

Salmon carcass subsidies in soil: implications for management of marine derived nitrogen in riparian areas

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Abstract

Pacific salmon acquire most of their biomass in the ocean before returning to spawn and die in coastal stream and lakes, thus providing subsidies of marine-derived nitrogen (MDN) to freshwater and terrestrial ecosystems. Recent declines in salmon abundance have raised questions of whether managers should mitigate for losses of salmon MDN subsidies. The ecological importance of salmon subsidies for direct consumers (e.g., bears, birds, insects) is well established; however, many studies examining the broader role of salmon nutrients have documented the presence of MDN, without demonstrating its ecological importance. This knowledge gap is particularly pronounced in terrestrial systems. To test the long-term importance of salmon to riparian ecosystems, a 20-year manipulation was performed where salmon carcasses were systematically removed from one bank and deposited on the opposite bank along the full length of a 2 km stream in southwestern Alaska. We examined the long-term effect of this manipulation on riparian soil fertility. Soil samples were taken from nine paired transects along the stream at distances 1, 3, 6, 10, and 20 m from the bank and measured for organic and inorganic nitrogen ($[\text{NH}_4^+]$, $[\text{NO}_3^-]$, $[\text{N}_{\text{Org}}]$) and nitrogen transformation rates (net mineralization and net nitrification). The potential presence of MDN was also measured using $^{15}\text{N}/^{14}\text{N}$ for bulk soils as well as NH_4^+ and NO_3^- soil pools. Stable isotope analyses confirmed $^{15}\text{N}/^{14}\text{N}$ was elevated on the salmon enhanced bank compared to the salmon depleted bank. However, $^{15}\text{N}/^{14}\text{N}$ values of plant-available inorganic nitrogen exceeded the $^{15}\text{N}/^{14}\text{N}$ of salmon inputs, highlighting N isotope fractionation in soils that raises significant methodological issues with standard MDN assessments. Surprisingly, despite 20 years of salmon supplementation, the presence of MDN did not cause a long-term increase in soil N availability measured immediately prior to salmon return during the peak vegetative growth season. This finding raises questions about the contribution of MDN subsidies to riparian vegetation and indicates their importance to ecosystem N

26 biogeochemistry may be overestimated. Our findings further suggest that other site factors
27 such as soil moisture and stand demography may influence riparian forest growth. Given that
28 essential nutrients can also be pollutants, we urge more critical analyses of the role of MDN
29 to inform compensatory mitigation programs targeting salmon nutrient enhancement.

Introduction

Pacific salmon (*Oncorhynchus* spp.) migration from marine environments to freshwater spawning grounds is a textbook case of cross-ecosystem nutrient subsidies, and dozens of studies have identified the presence of marine-derived nitrogen (MDN) from salmon as crossing ecosystem boundaries from oceans to freshwaters and into the terrestrial environment (sensu, Polis et al. 2004, Gende et al. 2002, Schindler et al. 2003). Declines in Pacific salmon populations in many areas, caused by human activities (overharvest, habitat degradation, dams) (Gustafson et al. 2007), and the concern over loss of MDN to coastal watersheds has made restoration of salmon nutrients a focal point for many management and mitigation strategies. For example, in the Columbia River Basin where Pacific salmon populations have declined, legislation requiring compensatory mitigation has led to nutrient enhancement programs, on the foundation that habitats have lost critical nutrients from salmon and therefore augmentation is necessary to maintain ecosystem function (Collins et al. 2015).

Salmon bring nutrients, including phosphorus (P) and other compounds in addition to nitrogen (N), into freshwater and terrestrial food webs through two pathways: 1) direct consumption of tissues by predators and scavengers, and 2) autotrophic or heterotrophic assimilation of nutrients released as salmon spawn, die, and eventually decay (Gende et al. 2002). Salmon are enriched in the heavy isotope of nitrogen (^{15}N) relative to the light isotope (^{14}N) when compared to terrestrial and watershed-derived N. This isotopic enrichment has been used to quantitatively trace the presence of salmon derived nutrients into watersheds (Schindler et al. 2003). For example, the proportion of N derived from salmon ranges from approximately 30% – 75% in fish and aquatic invertebrates (Naiman et al. 2002), 10 – 90% in piscivorous mammals such as bears, and 20 – 40% in piscivorous fishes near salmon

spawning grounds (Bilby et al. 1996, Hilderbrand et al. 1999, Chaloner et al. 2002, Claeson et al. 2006).

The annual return of this predictable and abundant, yet temporally limited, high quality resource drives the foraging ecology of both terrestrial and aquatic consumers (Quinn 2018). Carcasses and roe are documented food sources for over 22 species of mammals, birds (Cenderholm et al. 1989), fishes (Scheuerell et al. 2007), and invertebrates (Minakawa et al. 2002, Meehan et al. 2005; Winder et al. 2005). Bear population density, body size, and reproductive output has been correlated with meat (primarily salmon) consumption, with piscivorous populations having 55 times higher density than their meat-limited counterparts (Hilderbrand et al. 1999). In aquatic ecosystems, salmon carcass abundance has been correlated with elevated growth rates of invertebrates, and with size, density, and condition factor of juvenile salmonids (Bilby et al. 1998, Minakawa et al. 2002, Wipfli et al. 2003).

The presence of MDN has been documented in aquatic primary producers, though its overall ecological importance remains ambiguous. Via this bottom-up pathway, salmon supply critical limiting nutrients that can increase primary and/or bacterial productivity, which are subsequently transferred to consumers and up through the food web (Wipfli et al. 1998, Chaloner et al. 2002, Holtgrieve and Schindler 2011). Higher salmon returns are correlated with MDN signatures in lower trophic levels including zooplankton and periphyton (Kline et al. 1993, Finney et al. 2000, Holtgrieve et al. 2010). Both direct ecological and paleolimnological evidence suggest MDN and P positively influence primary production in lakes (Moore et al. 2007). For example, commercial fisheries remove upwards of two-thirds of MDN which would otherwise enter some freshwater lakes in Alaska, resulting in a 3-fold decline in algal production (Schindler et al. 2005). In stream ecosystems, the decomposition of salmon increases dissolved organic and inorganic nutrients, including highly available forms such as orthophosphate (PO_4^{3-}) and ammonia/ammonium ($\text{NH}_3/\text{NH}_4^+$).

These nutrients can stimulate epilithon growth (bacteria and algae), though the magnitude of this response is highly variable, and dependent on other growth limiting factors such as sunlight and disturbance, (Johnston et al. 2004, Mitchell and Lamberti 2005, Janetski et al. 2009).

In the terrestrial realm, bottom-up effects of MDN from salmon are also thought to be ecologically important, though this has been difficult to demonstrate rigorously. Studies across the range of salmon in North America have inferred that up to 26% of foliar N in riparian plants is marine derived, with foliar N levels often correlating with salmon abundance and distance from the salmon spawning location (e.g., Hocking and Reynolds 2012, Reimchen and Fox 2013). While MDN is clearly present in terrestrial producers, direct evidence of the importance of MDN for ecosystem function and productivity is much less evident. Helfield and Naiman (2001) measured tree growth increments in areas with and without salmon and found higher growth in one species (Sitka spruce) in areas where salmon nutrients were present, although these findings were later contested on statistical grounds (Kirchoff 2003). Hocking and Reynolds (2012) observed decreased understory plant diversity with increasing salmon abundance, though this pattern was largely attributed to increased dominance of a single N tolerant species (salmonberry). Reimchen and Fox (2013) suggested that salmon abundance increased tree growth, but tree ring $^{15}\text{N}/^{14}\text{N}$ values were not related to salmon abundance; other growth limiting factors such as temperature and location were important covariates. Most recently, Quinn et al. (2018) examined tree growth increments in the riparian zone of a small Alaskan stream before and after a 20-year, > 200,000 kg, salmon carcass manipulation. In the two decades prior to manipulation, white spruce (*Picea glauca*) on average grew faster on one bank compared to the other. The subsequent decades of carcass manipulation enriched the naturally slower growing side, and were associated with increased growth. However, the growth effect of the carcasses was smaller than the natural side-to-side

variation, and other important site factors such as forest demography, climate, aspect, and water availability were not fully considered.

Interpreting the contributions of MDN to terrestrial producers using stable isotopes is often highly simplified, and does not consider how variability of N sources and overall N availability may confound results. MDN analyses apply simple two-source mixing models to infer the proportion of total N derived from salmon. When applied to terrestrial vegetation, the terrestrial end-member for the mixing models is typically determined by sampling the $^{15}\text{N}/^{14}\text{N}$ of the same species of plant either laterally away from the stream (where MDN contribution is expected to be small), upstream of barriers to salmon migration, or in watersheds without salmon. For the salmon end-member, a single value equal to the average $^{15}\text{N}/^{14}\text{N}$ of salmon (12.62 ± 0.31 per mil for sockeye salmon) is typically used (S1). Inherent assumptions with these models therefore include: 1) reference sites are biogeochemically similar to salmon sites and 2) the isotopic signature of salmon is unchanged in the soils prior to plant uptake. N cycling in soils is strongly controlled by position in the landscape and contains a number of chemical reactions which fractionate N isotopically (Högberg 1997, Figure 1), therefore these assumptions may not be valid.

Experiments examining the contributions of MDN are often limited by short timescales, and relatively few experiments investigate changes in plant-available soil N pools important to plant nutrient uptake and growth (Collins et al. 2015). Studies examining spatial and temporal impacts of salmon on soil inorganic N have identified highly localized responses (effects only observed < 30 cm from carcasses) where soil ammonium (NH_4^+) and nitrate (NO_3^-) increase for weeks to months (Drake et al. 2005, Gende et al. 2007, Holtgrieve et al. 2009). Experiments typically examine the contributions of MDN by nutrient addition not nutrient removal; however, nutrient removal is important for understanding the effects of lower numbers of salmon returning to coastal watersheds due to fishing, habitat reduction,

and climate change. In addition, previous research observed a strong effect of watershed slope on $^{15}\text{N}/^{14}\text{N}$ in riparian plants and attributed this to topography concentrating carcasses near streams (Hockings and Reynolds, 2012). Watershed topography also influences soil water content and N cycling, which affect N isotopes (Högberg 1997) and may complicate MDN assessments.

To resolve the extent to which salmon carcasses contributed MDN to plant-available N pools and the long-term ecological response of this subsidy, we present a second study of the 20-year carcass manipulation experiment described in Quinn et al. (2018). While Quinn et al. focused on tree growth before and after the manipulation, the objective of this work was to determine whether prolonged enhancement and reduction of salmon subsidies altered long-term soil N cycling as documented previously with N fertilizer additions (Prescott et al. 1992, Prescott et al. 1995, Lu et al, 2010). If long-term changes in N availability due to salmon enhancement or reduction were observed, compensatory nutrient subsidies may be valuable for maintaining critical ecosystem functions in riparian areas with reduced salmon returns. If not, then the addition of nutrients as a management response to low salmon returns may have unintended negative consequences (*sensu* Compton et al. 2006). Specifically, the importance of MDN to riparian ecosystems was assessed by 1) evaluating the presence of MDN in soils enhanced and depleted in salmon through bulk stable isotope analysis of N, 2) quantifying the response of plant-available N pools ($[\text{NH}_4^+]$ and $[\text{NO}_3^-]$) and their rate of supply via mineralization and nitrification and 3) considering how fractionation in soils may impact mixing model results by measuring $^{15}\text{N}/^{14}\text{N}$ of NH_4^+ . This research fills key knowledge gaps by examining the long-term legacy of inorganic N pools, both salmon addition and removal, and considering site variability following a 20-year manipulation.

Methods

Site Description and Sample Collection

This study was conducted on Hansen Creek, a ~2 km long, 2nd order tributary to Lake Aleknagik in the Wood River system of Bristol Bay, AK and uses the same carcass manipulation described in Quinn et al. (2018). Briefly, from 1997-2016 an average of 10,853 sockeye salmon returned to the stream annually. Overstory vegetation is dominated by white spruce and paper birch (*Betula papyrifera*), and unlike many other watersheds in the region, it has a low density of symbiotic N₂-fixing alder (*Alnus spp.* Helfield and Naiman 2002). From 1997-2016 the stream was surveyed daily during the annual sockeye salmon (*Oncorhynchus nerka*) run and all dead salmon were removed from the creek and the river right bank to a distance of about 5 m and tossed onto the river left bank. Thus, the right side of the stream experienced a reduction in carcass density (depletion) while the left bank received an increase in carcasses (enhancement). Quinn et al. (2018) calculated approximately 108,530 individual fish (in many cases partially consumed by bears) were translocated over the 20-year period representing a total of 267,620 kg of salmon, 8,028 kg of N and 1,356 kg of phosphorus (P). To estimate the mass of nitrogen added per m² we assumed all salmon were tossed within 6 m of the creek's edge along the entire 2 km creek, thus within a 12,000 m² area.

Soil samples were collected from the riparian zone on 13 July, 2017 (prior to arrival of salmon and any carcass manipulation that season) along nine sets of paired transect sites. Transects covered the full 2 km length of the stream and were selected to represent typical riparian vegetation and high annual carcass abundance. Each transect included sampling sites at 1, 3, 6, 10, and 20 m from the bank-full point. Sampling occurred during peak growing season (i.e., during the typical time of maximum normalized difference vegetation index (NDVI); Kasischke and French 1995), approximately one week prior to the arrival of the first salmon in the creek. Thus, our sampling was intended to capture the long-term legacy of

MDN manipulations and specifically avoid short-term pulses following salmon return that may not represent a system-level change in N availability and recycling in soils. A 5 cm x 5 cm x 10 cm soil column was taken for each sample site and the litter layer was removed before storing at 4 °C in airtight plastic bags for 48 hours prior to processing. Nitrogen cycling decreases dramatically with depth, sampling at this depth includes the O and A horizons where a majority of nitrogen cycling occurs (Sparks et al. 1996).

Soil nitrogen concentrations and transformations

Soil $[\text{NH}_4^+]$, $[\text{NO}_3^-]$, and N transformations were measured according to Holtgrieve and Schindler (2009). Briefly, we extracted 10 to 12 g of field-moist sieved (< 2 mm) soil with 100 mL of 2 M potassium chloride (KCl) by shaking for 60 s, followed by settling for 24 hours prior to filtration through pre-leached Whatman #1 filter papers. Approximately 8 mL of filtered extracts were frozen and later analyzed colorimetrically for $[\text{NH}_4^+]$ and $[\text{NO}_3^-]$ with an Auto-Analyzer 500 Model (Perstorp Analytical Co, Analytical Service Station, Seattle, WA, USA). The remaining extract was frozen prior to stable isotope analyses (see below). To estimate inorganic N transformation rates, a second 10 to 12 g soil subsample was incubated aerobically in the dark for 15 d at 20°C prior to extraction, filtration, and analysis as above. Net mineralization was calculated as the sum of the change in $[\text{NH}_4^+]$ and $[\text{NO}_3^-]$ divided by the incubation duration, and net nitrification was calculated as the change in $[\text{NO}_3^-]$ over the incubation duration (Hart 1994). $[\text{N}_{\text{org}}]$ was calculated by taking total soil N concentration, $[\text{N}_{\text{tot}}]$ determined by mass spectrometry (see below) and subtracting $[\text{NH}_4^+]$ and $[\text{NO}_3^-]$. All soil N values were corrected for gravimetric soil water content (g H_2O /g dry soil) determined by drying 50 to 100 g of field-moist soil at 105°C for 48 h (Gardner, 1986).

Stable isotope analysis

Fresh soil was freeze dried for 48 h and ground into a uniform powder ($< 212 \mu\text{m}$) using a ball mill prior to analysis for nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) stable isotope

ratios at the University of Washington's IsoLab using a Costech Elemental Analyzer, ConFlo III MAT253 for continuous flow-based measurements. This procedure also provided total carbon and nitrogen concentrations, $[C_{\text{tot}}]$ and $[N_{\text{tot}}]$, of the soil samples. Data are reported using standard delta notation, which describes the per mil deviation in the ratio of heavy to light isotope relative to accepted international standards, in this case air and Vienna Pee Dee Belemite (VPDB) for N and C respectively (Schoeninger et al. 1983).

For $^{15}\text{N}/^{14}\text{N}$ stable isotope analysis of NH_4^+ and NO_3^- , KCl extracts were placed in Erlenmeyer flasks for diffusion using modified methods from Sigman et al. (1997) and Holmes et al. (1998). To retrieve NH_4^+ as gaseous NH_3 , 300 mg of MgO and an acid trap (1 cm glass fiber filter treated with KHSO_4 and sealed in Teflon) were added to each flask, immediately stoppered, sealed with parafilm, and shaken for six days prior to removal of acid traps to a desiccator for 3 to 4 days. The same extracts were then shaken uncovered for one day to remove any remaining NH_4^+ . To retrieve NO_3^- as NH_3 , another 300 mg of MgO were added to each extract and immediately followed with 75 mg of Devarda's alloy and an acid trap, then processed as above. Samples were run in four separate batches, for each batch three blanks (KCl with no soil extract) and three reference standards, NH_4Cl and KNO_3 with known $^{15}\text{N}/^{14}\text{N}$, were also run. Batch blanks showed quantifiable N from the KCl; therefore, a two-source mixing model correction was applied to both samples and reference standards using equation 1:

$$(1) \delta^{15}\text{N}_{\text{blank corrected}} = (\delta^{15}\text{N}_{\text{measured}} (N_{\text{blank}, x} + N_{\text{extracted}}) - (\delta^{15}\text{N}_{\text{blank}, x} N_{\text{blank}, x})) / N_{\text{extracted}}$$

Where x represents an individual batch, $N_{\text{blank}, x}$ is the average measured mass (μg) of nitrogen in a blank for a given batch, and $\delta^{15}\text{N}_{\text{blank}, x}$ is the average measured $\delta^{15}\text{N}$ of blanks for a given batch. $\delta^{15}\text{N}_{\text{measured}}$ is the $\delta^{15}\text{N}$ value for a given sample, and $N_{\text{extracted}}$ is the mass of nitrogen (μg) measured in the sample. A standard correction was then applied to the blank corrected measurements where:

$$(2) \delta^{15}\text{N}_{\text{corrected}} = \delta^{15}\text{N}_{\text{blank corrected}} - (\text{Standard}_{\text{measured}, x} - \text{Standard}_{\text{true}})$$

Where $\text{Standard}_{\text{measured}, x}$ is the average measured value of the standard for a given batch. All reported $\delta^{15}\text{N}$ of NH_4^+ and NO_3^- values are expressed as the $\delta^{15}\text{N}_{\text{corrected}}$, where a blank and standard correction has been applied. The internal standard of the $\delta^{15}\text{N}$ of NO_3^- had a -23.6 to 9.6 ‰ deviation from its true value, indicating a significant methodological issue. Given there was not enough sample to refine these methods and the potential for standard corrections of this magnitude to be misleading, $\delta^{15}\text{N}$ of NO_3^- data are not reported here.

C:N ratio, percent nitrification, and %C were also calculated to evaluate N availability and retention across the sites. C:N ratios were calculated from bulk isotope data by dividing %C by %N. Percent nitrification was calculated as:

$$(3) \text{Percent Nitrification} = 100 * \text{Net nitrification} / \text{Net Mineralization}$$

Statistical analyses

We used multi-model selection procedures via Akaike's information criterion (AIC) to identify how salmon carcass treatment governed a suite of response variables using the stats v3 and lme4 packages in R. These response variables were: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of bulk soil, $\delta^{15}\text{N}$ of NH_4^+ , $[\text{NH}_4^+]$ and $[\text{NO}_3^-]$, net mineralization and net nitrification, $[\text{N}_{\text{org}}]$, gravimetric water content (GW), and C:N. For all response variables, candidate models (S2) included bank (left vs. right) and distance from river's edge. A linear and quadratic interaction structure for bank and distance were fit for each response variable and these interaction terms allowed the effect of distance to vary by bank and the effect of bank to vary by distance. A \log_e transformation was used for the distance. GW was considered as a covariate for all response variables, soil $[\text{NH}_4^+]$ was considered as a covariate for net nitrification, and soil $[\text{N}_{\text{org}}]$ was considered as a covariate for net mineralization, given $[\text{N}_{\text{org}}]$ and $[\text{NH}_4^+]$ function as the substrate for mineralization and nitrification respectively. $[\text{N}_{\text{tot}}]$ was considered as a covariate for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of bulk soil, and for $\delta^{15}\text{N}$ of NH_4^+ . The best model was selected

from the candidate model set using AIC for each response variable. Under circumstances where multiple models had a ΔAIC value of < 2 , the most parsimonious model was selected.

Two model parameters – bank (left vs. right) and distance from the stream – were used to test salmon carcasses and site variability impacts to soil N cycling. Changing the number of salmon carcasses on each bank was the primary goal of the manipulation; however, the two banks potentially differ in aspect, soil type, and drainage, which can affect nutrient cycling and generate a bank effect unrelated to salmon manipulation (Chapin et al. 2011). Notably, the salmon enhanced bank has a northwest facing slope within 20 m of the creek edge. Distance from the stream reflects the magnitude of salmon manipulation because carcasses were not left immediately along the stream's edge, nor were they moved more than about 6 m from the stream. However, vegetation, soil type, and water availability can also change with distance. Therefore, model support for both distance and bank parameters and a peak response between 3 – 6 m indicates an effect of salmon on the response variables, but support for only one of these parameters or no response at 3 – 6 m demonstrates underlying site variability in the system. For each of the nine response variables, five competing hypotheses were compared, that the differences in response variables were due to H1) a bank and/or distance effect not caused by salmon manipulation, including a linear interaction, indicating a site variability not caused by salmon manipulation, H2) a bank and distance effect as a quadratic interaction with a peak between 3 – 6 m indicting a response to salmon manipulation or H3) no difference caused by distance and bank indicating support for the other covariates tested. These hypotheses were tested by categorizing each candidate model into one of the three hypotheses (S2, Table 1) and considering the hypothesis categorization for the model with the most support, and any additional competing models with relative support (ΔAIC value of < 2) (Burnham and Anderson 2002) for each response variable under consideration (e.g., $[NH_4^+]$, $[NO_3^-]$, $\delta^{15}N$, etc.). If models showed support for H2, the effect

of salmon was confirmed by examining whether the response variable peaked at the salmon enhanced bank between 3 – 6 m. If this did not occur, the response is likely due to site variability and not salmon.

Results

Bulk soil stable isotope analysis indicated that salmon carcasses enriched the N isotope pools (Table 1). $\delta^{15}\text{N}$ values peaked between 3 and 6 m from the stream edge, which was the distance salmon were typically relocated to during the experiment and declined at distances greater than 6 m. Maximum $\delta^{15}\text{N}$ of bulk soils was 11.8‰ for the salmon enhanced bank and 11.6‰ for the salmon depleted bank and no observations exceeded the sockeye salmon end-member value of 12.6‰ (Figure 2a). $\delta^{13}\text{C}$ was more enriched at greater distances from the bank and on average was highest at 20 m (Figure 2b). $\delta^{13}\text{C}$ was primarily governed by distance, with some evidence $[\text{N}_{\text{tot}}]$ and bank also had an effect (Table 1).

Salmon carcass manipulation also enriched $\delta^{15}\text{N}$ of NH_4^+ . Stable isotope values were enriched at 3 m from the stream edge on the salmon enhanced bank, and declined at distances > 3 m. On the salmon depleted bank, $\delta^{15}\text{N}$ of NH_4^+ was most enriched at 1 m and declined with distance (Figure 2c). The only model with support contained a quadratic interaction of distance and bank, which provides strong evidence that $\delta^{15}\text{N}$ of NH_4^+ was affected by salmon (Table 1). In contrast to bulk soil N, $\delta^{15}\text{N}$ values of NH_4^+ exceeded the salmon endmember of 12.6‰ for 23% of all observations ($n=21$).

Inorganic nitrogen concentrations were primarily governed by bank and GW, with some support for distance (Table 1). The salmon enhanced bank had a higher mean $[\text{NH}_4^+]$ and $[\text{NO}_3^-]$ compared to the salmon depleted bank (Figure 2d, e). The most supported models for both $[\text{NH}_4^+]$ and $[\text{NO}_3^-]$ showed evidence for H1. For $[\text{NH}_4^+]$ there was substantial model uncertainty, with six competing models receiving relative support ($\Delta\text{AIC} < 2$) (Table 1).

Similarly, the three competing models for $[\text{NO}_3^-]$ supported both H1 and H2 (Table 1). This indicates $[\text{NH}_4^+]$ was driven by site factors while $[\text{NO}_3^-]$ was driven by a combination of site variability and salmon enhancement. This result demonstrates that $[\text{NO}_3^-]$ concentrations differed between the two banks, but whether that effect resulted from salmon or other biogeochemical factors that may vary between the two banks is uncertain.

Nitrogen transformation rates were generally unaffected by salmon carcass manipulation. Both net nitrification and net mineralization models with relative support contained N substrate ($[\text{NH}_4^+]$ and $[\text{N}_{\text{org}}]$ respectively), and the models with the most support did not include distance or bank. Net mineralization had high model uncertainty, with five models receiving similar relative support; however, all of the competing models supported either H1 or H3 with no support for H2. $[\text{N}_{\text{org}}]$ was the only covariate included in all of the competing models, indicating $[\text{N}_{\text{org}}]$ was the most important covariate tested for determining net mineralization. Net nitrification had greater model certainty and both models that received relative support contained $[\text{NH}_4^+]$ and gravimetric water content. Similar to net mineralization, these models supported H1 and H3 with no support for H2, though net nitrification was slightly higher on average between 3 – 6 m on the salmon enhanced bank (Table 1). Overall, these results demonstrated the manipulation of salmon carcasses did not have clearly detectable effects on N transformation rates.

Both $[\text{N}_{\text{org}}]$ and GW indicated there are differences caused by distance and bank unrelated to salmon carcass manipulation. On average $[\text{N}_{\text{org}}]$ was higher on the salmon depleted bank than the salmon enhanced bank. There was model support H1 for both GW and $[\text{N}_{\text{org}}]$, indicating these variables decrease with distance (Table 1, Figure 2 h, i). While there was some evidence that there was both a distance and bank effect on GW, it is unlikely caused by salmon as the salmon enhanced bank does not show a peak GW at 3 - 6 m from the stream, which was where there was the highest observed isotopic enrichment and expected

MDN. However, one competing model for $[N_{org}]$ did support H2, indicating site factors and salmon may both affect $[N_{org}]$. However, the mean $[N_{org}]$ for the salmon enhanced bank was 18.42 mg/g and 18.97 mg/g for the salmon depleted bank demonstrating that salmon decrease $[N_{org}]$, if they affect it at all.

C:N, percent nitrification, and percent carbon indicate relatively high nitrogen availability across sampling sites in the Hansen Creek system. Percent carbon had means of 24.2 and 24.9 on the enhanced and depleted banks respectively (S3). C:N of bulk isotopes was less than 20 for all sites, with means of 15.8 (enhanced) and 14.2 (depleted). These values are well below the critical microbial C:N threshold of 29, demonstrating nitrogen is more available to meet microbial metabolic demands relative to carbon (Figure 2j). In contrast, percent nitrification was relatively high with a mean of 64% and 62% on the enhanced and depleted banks (S3).

Discussion

This study confirmed that MDN was both present in soils and increased on the bank enhanced with salmon carcasses for 20 years. However, plant-available inorganic N pools and N transformation rates measured in soil during the peak growing season immediately prior to the annual return of salmon were largely unaffected by salmon enhancement. Even though the salmon enhanced bank had increased net nitrification compared to the salmon depleted bank, our analysis found no pattern with distance from the stream, suggesting that elevated nitrification was caused by bank characteristics unrelated to salmon carcass density. Given numerous conventional long-term fertilization experiments worldwide have shown a consistent pattern of elevated soil inorganic N pools and N transformations, (Högberg 2006, Lu et al. 2010), it was surprising that 20 years of MDN inputs did not clearly accelerate soil N cycling in our study. Soils are the dominant (> 70%) sink for added N in forests worldwide

(Templer et al. 2012) and tree growth in high latitude conifer forests is often strongly N-limited (Nordin et al. 2001), both of which should have fostered retention of salmon N inputs to our site. Indeed, the 20 years of cumulative salmon N additions in the zone near the stream in our study ($\sim 6,690$ kg N/ha) greatly exceeded typical riparian surface soil N pools (500 to 2500 kg N/ha, Walker 1989, Morris and Stanford 2011, Perry et al. 2017), suggesting that even partial retention of salmon N inputs in soils should have increased soil $[N_{org}]$. The lack of increase in soil $[N_{org}]$ due to salmon that we observed is consistent with the lack of increase in N availability, because soil $[N_{org}]$ fuels long-term changes in N availability and recycling via plant uptake, litterfall, and decomposition (Chappel et al. 1999, Perakis and Sinkhorn 2011, Perakis et al. 2012). Overall, the lack of increase in soil organic and inorganic N concentrations and N transformations that we observed following 20-year salmon manipulation raises questions of whether plant growth responses should be expected at our site.

Prior work at Hansen Creek inferred that MDN stimulated white spruce growth based on tree ring analyses (Quinn et al. 2018). However, substantial salmon enhancement corresponding to approximately 669 g/m^2 ($6,690 \text{ kg/ha}$) of N and 113 g/m^2 ($1,130 \text{ kg/ha}$) of P over the past 20 years was unable to overcome pre-treatment differences in forest growth between banks. For reference, it is estimated white spruce in floodplain stands require approximately $1.35 \text{ g/m}^2/\text{y}$ of N (Chapin et al. 2006), which was far exceeded by the mean change of $33.45 \text{ g/m}^2/\text{y}$ of N added from this manipulation. Additionally, fertilization experiments apply N on the order of 100 - 1,000 kg/ha with clear results (Chappell et al. 1999), a much lower application rate than in this study. Factors such as climate, site, and landscape variability, and stand demography also affect tree growth in this system. Indeed, white spruce growth response to recent warming across southwest Alaska depends strongly on tree density (Wright et al. 2018). Basal area density is highly variable across our site,

differing on average 40% between salmon-enhanced and salmon-depleted banks, although the difference was not statistically significant (Quinn et al. 2018). Ultimately, the hierarchy of drivers of tree growth in this ecosystem appears to be landscape position (and associated forest demography) followed by climate and thirdly, nutrients. All told, a lack of long-term changes in soil nutrient dynamics and only marginal response in tree growth indicates that salmon nutrients are not a strong bottom-up force in northern riparian forest dynamics.

Our $^{15}\text{N}/^{14}\text{N}$ stable isotope data raise further questions of assessing MDN subsidies to tree growth. Vegetation typically takes up only 17% of added $^{15}\text{N}/^{14}\text{N}$ to forests, with soils instead being the dominant N sink (Templer et al. 2012). Thus, elevated bulk soil $^{15}\text{N}/^{14}\text{N}$ in our study suggests a potentially significant MDN sink in soil. On the other hand, elevated bulk soil $^{15}\text{N}/^{14}\text{N}$ may also reflect increases in soil N fractionation during N cycling and loss under salmon. Highly localized N pulses (as occur with MDN and other N subsidies) temporarily exceed plant and soil N sinks, leading to accelerated N loss via ammonia volatilization, nitrification and nitrate leaching, and/or denitrification (Perakis 2002). All of these N loss pathways favor ^{14}N and discriminate against ^{15}N (in some cases with a fractionation up to 30‰), and effects are strongest at high N availability, leading to high values of residual soil ^{15}N (Högberg et al. 1997). Prior work has shown that MDN inputs accelerate N losses from soil, particularly gaseous N losses (Holtgrieve et al. 2009) that are associated with large isotope fractionation (Högberg et al. 1997). Our finding that $\delta^{15}\text{N}$ of soil NH_4^+ was greater than bulk soil $\delta^{15}\text{N}$ for 95% of observations on the salmon enhanced bank and 84% of observations on the salmon depleted bank, further confirms that isotopic fractionation is important at Hansen Creek and likely elsewhere, but is rarely considered, leading to an overestimation of MDN importance.

There is a global trend for higher foliar $\delta^{15}\text{N}$ with increased soil N supply (Craine et al. 2009) indicating accelerated soil N cycling and $\delta^{15}\text{N}$ fractionation due to exogenous N

(from salmon or elsewhere) will alter plant foliar $\delta^{15}\text{N}$. This has important implications for using two-source mixing models to assess salmon N subsidies to riparian forests. Typical MDN mixing models assume 1) the isotopic signature of salmon is unchanged in the soils prior to plant uptake, and 2) reference sites are biogeochemically similar to salmon sites. However, our data suggest that both of these assumptions are likely violated at Hansen Creek. First, we observed that $\delta^{15}\text{N}$ of NH_4^+ , the dominant form of inorganic N in our soils, exceeded the 12.6‰ salmon end-member for 26% of our observations from the salmon enriched bank and 9% of observations from the salmon depleted bank, thus violating assumption (1) above. Our soil N data indicate Hansen Creek is a site of intermediate fertility relative to other boreal forests, so that soil NH_4^+ (rather than organic N or NO_3^-) is most likely the dominant N source taken up by plants (Chapin et al. 2011). Second, $[\text{N}_{\text{Org}}]$, C:N, $\delta^{13}\text{C}$, and GW varied with distance from the stream independent of salmon enhancement. This presents a challenge for selecting control sites to calculate terrestrial end members, as key N cycling factors vary longitudinally away from streams and simply selecting reference sites that are beyond the reach of salmon would likely violate the mixing model assumption of biogeochemical similarity. Additionally, observations of $\delta^{13}\text{C}$ increasing and GW decreasing from the creek edge are consistent with higher water use efficiency and less ^{13}C discrimination by vegetation, resulting in higher $\delta^{13}\text{C}$ in soil due to litterfall (Gabriel and Phillip 2016). These data identify systematic differences between salmon-enhanced vs. salmon-depleted banks that cannot be attributed to salmon, and which likely reflect landscape or soil differences. Previous studies examining contributions of MDN to riparian vegetation have not tested biogeochemical similarity across sites, an assumption that is likely violated beyond Hansen Creek specifically.

Violation of mixing model assumptions can lead to significant bias in calculations of MDN sources. To illustrate this point, we applied a typical mixing model framework to our

maximum observed $\delta^{15}\text{N}$ of NH_4^+ values to calculate the percent MDN contribution of salmon to NH_4^+ for the most extreme observation. Assuming soil processes have no effect on the isotopic signature yielded impossible result of 298% MDN contribution. To account for isotopic fractionation in soils, we applied our mean observed $\delta^{15}\text{N}$ of soil NH_4^+ at the 3 m distance (19.25‰) as the marine endmember to mean foliar $\delta^{15}\text{N}$ data from Quinn et al. (2018) and estimate 59.24% MDN on the salmon bank, which is 27.4% lower than the original estimate of 86.8% using salmon $\delta^{15}\text{N}$ as the marine endmember. Repeating this with our maximum observed value for $\delta^{15}\text{N}$ of NH_4 (41.2‰), we estimate only 28.9% of foliar N on salmon enhanced bank was MDN (a 57.9% reduction from Quinn et al. 2018 estimates). Thus, failure to account for isotopic enrichment associated with soil N transformations can lead to overestimates of MDN contributions to plants, and observed variability in $\delta^{15}\text{N}$ of NH_4^+ can produce a wide range of MDN estimates not previously considered, a result which is transferable to other studies that do not consider soil fractionation.

Our study is comprehensive in terms of the number of ecosystems factors considered but limited in that it includes only one seasonal timeframe. While MDN inputs do not affect the N pools and transformation rates during the summer growth period based on our results, N concentrations and transformations may be elevated in this system on shorter timescales (weeks to months after salmon return). As much as 40% of the annual inorganic N flux is released during the eight-month dormant season (September-May) and it has been posited spring and fall may be important for many biogeochemical processes in boreal forests (Hobbie and Chapin 1996, Chapin et al. 2006, Drake et al. 2006). The objective of this study was to identify the long-term legacy of salmon subsidies; short-term effects were both beyond the scope of this study and have been previously investigated (Holtgrieve et al. 2009). Considering long-term effect of N subsidies as opposed to short-term provides new

information on sustained N use and retention in the ecosystem and whether these salmon nutrients have lasting impacts on ecosystem function meaningful in a restoration context.

While this study is limited to one system, the results that N transformations cause a fractionation that can bias MDN mixing model estimates and that landscape factors are the primary driver of long-term N retention and use, are relevant to all systems where anadromous, semelparous salmon are abundant (Pacific, Atlantic, Great Lakes) (Quinn 2018). This result also agrees with related research examining fractionation of mineralization and nitrification (Högberg 1997), and fertilization studies (Lu et al. 2010). Additionally, it demonstrates salmon N subsidies may have a short-term and likely small spatial scale (Drake et al. 2005) legacy in soils and are not retained in the system.

Salmon provide critical food resources to many of terrestrial and aquatic consumers (Cederholm et al. 1999, Gende et al. 2002, Schindler et al. 2003), but the evidence that MDN stimulate terrestrial primary production is less certain. The salmon carcass manipulation experiment described here and in Quinn et al. (2018) represents an extreme case of carcass addition and depletion to riparian areas, as measured by bulk $\delta^{15}\text{N}$ and estimated percent contribution was approximately twice previous studies for both trees and soils (Helfield and Naiman 2002, Bartz and Naiman 2005). Generally, results of this manipulation were equivocal for soils and a statistically significant but ecologically small effect on trees. Simultaneously, other recent changes to boreal forest systems, such as moisture and temperature, appear to have a greater potential than MDN to alter biogeochemical pathways and primary production in these systems (Chapin et al. 2006, Yarie 2008, Lloyd et al. 2010, Wright et al. 2018). Additionally, this study demonstrates the importance of testing biogeochemical and site similarity between experimental and control sites in nutrient subsidy studies, as even banks on the same creek can have landscape and soil variability that alter N concentration, transformations, and vegetative growth. Altogether, while salmon have clear

benefits for consumers, management of salmon populations or application of compensatory restoration strategies based on terrestrial productivity response to salmon inputs is generally unfounded, and at least, hard to predict.

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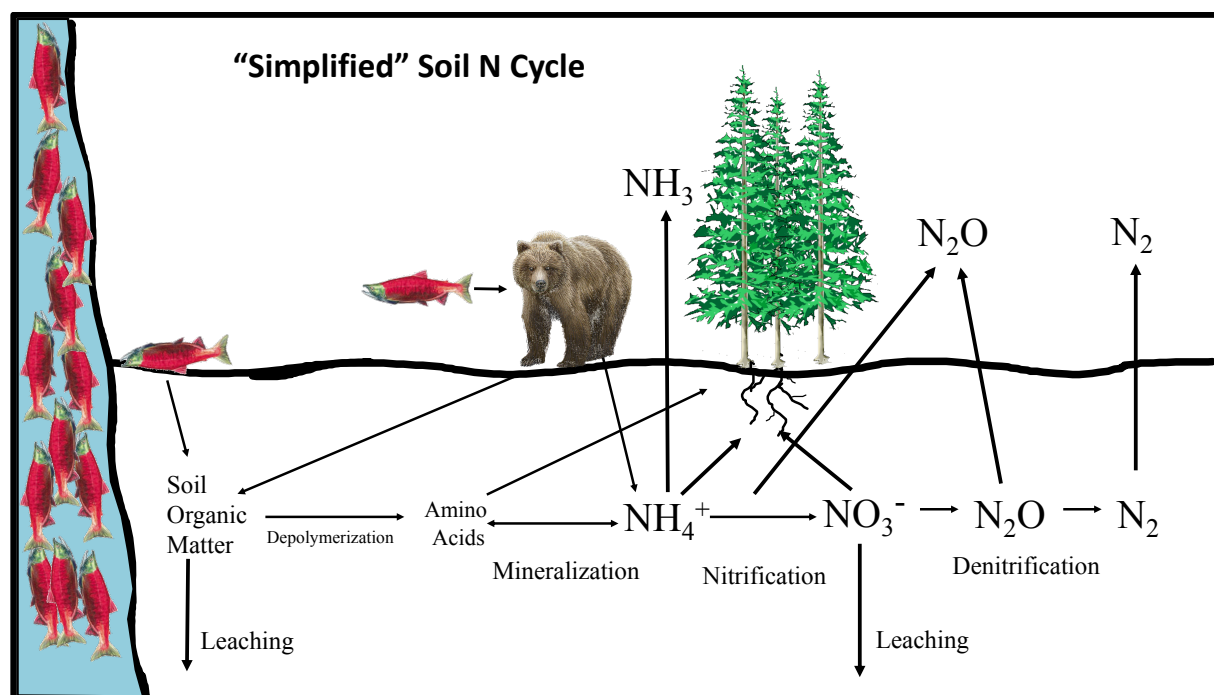
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Table 1: Competing models with relative support ($\Delta AIC < 2$) using AIC analysis for each response variable, where the most parsimonious models with the most support are shown in bold. Reported are ΔAIC and the hypothesis supported by each model: H1 is a bank effect not caused by salmon manipulation, H2 is a distance effect not caused by salmon manipulation, H3 is both a bank and distance effect indicating a response to salmon manipulation, and H4 indicates support for the other covariates tested.

Response Variable	Model Hypothesis	ΔAIC	Covariates Included in Models with Relative Support
Bulk $\delta^{15}N$	2	0.00	Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance)²
	2	0.41	Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance) ² , [N _{tot}]
Bulk $\delta^{13}C$	1	0.00	ln(Distance)
	1	0.22	Bank, ln(Distance)
	1	0.62	ln(Distance), [N _{tot}]
	1	1.23	Bank, ln(Distance), [N _{tot}]
$\delta^{15}N$ of NH_4^+	2	0.00	Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance)²
	1	0.00	Bank, ln(Distance)
[NH_4^+]	1	0.69	Bank, ln(Distance), Bank:ln(Distance)
	1	0.69	Bank
	1	0.95	Bank, GW
	1	1.10	Bank, ln(Distance), GW
	1	1.87	Bank, ln(Distance), Bank:ln(Distance), GW
	1	0.00	Bank, GW
[NO_3^-]	1	1.72	Bank, ln(Distance), GW
	2	1.87	Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance) ² , GW
	3	0.00	[N_{Org}]
Net Mineralization	3	0.61	GW, [N _{Org}]
	1	0.74	Bank, [N _{Org}]
	1	1.61	Bank, GW, [N _{Org}]
	3	0.00	[NH_4^+], GW
Net Nitrification	1	1.02	Bank, [NH_4^+], GW
	1	0.00	ln(Distance), GW
[N _{Org}]	1	0.22	Bank, ln(Distance), Bank:ln(Distance), GW
	2	0.33	Bank, ln(Distance), Bank:ln(Distance), Bank:ln(Distance) ² , GW
	1	1.94	Bank, ln(Distance), GW
	1	0.00	ln(Distance), Bank
Gravimetric Water Content (GW)	1	1.00	ln(Distance)
	1	1.80	Bank, ln(Distance), Bank:ln(Distance)
	1	0.00	ln(Distance), Bank

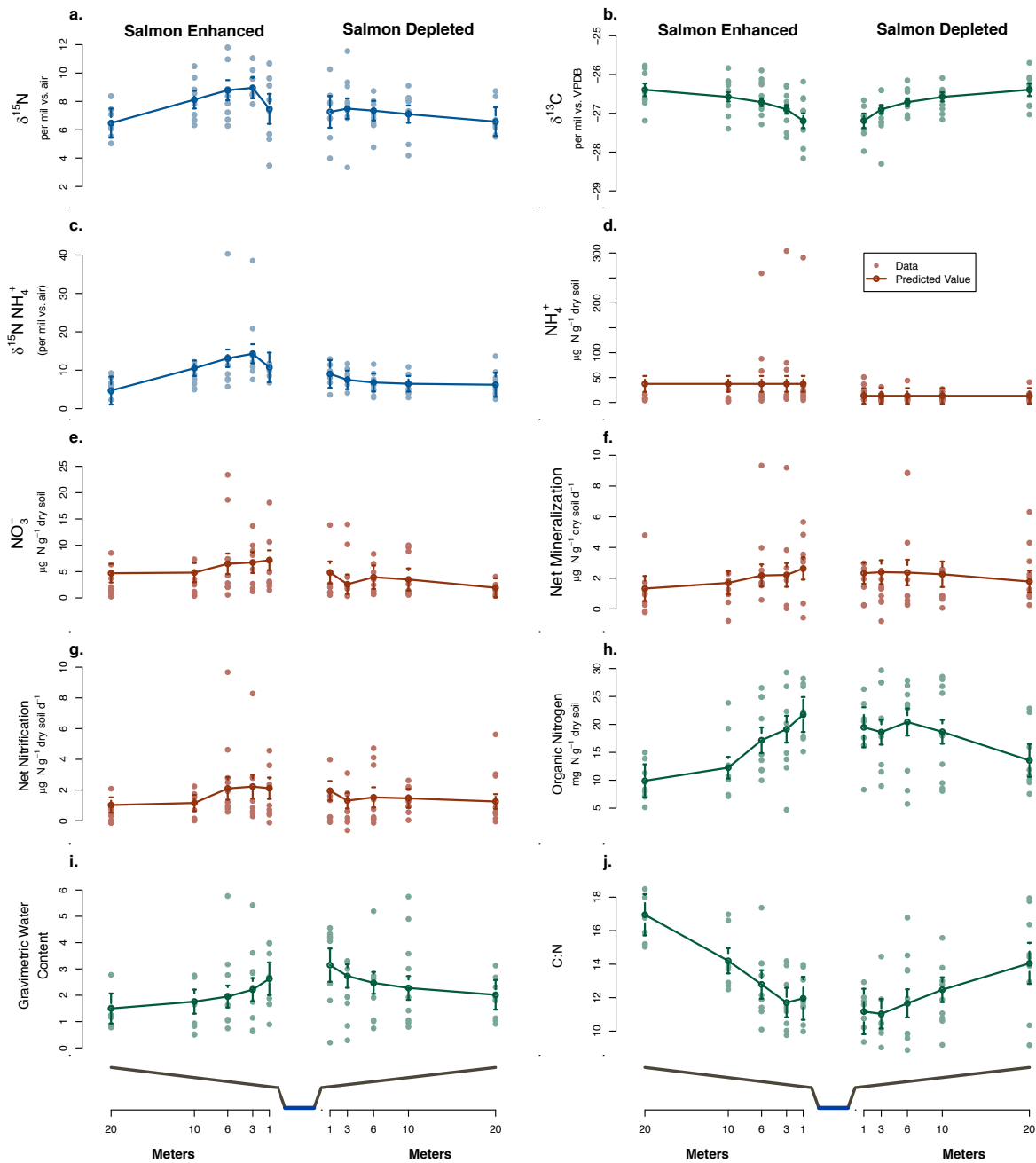
Figures

Figure 1: Nitrogen pathways in soil where MDN enters terrestrial systems via decay of salmon organic tissues or excretion from direct salmon consumers such as bears. Arrows represent conversion pathways with the potential to impart isotopic fractionations on plant available nitrogen (NH_4^+ or NO_3^-).



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711 Figure 2: Data and predicted values for the model with the most support (bolded, table 1) for
712 soil $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ of NH_4^+ , $[\text{NH}_4^+]$ and $[\text{NO}_3^-]$, and net mineralization and nitrification,
713 $[\text{N}_{\text{org}}]$, gravimetric water content, and C:N for both the salmon enhanced and the salmon
714 depleted banks of Hansen creek at 1 m, 3 m, 6 m, 10 m, and 20 m from the edge of the creek
715 bed with 95% confidence intervals for predicted values. Blue (a & c) denotes measures of
716 marine derived nitrogen, green (b, h, i, & j) denotes site variable factors, and red (d, e, f, g)
717 denotes measures of soil productivity.



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