Fungi, forests, and fish: the role of fungi in forest biogeochemical cycling

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Abstract

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Forests are threatened by a multitude of stressors and assessing how forests will respond to these stressors requires a comprehensive understanding of net primary productivity (Npp). However, one parameter of significant uncertainty is belowground Npp (bNpp), or total photosynthetic carbon allocated belowground. I evaluated the effect of climatic and soil variables on bNpp using a global productivity dataset and found that soil nutrient flux rates were the main drivers of bNpp across forest biomes. Within biomes, environmental constraints on bNpp varied between forests with low versus high bNpp, indicating that environmental drivers are site-specific and the development of within-biome, site-scale classifications for forest ecosystems could be useful. Finally, I found that soil variables caused abrupt and large decreases in bNpp for boreal, but not cold temperate forests, indicating that boreal forests might have lower adaptive capacity and higher sensitivity to disturbances than cold temperate forests. I then examined nutrient cycling in an Alaskan boreal riparian forest and evaluated the role of fungi in the flow of salmon-derived nitrogen (SDN). Pacific salmon subsidize terrestrial systems with SDN, which can have ecological significance for animals, plants, and soils. However, despite the crucial role of fungi in decomposition and nutrient cycling, the importance of fungal mycelium as an SDN sink in the soil has been largely overlooked. I found that SDN was present in fungal sporocarps, soils, and foliage, but only significantly increased N concentrations in fungi, suggesting that SDN was retained in fungal hyphae. Furthermore, SDN from recent salmon carcasses increased the relative abundance and diversity of medium-distance and long-distance ectomycorrhizal fungal types. In systems such as salmon streams where nutrients are available but patchily distributed and occur in pulses, these fungi might be preferred by plant hosts due to their strong ability to maintain large network structure, mine nutrient hotspots, and mobilize organically bound N and P. These results illustrate that fungi are essential to consider to accurately assess the flow and significance of SDN in riparian systems.

Chapter 1: Forest belowground productivity and carbon allocation predominantly driven by soil properties rather than climate

Abstract

Forests are threatened by a multitude of stressors, including anthropogenic disturbances and climate change. Assessing how forests will respond to these stressors requires a comprehensive understanding of net primary productivity (Npp), environmental constraints on growth, and adaptive capacity. A parameter of significant uncertainty is belowground Npp (bNpp), which can account for up to 80% of total Npp but is poorly estimated and rarely measured directly. We used a global dataset of direct, field-based measurements of aboveground and belowground primary productivity and 21 climatic and soil variables to identify potential constraints on bNpp and belowground carbon allocation. Soil variables, rather than climate variables, were the main drivers of bNpp and belowground allocation across biomes. The importance of soil variables suggests that soil nutrient dynamics, especially soil nutrient pool and flux variables, must be explicitly modeled to more accurately predict feedbacks between climate, productivity, and within-tree carbon allocation. Within biomes, environmental drivers of belowground allocation varied between low versus high allocation forests, indicating that environmental drivers are site-specific and the development of within-biome, site-scale classifications for forest ecosystems could be useful. Changes in soil variables, such as increasing soil nitrogen pools, caused abrupt and large decreases in bNpp for boreal, but not cold temperate forests. Threshold-like shifts indicate that boreal forests might have lower adaptive capacity and higher sensitivity to disturbances than cold temperate forests. With 70% of boreal forests characterized by low bNpp, disturbances such as anthropogenic nitrogen deposition could cause large-scale decreases in bNpp that could push these forests beyond their adaptive capacity.

Introduction

Forest ecosystems in the Anthropocene face multiple and compounding stressors, including changes in climate and soil chemistry, shifts in natural disturbance regimes, and anthropogenic activities such as deforestation (Case et al. 2021, Johnson and Johnson et al. 2019, Lilleskov et al. 2024, Popkin 2019). Forests have adapted to their ecological and geographical environmental niches through within-plant carbon (C) allocation shifts or shifts in their landscape distribution

(Körner 2015, White et al. 2016, Pagel et al. 2020). However, in the current climate crisis, many ecosystems are being pushed towards their biological tipping point as plants struggle to adapt to modified growing conditions (Pereira and Viola 2018, Hoegh-Guldberg et al. 2019). To assess how well a forest adapts to different stressors, there is a need for a more comprehensive understanding regarding the current productive capacity of forests, their genotypic and phenotypic adaptation to changing soil and climatic environments, and ecosystem fit – a measure of how well a forest is adapted to its site, defined as the ratio of field-collected total net primary productivity (tNpp) to the theoretical maximum tNpp (Gordon et al. 1983, Gordon et al. 1992). Furthermore, it is important to understand how changes in tree C allocation to the belowground components impact the acquisition of growth-limiting resources (Vogt et al. 1983, Clark et al. 2001, Scurlock et al. 2002). However, accurate estimates of a forest's current annual productive capacity, or net primary productivity (Npp), have been difficult to obtain (Clark et al. 2001, Scurlock et al. 2002). This has been due to poor predictions of belowground Npp (bNpp), which constitutes a significant portion of the total productivity of a forest and is therefore important to include in models estimating ecosystem C budgets. Yet, bNpp still remains the least known C pool in the C cycle (Vogt et al. 1993, Gherardi and Sala 2020, Klock et al. 2022a). This knowledge would provide further insights into how edaphic (factors relating to the structure and composition of soil) and climatic growth environments determine how much C is allocated to belowground tree components and whether restoring a site's primary productive capacity is realistic (Klock et al. 2022a).

Although studies focusing on bNpp and edaphic and climatic conditions exist (Xiao et al. 2023), the results are challenging to use in building a holistic model to explore the sensitivity of bNpp to edaphic and climatic conditions (Vogt et al. 2016, Klock et al. 2022a). Individual field studies across biomes are inconsistent and have found opposing effects of environmental variables on bNpp (Gherardi and Sala 2020), and therefore cannot be compared to develop general relationships of factors impacting bNpp since they do not include a comprehensive suite of both climate and edaphic variables (but see Vogt et al. 2016). This suggests that any relationships found may not be generalizable or realistically represent the diversity of forests found in a biome. For example, in boreal forests, bNpp is typically limited by both belowground and aboveground resources due to temperature-limited nutrient mineralization rates, such as belowground nutrient availability or solar radiation (Gherardi and Sala 2020). In contrast, in a temperate deciduous forest, soil moisture and nutrient availability determined bNpp levels (Newman et al. 2006). In tropical forests, bNpp is affected by limiting aboveground factors such as light and temperature (Gill and Finzi 2016, Nemani et al. 2003). However, Klock et al. (2022a) showed that tropical forests had significantly lower % allocation to bNpp in the Paleotropics compared to the Neotropics due to the more nutrient-poor soils of the Neotropics. In addition, a study assessing forest research sites across the tropics showed that the relationship between precipitation and total Npp (tNpp) varied for three soil textural classes, likely due to the differing soil moisture retention capabilities of these soils which then affect soil organic matter and nutrient availabilities. These results support the potential development of relationships between tNpp and certain soil texture classes, but not for all tropical forests. Finally, most current Earth system and productivity models assume climate is the primary driver of productivity and C dynamics, even though studies increasingly show that soil plays an important role in these dynamics (Luo et al. 2019, Todd-Brown et al. 2013).

Prior to 2000, bNpp estimates were based on field measures of changes in root biomass over time, but many indirect measures (*e.g.*, ecosystem models and proximate variables) emerged after this time because of the need to include bNpp estimates for many sites that did not have prior root research. A common indirect approach to model C allocation to the belowground was based on aboveground measures, such as aNpp:bNpp, which did not effectively capture how plants adapt to their site edaphic and climatic conditions at the plot scale (Klock et al. 2022a). Research has shown how C allocated belowground frequently cycles at different rates and is governed by different drivers than aboveground C, therefore these indirect estimates may generalize changes in forest growth at larger scales but would not adequately represent the diversity of site scale forest adaptations to environmental changes (Fortier et al. 2019, Klock et al. 2022a). Also, researchers lacking site-specific robust estimates of bNpp use indirect measures to calculate this variable based on relationships developed by other studies. The estimates of bNpp produced from direct and indirect methods often differ significantly, and it remains challenging to use indirect methods to identify the upper bounds of C available for root and mycorrhizal growth due to insufficient data availability from representative sites. To identify the mechanisms driving belowground productivity and allocation, we need to quantify the effect of a larger and more nuanced suite of edaphic and climatic variables on field-measured estimates of bNpp. This will allow for more accurate predictions of tNpp and a more detailed, quantifiable understanding of the global and biome scale patterns and drivers of bNpp and the % allocated to bNpp.

To better understand and identify the mechanisms controlling bNpp – the least understood part of the global C budget – we used random forest regression models to predict measures of tNpp, aboveground Npp (aNpp), bNpp, % allocation to bNpp, and ecosystem fit at two eco-physiological scales: phenological traits (evergreen, deciduous, mixed) and regional climatic zones (boreal, cold temperate), using a suite of 21 climate and edaphic variables in forests (Vogt et al. 1986, Vogt et al. 1995, Vogt et al. 1996, Klock et al. 2022a) and field-collected productivity measures. We hypothesized that climatic factors would primarily limit boreal forest tNpp, since tree growth is generally constrained by duration of the growing season, while temperate forests would be more limited by soil nutrients since a milder climate has less impact on forest productive capacity. To understand the drivers of bNpp, allocation, and ecosystem fit, our study main objectives were to:

(i) determine how bNpp, % allocation to bNpp, and ecosystem fit vary with biome and phenology,

(ii) assess the relative importance of climate vs. edaphic variables as predictors of bNpp, % allocation to bNpp, and ecosystem fit, and

(iii) evaluate the response of bNpp, % allocation to bNpp, and ecosystem fit to soil and climatic drivers, and how this response varies between boreal and temperate biomes.

Result and Discussion

What are the patterns of bNpp and % allocation to bNpp in cold temperate and boreal biomes?

We determined that bNpp differed by biome and phenology. Specifically, boreal evergreen forests had significantly lower bNpp than boreal deciduous forests and cold temperate evergreen forests (Figure S1; Figure S2). This difference could be due to the high nutrient retention of boreal evergreen species because of their long leaf longevity (up to 10 years for *Picea glauca* and *Picea mariana;* Reich et al. 2014), which would reduce the % allocation to bNpp, as annual nutrient requirements are lower than for boreal deciduous species, or cold temperate evergreens. In contrast, percent allocation to bNpp did not vary by phenology or biome, or when examining phenology by biome or biome within phenology (Table 1; Figure S1; Figure S2). Previous studies have shown variable and overlapping values for % allocation to bNpp between boreal and temperate forests (Gower et al. 2001, Raich and Nadelhoffer 1989). Generally, % allocation to bNpp increases with latitude from tropical to temperate to boreal forests, due to temperature-limited mineralization in higher latitudes that constrains belowground resources and induces greater allocation belowground to acquire limiting nutrients needed for growth and maintenance (Gherardi and Sala 2019). Boreal forests are thus typically more nutrient-limited than temperate forests due to slower rates of decomposition and nutrient cycling. Therefore, they are usually more dependent on symbiotic associations (*e.g.*, mycorrhizal fungi) to acquire growth limiting nutrients (Anthony et al. 2022), which leads to higher rates of belowground C allocation to roots and mycorrhizas (Vogt et al. 1982). This pattern, however, was not supported by a larger database where boreal forests had a significantly lower belowground biomass than temperate or tropical biomes (Klock et al. 2022a). Other studies have found that temperature-limited mineralization drives belowground resource limitation in both boreal and temperate forests in similar ways (Kicklighter et al. 2019). These differences in belowground allocation between studies show that biome-scale patterns of % allocation to bNpp are not consistent and suggest that many belowground studies do not adequately describe the role of mycorrhizas and C allocation to fungal biomass to acquire nutrients. However, Clemmensen et al. (2013) reported that roots and root-associated microorganisms are a dominant source of soil organic matter in boreal forests. Additionally, the functional balance theory proposes that plants allocate their resources to minimize resource limitation to growth and therefore gain access to further resources (Gherardi and Sala 2019). Therefore, plants generally increase the fraction of productivity allocated belowground with decreasing resource availability, such as drought conditions or soil nutrient limitation. The lack of difference in the % allocation to bNpp between boreal and temperate forests suggests that belowground resources are limiting in a way that similarly affects allocation patterns in both forests. However, it could also indicate that local site-scale factors and local site variability are primary drivers of % allocation to bNpp, and that biome-scale patterns are not sensitive to variation in these environmental variables, as shown by Klock et al. (2022a).

A wide variety of environmental conditions may influence allocation patterns, and site-specific factors can be more important than biome-scale differences when comparing C allocation patterns across forest types (Gower et al. 2001). Therefore, some authors caution against making broad generalizations based on forest type alone, which is further supported by the wide range of values reported in estimates of % allocation to bNpp (Körner 2003). For example, some studies estimate that % allocation to bNpp in boreal forests ranges from 45-65%, while others report 25-30%, whereas temperate forests generally fall within the range of 30-46% (Gill and Finzi 2016, Gower et al. 2001, Raich and Nadelhoffer 1989). Similar reasoning can be applied to the similarity we found in % allocation to bNpp between deciduous and evergreen forests in this study. Although some studies show that evergreen forests allocate a higher fraction of Npp belowground than deciduous forests (Gherardi and Sala 2020, Gower et al. 2001), our study shows that there can be considerable site-scale variation in % allocation to bNpp, particularly for evergreen forests (Figure S1).

When examining the distribution of % allocation to bNpp in boreal and temperate zones, we found that boreal % allocation to bNpp exhibited a bi-modal distribution, with clear peaks at 15% and 45%, suggesting site-scale variability and clustering in % allocation to bNpp within the boreal climate type. Cold temperate forests, on the other hand, had a mean % allocation to bNpp of 27%; however, the range for % allocation to bNpp was 20% higher for cold temperate (5-83%) than boreal (5-62%) forests, with some evergreen cold temperate forests allocating 83% of tNpp belowground (Table 1, Figure S1). The lack of difference between the two biomes and the larger range of % allocation to bNpp suggests that cold temperate forests have higher variability in their growing environmental conditions and site variation than boreal forests. This also further confirms that within-biome site-scale variation is important to consider when evaluating the drivers of belowground allocation patterns.

The very high values of % allocation to bNpp (60-80%, Figure S1; Figure S2) in cold temperate forests suggest release from aboveground resource limitation such as precipitation, leading to higher % allocation to bNpp due to belowground nutrient limitation to growth. Previous evidence suggests that bNpp in boreal forest systems is not driven by precipitation but controlled by nutrient limitation or solar radiation, indicating colimitation of above- and belowground resources to growth (Gherardi and Sala 2019). Tropical forests are also influenced by both above and belowground resource limitation, and especially by the diversity of growth limiting microsites (Klock et al. 2022a). Temperate forests, on the other hand, tend toward the average of tropical and boreal systems in productivity and diversity (Klock et al. 2022a, Reich and Bolstad 2001) and have milder climates and more variability in climate and geography.

Thus, they are limited more by belowground resources as they are released from the dominance of aboveground resource limitation.

How does ecosystem fit vary with forest biome and phenology?

Ecosystem fit was significantly higher for deciduous forests than evergreen forests. Ecosystem fit was also significantly higher in temperate than boreal forests, but only for evergreen forest types (Table 1, Figure S1). Ecosystem fit is the ratio of field-collected tNpp to the theoretical maximum tNpp and estimates how well a forest is adapted to its site and whether it has the capacity to grow more biomass beyond its current growth rate indicated by direct field measures of tNpp (Gordon et al. 1983, Gordon et al. 1992). Ecosystem fit depends on solar radiation and photosynthetic efficiency and is independent of local soil conditions, thus providing an independent measure of a forest's productive capacity (Klock et al. 2022b). Therefore, it is not surprising that deciduous traits typically involve higher photosynthetic efficiency, as the amount of total solar radiation generally limits boreal forest productivity. Importantly, phenology mediated the effect of forest biome on ecosystem fit. The overall ecosystem fit of deciduous trees was higher and did not differ between forest biomes, whereas the ecosystem fit of evergreen trees was lower and was influenced by forest biomes (Table 1, Figure S1), suggesting that deciduous forest types are more resilient to climate influences whereas evergreen traits are more sensitive to large-scale variations in climate.

What is the relative importance of soil variables versus climate variables in predicting belowground productivity, allocation, and ecosystem fit?

Soil variables, particularly soil nutrient flux rates, were the most important variables (Figure 1, Table S1). The effect of climate was secondary to the effect of soil variables (specifically soil flux rates), within and across biomes (Table 2). This suggests that soil characteristics, rather than climate variables, are the most important predictors of belowground productivity, allocation, and ecosystem fit. These results differ from a related study by Klock et al. (2022a), which found that a combination of climatic and edaphic variables explained productivity. However, Klock et al. (2022a) used a limited number of edaphic variables consisting of soil texture and soil taxonomic order, whereas this study employed a broad suite of aboveground and belowground soil variables which provided a more detailed analysis of specific environmental drivers of belowground productivity. The top five most important variables consisted of four soil flux rates (aboveground litter phosphorus (P) flux, soil nitrogen (N) flux, forest floor P mean residence time, and aboveground litter N flux), and one soil pool (forest floor P). The most important variables across and within biomes were P and N flux rates, suggesting colimitation of both N and P on productivity.

The effects of soil flux variables on productivity measures indicated that aNpp, tNpp and ecosystem fit increased with soil flux rates and soil pool size (Table S2). This is an expected pattern as productivity generally increases with nutrient cycling rates and availability as nutrient limitation is released and fuels growth (Wieder et al. 2015). However, these trends did not hold for bNpp and % allocation to bNpp. Individual soil flux rates and soil pools had differing and sometimes opposite effects for bNpp and % allocation to bNpp, and between measures of below- and aboveground productivity (Figure 2, Table S2). The fact that bNpp and % allocation to bNpp do not follow the same patterns as aboveground- or total productivity indicates that belowground processes are governed by different drivers than aboveground processes (Fortier et al. 2019), further emphasizing the need to fully understand and unravel the interactions between belowground processes, especially those of fungal symbionts, which are an important driver of soil nutrient cycling (Averill et al. 2014).

How did soil variables affect boreal forest productivity, allocation, and fit?

Soil flux variables had especially high variable importance for boreal forests, particularly for allocation belowground, where soil flux variables accounted for 72% of the relative importance of all environmental variables (Table 2). This was driven primarily by soil N flux and the soil N pool, which constituted 60% of the relative importance of all variables (Figure 1), indicating that these are main drivers of allocation belowground in boreal forests. Belowground productivity was primarily constrained by soil N flux and the forest floor P pool, also accounting for 60% of the relative variable importance (Figure 1). Allocation to the belowground was thus primarily limited by N, while bNpp was co-limited by N and P. Recent studies have provided new evidence that belowground productivity in boreal forests is not controlled by precipitation but driven by nutrient limitation or solar radiation (Gill and Finzi 2016, Nemani et al. 2003), supporting our results.

Our results also indicate that a few drivers constrain the system in unique ways. For example, the rate of soil N flux increased allocation belowground dramatically, with a hard threshold effect (sudden and large change) at 0.031 Mg/ha/yr that drove an increase in belowground allocation from 22% to 31% (Figure 2, Figure 1, Table S3). This indicates that soil N flux had a narrow range of effect on allocation but that effect on % allocation to bNpp was relatively strong. Furthermore, this suggests the existence of two states of belowground allocation in boreal forests – a low and high allocation state, driven by a critical environmental threshold determined by soil N flux rate. The effect of the soil N pool on allocation seems to confirm the presence of two distinct states of % allocation to bNpp – allocation decreases at a hard threshold of 2.6 Mg/ha of soil N, with a range of effect on % allocation to bNpp from 29% to 23% (Figure 2, Table S3). This also suggests that boreal forest allocation is split between two systems – one with low allocation (characterized by low rates of soil N cycling and a high soil N pool), and one with high allocation (characterized by high rates of soil N cycling and a low soil N pool). The high soil N flux at sites with high belowground allocation could reflect increased fungal activity, where low soil N levels would demand increased C allocation from tNpp (Wallenstein et al. 2006). The bi-modal distribution of % allocation to bNpp with clear peaks at 15% and 45% further confirmed this, suggesting site-scale variations and clustering in % allocation to bNpp within the boreal climate type.

For boreal bNpp, productivity increased with soil N flux and decreased with the forest floor N and P pools, and although hard threshold effects of a few dominant soil variables drove changes in bNpp, these changes were less impactful than those for % allocation to bNpp (Figure 2). The presence of hard threshold effects and the high % variable importance of just two soil variables suggests that belowground productivity and allocation in boreal forests have low adaptive capacity or resiliency (Seddon et al. 2011) and lack the ability to adapt to different environmental conditions within the variability of site variables. Furthermore, this suggests that these forest types could be prone to sudden changes in bNpp and % allocation to bNpp due to critical thresholds in soil flux rates, confirmed by the significantly lower ecosystem fit of boreal forests compared to temperate forests ($p < 0.001$; Figure S1).

Are soil variables driving % allocation to bNpp in boreal forests site-specific?

To further understand the drivers of these within-biome, site-scale groupings, we used random forest regression models to examine the effect of climate and edaphic variables on boreal forest systems characterized by low (≤ 20%) and high (> 20%) allocation patterns, clustered by the "sidClustering" function within the randomForestSRC package in R (Mantero and Ishwaran 2021, R Core Team 2020; Table S4). Results showed that boreal forests characterized by low belowground allocation were driven primarily by N-associated edaphic variables, while boreal forests with high belowground allocation were controlled by P-associated variables (Table S4; Figure S3). This suggests that belowground allocation in boreal forests is both N and P limited, but site-scale conditions drive these limitations and these differences were only observable within biomes. Furthermore, when examining the effects of dominant environmental drivers (soil N pool and soil N flux) for forests with high vs. low belowground allocation, we found that abrupt and large decreases in allocation were found in boreal forest sites with low allocation, and not in sites with high allocation (Figure S4). These abrupt allocation changes indicate that boreal forest stands with low belowground allocation are especially sensitive to changes in the environment and prone to sudden shifts in allocation with changing edaphic factors. For boreal forest productivity, the primary environmental drivers for low productivity sites (<2 Mg/ha/yr Npp) were aboveground litter N flux and aboveground litter flux, while for high productivity sites (> 2 Mg/ha/yr Npp) the dominant drivers were forest floor P and the soil P pool (Figure S5). These results demonstrate that scale is an important consideration in understanding drivers of productivity necessary for local forest assessments and management, especially because recent studies have confirmed that belowground allocation is highly variable within biomes, resulting in high uncertainty in global estimates of belowground processes. Furthermore, site-specific drivers of % allocation to bNpp provides evidence that plant communities and C allocation patterns adapt to local environmental site conditions (Luo et al. 2019).

How did soil variables affect cold temperate forest productivity, allocation, and fit?

Belowground productivity and allocation in cold temperate forests were driven primarily by soil pools and fluxes, although climate had a higher relative importance overall for productivity in cold temperate compared to boreal forests (Table 2). The fraction of productivity allocated belowground was driven by multiple soil variables, dominated primarily by soil flux rates, with relatively even variable importance (Figure 1). These variables were also split relatively evenly between aboveground and belowground N and P flux rates, suggesting colimitation of both N and P on allocation, which differed from boreal forests where N limitation seemed to be the main driver of % allocation to bNpp. Further confirming the differences in nutrient limitation, soil N was the dominant soil pool variable driving belowground allocation in boreal forests, while forest floor P was the dominant soil pool variable explaining allocation for cold temperate forests.

The large number of variables with similar percent values of relative importance for cold temperate forests suggests that there were no dominant drivers of % allocation to bNpp, with influence spread across many variables. Generally, soil variables affected allocation over a much wider range than in boreal forests, with more gradual non-threshold effects (Figure 1; Figure 3). However, soil variables had a much lower magnitude of effect on % allocation to bNpp in cold temperate forests (25-30%) than boreal forests (20-40%), indicating that allocation in boreal forests was much more sensitive to changes in soil nutrient cycling, and that these changes were more abrupt and intense.

Some variables had gradual non-monotonic effects on % allocation to bNpp, where a change in the direction of effect on the response occurred. For example, soil N flux decreased % allocation to bNpp for lower values of its range, but that effect was reversed for higher values of soil N flux, with trend change occurring at 0.025 Mg/ha/yr (Figure 3). The same trend was present for forest floor N mean residence time, and forest floor mean residence time (Figure 3), with % allocation to bNpp increasing for low rates of forest floor N flux and decreasing with high rates of forest floor N flux, the reverse of the trend observed for soil N flux on allocation. This illustrates that aboveground and belowground soil N cycling variables could have differing effects on % allocation to bNpp. These non-monotonic effects also suggest the presence of environmental thresholds that cause shifts in ecosystem properties.

Although some threshold-like effects were observed in several soil variables such as belowground litter flux and aboveground litter P flux, these were much less dramatic than those for boreal forests and indicative of some limitation release. These results show that cold temperate forests had many influential soil variables that affected belowground productivity and allocation in complex and non-linear ways, and with a large variability in responses. However, there was also the presence of some threshold values that indicated sudden changes or trend reversal in % allocation to bNpp. These results suggest that cold temperate forests, like boreal forests, exhibit a type of environmental threshold characterized by trend reversal. But unlike boreal forests, belowground productivity and allocation in cold temperate forests changed more gradually in response to environmental variables, suggesting higher adaptive capacity. This is further supported by the large number of variables with even variable importance, the lack of sharp threshold effects, and the lower magnitude of effect of soil variables on measures of productivity, all suggesting that bNpp and % allocation to bNpp in cold temperate forests are more resilient to changes in soil nutrient cycling. In addition, effects of soil variables on productivity within cold temperate forests was more variable and complex than those for boreal forests, indicating that cold temperate forests had higher variability of soil effects on productivity and a larger suite of interactions, making them potentially more adaptable to changes in the environment than boreal forests.

Soil variables for both boreal and cold temperate forests exhibited saturating effects on bNpp and % allocation to bNpp, where an increase in the soil variable had no effect on the productivity response variable. This suggests the presence of multiple limiting variables, where a variable limits productivity in the range of its effect, and limitation is removed upon saturation, whereupon some other environmental variable then limits the response variable. There is accumulating evidence that multiple (i.e., two or more) nutrient variable limitation is relatively common in forest ecosystems (Elser et al. 2007, Harpole et al. 2011, Fay et al. 2015). This colimitation can be defined as simultaneous colimitation, where both nutrients are needed to induce an increase in productivity, or independent colimitation, where productivity increase can be induced by either nutrient separately (Harpole et al. 2007), demonstrated in this study. These results further support the complex and non-linear interactions that regulate productivity and allocation.

Conclusion

Soil variables were the most important predictors of belowground productivity and allocation, whereas climate effects were tertiary after soil nutrient flux rates and soil nutrient pool variables. Therefore, soil flux rates and pools must be explicitly modeled to accurately predict feedback between climate, productivity, and allocation. This is contrary to most current Earth system and productivity models where climate is assumed to be the primary driver of productivity and C dynamics (Luo et al. 2019, Todd-Brown et al. 2013), indicating that more explicit and detailed representation of soil variables (e.g., the expansion of soil modules to include additional soil flux variables) needs to be incorporated to increase the accuracy of productivity and allocation predictions within forest ecosystems. Recent novel studies on global bNpp have shown that large-scale climate variables such as precipitation do not drive changes in bNpp or % allocation to bNpp in forest ecosystems (Gherardi and Sala 2020). Another recent study emphasized similar importance for global subsoil organic C turnover times, which were dominantly controlled by soil properties rather than climate at both local and global scales, providing similar insight on a previously unmapped albeit crucial belowground soil property (Luo et al. 2019).

Nitrogen and P soil pool and flux rates were the most important variables for predicting productivity and allocation in boreal and cold temperate forests, indicating the colimitation of both N and P across forest types. The type of limitation varied when forest belowground productivity was further subdivided into low and high productivity categories, indicating that within-biome site-level evaluation is important. Belowground productivity and allocation within boreal biomes were driven by few variables characterized by hard threshold effects resulting in sudden and large changes in productivity measures, signifying low adaptive capacity. Conversely, belowground productivity and allocation in cold temperate forests were influenced by many variables, a lack of hard threshold effects of environmental variables on productivity, and gradual changes in response variables, indicating a higher capacity to adapt to environmental change. This indicates that cold temperate forests might be more resilient to climate change while boreal forests could be more sensitive and could be more prone to sudden changes in productivity and allocation in response to changes in climate or other disturbances such as prescribed fire (Buonanduci et al. 2020, Harvey et al. 2023, Johnson and Johnson et al. 2019) or anthropogenic N deposition (Holtgrieve et al. 2011, Lilleskov et al. 2024). The lower resilience of boreal forests was further supported by lower ecosystem fit, and clustering of bNpp and % allocation to bNpp that showed that a higher percentage (70%) of boreal forest sites had lower bNpp than cold temperate sites (57%, Table S4). Importantly, increases in forest floor N and soil N led to state shifts and large decreases in belowground productivity and allocation in boreal forests, therefore N deposition has the potential to cause large decreases in bNpp and potentially push these forests beyond their adaptive capacity. Other disturbances such as drought could alter productivity by decreasing belowground cycling of N, leading to large and abrupt decreases in belowground productivity. However, boreal forests generally have the highest fungal diversity of all forest types (Li et al. 2022) and studies have reported strong associations between fungi and plant hosts, where mycorrhizal fungi can receive up to 20% of plant host C (Hobbie 2006, Konvalinková et al. 2017). Mycorrhizal fungal associations might help boreal forests maintain resilience to stressors such as drought and N deposition due to the ability of mycorrhizal fungi to supply water and mine nutrients for plant hosts.

Due to the lack of field-collected measures of productivity in a diversity of forest ecosystems globally, vegetation models are currently the best way to estimate C sequestration within forests and the effects that anthropogenic impacts and climate change will have on these C stores (Case et al. 2021). Using new modeling techniques in machine learning allows a more nuanced and detailed understanding of the mechanisms underpinning the controls on forest productivity, allocation, and adaptive capacity, specifically modeling non-linear effects and identifying thresholds of productivity and how these are driven by environmental variables, which are not able to be captured by traditional ecosystem vegetation models. Machine learning models can provide crucial information to forest management, such as quantifiable thresholds for biome-scale productivity at which state changes occur. In addition, our results showed that environmental drivers differed for varying productivity levels within biomes, indicating that development of within-biome classifications for forest systems could prove useful for management activities. Estimates of ecosystem fit can also allow managers to better understand a forest's productive capacity and predict whether forests can achieve higher levels of productivity and what drives the structure and function of these forests at the ecosystem scale. Although this information is important to assess and maintain forest health in response to climate change and other anthropogenic stressors, this research is also needed to inform communities that depend on forests to survive. Understanding the environmental drivers of a forest's productivity, allocation and ecosystem fit will determine if these forest ecosystems can provide ecosystem services for populations that rely on these forests (Chao 2012), and if forests can adapt to climate change within the constraints of edaphic controls. Our results allow for a more fine-scale assessment of forest regions sensitive to climate change, and further help guide site-specific policies and management for forest ecosystem health and effective C management. Furthermore, these results are essential to understanding and modeling the C cycle, especially as bNpp is the least known component of global C dynamics.

Materials and Methods

Dataset and variable selection

We used a unique and extensive multiple-biome dataset of field-based measurements conducted over 40 years to test the questions posed for this research (Table S6, Klock et al. 2022a). The dataset contained soil and climate variables, and tNpp, aNpp, and bNpp data collected per site (collection methodology is described in the literature listed in Table S6). The dataset described 181 natural forest sites, which were characterized at two spatio-ecological scales: leaf phenology types at the large scale (139 evergreen; 42 deciduous) and climatic regions at the meso-scale (69 boreal – 84% evergreen; 99 cold temperate – 74% evergreen; 13 warm temperate – 62% evergreen). Climatic and soil variables are listed in Table S1. By phenology and regional climate groupings, almost all soil and climate variables were used to predict ecosystem fit, tNpp, aNpp, bNpp, and % allocation to bNpp. The soil variables aboveground litter flux and belowground litter flux were only used to predict ecosystem fit, as these variables include production measures. A previous study examined this dataset with a focus on tNpp and ecosystem fit and used an expanded dataset that contained additional biomes such as tropical forests (Klock et al. 2022a). Our study provides a detailed look at sites that contain a larger suite of soil variables to comprehensively assess drivers of belowground productivity, allocation, and ecosystem fit.

We used ecosystem fit as a response variable to assess how well a forest was adapted to its site constraints to grow biomass. Ecosystem fit uses a reference maximum productivity level calculated with factors external to the site and not influenced by internal site conditions (Gordon et al. 1992, Gordon et al. 1995). The most important climatic and edaphic variables can be used to identify the “safe operating space” at each site; that is, where the upper and lower bounds of environmental conditions will determine the forests that are better adapted to their current growth environment and which forests might be more vulnerable to climate change and may need management intervention (Johnstone et al. 2016, Scheffer et al. 2015). Ecosystem fit uses the Theoretical Maximum Productive Capacity, which is modeled as the product of mean solar radiation (Fick and Hijmans 2017), interception efficiency, the efficiency with which forest canopies absorb solar radiation, and the conversion efficiency, or the rate at which solar radiation is absorbed by plants and converted to biomass (Delucia et al. 2014). Model parametrization, equations, and values were taken from Klock et al. (2022b). This model assumes that photorespiration is a constant fraction of photosynthesis, photosynthetically active radiation is 45% of total solar radiation, forest canopies absorb 90% of incoming photosynthetically active radiation during active growth, and growth is not limited by water or nutrients.

Model comparison and selection

We conducted model comparisons between linear regression (R package “MASS”), conditional forest (R package “party”), and random forest (R package “randomForest”) (R Core Team 2020) models using all soil and climatic variables to predict tNpp (Table S5). Although linear regression models are easier to interpret, random forest models work well with large datasets, work with missing data, and work better with non-linear trends (Lemon et al. 2003), which we identified with these data. Random forest models showed the lowest root mean squared error and mean absolute error for all measures of productivity (tNpp, aNpp, bNpp, % allocation to bNpp, and ecosystem fit). The random forest regression models were then used to predict the effect of soil and climatic variables on aNpp, bNpp, % allocation to bNpp, and ecosystem fit for boreal and cold temperate forests. For each model, we calculated root mean squared error (RMSE), % variance explained by the predictor variables (pseudo R^2), the mean squared error of out-of-bag errors, and model mean absolute error (MAE) (Table S2), as well as the percent relative importance of climatic and soil variables (Table 2) and the most important variables based on %IncMSE (Figure 1). To evaluate the overall relative importance of soil and climate variables, we summed the relative importance of individual variables for soil and climate, respectively.

This study used the “randomForest” package in the R-environment (Liaw and Wiener 2002, R Core Team 2020). The algorithm combines large sets of decision trees formed by selecting sets of variables to improve classification and regression analysis. The recursive feature elimination function was used to identify the most important predictor variables with respect to the response variable. For modeling, 2/3 of the samples were used for training the algorithm, and 1/3 (‘out of bag’ or OOB samples) were used for cross-validation to determine the model error (OOB error). The major parameters required for proper optimization of the random forest model included: ‘ntree’, the total number of regression trees grown from bootstrap samples of the observations, ‘mtry’ – the number of predictor variables examined at each node, ‘nodesize’ – the smallest size of the end nodes of the trees grown. Following multiple iterations, the optimum ‘ntree’ selected was 500 at ‘mtry’ = 8 as it resulted in the smaller OOB error. To avoid overfitting, we optimized a tuning parameter that governs the number of features that are randomly chosen to grow each tree from the bootstrapped data using K-fold cross-validation, where $K \in \{5,10\}$, and chose the tuning parameter that minimizes test sample prediction error. In addition, growing larger forests improved predictive accuracy, although there are usually diminishing returns once there are up to several hundred trees. Further information regarding partial dependence plots, multicollinearity and unbiased variable selection can be found in the SI.

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Table 1. Summary statistics of Aboveground Net Primary Productivity (aNpp) and Belowground Net Primary Productivity (bNpp), % allocation belowground (% allocation to bNpp), and ecosystem fit.

	Measure of productivity (mean ± SE)				
Type	tNpp (Mg/ha/yr)	aNpp (Mg/ha/yr)	bNpp (Mg/ha/yr)	Allocation to bNpp (%)	Ecosystem fit (%)
Boreal and temperate	11.4 ± 0.5	8.4 ± 0.4	3.0 ± 0.2	0.26 ± 0.01	5.5 ± 2.1
Phenology					
Deciduous	12.6 ± 0.7	9.1 ± 0.62	3.2 ± 0.3	0.3 ± 0.02	6.8 ± 0.5
Evergreen	11.1 ± 0.6	8.1 ± 0.5	2.9 ± 0.2	0.3 ± 0.01	5.1 ± 0.2
Climate zone					
Boreal	7.4 ± 0.5	5.6 ± 0.4	1.8 ± 0.2	0.2 ± 0.02	4.8 ± 0.3
Cold temperate	13.8 ± 0.6	10.0 ± 0.5	3.6 ± 0.2	0.3 ± 0.02	6.0 ± 0.3
Warm temperate	17.6 ± 2.1	13.2 ± 2.1	4.5 ± 0.9	0.3 ± 0.05	6.4 ± 0.9

Table 2. The % relative importance of predictor variables grouped by climate (mean air temperature, minimum air temperature, maximum air temperature, total annual precipitation), soil properties (soil taxonomic order, soil texture), soil pools (soil N, soil P, soil organic matter, forest floor mass, forest floor N, forest floor P), and soil fluxes (aboveground litter flux, belowground litter flux, aboveground litter N flux, aboveground litter P flux, soil N flux, forest floor mean residence time, forest floor N mean residence time, forest floor P mean residence time) for random forest models estimating the effects of these variables on the response variables of tNpp, bNpp, % allocation to bNpp, and ecosystem fit in boreal and cold temperate forests.

	Predictor variable groups (% relative importance)				
	Response	Climate	Soil properties	Soil pools	Soil fluxes
Boreal	tNpp	14	3	25	58
	bNpp	14	3	51	33
	% Allocation to bNpp	4	1	22	72
	Ecosystem fit	20	10	22	47
Cold temperate	tNpp	20	4	23	53
	bNpp	15	5	43	38
	% Allocation to bNpp	23	6	27	45
	Ecosystem fit	19	2	11	67

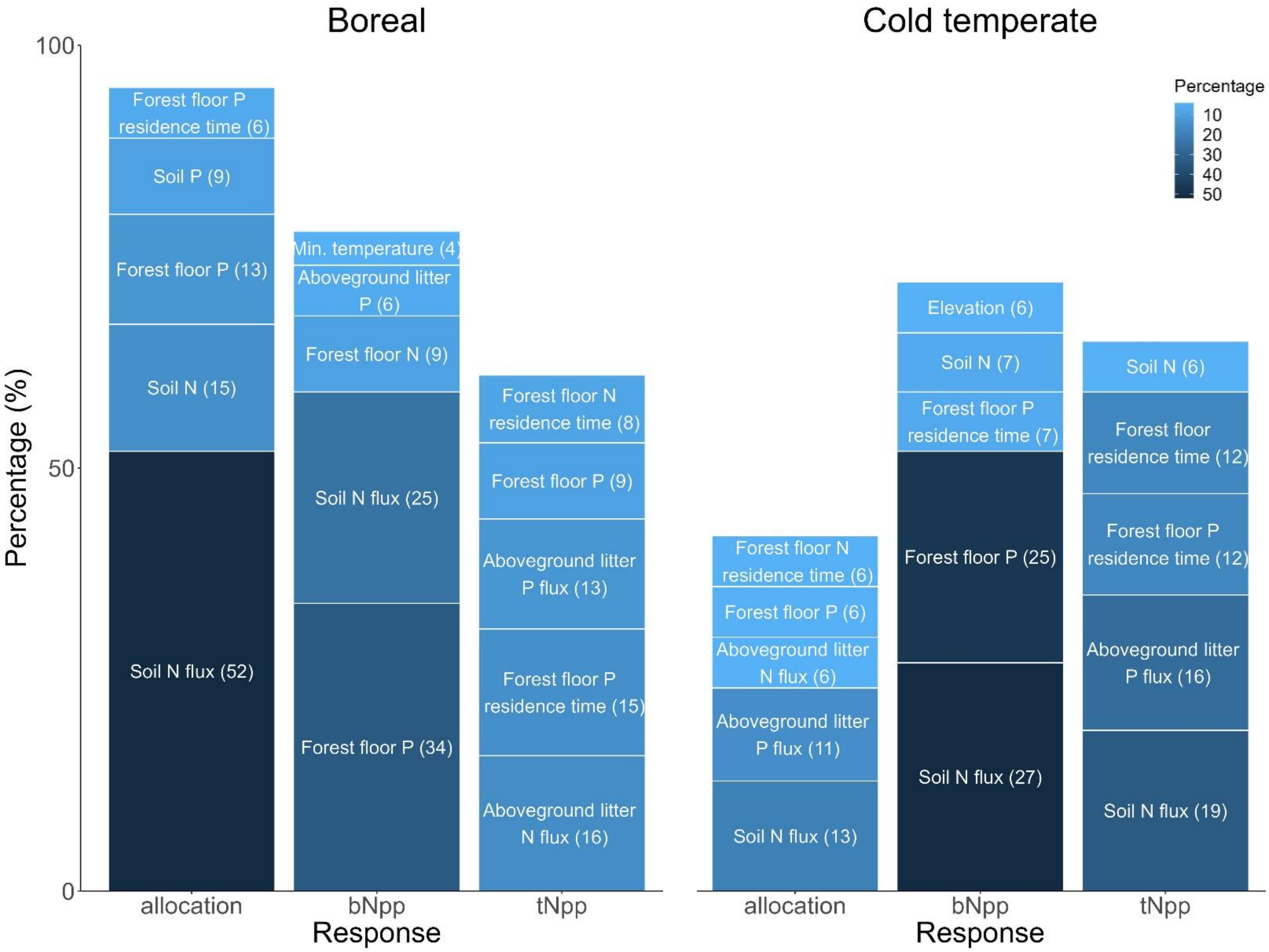

Figure 1. The top five most important variables identified by random forest regression models predicting total net primary productivity (tNpp), belowground net primary productivity (bNpp) and % allocation to bNpp, for boreal and cold temperate forests. For each model, the top five variables are stacked in order of importance. The height of each stack within the boxplot corresponds to the percentage of the variable’s importance for each model, and % variable importance is written alongside each variable.

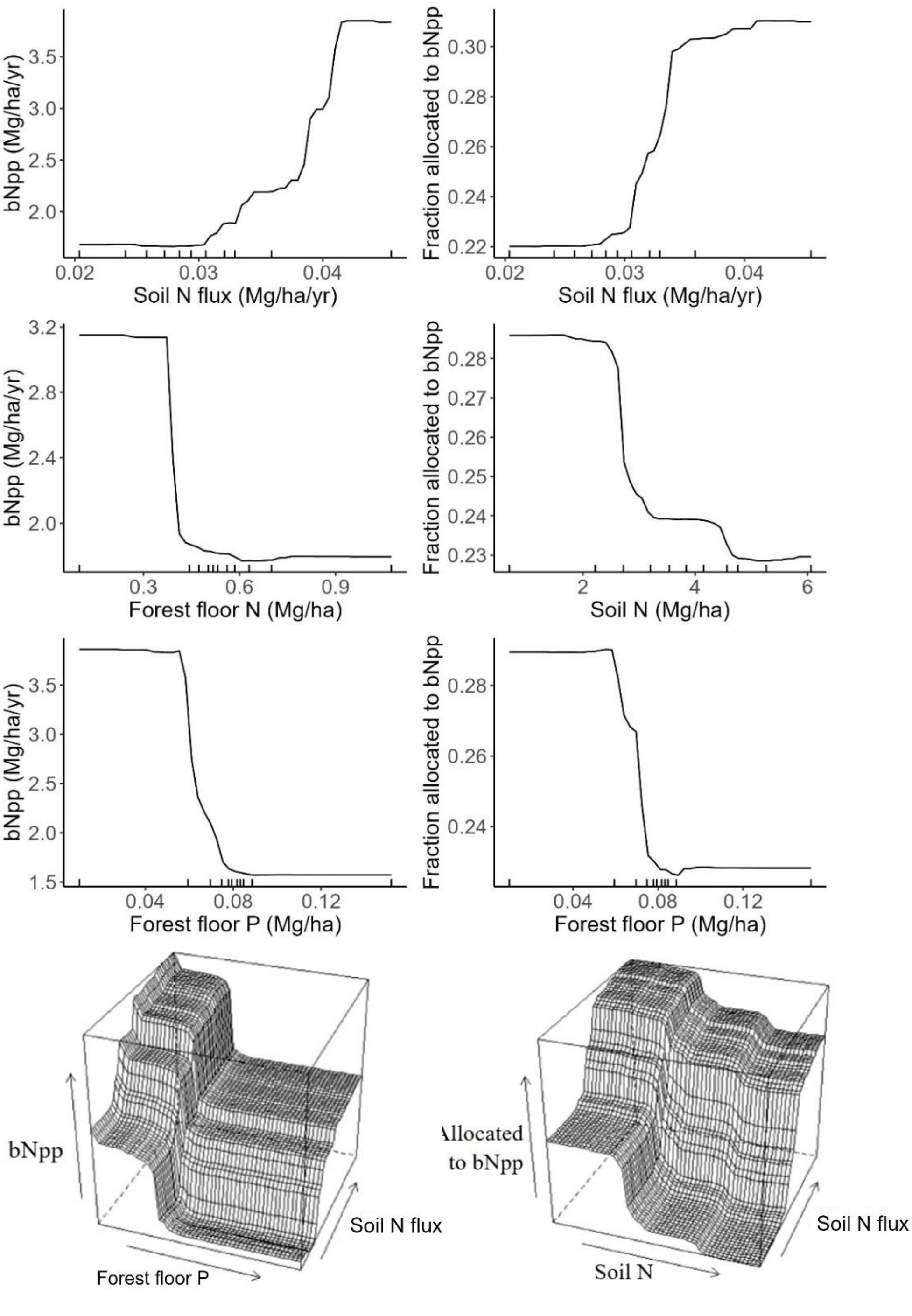

Figure 2. Partial dependence plots for boreal forests. Left panels illustrate the marginal effects of the most important variables on belowground net primary productivity (bNpp), which were soil N flux (top panel), forest floor N (second panel) and forest floor P (third panel). Right panels illustrate the effect of the most important variables on % allocation to bNpp, which were soil N flux (top panel), soil N (second panel), and forest floor P (third panel). The bottom panels show a three-dimensional partial dependence plot illustrating the effect of forest floor P and soil N flux on bNpp, and the effect of soil N and soil N flux on % allocation to bNpp.

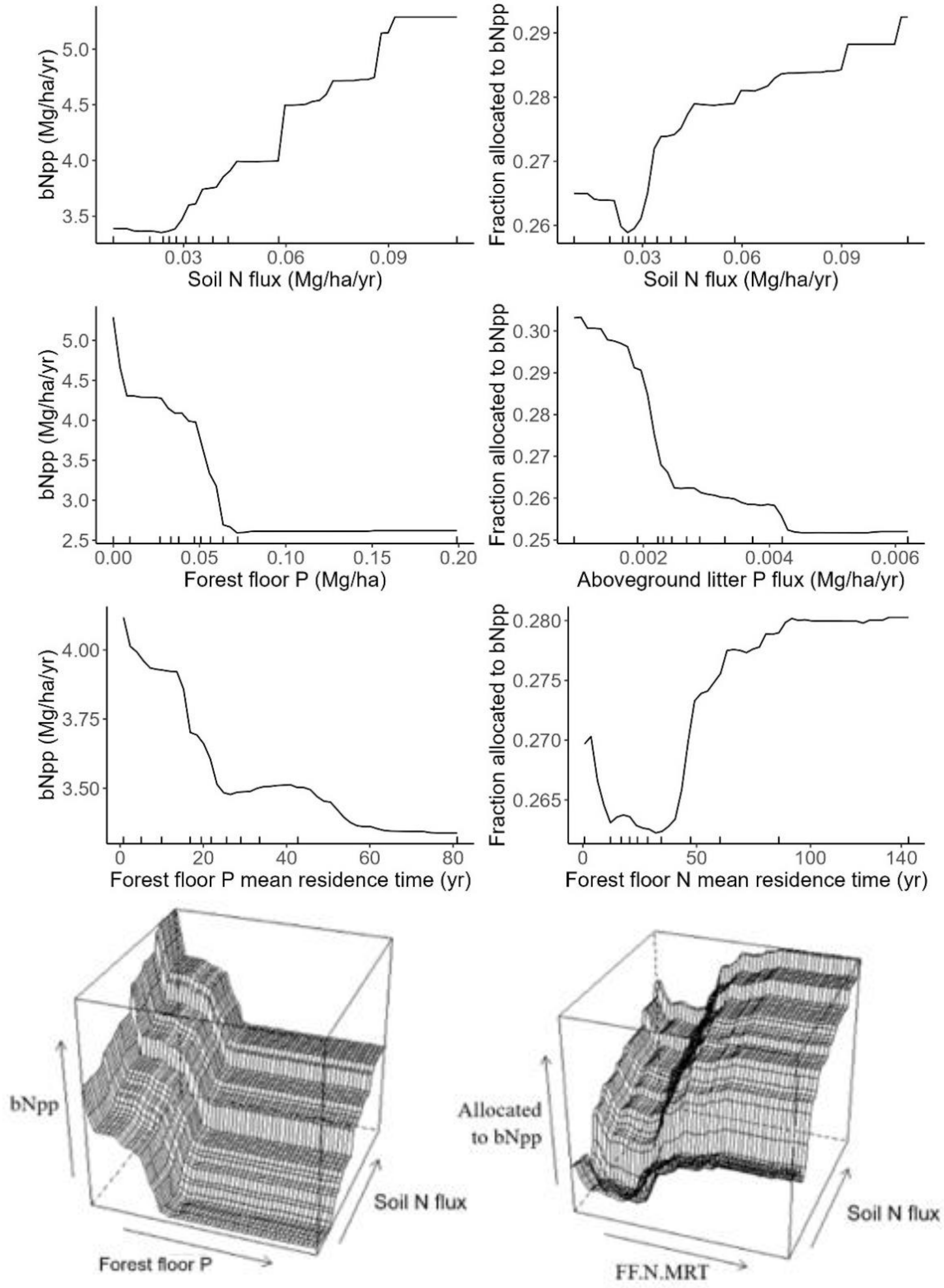

Figure 3. Partial dependence plots for cold temperate forests. Left panels illustrate the marginal effects of the most important variables on belowground net primary productivity (bNpp), which were soil N flux (top panel), forest floor P (second panel), and forest floor P mean residence time (third panel). Right panels illustrate the effect of the most important variables on % allocation to bNpp, which were soil N flux, aboveground litter P, and forest floor N mean residence time. The bottom panels show a three-dimensional partial dependence plot illustrating the effect of forest floor P and soil N flux on bNpp, and the effect of forest floor N mean residence time and soil N flux on % allocation to bNpp.

Supporting Information Text

Model comparison and selection. Results for random forest models typically consist of variable importance plots, and 1D and 2D partial dependency plots (Cutler et al. 2007). Variable (or feature) importance is the standard interpretation of random forest models and identifies variables with the best predictive power. The higher the importance, the more relevant the variable is according to the model. The mean decrease in accuracy, or percent increase in mean squared error, is the most robust and informative measure for the variable importance plot and shows how much model accuracy (model MSE) decreases if that variable is left out (or how much model accuracy increases if that variable is included). In other words, it is the increase in model MSE of predictions (estimated with out-of-bag-samples) as a result of variable j being permuted (values randomly shuffled). Partial dependency plots show the marginal effect that one (1D) or two (2D) features have on the predicted outcome of a machine learning model. A partial dependency plot can show whether the relationship between the target and a feature is linear, monotonic or more complex.

Random forest regression models have several advantages compared to linear models, since they do not require the typical assumptions of linear models to be met such as linearity, normality, no multicollinearity and homoscedastic variance. In addition, random forest models can work with large, unbalanced datasets with varying data types, are able to assess complex, non-linear interactions between variables and calculate variable importance (Lemon et al. 2003). Concerning correlated predictors in random forest models, multicollinearity is not an issue for random forest models. This is because each tree node is constructed by finding a single predictor and cut point, so only one candidate-predictor is examined at once. That is why relationships between predictors do not create problems since the random forest model never looks at more than one predictor at once. In addition, at each node, only a subset of predictors is taken into account, which is another anti-collinearity feature of random forest models.

However, although multicollinearity is not a problem for the random forest algorithm, it may be a problem for the random forest user. When the dataset has two (or more) correlated features, then from the model's point of view, any of these correlated features can be used as the predictor, with no concrete preference of one over the others. However, once one of them is used, the importance of others is significantly reduced, since the impurity they can remove is effectively already removed by the first feature. Consequently, they will have a lower reported importance. This is not an issue when we want to use feature selection to reduce overfitting, since removing features that are mostly duplicated by other features makes sense. But when interpreting the data, it can lead to the incorrect conclusion that one of the variables is a strong predictor while the others in the same group are unimportant, while they are actually very close in terms of their relationship with the response variable. This can lead to an inconsistent result of variable importance when predictors are highly correlated (Strobl et al. 2008). In order to overcome this limitation, we repeated the analysis with conditional forest models using the "cforest" function (Strobl et al. 2009) in the package party in the R environment (Hothorn et al. 2006). Conditional forest models, similar to random forests, use an ensemble method that combines collection of trees, but use conditional inference trees instead of a regression tree and run a permutation test that is conditioned on the correlated predictors and ensure unbiased variable selection and variable importance. Since the conditional forest model results had very similar variable importance to random forest models, we continued with random forest model analyses.

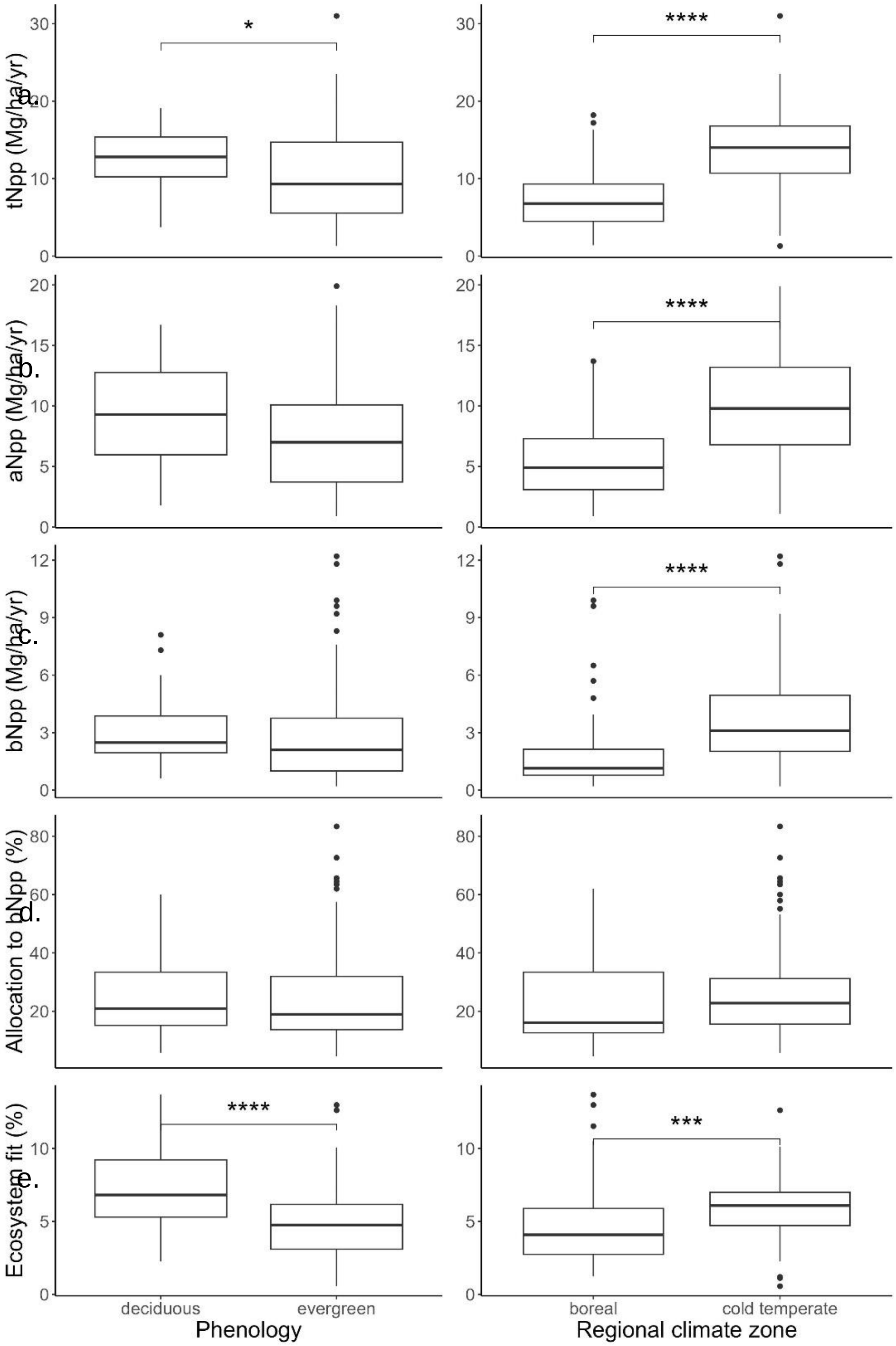

Fig. S1. Comparison of (a) Total Net Primary Productivity (tNpp), (b) Aboveground Net Primary Productivity (aNpp), (c) Belowground Net Primary Productivity (bNpp), (d) fraction allocated belowground (% allocation to bNpp or bNpp/tNpp), and (e) ecosystem fit (a measure of theoretical productivity potential) divided by phenology (deciduous or evergreen; left column) and climate type (boreal, cold temperate, and warm temperate; right column). Statistics reported at top are Wilcoxon rank sum test and p value. Significant pairwise differences are reported with brackets for each pair (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, **** $p \leq 0.0001$)

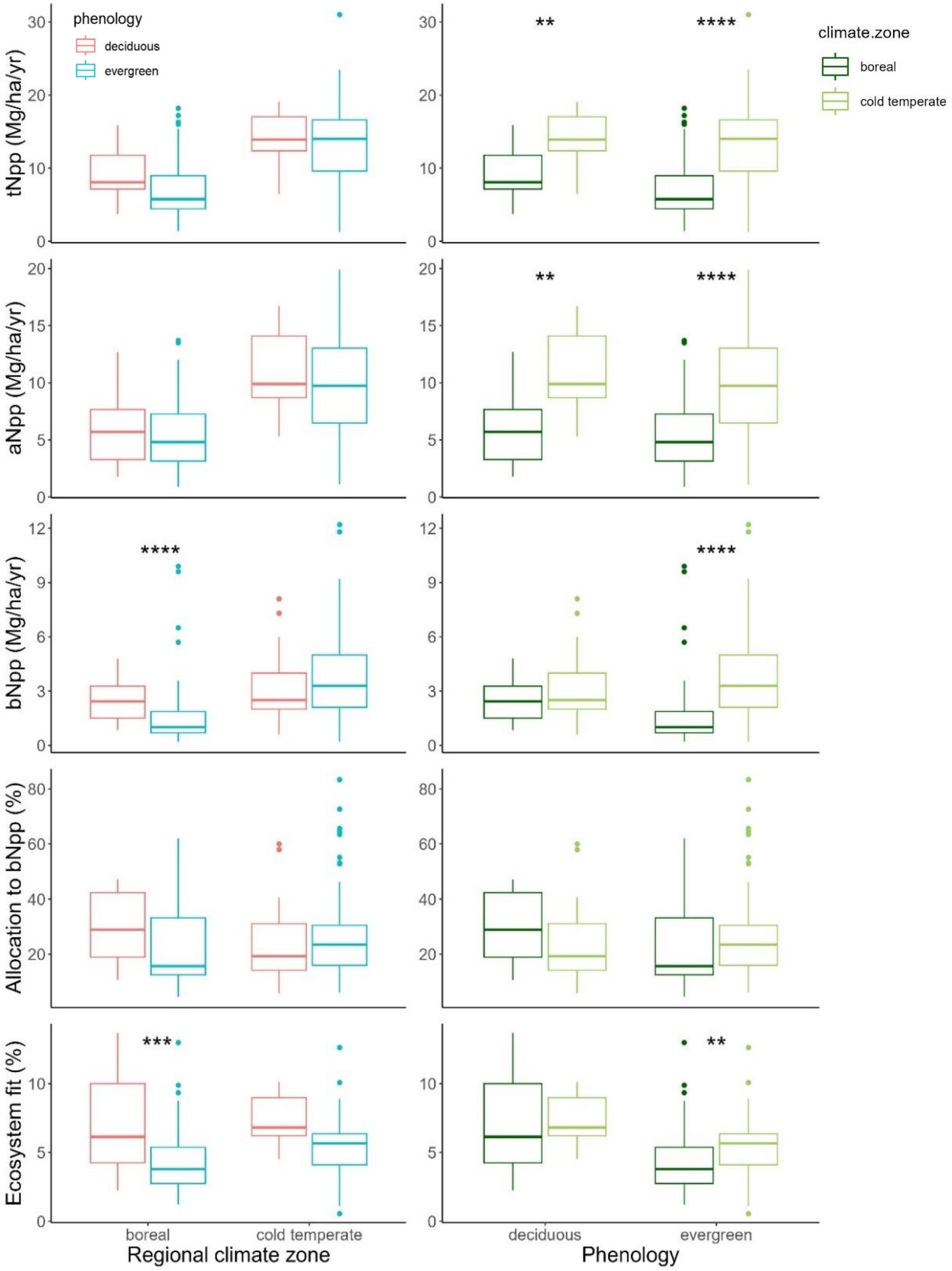

Figure S2. Comparison of (a) Total Net Primary Productivity (tNpp), (b) Aboveground Net Primary Productivity (aNpp), (c) Belowground Net Primary Productivity (bNpp), (d) fraction allocated belowground (% bNpp or bNpp/tNpp) and (e) ecosystem fit (a measure of theoretical productivity potential) divided by phenology (deciduous or evergreen) within climate type (boreal, cold temperate, and warm temperate; left column), and by climate type within phenology (right column). Statistics reported at top are Wilcoxon rank sum test and p value. Significant pairwise differences are reported with brackets for each pair (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, **** $p \leq 0.0001$).

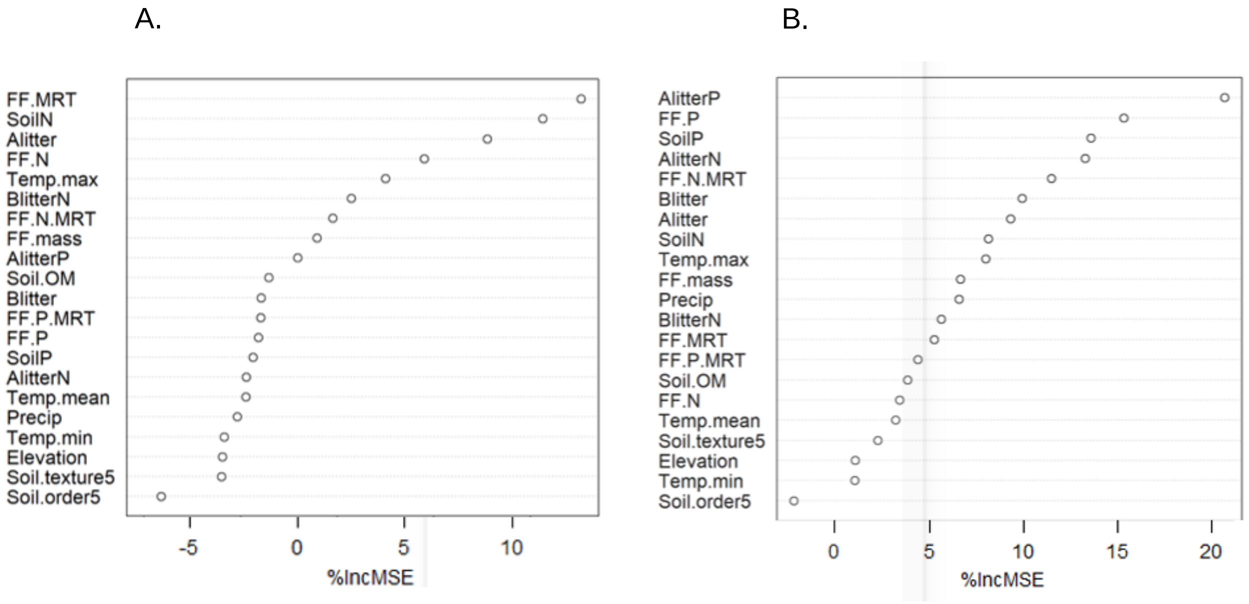

Figure S3. Variable importance plots generated from random forest regression modeling the effect of climatic and edaphic variables on percent allocation belowground (% bNpp) for boreal forests for A) low values of percent allocation belowground (< 20%) and B) high values of percent allocation belowground (> 20%).

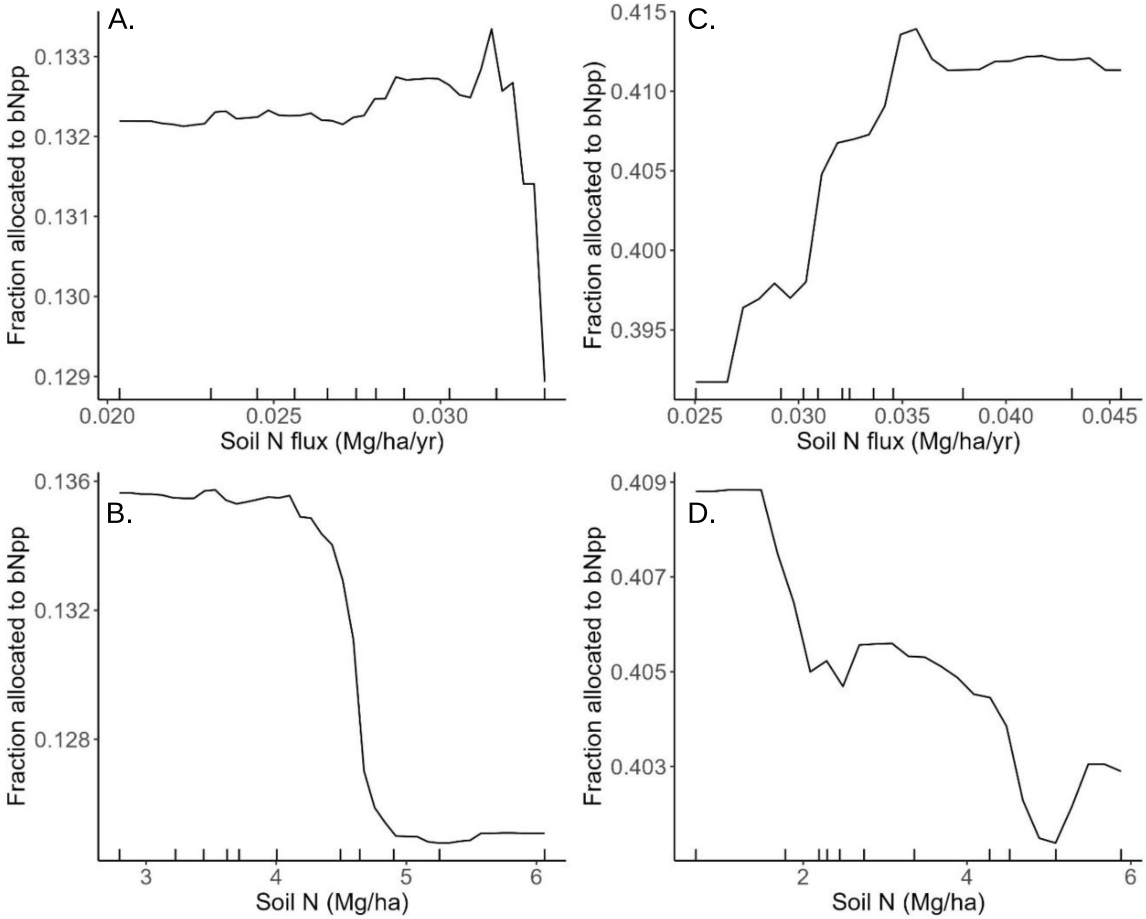

Figure S4. Partial dependence plots illustrating the effects of belowground litter N flux and the soil N pool on (A-B) low allocation (% bNpp < 20%) boreal forest sites and (C-D) high allocation (% bNpp > 20%) boreal forest sites.

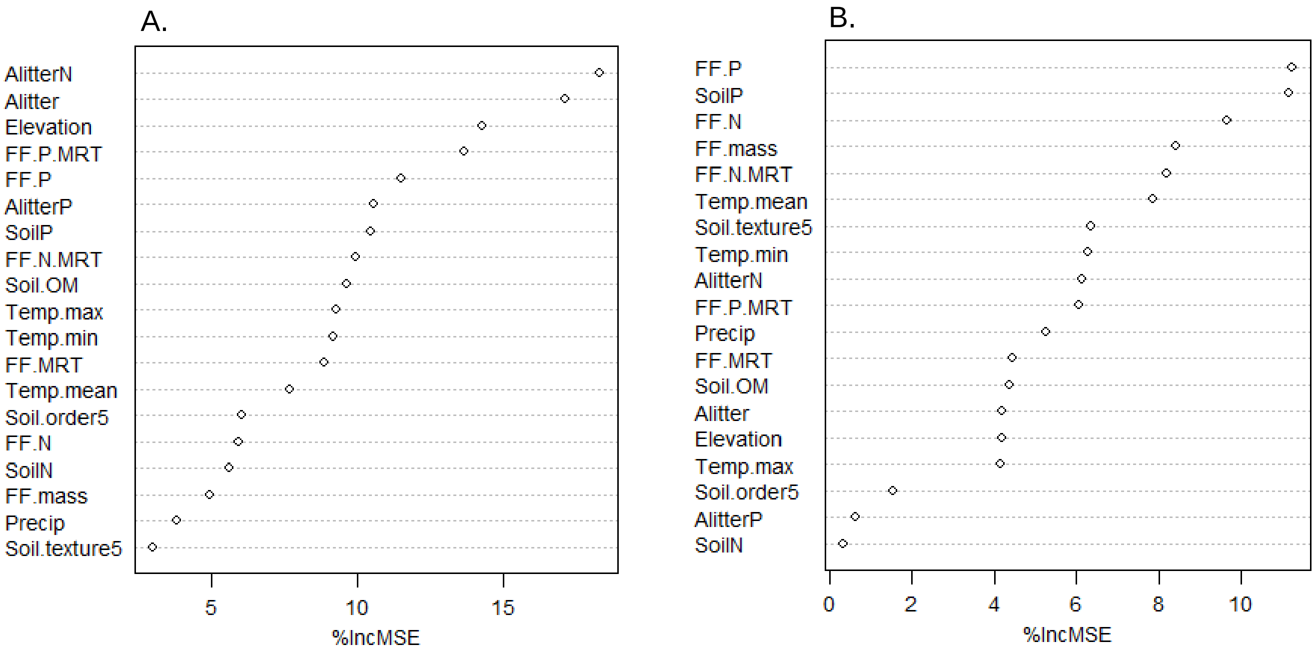

Figure S5. Variable importance plots generated from random forest regression modeling the effect of climatic and edaphic variables on belowground productivity (bNpp) for boreal forests for A) low values of percent allocation belowground (<2 Mg/ha/yr) and B) high values of percent allocation belowground (>2 Mg/ha/yr).

Table S1. Description of response variables and predictor variables used for this study. (Total Net Primary Productivity (tNpp), Above Net Primary Productivity (aNpp) and Belowground Net Primary Productivity (bNpp)).

Response Variables		**Predictor Variables**				
			Soil			
Variable Name	Description	Climate and elevation	Soil type	Soil pools (Mg/ha)	Soil fluxes (Mg/ha/yr)	Soil fluxes (yrs)
aNpp (Mg/ha/yr)	Aboveground net primary productivity	Mean air temperature (C)	Soil taxonomic order	Soil N	Aboveground litter flux	Forest floor mean residence time
bNpp (Mg/ha/yr)	Belowground net primary productivity	Minimum air temperature (C)	Soil texture	Soil P	Belowground litter flux	Forest floor N mean residence time
tNpp (Mg/ha/yr) [tNpp =aNpp+bNpp]	Total net primary productivity	Maximum air temperature (C)		Soil organic matter	Aboveground litter N flux	Forest floor P mean residence time
% allocation to bNpp [bNpp/tNpp*100]	% tNpp allocated belowground	Total annual precipitation (mm)		Forest floor mass	Aboveground litter P flux	
TMNPP (Mg/ha/yr) [solar radiation * photosynthetic efficiency * interception efficiency * inverse of biomass * absorption efficiency]	Theoretical maximum net primary productivity	Elevation (m)		Forest floor N	Soil N flux	
Ecosystem fit	tNpp/tmNpp			Forest floor P		

Table S2. Model summary for predicting tNpp, bNpp, and % allocation to bNpp for boreal and cold temperate forests. Pseudo R^2 is the percent variance explained by out-of-bag (OOB) predictions. MSE OOB error is the mean squared error of out-of-bag errors. Model root mean square error (RMSE) is the tuned model error rate in units of the response. Mean absolute error (MAE) is the error rate for the model robustness against outliers.

Model	Pseudo R^2	MSE OOB error	Model RMSE	MAE
Boreal forests (*n* = 69):				
tNpp	73.2	4.2	0.89	0.71
bNpp	74.51	0.9	0.44	0.27
% Allocation to bNpp	68.9	0.007	0.03	0.02
Cold temperate forests (*n* = 99):				
tNpp	64.17	8.44	1.25	0.85
bNpp	45.13	2.74	0.67	0.49
% Allocation to bNpp	44.06	0.01	0.05	0.03

Table S3. The most important predictor variables and their effect on response variables - TNPP, ANPP, BNPP, % BNPP, and ecosystem fit - by forest type (boreal, cold temperate, and warm temperate). Effects include trend (direction of effect), trend type (monotonic, non-monotonic, or hard saturation), threshold and saturating values for predictors, and the range of effect that each predictor had on the response variable.

TNPP

Climate	Variable	Trend	Trend type	Threshold & saturating values (predictor)	Range of effect on TNPP (Mg/ha/yr)
Boreal (n=69)	AlitterN (Mg/ha/yr)	+	m	0.02-0.035	6.5-9.5
	FF.P.MRT (yrs)	-	m	15-80	6.5-8.3
	Alitter (Mg /ha/yr)	+	m	1.5-1.6, 2.5-5	6.5-8
Cold temperate (n=99)	Soil N flux (Mg/ha/yr)	+	hs	0.02-0.037	13-15.5
	AlitterP (Mg/ha/yr)	+	m	0.002-0.004	12.5-15.5
	FF.P.MRT (yrs)	-	m	0-60	12-14.5
	FF.MRT (yrs)	-	(hs)	0-50	12.5-14

ANPP

Climate	Variable	Trend	Trend type	Threshold to saturating value (predictor)	Range of effect on ANPP (Mg/ha/yr)
Boreal (n=69)	AlitterN (Mg/ha/yr)	+	m	0.02-0.04	5-7.5
	Soil P (Mg/ha)	+	m	0.4-1.1	5-6.5
	FF.P.MRT (yr)	-	m	10-60	5-6
	FF.N.MRT (yr)	-	M,hs	10-30, 70-100	5-6.2
Cold temperate (n=99)	AlitterP (Mg/ha/yr)	+	m	0.002-0.004	8.5-11.5
	FF.MRT (yr)	-	(m)	30-50	8.5-10.5
	FF.N.MRT (yr)	-	m	30-70	9.4-10.4

BNPP

Climate	Variable	Trend	Trend type	Threshold to saturating value (predictor)	Range of effect on BNPP (Mg/ha/yr)
Boreal (n=69)	FF.P (Mg/ha)	-	hs	0.05-0.1	1.5-3.5
	Soil N flux (Mg/ha/yr)	+	m	0.03-0.04	1.5-3.5
	FF.N (Mg/ha)	-	hs	0.4-0.6	1.8-2.8
Cold temperate (n=99)	Soil N flux (Mg/ha/yr)	+	m	0.02-0.09	3.5-5.5
	FF.P (Mg/ha)	-	m	0-0.07	2.5-5.5

Percent BNPP

Climate	Variable	Trend	Trend type	Predictor: threshold and/or range of effect	Response: Range of effect
Boreal (n=69)	Soil N flux (Mg/ha/yr)	+	hs	0.031	20-40
	Soil N (Mg/ha)	-	hs	2.61	22-32
Cold temperate (n=99)	Soil N flux (Mg/ha/yr)	+	hs,m	4, 3-10	25-30, 30-33
	FF.N.MRT (yr)	-,+	nm	0-25 (-) 25-75(+)	26-28.5
	AlitterP (Mg/ha/yr)	-	hs,m	0.002, 0.002-0.004	30.5-26.5 25-26.5
	FF.P (Mg/ha)	-	m	0-0.1	26-29
	FF.MRT (yr)	-,+	nm	0-10 (-), 10-60 (+)	26.5-28.5
	Soil N flux (Mg/ha/yr)	-,+	nm	0.01-0.02 (-), 0.02-0.1 (+)	26-29

Ecosystem Fit

Climate	Variable	Trend	Trend type	Threshold to saturating value (predictor)	Range of effect on ecosystem fit
Boreal (n=69)	AlitterN (Mg/ha/yr)	+	m	0.02-0.035	0.045-0.058
	FF.P.MRT (yr)	-	m	No threshold, 10-80	0.044-0.054
	Alitter (Mg/ha/yr)	+	m	1.5-5	0.045-0.051
Cold temperate (n=99)	FF.P.MRT (yr)	-	m	20-60	0.048-0.064
	Alitter P (Mg/ha/yr)	+	m	0.002-0.004	0.05-0.075

Table S4. Ranked clusters of bNpp (belowground net primary productivity) and % allocation to bNpp (low, medium, and high) by ecophysiological scale. Notation shows mean ± SEM, [range], with number of samples (n) within each cluster. Clusters were selected using the partitioning around medoids (PAM) method. All bNpp and % allocation to bNpp mean values in the low, medium, and high ranks are significantly different within each row.

BNPP

	Low	Medium	High
Boreal and temperate (*n*=168)	1.1 ± 0.06 [0.2-2.1] *n*=77	3.2 ± 0.09 [2.2-4.8] *n*=61	6.8 ± 3.6 [5-12.2] *n*=30
Boreal (*n*=69)	0.93 ± 0.6 [0.2-1.9] *n* =47	2.9 ± 0.2 [2-5.1] *n*=18	7.9 ± 1 [5.7-9.9] *n*=4
Cold temperate (*n*=99)	2.1 ± 0.1 [0.2-3.4] *n*=57	4.9 ± 0.2 [3.6-6.5] *n*=35	9.2 ± 0.8 [7.3-12.2] *n*=7
Evergreen (*n*=139)	1.4 ± 0.08 [0.2-2.8] *n*=85	4.5 ± 0.18 [3-6.5] *n*=45	9.8 ± 0.49 [7.6-12.2] *n*=9
Deciduous (*n*=42)	1.5 ± 0.1 [0.6-2.1] *n*=14	3 ± 0.1 [2.3-4] *n*=18	6.2 ± 0.4 [4.8-8.1] *n*=10

% allocation to BNPP

	Low	Medium	High
Boreal and temperate (*n*=168)	15 ± 0.4 [4.5-23] *n*=92	31 ± 0.8 [23-43] *n*=53	55 ± 2 [43-84] *n*=23
Boreal (*n*=69)	13 ± 0.5 [4.5-20] *n*=42	31 ± 0.8 [26-35] *n*=11	48 ± 1.5 [40-62] *n*=16
Cold temperate (*n*=99)	17 ± 0.6 [5.8-24.7] *n*=59	33 ± 0.9 [25-46] *n*=30	63 ± 3 [52-83] *n*=10
Evergreen (*n*=139)	14 ± 0.4 [3.2-21] *n*=71	30 ± 0.8 [22-43] *n*=49	57 ± 2.4 [44-83] *n*=19
Deciduous (*n*=42)	16 ± 0.8 [6-21] *n*=22	29 ± 1.3 [23-37] *n*=10	48 ± 2.1 [39-60] *n*=10

Table S5. Model comparison between linear regression, conditional forest (Cforest), and random forest models predicting Total Net Primary Productivity (tNpp), Above Net Primary Productivity (aNpp) and Belowground Net Primary Productivity (bNpp) for climate and edaphic variables using random mean squared error (RMSE) and mean absolute error (MAE).

tNpp

Model type	RMSE	MAE
Linear regression	3.3	2.6
Cforest	1.77	2.46
Random forest	0.04	1.08

aNpp

Model type	RMSE	MAE
Linear regression	2.96	2.24
Cforest	6.75	1.7
Random forest	1.04	0.74

bNpp

Model type	RMSE	MAE
Linear regression	1.6	1.14
Cforest	1.43	0.88
Random forest	0.58	0.39

Table S6. Database ID, site location, dominant forest type and citations for boreal and cold temperate forests.

ID	Location	Forest Type	Citations
BOREAL FORESTS			
1	Alaska	*Picea mariana*, feather moss, no permafrost	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: *Dynamic Properties of Forest Ecosystems* (ed Reichle DE), pp. 341-409. International Biological Programme 23, Cambridge Univ. Press, London; DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle,ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Soil Survey of Greater Nenana Area, Alaska. MRCS. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alaska/AK655/0/GreaterNenana.pdf; Viereck LA, CT Dyrness, K Van Cleve, M J Foote. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Can. J. Forest Res. 13(5), 703-720.
2	Alaska	*Picea mariana*, muskeg, no permafrost	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: *Dynamic Properties of Forest Ecosystems* (ed Reichle DE), pp. 341-409. International Biological Programme 23, Cambridge Univ. Press, London; DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle,ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Soil Survey of Greater Nenana Area, Alaska. MRCS. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alaska/AK655/0/GreaterNenana.pdf; Viereck LA, CT Dyrness, K Van Cleve, M J Foote. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Can. J. Forest Res. 13(5), 703-720.
3	Alaska	*Picea mariana*, muskeg, permafrost 55 cm	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: *Dynamic Properties of Forest Ecosystems* (ed Reichle DE), pp. 341-409. International Biological Programme 23, Cambridge Univ. Press, London; DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle,ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Soil Survey of Greater Nenana Area, Alaska. MRCS. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alaska/AK655/0/GreaterNenana.pdf; Viereck LA, CT Dyrness, K Van Cleve, M J Foote. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Can. J. Forest Res. 13(5), 703-720.
4	Alaska, US [Bonanza Creek Experimental Forest LTER]	*Betula papyrifera*	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Soil Survey of Greater Nenana Area, Alaska. MRCS. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alaska/AK655/0/GreaterNenana.pdf; Van Cleve K, LA Viereck, CT Dyrness. 1996. State factor control of soils and forest succession along the Tanana River in interior Alaska, U.S.A. Arctic and Alpine Research 28:388-400.
5	Alaska	*Betula papyrifera*	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: *Dynamic Properties of Forest Ecosystems* (ed Reichle DE), pp. 341-409. International Biological Programme 23, Cambridge Univ. Press, London; Soil Survey of Greater Nenana Area, Alaska. MRCS. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alaska/AK655/0/GreaterNenana.pdf; Van Cleve K, LA Viereck, and CT Dyrness. 1996. State factor control of soils and forest succession along the Tanana River in interior Alaska, U.S.A. Arctic and Alpine Research 28:388-400; Viereck LA, CT Dyrness, K Van Cleve, MJ Foote. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Can. J. Forest Res. 13(5), 703-720.
6	Alaska	*Picea glauca*	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Soil Survey of Greater Nenana Area, Alaska. MRCS. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alaska/AK655/0/GreaterNenana.pdf
7	Alaska	*Picea glauca*	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Soil Survey

			of Greater Nenana Area, Alaska. MRCS. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alaska/AK655/0/GreaterNenana.pdf; Viereck LA, K Van Cleve, PC Adams, RE Schlentner. 1993. Climate of the Tanana River floodplain near Fairbanks, Alaska. CJFR 23, 899-913
8	Alaska	*Picea mariana* - black spruce	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Soil Survey of Greater Nenana Area, Alaska. MRCS. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alaska/AK655/0/GreaterNenana.pdf; Viereck LA, K Van Cleve, PC Adams, RE Schlentner. 1993. Climate of the Tanana River floodplain near Fairbanks, Alaska. CJFR 23, 899-913
9	Alaska	*Populus balsamifera*	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Soil Survey of Greater Nenana Area, Alaska. MRCS. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alaska/AK655/0/GreaterNenana.pdf
10	Alaska	*Populus/Alnus*	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Soil Survey of Greater Nenana Area, Alaska. MRCS. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/alaska/AK655/0/GreaterNenana.pdf
11	Canada, Manitoba [BOREAS NSA]	*Picea mariana*	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Gower ST, JG Vogel, JM Norman, CJ Kucharik, SJ Steele, TK Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J Geophysical Res 102, 29029-29041
12	Canada, Manitoba [BOREAS NSA]	*Pinus banksiana* - Jack pine	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Gower ST, JG Vogel, JM Norman, CJ Kucharik, SJ Steele, TK Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Res 102: 29,029-29,041
13	Canada, Manitoba [BOREAS NSA]	*Populus tremuloides* - trembling aspen	Gower ST, JG Vogel, JM Norman, CJ Kucharik, SJ Steele, TK Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Res 102: 29,029-29,041; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
14	Canada, Ontario	*Picea rubens*, dry	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle,ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Van Cleve K, LA Viereck, CT Dyrness. 1996. State factor control of soils and forest succession along the Tanana River in interior Alaska, U.S.A. Arctic and Alpine Research 28:388-400.
15	Canada, Ontario	*Picea rubens*, fresh	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle,ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
16	Canada, Ontario	*Picea rubens*, moist	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle,ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
17	Canada, Ontario	*Picea rubens*, wet	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle,ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
18	Canada, Saskatchewan [BOREAS SSA]	*Picea mariana* - black spruce	Gower ST, JG Vogel, JM Norman, CJ Kucharik, SJ Steele, TK Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Res 102, 29029-29041; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Van Cleve K, LA Viereck, CT Dyrness. 1996. State factor control of soils and forest succession along the Tanana River in interior Alaska, U.S.A. Arctic and Alpine Research 28, 388-400.

19	Canada, Saskatchewan [BOREAS SSA]	*Picea mariana* - closed canopy feathermoss ground cover (BSFM)	Gower ST, JG Vogel, JM Norman, CJ Kucharik, SJ Steele, TK Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Res 102, 29029-29041; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; O'Connell KEB, Gower ST, Norman JM. 2003. Comparison of Net Primary Production and light-use dynamics of two boreal black spruce forest communities. Ecosystems 6, 236-247.
20	Canada, Saskatchewan [BOREAS SSA]	*Picea mariana* - open canopy with Sphagnum ground cover (BSSP)	Gower ST, JG Vogel, JM Norman, CJ Kucharik, SJ Steele, TK Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Res 102, 2929-29041; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; O'Connell KEB, Gower ST, Norman JM. 2003. Comparison of Net Primary Production and light-use dynamics of two boreal black spruce forest communities. Ecosystems 6, 236-247.
21	Canada, Saskatchewan [BOREAS SSA]	*Pinus banksiana* - Jack pine	Gower ST, JG Vogel, JM Norman, CJ Kucharik, SJ Steele, TK Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Res 102, 29029-29041; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
22	Canada, Saskatchewan [BOREAS SSA]	*Populus tremuloides* - trembling aspen	Gower ST, JG Vogel, JM Norman, CJ Kucharik, SJ Steele, TK Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Res 102, 29029-29041; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
23	China, Tahe, Daxing'anling	*Larix gmelinii*	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Leuschner C, A Zach, G Moser, J Homeier, S Graefe, D Hertel, B Wittich, N Soethe, S Iost, M Röderstein, V Horna, K Wolf. 2013. The Carbon Balance of Tropical Mountain Forests Along an Altitudinal Transect. In: Bendix J. et al. (eds) Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Ecological Studies (Analysis and Synthesis), vol 221, pp. 117-139. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-38137-9_10; Wang C, ST Gower, Y Wang, H Zhao, P Yan, B. Bond-Lamberty. 2001. Influence of fire on carbon distribution and net primary production of boreal *Larix gmelinii* forests in northeastern China. Global Change Biol 7, 719– 730.
24	Finland	*Picea excelsa*	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle,ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kimmins JP, BC Hawkes. 1978. Distribution and chemistry of fine roots in a white spruce-subalpine fir stand in British Columbia: Implications for management. Can. J. For. Res. 8, 265-279.
25	Finland, Ilomantsi [RhNRmu], eastern Finland	*Betula pubescens*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
26	Finland, Ilomantsi [Mkmu]	*Picea abies*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
27	Finland, Ilomantsi [VNRmu]	*Pinus sylvestris*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
28	Finland, Ilomantsi [RhNRmu]	*Pinus sylvestris*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; O'Connell KEB, Gower ST,

			Norman JM. 2003. Net ecosystem production of two contrasting boreal black spruce forest communities. Ecosystems 6, 248-260
29	Finland, Kuusamo [Oulanka National Park]	*Picea abies*	Havas, P. 2013. NPP Boreal Forest: Kuusamo, Finland, 1967-1972, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA doi:10.3334/ORNLDAAC/466; O'Connell KEB, ST Gower, JM Norman. 2003. Net ecosystem production of two contrasting boreal black spruce forest communities. Ecosystems 6, 248-260.
30	Iceland, Eastern [Hallormsstadur]	*Betula pubescen*	Sigurdardottir R. 1999. Effects of different forest types on total ecosystem carbon sequestration in Hallormsstadur Forest, Eastern Iceland. (Dissertation, Yale)
31	Iceland, Eastern [Hallormsstadur]	*Larix sibirica*	Sigurdardottir R. 1999. Effects of different forest types on total ecosystem carbon sequestration in Hallormsstadur Forest, Eastern Iceland. (Dissertation, Yale)
32	Iceland, Eastern [Hallormsstadur]	*Pinus contorta*	Sigurdardottir R. 1999. Effects of different forest types on total ecosystem carbon sequestration in Hallormsstadur Forest, Eastern Iceland. (Dissertation, Yale)
33	Russia (Siberia), Irkutsk	*Pinus sylvestris*	Krankina O.N. 2013. NPP Boreal Forest: Siberian Scots Pine Forests, Russia, 1968-1974 Revision 1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA doi:10.3; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
34	Russia (Siberia), Irkutsk	*Pinus sylvestris*	Krankina O.N. 2013. NPP Boreal Forest: Siberian Scots Pine Forests, Russia, 1968-1974 Revision 1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA doi:10.3; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
35	Russia (Siberia), Irkutsk	*Pinus sylvestris*	Krankina O.N. 2013. NPP Boreal Forest: Siberian Scots Pine Forests, Russia, 1968-1974 Revision 1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA doi:10.3; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
36	Russia (Siberia), Tomsk (ssp1a)	*Pinus sylvestris*	Gower, S.T., O. Krankina, R.J. Olson, M. Apps, S. Linder, and C. Wang. 2012. NPP Boreal Forest: Consistent Worldwide Site Estimates, 1965-1995, R1. Data set. Available on-line [http://daac.ornl.gov] from the Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.
37	Russia (Siberia), Tomsk (ssp1b)	*Pinus sylvestris*	Gower, S.T., O. Krankina, R.J. Olson, M. Apps, S. Linder, C. Wang. 2012. NPP Boreal Forest: Consistent Worldwide Site Estimates, 1965-1995, R1. Data set. Available on-line [http://daac.ornl.gov] Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.
38	Russia (Siberia), Tomsk (ssp1c)	*Pinus sylvestris*	Gower, S.T., O. Krankina, R.J. Olson, M. Apps, S. Linder, and C. Wang. 2012. NPP Boreal Forest: Consistent Worldwide Site Estimates, 1965-1995, R1. Data set. Available on-line [http://daac.ornl.gov] Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.
39	Russia (Siberia), Tomsk (ssp1d)	*Pinus sylvestris*	Gower, S.T., O. Krankina, R.J. Olson, M. Apps, S. Linder, C. Wang. 2012. NPP Boreal Forest: Consistent Worldwide Site Estimates, 1965-1995, R1. Data set. Available on-line [http://daac.ornl.gov] Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.
40	Russia (Siberia), Tomsk (ssp1e)	*Pinus sylvestris*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411

41	Russia (Siberia), Tomsk (ssp1f)	*Pinus sylvestris*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
42	Russia (Siberia), Tomsk (ssp1g)	*Pinus sylvestris*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
43	Russia (Siberia), Tomsk (ssp1h)	*Pinus sylvestris*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
44	Russia (Siberia), Tomsk (ssp1i)	*Pinus sylvestris*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
45	Russia (Siberia), Tomsk (ssp1j)	*Pinus sylvestris*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
46	Russia (Siberia), Tomsk (ssp1k)	*Pinus sylvestris*	Finér L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208, 1-63; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
47	Russia (Southern Karelia) (Site 1)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
48	Russia (Southern Karelia) (Site 10)	*Picea abies* - Southern Karelian spruce	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed), pp. 341-409. International Biological Programme 23, Cambridge Univ. Press, London; DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
49	Russia (Southern Karelia), (Site 11)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.

50	Russia (Southern Karelia), (Site 12)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
51	Russia (Southern Karelia), (Site 13)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
52	Russia (Southern Karelia), (Site 14)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
53	Russia (Southern Karelia), (Site 15)	Picea abies - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
54	Russia (Southern Karelia), (Site 16)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
55	Russia (Southern Karelia), (Site 17)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
56	Russia (Southern Karelia), (Site 2)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
57	Russia (Southern Karelia), (Site 3)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
58	Russia (Southern Karelia), (Site 4)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
59	Russia (Southern Karelia), (Site 5)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
60	Russia (Southern Karelia), (Site 6)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.

61	Russia (Southern Karelia), (Site 7)	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
62	Russia (Southern Karelia), (Site 8	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
63	Russia (Southern Karelia), (Site 8	*Picea abies* - Southern Karelian spruce	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Kazimirov NI, RM Morozova. 1973. Biological cycling of matter in spruce forests of Karelia. NAUKA, Leningrad Branch, Academy of Sciences. 168 pp.
64	Russia (Southern Karelia), (Site 9)	*Picea abies* - Southern Karelian spruce	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
65	Russia, Karelia	*Picea abies*	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411
66	Russia, Tomsk	*Pinus sylvestris*	Kajimoto T, Y Matsuura, MA Sofronov, AV Volokitina, S Mori, A Osawa, AP Abaimov. 1999. Above- and belowground biomass and net primary productivity of a *Larix gmelinii* stand near Tura, central Siberia. Tree Physiology 19, 815-822; PokrovskyO.S, B Dupré, J Schott. 2005. Fe–Al–organic Colloids Control of Trace Elements in Peat Soil Solutions: Results of Ultrafiltration and Dialysis. Aquat Geochem 11, 241–278; Pokrovsky OS, J Schott, DI Kudryavtzev, B Dupré. 2005. Basalt weathering in Central Siberia under permafrost conditions. Geochim Cosmochim Acta 69:5659–5680; Wang S, L Zhou, J Chen, W Ju, X Feng, W Wu. 2011. Relationships between net primary productivity and stand age for several forest types and their influence on China's carbon balance. Journal of Environmental Management 92: 1651-1662.
67	Sweden	*Picea abies*	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Ladanai S. 2008. Nutrient relations in coniferous forests. Doctoral Thesis. Swedish University of Agricultural Sciences. Uppsala 2008. ISBN 978-91-86195-4. http://pub.epsilon.slu.se/1933/1/kapan.pdf; Linder S, GI Agren. 2013. NPP Boreal Forest: Jadraas, Sweden, 1973-1990, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. doi:10.3334/ORNLDAAC
68	Sweden, Jädraås [SWECON]	*Pinus sylvestris*	Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Ladanai S. 2008. Nutrient relations in coniferous forests. Doctoral Thesis. Swedish University of Agricultural Sciences. Uppsala 2008. ISBN 978-91-86195-4. http://pub.epsilon.slu.se/1933/1/kapan.pdf; Linder S, GI Agren. 2013. NPP Boreal Forest: Jadraas, Sweden, 1973-1990, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. doi:10.3334/ORNLDAAC
69	Sweden, Jädraås [SWECON]	*Pinus sylvestris*	Bergh J, Freeman M, Sigurdsson B, Kellomäki S, Laitinen K, Niinistö S, Peltola H, Linder S. 2003. Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. Forest Ecol Manage 183, 327-340; Eliasson, P.E. 2007. Impacts of climate change on carbon and nitrogen cycles in boreal forest ecosystems. PhD Dissertation. ISSN: 1652-6880, ISBN: 978-91-576-7388-6; Gower ST, O Krankina, RJ Olson, M Apps, S Linder, C Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol. Appl 11(5), 1395-1411; Linder S. 2013. NPP Boreal Forest: Flakaliden, Sweden, 1986-1996, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge

			National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. doi:10.3334/ORNLDAAC/201
70	Sweden, Northern [Flakaliden]	*Picea abies*	Linder S. 2013. NPP Boreal Forest: Flakaliden, Sweden, 1986-1996, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. doi:10.3334/ORNLDAAC/201
TEMPERATE FORESTS			
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72	Slovakia, southern part of the Veporske vrchy massif	*Picea abies* (L.) H Karst	Konôpka B, J Pajtík, K Noguchi, M Lukac. 2013. Replacing Norway spruce with European beech: A comparison of biomass and net primary production patterns in young stands. Forest Ecology Management 302, 185-192.
73	Belgium	*Pinus sylvestris* - Belgian Scots pine	Janssens IA, DA Sampson, J Cermák, L Meiresonne, F Riguzzi, S Overloop, R Ceulemans. 1999. Above- and below-ground phytomass and carbon storage in a Belgian Scots pine stand. Ann For Sci 56, 81–90; Yuste Curiel J, B Konôpka, IA Janssens, K Coenen, CW Xiao, R Ceulemans. 2005. Contrasting net primary productivity and carbon distribution between neighboring stands of *Quercus robur* and *Pinus sylvestris*. Tree Physio 25(6), 701-712.
74	Belgium	*Pinus sylvestris* - Belgian Scots pine	Xiao CW, J Curiel Yuste, IA Janssens, P Roskams, L Nachtergale, A Carrara, BY Sanchez, R Ceulemans. 2003. Above- and below-ground biomass and net primary production in a 73-year-old Scots pine forest. Tree Physiol 23, 505–516
75	Belgium	*Quercus robur*	Janssens IA, DA Sampson, J Cermák, L Meiresonne, F Riguzzi,S Overloop, R Ceulemans. 1999. Above- and below-ground phytomass and carbon storage in a Belgian Scots pine stand. Ann For Sci 56, 81–90; Yuste Curiel J, B Konôpka, IA Janssens, K Coenen, CW Xiao, R Ceulemans. 2005. Contrasting net primary productivity and carbon distribution between neighboring stands of *Quercus robur* and *Pinus sylvestris*. Tree Physio 25(6), 701-712.
76	Belgium	*Quercus* mixed	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed), pp. 341-409. International Biological Programme 23, Cambridge Univ. Press, London; Vogt, K.A.; Grier, C.C.; Vogt, D.J. 1986. Production, turnover, and nutrient dynamics of above and belowground detritus of world forests. In: Advances in Ecological Research. Vol. 15. (A MacFadyen, ED Ford, eds), pp. 303-377. London: Academic Press, Harcourt Brace Jovanovich Publishers
77	Canada, British Columbia	*Pinus contorta*, mesic	Comeau PG, JP Kimmins. 1989. Above- and below-ground biomass and production of Lodgepole pine on sites with differing soil moisture regimes. Can J of Forest Res 19(4), 447-454; Comeau PG, JP Kimmins. 2013. NPP Boreal Forest: Canal Flats, Canada, 1984, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee
78	Canada, British Columbia	*Pinus contorta*, xeric	Comeau PG, JP Kimmins. 1989. Above- and below-ground biomass and production of Lodgepole pine on sites with differing soil moisture regimes. Can J of Forest Res 19(4), 447-454; Comeau PG, JP Kimmins. 2013. NPP Boreal Forest: Canal Flats, Canada, 1984, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee
79	Canada, British Columbia	*Pinus contorta*, xeric	Comeau PG, JP Kimmins. 1989. Above- and below-ground biomass and production of Lodgepole pine on sites with differing soil moisture regimes. Can J of Forest Res 19(4), 447-454; Comeau PG, JP Kimmins. 2013. NPP Boreal Forest: Canal Flats, Canada, 1984, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee

80	Canada, British Columbia [Canal Flats]	*Pinus contorta*, mesic	Comeau PG, JP Kimmins. 1989. Above- and below-ground biomass and production of Lodgepole pine on sites with differing soil moisture regimes. Can J of Forest Res 19(4), 447-454; Comeau PG, JP Kimmins. 2013. NPP Boreal Forest: Canal Flats, Canada, 1984, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee
81	China	*Pinus koraiensis*	Jianping S, T Dali, W Miao, Z Shidong. 1993. Fine roots turnover in a broad-leaved Korean pine forest of Changbai mountain. Chinese J of Applied Ecology 3, 1993.
82	China - Liangshui National Nature Reserve	*Pinus koraiensis* old-growth	Cai H, X Di, SC Chang, C Wang, B Shi, P Geng, G Jin. 2016. Carbon storage, net primary production, and net ecosystem production in four major temperate forest types in northeastern China. Can J Forest Res 46(2), 143-151; Wang H, X Dong. 2017. Seed plant diversity of different forest types in Liangshui National Natural Reserve. Biodiversity Data Journal 5(10):e22167. DOI: 10.3897/BDJ.5.e22167
83	China - Liangshui National Nature Reserve	*Betula platyphylla* - secondary	Cai H, X Di, SC Chang, C Wang, B Shi, P Geng, G Jin. 2016. Carbon storage, net primary production, and net ecosystem production in four major temperate forest types in northeastern China. Can J Forest Res 46(2), 143-151; Wang H, X Dong. 2017. Seed plant diversity of different forest types in Liangshui National Natural Reserve. Biodiversity Data Journal 5(10):e22167. DOI: 10.3897/BDJ.5.e22167
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85	Denmark	*Fagus sylvatica*	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
86	England	*Quercus-Betula-Fraxinus*	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London; DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
87	Georgia, USA	*Cornus florida* L/*Acer rubrum* L/*Quercus prinus* L – *mature* mixed hardwood	Cromack K. 1973. Litter production and decomposition in a mixed hardwood watershed and a white pine watershed at Coweeta Hydrologic Station, North Carolina. PhD Dissertation, University of Georgia, Athens; McGinty DT. 1976. Comparative root and soil dynamics on a white pine watershed in the hardwood forest in the Coweeta Basin. PhD Dissertation. University of Georgia, Athen, Georgia; Swank WT, DA Crossley jr. 1988. Forest hydrology and ecology at Coweeta. Ecological Studies 66. Springer. 486 pp.
88	Germany	*Fagus sylvatica* – European beech	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Vogt, K.A.; Grier, C.C.; Vogt, D.J. 1986. Production, turnover, and nutrient dynamicsof above and belowground detritus of world forests. In: Advances in Ecological Research. Vol. 15. (A MacFadyen, ED Ford, eds), pp. 303-377. London: Academic Press, Harcourt Brace Jovanovich Publishers
89	Germany, Solling Project [SITE B 3]	*Fagus sylvatica* – European beech	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London.
90	Germany, Solling Project [Site F 2]	Quercus prinus	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London.

91	Germany, Solling Project [Site F 3]	Pinus strobus	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London.
92	Japan, Shigayama	Fagus sylvatica	Kimura M. 1963. Dynamics of vegetation in relation to soil development in northern Yatsugatake Mountains. Japanese J. Bot. 18, 255-287.
93	Japan	*Fagus sylvatica*	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
94	Japan, Kubotaniyama [JPTF-70 Yusuhara]	*Picea abies*	ORNL IBP-JIBP. ORNL Progress Report 1966-71 OF IBP-JIBP Special Committee in Japanese Science Congress 1966. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed), 605 p. Cambridge University Press, Cambridge, UK.
95	Japan, Kyoto [School forest, Ashu]	Evergreen broadleaf forest	ORNL IBP-JIBP. ORNL Progress Report 1966-71 OF IBP-JIBP Special Committee in Japanese Science Congress 1966. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed), 605 p. Cambridge University Press, Cambridge, UK.
96	Japan, Aya Research Site LTER	Evergreen broadleaf forest – old-growth	Do TV, T Sato, S Saito, O Kozan, H Yamagawa, D Nagamatsu, N Nishimura, T Manabe. 2015. Effects of micro-topograhies on stand structure and tree species diversity in an old-growth evergreen broad-leaved forest, southwestern Japan. Global ecology and Conservation 4, 185-196; Sato T, Y Kominami, S Saito, K Niiyama, T Manabe, H Tanouchi, N Noma, S Yamamoto. 1999. An introduction to the Aya Research Site, a longterm ecological research site, in a warm temperate evergreen broad-leaved forest ecosystems in southwestern Japan: research topics and design. Bull. Kitakyushu Mus. Nat. His. 18, 57–180; Sato T, Y Kominami, S Saito, K Niiyama, H Tanouchi, D Nagamatsu, H Nomiya. 2010. Temporal dynamics and resilience of fine litterfall in relation to typhoon disturbances over 14 years in an old-growth lucidophyllous forest in southwestern Japan. Plant Ecology 208, 187-198.
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98	Japan, Takatori-yama [JPTF-71 Yusuhara]	*Abies firma* - True fir	ORNL IBP-JIBP. ORNL Progress Report 1966-71 OF IBP-JIBP Special Committee in Japanese Science Congress 1966. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed), 605 p. Cambridge University Press, Cambridge, UK.
99	Massachusetts, USA	*Quercus-Acer* - red oak [*Q rubra*], sugar maple [*A saccharum*]	Aber JD, JM Melillo, KJ Nadelhoffer, CA McClaugherty, J. Pastor. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. Oecologica 66(3), 317-321; McClaugherty CA, JD Aber, JM Melillo. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63(5), 1481-1490; McClaugherty CA, JD Aber, JM Melillo. 1984. Decomposition dynamics of fine roots in forested ecosystems. Oikos 42, 378-386; Nadelhoffer KJ, JD Aber, JM Melillo. 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in Southern Wisconsin (U.S.A.). Can J Forest Res 13(1), 12-21; Pastor J, JD Aber, CA McClaugherty. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology 65(1), 256-268; Vitousek PM, JR Gosz, CC Grier, JM Melillo, WA Reiners. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecol. Monographs 52(2), 155-177.
100	Massachusetts, USA	*Pinus resinosa*	Aber JD, JM Melillo, KJ Nadelhoffer, CA McClaugherty, J. Pastor. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. Oecologica 66(3), 317-321; McClaugherty CA, JD Aber, JM Melillo. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63(5), 1481-1490; McClaugherty CA, JD Aber, JM Melillo. 1984. Decomposition dynamics of fine roots in forested ecosystems. Oikos 42, 378-386; Vogt KA, CC Grier, DJ Vogt. 1986. Production, turnover, and nutrient dynamics of above and belowground detritus of world forests. In: MacFadyen, A.; Ford, E.D., eds. Advances in ecological research. Vol. 15. London: Academic Press, Harcourt Brace Jovanovich Publishers: 303-377.

101	Michigan, USA	*Acer saccharum* - hardwood mix, southern	Hendrick KS, RL Hendrick, R Fogel. 1993. The demography of fine roots in response to patches of water and nitrogen. New Phytologist 125(3), 575-580.
102	Michigan, USA	*Quercus alba*	Hendrick KS, RL Hendrick, R Fogel. 1993. The demography of fine roots in response to patches of water and nitrogen. New Phytologist 125(3), 575-580.
103	New Hampshire, USA	*Acer spitcatum, Betula lutea, Fagus grandifolia*	Bormann FH, GE Likens, TG Siccama, RS Pierce, JS Eaton. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. Ecol Monographs 44(3), 255-277; Gosz JR, GE Likens, FH Bormann. Nutrient content of litter fall on the Hubbard Brook Experimental Forest, New Hampshire. 1972. Ecology 53(5), 769-784; Safford LO. 1974. Effect of fertilization on biomass and nutrient content of fine roots in a beech-birch-maple stand. Plant Soil 40, 349-363; Siccama TG, FH Bormann, GE Likens. 1970. The Hubbard Brook Ecosystem Study: Productivity, nutrients, and phytosociology of the herbaceous layer. Ecological Monograph 40(4), 389-402.
104	New Hampshire, USA	Northern hardwoods - mix sugar maple, beech, yellow birch, red maple and white ash	Bormann FH, G Likens. 1979. Pattern and Process in a Forested Ecosystems. Springer- Verlag, New York Inc., 253 pp.; Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London; Covington WW. 1976. Forest floor organic matter and nutrient content and leaf fall during secondary succession in Northern Hardwoods. Dissertation. Yale University; Covington WW. 1981. Changes in forest floor organic matter and nutrient content following clearcutting in Northern Hardwoods. Ecology 62(1), 41-48; Fahey TJ, JW Hughes. 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Ex0perimental Forest, NH. J of Ecology 82(3), 533-548; Harmon ME, WL Silver, B Fasth, H Chen, IC Burke, WJ Parton, SC Hart, WS Currie and Lidet. 2009. Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. Global Change Biol 15(5): 1320-1338.
105	New Mexico, Mt Taylor [Cibola National Forest]	*Pseudotsuga menziesii var glauca* -Rocky Mt. mixed conifer, control	Horner JT. 1987. The effects of manipulation of nitrogen and water availability on the polyphenol content of Douglas-fir foliage: Implications for ecosystem theory. Dissertation University of New Mexico, Albuquerque, New Mexico; HornerJD, RG Cates, JR Gosz. 1987. Tannin, nitrogen, and cell wall composition of green vs. senescent Douglas-fir foliage. Oecologia 72, 515-519; Gower ST, KA Vogt, CC Grier. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: Influence of water and nutrient availability. Ecological Monographs 62(1), 43-65; White CS, JR Gosz, JD Horner, DI Moore. 1988. Seasonal, annual, and treatment-induced variation in available nitrogen pools and nitrogen-cycling processes in soils of two Douglas-fir stands. Biology Fertility of Soils 6, 93-99.et al 1988.
106	New Mexico, Mt Taylor [Cibola National Forest]	*Pseudotsuga menziesii var glauca* -Rocky Mt. mixed conifer, fertilized	Gower ST, KA Vogt, CC Grier. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: Influence of water and nutrient availability. Ecological Monographs 62(1), 43-65.
107	New Mexico, Mt Taylor [Cibola National Forest]	*Pseudotsuga menziesii var glauca* -Rocky Mt. mixed conifer, irrigation	Gower ST, KA Vogt, CC Grier. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: Influence of water and nutrient availability. Ecological Monographs 62(1), 43-65.
108	New Mexico, Mt Taylor [Cibola National Forest]	*Pseudotsuga menziesii var glauca* -Rocky Mt. mixed conifer, wood chips added	Gower ST, KA Vogt, CC Grier. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: Influence of water and nutrient availability. Ecological Monographs 62(1), 43-65.
109	New Mexico, Mt Taylor [Cibola National Forest]	*Pseudotsuga menziesii var glauca* -Rocky Mt. mixed conifer, wood chip/irrigation	Gower ST, KA Vogt, CC Grier. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: Influence of water and nutrient availability. Ecological Monographs 62(1), 43-65.

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112	Oregon	*Tsuga heterophylla/Picea sitchensis*	Grier CC. 1976. Biomass, productivity and nitrogen-phosphorus cycles in hemlock-spruce stands of the central Oregon coast. IN: *Western hemlock management* (WA Atkinson, RJ Zasoski, eds) pp. 71-81. College of Forest Resources, University of Washington, Seattle, WA Contribution No. 34; Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London.
113	Oregon	*Tsuga heterophylla/Picea sitchensis*	Grier CC. 1976. Biomass, productivity and nitrogen-phosphorus cycles in hemlock-spruce stands of the central Oregon coast. IN: *Western hemlock management* (WA Atkinson, RJ Zasoski, eds) pp. 71-81. College of Forest Resources, University of Washington, Seattle, WA Contribution No. 34.
114	Oregon	*Pinus ponderosa*	Law BE, PE Thornton, J Irvine, PM Anthoni, S Van Tuyl. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biol. 7, 755-777; Pierce LL, SW Running, J Walker. 1994. Regional-scale relationships of leaf area index to specific leaf area and leaf nitrogen content. Ecol Appl 4, 313-321.
115	Oregon	*Pinus ponderosa*	Law BE, PE Thornton, J Irvine, PM Anthoni, S Van Tuyl. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biol. 7, 755-777; Peterson DL, RH Waring. 1994. Overview of the Oregon Transect Ecosystem Research Project. Ecological Applications 4(2), 211-225.
116	Oregon	*Pseudotsuga menziesii/ Tsuga heterophylla*	Harmon ME, K Bible, MG Ryan, DC Shaw, H Chen, J Klopatek, X Li. 2004. Production, respiration, and overall carbon balance in an old-growth *Pseudotsuga-Tsuga* forest ecosystem. Ecosystems 7, 498-512; Shaw DC, JF Franklin, K Bible, J Klopatek, E Freeman, S Greene, GG Parker. 2004. Ecological setting of the Wind River old-growth forest. Ecosystems 7, 427-439.
117	Oregon, Cascade Head, coast range [OTTER sites, Site 1]	*Picea sitchensis-Tsuga heterophylla*	Runyon J, RH Waring, SN Goward, JM Welles. 1994. Environmental limits on net primary production and light-use efficiency across the Oregon Transect. Ecol. Applications 4(2), 226-237; Waring RH, JJ Landsberg, M Williams. 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Physiology 18(2), 129-134; Waring RH, B Law, B Bond. 2013. NPP Temperate Forest: OTTER Project Sites, Oregon, USA, 1989-1991, R1. Data set available on-line: https://doi.org/10.3334/ORNLDAAC/472
118	Oregon, Eastern High Cascades (Control) [OTTER site, Site 5]	*Ponderosa pine*	Runyon J, RH Waring, SN Goward, JM Welles. 1994. Environmental limits on net primary production and light-use efficiency across the Oregon Transect. Ecol. Applications 4(2), 226-237; Waring RH, JJ Landsberg, M Williams. 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Physiology 18(2), 129-134; Waring RH, B Law, B Bond. 2013. NPP Temperate Forest: OTTER Project Sites, Oregon, USA, 1989-1991, R1. Data set available on-line: https://doi.org/10.3334/ORNLDAAC/472
119	Oregon, HJ Andrews Experiimental Forest [Watershed 10]	*Pseudotsuga-Acer-Olystichum* (Cool-moist)	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London; Cromack K Jr, P Sollins, WC Graustein, K Speidel, AW Todd, G Spycher, CY Li, RL Todd. 1979. Calcium oxalate accumulation and soil weathering in mats of the hypogeous fungus *Hysterangium crassum*. Soil Bio Biochemistry 11(5), 463-468; Grier CC, RS Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. Ecol Monogr 47(4), 373-400; Sollins P, CC Grier, FM McCorison, K Cromack Jr, R Fogel. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecol Monogr 50 (3): 261-285.
120	Oregon, HJ Andrews Experimental Forest	*Pseudotsuga-Castganopsis* (Xeric), north slope	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London; Cromack K Jr, P Sollins, WC Graustein, K Speidel, AW Todd, G Spycher, CY Li, RL Todd. 1979. Calcium oxalate accumulation and soil weathering in mats of the hypogeous fungus *Hysterangium crassum*. Soil Bio Biochemistry 11(5), 463-468; Grier CC, RS Logan. 1977. Old-growth

	[Watershed 10]		*Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. Ecol Monogr 47(4), 373-400; Sollins P, CC Grier, FM McCorison, K Cromack Jr, R Fogel. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecol Monogr 50 (3): 261-285.
121	Oregon, HJ Andrews Experimental Forest [Watershed 10]	*Pseudotsuga-Castganopsis* (Xeric), south slope	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London; Cromack K Jr, P Sollins, WC Graustein, K Speidel, AW Todd, G Spycher, CY Li, RL Todd. 1979. Calcium oxalate accumulation and soil weathering in mats of the hypogeous fungus *Hysterangium crassum*. Soil Bio Biochemistry 11(5), 463-468; Grier CC, RS Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. Ecol Monogr 47(4), 373-400; Sollins P, CC Grier, FM McCorison, K Cromack Jr, R Fogel. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecol Monogr 50 (3): 261-285.
122	Oregon, HJ Andrews Experimental Forest [Watershed 10]	*Pseudotsuga-Rhododenron-Berberis* (Mesic)	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London; Cromack K Jr, P Sollins, WC Graustein, K Speidel, AW Todd, G Spycher, CY Li, RL Todd. 1979. Calcium oxalate accumulation and soil weathering in mats of the hypogeous fungus *Hysterangium crassum*. Soil Bio Biochemistry 11(5), 463-468; Grier CC, RS Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. Ecol Monogr 47(4), 373-400; Sollins P, CC Grier, FM McCorison, K Cromack Jr, R Fogel. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecol Monogr 50 (3): 261-285.
123	Oregon, Santiam Pass, High Cascades summit [OTTER sites, Site 4]	*Tsuga mertensiana*	Pierce LL, SW Running, J Walker. 1994. Regional-scale relationships of leaf area index to specific leaf area and leaf nitrogen content. Ecol Appl 4(2), 313-321; Runyon J, RH Waring, SN Goward, JM Welles. 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. Ecological Applications 4(2), 226-237; Waring RH, B Law, B Bond. 2013. NPP Temperate Forest: OTTER Project Sites, Oregon, USA, 1989-1991, R1. Data set available on-line: https://doi.org/10.3334/ORNLDAAC/472.
124	Oregon, Scio (control, west Cascades) [OTTER sites, Site 3]	*Tsuga heterophylla-Pseudotsuga menziesii*	Pierce LL, SW Running, J Walker. 1994. Regional-scale relationships of leaf area index to specific leaf area and leaf nitrogen content. Ecol Appl 4(2), 313-321; Runyon J, RH Waring, SN Goward, JM Welles. 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. Ecological Applications 4(2), 226-237; Waring RH, B Law, B Bond. 2013. NPP Temperate Forest: OTTER Project Sites, Oregon, USA, 1989-1991, R1. Data set available on-line: https://doi.org/10.3334/ORNLDAAC/472.
125	Oregon, Waring's Woods, interior valley [OTTER sites, Site 2]	*Pseudotsuga menziesii*	Pierce LL, SW Running, J Walker. 1994. Regional-scale relationships of leaf area index to specific leaf area and leaf nitrogen content. Ecol Appl 4(2), 313-321; Runyon J, RH Waring, SN Goward, JM Welles. 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. Ecological Applications 4(2), 226-237; Waring RH, B Law, B Bond. 2013. NPP Temperate Forest: OTTER Project Sites, Oregon, USA, 1989-1991, R1. Data set available on-line: https://doi.org/10.3334/ORNLDAAC/472.
126	Poland, Ispina, Niepolomice near Krakow	Tilio-Carpinetum, oak-hornbeam forest [*Quercus patraea, Carpinus betulus*]	Bandolo-Ciolczyk E. 1974. Production of tree leaves and energy flow through the litter in Tilio-Carpinetum association (International Biological Programme area). Stud Nat Sci A 9, 29-91.
127	Russia, Koinas [Arkangelsk Region]	*Picea abies, Juniperus communis, Vaccinium myrtillus*	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
128	Sweden	*Fagus sylvatica*	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK.

129	Sweden	*Fagus sylvatica*	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
130	Sweden	*Picea abies*	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
131	Sweden	*Quercus robus-Tilia cordata*	Andersson F. 1970. Ecological studies in a Scanian woodland and meadow area, Southern Sweden. I. Vegetational and environmental structure. Opera Botanica 27, 190 pp.; Andersson F. 1970. Ecological studies in a Scanian woodland and meadow area, Southern Sweden. II. Plant biomass, primary production and turnover of organic matter. Bot Notiser 123, 8-51; Andersson F. 1973. In Modeling Forest Ecosystems. EDFB-IBP 73-7, OAK RIDGE, USA; Nihlgård B. 1969. Microclimate in a beech and a spruce forest; a comparative study from Kongalund, Scania, Sweden. Bot Notiser 122, 333-352; Nihlgård B. 1970. Precipitation, its chemical composition and effect on soil water in a beech and a spruce forest in South Sweden. Oikos 21, 208-17; Nihlgård B. 1971. Pedological influence of spruce planted on former beech forest soils in Scania, South Sweden. Oikos 22, 301-13; Nihlgård B. 1972. Plant biomass, primary production and distribution of chemical elements in a beech and a planted spruce forest in South Sweden. OIKOS 23(1), 69-81.
132	Sweden [Kongalund Beech Site]	*Fagus sylvatica, Stellaria nemorum* - Beech forest	Andersson F. 1970. Ecological studies in a Scanian woodland and meadow area, Southern Sweden. I. Vegetational and environmental structure. Opera Botanica 27, 190 pp.; Andersson F. 1970. Ecological studies in a Scanian woodland and meadow area, Southern Sweden. II. Plant biomass, primary production and turnover of organic matter. Bot Notiser 123, 8-51; Andersson F. 1973. In Modeling Forest Ecosystems. EDFB-IBP 73-7, OAK RIDGE, USA; Nihlgård B. 1969. Microclimate in a beech and a spruce forest; a comparative study from Kongalund, Scania, Sweden. Bot Notiser 122, 333-352; Nihlgård B. 1970. Precipitation, its chemical composition and effect on soil water in a beech and a spruce forest in South Sweden. Oikos 21, 208-17; Nihlgård B. 1971. Pedological influence of spruce planted on former beech forest soils in Scania, South Sweden. Oikos 22, 301-13; Nihlgård B. 1972. Plant biomass, primary production and distribution of chemical elements in a beech and a planted spruce forest in South Sweden. OIKOS 23(1), 69-81.
133	Sweden [Kongalund Spruce Site]	*Picea abies*	Nihlgård B, L Lindregn. 1977. Plant biomass, primary production and bioelements of three mature beech forests in South Sweden. Oikos 28, 95-104; Lindgren L. 1970. Beech forest vegetation in Sweden - a survey. Botaniska notiser 123: 401–24.
134	Sweden, Oved	*Fagus sylvatica*	DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
135	Tennessee, Walker Branch, USA	*Liriodendron tulipifera*	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 341-409. Cambridge University Press, Cambridge, UK. International Biological Programme 23, Cambridge Univ. Press, London; Cox TL, TL Harris, BS Ausmus, NT Edwards. 1978. The role of roots in biogeochemical cycles in an eastern deciduous forest. Pedobiologica 18, 264-271; DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK; Harris WF, RS Kinerson Jr, NT Edwards. 1977. Comparison of below-ground biomass of natural deciduous forest and loblolly pine plantations. Pedobiologia 17, 369-381.
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137	Tennessee, Walker Branch, USA	*Pinus echinata*	Climate of the States. 1980. NOAA National Centers for Environmental Information. https://www.ncdc.noaa.gov/climateatlas/; Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed), pp. 341-409. International Biological Programme 23, Cambridge Univ. Press, London; DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK.

138	Tennessee, Walker Branch, USA	*Quercus alba/Carya* spp.	Cole DW, M Rapp. 1981. Elemental cycling in forests. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed), pp. 341-409. International Biological Programme 23, Cambridge Univ. Press, London; DeAngelis DL, RH Gardner, HH Shugart. 1981. Productivity of forest ecosystems studies during the IBP: the woodlands data set. In: Dynamic Properties of Forest Ecosystems (DE Reichle, ed) pp. 567-672. Cambridge University Press, Cambridge, UK.
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140	Virginia, USA	*Chamae-cyparis thyoides*, wetland site [Atlantic White Cedar]	Day FP Jr. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63, 670-678; Day FP. 1984. Biomass and litter accumulation in the Great Dismal Swamp. In, Cypress swamps (KC Ewel, HT Odum, eds.) pp. 386-392. University Presses of Florida, Gainesville; Gomez MM, FP Day Jr. 1982. Litter nutrient content and production in the Great Dismal Swamp. Am. J. Bot. 69, 1314-1321; Megonigal JP, FP Day Jr. 1988. Organic matter dynamics in four seasonally flooded forest communities of the Dismal Swamp. Am. J. Bot. 75, 1334-1343; Powell SW, FP Day Jr. 1991. Root production in four communities in the Great Dismal Swamp. American J of Botany 78(2), 288-297.
141	Virginia, USA	*Acer rubrum, Nyssa Aquatica* [maple-gum] and oak (*Quercus* spp.) Hardwood mixture Dismal Swamp Upland sites	Day FP Jr. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63, 670-678; Day FP. 1984. Biomass and litter accumulation in the Great Dismal Swamp. In, Cypress swamps (KC Ewel, HT Odum, eds.) pp. 386-392. University Presses of Florida, Gainesville; Gomez MM, FP Day Jr. 1982. Litter nutrient content and production in the Great Dismal Swamp. Am. J. Bot. 69, 1314-1321; Megonigal JP, FP Day Jr. 1988. Organic matter dynamics in four seasonally flooded forest communities of the Dismal Swamp. Am. J. Bot. 75, 1334-1343; Powell SW, FP Day Jr. 1991. Root production in four communities in the Great Dismal Swamp. American J of Botany 78(2), 288-297.
142	Virginia, USA	*Nyssa aquatica, Acer rubrum, N. sylvatica* [water tupelo, cottongum, wild olive, large tupelo, sourgum] Wetland site	Day FP Jr. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63, 670-678; Day FP. 1984. Biomass and litter accumulation in the Great Dismal Swamp. In, Cypress swamps (KC Ewel, HT Odum, eds.) pp. 386-392. University Presses of Florida, Gainesville; Gomez MM, FP Day Jr. 1982. Litter nutrient content and production in the Great Dismal Swamp. Am. J. Bot. 69, 1314-1321; Megonigal JP, FP Day Jr. 1988. Organic matter dynamics in four seasonally flooded forest communities of the Dismal Swamp. Am. J. Bot. 75, 1334-1343; Powell SW, FP Day Jr. 1991. Root production in four communities in the Great Dismal Swamp. American J of Botany 78(2), 288-297.
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144	Washington, USA	*Pseudotsuga menziesii*	Vogt DJ. 1987. Douglas-fir ecosystems in western Washington biomass and production as related to site quality and stand age. PhD Dissertation. University of Washington, Seattle, Washington, USA.
145	Washington	*Pseudotsuga menziesii*	Vogt DJ. 1987. Douglas-fir ecosystems in western Washington biomass and production as related to site quality and stand age. PhD Dissertation. University of Washington, Seattle, Washington, USA.
146	Washington, USA	*Pseudotsuga menziesii*	Vogt DJ. 1987. Douglas-fir ecosystems in western Washington biomass and production as related to site quality and stand age. PhD Dissertation. University of Washington, Seattle, Washington, USA.
147	Washington, USA	*Pseudotsuga menziesii*	Vogt DJ. 1987. Douglas-fir ecosystems in western Washington biomass and production as related to site quality and stand age. PhD Dissertation. University of Washington, Seattle, Washington, USA.

148	Washington, USA	*Pseudotsuga menziesii*	Vogt DJ. 1987. Douglas-fir ecosystems in western Washington biomass and production as related to site quality and stand age. PhD Dissertation. University of Washington, Seattle, Washington, USA.
149	Washington, USA	*Pseudotsuga menziesii*	Vogt DJ. 1987. Douglas-fir ecosystems in western Washington biomass and production as related to site quality and stand age. PhD Dissertation. University of Washington, Seattle, Washington, USA.
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162	Washington, USA	*Pseudotsuga menziesii*	Grier CC, JG McColl. 1971. Forest floor characteristics within a small plot in Douglas-fir in Western Washington. Soil Sci Soc Am Proc 35, 988-991; Vogt KA, DJ Vogt, ST Gower, CC Grier. 1990. Carbon and nitrogen interactions for forest ecosystems. In Above- and below-ground interactions in forest trees in acidified soils. Air Pollution Report 32. (H Persson, ed), pp. 203-235. Commission of the European Communities. Directorate-General for Science, Research and Development. Environment Research Programme, Brussels, Belgium
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Chapter 2: Mycorrhizal fungi take up and store salmon nitrogen

Abstract

Pacific salmon subsidize terrestrial systems with marine-derived nitrogen (MDN), which have ecological significance for soils, animals, and plants in riparian systems. However, despite the crucial role of fungi in decomposition and nutrient cycling, the importance of fungal mycelium as an MDN sink in the soil has been largely overlooked. We examined the effects of MDN on fungi, dominant trees (white spruce and paper birch), and soils using $\delta^{15}N$, and also measured $\delta^{13}C$ and carbon and nitrogen concentrations along three salmon streams in SW Alaska. MDN was present in ectomycorrhizal fungal (EMF) sporocarps, soils, and vegetation, but only significantly increased N concentrations in EMF, indicating that MDN was retained in EMF hyphae. This study illustrates that fungi are essential to include to accurately assess the flow and significance of MDN in riparian systems.

Introduction

The migration of anadromous fish such as Pacific salmon (*Oncorhynchus* spp.) from marine to freshwater environments transports a large nutrient pulse, which subsidizes freshwater and riparian ecosystems with marine-derived nitrogen (MDN) (Feddern et al. 2019, Gende et al. 2002, Quinn et al. 2018, Schindler et al. 2003). After salmon spawn and die, their carcasses are a significant food and nutrient source for numerous aquatic and terrestrial species, and these carcasses are also associated with higher growth rates and population densities across taxa (Field and Reynolds 2013, Schindler et al. 2013, Minakawa et al. 2002, Hilderbrand et al. 1999a). Nitrogen in salmon has a higher ratio of ^{15}N to ^{14}N than most N pools in freshwater and terrestrial ecosystems. Thus, salmon-derived N can be tracked quantitatively by measuring $^{15}N/^{14}N$ (expressed as $\delta^{15}N$) (Schindler et al. 2013). Some studies found that, when salmon are abundant, MDN can contribute from 40-90% of the N in bears, fish and aquatic invertebrates comes from MDN (Bilby et al. 1996, Hilderbrand et al. 1999b, Chaloner et al. 2002, Claeson et al. 2006, Naiman et al. 2002), and marine-derived nutrients provide important limiting nutrients to aquatic plants and microbes that can increase primary and bacterial productivity (Moore et al. 2007). Nutrient from salmon carcasses, which include not only nitrogen (N), but also phosphorus (P) and other elements such as calcium and magnesium, enter riparian forests from salmon streams in three ways: transfer by predators and floods (Ben-David et al. 1998), excreta of predators and scavengers consuming carcasses (Hilderbrand et al. 1999), and transfer of dissolved marine-derived nutrients from stream water through hyporheic flow and diffusion (O'Keefe and Edwards 2003). The presence of MDN is well-documented in terrestrial systems. Although MDN has been found in plant tissues (foliage and wood) and in riparian soils along salmon streams (Bilby et al. 1996, Ben-David et al. 1998, Hilderbrand et al. 1999b, Reimchen et al. 2003, Reimchen and Fox 2013, Bartz and Naiman 2005), the ecological significance of MDN for terrestrial productivity and function is less clear. For example, several studies reported foliar N concentrations positively correlated with both salmon abundance and proximity to stream bank (Helfield and Naiman 2001, 2002, Bilby et al. 2003, Mathewson et al. 2003), and MDN has been shown to account for up to 86% of the foliage N in vegetation growing in the riparian area (Hocking and Reynolds 2012, Reimchen and Fox 2013, Quinn et al. 2018). In contrast, other studies show that foliar N and MDN were not correlated (Ben-David et al. 1998, Bartz and Naiman 2005, Drake et al. 2006), although this can be confounded by increased plant biomass (Bryant et al. 1987, Quinn et al. 2018). Many studies have found significant correlations between salmon density and riparian tree growth rates across boreal and temperate forests (Helfield and Naiman 2002, Reimchen and Fox 2013, Drake et al. 2002, Drake and Naiman 2007), although Helfield and Naiman was later contested because considerable variability in the soil characteristics between the reference and spawning sites was not considered (Kirchoff 2003). MDN has also been shown to have ecological significance for physiological and reproductive processes in vegetation, such as increased stomatal density and fruit production in salmonberry (*Rubus spectabilis*) (van den Top 2018, Siemens et al. 2020*)*. Importantly, Quinn et al. (2018) reported increased tree growth rates after a 21-year salmon carcass manipulation experiment, equating to ~267,000 kg of salmon, was added to a riparian area over several decades at the site of our study system.

Given that N can be a limiting nutrient in boreal forest ecosystems and is subsidized to an unknown degree by MDN in riparian boreal forests, it is important to understand the influence of MDN on soil N cycles. MDN has been shown to increase soil N, P, sulfur, potassium, and dissolved organic C pools, with varying lag times in nutrient availability (Drake et al. 2005, Larocque et al. 2023, Gende et al. 2007, D'amore et al. 2020, Wheeler and Kavanagh 2017). For example, Drake et al. (2005) found that NH_4 was available within weeks, NO_3 within months, and P and Ca within months to year. However, these changes were highly localized, with effects primarily occurring < 1 m surrounding the carcass (Drake et al. 2005, Gende et al. 2007, Holtgrieve et al. 2009). Feddern et al. (2019) examined the effect of long-term retention of MDN by soils at the same 21-year carcass experiment site used in the Quinn et al. (2018) study. They found that MDN enriched soil in ^{15}N but soil N availability and N cycling rates did not increase. In addition, δ^{15}N of available soil N was higher than salmon N due to isotopic fractionation against ^{15}N during N transformations, indicating a serious issue with using standard two-source mixing models to estimate the proportion of N derived from MDN in plants. Salmon return to natal streams during discrete periods of time over a few weeks. Large amounts of N patchily deposited within a short time frame likely surpass the capacity of plant and soil N pools at sites of deposition to retain these influxes. This overabundance of N results in increased N loss through ammonia volatilization, nitrification, nitrate leaching, and denitrification (Holtgrieve et al. 2009, Perakis 2002). All these processes fractionate against ^{15}N and discrimination increases with soil N availability, resulting in increased residual soil δ^{15}N values (Högberg 1997). In fact, Wheeler and Kavanaugh (2017) observed that ammonia volatilization of specifically salmon carcasses isotopically enriched carcass fluid by 1.5‰. Therefore, the isotopic enrichment observed in soil and plant N could result from either the direct uptake of MDN and/or the uptake of soil N enriched due to microbial processes such as denitrification and ammonia volatilization. Because isotopic fractionation is generally not considered, it is likely that MDN contribution is generally overestimated in many studies.

In addition, considering these processes further complicates the process of choosing a reference site, as many N cycling factors are highly spatially variable and vary considerably with distance from stream (Feddern et al. 2019), slope, and certainly between watersheds. This subsequently affects N isotopes (Hogberg 1997) and ultimately violates the assumption that reference and salmon sites are biogeochemically similar and that the only factor affecting ^{15}N values is salmon. Specifically, N cycling generally decreases with distance from stream and with higher slopes due to changes in soil water content and drainage (Hogberg 1997, Kirchoff 2003), thus leading to increased plant δ^{15}N with lower slopes, which some studies have attributed to salmon carcasses (Hocking and Reynolds 2012). This also applies to sites above and below waterfalls, as sites below waterfalls tend to have higher rates of N cycling, drainage and soil water content than sites above waterfalls, leading to higher δ^{15}N values at lower elevations due to factors unrelated to salmon. Differences in elevation have also been used to contest increased tree growth rates due to salmon abundance, as high forest productivity in floodplains, valley bottoms and stream sides (where salmon are found) is driven strongly by fluvial processes such as frequency and intensity of flooding (McKee et al. 1982, Hanley and Hoel 1996), factors unrelated to salmon.

However, to further add to this complexity, plant $\delta^{15}N$ is affected not only by the fractionation processes in the soil, but also by associations with symbionts such as N_2-fixing bacteria and mycorrhizal fungi (MF). Almost all terrestrial plants partner with MF and exchange photosynthetically-derived C for fungal-foraged N (Smith and Read 2008). Specifically, for ectomycorrhizal fungi (EMF), isotopic fractionation occurs upon ectomycorrhizal transfer of N to plant hosts, which discriminates against ^{15}N and results in plants depleted in ^{15}N and fungi enriched in ^{15}N relative to the ^{15}N of soil N (Hobbie and Hobbie 2006, Hobbie et al. 2019). In boreal forests, dominant tree species such as spruce and birch form symbiotic associations with EMF, which can provide up to 80% of plant-derived N (van der Heijden et al. 2015). This indicates that this N pathway is important when evaluating the movement of salmon N through the ecosystem. Disregarding this fractionation pathway would underestimate the contribution of MDN to plants, since plants receive a ^{15}N-depleted form of N from MF. This counteracts the overestimation of MDN contribution when disregarding isotopic fractionation in the soil. Thus, the $\delta^{15}N$ signature of salmon-derived N undergoes considerable changes as the salmon carcass decomposes, moves through the soil, is taken up by MF, and is transferred to plants. These changes must be accounted for when assessing MDN's proportional contribution to these ecosystems' N budgets.

Although studies have shown the presence and importance of MDN for animals, vegetation, and soils near and in salmon spawning streams (Quinn et al. 2018, Feddern et al. 2019, Field and Reynolds 2013), the presence and ecological significance of MDN for riparian fungal processes and the capacity of riparian fungi as an MDN sink in the soil remains unexplored. One exception is Larocque’s (2022) PhD thesis which reports increasing fungal $\delta^{15}N$ but no change in fungal %N along a salmon density gradient across streams. In addition to the crucial role of fungi in organic matter decomposition, soil N and C cycling, and C storage through important processes including fungal-plant nutrient exchange, MF specifically can form large and interconnected networks that allow for inter-plant carbon and nutrient transfer. If MF are a sink for MDN, they can mediate the transfer of MDN to plants. If MDN provides an ecologically significant amount of N for fungal needs, it will further affect fungal-plant trading patterns. Furthermore, MDN could be distributed through belowground mycorrhizal fungal or plant root networks and transferred away from the stream to areas with lower N availability, as these networks typically operate based on source-sink dynamics (Walder and Heijden 2015). This would provide a nutrient subsidy to the surrounding forest beyond the salmon-bearing streams and rivers. Fungi could be sequestering MDN in fungal hyphae or concentrating MDN in sporocarps, which would further affect the sequestration and cycling of MDN. It is important to know whether fungi absorb MDN and if MDN is ecologically important for fungal taxa to assess the flow and significance of MDN in riparian systems more accurately.

We examined the effect of the 21-year salmon carcass addition (considered a long-term effect) and recently decomposing salmon carcasses from the current salmon run (considered a short-term effect) on $\delta^{15}N$, C:N, and $\delta^{13}C$ of fungal sporocarps, the dominant plant species (white spruce and paper birch, *Betula papyrifera*) and the major soil layers (organic and mineral soils). This data allowed us to create an isotopic map of MDN flow through these ecosystem compartments of riparian areas. While Quinn et al. (2018) examined tree growth before and after the experiment, and Feddern et al. (2019) quantified the contribution and long-term effect of MDN from the experiment on soil N pools, we evaluated the ecological significance of MDN for fungi and fungal processes and quantified fungal use of MDN. The importance of MDN to fungal processes was determined by (1) evaluating the presence of MDN in fungi by performing stable isotope analysis of fungal sporocarps, (2) examining the effect of MDN on fungal sporocarp %N and %C to evaluate the ecological significance of carcass manipulation, and (3) evaluating the effect of MDN input on mycorrhizal fungal-plant trading patterns. Since MDN is present in the organic bulk soil, soil ammonium pools (Feddern et al. 2019) and white spruce foliage (Quinn et al. 2018), it is likely that fungi also take up MDN. However, the extent of N limitation will affect long-term retention of MDN within the system. If N is strongly limiting plant growth, MDN will likely be tightly cycled among plants, soils, and fungi and retained within the system. However, if N is not strongly limiting, carcass manipulation will likely lead to high N losses through volatilization, nitrification, and leaching, and the contribution of MDN to plants, soils, and fungi will be less. We hypothesized that (H1) MDN from the 21-year carcass manipulation and nearby decomposing carcasses would be present in all ecosystem components, including white spruce and paper birch foliage, organic and mineral soil layers, and fungal sporocarps, specifically in mostly N-tolerant fungal genera such as *Laccaria,* and some species of *Lactarius* such as *Lactarius tabidus* (Lilleskov et al. 2011). We also hypothesized that (H2) MDN input would not affect N concentrations in any of the ecosystem components, due to previous evidence showing no effect of MDN on white spruce C:N (Quinn et al. 2018), soil C:N (Feddern et al. 2019), or fungal C:N (Larocque 2022). Nitrogen manipulation typically decreases mycorrhizal fungal-plant trading of N and C as plants can directly obtain N without incurring C costs from mycorrhizal fungal partners (Kutorga et al. 2013, Jach-Smith et al. 2020). Therefore, we hypothesized that (H3) large inputs of MDN and the consequent high N loading would decrease mycorrhizal fungal-plant trading of N and C.

Methods

Description of site and salmon carcass manipulation – We conducted this study at Hansen Creek (59°19'18.2"N 158°42'04.2"W), Happy Creek (59°19'22.0"N 158°43'02.1"W), and Yako Creek (59°16'34.0"N 158°42'22.5"W), three unconnected sockeye salmon streams that flow into Lake Aleknagik within the Wood River System north of Bristol Bay in southwest Alaska. Salmon spawn in the entire 2 km length of Hansen Creek and primarily in the lower 3.2 km and 1.6 km of Happy Creek and Yako Creek, respectively. Hansen and Happy Creeks are neighboring creeks ~1 km apart, while Yako Creek is located across Lake Alekgnagik. A boreal forest surrounds the streams, where white spruce and paper birch are codominant tree species. Other vegetation includes willow (*Salix* spp.), *Vaccinium* spp., bracken fern (*Pteridium aquilinum*), horsetail (*Equisetum arvense*), fireweed (*Epilobium angustifolium*), and dwarf birch (*Betula nana*). In addition, cotton grass (*Eriophorum* spp.) is found closer to the stream edge, while moss (Bryophyta spp.) and heather (*Calluna* spp.) are found further away from the stream edge. Our sampling sites at Hansen and Yako Creeks did not contain green alder (*Alnus crispa*), a species that contributes N through symbiotic fixation of atmospheric N_2 and would make it more difficult to trace MDN in riparian systems as some vegetation such as white spruce preferentially use alder-fixed N over MDN (Helfield and Naiman 2002). However, our sampling sites at Happy Creek did contain green alder. At Hansen Creek, the topography is low-gradient (7.7% slope) than other streams in the area and this leads to very stable flows with minimal flooding (Lisi et al. 2013, Quinn et al. 2018). Therefore, high flows do not distribute salmon carcasses into the riparian zone, which indicates that the dominant form of transport into the riparian zone is by brown bears, although it is possible that hyporheic transport occurs (O'Keefe and Edwards 2002). A large proportion of sockeye salmon at Hansen Creek and other streams in the area are transferred to the riparian zone by brown bears, and other studies have shown that vegetation by the stream bank receives a significant amount of MDN (Quinn et al. 2009, Helfield and Naiman 2002). In fact, surveys have shown that 35% of salmon carcasses were found on land, 44% partially submerged, and 21% fully submerged at streams in the area (Meehan et al. 2005). Furthermore, additional studies at Hansen Creek have shown that the close banks from 1-6 m did not differ significantly in stem density, basal area density, and overstory species composition (Quinn et al. 2018).

We observed multiple decomposing salmon carcasses at all streams, with some found within bear middens (areas where bears consistently bring carcasses to consume). Hansen Creek was the site of a 21-year salmon carcass fertilization experiment established by Quinn et al. (2018). From 1997 to 2018, the stream was surveyed daily for salmon carcasses throughout the annual sockeye salmon run. During these surveys, all dead salmon located in the creek and up to 5 m on the river-right stream bank were thrown onto the river-left stream bank, facing downstream. In addition, all salmon on the left bank were moved to a distance of 5 m to avoid double-counting. As a result, all salmon carcasses at Hansen Creek were located 3-6 m from the left bank of the stream, except for those relocated by wildlife. This resulted in a decrease in salmon carcass density on the right side of the stream and an increase in salmon carcass density on the left side. Before the manipulation began, each bank received 4500 kg of salmon annually, where after the manipulation began, the left bank received almost 10 times more salmon carcasses than the right bank, averaging 13,400 kg of salmon while the right bank averaged 2,300 kg of salmon annually (due to some live salmon still present on the last survey date, which were assigned evenly between both banks; Quinn et al. 2018). Over the entire 21-year period, about 108,530 salmon were moved to a 3 m wide zone along the entire 2 km-long left bank of Hansen Creek. This equated to 267,620 kg of salmon carcasses that contributed 8,028 kg of N and 1,356 kg of P to the bank (Quinn et al. 2018), or 0.064 kg N/m^2/yr and 0.011 kg P/m^2/yr. We performed this study in 2020, two years after the conclusion of the carcass manipulation experiment.

Sample collection and processing - We established three sets of paired transects on opposing banks at Hansen Creek, and three unpaired transects each at Happy and Yako Creek, for a total of 12 transects. At each transect, we established sampling points at 1, 3, 6, 10, 20, 40, 60, and 100 meters from the edge of the active channel, and transects were selected to cover the stream's lower, middle, and upper sections, representing typical riparian vegetation and high annual salmon carcass abundance. Sampling took place in 2020, two years after the carcass deposition experiment described above ended. At each sampling location, we collected a soil sample from the organic O horizon (with potentially some soil from the A horizon for some locations) approximately 10-15 cm deep, and from the mineral A horizon approximately 25-30 cm deep (USDA 2022). At each sampling point (except for the 3 m location), we established a 10 m sampling transect to each side perpendicular to the 100 m transect away from the bank. We visually scanned an area approximately 2 m wide in each direction for fungal sporocarps, resulting in a total sampling area of 80 m^2 area surrounding the soil core (4 m × 10 m in each direction). We counted all sporocarps in this area and collected a representative sampling of these sporocarps (a sporocarp from each clump of sporocarps) for a total of 267 fungal sporocarps to be further analyzed (SI Methods). We sorted, photographed, and then dried all sporocarps in a dehydrator, and sent for nanopore sequencing (253 fungal sporocarps were identified to species). We classified fungal sporocarps into exploration types based on the FungalTraits, FunGuild database, and other sources (Bahr 2013, Hobbie and Agerer 2010, Nguyen et al. 2016, Põlme et al 2020). We collected foliage samples from all plant species within a 2 m radius of each soil core (except for the 3 m location). These samples included the moss and herb layer such as heather, kinnikinnick (*Arctostaphylos uva-ursi*), and cotton grass; the shrub layer (*Vaccinium alaskanse*, *Rhododendron* spp.); and the dominant tree species white spruce and paper birch. For trees, we selected a 3-5 g wet mass sample of new annual growth at a height of 1-2 m from unshaded branch tips where possible, for each species closest to the soil core (SI Methods). We froze plant foliage samples at -20°C for later isotopic analysis. We collected samples over six days and no precipitation occurred during this time. We dried plant foliage tissue, fungal sporocarp tissue, and soil samples at 60°C for 48 hours and then ground them into uniform powder (<212 µm) using a ball mill grinder. We analyzed samples for ^{15}N: ^{14}N and ^{13}C: ^{12}C ratios at the Washington State University Stable Isotope Core Laboratory.

Normalization reference materials were two glutamic acids and quality control material was NIST1547, a peach leaf. Stable isotope ratios are presented as δ^{15}N and δ^{13}C values, which is the per mil deviation in ^{15}N: ^{14}N and ^{13}C: ^{12}C, respectively, relative to air and Vienna PeeDee Belemnite for N and C using the equation $\delta^{15}N/\ \delta^{13}C = R_{sample}/R_{standard} - 1$, where R is the ^{15}N:^{14}N or ^{13}C:^{12}C ratio. This analysis also yielded data on C and N concentrations by mass of samples (Schoeninger et al. 1983). Gravimetric soil water content (g H_2O/g dry soil) was determined by drying 50-100 g of field-moist soil at 105°C for 48 hours (Gardner 1986). Due to funding constraints, we were only able to analyze 14 white spruce, 12 paper birch, 4 fungal sporocarps (two *Lactarius* and two *Paxillus*) and 3 organic soil samples for total P concentration (Figure S4). For this analysis, we used 1 g of dried sample material and digested with repeated additions of nitric acid and hydrogen peroxide. The resultant digestate was then reduced in volume while heating and diluted to a final volume of 100 mL (US EPA 1996). The solution was then analyzed for total P and 22 other elements using ICP-MS on an ICAP 6300 (Thermo Scientific Inc.).

DNA extraction and sequencing – We used the nanopore sequencing workflow described in Russell (2023b) to extract and sequence fungal sporocarp samples. We extracted fungal tissue into 0.2 mL8-strip PCR tubes. We then added 20 µL ofX-Amp (IBI Scientific, Peosta, Iowa, United States) into each well of the 8-strip tubes and heated at 80 °C for 1 h to begin DNA extraction. We added 50 µL of water to each well to create the PCR template, and performed PCR for the full ITS region using ITS1F and ITS4 primers. We created dual-index primer-master mix plates by hand or using a Opentrons OT-2 robotic pipetting platform as described in Russell (2023c). Each amplification reaction contained 12.5 µL of MeanGreen 2× Master Mix (Empirical Bioscience, Grand Rapids, Michigan, USA), 9 µL water, 1.25 µL forward primer, 1.25 µL reverse primer, and 1 µL DNA template for a total PCR volume of 25 µL. The following PCR protocol was used: (i) initial denaturation at 94 °C for 60 s; (ii) 30 cycles of denaturation at 94 °C for 60 s, annealing at 51 °C for 60 s, and extension at 72 °C for 60 s; (iii) hold at 72 °C for 8 min. We used electrophoresis with a 1 % agarose gel to verify successful amplification. We pooled the resulting amplicons and created a library with the Oxford Nanopore Technologies (ONT) LSK 112 or LSK114 chemistry (Oxford Nanopore Technologies, Oxford, UK). We performed sequencing on an ONT Minion & Flongle device with a Flongle 9.4.1 or 10.4.1 flowcell. Raw data were base called, demultiplexed, consensus sequences were formed, and the final data were uploaded to MycoMap using protocols from Russell (2023b). All curated sequence data were compared against data contained in public (GenBank, BOLD & UNITE) and in-house databases. The raw DNA sequence data (FASTQ) are available within the Macrolepiota of North America MycoMap project (MycoMap 2023). Final consensus sequence data were deposited in GenBank.

Statistical Analysis – We fit linear mixed effect models for $\delta^{15}N$, $\delta^{13}C$, and C:N ratio of fungi, white spruce, paper birch, organic soil, and mineral soil from 1-100 m at all streams, resulting in a total of 15 model sets (Tables 1-3). We included a random effect of transect nested within stream, and fixed effects of distance and three salmon carcass variables – the carcass manipulation, carcass density, and decomposing carcass for all models. The carcass manipulation variable referred to the 21-year carcass manipulation experiment, where all carcasses in the stream and on one bank were placed onto the other bank for 21 years, which created a large carcass fertilization experiment from 1-6 m. We defined carcass manipulation as a categorical presence/absence variable, and recorded presence at 1 m and 6 m at Hansen Creek for all components (soils, fungi, and plants) and absence at all other locations. Further, we defined recently decomposing salmon carcasses as a presence/absence categorical variable and recorded presence for soils, plants, and fungi at each sampling location < 2 m to a decomposing salmon carcass, similar to Drake et al. (2005), and absence for all other locations. Although we recorded presence for fungi within sampling locations with nearby carcasses, the large areas for sporocarp sampling meant that an effect of single carcasses on fungi was less likely. All models for fungi included trophic status and a random effect of genus. Additional predictor variables differed depending on the response variable and are described in SI Methods. We used stepwise model selection to confirm the best fitting model using Akaike's Information Criterion corrected for small sample size (AICc) using the R package lmer for each model set. We also ran a set of candidate models with variable sets of predictors (SI Methods). Both analyses yielded similar results. To examine for over-fitting, we used the variance inflation factor which measures the strength of correlation between predictor variables in a regression model. A VIF value of > 3 typically indicates high correlation (Everitt and Anders 2010).

Transfer ratios derived from ^{15}N *mass balance calculations* – We estimated the percentage of N from the available N pool entering the ectomycorrhizal fungal hyphae that is transferred to plant hosts (T_r) using mass balance calculations as described in Hobbie and Hobbie (2006) for each sampling location. We assumed that the available N pool was the soil ammonium pool for 1-6 m on the salmon-enhanced bank (Table S3), and the fractionation factor during N transfer from EMF to plants hosts was set to 9‰ based on fractionation rates from similar systems (Hobbie et al. 2019). We averaged values of δ^{15}N for fungi, soil, and foliage (white spruce and paper birch) for every distance sampled on both banks (Table 5).

Results

Environmental drivers of δ^{15}N in soil, fungi, and vegetation - Mean δ^{15}N of fungal sporocarps was significantly higher on the salmon-enhanced bank than the salmon-depleted bank at 1-6 m (13.6 ± 0.6 and 10.6 ± 0.8, respectively, n = 265; Figure 1, Table 1). Mean white spruce δ^{15}N was significantly higher on the salmon-enhanced bank than the salmon-depleted bank at 1-6 m (8.9 ± 0.4 and 4.9 ± 0.9, respectively, n = 74; Figure 1, Table 1). Mean paper birch δ^{15}N was significantly higher on the salmon-enhanced bank than the salmon-depleted bank at 1-6 m (8.3 ± 0.9 and 4.2 ± 0.9, respectively, n = 69; Figure 1, Table 1). Mean δ^{15}N of organic soil was significantly higher on the salmon-enhanced bank than the salmon-depleted bank (8.3 ± 0.9 and 4.2 ± 0.9, respectively, n = 97; Figure 1, Table 1). Mean δ^{15}N of organic soil was significantly higher on the salmon-enhanced bank than the salmon-depleted bank (8.3 ± 0.9 and 4.2 ± 0.9, respectively; Figure 1, Table 1). Mean δ^{15}N of mineral soil was not significantly different between the salmon-enhanced bank and the salmon-depleted bank at 1-6 m (n = 96, Table 1).

Fungal δ^{15}N ranged from -4.88 to 18.56, with a maximum δ^{15}N value of 18.56 for the salmon-enhanced side and 16.62 for the salmon-depleted side (Figure 2). Fungal δ^{15}N increased with both the presence of the carcass manipulation and the presence of a nearby decomposing salmon carcass (β = 3.98 ± 0.76, β = 1.89 ± 0.81, respectively; Table 1). Fungal δ^{15}N also increased with organic soil δ^{15}N but decreased with organic soil GWC (β = 0.40 ± 0.10 and β = -0.11 ± 0.04, respectively; Table 1). Fungal δ^{15}N was further affected by fungal trophic status, with saprotrophic fungi having significantly lower δ^{15}N than mycorrhizal fungi (β = -2.74 ± 0.97). Fungal δ^{15}N decreased with distance from stream bank and mineral soil C:N (β = -0.98 ± 0.17 and β = -0.11 ± 0.06, respectively; Table 1). White spruce δ^{15}N ranged from -4.93 to 10.18, with a maximum δ^{15}N of 10.18 on the salmon-enhanced side and 6.77 on the salmon-depleted side (Figure 2). White spruce δ^{15}N increased with the presence of the carcass manipulation (β = 3.00 ± 0.67), as well as with mean fungal δ^{15}N and organic soil δ^{15}N (β = 0.1 ± 0.05, β = 0.47 ±

0.11, respectively; Table 1). White spruce $\delta^{15}N$ increased with distance from the stream bank and organic soil GWC (β = 0.84 ± 0.14 and β = 0.28 ± 0.13, respectively; Table 1). Paper birch $\delta^{15}N$ ranged from -3.14 to 9.37, with a maximum $\delta^{15}N$ value of 9.37 for the salmon-enhanced side and 6.77 for the salmon-depleted side (Figure 2). Paper birch $\delta^{15}N$ increased with the presence of the carcass manipulation (β = 3.46 ± 0.76), as well as with organic soil GWC and organic soil $\delta^{15}N$ (β = 0.46 ± 0.12 and β = 0.37 ± 0.11, respectively, Table 1). Paper birch also increased with mean mycorrhizal fungal $\delta^{15}N$ but decreased with distance (β = 0.11 ± 0.05 and β = -0.5 ± 0.15, respectively, Table 1). For organic soils, $\delta^{15}N$ ranged from 0.51 to 12.83, and the maximum $\delta^{15}N$ of organic soils was 11.18% for the salmon-enhanced side and 12.83% for the salmon-depleted side (Figure 2). Organic soil $\delta^{15}N$ increased with the carcass manipulation and the presence of a decomposing carcass (β = 1.81 ± 0.63 and β = 1.18 ± 0.51, respectively; Table 1). Organic soil $\delta^{15}N$ also increased with organic soil GWC and decreased with distance from stream edge (β = 0.49 ± 0.12 and β = 0.94 ± 0.12; Table 1). Mineral soil $\delta^{15}N$ ranged from 3 to 10.61 %, and maximum $\delta^{15}N$ of mineral soils was 10.61 for the salmon-enhanced side, and 9.72 for the salmon-depleted side (Figure 2). Mineral soil $\delta^{15}N$ decreased with distance from stream edge (β = -0.53 ± 0.09; Table 1).

Environmental drivers of C:N in soil, fungi, and vegetation - Mean C:N of fungal sporocarps was significantly higher on the salmon-enhanced close bank than the salmon-depleted close bank (7.9 ± 0.35 and 9.5 ± 0.5; respectively, Figure 1, Table 2). The C:N ratio of white spruce, paper birch, organic soil and mineral soil did not differ significantly between the salmon-enhanced and salmon-depleted close banks (Figure 1, Table 2). Fungal C:N decreased with carcass manipulation and paper birch C:N (β = -0.13 ± 0.07 and β = -0.01 ± 0.006), but increased with white spruce C:N (β = 0.005 ± 0.002; Table 2). Fungal C:N was also significantly lower for saprotroph than mycorrhizal fungi (β = -0.25 ± 0.04, Table 2). White spruce C:N increased with distance from stream bank (β = 1.55 ± 0.44, Table 2). Although white spruce C:N also increased with mean fungal C:N (β = 0.87 ± 0.50), this effect was not significant (Table 2). Paper birch C:N increased with distance from stream bank (β = 0.72 ± 0.23, Table 2). Organic soil C:N increased with distance and organic soil GWC (β = 2.23 ± 0.34, β = 0.69 ± 0.30; Table 2). Mineral soil C:N increased with distance from stream bank (β = -0.36 ± 0.14, Table 2).

Environmental drivers of $\delta^{13}C$ in soil, fungi, and vegetation - Fungal δ^{13}C increased with fungal %N and distance from stream bank (β = 0.19 ± 0.06, β = 0.16 ± 0.06, Table 3). Fungal δ^{13}C also increased with distance from stream bank (β = 0.16 ± 0.06, Table 3). Saprotroph fungi had higher δ^{13}C than mycorrhizal fungi (β = 0.85 ± 0.23, Table 3). Although fungal δ^{13}C increased with the presence of a decomposing carcass, this effect was not significant (β = 0.52 ± 0.30, Table 3). Both white spruce and paper birch δ^{13}C declined with the presence of a decomposing carcass (β = -1.00 ± 0.44 and β = -0.83 ± 0.43, respectively; Table 3). Organic soil δ^{13}C decreased with organic soil %N (β = -0.52 ± 0.12, Table 3). Mineral soil δ^{13}C decreased with mineral soil %N (β = -0.40 ± 0.13, Table 3). Mineral soil δ^{13}C also increased with distance from stream bank (β = 0.11 ± 0.04), but this effect was not significant (Table 3).

Fungal sporocarps by genus, trophic, and function specific patterns of $\delta^{15}N$ – We observed a total of 828 fungal sporocarps. We sequenced all 267 fungal sporocarps that were collected, and were able to identify 253 samples to genus and 223 to species. We identified a total of 32 genera and 74 species of fungi, including 17 previously unidentified species (Table 4, Table S1). EMF represented 83% of sporocarps, whereas saprotroph fungi represented 17% of identified sporocarps (Table 4). The most common genera included *Lactarius* (66), *Cortinarius* (33), *Paxillus* (32), and *Russula* (30) (Table 4). Five species – *Lactarius tabidus* (59), *Paxillus involutus* (26), *Hebeloma leucosarx* (13), *Russula betularum* (11), and *Laccaria sp-AK01* (9) – constituted ~50% of all collected sporocarps, while the genus *Cortinarius* had the highest species diversity with 14 species and *Russula* consisted of 9 species (Table 4). *Xerocomus* had the highest mean δ^{15}N of 17.9‰, followed by *Tricholoma* at 12.7‰ and *Paxillus* at 10.7‰ (Table 4). Genera with the lowest mean δ^{15}N were *Tubaria* at -0.7‰ and *Cystoderma* at -0.1‰ (Table 4). Mean δ^{15}N for all genera are listed in Table 4. *Entoloma* species were divided into saprotroph (*Entoloma certratum*, *Entoloma turbidum*) and mycorrhizal (*Entoloma sericatum*) species (Table 4, Table Table S1).

Saprotrophic fungi had significantly lower δ^{15}N than mycorrhizal fungi (saprotroph δ^{15}N = 3.4 ± 2.3, *n* =45, mycorrhizal δ^{15}N = 8.9 ± 3.1, *n* = 222; Table 1, Table 4). Saprotrophic fungi were not found < 10 m from either bank, except for one *Stropharia pseudocyanea*, whereas mycorrhizal fungi were abundant across all distances from stream bank. We classified fungal sporocarps into exploration types based on the FunGuild Database and other sources (Nguyen et al. 2016, Hobbie and Agerer 2010, Bahr 2013). Functional groups included long-distance types (*Paxillus* spp., *Xerocomus* spp., and species from the order Boletales), medium-distance fringe types (*Cortinarius* spp., *Tricholoma* spp., *Hebeloma* spp.), medium-distance smooth (*Lactarius* spp., *Laccaria* spp., *Naucoria* spp., *Entoloma* spp., *Amanita* spp.), and short-distance types (*Russula* spp., *Inocybe* spp.; Table S4).

Variation in $\delta^{15}N$ over time from the carcass manipulation – In 2016, white spruce mean δ^{15}N was 10.7‰ from 1-5 m for the salmon-enhanced (Quinn et al. 2018), while our study in 2020 showed a mean δ^{15}N of 8.9‰ at 1-6 m for the salmon-enhanced bank, a significant decrease of 1.8‰ (t-test, $p < 0.05$; Table S2). In 2017, organic soil mean δ^{15}N was 8.9‰, while this study recorded organic soil mean δ^{15}N of 7.2‰ at 3-6 m on the salmon-enhanced bank 3 years later (Table S2), showing a 1.7‰ decrease in 3 years, a significant difference (t-test, $p < 0.05$; Table S2; Feddern et al. 2019). However, organic soil δ^{15}N also decreased on the salmon-depleted bank, from 7.36‰ in 2017 to 6.82‰ in 2020, a 0.54‰ difference, although not significant (t-test, $p = 0.3$, Table S2).

White spruce and paper birch N:P – White spruce and paper birch N:P was not significantly different between the salmon-enhanced and salmon-depleted banks at Hansen Creek for 1-6 m (t-test, $p = 0.3$ and $p = 0.5$, respectively; Figure S4). In addition, mean white spruce N:P (7.3 ± 1.1) and mean white spruce %N (1.08 ± 0.11) at Hansen Creek from 1-6 m suggested that N was limiting to white spruce growth, while mean %P (0.15 ± 0.02) indicated mostly sufficient P for white spruce (Carter 1992, Güsewell et al. 2004; Figure S4). Mean white spruce %N (1.06 ±0.14) from 1-100 m at Hansen Creek further confirmed that N was the primary limiting nutrient to white spruce growth (Carter 1992, Figure 3). Values for paper birch %N that indicate N limitation vary widely from 1.24 – 3% N, with a mean of 2.12 %N (Keski-Saari and Julkunen-Tiitto 2003, Wang et al. 1998). Mean paper birch %N (2.18 ± 0.31) from 1-100 m at Hansen Creek (Figure 3) indicated that paper birch is somewhat limited by N. Paper birch N:P (9.8 ± 2.3) from 1-6 m at Hansen Creek suggested potential co-limitation of N and P (Güsewell et al. 2004; Figure S4).

Discussion

Fungi, soil, and plants take up MDN – We predicted that MDN would be present in fungi, plants, and soil (H1). We found that the carcass manipulation increased δ^{15}N in white spruce, paper birch, organic soil, and fungal sporocarps, indicating that MDN from the carcass manipulation was likely present in these ecological components (Figure 1, Table 1). For plants and soils, this result is not surprising as MDN from the carcass manipulation was shown to be present in white spruce in 2016 (Quinn et al. 2018) and bulk soils in 2017 (Feddern et al. 2019). However, fungi have not been examined in this system, and we showed that MDN was present in fungal sporocarps as well, specifically EMF fungal sporocarps, indicating that EMF likely immobilized MDN from salmon carcasses. Saprotrophic (decomposer) fungi only represented < 5% of samples at the site of carcass manipulation and sites close to decomposing carcasses, therefore we cannot draw any conclusion about saprotrophic fungal capacity to absorb MDN. We found that although both organic soil and EMF incorporated MDN from recent decomposing salmon carcasses in the current season (within ~1-2 months), MDN from decomposing carcasses was not present in white spruce or paper birch foliage (Table 1). This suggests that fungi potentially incorporate short-term MDN faster than plant tissues. This is further supported by studies showing that many spruce species remobilize N from previous year needles for new shoot growth, making it less likely that new shoot growth would contain recent MDN from nearby decomposing carcasses (Millard and Grilet 2010). However, it can also signify that plants have a larger residual pool of N that dilutes new inputs, and the radius of uptake is much larger for tree roots than fungal hyphae. These results suggest that EMF can take up MDN quickly from salmon as carcasses decompose and also immobilize MDN from long-term salmon carcass deposition events, likely from soil N pools enriched with MDN (Feddern et al. 2019). Feddern et al. (2019) showed that carcass manipulation enriched both bulk soil and soil ammonium pools in ^{15}N. If EMF draw nutrients from either or both of these pools, it is likely that they take up MDN and become enriched in ^{15}N, as did the soil, relative to the salmon-depleted side. These results are supported by only one other study examining the effects of MDN on fungi, which showed increased fungal sporocarp δ^{15}N along a salmon density gradient across streams (Larocque 2022). It is not surprising that EMF are incorporating MDN into hyphae and sporocarps. The primary source of N and P in most boreal forests is litter, which decomposes and releases nutrients relatively slowly (Chapin et al. 2002). Salmon tissues are nutrient-rich and are quickly broken down by decomposers, with skeletonization occurring within 6-10 weeks (Drake et al. 2005, Drake et al. 2006). Salmon carcass decomposition is a highly spatially localized and temporally limited N pulse, where inorganic N (ammonium and nitrate) increases within a few meters around the carcass for up to 5 months (from a study in a coastal temperate rainforest; Drake et al. 2005). EMF are efficient nutrient scavengers and would readily take advantage of the available N in their vicinity. EMF likely immobilize MDN from both the inorganic and organic soil N pools and utilize these nutrients to support maintenance, growth, sporocarp production, and N transfer to plant hosts in exchange for C.

We found significantly higher $\delta^{15}N$ in plants, soils, and fungi on the salmon-enhanced bank relative to the salmon-depleted bank from 1-6 m at Hansen Creek 2 years after the termination of the carcass manipulation experiment in 2018. This could potentially indicate that this large, continuous, and annual supply of salmon carcasses resulted in some amount of MDN that was retained in the area and continuously cycled through ecosystem components. Some studies have shown that MDN persists in vegetation for months to years. For example, forest productivity was affected by salmon abundance 13 months after spawning (Kieran et al. 2021), and understory plants used N from salmon during important period of plant growth many months following carcass placement (Hocking and Reynolds 2012). Drake et al. (2006) found that ^{15}N tracer used to simulate carcass deposition was retained in trees for at least one year, and allocated to leaves and stems the following spring after application in the fall. However, it is also important to note that localized N pulses such as carcass addition can temporarily surpass soil and plant N pools and lead to increasing N loss through ammonia volatilization, nitrate leaching, and denitrification (Perakis 2002). All these processes fractionate against ^{15}N and discrimination increases with soil N availability, resulting in increased residual soil $\delta^{15}N$ values (Högberg 1997). Elevated soil N from salmon carcasses can persist for up to 6 months following carcass placement, suggesting that the N demands of both plants and microbes near carcasses are saturated by carcass inputs at small scales (Drake et al. 2005). In addition, MDN has been shown to increase particularly gaseous N losses (Holtgrieve et al. 2009), and ammonia volatilization has been shown to isotopically enrich carcasses by 1.5‰ (Wheeler and Kavanaugh 2017). Furthermore, Feddern et al. 2019 showed that $\delta^{15}N$ of inorganic N was frequently higher than $\delta^{15}N$ of salmon inputs, indicating that isotopic fractionation is likely important at Hansen Creek. Therefore, it is possible that some amount of the increased $\delta^{15}N$ observed in plants, soils, and fungi was due to increases in soil N cycling and N losses within the system due to the large input of MDN. This increased $\delta^{15}N$ would still be a result of the carcass manipulation, however, $\delta^{15}N$ would be increased due to N losses in addition to MDN input, potentially artificially amplifying the amount of MDN present in the system. Furthermore, although we found significantly higher $\delta^{15}N$ in plants and soils on the salmon-enhanced bank from 1-6 m due to the carcass manipulation, both plant and soil $\delta^{15}N$ decreased significantly over the span of 3-4 years (Table S2), indicating that the amount of MDN stored in the soil from the carcass manipulation has declined since the end of the carcass manipulation, and suggesting that some N loss is occurring, or that MDN is being diluted by other forms of N following the termination of the carcass manipulation.

MDN increases fungal, but not soil or plant, N concentrations - We predicted that MDN would not affect N concentrations in soil, plants, or fungi (H2) due to previous studies that showed that MDN did not significantly alter C:N ratios of fungal, white spruce, or bulk soil (Feddern et al. 2019, Larocque 2022, Quinn et al. 2018). We found that MDN did not increase N concentrations in soils or plant foliage, as expected (Figure 1, Table 2). However, we found that the C:N ratio for EMF was significantly lower on the salmon-enhanced bank relative to the salmon-depleted bank (Figure 1; Figure 2; Table 2). This indicates that MDN increased N concentrations in fungi and the N uptake per unit fungal growth, contrary to our second hypothesis, and suggests that MDN was ecologically significant for fungi. Although lower C:N in EMF could also indicate lower photosynthetic C transfer to EMF by plant hosts, this is unlikely as fungal-plant trading patterns were not altered by the carcass manipulation (discussed below). In addition, the %C of EMF was similar between banks while the %N of EMF was significantly higher on the salmon-enhanced bank than the salmon-depleted bank (mean EMF %N = 5.3 and 4.6, respectively, $p < 0.05$, $n = 32$). The C:N ratio of EMF did not vary with short-term MDN from nearby decomposing carcasses, indicating that changes to fungal C:N from MDN require larger amounts of nutrient input. Although the carcass manipulation artificially inflated carcass input to one bank of Hansen Creek, signifying that fungal response might not represent the natural response to MDN input throughout this system, it might be more representative of fungal response to MDN input prior to commercial fishing operations, which harvest 60-75% of the sockeye salmon run in this system each season and thus considerably reduce the abundance of sockeye salmon returning to Hansen Creek (Alaska Department of Fish and Wildlife 2022).

It is possible that fungi incorporate some amount of MDN before it is lost from the soil through volatilization, leaching, and denitrification, leading to an increased N pool from MDN in fungi, but not in soil or plants. This is further confirmed by the fact that fungi took up MDN from nearby decomposing carcasses but plants did not, which suggests that fungi can access MDN more quickly than plants. Feddern et al. (2019) found that MDN did not increase soil organic and inorganic N concentrations and N mineralization rates, indicating that much of the MDN from the carcass manipulation was not being retained in the soil. It is possible that some of this MDN is being retained in EMF hyphae and sporocarps, due to the increased N concentrations in EMF sporocarps from the carcass manipulation. The majority (80%) of EMF in this study were classified as medium and long-distance types (Table 4). These fungi have significant N retention capacity and prevent N leaching due to the presence of rhizomorphs and thick hyphal mats. EMF also have high standing mycelial biomass, with some EMF storing N for up to 2 years (Bahr 2013, Ekblad et al. 2013), suggesting that some long-term MDN retention in EMF hyphae is possibly and likely occurring. In fact, Bahr (2013) found that recently produced EMF mycelium could assimilate 6 kg/ha/month of inorganic N, which would indicate that EMF could assimilate ~11% of the 637 kg N/ha/yr deposited by the carcass manipulation. The only other study to examine the effects of MDN on fungi observed no changes in fungal C:N with a salmon density gradient across 16 salmon streams (Larocque 2022). However, high biogeochemical variability within streams may make it challenging to capture the response of fungal C:N to increasing salmon density, whereas a more fine-scale, within-stream comparison with a relatively precise carcass manipulation experiment was able to capture this response. Furthermore, other N addition studies have shown increases in fungal %N with N addition (Hobbie et al. 2019), although these studies did not add P. The ecological significance of MDN in riparian systems has been debated for several decades, and the results are mixed (Walsh et al. 2020). However, few studies have quantified the effect of MDN on ecosystem-level responses such as C:N, or even nutrient enhancement such as increases in %N. In this study, MDN significantly decreased fungal C:N, indicating that MDN increased the fungal N absorption rate and the fungal N pool size within the system. We accounted for multiple soil biogeochemical and other variables when evaluating the effect of the carcass manipulation on fungal C:N, and previous studies have shown no significant differences in stem density, basal area density, and overstory species composition between banks at Hansen Creek from 1-6 m (Quinn et al. 2018). Therefore, we conclude that the decreased fungal C:N is primarily due to the carcass manipulation. This result suggests that MDN is retained in fungal hyphae for years, as this study was performed two years after the end of carcass manipulation, and indicates that MDN has ecosystem-level significance for fungal organisms.

The lack of effect of the carcass manipulation on organic soil C:N indicates that this large nutrient fertilization did not increase soil N pools (Figure 1, Table 2). Salmon carcasses contribute nutrients to soils and vegetation at high rates, but over small areas and short time periods, and the small spatio-temporal scale and patchy distribution of these nutrients is expected to lead to high rates of loss (Drake et al. 2006). Since the carcass manipulation increased organic soil δ^{15}N, this suggests that MDN replaced existing N rather than adding to the soil N pool. This is further confirmed by a lack of increase in inorganic and organic soil N concentrations from the carcass manipulation and high fractionation rates due to N losses at Hansen Creek, which indicate that N inputs likely surpass the capacity of soil N pools and lead to accelerated N loss due to leaching, denitrification, and ammonia volatilization (Feddern et al. 2019). The lack of effect of the carcass manipulation on white spruce C:N also suggests that this large nutrient fertilization likely did not increase the white spruce N pool (Figure 1, Table 2). However, this is complicated by the fact that the carcass manipulation increased the growth rate of white spruce at Hansen Creek (Quinn et al. 2018). This suggests that N in the plant pool may have been diluted by growth, which has been shown to occur during rapid growth (Quinn et al. 2018, Bryant 1987, Drake et al. 2006). Therefore, it is also possible that some of this MDN was retained in white spruce biomass through increased biomass instead of increased N concentration. This is further supported by the fact that N is typically a limiting nutrient for growth in Alaskan white spruce forests (Chapin et al. 1986, Schulze et al. 1994), and white spruce at our sites were N-limited (Figure 3), suggesting that large nutrient inputs from the carcass manipulation should impact white spruce N concentrations or growth rates. In addition, many other studies have shown increased tree growth rates from MDN input (Helfield and Naiman 2001, 2002, Bilby et al. 2003, Mathewson et al. 2003, Reimchen and Fox 2013, Drake et al. 2002, Drake and Naiman 2007, Hocking and Reynold 2012). Interestingly enough, a few previous studies have been conducted on white spruce at Hansen Creek prior to Quinn et al. 2018. Drake et al. 2006 found that annual growth rate of white spruce at Hansen Creek did not correlate with either salmon abundance, precipitation, or temperature. Helfield and Naiman 2002 showed that white spruce at Hansen Creek had higher growth rates than spruce at reference sites without salmon. Therefore, there is mixed evidence concerning white spruce growth response to MDN input. Paper birch was likely co-limited by N and P (Figure 3, Figure S4), however information on paper birch growth rates are unavailable, making it difficult to fully assess the impact of N inputs on paper birch.

Fungal MDN use varied by functional type – We further examined the effects of MDN by functional exploration type, and found that long-term carcass manipulation significantly increased $\delta^{15}N$ in long- and medium-distance smooth types, while recently decomposing carcasses significantly increased $\delta^{15}N$ in medium-distance fringe types (Table S4). Long- and medium-distance EMF have long-distance transport structures called rhizomorphs and large amounts of extraradical hyphae that allow them to maintain a large network structure, forage over large distances, and exploit nutrient patches (Lilleskov et al. 2011 Moeller et al. 2014). Some of these species can even break down organic N and increase available nutrient pools (Lilleskov et al. 2024, Northrup et al. 1995). These fungi incur a high C cost for plant hosts and are competitively dominant in low-nutrient (N or P) environments, where resources are rare or patchy (Moeller et al. 2014). Short-distance EMF forage over much smaller areas, have more fluid and adaptive hyphae, and a lower C cost for plant hosts relative to long and medium distance types (Moeller et al. 2014). Plants generally prefer these fungi in nutrient-rich environments (Lilleskov et al. 2011). It is possible that only long- and medium-distance foragers absorbed MDN because of their capacity to maintain large networks, mine nutrient hotspots, forage over large distances, and access organic N (Lilleskov et al. 2024), all of which would be beneficial for plants to gain access to nutrients from carcasses more efficiently. These EMF have fungal rhizomorphs that allow for distributing and mining nutrients in spatially heterogenous and patchy nutrient environments, and thus could be prioritized by plant hosts in areas of high soil nutrient levels due to their capability to obtain patchily-distributed nutrients for plant hosts efficiently (Larocque 2022). In fact, studies have shown that fungal-plant trading increases when nutrient patches are unevenly distributed as fungal hyphae have higher search efficiency and lower metabolic maintenance costs than plant roots, leading to higher plant C allocation belowground to fungal partners (Bending and Read 1995, Peay et al. 2011). Long-distance and some medium-distance exploration types also generally have higher proteolytic capacity to decompose complex organic compounds and access organic N (Lilleskov et al. 2024, Vaario et al. 2019), thus giving this functional group an advantage at the site of carcass manipulation. In addition, these fungal types have high N retention due to their capacity to form rhizomorphs that can store and retain N and prevent leaching (Bahr 2013). These traits allow these exploration types to have high-standing mycelial biomass in boreal forests and indicates that these fungal functional groups could retain, utilize, and trade MDN with plant hosts for a substantial amount of time, from months to years, after initial absorption within this system.

Other drivers of $\delta^{15}N$ *in fungi, soil, and vegetation* – In addition to the carcass manipulation and nearby decomposing carcasses, EMF δ^{15}N increased with soil organic δ^{15}N, suggesting that EMF are incorporating N from the organic soil layer (Table 1). However, when examining by functional type, models showed that medium-distance fringe EMF acquired nutrients primarily from mineral soil, while medium-distance smooth and short-distance EMF utilized the organic soil layer (Table S4, Figure S5). Given that soil N is not homogenous within a horizon, another interpretation is that medium-distance fringe EMF acquired N that turned over more slowly (more recalcitrant) than the forms of N acquired by the other EMF types (Hobbie et al. 2014). Interestingly, EMF δ^{15}N decreased much slower on the salmon-enhanced bank relative to the salmon-depleted bank, with EMF δ^{15}N more than 4‰ higher on the salmon-enhanced than the salmon-depleted bank at 20 m, a significant difference (t-test, $p = 0.02$). This could possibly be due to the presence of a slope at 20 m on the salmon-enhanced bank, which could increase soil N cycling, soil water content and drainage at the bottom of the slope at 20 m, and therefore increase EMF δ^{15}N (Hogberg 1997, Kirchoff 2003). However, soil δ^{15}N was not significantly different at 20 m between banks. Therefore, this could indicate some potential re-distribution of MDN from the carcass manipulation through EMF networks to more N limited sites further away from the stream edge on the salmon-enhanced bank (Figure 2). White spruce and paper birch δ^{15}N also increased with soil organic δ^{15}N, indicating that these species also take up N from the organic soil layer. White spruce and paper birch δ^{15}N increased with mean mycorrhizal fungal δ^{15}N, which could indicate either that organic soil N was the primary N source for both plants and fungi, or that fungal N exchange with white spruce and paper birch hosts was occurring in this system. Fungal δ^{15}N generally also increased from short-distance to long-distance exploration types (Table 4), which is expected, likely due to increased N sequestration for higher biomass requirements in long-distance types (Hobbie and Agerer 2010), but also because medium-distance and long-distance types were the primary fungi to take up MDN. Fungal δ^{15}N was also significantly lower for saprotrophic fungi than mycorrhizal fungi, which is expected as isotopic fractionation during N exchange between mycorrhizal fungi and plant hosts results in mycorrhizal fungi enriched in δ^{15}N and plant hosts depleted in δ^{15}N (Figure 4, Table 1). Saprotrophic fungi had higher %N and lower %C than mycorrhizal fungi (Figure 4). Saprotrophic fungi were also only found > 10 m away from either side of the stream bank (Figure 5), possibly due to their preference for higher soil organic matter further away from the stream bank due to decreased soil N cycling (Feddern et al. 2019, Janowski and Leski 2022). Studies have also shown that EMF compete with free-living saprotrophs for N, and EMF can suppress saprotrophic activity and litter decomposition and drive soil C accumulation, with effects most pronounced with increasing N fertilization (Averill and Hawkes 2016, Liang et al. 2022). Therefore, it is possible that EMF are outcompeting saprotrophs with higher soil N levels closer to the stream bank. However, EMF have poor ability to access cellulose and hemicellulose in litter or wood, which could make competition less likely.

Fungal-plant trading patterns – The dominant tree species at the study site, white spruce and paper birch, form strong mutualisms and are obligate partners with mycorrhizal fungi. Trees trade photosynthetically derived C for fungal-foraged N, with up to 80% of plant N derived from mycorrhizal fungal networks (Hobbie and Hobbie 2006, Smith and Read 2008). Since most of the fungi we collected were ectomycorrhizal fungi (85%, Table 1), C and N exchange is likely occurring in this system. This supposition was supported by the fact that mean mycorrhizal δ^{15}N was a significant predictor for white spruce and paper birch δ^{15}N (Table 1). However, fungal-plant trading is strongly driven by N availability, and some studies have shown that fungal N transfer to plant hosts decreases with higher soil N availability as plant hosts can attain labile N directly from the soil without the C cost associated with fungal-mediated N uptake and transfer (Jach-Smith et al. 2020, Nylund and Wallander 1992, Hogberg 2010, Kranabetter and MacKenzie 2009). However, other studies have shown that EMF can actually reinforce N limitation and direct uptake of nutrients is limited when EMF colonizes plants (Franklin et al. 2014, van't Padje et al. 2020). Plants were primarily N-limited in this system (Figure S4), therefore we might expect trading to be high across the entire site and potentially lower at the site of carcass manipulation. Stable isotope analysis can be used to detect the presence and intensity of fungal-plant trading due to isotopic fractionation that occurs during the trading process. After taking up N from the soil, mycorrhizal fungi create transfer compounds within the hyphae that will transfer N to plant hosts. The creation of transfer compounds fractionates against ^{15}N, leading to plant hosts receiving ^{15}N-depleted N, while N that remains within the hyphae is enriched in ^{15}N (Hobbie and Hobbie 2006). This leads to mycorrhizal fungi being enriched and mycorrhizal plants being depleted in ^{15}N relative to bulk soil and inorganic soil N. In this study, plant δ^{15}N was lower than soil δ^{15}N while fungal δ^{15}N was higher than soil δ^{15}N by similar values of ~3‰ on the salmon-depleted bank from 1-6 m (soil δ^{15}N = 8.3‰, plant δ^{15}N = 5.7‰, fungal δ^{15}N = 12‰; Figure 2). This indicates that N and C exchange is occurring between mycorrhizal fungi and their plant hosts, with an average of 28% fungal N transferred to plant hosts from 1-6 m (Table S3). However, on the salmon-enhanced bank from 1-6 m, soil and plant δ^{15}N are approximately the same, while fungi are 5‰ and 6‰ higher in δ^{15}N than plants or organic soil, respectively (fungal δ^{15}N = 13.56‰, plant δ^{15}N = 8.6‰, organic soil δ^{15}N = 7.6‰; Figure 2). At first glance, this might suggest that no fungal-plant N exchange is occurring, because we do not see the expected pattern of lower plant δ^{15}N and higher fungal δ^{15}N relative to soil δ^{15}N. If fungal-plant trading were occurring, fungi would have to be drawing from a N pool considerably more enriched than the organic bulk soil pool. Based on available evidence, it is likely that fungi are taking up MDN from the ^{15}N-enriched soil ammonium pool, and then trading this MDN with plant hosts. Although this study did not evaluate soil ammonium concentration or δ^{15}N, we note that in 2017, organic soil δ^{15}N and ammonium δ^{15}N was approximately the same at 6 m on the salmon-depleted bank, while soil ammonium δ^{15}N was approximately 3‰ higher than organic soil δ^{15}N on the salmon-enhanced bank (Feddern et al. 2019; Table S2). This difference was due to high nitrification rates on the salmon-enhanced bank from carcass manipulation. Since soil ammonium is the dominant available N pool and is considerably enriched in ^{15}N relative to bulk soil, it is likely that fungi are taking up MDN from this enriched pool and trading with plant hosts, leading to the patterns seen in Figure 2, with plant δ^{15}N and fungal δ^{15}N higher than bulk soil δ^{15}N. In 2017, δ^{15}N of soil ammonium averaged 11.85‰ at 1-6 m on the salmon-enhanced bank (Table S2). If we assume that soil ammonium δ^{15}N changes by the same amount as bulk soil δ^{15}N for each sampling location from 2017 to

2020, then soil ammonium δ^{15}N = ~11.48‰ from 1-6 m in 2020 (Table S2). If fungi are taking up MDN from the soil ammonium pool and trading with plants at the site of carcass manipulation (soil δ^{15}N = 11.48‰, plant δ^{15}N = 8.6‰, fungal δ^{15}N = 13.9‰; Figure 2), calculations show that ~20% of fungal N is transferred to plant hosts from 1-6 m on the salmon-enhanced bank. This amount is 8% less N than the 28% of fungal N transferred to plant hosts on the salmon-depleted bank from 1-6 m (Table S3), not a considerably large difference and minimal support for our hypothesis that MDN would decrease plant-fungal trading.

Incorporating fungal-plant trading in estimating contributions of MDN - Multiple other studies have used two-source mixing models (Kline et al. 1990, Bilby et al. 1996) to estimate the % marine-derived nitrogen (MDN) contribution to vegetation and soil (Quinn et al. 2018, Feddern et al. 2019), where %MDN = ((SAM – TEM)/(MEM-TEM)) × 100. In this model, %MDN is the percent of MDN in a sample, SAM is the δ^{15}N of the sample, TEM is the terrestrial end member (δ^{15}N value with 0% MDN), and MEM is the marine end member (δ^{15}N value with 100% MDN). However, this model assumes that the δ^{15}N of MDN is not altered between carcass decomposition and absorption by plants or fungi, and that reference sites have similar biogeochemical properties to sites with salmon. Both assumptions are false at Hansen Creek, and likely other riparian systems as well (Feddern et al. 2019). Many factors affect the δ^{15}N of soil, fungi, and plants (Table 1; Craine et al. 2019), and the δ^{15}N of these components can decrease dramatically with distance from the stream edge (Figure 2), indicating that selecting a site outside the reach of salmon would not only violate the assumption that sites are biogeochemically similar, but would also lead to over-estimation of the %MDN contribution. Feddern et al. (2019) showed that salmon N undergoes N transformations that dramatically increase the δ^{15}N of salmon N in the ammonium pool, the likely pool used by plants (and fungi), suggesting an overestimation of the % MDN contribution to plants in studies that use the two-source mixing model. However, there is an additional N transformation step that occurs before MDN reaches plants. White spruce and paper birch form strong partnerships with ectomycorrhizal fungi in boreal forests, with high levels of N exchange between ectomycorrhizal fungi and plant hosts (up to 80% of plant N derived from mycorrhizal fungal partners in similar systems; Hobbie and Hobbie 2006). This indicates that MDN is taken up by fungal organisms from available soil N, and then ^{15}N-depleted MDN is transferred to plant hosts, while fungi become enriched in ^{15}N, relative to $\delta^{15}N$ of available soil N. Therefore, this indicates an un-accounted for underestimation of %MDN contribution to plants, as the ultimate $\delta^{15}N$ value that is used for the sample (in this case, plants) is lower due to $\delta^{15}N$ fractionation during fungal N transfer. With high levels of trading in these systems, this suggests that MDN studies could be significantly underestimating salmon N contributions to riparian systems. This component would be very useful to incorporate in MDN mixing models.

Conclusion – We examined the presence and ecological significance of MDN to soils, plants, and fungi in riparian zones. We found that EMF hold an important role in riparian systems, as these fungi incorporate and retain MDN. MDN is primarily immobilized by medium-distance and long-distance EMF, which are efficient at mining and obtaining nutrients in patchy environments, have high N retention capacity and standing mycelial biomass, and prevent N leaching due to the presence of rhizomorphs and thick hyphal mats. MDN increased N uptake and N concentrations in EMF, indicating that EMF represent a potentially significant MDN sink in the soil and that MDN is ecologically significant for fungal processes. This suggests that removing large amounts of MDN might affect ecosystem-level processes through fungal organisms. In many parts of the world, salmon stocks are declining (Mills et al. 2013), but the effect of this decrease in MDN on fungal communities, and subsequently the cycling of C and N, is unknown. Decreasing N for fungal processes might lead to decreased N transfer to plant hosts, which could then increase plant C allocation belowground to fungi to attain additional N. We also found MDN in white spruce, paper birch, and organic soil, and could indicate that MDN from long-term carcass manipulation is cycled between soil, fungi, and plants and persist in riparian system for years. However, MDN did not alter N concentrations in these components, and the relative contribution of MDN vs. accelerated N cycling to value of $\delta^{15}N$ is difficult to assess, as both isotopic fractionation and MDN increase $\delta^{15}N$. It is important to consider all pathways that alter $\delta^{15}N$ of MDN to understand its contributions to an ecosystem. For example, disregarding fractionation in the soil can overestimate how much MDN is retained in vegetation, but disregarding fungal-plant dynamics underestimate MDN contribution to plants. This study illustrates that to attain a comprehensive understanding of the flow of MDN in riparian systems, all ecosystem components including fungi, soil, and plants must be considered.

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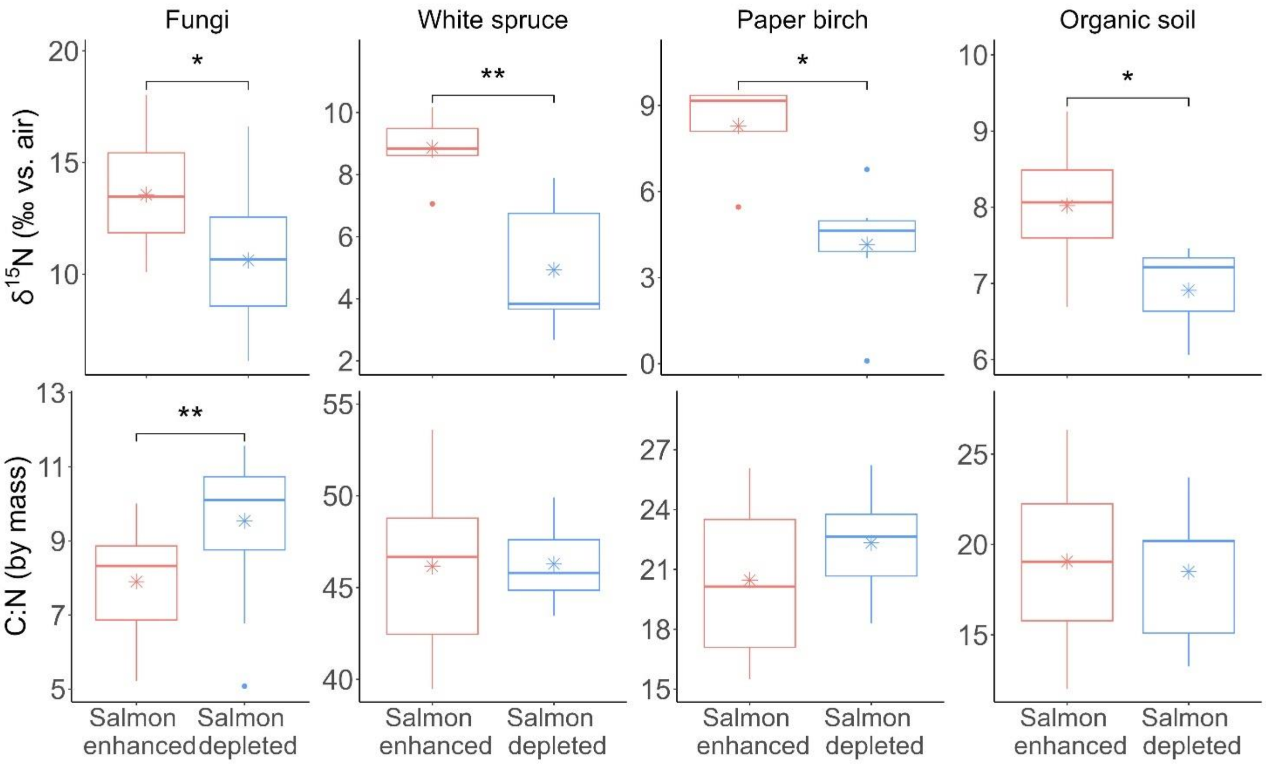


Figure 1. Mean values of δ^{15}N and C:N for fungal sporocarps, paper birch and white spruce foliage, and organic soil from 1-6 meters from the stream edge on salmon carcass enhanced and salmon carcass depleted banks of Hansen Creek, Alaska. Statistics reported at top are Wilcoxon rank sum test and p value. Significant pairwise differences are reported with brackets for each pair (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, **** $p \leq 0.0001$). Boxplots indicate the minimum, lower quartile, median, upper quartiles, and maximum values for each component.

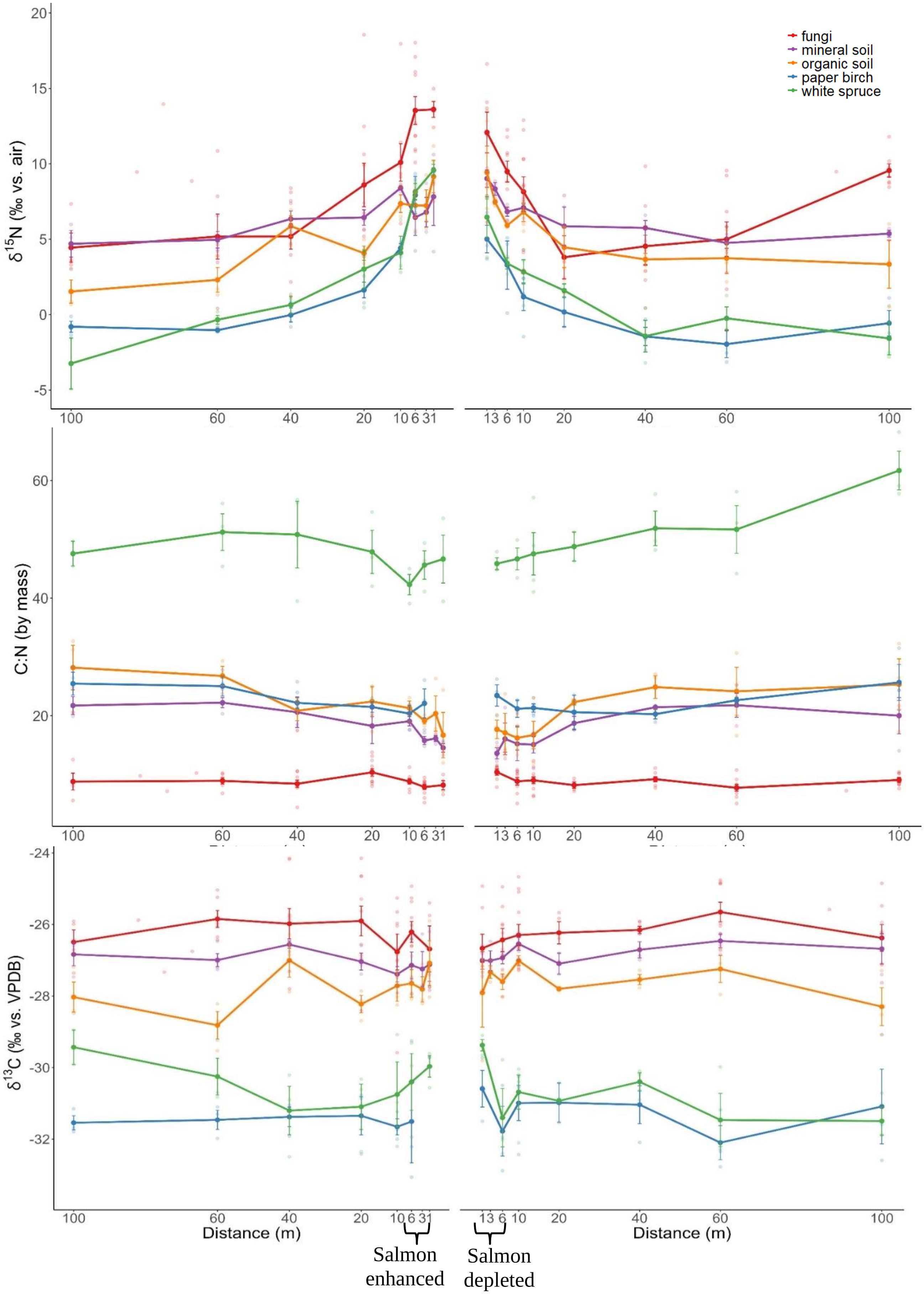


Figure 2. Mean values of δ^{15}N, C:N, and δ^{13}C for fungi, white spruce, paper birch, organic soil and mineral soil 1-100 m away from the bank of Hansen Creek on both sides.

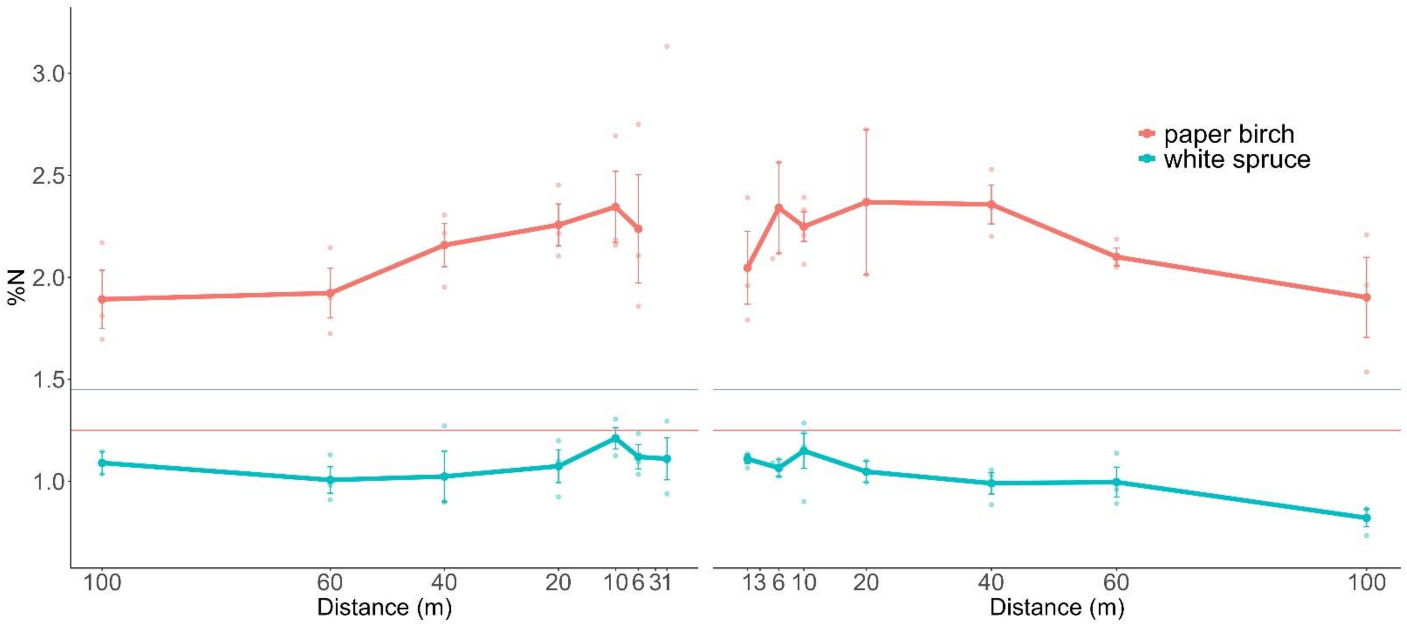


Figure 3. Mean values of %N for white spruce and paper birch from 1-100 m away from the bank on both sides of Hansen Creek. Horizontal lines indicate values of N deficiency.

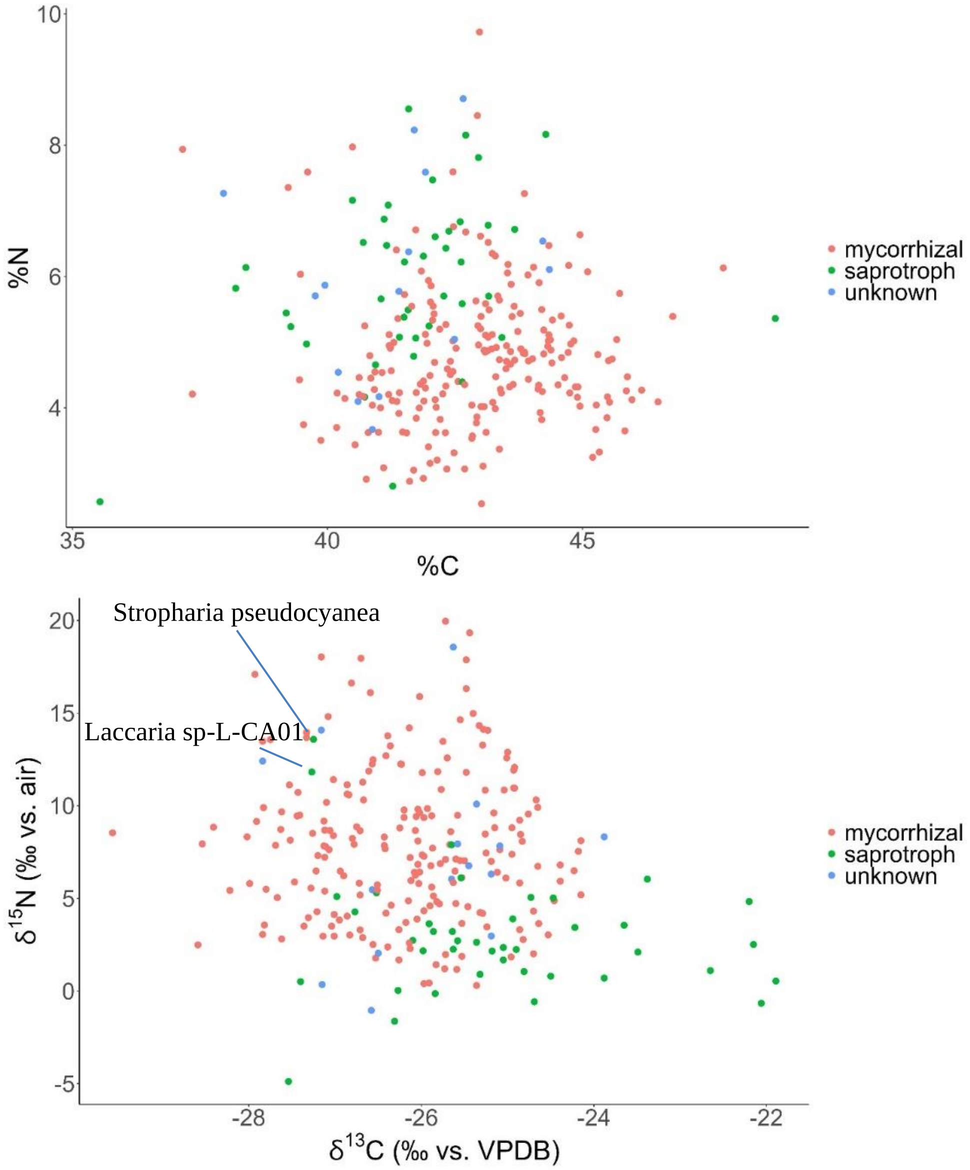


Figure 4. Scatterplot of mycorrhizal, saprotrophic, and unknown trophic status fungal %C and %N, and fungal $\delta^{15}N$ and $\delta^{13}C$. Species listed indicate saprotrophs that might have some mycorrhizal capacity.

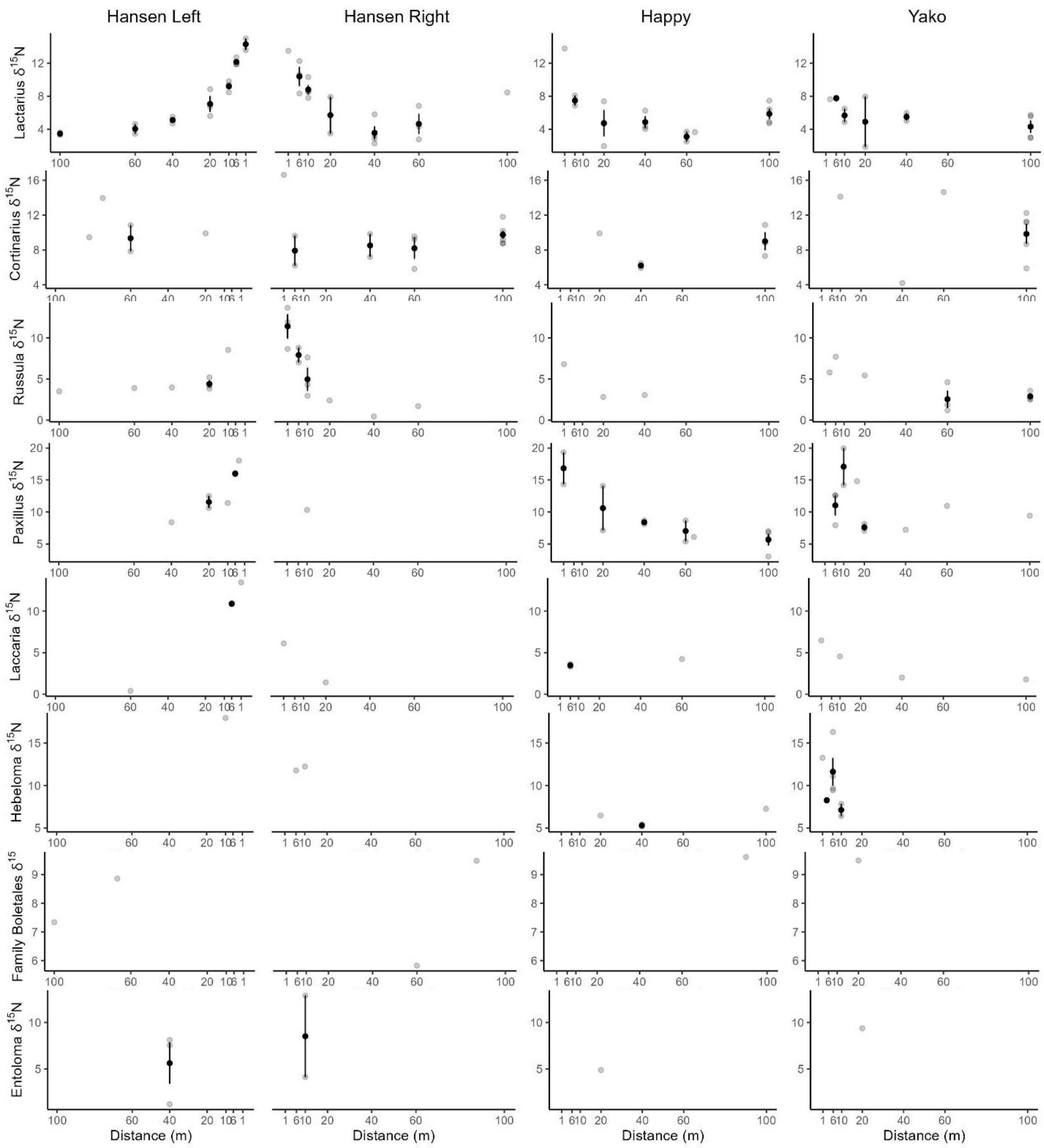


Figure 5. Values of fungal $\delta^{15}N$ by genera, distance, and side (at Hansen Creek) along three sockeye salmon streams in southwest Alaska. Genera with > 5 sporocarps are included.

Table 1. Significant predictors from the top linear mixed models for fungal, white spruce, paper birch, organic soil, and mineral soil $\delta^{15}N$ from 1-100 m away along three salmon streams in SW Alaska. Models include predictive R^2, all predictor variables, beta coefficient estimates ± SE, P values and VIF (variance inflation factor). All models included a random effect of transect nested within stream, and fungal $\delta^{15}N$ included an additional random effect of genus. GWC indicates gravimetric water content. For trophic status (mycorrhizal, saprotroph, or unknown), the intercept gives an estimate for mean mycorrhizal $\delta^{15}N$, and the coefficient for trophic status gives the difference between mycorrhizal and saprotrophic mean $\delta^{15}N$. This indicates that saprotrophic fungi have significantly lower $\delta^{15}N$ than mycorrhizal fungi.

Response variable	Conditional R^2	Covariates	Value ± SE	P-value	VIF
Fungi $\delta^{15}N$ (n = 265)	0.79	Intercept	9.99 ± 0.87	< 0.001	NA
		Carcass manipulation	3.98 ± 0.76	0.007	1.14
		Decomposing carcass	1.89 ± 0.81	0.04	1.25
		Ln(distance)	-0.98 ± 0.17	< 0.001	2.10
		Organic soil GWC	-0.11 ± 0.04	0.02	1.23
		Organic soil $\delta^{15}N$	0.40 ± 0.10	< 0.001	2.33
		Trophic status:saprotroph	-2.74 ± 0.97	0.007	1.03
		Trophic status:unknown	-0.12 ± 0.85	0.89	NA
		Mineral soil C:N	-0.11 ± 0.06	0.05	1.72
White spruce $\delta^{15}N$ (n = 74)	0.86	Intercept	4.00 ± 0.48	< 0.001	NA
		Carcass manipulation	3.00 ± 0.67	< 0.001	1.65
		Ln(distance)	0.84 ± 0.14	< 0.001	2.03
		Organic soil GWC	0.28 ± 0.13	0.03	1.25
		Organic soil $\delta^{15}N$	0.47 ± 0.11	< 0.001	2.23
		Mineral soil $\delta^{15}N$	0.29 ± 0.15	0.06	1.82
		Mean fungal $\delta^{15}N$	0.10 ± 0.05	0.06	1.28
Paper birch $\delta^{15}N$ (n = 69)	0.83	Intercept	2.89 ± 0.53	< 0.001	NA
		Carcass manipulation	3.46 ± 0.76	< 0.001	1.55
		Ln(distance)	-0.50 ± 0.15	0.002	2.32
		Mean mycorrhizal fungal $\delta^{15}N$	0.11 ± 0.05	0.01	1.83
		Organic soil GWC	0.46 ± 0.12	< 0.001	1.45
		Organic soil $\delta^{15}N$	0.37 ± 0.11	0.001	2.30
Organic soil $\delta^{15}N$ (n = 97)	0.51	Intercept	7.37 ± 0.38	< 0.001	NA
		Carcass manipulation	1.81 ± 0.63	0.005	1.33
		Decomposing carcass	1.18 ± 0.51	0.02	1.85
		Organic soil GWC	0.49 ± 0.12	< 0.001	2.24
		Ln(Distance)	-0.94 ± 0.12	< 0.001	1.41
Mineral soil $\delta^{15}N$ (n = 96)	0.34	Intercept	7.09 ± 0.42	< 0.001	NA
		Ln(distance)	-0.53 ± 0.09	< 0.001	1.30

Table 2. Significant predictors from the top models for fungal, white spruce, paper birch, organic soil, and mineral soil C:N from 1-100 m away from both stream banks of Hansen Creek, AK. Models include predictive R^2, all predictor variables, beta coefficient estimates ± SE, P values and VIF (variance inflation factor). GWC indicates gravimetric water content. All models included a random effect of transect nested within stream, and fungal C:N additionally included a random effect of genus. For trophic status (mycorrhizal, saprotroph, or unknown), the intercept gives an estimate for mean mycorrhizal C:N, and the coefficient for trophic status gives the difference between mycorrhizal and saprotrophic mean C:N. This indicates that saprotrophic fungi have significantly lower C:N than mycorrhizal fungi.

Response variable	Conditional R^2	Covariates	Estimate ± SE	P-value	VIF
log(fungal C:N) (n = 231)	0.44	Intercept	8.52 ± 1.26	< 0.001	NA
		Paper birch C:N	-0.01 ± 0.006	0.03	1.07
		White spruce C:N	0.005 ± 0.002	0.06	1.06
		Trophic status:saprotroph	-0.25 ± 0.04	< 0.001	1.02
		Trophic status:unknown	-0.23 ± 0.06	< 0.001	NA
		Carcass deposition	-0.13 ± 0.07	0.05	1.38
log(white spruce C:N) (n = 70)	0.41	Intercept	42.30 ± 1.77	< 0.001	NA
		Ln(Distance)	1.55 ± 0.44	< 0.001	2.1
		Mean fungal C:N	0.87 ± 0.50	0.08	1.10
log(paper birch C:N) (n = 69)	0.16	Intercept	17.84 ± 1.81	< 0.001	NA
		Ln(Distance)	0.72 ± 0.23	0.007	1.73
log(organic soil C:N) (n = 97)	0.54	Intercept	7.06 ± 0.42	< 0.001	NA
		Ln(distance)	2.23 ± 0.34	< 0.001	1.00
		Organic soil GWC	0.69 ± 0.30	0.02	1.00
log(mineral soil C:N) (n = 96)	0.35	Intercept	7.09 ± 0.42	< 0.001	NA
		Ln(Distance)	-0.36 ± 0.14	0.01	1.30

Table 3. Significant covariates from the top models for fungal, white spruce, paper birch, organic soil, and mineral soil $\delta^{13}C$ from 1-100 m away from both stream banks of Hansen Creek, AK. Models include predictive R^2, all predictor variables, beta coefficient estimates ± SE, P values and VIF (variance inflation factor). GWC indicates gravimetric water content. All models included a random effect of transect, and fungal $\delta^{13}C$ included a random effect of genus. For trophic status (mycorrhizal, saprotroph, or unknown), the intercept gives an estimate for mean mycorrhizal $\delta^{13}C$, and the coefficient for trophic status gives the difference between mycorrhizal and saprotrophic mean $\delta^{13}C$. This indicates that saprotrophic fungi have significantly higher $\delta^{13}C$ than mycorrhizal fungi.

Response variable	Conditional R^2	Covariates	Estimate ± SE	P-value	VIF
Fungi $\delta^{13}C$ (n = 131)	0.21	Intercept	-26.64 ± 0.23	< 0.001	NA
		Ln(distance)	0.16 ± 0.06	0.01	1.09
		Mineral soil $\delta^{13}C$	-0.40 ± 0.17	0.02	1.01
		Trophic status:saprotroph	0.85 ± 0.23	0.003	1.14
		Trophic status:unknown	-0.38 ± 0.29	0.19	NA
		Fungal %N	0.19 ± 0.06	0.01	1.08
		Decomposing carcass	0.52 ± 0.30	0.08	1.32
White spruce $\delta^{13}C$ (n = 77)	0.22	Intercept	-29.78 ± 0.31	< 0.001	NA
		Decomposing carcass	-1.00 ± 0.44	0.02	1.27
Paper birch $\delta^{13}C$ (n = 77)	0.14	Intercept	-30.53 ± 0.36	< 0.001	NA
		Decomposing carcass	-0.83 ± 0.43	0.05	1.29
Organic soil $\delta^{13}C$ (n = 97)	0.17	Intercept	-27.59 ± 0.10	< 0.001	NA
		Organic soil %N	-0.52 ± 0.12	< 0.001	NA
Mineral soil $\delta^{13}C$ (n = 96)	0.27	Intercept	-26.94 ± 0.10	< 0.001	NA
		Ln(distance)	0.11 ± 0.04	0.08	1.20
		Mineral soil %N	-0.40 ± 0.13	0.002	1.20

Table 4. The trophic status, exploration type (for mycorrhizal fungi), count, mean δ^{15}N and SD, and mean δ^{13}C of all fungal genera (and two families – *Lyophyllaceae* and *Boletaceae*) found at three salmon streams in SW Alaska. Genera are ordered with increasing δ^{15}N values. For *Lyophyllaceae*, the species found was previously undescribed, therefore, no information about trophic status is available.

Genus	**Trophic status**	**Exploration type**	**Count**	**δ^{15}N (‰ vs. air)**	**δ^{15}N SD (‰ vs. air)**	**δ^{13}C (‰ vs. VPDB)**
Tubaria	saprotroph		1	-0.7	0.0	-22.1
Cystoderma	saprotroph		1	-0.1	0.0	-25.8
Psathyrella	saprotroph		6	-0.1	3.1	-25.8
Ampulloclitocybe	saprotroph		9	2.4	1.4	-25.7
Gymnopilus	saprotroph		1	2.7	0.0	-26.1
Hypholoma	saprotroph		7	2.9	2.2	-24.4
Entoloma cetratum/turbidum	saprotroph		2	3.0	4.1	-25.1
Family *Lycoperdaceae*	saprotroph		1	3.2	0.0	-25.9
Pholiota	saprotroph		2	3.3	3.9	-22.6
Clitocybe	saprotroph		3	3.4	3.4	-24.8
Pluteus	saprotroph		1	3.6	0.0	-23.7
Rhodocollybia	saprotroph		2	3.9	0.0	-24.6
Protostropharia	saprotroph		1	4.3	0.0	-26.8
Stropharia	saprotroph		4	4.7	6.0	-24.2
Apioperdon	saprotroph		1	4.8	0.0	-22.2
Russula	mycorrhizal	short	30	5.0	3.1	-26.5
Pseudoclitocybe	saprotroph		1	5.1	0.0	-27.0
Laccaria	mycorrhizal	Short/medium smooth	13	5.3	4.1	-25.5
Cystodermella	saprotroph		1	6.1	0.0	-25.5
Inocybe	mycorrhizal	short	1	6.4	0.0	-26.0
Lactarius	mycorrhizal	medium smooth	66	6.7	3.2	-26.3
Lyophyllaceae	unknown		1	6.8	0.0	-25.5
Amanita	mycorrhizal	Short/medium smooth	1	7.1	0.0	-25.7
(blank)				7.2	5.1	-26.3
Entoloma sericatum	mycorrhizal	medium smooth	4	7.3	4.7	-25.4
Melanoleuca	saprotroph		1	7.9	0.0	-25.7
Order Boletales	mycorrhizal	long	6	8.4	1.5	-26.0
Limacella	unknown		2	8.6	4.6	-26.9
Naucoria	mycorrhizal	Short/medium smooth	3	9.4	8.5	-26.9
Cortinarius	mycorrhizal	Medium fringe	33	9.6	2.8	-26.2
Hebeloma	mycorrhizal	Medium fringe	16	9.8	3.7	-26.4

Paxillus	mycorrhizal	long	32	10.7	4.3	-26.0
Tricholoma	mycorrhizal	Medium fringe	2	12.7	0.8	-25.6
Xerocomus	mycorrhizal	long	1	17.9	0.0	-25.5

Supplementary Section Methods

We analyzed ^{15}N:^{14}N, ^{13}C:^{12}C, %N, %C of fungal sporocarps, white spruce foliage, paper birch foliage, mineral soil and organic soil to achieve these goals. Additionally, we genetically sequenced all fungal sporocarps to further assist in assigning functional traits and interpreting isotopic signatures, as characteristics influencing isotopic signatures of fungal sporocarps are typically genus- or species-specific. Furthermore, sequencing contributed to the characterization of fungal species in Alaska, as Alaska mycota are not well characterized and include many undescribed species (Dr. Steve Trudell, personal communication).

To accurately model the effect of the salmon carcass manipulation, we considered how placement of carcasses could affect nearby trees, fungi, and soil, and how sampling the soil environment differs from sampling foliage from a tree or a fungal sporocarp. Soil is a physical substrate through which nutrients from a carcass diffuse outwards from the carcass source. Tree roots extend through the soil several meters outward from the trunk to search for nutrients, which are then up taken through directed movement through the roots, and subsequently sent to varying parts of the tree, such as the roots, stem, or foliage. Fungi form thick mats of hyphae belowground that can transfer nutrients up to several meters, and possibly further distances from a nutrient source (Beiler et al. 2015, Simard et al. 2012). In this way, the soil receives nutrients at a point and nutrients then passively diffuse through the soil, while trees and fungi actively uptake nutrients using roots or hyphae within at least a several meter radius, thus re-distributing and accumulating nutrients from the surrounding area to a source. Thus, the area of effect from a nutrient source such as a carcass is much wider when sampling foliage or fungal sporocarps than when sampling soil, because of the uptake and directed movement of nutrients through roots and hyphae. Salmon carcasses were thrown onto the soil from 3-6 m from the bank each year in late summer, where they would decompose into the soil. It is important to evaluate whether the fungi, soil, and plants sampled along transects reasonably had access to nutrients from these decomposing salmon carcasses. Soil cores were taken at points 1, 3, and 6 m away from the stream bank. Therefore, soils sampled at 3 and 6 m were affected by carcass manipulation, and also likely the soils at 1 m as salmon nutrients potentially move through the soil towards the stream bank due to diffusion and mass flow of soluble N, and also via foliage, roots, and fungal hyphae. Sporocarps that were sampled at the 1 m sampling location were collected (and data were averaged) across a 10 × 2 m area on each side of the soil core at 1 m, stretching 10 m away parallel to the bank on either side, and from 1-3 m perpendicularly away from the bank. Therefore, it is very likely that the fungi that produced these sporocarps had hyphae present beyond 3 m from the bank, into the carcass manipulation zone. The fungi that we sampled at the 6 m soil core plot were collected from 4-8 m away from the bank, and 10 m parallel to the bank on either side, across a 10 × 4 m area. Thus, the carcass manipulation affected fungi sampled at both the 1 and 6 m locations away from the stream bank. Plants were sampled in a 2 m radius of the soil core at each sampling location, and plants sampled in the 2 m radius around the 1 m soil core likely had roots extending into the carcass manipulation zone at 3-6 m. Thus, plants sampled at both the 1 and 6 m locations away from the stream bank were affected by the carcass manipulation. This is similar to the methodology of sampling white spruce at Hansen Creek performed by Quinn et al. (2018), where spruce from 1-5 m from both stream banks were sampled. In addition, Feddern et al. (2019) found that the carcass manipulation increased the ^{15}N of the soil ammonium pool, the most likely N source for plants and fungi in this system, and that enrichment was highest at 3 m and declined with distances < 3 m. This suggests that salmon-derived N was present in larger quantities closer to the 3 m area of the manipulation. Therefore, this makes it even more likely that fungi and plants sampled from 1-3 m had the possibility of taking up MDN, and in fact could even imply that uptake of MDN could be higher for plants and fungi at the 1 m sampling location than the 6 m sampling location, due to the 1-3 m samples being closer to the 3 m site than the 4-8 m samples.

Supplementary Section Models

Models for δ^{15}N

Fungal δ^{15}N ~ carcass manipulation + decomposing carcass + salmon density + fungal %N + ln(Distance) + organic soil GWC + organic soil δ^{15}N + organic soil C:N + mineral soil GWC + mineral soil δ^{15}N + mineral soil C:N + trophic status (mycorrhizal, saprotrophic, or unknown) + (1|Genus) + (1|Stream:Transect)

White spruce δ^{15}N ~ carcass manipulation + decomposing carcass + salmon density + white spruce %N + ln(Distance) + mean fungal δ^{15}N + soil organic GWC + soil organic δ^{15}N + mineral soil GWC + mineral soil δ^{15}N + (1|Stream:Transect)

Paper birch δ^{15}N ~ carcass manipulation + decomposing carcass + salmon density + paper birch %N + ln(Distance) + mean fungal δ^{15}N + soil organic GWC + soil organic δ^{15}N + mineral soil GWC + mineral soil δ^{15}N + (1|Stream:Transect)

Organic soil δ^{15}N ~ carcass manipulation + decomposing carcass + salmon density + ln(Distance) + organic soil %N + organic soil GWC + (1|Stream:Transect)

Mineral soil δ^{15}N ~ carcass manipulation + decomposing carcass + salmon density + ln(Distance) + mineral soil %N + mineral soil GWC + (1|Stream:Transect)

Models for δ^{13}C

Fungal δ^{13}C ~ carcass manipulation + decomposing carcass + salmon density + fungal %N + ln(Distance) + trophic status + organic soil GWC + organic soil δ^{13}C + mineral GWC + mineral soil δ^{13}C + paper birch δ^{13}C + white spruce δ^{13}C + (1|Genus) + (1|Stream:Transect)

White spruce δ^{13}C ~ carcass manipulation + decomposing carcass + salmon density + white spruce %N + ln(Distance) + soil organic GWC + (1|Stream:Transect)

Paper birch δ^{13}C ~ carcass manipulation + decomposing carcass + salmon density + paper birch %N + ln(Distance) + soil organic GWC + (1|Stream:Transect)

Organic soil δ^{13}C ~ carcass manipulation + decomposing carcass + salmon density + organic soil %N + ln(Distance) + organic soil GWC + (1|Stream:Transect)

Mineral soil δ^{13}C ~ carcass manipulation + decomposing carcass + salmon density + mineral soil %N + ln(Distance) + mineral soil GWC + (1|Stream:Transect)

Models for C:N

Fungal C:N ~ carcass manipulation + decomposing carcass + salmon density + ln(Distance) + trophic status + organic soil C:N + mineral soil C:N + white spruce C:N + paper birch C:N + organic soil GWC + mineral soil GWC + (1|Genus) + (1|Stream:Transect)

White spruce C:N ~ carcass manipulation + decomposing carcass + salmon density + ln(Distance) + organic soil GWC + mineral soil GWC + (1|Stream:Transect)

Paper birch C:N ~ carcass manipulation + decomposing carcass + salmon density + ln(Distance) + organic soil GWC + mineral soil GWC + (1|Stream:Transect)

Organic soil C:N ~ carcass manipulation + decomposing carcass + salmon density + ln(Distance) + organic soil GWC + (1|Stream:Transect)

Mineral soil C:N ~ carcass manipulation + decomposing carcass + salmon density + ln(Distance) + mineral soil GWC + (1|Stream:Transect)

Table S1. Fungal species found at three salmon streams in SW Alaska, accompanied by trophic guild and exploration type (if applicable) from three databases: FunGuild (has species-level data available, but only trophic guild), FungalTraits (has only genus-level data, both trophic and exploration type available), and Determination of Ectomycorrhizae, or DEEMY (has species-level data and trophic and exploration type information. Fungal species with numbers are new, undescribed species. ND = no data. NA = not applicable.

Species	**FunGuild**	**FungalTraits**	**DEEMY**	**Literature**
Amanita betulae	Pathotroph-Saprotroph-Symbiotroph	Ectomycorrhizal, medium distance smooth	ND	
Ampulloclitocybe clavipes	Saprotroph-Symbiotroph	Litter saprotroph	ND	
Apioperdon pyriforme	Saprotroph	Wood saprotroph	ND	
Boletaceae (family)				
Clitocybe odora	Pathotroph-Saprotroph-Symbiotroph	Litter saprotroph	ND	
Clitocybe PNW06	NA	Litter saprotroph	NA	
Clitocybe sp-PNW01	NA	Litter saprotroph	NA	
Cortinarius alboviolaceus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius armillatus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	Medium distance fringe	
Cortinarius caperatus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius hirtus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius illibatus-AK01	NA	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius modestus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius nigrocuspidatus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius pellstonianus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius pholideus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius vibratilis	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	Medium distance fringe	

Cortinarius semisanguineus-PA01	NA	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius subparvannulatus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius tabularis	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	ND	
Cortinarius umbrinolens	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance fringe	ND	
Cystoderma amianthinum-PA01	Saprotroph	Litter saprotroph	ND	
Cystodermella adnatifolia	Saprotroph	Litter saprotroph	ND	
Entoloma cetratum	Pathotroph-Saprotroph-Symbiotroph, Ectomycorrhizal-Fungal Parasite-Soil Saprotroph-Undefined Saprotroph	Soil saprotroph and unspecified symbiotroph, ectomycorrhizal ~ 10% of species, Medium distance smooth	ND	Saprotrophic. Source: Termorshuizen, Aad J., and Mirjam T. Veerkamp. "Fungi in spontaneous stands of Scots pine (Pinus sylvestris) in drift sands." *Field Mycology* 13, no. 4 (2012): 118-123.
Entoloma sericatum	Pathotroph-Saprotroph-Symbiotroph, Ectomycorrhizal-Fungal Parasite-Soil Saprotroph-Undefined Saprotroph	Soil saprotroph and unspecified symbiotroph, ectomycorrhizal ~ 10% of species, Medium distance smooth	ND	Mycorrhizal. Source: Brandrud, Tor Erik, Egil Bendiksen, John Bjarne Jordal, Øyvind Weholt, Siw Elin Eidissen, Jostein Arve Lorås, Bálint Dima, and Machiel E. Noordeloos. "Entoloma species of the rhodopolioid clade (subgenus Entoloma; Tricholomatinae, Basidiomycota) in Norway." (2018).
Entoloma turbidum	Pathotroph-Saprotroph-Symbiotroph, Ectomycorrhizal-Fungal Parasite-Soil Saprotroph-Undefined Saprotroph	Soil saprotroph and unspecified symbiotroph, ectomycorrhizal ~ 10% of species, Medium distance smooth	ND	Saprotrophic. Source: Termorshuizen, Aad J., and Mirjam T. Veerkamp. "Fungi in spontaneous stands of Scots pine (Pinus sylvestris) in drift sands." *Field Mycology* 13, no. 4 (2012): 118-123.
Gymnopilus decipiens	Pathotroph-Saprotroph-Symbiotroph; Bryophyte Parasite-Dung Saprotroph-Ectomycorrhizal-Fungal Parasite-Leaf Saprotroph-Plant Parasite-Undefined	Wood saprotroph	ND	

	Saprotroph-Wood Saprotroph			
Hebeloma aurantioumbrinum	Pathotroph-Saprotroph-Symbiotroph; Bryophyte Parasite-Dung Saprotroph-Ectomycorrhizal-Fungal Parasite-Leaf Saprotroph-Plant Parasite-Undefined Saprotroph-Wood Saprotroph	Ectomycorrhizal; short distance delicate	ND	
Hebeloma leucosarx	Pathotroph-Saprotroph-Symbiotroph; Bryophyte Parasite-Dung Saprotroph-Ectomycorrhizal-Fungal Parasite-Leaf Saprotroph-Plant Parasite-Undefined Saprotroph-Wood Saprotroph	Ectomycorrhizal; short distance delicate	ND	
Hebeloma monticola	Pathotroph-Saprotroph-Symbiotroph; Bryophyte Parasite-Dung Saprotroph-Ectomycorrhizal-Fungal Parasite-Leaf Saprotroph-Plant Parasite-Undefined Saprotroph-Wood Saprotroph	Ectomycorrhizal; short distance delicate	ND	
Hebeloma sordescens	Pathotroph-Saprotroph-Symbiotroph; Bryophyte Parasite-Dung Saprotroph-Ectomycorrhizal-Fungal Parasite-Leaf Saprotroph-Plant Parasite-Undefined Saprotroph-Wood Saprotroph	Ectomycorrhizal; short distance delicate	ND	
Hypholoma capnoides	Pathotroph-Saprotroph; Dung	Wood saprotroph	ND	

	Saprotroph-Plant Parasite-Soil Saprotroph-Undefined Saprotroph-Wood Saprotroph			
Inocybe sp-AK01	NA	Ectomycorrhizal; short distance delicate	NA	
Laccaria glabripes	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; short distance delicate	ND	
Laccaria sp-AK01	Likely Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; short distance delicate	NA	
Laccaria sp-PA01	Likely Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; short distance delicate	NA	
Lactarius glyciosmus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance smooth	No information on exploration type, no rhizomorphs present	
Lactarius rufus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance smooth	No information on exploration type, rhizomorphs infrequent	
Lactarius tabidus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance smooth	ND	
Lactarius turpis	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, medium distance smooth	ND	
Limacella sp-L-CA01	NA	Soil saprotroph	NA	
Limacella sp-L-CO01	NA	Soil saprotroph	NA	
Lyophyllaceae sp-AK01	NA	This family had two saprotrophic and one ectomycorrhizal genera which was medium distance fringe	NA	
Melanoleuca alboflavida	Soil saprotroph	Soil saprotroph	ND	
Naucoria bohemica	Pathotroph-Saprotroph-Symbiotroph; Bryophyte Parasite-Dung Saprotroph-	Ectomycorrhizal; short distance delicate	ND	

	Ectomycorrhizal-Fungal Parasite-Leaf Saprotroph-Plant Parasite-Undefined Saprotroph-Wood Saprotroph			
Naucoria sp-AK01	NA	Ectomycorrhizal; short distance delicate	NA	
Paxillus involutus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; long distance	Long distance	
Pholiota lurida	Pathotroph-Saprotroph; Dung Saprotroph-Plant Parasite-Soil Saprotroph-Undefined Saprotroph-Wood Saprotroph	Wood saprotroph	ND	
Pholiota mixta	Pathotroph-Saprotroph; Dung Saprotroph-Plant Parasite-Soil Saprotroph-Undefined Saprotroph-Wood Saprotroph	Wood saprotroph	ND	
Pluteus elaphinus	Pathotroph-Saprotroph; Bryophyte Parasite-Ectomycorrhizal-Litter Saprotroph-Wood Saprotroph	Litter saprotroph	ND	
Protostropharia alcis	Pathotroph-Saprotroph; Dung Saprotroph-Plant Parasite-Soil Saprotroph-Undefined Saprotroph-Wood Saprotroph	Dung saprotroph	ND	
Psathyrella borealis	Saprotroph; Dung Saprotroph-Plant Saprotroph-Wood Saprotroph	Wood saprotroph	ND	
Psathyrella fennoscandica	Saprotroph; Dung Saprotroph-Plant Saprotroph-Wood Saprotroph	Wood saprotroph	ND	
Psathyrella fibrillosa	Saprotroph; Dung Saprotroph-Plant Saprotroph-Wood Saprotroph	Wood saprotroph	ND	

Pseudoclitocybe cyathiformis-02	Pathotroph-Saprotroph-Symbiotroph; Bryophyte Parasite-Dung Saprotroph-Ectomycorrhizal-Fungal Parasite-Leaf Saprotroph-Plant Parasite-Undefined Saprotroph-Wood Saprotroph	Litter saprotroph	ND	
Rhodocollybia badiialba	Wood saprotroph	Litter saprotroph	ND	
Rhodocollybia butyracea	Wood saprotroph	Litter saprotroph	ND	
Russula betularum	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; contact	contact	
Russula claroflava	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; contact	medium distance smooth	
Russula decolorans	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; contact	Contact	
Russula serissima	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; contact	ND	
Russula nitida	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; contact	ND	
Russula paludosa	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; contact	Contact	
Russula pubescens	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; contact	ND	
Russula sp-AK01	NA	Ectomycorrhizal; contact	NA	
Russula viscida	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal; contact	Contact	
Stropharia caerulea	Pathotroph-Saprotroph; Dung Saprotroph-Plant Parasite-Soil Saprotroph-Undefined Saprotroph-Wood Saprotroph	Litter saprotroph	ND	
Stropharia hornemannii	Pathotroph-Saprotroph; Dung Saprotroph-Plant Parasite-Soil Saprotroph-Undefined Saprotroph-Wood Saprotroph	Litter saprotroph	ND	

Stropharia pseudocyanea	Pathotroph-Saprotroph; Dung Saprotroph-Plant Parasite-Soil Saprotroph-Undefined Saprotroph-Wood Saprotroph	Litter saprotroph	ND	
Tricholoma fulvum-IN01	NA	Ectomycorrhizal, medium distance fringe	ND	
Tricholoma stiparophyllum-AK01	NA	Ectomycorrhizal, medium distance fringe	ND	
Tubaria sp-AK01	NA	Litter saprotroph	NA	
Xerocomus ferrugineus	Symbiotroph, Ectomycorrhizal	Ectomycorrhizal, long distance	ND	

Additionally, one *Laccaria* sp-PA01 and *Galerina paludosa* not sampled for isotopic analysis

Table S2. The $\delta^{15}N$ of (a) white spruce needles from studies in 2016 and 2020, (b) bulk soil $\delta^{15}N$ in 2017 and 2020 from 1-20 m, and (c) soil ammonium $\delta^{15}N$ in 2017 and predicted soil ammonium $\delta^{15}N$ in 2020 from 1-6 m.

(a)

Year	White spruce $\delta^{15}N$	
	Salmon-enhanced bank	Salmon-depleted bank
2016	10.7 (1-5 m)	6.4 (1-5 m)
2020	8.9 (1-6 m)	5.4

(b)

Bulk soil $\delta^{15}N$			
Year	Distance	Salmon-enhanced bank	Salmon-depleted bank
2017	1	7.02	7.19
	3	9.17	7.8
	6	8.55	6.92
	10	8.14	7.27
	20	6.36	6.58
2020	1	9.15	9.43
	3	7.23	7.47
	6	7.25	5.92
	10	7.36	6.8
	20	4.07	4.47

(c)

Ammonium soil $\delta^{15}N$			
Year	Distance	Salmon-enhanced bank	Salmon-depleted bank
2017	1	11.32	9.93
	3	12.51	10.21
	6	11.73	6.69
	10	9.56	6.53
	20	6.25	7.16
2020 (predicted)	1	13.45	12.17
	3	10.57	9.88
	6	10.43	5.69
	10	8.78	6.06
	20	3.96	5.05

Table S3. Estimates of T_r(%), or %N in fungi that is transferred to plant hosts, at varying distances from the stream bank on both the salmon-enhanced and salmon-depleted sides. This model assumes that fungi are incorporating N from the soil ammonium pool. T_r(%) was calculated using the mean plant $\delta^{15}N$, mean mycorrhizal fungal $\delta^{15}N$, and predicted soil ammonium $\delta^{15}N$ based on values of bulk soil $\delta^{15}N$.

Distance from bank (m)	T_r(%)	
	Salmon-enhanced	Salmon-depleted
1-6	20	28
10	26	9
20	25	0
40	0	0
60	24	15
100	12	41

Table S4. Significant predictors from linear mixed models for EMF $\delta^{15}N$ for exploration types (long distance, medium distance fringe, medium distance smooth, and short distance) from 1-100 m away along three salmon streams in SW Alaska. Models include predictive R^2, all predictor variables, beta coefficient estimates ± SE, P values and VIF (variance inflation factor). All models included a random effect of transect nested within stream. GWC indicates gravimetric water content.

Response variable	Conditional R^2	Covariates	Value ± SE	P-value	VIF
Long distance EMF $\delta^{15}N$ (n = 39)	0.82	Intercept Carcass manipulation Ln(Distance)	19.57 ± 3.09 3.52 ± 1.67 -2.22 ± 0.38	0.01 0.04 < 0.001	NA 1.14 1.14
Medium distance fringe EMF $\delta^{15}N$ (n = 51)	0.30	Intercept Decomposing carcass Mineral soil $\delta^{15}N$	9.36 ± 0.41 4.62 ± 1.41 0.47 ± 0.23	< 0.001 0.002 0.05	NA 1.01 1.01
Medium distance smooth EMF $\delta^{15}N$ (n = 90)	0.69	Intercept Ln(distance) %N Carcass manipulation Organic soil GWC Organic soil $\delta^{15}N$ Mineral soil C:N	8.84 ± 1.02 -0.88 ± 0.23 -0.47 ± 0.24 2.86 ± 0.99 0.46 ± 0.18 0.53 ± 0.17 -0.17 ± 0.06	< 0.001 < 0.001 0.05 0.005 0.01 0.002 0.005	NA 1.80 1.02 2.08 1.93 2.17 1.37
Short distance EMF $\delta^{15}N$ (n = 31)	0.72	Intercept Ln(Distance) Organic soil $\delta^{15}N$	8.96 ± 0.72 -1.41 ± 0.24 0.44 ± 0.15	< 0.001 < 0.001 0.008	NA 1.31 1.31

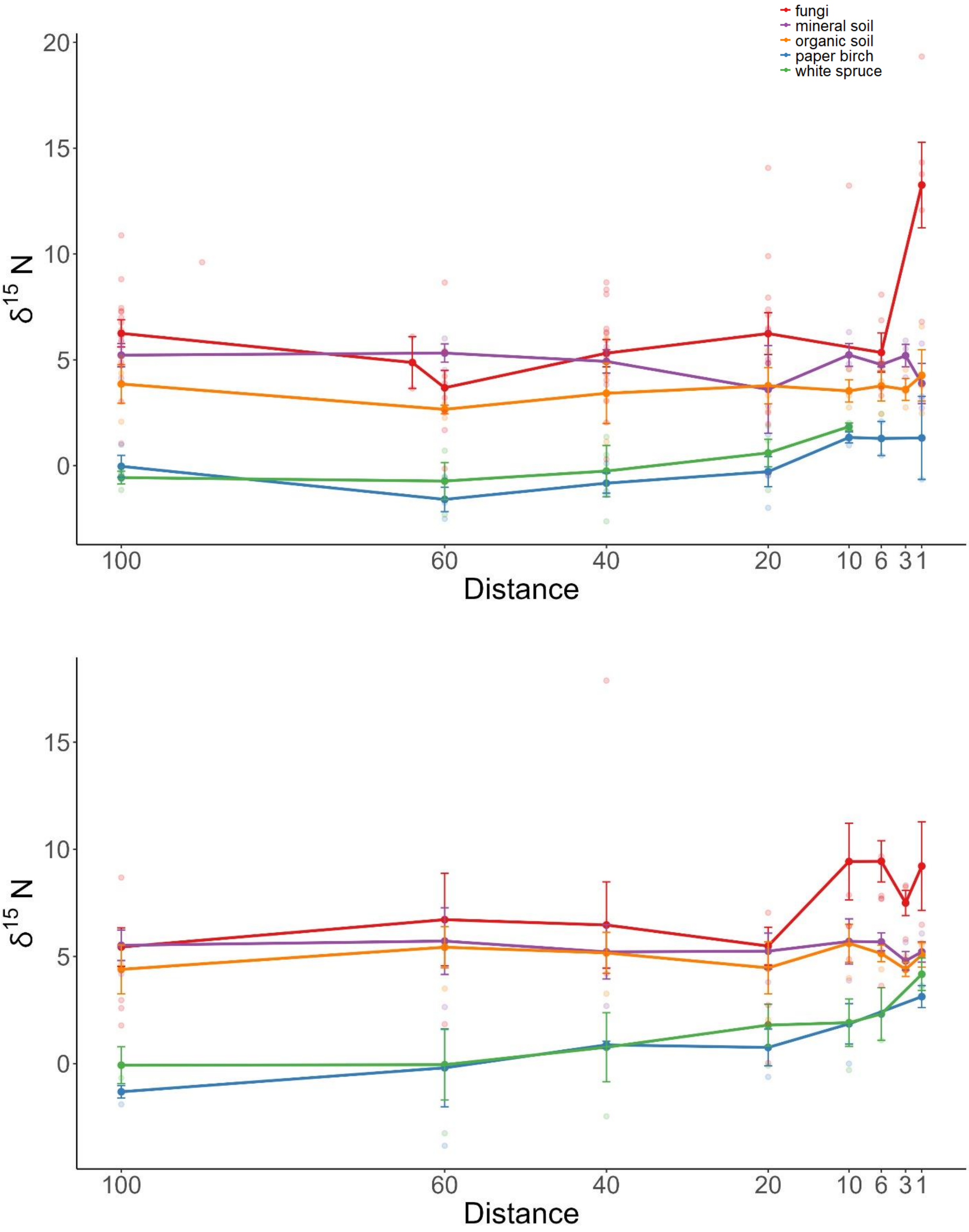


Figure S1. Mean values of δ^{15}N for fungal sporocarps, white spruce and paper birch foliage, and organic and mineral soil 1-100 m away from the bank of (a) Happy and (b) Yako Creek.

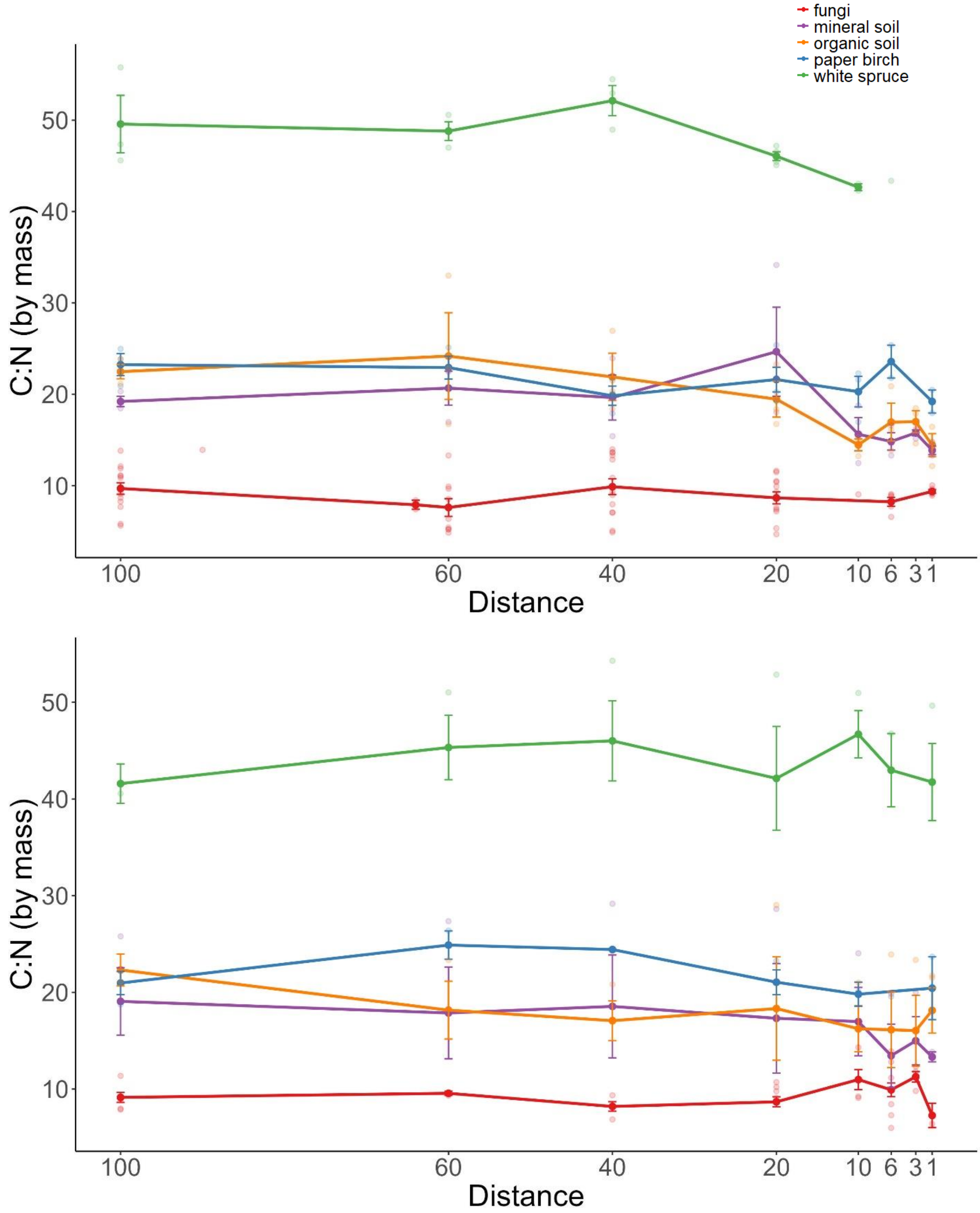


Figure S2. Mean values of C:N for fungal sporocarps, white spruce and paper birch foliage, and organic and mineral soil 1-100 m away from the bank of (a) Happy and (b) Yako Creek.

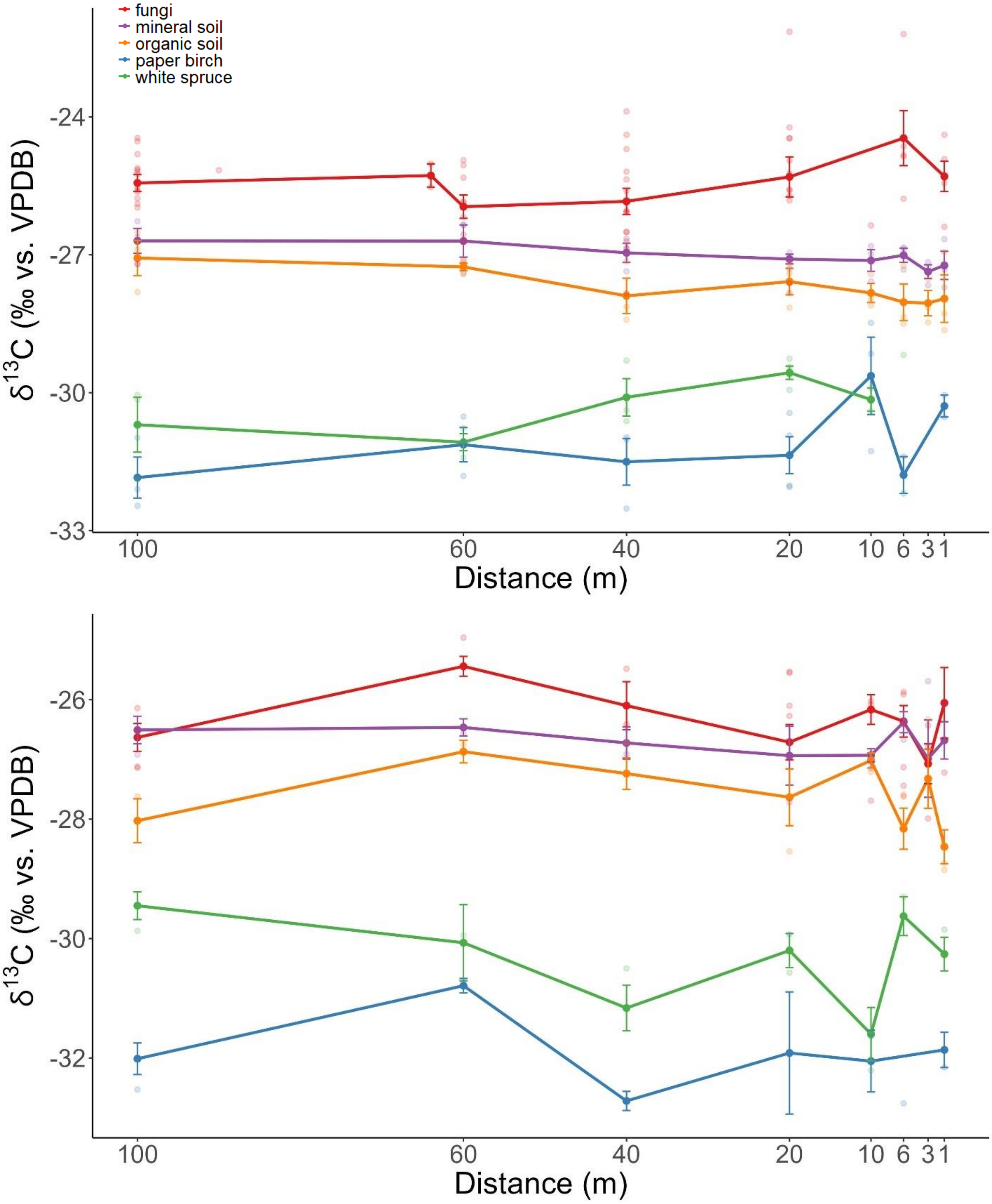
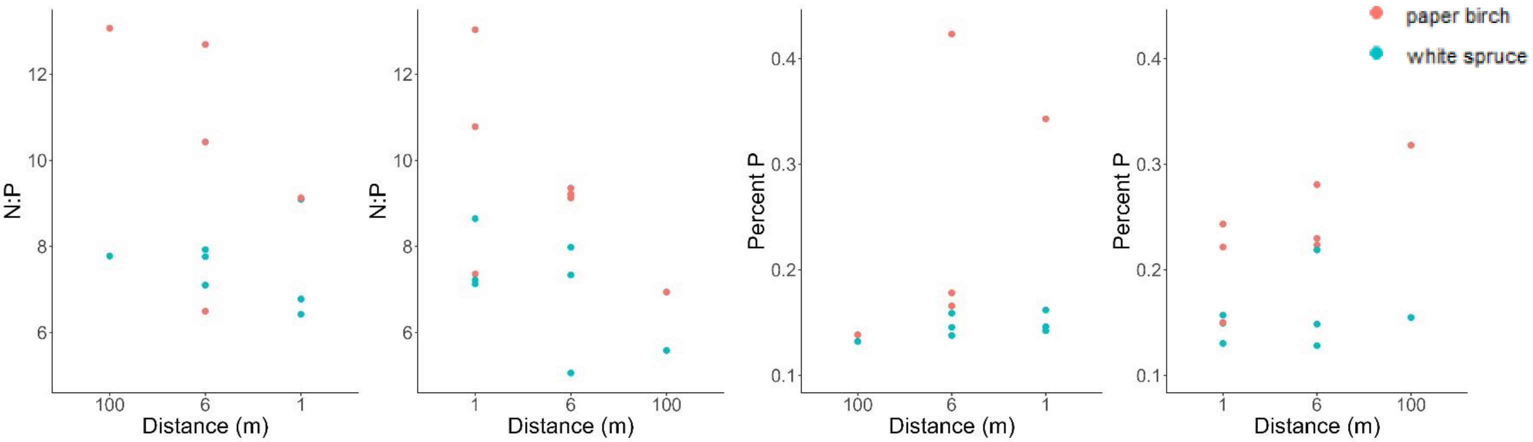
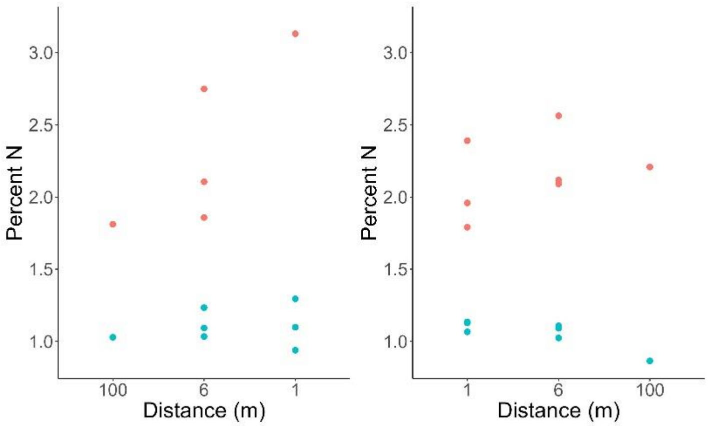


Figure S3. Mean values of δ^{13}C for fungal sporocarps, white spruce and paper birch foliage, and organic and mineral soil 1-100 m away from the bank of (a) Happy and (b) Yako Creek.



Salmon-enhanced Salmon-depleted Salmon-enhanced Salmon-depleted



Salmon-enhanced Salmon-depleted

Type	Transect	Side	Distance	%P	N:P	%N
Lactarius tabidus	S6	SL	6	0.382	13.13	5.02
Lactarius tabidus	S6	SR	1	0.528	7.74	4.09
Paxillus involutus	S4	SL	4	0.791	5.34	4.23
Paxillus involutus	S1	SR	10	0.694	6.91	4.8
organic soil	S4	SL	1	0.137	5.13	0.71
organic soil	S4	SL	100	0.081	16.16	1.3
organic soil	S4	SR	1	0.115	22	2.54

Figure S4. The %P, %N, and N:P values for paper birch, and white spruce samples at Hansen Creek from 1-6 m on both the salmon-enhanced (SL) and salmon-depleted (SR) banks, in addition to four ectomycorrhizal fungal sporocarps and three organic soil samples.

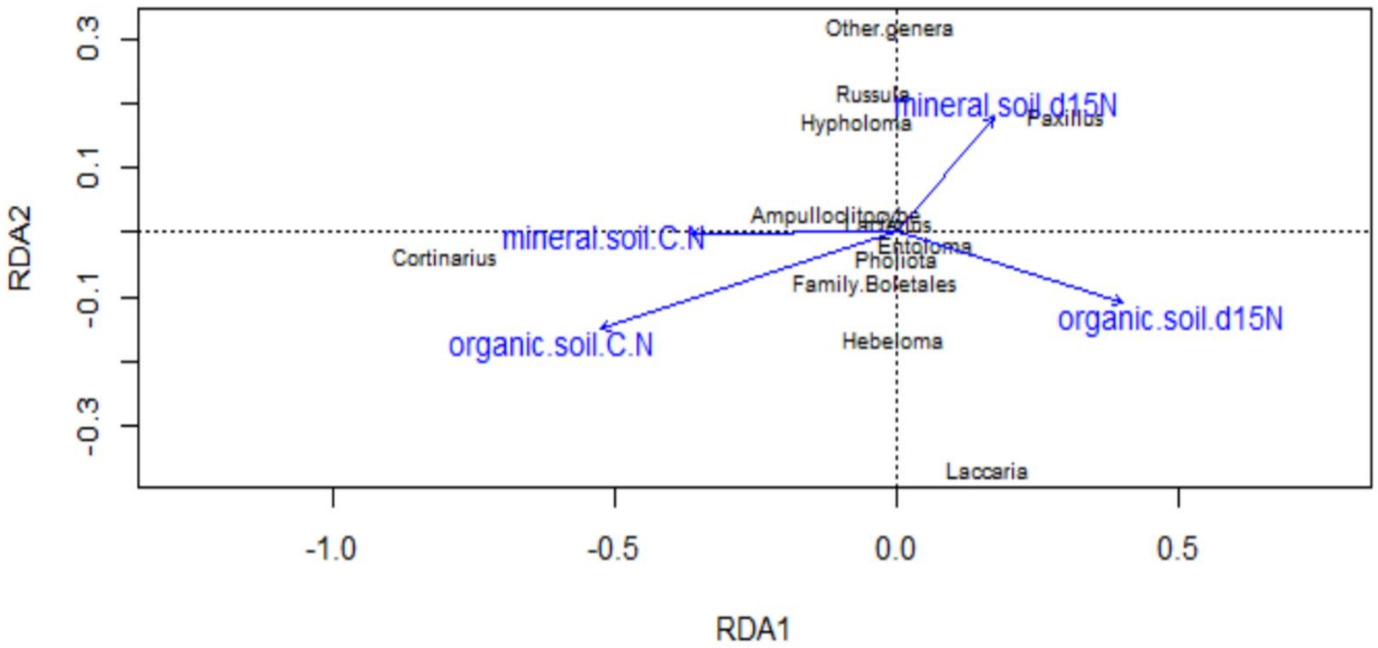


Figure S5. Correlation biplot based on redundancy analysis using the genus-level fungal community and environmental variables along a natural nitrogen gradient perpendicular to salmon streams in southwest Alaska. The first and second axes explain 54% and 27% of the species data, respectively. Lines represent environmental variables. The projection (perpendicular to the axis) from a genus or endpoint for an environmental variable to an axis indicates the correlation of that taxon with that axis. The correlation of a taxon with an environmental variable is shown by the projection from the taxon perpendicular to the line for the environmental variable.

Chapter 3: Salmon carcass effects on saprotrophic and ectomycorrhizal fungi in riparian soils of southwest Alaska

Abstract

Nutrient limitation plays a crucial role in structuring fungal community composition. Typically, plants reduce belowground carbon (C) flux to mycorrhizal fungi with increasing nutrient availability, but the type of nutrient limitation and the spatial distribution of nutrients can also influence belowground C allocation. We characterized fungal communities using metabarcoding along a natural nutrient gradient and in response to salmon carcass input near three salmon-bearing streams in southwest Alaska. A 21-year salmon carcass experiment annually removed all salmon carcasses from the stream and one bank and placed them on the opposite bank. This carcass manipulation decreased the relative abundance and species richness of ectomycorrhizal fungi (EMF) species differing in their spatial extent of exploration. Specifically, the medium-distance fringe group, particularly *Cortinarius,* declined on the salmon-enhanced bank, likely due to selection against C-demanding EMF with class II peroxidases under high N conditions. However, recent decomposing carcasses naturally placed by wildlife increased the relative abundance and diversity of medium-distance fringe, particularly *Cortinarius* species, and long-distance EMF. In systems such as salmon streams where nutrients are available but patchily distributed and occur in pulses, these EMF might predominate even at higher nutrient levels due to their strong ability to maintain large network structure, mine nutrient hotspots, and mobilize organically-bound N and P. These results also indicate that fungal communities are affected not only by the availability of nutrients, but also by their distribution in the environment, and the spatiotemporal scale of nutrient input is a driver of fungal community structure. Decomposing carcasses also increased the species richness and diversity of saprotrophic fungi, and these communities are likely associated with the decomposition of salmon carcasses. Responses of EMF to a natural N gradient along salmon streams varied widely within functional group and genera, indicating that the full suite of functional mechanisms underlying these responses are still underexplored, and additional traits must be characterized to better understand how

environmental conditions drive fungal community structure. Furthermore, we identified multiple nitrophilic EMF taxa that might be adapted to respond positively to anthropogenic N deposition.

Introduction

Growth-limiting resources are essential drivers of ecosystem structure and function because they limit ecosystem primary productive capacity (Klock et al. 2022). The migration of Pacific salmon (*Oncorhynchus* spp.) from marine to freshwater systems creates a significant flux of marine-derived nutrients (MDN) to terrestrial environments. These MDN are then consumed directly by animals or incorporated into the ecosystem carbon and nutrient cycles after decomposition (Holtgrieve et al. 2010, Minakawa et al. 2002, Field and Reynolds 2013, Larocque 2022). MDN in salmon carcasses include potentially important growth-limiting nutrients including nitrogen (N), phosphorus (P), magnesium (Mg), and calcium (Ca) that can significantly alter plant and animal community structure (Hocking and Reynolds 2011, Wagner and Reynolds 2019). For example, MDN can increase plant growth (Quinn et al. 2018) and reproductive allocation (Siemens et al. 2020), reduce plant diversity, and alter plant composition to increasingly nitrophilic and phylogenetically dispersed communities (Hocking and Reynolds 2011, Hurteau et al. 2016).

Although fungi have essential ecosystem roles as decomposers of complex organic materials that increase the availability of limiting nutrients to plants, little is known about MDN effects on fungi. Mycorrhizal fungi are critical in improving tree nutrition and soil C storage (Averill et al. 2016, Hawkins et al. 2023) by allowing plants to absorb nutrients released in the soil more efficiently or to convert non-soluble nutrients to available forms for their host plants (Northrup et al. 1995, Averill et al. 2014, Read et al. 2004). Therefore, their potential to mediate the long-term effects of MDN on plant communities is important to understand. In the only study to examine the effects of MDN on fungal communities, fungal species richness and diversity increased with higher salmon densities (Larocque 2022). Furthermore, fungi can quickly react to changes in environmental conditions and along environmental gradients, and are especially sensitive to changes in important limiting nutrients such as N (Zhao et al. 2020). Functional classifications based on feeding strategies (saprotrophic or mycorrhizal) or other functional traits such as hyphal properties and exploration strategies (Hobbie et al. 2014) allows for examining trait-based hypotheses (Nguyen et al. 2016, Zanne et al. 2020, Moeller et al 2014). While saprotrophic fungi typically increase in relative abundance with increasing soil nutrient levels

(Geng et al. 2023), long-term N addition has been shown to decrease N exchange between mycorrhizal fungi and plant hosts (Jach-Smith et al. 2020) and generally reduces mycorrhizal fungal biomass, richness, and diversity (Fierer 2017, Lilleskov et al. 2011, Treseder 2008), although effects vary strongly by functional groups (Lilleskov et al. 2024). In fact, nutrient availability and limitation play a critical role in driving mycorrhizal fungal community composition (Moeller et al. 2014), and distinct communities of ectomycorrhizal fungi (EMF) are associated with variable functional capabilities such as hyphal properties and exploration strategies (Hobbie et al. 2014). In environments with low N or low P, where these nutrients are rare or patchy, EMF with long-distance exploration types are preferred by plant hosts, as species in this functional group exhibit long-distance transport structures and large amounts of extraradical hyphae that allow them to forage over large distances and exploit nutrient patches (Moeller et al. 2014). These fungal taxa also have strong enzymatic capabilities to break down and acquire organic N, thus increasing accessible N pools (Hobbie and Agerer 2010). Similar to long-distance types, medium-fringe type EMF have hydrophobic hyphae, high hyphal density, and extensive capacity for organic N use. Unlike medium-distance fringe types, medium-distance smooth type EMF have hydrophilic exploration types with less abundant rhizomorphic structure and limited organic N mining capabilities (Lilleskov et al. 2011). Medium-distance smooth type EMF are selectively dominant with increasing nutrient availability, in addition to EMF with much less energy intensive exploration strategies such as short distance and contact foragers (Moeller et al. 2014). Relative to other types, short-distance and contact EMF typically forage over small areas, have less C intensive exploration strategies, and are favored under conditions of low belowground C allocation and high nutrient environments (Nara 2015).

Although altering soil N availability has direct consequences for EMF community composition and relative abundance, the specific mechanisms by which these effects take place are still poorly understood (Lilleskov et al. 2019) and these functional groups are not well characterized (Hobbie et al. 2019). For example, the response of mycorrhizal fungi to increasing soil nutrient levels has been shown to vary not just among, but also within functional groups. For example, although some long-distance species such as the nitrophobic *Suillus bovinus* decline with increasing soil N, other long-distance species such as the nitrophilic *Paxillus involutus* are specialized for P acquisition under high N, low P conditions and increase with soil N levels in conditions where P becomes limiting (Lilleskov et al. 2024). This indicates that additional functional traits must be considered to fully understand responses to nutrient availability. Furthermore, the spatiotemporal distribution of nutrients can also drive changes in fungal community composition. Typically, as overall nutrient availability increases, long-distance and medium-distance fringe type mycorrhizal fungi decrease in relative abundance and richness as plants decrease belowground C flux (Lilleskov et al. 2011, Kutorga et al. 2013, Jach-Smith et al. 2020). However, in systems where nutrients are available but patchily distributed or where nutrient input occurs in pulses such as riparian zones along salmon streams, these functional groups might increase in relative abundance and richness due to their ability to maintain large network structures and mobilize organic N, making them more efficient at mining nutrient hotspots than plant roots (Moeller and Neubert 2015). In addition, increased soil N availability due to anthropogenic factors such as N pollution is causing the global decline of functionally related EMF taxa with long-distance exploration types (Lilleskov et al. 2011). DNA-based molecular tools can provide us with new insights concerning the diversity of these fungal communities to help us better assess the implications of losing them for fungal conservation biology and ecosystem function.

Salmon streams with recurring annual spawning salmon runs typically create a long-term natural, decreasing N gradient away from the stream edge due to continual annual input of salmon-derived N over millennia (Feddern et al. 2019). However, other factors also contribute to this N gradient, as N cycling generally decreases with distance from stream and with slope due to changes in soil water content and drainage, and N fixed uphill will migrate down to the streams over time (Hogberg 1997, Kirchoff 2003). This natural N gradient is especially prevalent in streams within boreal forests and likely associated with EMF communities adapted to variable levels of soil N. However, research has not characterized how the abundance, diversity, and associated functional traits of these communities shift with increasing N availability along a continuous N gradient. With such research, we could characterize EMF functional groups associated with higher soil N levels that will respond positively to pulses of anthropogenic N enrichment. In addition, although fungal taxa associated with carcasses of some species such as pigs and humans have been studied (Procopio et al. 2020, Metcalf et al. 2015), unique fungal taxa associated with salmon carcasses have never been characterized. Salmon runs are declining in many parts of the world, likely negatively affecting salmon carcass-adapted fungal taxa in the riparian zone. Characterizing these fungal taxa and their functional roles near streams with high populations of spawning salmon could serve as a reference system to better identify these potentially declining and threatened EMF communities in other regions, such as the Pacific Northwest, where salmon runs are decreasing or no longer present.

This study examined fungal communities along three salmon streams located in a southwest Alaskan boreal forest. At all streams, the natural soil C:N ratio increased with increasing distance from the stream bank, and wildlife had recently deposited multiple decomposing salmon carcasses 1-10 m from the stream bank. One of the streams, Hansen Creek, represents a unique site with an unprecedented in-situ nutrient manipulation experiment. For 21 years (1997-2018), all dead salmon were removed from the stream and from one bank and thrown onto the opposite bank of the creek to avoid double-counting during stream surveys. This experiment deposited 200,000 kg of salmon on one side of the creek but not the other, creating a large nutrient fertilization experiment (Quinn et al. 2018). Our objectives were to characterize the response of fungal relative abundance, species richness, species diversity, and community structure to (a) the long-term, large-scale carcass manipulation experiment, (b) single, decomposing carcasses recently placed by wildlife along stream banks, and (c) to a natural N gradient away from the stream edge along the three salmon streams. We examined responses of fungal trophic guilds, EMF functional groups, and individual fungal genera separately. Since the carcass manipulation deposited considerably higher N than critical N loads associated with changes in fungal community structure (Lilleskov et al. 2024), we hypothesized that (H1) community composition would shift in response to the carcass manipulation. We also hypothesized that (H2) higher soil N levels from both MDN and along the N gradient would increase the relative abundance, richness, and diversity of saprotrophic fungi but (H3) decrease the overall relative abundance, richness, and diversity of nitrophobic long-distance and medium-distance fringe EMF. However, we also hypothesized that (H4) nitrophilic long-distance and medium-distance fringe EMF would increase in relative abundance with salmon carcass input due to the increased capacity of these functional guilds to access organic N and mine nutrient hotspots created by salmon carcasses.

Methods

Site description - This study was conducted at three salmon streams – Hansen Creek, Happy Creek, and Yako Creek - that flow into Lake Aleknagik, located within the Wood River System north of Bristol Bay, southwest Alaska (Figure 1a). A boreal forest surrounds the streams, where white spruce (*Picea glauca*) and paper birch (*Betula papyrifera*) are codominant. Other vegetation includes willow (*Salix* spp.), cottongrass (*Eriophorum* spp.), bracken fern (*Pteridium aquilinum*), horsetail (*Equisetum arvense*), fireweed (*Chamerion angustifolium*), and dwarf birch (*Betula nana*), found closer to the stream edge, and *Vaccinium* species, mosses and heather (*Harrimanella stelleriana*), found further away from the steam edge (Figure 1b). Although green alder (*Alnus crispa*) was present at Happy Creek, we did not record green alder at sampling sites for Hansen or Yako Creek, which would contribute N through the symbiotic fixation of atmospheric N_2 and makes it more difficult to trace MDN in riparian systems (Helfield and Naiman 2002). Hansen Creek was the site of a 21-year salmon carcass fertilization experiment, described both in Quinn et al. (2018) and Feddern et al. (2019). From 1997 to 2018, daily stream surveys were conducted during the entirety of the annual sockeye salmon run (approximately July 20 – August 20). During these surveys, all dead salmon in the creek and on the right stream bank up to 5 m were thrown onto the left stream bank. In addition, all salmon on the left bank were moved to a distance of about 3-6 m to avoid double-counting. As a result, almost all salmon carcasses at Hansen Creek were located roughly 3-6 m from the left bank of the stream, except for those relocated by wildlife and the salmon present following the end of stream surveys. This led to a decrease in salmon carcass density on the right side of the stream and an increase in salmon carcass density on the left side. Before the manipulation began in 1997, each bank of Hansen Creek received an average of 4,500 kg of salmon annually over an area of 1.2 ha (assuming an area 6 m wide by 2 km long), while after the manipulation began, the left bank received almost 10 times more salmon carcasses than the right bank, averaging 13,400 kg of salmon while the right bank averaged 2,300 kg of salmon annually (due to some live salmon still present on the last survey date, which were assigned evenly between both banks; Quinn et al. 2018). Over the entire 20-year period, about 268,000 kg of salmon were moved to the left bank of Hansen Creek, equating to 8,000 kg of N and 1,400 kg of P, or 317 kg N/ha/year and 56 P/ha/year (Quinn et al. 2018, Feddern et al. 2019). After the cessation of the manipulations natural rates of salmon input were re-established. We observed multiple decomposing salmon carcasses that were presumably deposited recently by wildlife along all three streams.

Sample collection and processing - At Hansen Creek, three sets of paired transects were established (one transect on the left bank and one transect on the opposing right bank) for a total of 6 transects perpendicular to the stream bank. At Happy and Yako Creeks, three transects were established for each creek. Transects covered the lower, middle, and upper sections of the stream, and were selected to represent typical riparian vegetation (primarily white spruce and paper birch) and a high annual input of salmon carcasses. At each transect, sampling points were established at 1, 3, 6, 10, 20, 40, 60, and 100 meters from the edge of the active channel. At each sampling location, we collected a soil sample from the Oe horizon at 10 cm deep, and from the Ah horizon at 25 cm deep (USDA 2022). Gravimetric soil water content (g H_2O/g dry soil) was determined by drying 50-100 g of field-moist soil at 105°C for 48 hours (Gardner 1986). All soil samples were frozen at -20 °C and transported in a high-grade cooler to the University of Washington.

Molecular analysis –The PowerSoil Pro DNA Extraction Kit (Qiagen, Benelux BV) was used to extract DNA from 5 mg of moist soil from the Oe layer at each sampling location. The concentration of DNA was quantified using a Qubit 4 Fluorometer (Invitrogen, Carlsbad, California, USA) and the Qubit dsDNA HS assay kit (Thermo Fisher Scientific Inc, Wilmington, DE, USA). DNA amplicon sequencing was conducted at the University of Oregon Genomics Laboratory according to Caporaso et al. 2012. Polymerase chain reaction (PCR) amplification utilized the ITS2 and ITS1-F primers (White et al. 1990) targeting the fungal ITS1 region. Primers were fitted with Illumina adaptors, samples were pooled into equimolar portions and sequenced on an Illumina MiSeq platform using a 2 x 250 bp chemistry.

Bioinformatics – Raw reads were trimmed from adaptors using CUTADAPT (Martin 2011), and the DADA2 pipeline was then used to filter (maximum expected errors: 2, minimum length: 500 bp) and dereplicate the reads, trim low-quality sequences, merge paired-ends, and remove chimeras (Callahan et al. 2016). The parameters maxEE = 4, 6 and truncLen = 270, 250, and minOverlap = 50 were used for ITS regions. The resulting amplicon sequence variants (ASVs) were clustered by 97% similarity with the R package DECIPHER (v. 2.16.1), and a naïve Bayesian classifier from the ribosomal database project RDP (Wang et al. 2007) was used to assign taxonomy based on the UNITE database (Nilsson et al. 2019). Metabarcoding data were analyzed using the Phyloseq package in R. Funguild (Nguyen et al. 2016) was used to assign trophic status and exploration types to fungal taxa, with only guild confidence rankings of "highly probable" and "probable" used for guild assignment. For genera categorized as mixed trophic strategies such as *Entoloma, Oidiodendron, Sistotrema,* and *Cadophora,* trophic strategy was assigned for individual species (Brandrud et al. 2018).

Statistical Analysis – A set of generalized linear mixed effect models was implemented to examine the effect of environmental variables on fungal community metrics by trophic guild, EMF functional group, and individual EMF genera. The first set of models examined environmental effects on the relative abundance, species richness, and species diversity of saprotrophic and symbiotoph fungal trophic guilds. The second set of models examined environmental effects on the relative abundance, richness, and diversity of EMF functional guilds, consisting of short-distance, medium-distance fringe, medium-distance smooth, and long-distance functional types (Table 1, Table S6). The third set of models examined environmental effects on the relative abundance of individual EMF genera. Negative binomial generalized linear mixed models were used for species richness and linear mixed effects models were used for relative abundance and Shannon's diversity index response variables. Covariates included organic soil C:N ratio, mineral soil C:N ratio, organic soil gravimetric water content, organic soil pH, the presence of a nearby decomposing carcass < 1 m from the sampling location (as salmon N can be found up to 1 m away from decomposing carcasses, Drake et al. 2005), the carcass manipulation (represented as a binary variable with presence from 1-6 m on the salmon-enhanced bank of Hansen Creek), presence of a slope > 10° (as a binary variable using visual field observations), distance from the stream bank, and plant community composition. Plant communities were recorded as the presence of tree, shrub, herb, and moss species in the 5 m radius (25π m^2) surrounding the soil sampling location. Due to the high species diversity, multiple correspondence analysis was used to represent the data as points in a low-dimensional space and the first five vectors representing 60% of the explained variance were used as predictor variables in all models (Figure S4). A full list of plant species is in Table S4. A random effect of transect nested within stream was included for all models. Stepwise AIC model selection was used to select the best fitting model. Species indicator analysis was used to identify indicator species associated with the carcass manipulation and the presence of a nearby decomposing carcass using the indicspecies package in R (Table S5; Cáceres and Legendre 2009). Threshold Indicator Taxa Analysis (TITAN) using the TITAN2 package in R (Baker and King 2010) was implemented to identify the responses of individual fungal taxa to changes in organic soil C:N ratio (Figure 4).

To examine the effect of the carcass manipulation on fungal community structure, the matrices of the pairwise taxonomic distance (Bray-Curtis) were calculated. Correlations between fungal community composition and environmental variables were evaluated using Mantel tests and the Bray-Curtis dissimilarity metric using the R package ecodist (Goslee and Dean 2007). The significance of environmental variables on fungal community composition was evaluated with analysis of variance using distance matrices within the adonis2 function in the R package vegan (Oksanen et al. 2016). Redundancy analysis (RDA) was conducted with forward selection of the explanatory variables.

Results

Overall fungal community composition - We identified a total of 8754 fungal ASVs. Of these, 4155 were identified to species (classified maximally), 5583 to genus, 6217 to family, and 8045 to phylum. The identified ASVs included 10 phyla, 154 families, and 308 genera, and 532 species. Dominant phyla consisted of *Basidiomycota*, *Mortierellomycota*, and *Ascomycota*, with an average relative abundance of 67%, 18%, and 11% across all samples. Importantly, *Ascomycota* can be undersampled in the ITS1 region due to group 1 introns (Bellemain et al. 2010). The top ten most abundant genera were *Mortierella* (19%), *Russula* (13%), *Laccaria* (9%), *Inocybe* (8%), *Tylospora* (7%), *Cortinarius* (6%), *Solicoccozyma* (5%), *Lactarius* (3%), *Tomentella* (2%), and *Naucoria* (2%), which constituted 84% of all sequences, indicating dominance of symbiotrophs (specifically EMF), relative to saprotrophic fungi (45% and 9% of total abundance, respectively). Within EMF, short-distance exploration types dominated (42% of total abundance).

Effects of carcass input on fungal communities - Fungal community composition significantly differed between the banks of Hansen Creek due to the carcass experiment ($p = 0.05$, $R^2 = 0.13$, Figure S1). The carcass manipulation specifically reduced the relative abundance and species richness of medium-distance fringe EMF (Table 1, Table S6, Figure 2a). When examining the effect of carcass input by genera, the carcass manipulation increased the relative abundance of *Boletus*, *Tomentella, Thelephora, Tylospora, Meliniomyces*, and *Alnicola,* and decreased the relative abundance of *Cortinarius* and *Clavulina.* Species indicator analysis identified seven species associated with the carcass manipulation (Table S5a). Nearby decomposing carcasses increased the relative abundance of long-distance exploration type fungi and the species diversity of medium-distance fringe EMF (Figure 2b). When examining the effect of carcass input by genera, nearby decomposing carcasses increased the relative abundance of *Paxillus, Xerocomus, Piloderma, Sistotrema, Hydnum, Geopora,* and *Helvellosebacina,* and decreased the relative abundance of *Trichophaea* and *Hebeloma.* Species indicator analysis identified ten species associated with the presence of a nearby decomposing carcass (Table S5a). Nearby decomposing carcasses also increased the richness and diversity of saprotrophic fungi (Figure 3), and we identified 35 genera (Table 2) and 51 species of saprotrophic fungi that were only found nearby decomposing carcasses, including multiple saprotrophic *Entoloma* and *Mortierella* species (Table S1, Table S5a).

Fungal communities along soil N gradients - Both saprotrophic and symbiotrophic species richness and diversity increased with organic soil C:N ratio and decreased with mineral soil C:N ratio (Table 2). For symbiotrophs, medium-distance fringe EMF increased in relative abundance and species richness, whereas long distance EMF increased in relative abundance, with organic soil C:N ratio (Table 2). However, in TITAN analysis, responses to soil C:N ratio varied considerably within functional group and even within genera by species, indicating considerable interspecific variation in strategy within genera (Figure 4). Multiple EMF species increased and decreased in relative abundance with increasing soil N availability (Figure 4A). Many *Cortinarius* species increased with organic soil C:N ratio, but *Cortinarius caninus* decreased with organic soil C:N ratio (Table 4). While *Russula favrei* increased with lower soil C:N ratio, *Russula suecica, Russula paludosa, Russula consobrina,* and *Russula claroflava* increased in relative abundance with higher soil C:N ratio (Table 4). *Lactarius rufus* and *Lactarius atroviridis* increased with higher soil C:N ratio while *Lactarius necator* and *Lactarius glyciosmus* decreased with higher soil C:N ratio (Table 4). Many *Entoloma* species, both symbiotrophic and saprotrophic species, increased in relative abundance with higher soil N (Table 4). The relative abundance of long-distance EMF types *Paxillus involutus* and *Alpova corsicus* decreased with organic soil C:N ratio (Figure 4).

White spruce and paper birch N:P – White spruce and paper birch N:P was not significantly different between the salmon-enhanced and salmon-depleted banks at Hansen Creek for 1-6 m (t-test, $p = 0.3$ and $p = 0.5$, respectively; Figure S2). In addition, mean white spruce N:P (7.3 ± 1.1) and mean white spruce %N (1.08 ± 0.11) at Hansen Creek from 1-6 m suggested that N was limiting to white spruce growth, while mean %P (0.15 ± 0.02) indicated mostly sufficient P for white spruce (Carter 1992, Güsewell et al. 2004; Figure S2). Mean white spruce %N (1.06 ±0.14) from 1-100 m at Hansen Creek further confirmed that N was the primary limiting nutrient to white spruce growth (Carter 1992, Figure S2). Values for paper birch %N that indicate N limitation vary widely from 1.24 – 3% N, with a mean of 2.12 %N (Keski-Saari and Julkunen-Tiitto 2003, Wang et al. 1998). Mean paper birch %N (2.18 ± 0.31) from 1-100 m at Hansen Creek (Figure S2) indicated that paper birch is somewhat limited by N. Paper birch N:P (9.8 ± 2.3) from 1-6 m at Hansen Creek suggested potential co-limitation of N and P (Güsewell et al. 2004; Figure S2).

Discussion

Effects of carcass manipulation on fungi – In agreement with hypothesis H1, fungal community composition significantly differed between the banks of Hansen Creek due to the carcass experiment ($p = 0.05$, $R^2 = 0.13$, Figure S1), where salmon carcasses were deposited for 21 years during the salmon manipulation experiment. Medium-distance fringe EMF (Table 1, Table S6) had significantly lower relative abundance and species richness from 1-6 m on the salmon-enhanced bank than the salmon-depleted stream bank at Hansen Creek (Figure 2a), suggesting that the long-term carcass manipulation negatively affected these EMF types in this system and supporting hypothesis H3. Medium-distance fringe exploration types are consistently the most N-sensitive EMF functional group and typically decline in relative abundance and richness with N fertilization (Lilleskov et al. 2019), and this manipulation added an amount of N that far exceeds the amounts typically used in fertilization experiments. These fungi are characterized by large amounts of extraradical hyphae connected by hydrophobic rhizomorphs and some species possess oxidative enzymes that include but are not limited to class II peroxidases, alongside hydrolytic enzymes such as proteases, that are all hypothesized to be important enzymes for organic N mobilization (Agerer 2001, Lilleskov et al. 2011, Lindahl and Tunlid 2015). The ability of these fungi to acquire organic N could explain the functional shift away from these fungi under high N availability, as plants would decrease C allocation to these more C-demanding fungal partners and replace them with shorter-distance exploration types with lower C cost (Lilleskov et al. 2024), or access soil nutrients directly with their roots (Jach-Smith et al. 2020). When we examined the effects of the carcass manipulation by genus, many *Cortinarius* species declined in relative abundance with the carcass manipulation (Table S2). Peroxidase genes are common in *Cortinarius* species (Bödeker et al. 2014), a nitrophobic and N-sensitive genus (Lilleskov et al. 2024). The carcass experiment was halted in 2018, two years before this study, indicating that these changes in fungal community composition can continue for years. In many studies, the legacy of N deposition persists for years after fertilization levels are reduced or removed due to plant-soil microbe-soil feedbacks and acidification, and recovery of EMF communities occurs very slowly following N fertilization, with estimates ranging from 14-47 years (Lilleskov et al. 2024).

Effects of decomposing carcasses on fungi - In contrast with the long-term effect of the carcass manipulations at Hansen Creek, nearby decomposing carcasses increased the relative abundance of long-distance exploration type fungi and the species diversity of medium-distance fringe EMF (Figure 2b), which was not supported by hypothesis H3. For example, the genera *Piloderma* and *Sistotrema* increased in relative abundance with the presence of decomposing carcasses (Table S2). Multiple medium-distance species were found only at sites with decomposing carcasses, especially from *Cortinarius* (Table S1). In species indicator analysis, *Cortinarius casimiri* was significantly associated with the presence of decomposing carcasses (Table S5a). This is particularly striking as long-term carcass deposition from the manipulation experiment significantly decreased the relative abundance of *Cortinarius*. This suggests that the spatial and temporal scale of salmon carcass placement had opposite effects on the response of this fungal genera, where the large-scale, long-term nutrient fertilization from the carcass experiment decreased the relative abundance of *Cortinarius* species, while the small-scale, short-term nutrient input from single decomposing carcasses increased the relative abundance of

Cortinarius species. Long-distance and medium-distance fringe exploration type fungi form rhizomorphs, which are long-distance transport structures, and large amounts of extraradical, hydrophobic hyphae, which allows for nutrient foraging over large distances and exploiting nutrient patches. Furthermore, these fungi have hydrophobic hyphae prevent leakage of solutes during transport (Moeller et al. 2014, Lilleskov et al. 2024). Therefore, these functional groups are typically competitively dominant in environments where resources are rare or patchy (Moeller et al. 2014). We hypothesize that the increased relative abundance and diversity of long-distance and medium-distance fringe foragers at sites of recently decomposing carcasses may be because these fungi are particularly well suited to the spatial and temporal heterogeneity created by salmon inputs, due to their morphology and ability to maintain extensive network structure effective at mining patchily-distributed nutrient hotspots deposited in pulses (Moeller and Neubert 2015). This subsequently increases the ability of plant hosts to access nutrients from nearby decomposing carcasses. Furthermore, foliar analysis indicated that white spruce were N-limited and paper birch were likely co-limited by N and P at these sites (Figure 3, Figure S4). Therefore, we hypothesize that plant hosts could increase C allocation to long-distance and medium-distance fringe foragers near decomposing carcasses to efficiently acquire resources from these nutrient patches. Salmon carcasses also contain other important nutrients such as P, Mg, and Ca (Wagner and Reynolds 2019), and we hypothesize that long-distance and medium-distance foragers might be particularly effective at increasing plant access to a diversity of nutrients besides N due to their extensive network structure and ability to mine nutrient hotspots.

The long-distance fungal species *Paxillus involutus* increased in relative abundance with the presence of a decomposing salmon carcass (Table 1, Figure 2b, Table S2). This species is believed to be specialized for P uptake under high-N and low-P conditions (Lilleskov et al. 2024), and the average C:N ratio (< 20) near the bank at all three streams suggests relatively high N availability close to the banks of these streams, where decomposing carcasses were found (Feddern et al. 2019). This could indicate increasing limitation near the stream bank by P, another essential nutrient for plants and fungi (Plassard and Dell 2010). White spruce was N limited at these sites, while paper birch was potential co-limited by N and P (Figure S2; Table S3). Furthermore, organic soils were highly acidic across all streams (soil pH = 4.2 ± 0.5), which typically reduces P availability as P complexes with aluminum and iron (Rahman et al. 2018). However, *Equisetum*, which was present at 35% of the sites, has deep roots that act as nutrient pumps and transport P to the surface of the soil where plants and microbes can access these nutrients (Husby 2013), which might alleviate P limitation to some degree. Overall, these sites were potentially characterized by co-limitation of N and P. This was supported by the presence of fungal species specialized for both N uptake (some *Cortinarius* species) and P uptake (*Paxillus involutus* and *Alpova corsicus*). Therefore, it is possible that plants increase C allocation to long-distance foragers such as *Paxillus involutus* to access P from decomposing carcasses. In fact, both nitrophilic taxa such as *Paxillus* and nitrophobic taxa such as *Cortinarius* (Plassard et al. 2011) have high rates of organic acid production, which mobilizes inorganic and organic P (Lambers et al. 2006). This further supports that these genera might be particularly effective at mobilizing P from carcasses.

Nearby decomposing carcasses also increased the richness and diversity of saprotrophic fungi (Figure 3). Saprotrophic fungi can effectively break down organic matter and readily decompose carcasses (Metcalf et al. 2015). Although fungal communities associated with carcasses have been examined for pigs, mice, human cadavers, and other mammals (Metcalf et a. 2015, Procopio et al. 2020, Sagara et al. 2008, Sagara 1976), unique fungal taxa associated with salmon carcasses have never been studied with modern molecular methods. Here, 35 genera (Table 2) and 51 species of saprotrophic fungi were only found near decomposing carcasses, including multiple saprotrophic *Entoloma* and *Mortierella* species (Table S1, Table S5a). These fungi might be associated with salmon carcass decomposition.

Fungal taxa response to a gradient of organic soil C:N ratio – Both saprotrophic and symbiotrophic species richness and diversity increased with organic soil C:N ratio and decreased with mineral soil C:N ratio (Table 2). For symbiotrophs, medium-distance fringe EMF increased in relative abundance and species richness, whereas long distance EMF increased in relative abundance, with organic soil C:N ratio (Table 2). However, in TITAN analysis, responses to soil C:N ratio varied considerably within functional group and even within genera by species, indicating considerable interspecific variation in strategy within genera (Figure 4). For example, while many *Cortinarius* species increased with organic soil C:N ratio, *Cortinarius caninus* decreased with organic soil C:N ratio. *Cortinarius* species are one of the most N-sensitive genera (Lilleskov et al. 2019), and most *Cortinarius* species decreased with higher organic soil C:N ratio (Figure 4A, Table S2). Many *Cortinarius* species possess oxidative and hydrolytic enzymes such as peroxidases that can mobilize organically-bound N (Bödeker et al. 2014). The high sensitivity of *Cortinarius* to N fertilization might be due to the selection against EMF that can mobilize organic N under high N conditions, although it is unclear whether the mechanism underlying this selection is due to changes in host allocation, host selection, or soil-mediated direct effects (Lilleskov et al. 2024). *Cortinarius* species vary in their sensitivity to N deposition, which may relate to peroxidase activity. The relative abundance of *Cortinarius caninus* increases with decreasing soil C:N ratio, but its peroxidase activity is unknown. However, our results suggest that *Cortinarius caninus* could potentially have fewer peroxidase copy numbers or lower peroxidase activity than other *Cortinarius* species.

Russula species differ widely in their sensitivity to N (Lilleskov et al. 2011, Van der Linde et al. 2018), and our results showed variable responses of *Russula* species to soil C:N ratio. While *Russula favrei* increased with lower soil C:N ratio, *Russula suecica*, *Russula paludosa*, *Russula consobrina*, and *Russula claroflava* increased in relative abundance with higher soil C:N ratio, indicating potential N sensitivity for these species. Some *Russula* species have retained peroxidase genes (Looney et al. 2022), and these four species could be candidates for some retention of peroxidase genes due to their response to N. Surprisingly, although *Russula consobrina* is a member of a nitrophilic group of *Russula* (Avis 2012) and was associated with sites with decomposing carcasses (Table S5a), the species decreased with higher soil N levels along a gradient (Figure 4). Therefore, for this species, the effects of nutrients from carcasses and soil N along a gradient had opposing effects on relative abundance. Although *Lactarius* is generally considered nitrophilic (Moeller et al. 2015, Lilleskov et al. 2019), *Lactarius* species have variable responses to elevated N. Here, *Lactarius rufus* and *Lactarius atroviridis* increased with higher soil C:N ratio while *Lactarius necator* and *Lactarius glyciosmus* decreased with higher soil C:N ratio, suggesting that the former *Lactarius* species are N-sensitive while the latter species are N-tolerant. Interestingly, *Lactarius rufus* was significantly associated with sites nearby decomposing carcasses (Table S5a), similar to *Russula consobrina,* although *Lactarius rufus* varies in its response to N (Lilleskov et al. 2011). Little is known about the response of *Entoloma* to N fertilization. Here, many *Entoloma* species, both symbiotrophic and saprotrophic species, increased in relative abundance with higher soil N, indicating that this genus might be relatively N-tolerant (Table 4). Its very high N concentrations in sporocarps (roughly twice that of co-occurring genera) (Chen et al. 2019) suggests that its N demand must be quite high. In this study, multiple EMF species increased in relative abundance with increasing soil N availability (Figure 4A), indicating that these species might be adapted to respond positively to anthropogenic N enrichment. Further study is required to better understand the functional attributes of these N-tolerant species. Overall, there was a large variability in response to increasing soil N not only within functional group, but within genera, indicating that the functional mechanisms underlying these responses are still imperfectly understood and underexplored.

The relative abundance of long-distance EMF types *Paxillus involutus* and *Alpova corsicus* decreased with organic soil C:N ratio (Figure 4A). Although some groups of long-distance EMF such as *Suillus* species are highly sensitive to N deposition, others such as *Paxillus involutus* and *Alpova corsicus* are nitrophilic species that increase with higher soil N levels (Lilleskov et al. 2024) and are associated with P limitation. *Alpova corsicus* is highly associated with N-fixing plant hsots, and likely specializes in other resources such as P (Rochet et al. 2011). *Paxillus involutus* is hypothesized to be specialized for P acquisition in high N, low P environments (Lilleskov et al. 2024). It is likely that distinct clades of long-distance EMF are associated with either N limitation or P limitation, but not both, and are specialized for either P uptake under P limitation or N uptake under N limitation. This exploration type could be associated with high belowground C allocation when aboveground growth is limited by either N or P (Lilleskov et al. 2024). Furthermore, there may be a link between high N and alder-associated communities, as both *Alpova corsicus* and *Paxillus involutus* are associated with N-fixing alders (Walker et al. 2014), and the presence of other alder-associated generas such as *Naucoria* further suggests this. In fact, some species of nitrophilic *Cortinarius* and *Tomentella* are also alder associates (Walker et al. 2014). However, *Cortinarius caninus*¸which responded positively to higher N at these sites, has no evidence of associating with alder, and was not found at sites with alder. Furthermore, *Naucoria bohemica*, which also increased with higher soil N, was found at many sites without alder. Therefore, the high N communities at these sites are not restricted to alder communities.

Based on the peaks of cumulative distributions of change points for fungal species with negative and positive associations with organic soil C:N ratio, there was a significant shift in mycorrhizal community composition at an organic soil C:N ratio of 19, and an additional shift in composition for positively affected fungi at an organic soil C:N ratio of 25. This reflects that species responding negatively to C:N ratio were most often found at organic soil C:N ratio values below 19, while species responding positively to C:N ratio were most often found at values of organic soil C:N ratio above 25 (Figure 4B). An organic soil C:N ratio of < 29 typically indicates N limiting conditions (Brust 2019). These results suggest that nitrophobic species are typically found at organic soil C:N ratio values > 25 where N is limiting, while nitrophilic fungal species are typically found at organic soil C:N ratio values < 19 where N is not limiting.

Effects of salmon on fungi varied with spatiotemporal scale - The effect of salmon carcasses on symbiotrophic fungi contrasted sharply between sites of short-term, naturally placed decomposing carcasses and the long-term salmon carcass manipulation experiment. While the long-term carcass manipulation decreased medium-distance fringe richness and relative abundance, recently decomposing carcasses increased long-distance relative abundance and medium-distance fringe diversity. These opposing effects might be due to differences in the spatial and temporal scales of carcass placement, as well as the manipulated versus natural aspect of carcass input. These decomposing carcasses placed by wildlife are a N source that has been occurring in the system for as long as salmon have been migrating up this river, likely millennia, making it likely that the fungal and plant mechanisms for nutrient uptake have to some degree co-evolved with this type of nutrient input, specifically small-scale and patchy nutrient hotspots. Similarly, the natural N gradient away from the stream edge has also existed within the system for some time. In contrast, the carcass manipulation artificially increased carcass abundance dramatically on the left bank over 21 years of sockeye salmon runs at this stream, equating to a very large fertilization experiment. We would then expect fungal taxa to respond in different ways to the artificial type of N variation relative to the natural or pre-existing types of N variation. For example, fungal taxa along the natural N gradient are likely pre-adapted to varying levels of soil N, while decomposing carcasses likely select for fungal taxa that can efficiently mine nutrient patches and access organic N. The placement of all salmon carcasses on a narrow strip of bank would fall outside of the natural nutrient placement within this system, therefore, we might expect that fungal taxa would respond to this large nutrient load created by the carcass manipulation experiment with similar responses to those for N fertilization or N deposition. Consistent with this interpretation, the carcass manipulation decreased the richness of medium-distance fringe EMF, as has been found in response to N fertilization and N deposition (Lilleskov et al. 2011). Alternatively, single decomposing carcasses placed naturally by wildlife in the riparian area (from 1-10 m away from the stream bank) increased the relative abundance and richness of long-distance and medium-distance EMF within 1-2 m from the site of the carcass, potentially due to increased plant C allocation to these foragers to mine these nutrient hotspots, supporting the hypothesis that some types of mycorrhizal fungi will predominate in areas of higher soil nutrient levels due to their ability to mine nutrient hotspots and maintain large network structures (Moeller and Neubert 2015). This suggests that fungal communities are affected not only by the availability of nutrients, but also by their spatiotemporal dynamics in the environment. In fact, there are differences between continuous and pulsed nutrient additions, and some evidence shows that nutrient pulses lead to higher diversity than continuous additions (Lodge et al. 1994, Weber and Brown 2013). These results indicate that the spatial scale and temporal scale of nutrient input are drivers of EMF community structure, and that scale mediates the effect of nutrient inputs on EMF community composition.

Conclusions

We found that a large-scale, long-term carcass manipulation experiment decreased medium-distance fringe EMF relative abundance and species richness, likely due to the selection against the C-demanding medium-distance fringe EMF with peroxidase activity at higher N levels. However, individual decomposing salmon carcasses placed on the stream banks by wildlife increased relative abundance of long-distance EMF and species diversity of medium-distance fringe types, especially of *Cortinarius* species, likely due to the ability of these EMF to maintain large network structure, mine nutrient hotspots, and access organic N and P. These results indicate that spatiotemporal scale mediates the effect of N inputs on EMF community structure. Decomposing carcasses also increased the species richness and diversity of saprotrophic fungi. We identified unique saprotrophic communities associated with the decomposition of salmon carcasses. Preserving salmon habitat and salmon populations might be important for maintaining the diversity in riparian areas of EMF and salmon carcass-associated saprotrophic fungi. Finally, responses of fungal taxa to soil N gradients varied widely by species, indicating that the functional mechanisms underlying these responses need further study.

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Table 1. Fungal genera placed into exploration type categories (long-distance, medium-distance fringe, medium-distance smooth, and short-distance (grouped by short-distance delicate, short-distance coarse, and contact) types from soil samples sampled along three salmon streams in Alaska. A list of species for each genus can be found in Table S5.

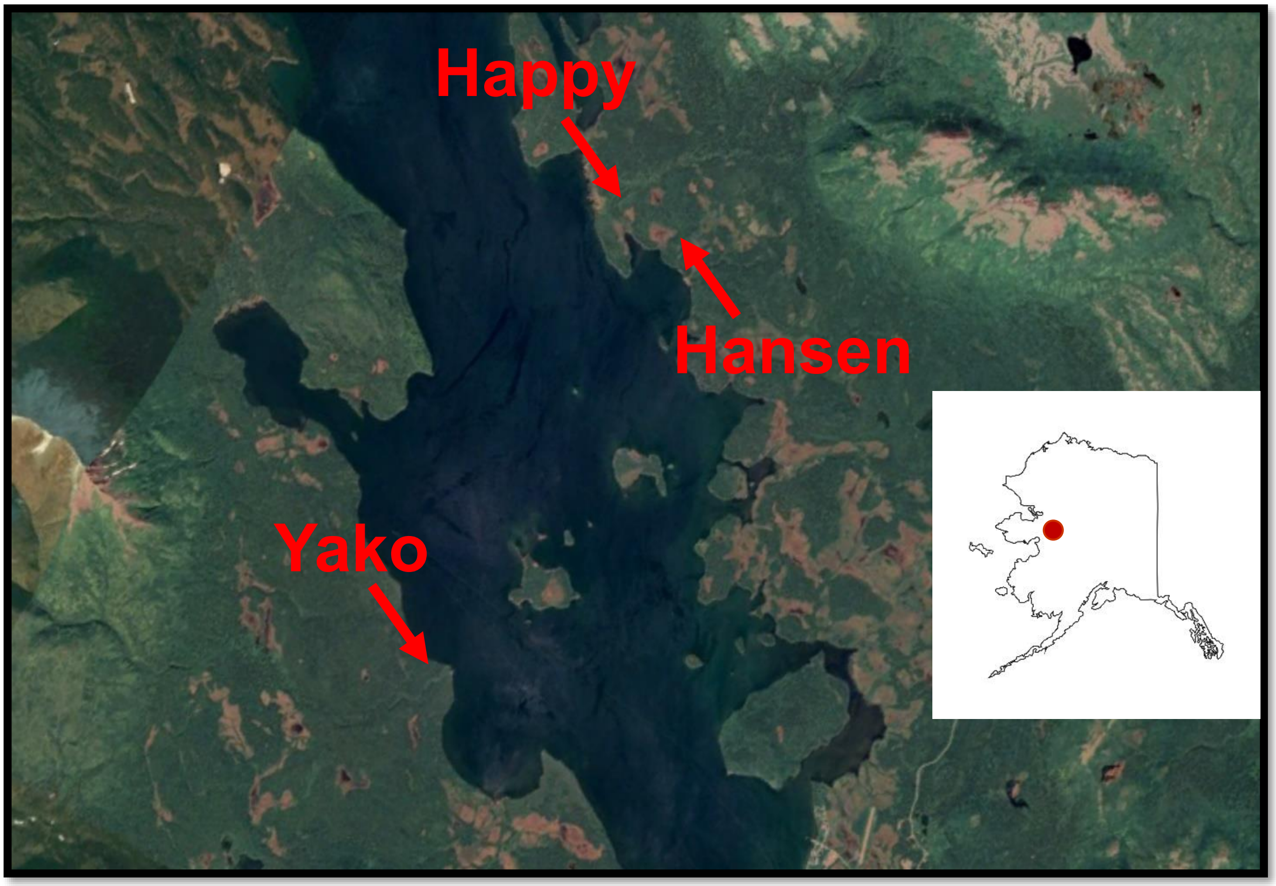
Long distance	**Medium distance fringe**	**Medium distance smooth**	**Short distance delicate**	**Short distance coarse**	**Contact**
Xerocomus	*Cortinarius*	*Hydnum*	*Laccaria*	*Trichophaea*	*Russula*
Paxillus	*Amphinema*	*Tomentella*	*Inocybe*	*Wilcoxina*	*Amanita*
Alpova	*Piloderma*	*Pseudotomentella*	*Naucoria*	*Cenococcum*	*Hygrophorus*
Boletus	*Sistotrema* (mycorrhizal species)	*Thelephora*	*Tylospora*	*Genabea*	*Clavulina*
	Tricholoma	*Lactarius*	*Hymenogaster*	*Otidea*	*Helvellosebacina*
	Lyophyllum (mycorrhizal species)	*Entoloma* (mycorrhizal species, see Table S5)	*Tuber*	*Geopora*	
		Tomentellopsis	*Leotia*		
			Hebeloma		
			Sebacina		
			Alnicola		
			Pulvinula		
			Endogone		

Table 2. Predictors from the top linear mixed effect models for relative abundance, species richness, and species diversity of saprotrophic and symbiotrophic (long-distance, medium-distance fringe, medium-distance smooth, and short-distance) fungi along three salmon streams in SW Alaska. Models include conditional R^2, all predictor variables, beta coefficient estimates ± SE, P values and VIF (variance inflation factor). All models included a random effect of transect nested within stream. GWC indicates gravimetric water content. Dim1-Dim4 describe plant community composition based on multiple correspondence analysis (Figure S4).

Trophic guild	**Response variable**	**R^2**	**Predictors**	**Value ± SE**	**P-value**	**VIF**
Sapro-trophic fungi	relative abundance	0.09	Intercept	0.23 ± 0.03	< 0.001	NA
			Organic soil C:N	-0.005 ± 0.001	< 0.001	1.23
			pH	0.06 ± 0.01	< 0.001	1.72
	species richness	0.28	Intercept	-30.62 ± 13.43	0.02	NA
			Organic soil C:N	0.78 ± 0.27	0.004	1.85
			Mineral soil C:N	-0.76 ± 0.28	0.009	1.12
			Ln(Distance)	-1.12 ± 0.73	0.13	1.23
			pH	11.59 ± 2.29	< 0.001	1.82
			Decomposing carcass	6.09 ± 2.80	0.03	1.63
	species diversity	0.22	Intercept	1.40 ± 0.20	< 0.001	NA
			Organic soil C:N	0.02 ± 0.01	0.02	2.15
			Mineral soil C:N	-0.04 ± 0.01	0.005	2.50
			Slope	0.23 ± 0.13	0.08	1.54
			Ln(Distance)	-0.07 ± 0.03	0.05	1.62
			pH	0.24 ± 0.10	0.01	1.27
			Decomposing carcass	0.35 ± 0.13	0.006	1.46
Symbio-trophic fungi	Short distance relative abundance	0.11	Intercept	0.51 ± 0.05	< 0.001	NA
			Dim1	0.13 ± 0.05	0.01	1.32
			Dim2	-0.17 ± 0.07	0.01	1.01
			Dim3	0.17 ± 0.08	0.04	1.12
			Ln(Distance)	-0.04 ± 0.02	0.03	1.45
	Short distance species richness	0.15	Intercept	0.72 ± 0.33	0.03	NA
			Mineral soil C:N	0.003 ± 0.007	0.64	1.85
			Dim4	0.08 ± 0.09	0.36	1.12
			pH	-0.08 ± 0.06	0.19	1.62
			Ln(Distance)	-0.02 ± 0.02	0.36	1.42
	Short distance species diversity	0.15	Intercept	0.30 ± 0.11	< 0.001	NA
			Mineral soil C:N	0.008 ± 0.006	0.17	1.38
			Ln(Distance)	-0.01 ± 0.02	0.49	1.28
			Carcass deposition	0.09 ± 0.09	0.30	1.39
			Decomposing carcass	-0.02 ± 0.08	0.82	1.47
	Medium distance smooth relative abundance	0.23	Intercept	0.12 ± 0.02	< 0.001	NA
			Ln(Distance)	-0.02 ± 0.005	< 0.001	1.74
			Carcass deposition	-0.05 ± 0.03	0.07	1.25

	Medium distance smooth species richness	0.50	Intercept	4.90 ± 0.25	< 0.001	NA
			Dim1	-3.14 ± 0.50	< 0.001	1.35
			Dim2	1.65 ± 0.63	0.01	1.11
			Dim4	1.62 ± 0.75	0.03	1.19
			slope	-0.88 ± 0.63	0.16	1.52
			carcass deposition	-1.12 ± 0.72	0.13	1.73
	Medium distance smooth species diversity	0.15	Intercept	0.09 ± 0.44	0.83	NA
			Dim1	-0.21 ± 0.19	0.08	1.16
			pH	0.15 ± 0.10	0.16	1.03
			Decomposing carcass	0.22 ± 0.14	0.10	1.38
	Medium distance fringe relative abundance	0.27	Intercept	0.02 ± 0.03	0.45	NA
			Organic soil C:N	0.007 ± 0.001	< 0.001	2.08
			Mineral soil C:N	-0.006 ± 0.002	< 0.001	2.36
			Slope	0.09 ± 0.02	< 0.001	1.74
			Carcass deposition	-0.05 ± 0.02	0.03	1.06
	Medium distance fringe species richness	0.23	Intercept	-0.003 ± 0.01	0.90	NA
			Organic soil C:N	0.005 ± 0.002	0.03	2.18
			pH	-0.006 ± 0.02	0.72	1.08
			Dim1	-0.01 ± 0.02	0.63	1.11
			Dim2	0.01 ± 0.02	0.65	1.14
			Dim3	0.03 ± 0.03	0.29	1.55
			Carcass deposition	-0.05 ± 0.03	0.05	1.73
	Medium distance fringe species diversity	0.27	Intercept	-0.17 ± 0.41	0.005	NA
			Mineral soil C:N	0.03 ± 0.008	0.001	1.37
			Carcass load	0.003 ± 0.001	0.08	1.72
			Dim1	-0.16 ± 0.08	0.05	1.25
			Dim2	0.15 ± 0.09	0.08	1.83
			Dim3	0.36 ± 0.10	0.003	1.82
			pH	0.20 ± 0.07	0.005	1.52
			Ln(Distance)	0.07 ± 0.03	0.02	1.73
			Decomposing carcass	0.37 ± 0.09	0.001	1.26
	Long distance relative abundance	0.27	Intercept	-0.02 ± 0.008	0.008	NA
			Organic soil C:N	0.002 ± 0.001	0.09	1.21
			Dim3	-0.007 ± 0.002	0.001	1.21
			pH	0.004 ± 0.001	0.002	1.49
			Decomposing carcass	0.005 ± 0.001	0.004	1.72
	Long distance species richness	0.39	Intercept	-4.60 ± 1.10	< 0.001	NA
			Organic soil C:N	0.07 ± 0.02	0.001	1.34
			Dim1	-0.68 ± 0.23	0.003	1.49
			Dim3	-1.05 ± 0.27	< 0.001	1.36
			pH	1.09 ± 0.19	< 0.001	1.28
	Long distance species diversity	0.41	Intercept	-1.37 ± 0.30	< 0.001	NA
			Mineral soil C:N	0.02 ± 0.007	0.01	1.08
			Dim4	-0.29 ± 0.10	0.005	1.38
			pH	0.31 ± 0.05	< 0.001	1.92
			ln(Distance)	-0.03 ± 0.02	0.09	1.63
			carcass deposition	-0.11 ± 0.08	0.17	1.23

(a)



(b) The stream bank

(c) Further from the stream bank into the forest

Figure 1. (a) A map of the study area, including the three salmon streams on Lake Aleknagik where soil samples were collected. (b) Photograph of a study site at Hansen Creek close to the stream bank. (c) Photograph of a study site at Hansen Creek 40 m into the forest.

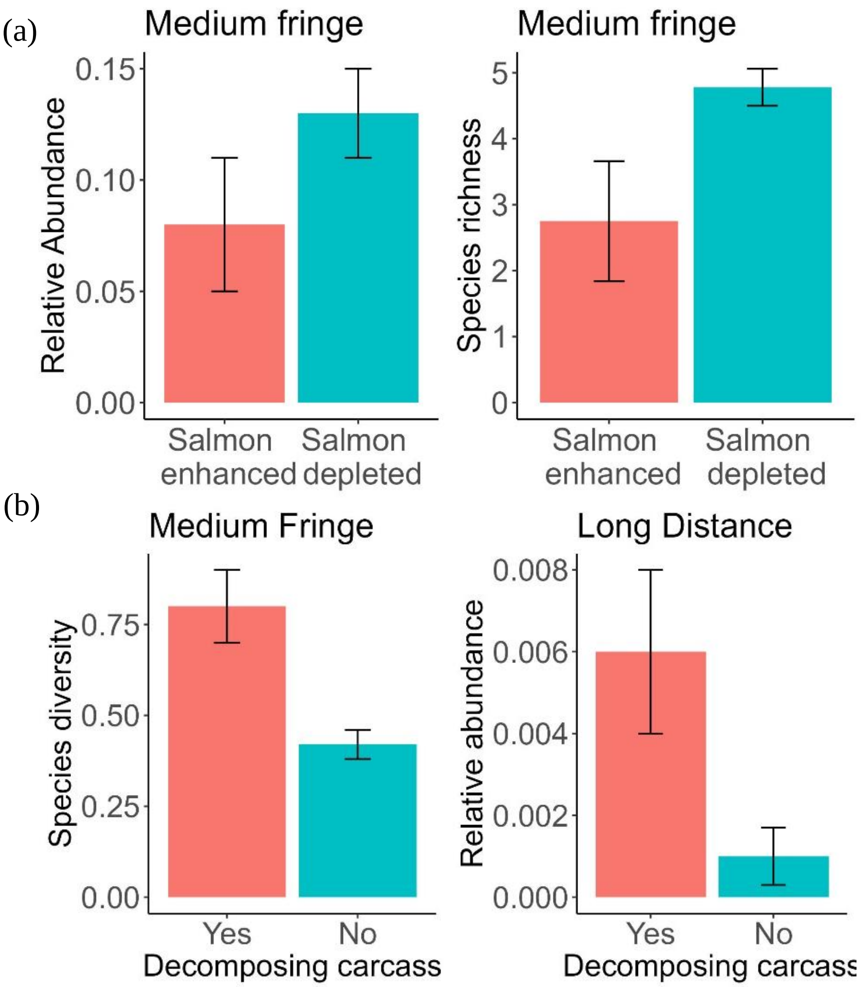


Figure 2. (a) Predicted fractional relative abundance and species richness of medium-distance fringe on the salmon-enhanced and salmon-depleted banks of Hansen Creek following a 21-year salmon carcass manipulation experiment, and (b) species diversity of medium-distance fringe types and predicted fractional relative abundance of long-distance types at locations <1 m from a decomposing salmon carcass along three salmon streams in SW Alaska.

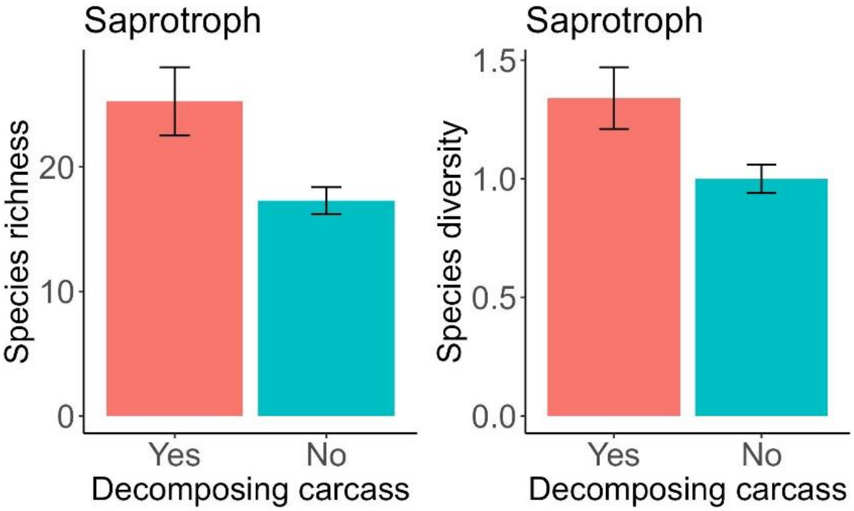


Figure 3. Predicted species richness and diversity of saprotroph fungi at locations <1 m from a decomposing salmon carcass along three salmon streams in SW Alaska.

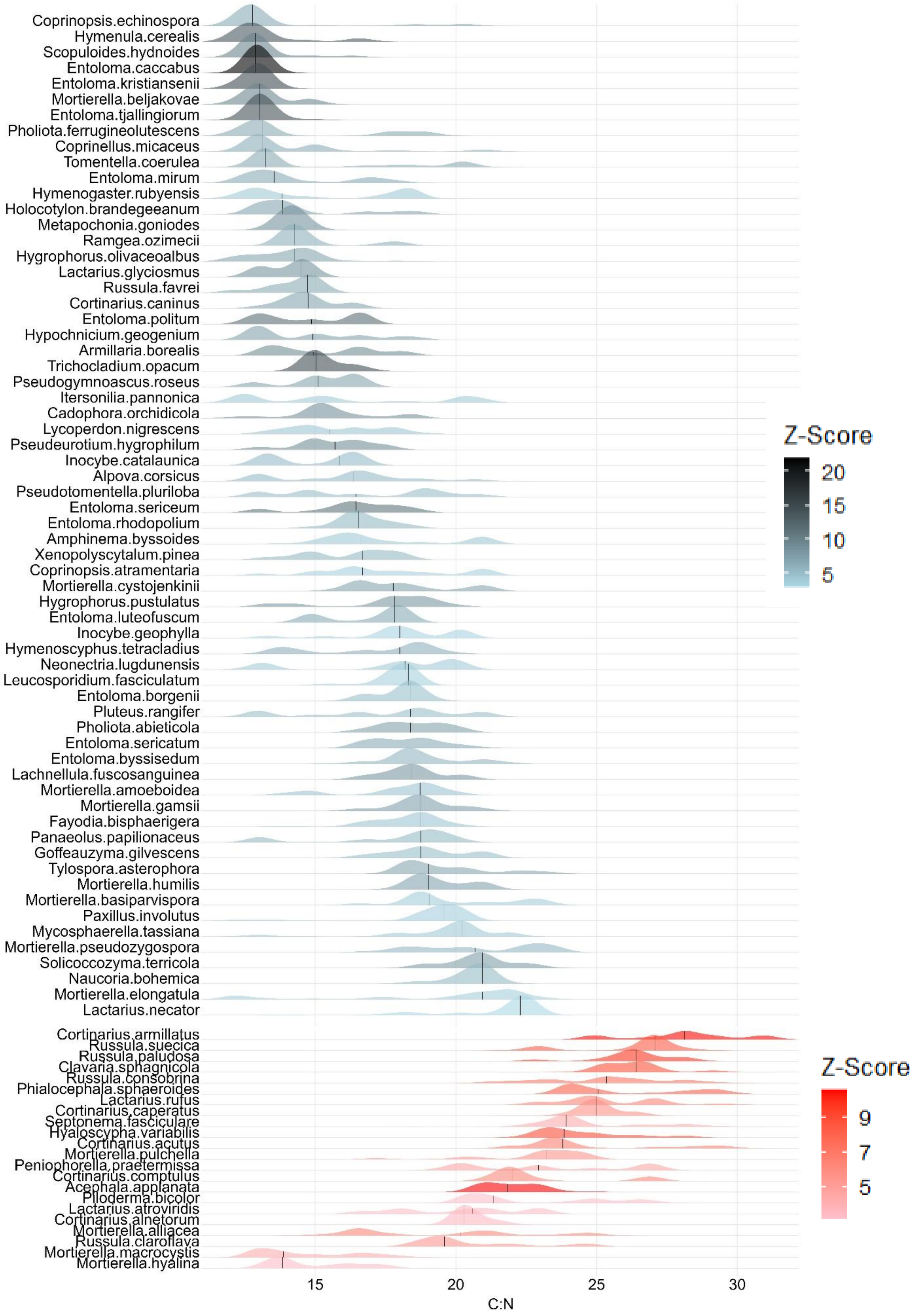


Figure 4A. Probability densities of change points for fungal species with negative (blue) and positive (red) responses to increasing organic soil C:N along three salmon streams in SW Alaska.

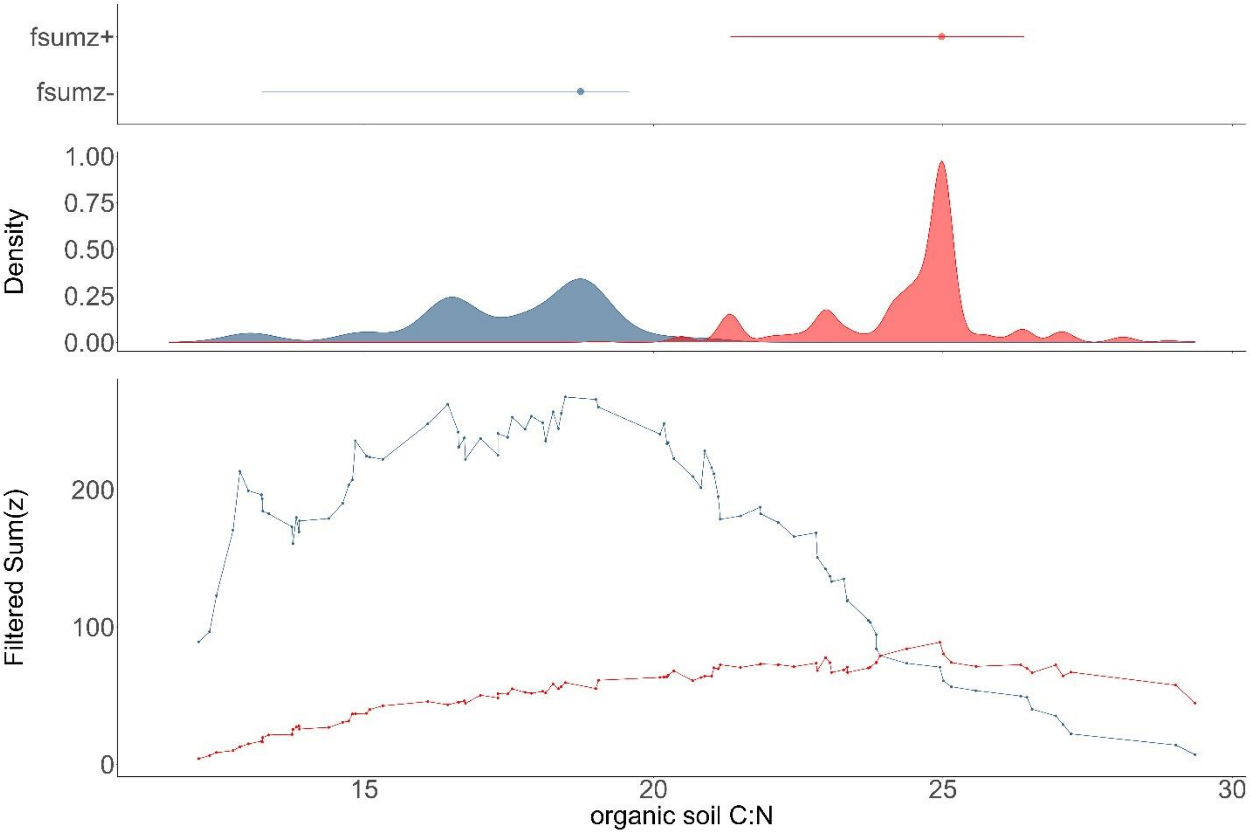


Figure 4B. Probability densities of change points for decreases (blue) and increases (red) as determined from bootstrap replicates, and the sum of z-scores for fungal species with negative (blue) and positive (red) z-scores. Peaks represent fungal community thresholds for change along organic soil C:N gradient along three salmon streams in SW Alaska.

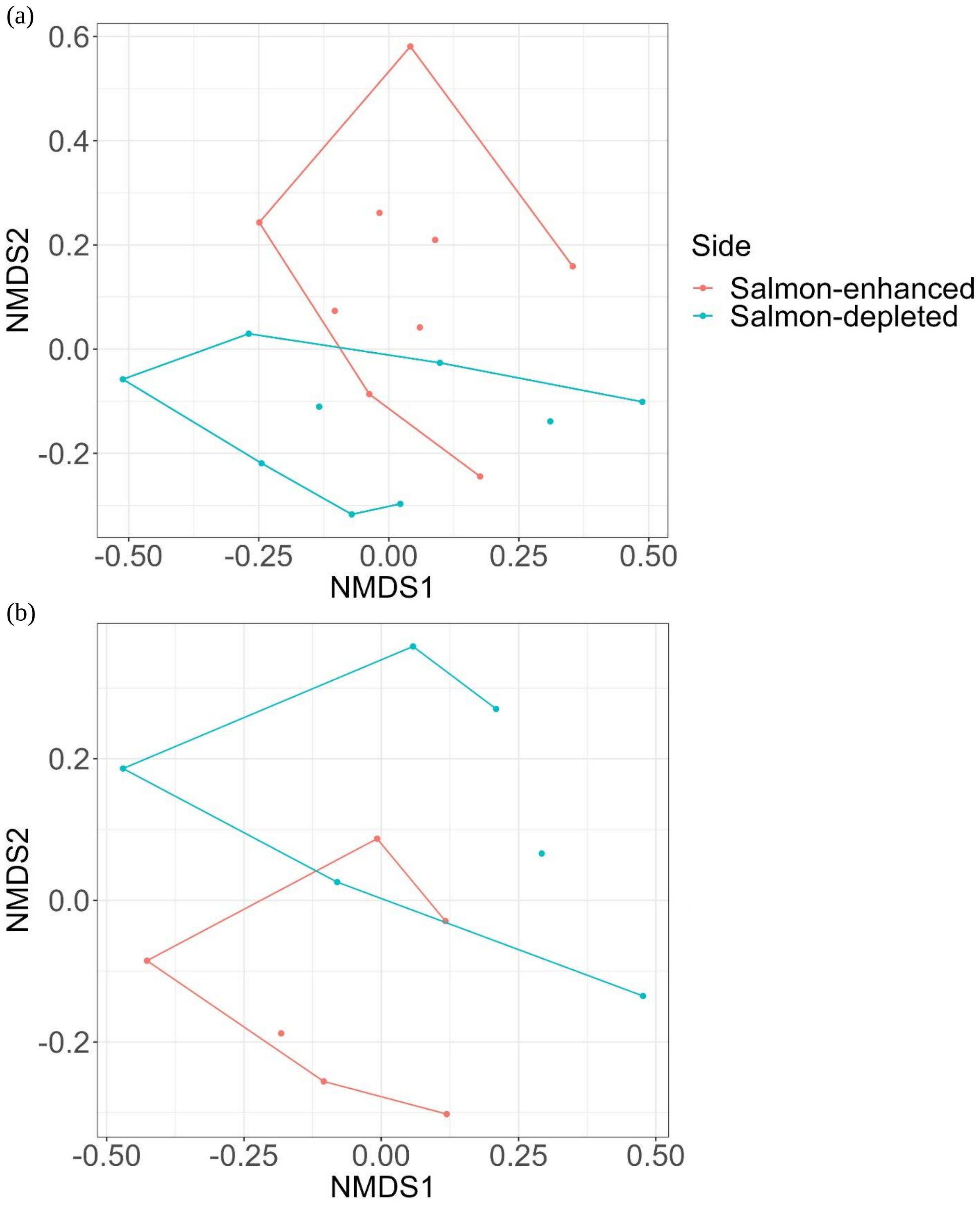


Figure S1. NMDS plot with lines connecting the outermost points for each group visualizing the effect of the salmon carcass deposition (on the salmon-enhanced bank) on fungal communities for (a) 1-6 m and (b) 3-6 m at Hansen Creek.

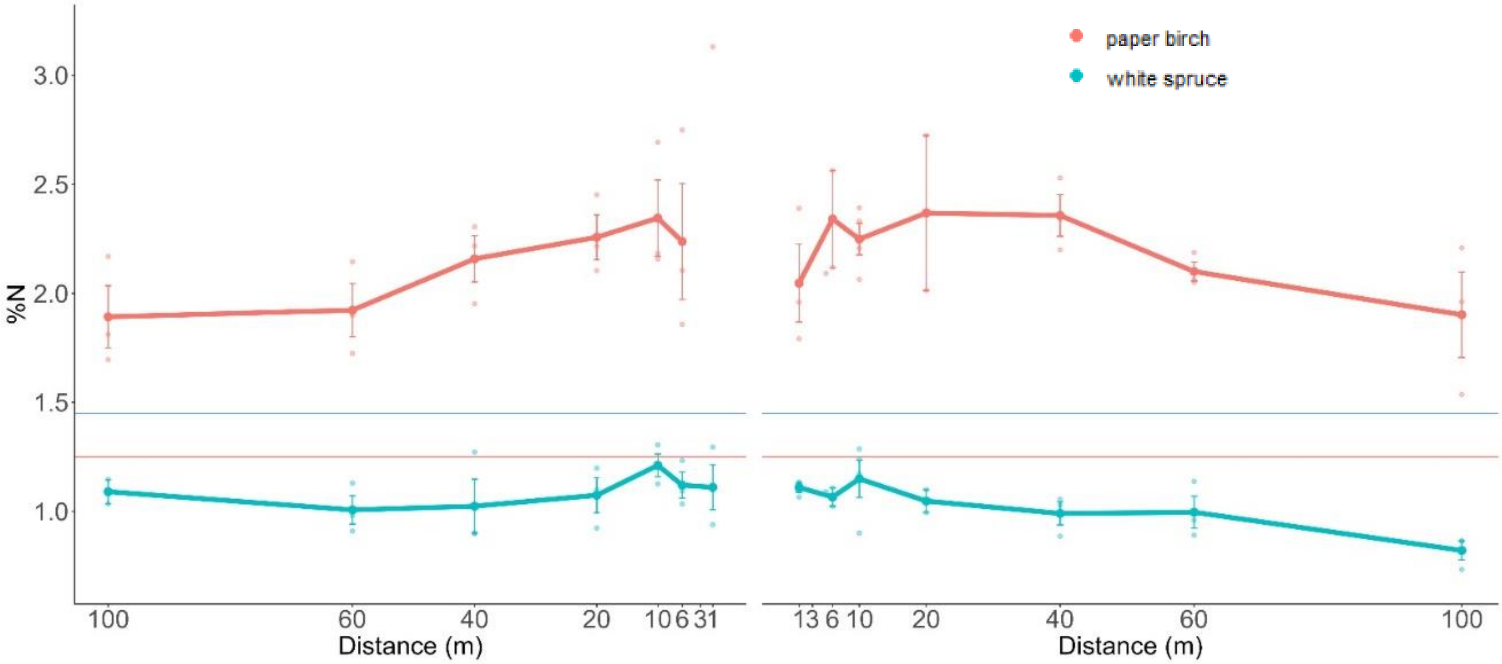


Figure S2. Mean values of foliar %N for white spruce and paper birch from 1-100 m away from the bank on both sides of Hansen Creek. Horizontal lines indicate values of N deficiency.

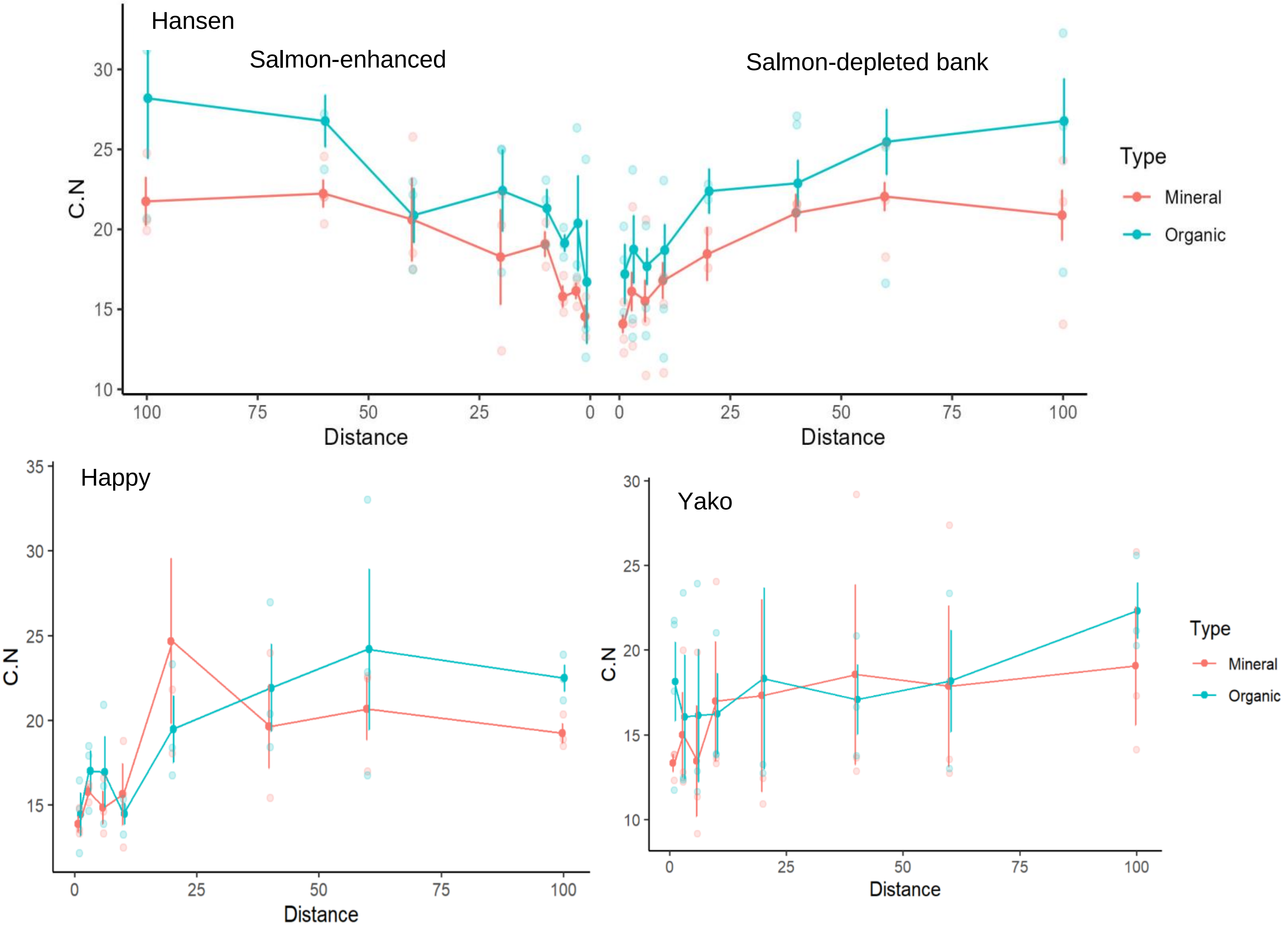
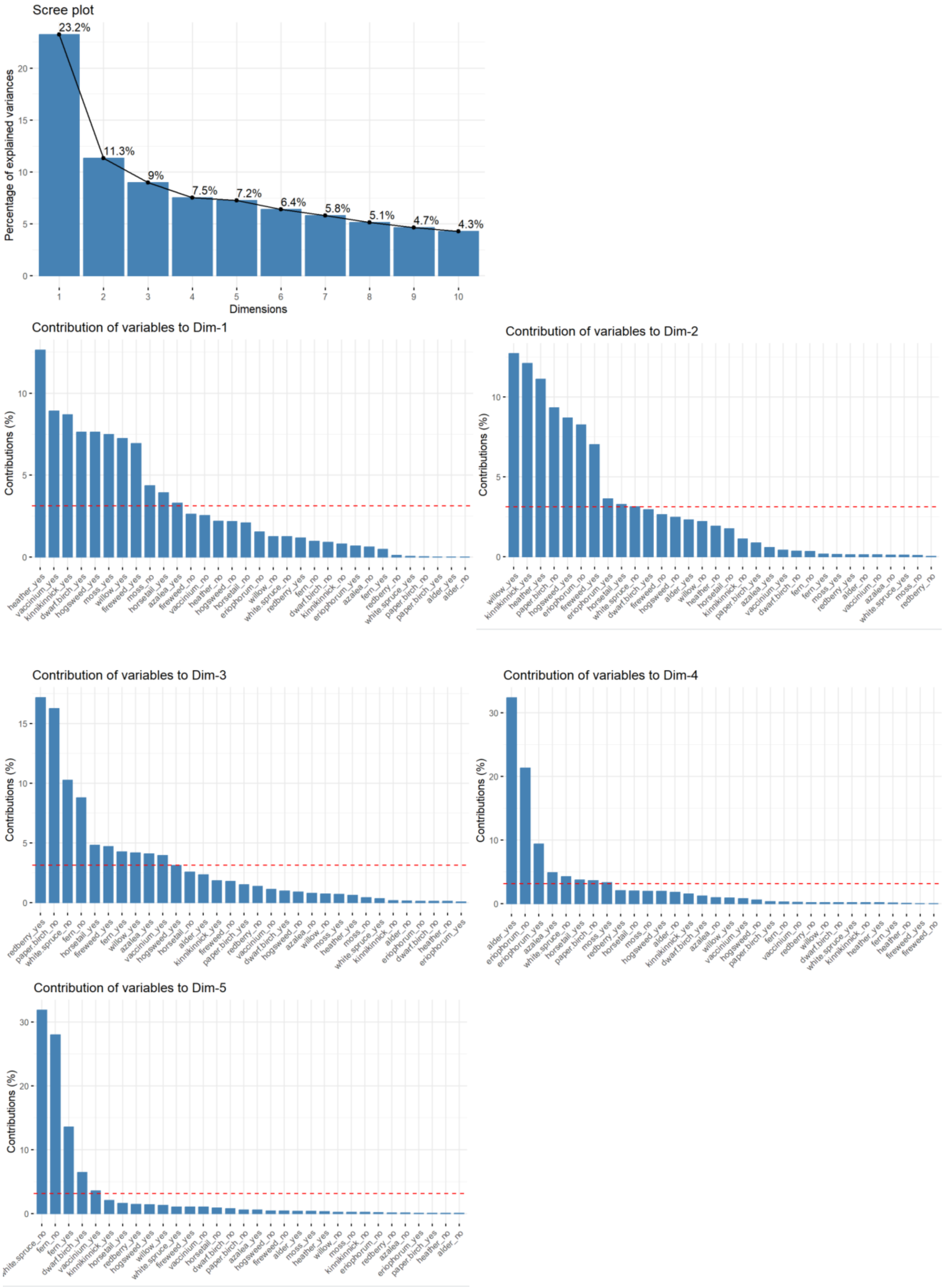


Figure S3. Organic and mineral soil C:N from 1-100 m away from both banks of Hansen Creek, and from 1-100 m away from the banks of Happy and Yako Creek.


Scree plot

Contribution of variables to Dim-1

Contribution of variables to Dim-2

Contribution of variables to Dim-3

Contribution of variables to Dim-4

Contribution of variables to Dim-5

Figure S4. Plot of dimensions resulting from multiple correspondence analysis of plant community composition in a 5 m^2 radius surrounding soil sampling locations.

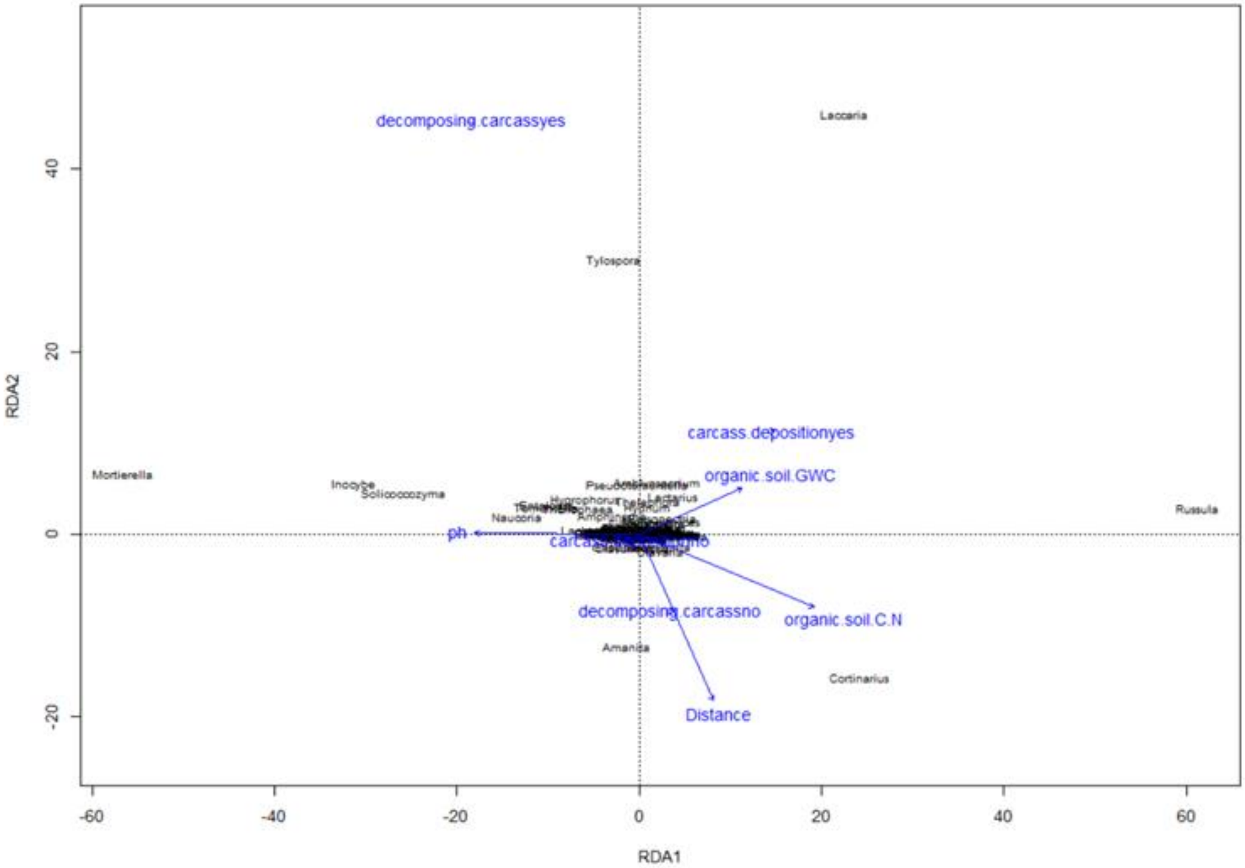


Figure S5. A correlation biplot representing redundancy analysis using 308 fungal genera and 6 environmental variables.

Table S1. Fungal species that were found only at sites near decomposing carcasses at three salmon streams in SW Alaska, ordered by trophic guild.

Genus	**Species**	**Trophic Guild**	**Type**
Metarhizium	*carneum*	animal_parasite	none
Beauveria	*pseudobassiana*	animal_parasite	none
Exophiala	*bonariae*	animal_parasite	none
Coprinus	*phaeopunctatus*	dung_saprotroph	none
Tomentella	*viridula*	ectomycorrhizal	medium-distance_smooth
Thelephora	*palmata*	ectomycorrhizal	medium-distance_smooth
Inocybe	*mixtilis*	ectomycorrhizal	short-distance_delicate
Cortinarius	*annae-maritae*	ectomycorrhizal	medium-distance_fringe
Hygrophorus	*discoideus*	ectomycorrhizal	contact
Inocybe	*pseudodestricta*	ectomycorrhizal	short-distance_delicate
Tomentella	*clavigera*	ectomycorrhizal	medium-distance_smooth
Otidea	*nannfeldtii*	ectomycorrhizal	short-distance_coarse
Cortinarius	*glandicolor*	ectomycorrhizal	medium-distance_fringe
Russula	*helodes*	ectomycorrhizal	contact
Cortinarius	*pluvius*	ectomycorrhizal	medium-distance_fringe
Cortinarius	*disjungendulus*	ectomycorrhizal	medium-distance_fringe
Alnicola	*spectabilis*	ectomycorrhizal	short-distance_delicate
Pseudotomentella	*alnophila*	ectomycorrhizal	medium-distance_smooth
Cortinarius	*pluviorum*	ectomycorrhizal	medium-distance_fringe
Cortinarius	*pseudoturmalis*	ectomycorrhizal	medium-distance_fringe
Cortinarius	*acetosus*	ectomycorrhizal	medium-distance_fringe
Cortinarius	*illuminoides*	ectomycorrhizal	medium-distance_fringe
Triposporium	*cycadicola*	foliar_endophyte	none
Monodictys	*arctica*	lichen_parasite	none
Psilocybe	*medullosa*	litter_saprotroph	none
Pyxidiophora	*arvernensis*	litter_saprotroph	none
Cystoderma	*carpaticum*	litter_saprotroph	none
Crocicreas	*cyathoideum*	litter_saprotroph	none
Deconica	*merdaria*	litter_saprotroph	none
Pluteus	*leoninus*	litter_saprotroph	none
Lepiota	*magnispora*	litter_saprotroph	none
Cystofilobasidium	*capitatum*	litter_saprotroph	none
Mycena	*metata*	litter_saprotroph	none
Neosetophoma	*samararum*	litter_saprotroph	none
Arrhenia	*acerosa*	litter_saprotroph	none
Deconica	*bayliasiana*	litter_saprotroph	none
Pluteus	*eos*	litter_saprotroph	none
Colacogloea	*philyla*	mycoparasite	none
Debaryomyces	*hansenii*	nectar/tap_saprotroph	none

Typhula	*micans*	plant_pathogen	none
Ilyonectria	*mors-panacis*	plant_pathogen	none
Polyscytalum	*neofecundissimum*	plant_pathogen	none
Microcyclospora	*tardicrescens*	plant_pathogen	none
Mortierella	*sclerotiella*	soil_saprotroph	none
Mortierella	*rishikesha*	soil_saprotroph	none
Phialocephala	*virens*	soil_saprotroph	none
Entoloma	*nitens*	soil_saprotroph	none
Coprinopsis	*clastophylla*	soil_saprotroph	none
Entoloma	*calobrunneum*	soil_saprotroph	none
Coprinopsis	*romagnesiana*	soil_saprotroph	none
Agaricus	*macrocarpus*	soil_saprotroph	none
Capronia	*pulcherrima*	soil_saprotroph	none
Leucosporidium	*fellii*	soil_saprotroph	none
Blastocladiella	*britannica*	soil_saprotroph	none
Entoloma	*cuspidiferum*	soil_saprotroph	none
Entoloma	*rhombisporum*	soil_saprotroph	none
Entoloma	*vernum*	soil_saprotroph	none
Solicoccozyma	*terrea*	soil_saprotroph	none
Entoloma	*jubatum*	soil_saprotroph	none
Entoloma	*hirtipes*	soil_saprotroph	none
Cuphophyllus	*cinerellus*	soil_saprotroph	none
Mrakia	*niccombsii*	unspecified_saprotroph	none
Claussenomyces	*prasinulus*	wood_saprotroph	none
Psathyrella	*rostellata*	wood_saprotroph	none
Lachnellula	*calyciformis*	wood_saprotroph	none
Coniophora	*puteana*	wood_saprotroph	none
Kuehneromyces	*mutabilis*	wood_saprotroph	none
Hyphodontiella	*multiseptata*	wood_saprotroph	none
Psathyrella	*boreifasciculata*	wood_saprotroph	none

Table S2. Predictors from the top linear mixed effect models for relative abundance of each ectomycorrhizal fungal genus along three salmon streams in SW Alaska. Models include beta coefficient estimates ± SE, and P-values. Dim1 through Dim5 refer to the plant community metric vectors defined through multiple correspondence analysis (Figure S4). All models included a random effect of transect nested within stream. Organic soil GWC indicates organic soil gravimetric water content.

Long distance EMF				
Genus	**term**	**estimate**	**std.error**	**P value**
Paxillus	(Intercept)	-0.00343	0.002499	0.173201
	Dim3	-0.00308	0.000997	0.002671
	pH	0.001002	0.000592	0.093636
	decomposing.carcassyes	0.002241	0.000846	0.009512
Boletus	(Intercept)	-5E-05	1.71E-05	0.004448
	organic.soil.GWC	6.29E-06	1.44E-06	3.49E-05
	pH	8.81E-06	3.9E-06	0.026156
	carcass.depositionyes	1.41E-05	7.29E-06	0.056532
Alpova	(Intercept)	-0.01112	0.003356	0.001318
	Dim3	-0.0043	0.001363	0.002174
	pH	0.002901	0.000785	0.000375
Xerocomus	(Intercept)	-0.00158	0.001031	0.12894
	organic.soil.C.N	0.000134	5.48E-05	0.01671
	organic.soil.GWC	-0.00031	0.000171	0.070623
	slopeyes	-0.00108	0.000697	0.125802
	decomposing.carcassyes	0.001514	0.000701	0.033365

Medium distance fringe EMF				
Genus	**term**	**estimate**	**std.error**	**p.value**
Cortinarius	(Intercept)	0.00871	0.030503	0.775885
	organic.soil.C.N	0.006641	0.001807	0.000405
	mineral.soil.C.N	-0.00545	0.002155	0.013213
	slopeyes	0.078337	0.020589	0.000258
	carcass.depositionyes	-0.04496	0.022849	0.052161
Amphinema	(Intercept)	0.018615	0.005441	0.000939
	mineral.soil.C.N	-0.00072	0.000291	0.015161
	carcass.load	-4.7E-06	2.65E-06	0.081939
	Dim3	-0.0103	0.00454	0.025653
	Dim5	-0.00727	0.004977	0.147558
Piloderma	(Intercept)	0.001527	0.001645	0.355468
	Dim3	0.00941	0.005147	0.070757
	decomposing.carcassyes	0.008582	0.004305	0.049191
Sistotrema	(Intercept)	5.97E-05	4.45E-05	0.183257

	Dim1	-0.00013	9.16E-05	0.155359
	Dim2	0.00024	0.000129	0.065484
	Dim5	-0.00023	0.000148	0.122327
	decomposing.carcassyes	0.000308	0.000131	0.02131
Tricholoma	(Intercept)	6.56E-05	3.26E-05	0.047048
	Dim3	0.000369	0.00011	0.001142
Lyophyllum	(Intercept)	1.24E-05	7.64E-06	0.106739
	Dim2	5.03E-05	2.29E-05	0.030608
	Dim3	-5.8E-05	2.58E-05	0.025886

Medium distance smooth EMF				
Genus	**term**	**estimate**	**std.error**	**p.value**
Lactarius	(Intercept)	0.040211	0.008223	4.2E-06
	organic.soil.GWC	-0.00611	0.003156	0.056082
Tomentella	(Intercept)	0.017052	0.004972	0.000907
	Dim1	-0.02979	0.009922	0.003443
	carcass.depositionyes	0.023465	0.016153	0.149725
Entoloma	(Intercept)	0.030067	0.008584	0.000722
	ln(Distance)	-0.0057	0.00265	0.034128
	Dim1	-0.01947	0.007259	0.008717
	Dim2	0.027476	0.009432	0.004526
	decomposing.carcassyes	-0.01429	0.010297	0.168759
	carcass.depositionyes	-0.01691	0.011439	0.142899
Pseudotomentella	(Intercept)	0.006971	0.002338	0.003665
	Dim5	-0.01546	0.008674	0.077937
Hydnum	(Intercept)	-0.00712	0.010415	0.495881
	organic.soil.C.N	0.000829	0.000529	0.120352
	ln(Distance)	-0.00355	0.001976	0.075737
	Dim3	0.01413	0.008428	0.097097
	decomposing.carcassyes	0.016035	0.007478	0.034712
Thelephora	(Intercept)	0.005351	0.003068	0.084373
	carcass.depositionyes	0.019619	0.009966	0.051986
Tomentellopsis	(Intercept)	-0.00055	0.000223	0.01512
	organic.soil.C.N	-1.7E-05	1.1E-05	0.130362
	mineral.soil.C.N	5.51E-05	1.24E-05	2.37E-05
	slopeyes	-0.0002	0.000116	0.082141
	Dim1	-0.00023	0.000113	0.043887

Short distance EMF				
Genus	**term**	**estimate**	**std.error**	**p.value**
Russula	(Intercept)	0.413231	0.194111	0.035969
	Dim1	0.092489	0.048111	0.057681
	Dim3	0.137644	0.067414	0.044069

	pH	-0.064	0.045548	0.163362
Naucoria	(Intercept)	-0.17325	0.045458	0.00025
	organic.soil.GWC	0.00806	0.003601	0.027593
	pH	0.040182	0.010365	0.000198
Inocybe	(Intercept)	0.081947	0.013727	4.41E-08
	Dim5	0.082717	0.048493	0.091428
	carcass.depositionyes	-0.07819	0.044634	0.083155
Clavulina	(Intercept)	-0.01442	0.007338	0.052553
	organic.soil.GWC	0.001016	0.000616	0.102483
	carcass.load	4.06E-06	1.72E-06	0.020674
	Dim3	0.004581	0.002944	0.123211
	pH	0.003353	0.001681	0.049086
	carcass.depositionyes	-0.00631	0.003273	0.056921
Laccaria	(Intercept)	0.397047	0.112501	0.000653
	ln(Distance)	-0.0268	0.008384	0.00191
	pH	-0.06008	0.024131	0.014586
Tylospora	(Intercept)	0.179398	0.066568	0.008432
	organic.soil.C.N	-0.01089	0.003219	0.001068
	mineral.soil.C.N	0.005056	0.003406	0.141236
	carcass.load	3.52E-05	2.14E-05	0.104168
	Dim1	0.063893	0.032256	0.050735
	Dim3	0.061346	0.036802	0.09909
	carcass.depositionyes	0.090083	0.037586	0.01866
Hebeloma	(Intercept)	-0.00502	0.002056	0.016688
	organic.soil.GWC	0.000333	0.000153	0.031878
	Dim1	-0.00114	0.000561	0.045865
	Dim2	0.001716	0.000722	0.019555
	pH	0.00118	0.000485	0.017008
	decomposing.carcassyes	-0.00134	0.000682	0.052746
Meliniomyces	(Intercept)	-0.00435	0.002168	0.04781
	organic.soil.C.N	0.000522	0.000122	4.8E-05
	ln(Distance)	-0.00091	0.000461	0.051291
	carcass.depositionyes	0.004533	0.00204	0.028749
Tuber	(Intercept)	-0.01021	0.002913	0.000719
	mineral.soil.C.N	0.000162	6.18E-05	0.010137
	organic.soil.GWC	-0.00033	0.000149	0.029527
	ln(Distance)	-0.00062	0.000181	0.000955
	Dim3	-0.00122	0.000775	0.118992
	Dim5	0.004606	0.000826	2.64E-07
	pH	0.002438	0.000523	1.1E-05
Leotia	(Intercept)	0.006415	0.003228	0.049905
	mineral.soil.C.N	-0.00013	6.73E-05	0.060028
	ln(Distance)	0.000463	0.000189	0.016053

	Dim4	0.001537	0.000903	0.092286
	pH	-0.00116	0.000579	0.047838
Sebacina	(Intercept)	-0.00659	0.002976	0.029201
	organic.soil.C.N	8.7E-05	5.41E-05	0.111365
	organic.soil.GWC	-0.00027	0.000149	0.072397
	Dim5	-0.00116	0.00077	0.135333
	pH	0.001387	0.000526	0.00984
Alnicola	(Intercept)	-0.00198	0.001062	0.066006
	mineral.soil.C.N	3.34E-05	2.11E-05	0.11591
	organic.soil.GWC	-0.00016	5.87E-05	0.009548
	carcass.load	2.97E-07	1.57E-07	0.062577
	Dim2	-0.00039	0.000246	0.112132
	pH	0.000402	0.000188	0.034994
	carcass.depositionyes	0.000853	0.000298	0.005262
Hymenogaster	(Intercept)	0.001379	0.000879	0.120139
	organic.soil.C.N	-8.2E-05	4.52E-05	0.073243
	organic.soil.GWC	0.000248	0.00016	0.125241
Pulvinula	(Intercept)	-0.00076	0.000291	0.010704
	Dim3	0.000255	0.000118	0.033319
	Dim5	-0.00023	0.000127	0.068934
	pH	0.000187	6.81E-05	0.007201
Endogone	(Intercept)	-0.00076	0.000291	0.010704
	Dim3	0.000255	0.000118	0.033319
	Dim5	-0.00023	0.000127	0.068934
	pH	0.000187	6.81E-05	0.007201
Trichophaea	(Intercept)	0.05578	0.010149	3.58E-07
	organic.soil.C.N	-0.00099	0.000584	0.092916
	mineral.soil.C.N	-0.0013	0.000662	0.053078
	decomposing.carcassyes	-0.01369	0.006567	0.039895
	carcass.depositionyes	-0.01144	0.007475	0.129512
Wilcoxina	(Intercept)	0.005395	0.003897	0.169613
	organic.soil.C.N	-0.0006	0.000196	0.002783
	mineral.soil.C.N	0.000448	0.00021	0.035055
	Dim1	0.004581	0.001995	0.023929
Cenococcum	(Intercept)	-0.00711	0.003632	0.05329
	organic.soil.C.N	0.000412	0.000183	0.027282
	slopeyes	0.003975	0.002078	0.058915
	Dim1	-0.00572	0.002064	0.006786
	Dim4	-0.0071	0.002519	0.005936
Genabea	(Intercept)	-0.00223	0.000854	0.010704
	Dim3	0.000749	0.000347	0.033319
	Dim5	-0.00069	0.000373	0.068934
	pH	0.00055	0.0002	0.007201

Otidea	(Intercept)	5.47E-06	1.58E-05	0.730311
	Dim2	9.86E-05	4.61E-05	0.035099
	decomposing.carcassyes	7.02E-05	4.34E-05	0.108929
Geopora	(Intercept)	1.32E-08	1.07E-06	0.990155
	Dim5	-5.5E-06	3.65E-06	0.134006
	decomposing.carcassyes	6.95E-06	2.78E-06	0.014083
	(Intercept)	0.003625	0.010886	0.73988
Amanita	organic.soil.GWC	-0.00622	0.003032	0.043071
	slopeyes	-0.02022	0.012682	0.114307
	ln(Distance)	0.008358	0.003271	0.012286
	Dim2	-0.02425	0.013585	0.077588
Hygrophorus	(Intercept)	0.050716	0.011501	2.83E-05
	organic.soil.C.N	-0.0015	0.00058	0.011345
	mineral.soil.C.N	-0.00089	0.000618	0.155464
	Dim1	0.014642	0.005887	0.014693
Helvellosebacina	(Intercept)	8.58E-08	6.93E-06	0.990155
	Dim5	-3.6E-05	2.37E-05	0.134006
	decomposing.carcassyes	4.52E-05	1.81E-05	0.014083

Table S3. The %P, %N, and N:P values for paper birch, and white spruce samples at Hansen Creek at 1, 6, and 100 m on both the salmon-enhanced (SL) and salmon-depleted (SR) banks, in addition to four ectomycorrhizal fungal sporocarps and three organic soil samples.

Stream	**Transect**	**Side**	**Distance**	**% P**	**% N**	**N:P**
Hansen	S6	SL	6	0.38	5.02	13.13
Hansen	S6	SR	1	0.53	4.09	7.74
Hansen	S4	SL	1	0.14	0.71	5.13
Hansen	S4	SL	100	0.08	1.30	16.16
Hansen	S4	SR	1	0.12	2.54	22.00
Hansen	S1	SL	1	0.34	3.13	9.13
Hansen	S4	SL	6	0.17	2.11	12.69
Hansen	S6	SL	6	0.18	1.86	10.43
Hansen	S1	SL	6	0.42	2.75	6.49
Hansen	S4	SL	100	0.14	1.81	13.07
Hansen	S4	SR	1	0.22	2.39	10.78
Hansen	S1	SR	1	0.24	1.79	7.36
Hansen	S6	SR	1	0.15	1.96	13.04
Hansen	S6	SR	5	0.22	2.09	9.35
Hansen	S4	SR	6	0.23	2.12	9.21
Hansen	S1	SR	6	0.28	2.56	9.13
Hansen	S4	SR	100	0.32	2.21	6.94
Hansen	S4	SL	4	0.79	4.23	5.34
Hansen	S1	SR	10	0.69	4.80	6.91
Hansen	S4	SL	1	0.14	1.29	9.10
Hansen	S1	SL	1	0.15	0.94	6.42
Hansen	S6	SL	1	0.16	1.10	6.78
Hansen	S4	SL	6	0.15	1.03	7.10
Hansen	S1	SL	6	0.14	1.09	7.93
Hansen	S6	SL	6	0.16	1.23	7.76
Hansen	S4	SL	100	0.13	1.03	7.78
Hansen	S4	SR	1	0.13	1.13	8.65
Hansen	S1	SR	1	0.15	1.07	7.13
Hansen	S6	SR	1	0.16	1.14	7.22
Hansen	S6	SR	5	0.15	1.09	7.34
Hansen	S4	SR	6	0.22	1.11	5.06
Hansen	S1	SR	6	0.13	1.02	7.98
Hansen	S4	SR	100	0.15	0.87	5.58

Table S4. List of all plant species observed within a 5 m^2 radius of soil sampling locations along transects perpendicular to three salmon streams in SW Alaska.

Latin name	**Common name**
Picea glauca	White spruce
Betula papyrifera	Paper birch
Betula nana	Dwarf birch
Vaccinium ovalifolium	Alaskan blueberry
Pteridium aquilinum	Bracken fern
Harrimanella stelleriana	Alaskan moss heather
Eriophorum spp.	Cotton grass
Alnus crispa	Green alder
Chamaenerion angustifolium	Fireweed
Equisetum arvense	Horsetail
Salix alaxensis	Felt leaf willow
Vaccinium vitis-idaea	Lowbush mountain lingonberry
Arctostaphylos uva-ursi	Kinnikinnick Bearberry
Sphagnum spp.	Mosses
Heracleum mantegazzianum	Hogsweed

Table S5. Indicator species and primary lifestyles significantly associated with (a) the presence of nearby decomposing carcasses across three salmon streams in SW Alaska, and (b) indicator species significantly associated with the salmon-enhanced bank where salmon carcasses were deposited or the salmon-depleted bank where salmon carcasses were removed from 1-6 m at Hansen Creek during a 21-year salmon carcass manipulation experiment at Hansen Creek in SW Alaska.

(a)

Species	**Lifestyle**
Lophium arboricola	litter saprotroph
Trichocladium opacum	unspecified saprotroph
Russula consobrina	ectomycorrhizal, short-distance type
Hypholoma frowardii	wood saprotroph
Mortierella globulifera	soil saprotroph
Acrodontium hydnicola	plant pathogen and litter saprotroph
Hygrophorus olivaceoalbus	ectomycorrhizal, short-distance type
Lactarius rufus	ectomycorrhizal, medium-distance type
Mortierella sclerotiella	soil saprotroph
Cortinarius casimiri	ectomycorrhizal, medium-distance fringe

(b)

Genus	**Lifestyle**	**Side**
Ophiocordycipitacea inflatum	Animal parasite/decomposer	Salmon-enhanced
Oidiodendron trunca	Soil saprotroph/root endophyte	Salmon-enhanced
Amblyosporium botryt	Mycoparasite/fungal decomposer	Salmon-enhanced
Tomentella sublilacina	ectomycorrhizal, medium smooth type	Salmon-enhanced
Inocybe napipes	ectomycorrhizal, short-distance type	Salmon-depleted
Mortierella cystojenkinii	soil saprotroph	Salmon-depleted
Lactarius vietus	ectomycorrhizal, medium-smooth type	Salmon-depleted

Table S6. All ectomycorrhizal fungal species found along three salmon streams in SW Alaska, categorized by exploration types based on genus.

Long distance species
Paxillus involutus
Alpova corsicus
Alpova NA
Xerocomus NA
Boletus edulis

Medium distance fringe species
Amphinema byssoides
Amphinema diadema
Amphinema NA
Cortinarius acetosus
Cortinarius acutovelatus
Cortinarius acutus
Cortinarius adalbertii
Cortinarius alboamarescens
Cortinarius alnetorum
Cortinarius alpinus
Cortinarius annae-maritae
Cortinarius anomalus
Cortinarius armillatus
Cortinarius aurantiobasis
Cortinarius badiolatus
Cortinarius barlowensis
Cortinarius caninus
Cortinarius caperatus
Cortinarius casimiri
Cortinarius comptulus
Cortinarius delibutus
Cortinarius disjungendulus
Cortinarius duristipes
Cortinarius evernius
Cortinarius fennoscandicus
Cortinarius ferruginosus
Cortinarius fulvescens
Cortinarius fuscescens
Cortinarius glandicolor

Cortinarius illibatus
Cortinarius illuminoides
Cortinarius ionophyllus
Cortinarius ionosmus
Cortinarius jonimitchelliae
Cortinarius leiocastaneus
Cortinarius lucorum
Cortinarius luteo-ornatus
Cortinarius malicorius
Cortinarius millaresensis
Cortinarius multiformis
Cortinarius NA
Cortinarius obtusus
Cortinarius ochrophyllus
Cortinarius panellus
Cortinarius pluviorum
Cortinarius pluvius
Cortinarius pseudoturmalis
Cortinarius rufolatus
Cortinarius scaurus
Cortinarius septentrionalis
Cortinarius spilomeus
Cortinarius subpaleaceus
Cortinarius transatlanticus
Cortinarius valgus
Cortinarius var._notandus
Cortinarius vibratilis
Cortinarius violaceus
Cortinarius xanthocephalus
Lyophyllum NA
Piloderma bicolor
Piloderma lanatum
Piloderma sphaerosporum
Sistotrema luteoviride
Sistotrema muscicola
Tricholoma fulvum
Tricholoma NA
Tricholoma saponaceum
Tricholoma stiparophyllum

Medium distance smooth species
Entoloma borgenii
Entoloma paludicola
Entoloma politum
Entoloma rhodopolium
Entoloma rubrobasis
Entoloma sericatum
Entoloma serpens
Hydnum NA
Lactarius atroviridis
Lactarius flexuosus
Lactarius glyciosmus
Lactarius hengduanensis
Lactarius lapponicus
Lactarius NA
Lactarius necator
Lactarius rufus
Lactarius tabidus
Lactarius tesquorum
Lactarius trivialis
Lactarius vietus
Pseudotomentella alnophila
Pseudotomentella mucidula
Pseudotomentella NA
Pseudotomentella pluriloba
Pseudotomentella umbrina
Tomentella badia
Tomentella bryophila
Tomentella clavigera
Tomentella coerulea
Tomentella ellisii
Tomentella lapida
Tomentella lateritia
Tomentella NA
Tomentella stuposa
Tomentella subclavigera
Tomentella sublilacina
Tomentella viridula

Tomentellopsis NA
Tomentellopsis submollis

Short distance species
Alnicola cholea
Alnicola NA
Alnicola spectabilis
Amanita constricta
Amanita magnivolvata
Amanita NA
Ambispora NA
Aspicilia NA
Cadophora orchidicola
Cenococcum geophilum
Cenococcum NA
Clavulina coralloides
Clavulina NA
Clavulina ornatipes
Cryptodiscus NA
Genabea NA
Geopora NA
Gymnopilus penetrans
Hebeloma aurantioumbrinum
Hebeloma cavipes
Hebeloma hetieri
Hebeloma hiemale
Hebeloma mesophaeum
Hebeloma NA
Helvellosebacina NA
Hygrophorus discoideus
Hygrophorus monticola
Hygrophorus olivaceoalbus
Hygrophorus pustulatus
Hymenogaster NA
Hymenogaster rubyensis
Inocybe acuta
Inocybe ambigua
Inocybe assimilata
Inocybe borealis
Inocybe catalaunica

Inocybe flavella
Inocybe geophylla
Inocybe grammata
Inocybe impexa
Inocybe lacera
Inocybe lanuginosa
Inocybe lapponica
Inocybe mixtilis
Inocybe NA
Inocybe napipes
Inocybe nitidiuscula
Inocybe nothomixtilis
Inocybe pallidicremea
Inocybe posterula
Inocybe pseudodestricta
Inocybe rufoalba
Inocybe soluta
Inocybe stellatospora
Inocybe substellata
Inocybe teraturgus
Inocybe tetragonospora
Inocybe whitei
Laccaria laccata
Laccaria NA
Laccaria pseudomontana
NA NA
Naucoria bohemica
Naucoria NA
Oidiodendron maius
Otidea nannfeldtii
Pulvinula NA
Rhodoscypha NA
Russula adusta
Russula amoenoides
Russula cessans
Russula citrinochlora
Russula claroflava
Russula consobrina
Russula cupreola
Russula decolorans

Russula emetica
Russula favrei
Russula griseascens
Russula helodes
Russula intermedia
Russula murrillii
Russula NA
Russula nuoljae
Russula paludosa
Russula sapinea
Russula suecica
Russula versicolor
Russula vinososordida
Russula violaceoincarnata
Russula viscida
Sebacina NA
Tomentellopsis NA
Tomentellopsis submollis
Trichophaea NA
Tuber NA
Tuber wenchuanense
Tylospora asterophora
Tylospora fibrillosa
Wilcoxina mikolae