and biodiversity are dependent on regional climate in Douglas-fir forests of British Columbia. *Front. For. Glob. Change* 3:88. doi: 10.3389/ffgc.2020.00088

Song, Y. Y., Simard, S. W., Carroll, A., Mohn, W. W., and Zeng, R. S. (2015). Defoliation of interior Douglas-fir elicits carbon transfer and stress signaling to ponderosa pine neighbors through ectomycorrhizal networks. *Sci. Rep.* 5:8495. doi: 10.1038/srep08495

Tedersoo, L., Bahram, M., and Zobel, M. (2020). How mycorrhizal associations drive plant population and community biology. *Science* 367:eaba1223. doi: 10.1126/science.aba1223

Teste, F. P., and Simard, S. W. (2008). Mycorrhizal networks and distance from mature trees alter patterns of competition and facilitation in dry Douglas-fir forests. *Oecologia* 158, 193–203. doi: 10.1016/j.funeco.2008.11.003

Teste, F. P., Simard, S. W., Durall, D. M., Guy, R. D., and Berch, S. M. (2010). Net carbon transfer occurs under soil disturbance between *Pseudotsuga menziesii* var. glauca seedlings in the field. *J. Ecol.* 98, 429–439. doi: 10.1111/j.1365-2745.2009.01624.x

Teste, F. P., Simard, S. W., Durall, D. M., Guy, R. D., Jones, M. D., and Schoonmaker, A. L. (2009). Access to mycorrhizal networks and roots of trees: importance for seedling survival and resource transfer. *Ecology* 90, 2808–2822. doi: 10.1890/08-1884.1

Turner, N. J. (2008). *The Earth's Blanket: Traditional Teachings for Sustainable Living.* Madeira Park, BC: D&M Publishers.

Turner, N. J., Ignace, M. B., and Ignace, R. (2000). Traditional ecological knowledge and wisdom of Aboriginal peoples in British Columbia. *Ecol. Appl.* 10, 1275–1287. doi: 10.1890/1051-0761(2000)010[1275:TEKAWO]2.0.CO;2

Twieg, B. D., Durall, D. M., and Simard, S. W. (2007). Ectomycorrhizal fungal succession in mixed temperate forests. *New Phytol.* 176, 437–447. doi: 10.1111/j.1469-8137.2007.02173.x

Van Der Heijden, M. G., and Horton, T. R. (2009). Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *J. Ecol.* 97, 1139–11150. doi: 10.1111/j.1365-2745.2009.01570.x

Van Dorp, C. H., Simard, S. W., and Durall, D. M. (2020). Resilience of *Rhizopogon*-Douglas-fir mycorrhizal networks 25 years after selective logging. *Mycorrhiza* 30, 467–474. doi: 10.1007/s00572-020-00968-6

Wickham, S. B., Augustine, S., Forney, A., Mathews, D. L., Shackelford, N., Trant, A. J., et al. (2022). Incorporating place-based values into ecological restoration. *Ecol. Soc.* 27:32. doi: 10.5751/ES-13370-270332

Zahra, S., Novotny, V., and Fayle, T. M. (2021). Do reverse Jansen-Connell effects reduce diversity? *Trends Ecol. Evol.* 36, 387–390. doi: 10.1016/j.tree.2021.02.002