**Working title:** Effects of long term enrichment of riparian areas with salmon carcasses on inorganic soil nitrogen pools, nitrogen transformations, and stable isotopic ratios.

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**Abstract** *(350 words for ecology)*

**Introduction**

The migration of Pacific salmon (*Oncorhynchus* spp.) from marine environments to freshwater spawning grounds contributes nutrients and organic material to freshwater and terrestrial ecosystems (Gende et al. 2002). Given a majority of salmon growth occurs in the ocean, these annual events provide an influx of marine derived nutrients (MDN). Carcasses and roe are prey for a variety of organisms, and this resource pulse is linked to variable responses in periphyton density, stream biofilms, freshwater nutrient concentration, and insect abundance (Mitchell and Lamberti 2005; Rüegg et al. 2011). A majority of these nutrients are directly deposited to freshwater systems, and aquatic ecosystems demonstrate strong influences on their riparian counterparts. Flooding, erosion, and sediment deposition can alter nutrient dynamics and soil composition in adjacent ecosystems (Naiman 1998; Naiman and Decamps 1997). Transport of salmon carcasses by bears increases soil ammonium (NH4+) concentrations (Holtgrieve et al. 2009), and the spatial distribution of MDN in foliar material is linked to flooding and piscivorous predator activity (Ben-David et al. 1998).

The body of research focused on the contributions of MDN from anadromous, semelparous, fish species to surrounding ecosystems is primarily based on stable isotope analysis of δ15N (15N/14N). Salmon tend to be enriched in 15N relative to 14N when compared to freshwater nitrogen; this elevation of the heavier isotope can be used to trace the fate and distribution of MDN (Schindler et al. 2003). Higher salmon returns have demonstrated elevated δ15N in zooplankton and periphyton (Finney et al. 2000; Holtgrieve et al. 2010). Stable isotope analysis is used to understand utilization of MDN by juvenile and adult salmon, plankton, and piscivorous predators (Hicks et al. 2005; Chaloner et al 2002; Claeson et al. 2006; Rinella et al. 2013)*.* Additionally, salmon has been identified as an important source of terrestrial nitrogen and a contributor to plant growth and distribution (Bilby et al. 2003; Helfield and Naiman 2001, 2006; Ben-David et al. 1998).

Studies using δ15N as an MDN tracer for plants frequently assume nitrogen from salmon is directly assimilated by plants by using salmon δ15N as a mixing model end member, an assumption that is demonstrably false. The nitrogen cycle in soils contains a number of potentially fractionating steps (Figure 1). Organic material from decomposing salmon must undergo mineralization, or the conversion of organic compounds to ammonium by nitrogen fixing bacteria. Ammonium then must then be converted to nitrate (NO3-) by nitrifying bacteria before it can be assimilated into plant tissues. Therefore, processes such as mineralization and nitrification control plant available nitrogen pools and ultimately its corresponding δ15N. These conversions also have the potential to enrich nitrogen pools in 15N (Gende et al. 2002; Schindler et al. 2003) which is likely to provide misleading estimates of the contributions of MDN to terrestrial flora and its consumers. Additionally, there is evidence δ15N and nitrogen availability are correlated, with foliar δ15N becoming more enriched when plant available nitrogen is abundant. Therefore, foliar δ15N is a signature of both the source δ15N of inorganic nitrogen in soils and nitrogen availability (Craine et al. 2009). Given plants assimilate nitrogen that has been converted to inorganic forms in soil rather than direct uptake of organic matter from salmon, fractionation in soils and nitrogen availability must be accounted for when calculating the relative contribution of MDN to terrestrial communities via pathways that do not involve direct consumption of salmon.

Experiments examining the contributions of MDN are often limited by short timescales and few experiments investigate plant available nitrogen pools. Collins et al. 2015 demonstrated the need to evaluate ecosystem responses over longer periods of time to understand the magnitude and timescale of the effects of salmon on ecosystems. Studies examining spatial and temporal impacts of salmon on inorganic nitrogen pools have identified responses are highly localized (effects only observed less than 30 cm from carcasses), and NH4+ and NO3- become biologically available on the order of weeks to months respectively (Gende et al. 2007; Drake et al. 2005). Predator exclosure experiments determined impacts to soil N processing only persist for a year (Holtgrieve et al. 2009). While these results provide a framework of the importance of soil processing of MDN on inorganic nitrogen pools, no experiment has examined the impacts of salmon removal on soil nitrogen pools on long time scales

To resolve the extent to which salmon carcasses impact plant available nitrogen pools (NH4+ and NO3-) and the rate of supply of these pools (via nitrification and mineralization), we present the results of a long-term fertilization experiment in southwestern Alaska. We also evaluate the impacts of soil nitrogen conversions on δ15N by examining the δ15N of NH4+ and NO3- in soils. Finally, we assess the relationship between nitrogen availability on stable isotope signatures of inorganic nitrogen pools.

**Methods**

*Sample Collection*

This study was conducted on Hansen Creek, a small stream flowing from a beaver pond to Lake Aleknagik in the Wood River system of Bristol Bay, AK. For the last 20 years adult spawned out sockeye salmon (*Oncorhynchus nerka*) were removed from Hansen Creek and its river right bank (decreasing salmon density) and tossed on the river left bank (increasing salmon density). Unlike some watersheds in the region, Hansen Creek has a low density of alder (*Alnus crispa*) which can be a source of nitrogen via symbiotic fixation of atmospheric N2, making it a useful system for studying MDN in plant available nitrogen in soils.

Soil samples were collected from on July 13th 2017 along nine sets of paired transects on the river left and river right banks at 1m, 3m, 6m, 10m, and 20m from the proper bank. Sampling was conducted during peak growing season when plants are removing the most nitrogen from soils thus incorporating the available nitrogen. Studies examining the normalized difference vegetation index (NDVI) for boreal forests in Alaska indicate peak growing season of vegetation occurs during early July (Kasischke and French 1995). Sites were selected to be representative of typical riparian vegetation and high spawning intensity. An approximate 5cm x 5cm x 10cm soil column was taken for each sample and plant matter was removed from the samples. Samples were stored at 4 degrees C in airtight plastic bags for 48 hours prior to processing. To determine soil water content 50 – 100 g of soil (wet weight) were dried at 105°C until dry soil reached a constant mass, and gravimetric water content was calculated.

*Soil nutrient concentrations (NH4+ and NO3-) and N transformations*

Soil nutrient concentration and N transformations were conducted according to Holtgrieve and Schindler 2009. Briefly, to determine the initial NH4+ and NO3- concentrations, subsamples (10-12 g wet weight) of sieved soils were extracted within 48 hours of collection in 100 ml of 2 M potassium chloride (KCl) (Hart et al. 1994). Soil extracts were shaken for 60 s then left to settle for 24-48 h before being filtered through Whatman #1paper filters pre-leached with 100 ml of KCl. Approximately 8 ml of filtered extracts were frozen and later analyzed colorimetrically with an Alpkem Flow Solution IV (OI Analytical, College Station, TX, USA). All leftover filtered extracts were frozen and stored for inorganic nitrogen stable isotope analysis. A second 10-12 g soil subsample was incubated aerobically in the dark for 15 days at 12-16°C prior to extraction with KCl as above, an 8ml were frozen and stored for colormetric analysis. Net mineralization calculated as the change in inorganic N concentration (NH4+ and NO3-) divided by the incubation duration, while net nitrification was calculated as the change in NO3- concentration over the incubation.

*Stable isotope analysis*

Soil subsamples were freeze dried for 48 hours, sieved, and ground into a uniform powder (< 212 μm) using a ball mill grinder for bulk isotope analysis. 2 mg of soil were packed in tin capsules and analyzed for nitrogen stable isotope ratios (15N/14N) using Air-N2 for reference and carbon (13C/12C) stable isotope ratios using VPDB for reference. Samples were analyzed at University of Washington’s IsoLab using a Costech Elemental Analyzer, Conflo III MAT253 for continuous flow-based measurements. Measurements are reported as δ15N or δ13C which represent the per mil deviation in heavy isotope abundance from the isotopic standard (Schoeninger et al. 1983). Total nitrogen concentration was also calculated based on percent nitrogen from the isotope data. Percent nitrogen was converted to mg nitrogen per gram dry soil.

For inorganic stable isotope analysis of NH4+ and NO3-, total volume of formerly frozen filtered extracts was measured and placed in Erlenmeyer flasks. To retrieve NH4+,300 mg of MgO and an acid trap (1 cm glass fiber filter treated with KHSO4 and sealed in Teflon tape) were added to each flask, which were immediately stoppered, sealed with parafilm, and placed on a shaker table. Samples shook continuously for six days after which acid traps were removed and stored in desiccator for 3-4 days before filters were removed and packed in tin capsules for analysis. Extracts were returned to the shaker table and left open to the atmosphere to remove remaining NH4+. To retrieve NO3-, 300 mg of MgO were added to each extract and immediately followed with 75 mg of Devarda’s alloy and an acid trap. Extracts were immediately stoppered, sealed with parafilm, and placed on a shaker table for six days before acid traps were removed and filters were packed as described above. For each batch blanks (KCl with no soil extract) and standards were also run.

*Statistical analyses*

Our study design resulted in samples being collected at 9 sites (transects) across three reaches of Hansen Creek. Samples were also collected at 5 distances from the stream edge on two different banks for a total of 90 samples. Linear models and mixed effects models were fit to the data for each response variables: initial NH4+ and NO3- concentration, net mineralization and net nitrification, δ15N and δ13C of bulk isotopes, and δ15N of NH4+ and NO3-, and total nitrogen concentration. For all response variables, candidate models (supplementary material 1) included the interaction between bank and distance from rivers edge. Reach and site were considered in the candidate model set as nested random effects and the random effects structure was tested first for the candidate model set using model selection methods described by Zuur et al. 2009. Gravimetric water content was considered as a fixed effect, and NH4+ concentration was considered as a fixed effect for net nitrification, and organic nitrogen concentration was considered as a fixed effect for net mineralization, given NH4+ concentration and organic nitrogen concentration function as the substrate for the corresponding reactions. The best model was selected from the candidate models set using Akaike’s information criterion (AIC) for each response variable. Under circumstances where multiple models had a difference in AIC value of < 2 relative to the best model, the most parsimonious model was selected. To test the hypothesis MDN provided by salmon carcasses impacts plant available nitrogen, the significance of the bank effect was tested for the model with the most support for each response variable.

To determine how nitrogen availability impacts stable isotope signatures of plant available nitrogen pools, linear models comparing δ15N of NH4+ and NO3- and nitrogen concentration in soils were used. Nitrogen concentration was calculated using the percent nitrogen for a dry sample and converted to mg nitrogen per g of dry soil. The slopes of these models were used to determine the significance of the relationship between nitrogen availability and stable isotope signature.

**Results**

*Model selection*

Linear models with no random effects had the most support for all response variables. For δ15N, δ13C, NO3- concentration, δ15N of NH4+ and δ15N of NO3- , the selected models indicated a polynomial relationship between response variable and distance from the edge of the creek. The selected models for NH4+ concentration, net mineralization, net nitrification, and total nitrogen concentration each had a linear relationship between the response variable and distance from the creek edge. Gravimetric water content was not supported as a covariate except for net nitrification and total nitrogen concentration. For both net nitrification and net mineralization, inclusion of the reaction substrates (organic nitrogen and NH4+ concentration respectively) were supported and included in the selected models (Table 1).

*Effect of salmon enrichment*

There was no significant effect of salmon enrichment on plant available nitrogen pools and nitrogen transformation rates. Both net mineralization and net nitrification did not have a significant difference on the salmon enriched bank of Hansen Creek compared to the non-enriched bank (p > 0.1). Similarly, there was no significant difference for NO3- and NH4+ concentration between the salmon enriched and the non-salmon enriched banks (p > 0.1; Figure 2). Net nitrification rates demonstrated a significant distance effect (p < 0.1) with net nitrification decreasing with distance from the creek edge. NO3- and NH4+ concentrations, and net mineralization did not have a significant distance effect (p > 0.1; Figure 2). However, there was a significantly higher total nitrogen concentration on the salmon enriched bank relative to the non-enriched bank.

Salmon enrichment did have an effect on stable isotope values of nitrogen pools. δ15N of NH4+, δ15N of NO3-, and bulk δ15N each had significantly higher isotopic enrichment on the salmon enriched bank of the creek compared to the non-salmon enriched bank (p < 0.05; Figure 3). The δ13C was not significantly different between the two banks. δ15N of NH4+ and δ15N of NO3- also had a significant distance effect (p<0.05; Figure 2).

*Effect of nitrogen availability on stable isotope signatures*

Both δ15N of NH4+ and NO3- were more enriched with a higher concentration of nitrogen in soil. This relationship was not significant for δ15N of NH4+ (p < 0.05) but was significant for δ15N of NO3- (Figure 4). It was also observed δ15N values of both NH4+ (n=11) and NO3- (n=2) exceeded 12‰.

**Discussion**

These results confirmed the presence of MDN in soils and that salmon enrichment increases nitrogen concentration in soils. The salmon enriched bank had significantly elevated total nitrogen concentration and the total nitrogen pool also demonstrated a significantly enriched δ15N. Given soils were sampled prior to the return of salmon for the year, these results indicate elevated nitrogen and δ15N persist through the winter and are available even when salmon are not present in the system. δ15N was the most enriched at 3m from the edge of the enriched edge and declined significantly with distance, indicating the presence of MDN is somewhat localized to areas where salmon carcasses are placed.

Despite increased total nitrogen concentration, fertilization from salmon carcasses did not increase plant available nitrogen pools and transformation rates during peak vegetative growing season. Given vegetation incorporates the largest quantities of nitrogen during the growing season, these results indicate long term fertilization does not increase nitrogen sources that are seasonally accessible to plants. While carcass fertilization may increase total nitrogen concentration, NH4+ and NO3- only represent a small fraction of total nitrogen, and total nitrogen is not reflective of nitrogen sources accessible to plants (Chapin et al. 2002). While vegetation in salmon enriched areas may demonstrate elevated stable isotope signatures, this reflects the presence of MDN and not necessarily the contributions MDN has made to plants.

Stable isotope values of inorganic nitrogen sources had values that exceeded salmon stable isotope end members commonly used in plant MDN mixing models. This indicates soil nitrogen pathways can enrich stable isotope values. As a result, using a mixing model end member of 12‰ to represent a nitrogen signature 100% derived from salmon is inaccurate, as under some circumstances plant available nitrogen pools can exceed that value. This demonstrates incorporating isotopic enrichment associated with nitrogen transformations in soils is important and necessary to accurately assess the contributions of MDN to plants. If these transformations are not considered, it is likely calculations may overstate the importance of MDN to plants.

Global declines in Pacific salmon populations caused by anthropogenic impacts (overharvest, habitat degradation, hydropower dams) and the preservation of this ecosystem service and has been a focal point for many management and mitigation strategies (Collins et al. 2015; Lichatowich 1999). It has been established salmon provide supplementary nutrients to aquatic systems and direct consumers, however the necessity of MDN for plant communities and their consumers is less certain. While these results support the presence of MDN in soils, the utility of these nutrients as represented by δ15N is dependent on what nutrients are limiting to plant growth, and whether they are available during the growing season. The relationship between fractionation and nitrogen concentration, and the fractionation caused by nitrogen transformations has the potential to mislead results linking MDN to growth.

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**Tables**

Table 1: Models with the most support using AIC analysis for each response variable

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| --- | --- |
| **Response Variable** | **Selected Models** |
| Bulk δ15N | δ15N = bank\*log10(distance)+I(log10(distance)2)\*bank + ε |
| Bulk δ13C | δ13C = bank\*log10(distance)+I(log10(distance)2)\*bank + ε |
| NO3- concentration | NO3- concentration = bank\*log10(distance)+I(log10(distance)2)\*bank + ε |
| NH4+ concentration | NH4+ concentration = bank\*log10(distance) + ε |
| Net Mineralization | Net Mineralization = bank\*log10(distance) + organic nitrogen concentration + ε |
| Net Nitrification | Net Nitrification = bank\*log10(distance) + NH4+ concentration + gravimetric water content + ε |
| δ15N of NO3- | δ15N of NO3- = bank\*log10(distance)+I(log10(distance)2) + ε |
| δ15N of NH4+ | δ15N of NH4+ = bank\*log10(distance)+I(log10(distance)2) + ε |
| Mass Nitrogen | Mass Nitrogen = bank\*log10(distance)+ gravimetric water content + ε |

**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 a fractionation on plant available nitrogen (NH4+ or NO3-).

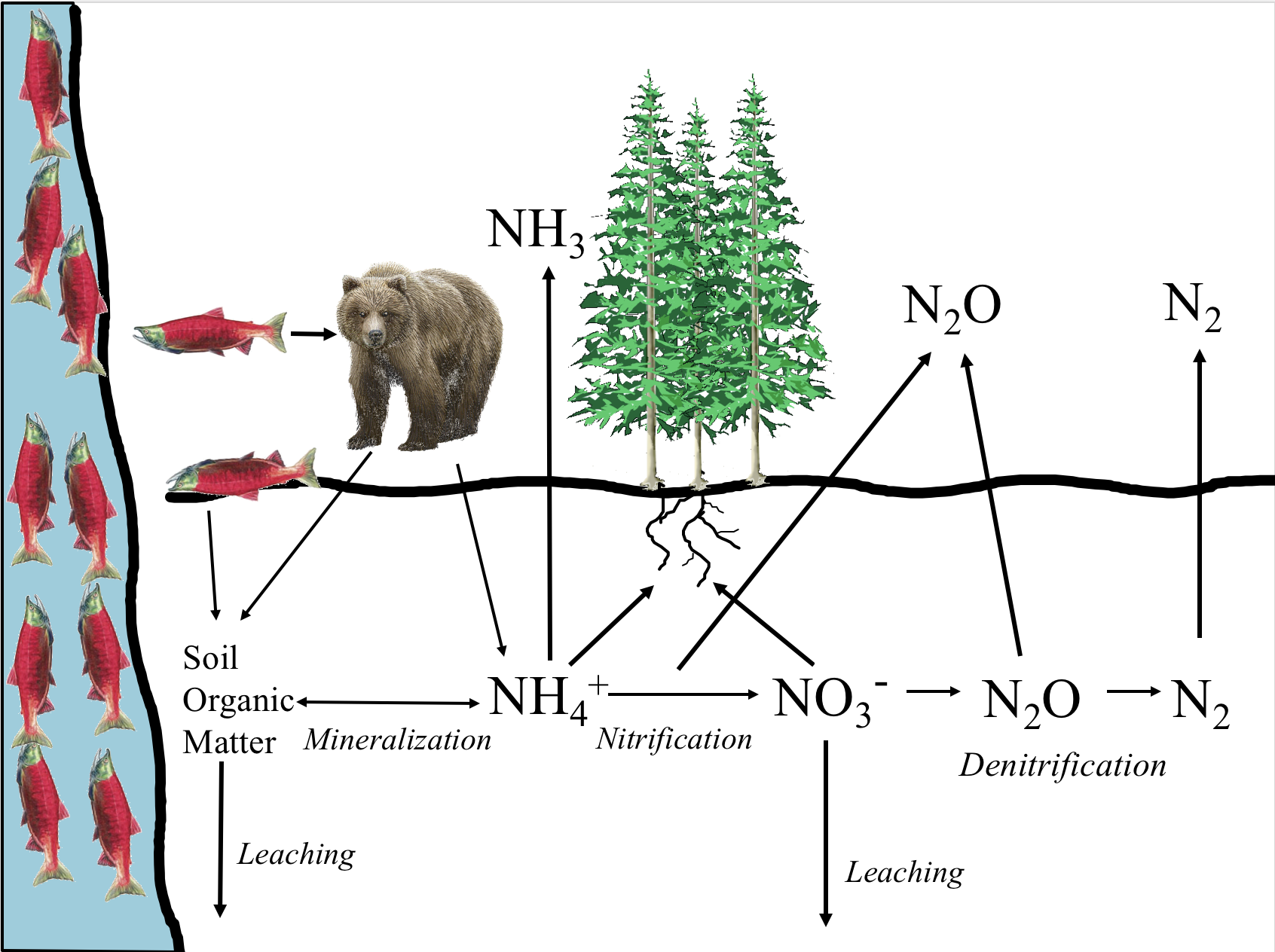
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Figure 2: Data (grey) and predicted (black) values of NH4+ and NO3- concentration, and net mineralization and nitrification for both the salmon enriched and the non-salmon enriched banks of Hansen creek at 1m, 3m, 6m, 10m, and 20m from the edge of the creek bed with 95% confidence intervals for predicted values.



Figure 3: Data (grey) and predicted (black) stable isotope values for organic and inorganic nitrogen pools on both the salmon enriched and the non-salmon enriched banks of Hansen creek at 1m, 3m, 6m, 10m, and 20m from the edge of the creek bed with 95% confidence intervals for predicted values.



Figure 4: Relationship between stable isotope signatures of inorganic nitrogen pools and nitrogen concentration expressed as total mass of nitrogen per gram dry soil.



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**Supplementary Material**

SI 1: The candidate model set tested for each response variable using AIC analysis. \* denotes a mixed effects model where reach and site are random effects and all other variable are fixed effects. All other candidate models are linear models. For net nitrification and net mineralization, NH4+ concentration and organic nitrogen concentration were considered as fixed effects respectively.

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| --- |
| **Candidate Model Set** |
| **\*** Response Variable = bank\*log10(distance)+I(log10(distance)2)\*bank + gravimetric water content + (1|Reach/Site) + ε |
| \* Response Variable = bank\*log10(distance)+I(log10(distance)2)\*bank + gravimetric water content + (1|Reach) + ε |
| \* Response Variable = bank\*log10(distance)+I(log10(distance)2)\*bank + gravimetric water content + (1|Site) + ε |
| Response Variable = bank\*log10(distance)+I(log10(distance)2)\*bank + gravimetric water content + ε |
| Response Variable = bank\*log10(distance) + gravimetric water content + ε |
| Response Variable = bank\*log10(distance)+I(log10(distance)2)\*bank + ε |
| Response Variable = bank\*log10(distance) + ε |