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Nitrogen dynamics vary across hydrologic gradients and by forest community composition in the perhumid coastal temperate rainforest of southeast Alaska

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Abstract: Nitrogen (N) limitation constrains plant growth, but complex interactions among species and ecosystems hinder our ability to identify primary drivers of N availability. Hydrologic, biogeochemical, and ecological processes interact spatially and temporally, requiring measurements of N across diverse ecosystem types and as a function of both site conditions and vegetation composition. We measured initial exchangeable and mineralized N along a hydrologic gradient in the Alaskan perhumid coastal temperate rainforest to test a conceptual model of linkages between N availability and landscape, hydrologic, and ecosystem characteristics in temperate forests. Mineralization was closely associated with inorganic N concentrations. Inorganic N as NH_4^+ generally increased with increasing depth to groundwater but was strongly determined by plant–water interactions. Exchangeable and mineralized N were closely linked to tree species, forest biomass, and hydrologic regime regardless of ecosystem type. The emergence of tree species as indicators of N cycling highlights the effect that species have on nutrient dynamics, while the trend of increasing inorganic N with increasing soil saturation points to the role of hydrology in driving N availability. Our research quantified N dynamics for an understudied, yet critical, system and provides a framework for exploring feedbacks among soil saturation, forest composition, and nutrient cycling in temperate forests.

Key words: nitrogen mineralization, plant–soil feedbacks, perhumid coastal temperate rainforest, North Pacific coastal temperate rainforest, hydrologic gradient.

Résumé : La faible quantité d'azote (N) limite la croissance des plantes mais les interactions complexes entre les espèces et les écosystèmes entravent notre capacité à identifier les principaux facteurs responsables de la disponibilité de N. Les processus hydrologiques, biochimiques et écologiques interagissent dans l'espace et le temps, ce qui nécessite des mesures de N dans divers types d'écosystèmes en tenant compte des conditions de la station et de la composition de la végétation. Nous avons mesuré la quantité initiale de N échangeable et de N minéralisé le long d'un gradient hydrologique dans la forêt pluviale tempérée en zone côtière perhumide, en Alaska, pour tester le modèle conceptuel des liens entre la disponibilité de N et les caractéristiques du paysage, de l'hydrologie et de l'écosystème dans les forêts tempérées. La minéralisation était étroitement liée à la concentration de N inorganique. L'azote inorganique sous forme de NH_4^+ augmentait généralement avec la profondeur de l'eau souterraine mais était fortement fonction des interactions entre la végétation et l'eau. L'azote échangeable et N minéralisé étaient étroitement liés à l'espèce d'arbre, à la biomasse forestière et au régime hydrologique peu importe le type d'écosystème. L'émergence des espèces arborescentes en tant qu'indicateurs du recyclage de N met en évidence l'effet qu'ont les espèces sur la dynamique des nutriments, tandis que le fait que N inorganique ait tendance à augmenter à mesure que la saturation du sol augmente fait ressortir le rôle déterminant de l'hydrologie comme facteur responsable de la disponibilité de N. Nos travaux de recherche quantifient la dynamique de N pour un système peu étudié, bien qu'essentiel, et fournissent un cadre pour explorer les rétroactions parmi la saturation du sol, la composition de la forêt et le recyclage des nutriments dans les forêts tempérées. [Traduit par la Rédaction]

Mots-clés : minéralisation de l'azote, rétroactions plante–sol, forêt pluviale tempérée en zone côtière perhumide, forêt pluviale côtière du Pacifique Nord, gradient hydrologique.

Introduction

Landscapes are mosaics of ecosystems that vary in edaphic, hydrologic, and biological processes (Chapin et al. 2002). These processes structure plant community composition (Silvertown et al. 2015) but also interact to determine nitrogen (N) availability or limitation (Vitousek et al. 1982). Limitation of N is a widespread phenomenon in temperate ecosystems — from wetlands to forests — (LeBauer and Treseder 2008) that can constrain productivity and community composition (Vitousek et al. 2002). For plant

communities, growth is regulated by the availability of N mineralized from soil organic matter (Binkley and Hart 1989), and N concentrations shape composition in grassland and forest ecosystems (Huston 1980; Goldberg and Miller 1990). Plant-available N is governed by soil temperature, which regulates microbial-driven N release (Kaye and Hart 1997) through decomposition of organic substrate (Davidson and Janssens 2006), and soil moisture, which influences N turnover and loss (Borken and Matzner 2009). Additionally, soil physical and chemical properties, including soil texture

and carbon (C) to nitrogen ratios (C:N), influence N mineralization directly via substrate quality (Reich et al. 1997) and indirectly through regulation of soil moisture (Sleutel et al. 2008). Landscape-level differences in edaphic and hydrologic settings drive variation in the exchangeable form and availability of N, and plant communities occurring across hydrologic gradients (e.g., from emergent wetland to upland forest) are structured by, and uniquely subject to, edaphic–hydrologic interactions (Silvertown et al. 2015).

Tightly linked soil–hydrologic–biogeochemical processes control nutrient concentrations and fluxes (Noe et al. 2013), which can lead to distinct patterns of nutrient availability and plant community composition (Bedford et al. 1999). Wetlands have been the primary focus of plant–soil–water research, and the literature is clear on the effect of wetland hydrology on N dynamics. The source and flow of water and degree of saturation determine the lability of nutrients (Noe et al. 2013) and forms of available N (Bridgham et al. 1998; Hefting et al. 2004). Under anaerobic conditions of saturated soil, nitrate (NO_3^--N) becomes more dominant, and ammonium (NH_4^+-N) is diminished (Reddy et al. 1989), with lower overall turnover in anaerobic than aerobic soils (Bridgham et al. 2001). Mineralization rates often increase under decreasing soil moisture (Bridgham et al. 1998; Yu and Ehrenfeld 2009), while low moisture increases nitrification (Yu and Ehrenfeld 2009). Although we have this knowledge for wetland ecosystems, we lack understanding of N dynamics over landscape gradients of hydrologic regimes and ecosystem types. Spatial and temporal changes in duration of saturation and (or) soil temperature are common in topographically heterogeneous landscapes (Moore et al. 1988), where plant communities are structured by topographically driven hydrologic regimes across wetland to forest gradients (Bisbing et al. 2016). Slight changes in microclimate can shift N cycling dynamics (e.g., rates of mineralization and nitrification; Reddy et al. 1989; Bridgham et al. 2001) and associated ecosystem function (e.g., microbial use and plant uptake; Kaye and Hart 1997), which have direct effects on plant-available N and aboveground plant productivity (Rustad et al. 2001).

Climatic, edaphic, and hydrologic interactions are not exclusive drivers of available N, as feedbacks from vegetation can also influence the N pool. Most notably, tree species are often associated with specific soils, nutrient availability, and site conditions (John et al. 2007). Species, in turn, influence soils through litterfall, microclimate effects, nutrient uptake, root turnover, and associated soil organisms (Prescott and Vesterdal 2013; Ribbons et al. 2016). These feedbacks from forest composition shape soil properties (e.g., Hobbie et al. 2006), including rates of N uptake and development of C and N stocks (Hansson et al. 2013) and N dynamics (Aponte et al. 2013; Gurmesa et al. 2013). Species-specific litterfall, for instance, can influence C turnover, affecting C:N and subsequently controlling N retention (Swift et al. 1979). Understanding N dynamics across diverse ecosystem types therefore requires measurements of N availability as a function of both site conditions and community composition.

A major gap in our understanding of plant–soil interactions is a model of biological linkages between hydrologic regime, forest community composition, and N cycling for temperate forest ecosystems. The need for this model is magnified by the potential for global alteration of nutrient cycling due to climate change (Greaver et al. 2016). Trajectories of N cycling are difficult to predict, but alterations to regional climate will increase temperatures, which may enhance mineralization (Rustad et al. 2001), and impact local hydrologic regimes and associated community composition and function. Although experimental manipulation provides the ideal test of nutrient availability and turnover, natural ecosystems are inherently complex, with N availability, limitations, and requirements varying across space, time, and species (Sullivan et al. 2014). Intact ecosystems that span a range of states can provide surrogate, more realistic conditions for examining N

Fig. 1. Conceptual model for the influence of landscape, hydrologic, and ecological characteristics on the forest community and feedbacks from the forest community to ecosystem function. Landscape slope and ecosystem position on the landscape determine soil weathering, soil development, nutrient dynamics, and period of inundation (D'Amore et al. 2015a). Inundation and soil nutrients directly influence the occurrence and productivity of local conifers (Bisbing et al. 2016). Plant–soil feedback is hypothesized, where interactions between hydrologic regime and conifer biomass directly shape nutrient availability in coastal temperate forest ecosystems. 1, D'Amore et al. 2015a; 2, Bisbing et al. 2016; 3, this study. [Colour online.]
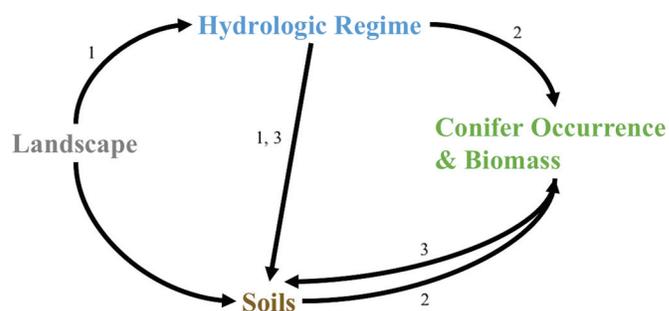
dynamics (e.g., Perakis and Sinkhorn 2011) and insight into potential alteration of N cycling with climate change (Greaver et al. 2016).

The perhumid coastal temperate rainforest (PCTR; D'Amore et al. 2016) offers an unparalleled natural system for evaluating coupled hydrologic and biological linkages driving N stock and availability. Regional forest communities vary across local hydrologic gradients (Bisbing et al. 2016) but are influenced by the same geographic and climate context (Nowacki et al. 2001), allowing for examination of plant–soil–water feedbacks without confounding effects. Nutrient turnover in these low N deposition forests is limited by excessive moisture and low temperatures (Sidle and Shaw 1983), and PCTR forests are characterized as N poor (Fenn et al. 1998). Predictions under rapid climate change, however, indicate warming and wetting of the PCTR and transitions from snow- to rain-dominated precipitation (McAfee et al. 2014), which may alter the stability of soil nutrient turnover. In addition to serving as a model system for testing linkages, PCTR forests are also emerging as important ecosystems for maintenance of natural ecological function and sustainability of intact coniferous forests in an era of increasing anthropogenic disturbance and rapid climate change (DellaSala 2011).

In this study, we used a hydrologic gradient in the PCTR to test a conceptual model of quantified (D'Amore et al. 2015a; Bisbing et al. 2016) and hypothesized linkages between N availability and landscape, hydrologic, and ecosystem characteristics in temperate forests (Fig. 1). Topography and landform determine soil weathering, soil development, nutrient content, and period of inundation (indicated by "1" in Fig. 1; D'Amore et al. 2015a). Inundation and soil nutrients then directly influence the occurrence and biomass of local conifers (indicated by "2" in Fig. 1; Bisbing et al. 2016). We further hypothesized, and subsequently tested, the direct effect of site condition and forest community composition on soil N and linkages where interactions between hydrologic regime and conifer biomass directly shape nutrient availability in temperate forest ecosystems (indicated by "3" in Fig. 1; this study). Our goal was to quantify N availability across the range of ecosystem types dominated by different conifers along a topographically driven wetness gradient in the PCTR. Two potential controls of N cycling in the PCTR were of particular interest: (i) the extent and duration of soil saturation and (ii) feedbacks to soil N associated with regionally dominant conifers. We aimed to expand our understanding of how landscape, hydrologic, and ecosystem char-

acteristics may influence the concentration and utilization of nitrogen in temperate forests.

Methods

Study region

The PCTR extends along the west coast of North America from northern California to Kodiak Island, Alaska. Although the southern PCTR, from California through southern British Columbia, has experienced heavy anthropogenic disturbance, the northern portion of the PCTR is the least impacted and largest contiguous area of coastal temperate rainforest in the world (Albert and Schoen 2013), providing habitat for species declining in disturbed portions of their ranges (Albert and Schoen 2013), sequestering large amounts of carbon (Heath et al. 2011), and transporting abundant terrestrial organic matter to aquatic systems (D'Amore et al. 2016).

This study occurred in the northern PCTR in the Alexander Archipelago on the Juneau – Douglas Island complex of southeast Alaska (58°26′40″N, 134°13′47″W). Local climate is a hypermaritime regime of mild, wet winters and cool, wet summers (D'Amore et al. 2015a) that is heavily influenced by oceanic pressure systems, glacial runoff, and a recent history of glacial recession. Mean annual precipitation exceeds 300 cm in many areas of the Alexander Archipelago but averages 150 cm in the Juneau area.

Geologic history, topography, and slope create a distinct hydrologic gradient, dividing the landscape into hydrologically partitioned ecosystem types (Nowacki et al. 2001; D'Amore et al. 2015a). Soils are closely tied to landscape position and strongly influenced by glacial drift from geomorphic forces, including compact and ablation till, lateral moraines, and outwash deposits. Mature soils occur on well-drained landscape positions with various stages of podsolization and on poorly drained landscape positions as Histosols. All mature soils have surface organic matter accumulation in both folistic (well-drained) and histic (poorly drained) epipedons.

Ecosystem types of the PCTR are distinguishable by vegetative cover and classified as palustrine emergent wetland (PEM), palustrine scrub–shrub wetland (PSS), palustrine forested wetland (PFO), or forested upland (U) (according to the National Wetland Inventory (NWI) classifications; Cowardin et al. 1979). Palustrine sites are all nontidal wetlands, and the terms "emergent", "scrub–shrub", and "forested" denote the dominant life form and appearance of the habitat. In the PCTR, PEM and PSS communities occur on flat to sloping sites, often carpeted with *Sphagnum* spp. and dominated by shore pine (*Pinus contorta* Douglas ex Loudon ssp. *contorta*); co-occurring species include western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Labrador-tea (*Ledum groenlandicum* Oeder), bog laurel (*Kalmia polifolia* Wangenh.), and skunk cabbage (*Lysichiton americanus* Hultén & H. St. John). Steeper PFO and U communities are mixed-conifer forests with a western hemlock and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) canopy; co-occurring species include devilsclub (*Oplopanax horridus* (Sm.) Miq.), Alaska blueberry (*Vaccinium alaskaense* Howell), and oval-leaf blueberry (*Vaccinium ovalifolium* Sm.).

Site selection and installation

This study leveraged existing field sites used by Bisbing and colleagues (2016), which stratified the landscape by NWI-defined ecosystem types (Cowardin et al. 1979). Sites were randomly selected with the generalized random tessellation stratified (GRTS) selection process in R 2.9.2 (R Core Team 2017) using the GRTS function and spsurvey package (Kincaid 2008). Three replicate sites of each ecosystem type (N = 12) were selected and established across the Juneau – Douglas Island complex. Upland and PFO sites arose following landscape-level windthrow in the 1880s (Nowacki

and Kramer 1998). No sites showed evidence of recent harvest (i.e., no visible stumps).

Soil map units were obtained for each site from the Tongass National Forest Soil Resource Inventory (USDA Forest Service 1997). Soil taxonomic descriptions are provided in Table 1, and soil pedon descriptions for these soil types are available from pedons sampled in the vicinity (D'Amore et al. 2015a). Surface horizons at all sites were organic material and identified by decomposition class according to field identification (Table 1).

To capture within-site environmental heterogeneity, sites were stratified into four topographically distinct units. One groundwater-monitoring well was installed at each unit and used as the plot center where data were collected on elevation, aspect, slope, landform, understory species percent cover (including bryophytes), and presence or absence of all tree species.

Sampling methods

Water table

Depth to water was manually measured biweekly in each of the four wells during the seasonal aerated period of higher temperature (May–August) to quantify temporal and spatial variation in the water table. Additionally, a pressure transducer (In Situ Co., Fort Collins, Colorado) was installed in the well most representative of each site for recording hourly depth and monitoring fine-scale fluctuations in depth to water. Transducer data were corrected for atmospheric pressure using a barometric pressure logger. Manual and logger-derived water table data were summarized into variables considered potentially important to nutrient dynamics: depth to water at day 0 (DTW at in situ incubation start), depth to water at day 30 (DTW at incubation end), and the number of growing season days when the water table was within the rooting zone (Days, >−20 cm depth; Coutts and Philipson 1978; Wang et al. 2002). The growing season was defined as the 138-day period between 15 May and 30 September (NOAA/NWS Juneau, Alaska). Monthly groundwater pH measurements were taken in each well using an Orion 3-star pH meter, and mean growing season values were used in analysis.

Tree biomass

Overstory communities were sampled around a 0.1 ha plot at each well location, with species and diameter measured for all trees. Trees < 10 cm in diameter were tallied by midpoint diameter class (0–2.5, 2.5–5, 5–10 cm), while trees > 10 cm were sampled for diameter at breast height (DBH, >1.37 m). Tree biomass was derived from diameters using established biomass regression equations (Jenkins et al. 2003). Plot-level biomass was calculated for each species by summing individual-tree biomass values and scaling to a per-hectare basis (Mg·ha^{-1}).

Moss productivity

We measured *Sphagnum* growth and production over the growing season to account for ecosystem productivity and competition for N across ecosystem types. Using a modified crank wire method (for details, see Gunnarsson and Rydin 2000), we tracked growth along ten 20 cm long crank wires inserted adjacent to each well location (n_{wires} = 10 wires per well × 4 wells per site = 40 wires per site). Height growth was measured biweekly, and 5 cm diameter cores were extracted at the end of the growing season. Cores were dried to a constant mass at 70 °C and weighed. We multiplied length increments by core bulk density to convert values into biomass production and scaled up to Mg·ha^{-1}·year^{-1} (Gunnarsson and Rydin 2000).

Soil nitrogen

Exchangeable and mineralized N were assessed using in situ soil incubation methods originally described by Hart et al. (1994), with additional details and modifications from Robertson et al. (1999a). Each incubation experiment ran for 30 days, with installation

Table 1. Landscape, aboveground, and belowground attributes for sites near Juneau in the southeast Alaska perhumid coastal temperate rainforest.

Site name	Ecosystem type	Soil	Horizon	Landform	Bulk density (g·cm⁻³)	PICO	PISI (Mg·ha⁻¹)	TSHE	DTW day 1 (cm)	DTW day 30 (cm)	Days	Groundwater pH	Moss productivity (Mg·ha⁻¹·year⁻¹)
FAA Bog	PEM	Typic Cryohemist	O$_i$	Flat lowlands	0.12±0.00	17.67±0.6	0	0.53±0.1	−26±3	−28±2	123	4.11±0.04	3.48±0.25
Water Tower PEM	PEM	Typic Cryohemist	O$_i$	Gently sloping lowlands	0.23±0.03	27.86±2.4	0	3.37±2.2	−14±6	−20±10	123	4.92±0.08	2.85±0.27
Ski Area Fen	PEM	Typic Cryohemist	O$_e$	Gently sloping lowlands	0.14±0.01	6.97±2.5	0	1.29±0.4	−20±3	−26±4	118	4.81±0.04	1.44±0.17
Eagle River PSS	PSS	Typic Cryohemist	O$_i$	Flat lowlands	0.11±0.00	2.71±1.4	4.27±0.9	3.97±1.4	−15±3	−21±2	64	4.57±0.04	1.80±0.14
Water Tower PSS	PSS	Typic Cryohemist	O$_e$	Gently sloping lowlands	0.16±0.01	48.41±0.8	0	2.52±0.6	−26±2	−31±2	109	4.56±0.04	0.77±0.04
Mt Jumbo Bog	PSS	Typic Cryohemist	O$_i$	Gently sloping lowlands	0.15±0.01	37.35±2.8	0	4.48±0.8	−17±4	−17±4	132	4.37±0.15	1.93±0.18
Tee Harbor PFO	PFO	Typic Cryaquod	O$_e$	Smooth hillslopes	0.18±0.01	0	68.07±16.4	267.61±22.6	−67±19	−68±19	108	5.41±0.08	0.42±0.28
Fish Creek PFO	PFO	Typic Cryaquod	O$_e$	Gently sloping lowlands	0.19±0.01	0	91.35±28.5	267.58±10.7	−28±7	−20±2	105	5.84±0.11	0.68±0.04
Ski Area PFO	PFO	Typic Cryaquod	O$_e$	Gently sloping lowlands	0.29±0.09	0	75.27±10.6	335.95±12.9	−69±20	−72±18	0	4.95±0.05	0.51±0.06
Eagle River U	U	Typic Humicryod	O$_e$	Smooth hillslopes	0.24±0.04	0	96.42±9.0	307.33±5.8	Dry to −120 cm	Dry to −120 cm	0	5.86±0.12	0.46±0.04
Peterson U	U	Typic Humicryod	O$_e$	Smooth hillslopes	0.20±0.01	0	31.18±13.3	585.50±93.9	Dry to −120 cm	Dry to −120 cm	0	5.88±0.11	0.64±0.05
Sheep Creek U	U	Typic Humicryod	O$_e$	Low incised mountain slope	0.39±0.07	0	213.62±38.8	451.36±63.4	Dry to −120 cm	Dry to −120 cm	0	5.94±0.14	0.45±0.02

Note: Ecosystem types are classified as palustrine emergent (PEM), palustrine scrub–shrub (PSS), palustrine forested wetland (PFO), or forested upland (U). Total tree biomass was quantified for *Pinus contorta* (PICO), *Picea sitchensis* (PISI), and *Tsuga heterophylla* (TSHE). Depth to water (DTW) measurements presented correspond to the dates of the incubation study on day 1 and on day 30. The number of growing season days when water was in the rooting zone (>−20 cm depth, Days) was defined as the 138-day period between 15 May and 30 September for the experiment year (NWS/NOAA, Juneau, Alaska). Values are mean ± SE at individual sites. Bulk density, DTW day 1, DTW day 30, Days, groundwater pH, and moss productivity are significantly different among ecosystem types at $p < 0.01$. PICO, PISI, and TSHE are significantly different among ecosystem types at $p < 0.05$.

staggered to ensure extraction of all cores on day 30. Installation and incubation procedures were implemented using an intact PVC core-extraction method of beveled-edge 10 cm ID PVC cores. Soil core samples were taken adjacent to each well from each site at each sampling time period (per site, $n = 4$ at day 0 and $n = 4$ at day 30). All field mineralization methods have limitations (see Robertson et al. 1999a). We used the in situ PVC core method to maintain soil structure and minimize soil disturbance while subjecting cores to similar environmental conditions (i.e., ambient precipitation and temperature). We did not cap cores due to the threat of wind and animal action removing the caps and creating confounding conditions across replicates. Therefore, cores were exposed to rainfall, which may have created a leaching vector through the cores. However, the seasonal rainfall during the period of incubation was low, and vertical N loss through soil horizons was minimal compared with lateral flow (see D'Amore et al. 2015b).

The influence of the forest community is most evident in the uppermost soil layers (Hansson et al. 2013), so we focused our sampling efforts on the top 10 cm of the soil surface. Core depth of 10 cm corresponded to surface organic horizons in all soils (O horizon > 10 cm at all sites), so mineral soil was not sampled. Live plant roots and stems were severed at the cutting edge of each core, leaving two intact cores free of plant roots. One core was immediately returned to the lab for analysis. The second core was returned to its extraction site and left for the 30-day in situ incubation period. All samples were processed and analyzed within 48 h of collection. One bulk density sample was also collected per site. Large blocks of soil were initially removed adjacent to the cores. Smaller volumetric subsamples (125 cm⁻³) were carefully carved from the larger block and dried to a constant mass. Bulk density was calculated based on the final dry mass and volume and expressed as g·cm⁻³.

Sample analysis

Soils were treated following the procedure described in Robertson et al. (1999b). Duplicate 15 g samples were mixed with 100 mL of $1.0 \ \mathrm{mol \cdot L^{-1}}$ KCl in 120 mL Falcon specimen cups. Samples were shaken for 1 min on a shaker table, left to sit overnight, and shaken again for 1 min the following morning. After settling for at least 45 min, the supernatant in each specimen cup was drawn into a large syringe through a Whatman GF/D filter. Three laboratory replicates were split among 20 mL scintillation vials and kept cold until analyzed (~1 month). All extracted subsamples were analyzed for dissolved NO_3^--N and NH_4^+-N by flow-through colorimetry at the University of Georgia's analytical laboratory (Athens, Georgia). Carbon and N were measured on a LECO CN analyzer from samples dried at 70 C to a constant mass.

Initial exchangeable inorganic N was converted to (*i*) a gravimetric basis ($\mu g \cdot g^{-1}$) using extract volume and moisture corrected for soil mass and (*ii*) mass per unit area (g·m⁻²) using the bulk density for each sample location. Total inorganic N (TIN) was calculated as the sum of NH_4^+-N and NO_3^--N at each time step. Net mineralization rates (TIN, NH_4^+-N, NO_3^--N) were calculated as the difference between initial and final (30 day) exchangeable values (Robertson et al. 1999a).

Statistical analysis

We first completed exploratory analyses on soil nutrient concentrations and examined the dataset for correlations among predictor variables. Exploratory analyses included one-way ANOVAs to compare soil and water attributes across ecosystem types, including groundwater pH, bulk density, C, N, and C:N. Kruskal–Wallis rank sum tests were used to evaluate differences in species' biomass and both initial exchangeable and mineralized N as a function of ecosystem type and hydrologic conditions.

We then identified a candidate model for testing our hypothesis of and previous knowledge on (D'Amore et al. 2015a; Bisbing et al.

2016) ecosystem function in the PCTR (Fig. 1), including the measured landscape (e.g., slope), hydrologic (e.g., DTW), and ecosystem characteristics (e.g., conifer biomass) directly and indirectly influencing the forest community and ecosystem processes. In initial exploration of all landscape and ecosystem variables, a correlation analysis revealed high correlation among potential predictor variables (see Appendix Table A1). Slope, for instance, was highly correlated with landform (0.92), depth to groundwater (DTW, −0.92), days when the water table was within the rooting zone (Days, −0.83), pH (0.77), and moss productivity (−0.81). We therefore utilized structural equation modeling (SEM) to avoid eliminating important variables or key connections while simultaneously examining potential pathways of influence on initial exchangeable and mineralized N. The SEM provided a framework for investigating causal relationships, evaluating both direct and indirect effects, and generating a graphical model for visualization of pathways (Grace et al. 2012).

With the SEM, we tested the indirect influence of slope on initial exchangeable and mineralized N through its direct influence on hydrologic regime (DTW and Days) and indirect effect on soils (pH and C:N) and conifer biomass. We further examined the relationship between hydrologic regime and its direct effect on conifer species' biomass and interaction with conifers to influence initial exchangeable and mineralized N. Finally, we tested the direct effect of conifer species' biomass on N, including interactions with hydrologic regime (DTW). To examine all potential causal pathways, our full model included direct and indirect paths from landscape topography to all ecosystem characteristics potentially influencing initial exchangeable and mineralized N, including pH, C:N, and moss productivity.

We ran separate SEMs on the following response variables: (*i*) initial model for the initial exchangeable N (NH_4^+-N, NO_3^--N, and TIN, in $\mu g \cdot (g \text{ of dry soil})^{-1}$) and (*ii*) rate model for N mineralized over the 30-day incubation period (NH_4^+-N, NO_3^--N, and TIN, in $\mu g \cdot (g \text{ of dry soil})^{-1}$). Exchangeable and mineralized N data were log-transformed to fit a Gaussian distribution, and all predictor variables were examined for linearity. In a previous exploration of hydrologic variables (Bisbing et al. 2016), we identified Days as a driver of conifer biomass and DTW as significant in conifer occurrence, so we utilized both measures of the hydrologic regime in our SEM. The relationship between Days and conifer biomass was quadratic, so a quadratic Days term ($Days^2$) was used in the model, but all other relationships were observed to be linear. Species' influences were tested as separate direct effects and included *P. contorta* biomass ($Mg \cdot ha^{-1}$, PICO), *T. heterophylla* biomass ($Mg \cdot ha^{-1}$, TSHE), and *P. sitchensis* biomass ($Mg \cdot ha^{-1}$, PISI). Extraction time (TIME) was included as an interaction term in the rate model to incorporate changes in N and DTW over the 30-day incubation period. An interaction term was also included to test the interactive direct effect between DTW and conifer biomass on exchangeable and mineralized N (e.g., PISI × DTW). Model fit was evaluated using Shipley's *d*-separation test (Shipley 2009), which yields a Fisher's *C* statistic and associated *p* value (strong model fit *p* > 0.05; Grace and Keeley 2006). All analyses were run in R 3.4.1 (R Core Team 2017), and SEM models were fit using the piecewiseSEM package (Lefcheck 2016).

Results

Hydrologic regime and ecosystem properties

Hydrology and soils

Soil saturation (both Days and DTW) corresponded to ecosystem type (*p* < 0.001) and position along the hydrologic gradient (slope and landform, *p* < 0.001). All U wells were dry during the growing season, with no water in the rooting zone (Table 1). All PFOs had water in the rooting zone during some point over the period of observation, but depth to water was ≤−20 cm over the incubation period. Conversely, PEM and PSS sites had the longest duration of

saturation, and the depth to water was rarely below the plant-rooting zone (<−20 cm) over the observation period (Table 1). Cores were free of groundwater (<−10 cm) at all sites over the 30-day incubation period (Table 1). Groundwater pH was lowest at the wettest end of the hydrologic gradient (PEM and PSS sites), averaging from 4.11 at the FAA Bog to 4.92 at WT PEM (Table 1), and highest at the driest sites with U values closer to 6.0 (e.g., 5.94 at Sheep U; Table 1). Measurements were significantly different among ecosystem types (*p* < 0.01). Soil bulk density was also significantly related to ecosystem type (*p* < 0.01), increasing from saturated to well-drained sites (PEM to U; Table 1). The lowest mean bulk densities were in PEM and PSS sites, with values generally <0.15 $g \cdot cm^{-3}$ (Table 1).

Forest community composition and productivity

Conifer biomass and moss productivity varied as a function of hydrologic regime and landscape position (Table 1) and were significantly different among ecosystem types (*p* < 0.05 and *p* < 0.01, respectively). *Pinus contorta* was absent from PFO and U sites (Table 1), while *P. sitchensis* occurred in only one wetland site (Eagle River PSS). *Tsuga heterophylla* was distributed across the entire hydrological gradient but achieved maximum biomass at the driest U sites (Peterson and Sheep U; Table 1). Moss productivity was highest in *Sphagnum*-dominated wetland sites (PEM and PSS) and declined with increasing depth to groundwater and increasing canopy cover (Table 1).

Soil C and N

Carbon pools were high across all sites (>7 kg $C \cdot m^{-2}$), and most were within 5–10 kg $C \cdot m^{-2}$ (10 cm depth; Table 2). The lowest values were measured at the PEM and PSS sites where lower bulk density values dominate the surface soil (Table 2). The highest values were in the U sites, but U sites also had the highest variability (Table 2). Soil C:N was significantly related to ecosystem type (*p* < 0.01) and depth to water (*p* < 0.05). Nitrogen values varied widely among sites, with low N at the FAA Bog PEM and Eagle River PSS that drove C:N up to >80:1 (Table 2). At the other extreme, high N content at the Water Tower PEM and Water Tower PSS resulted in C:N values near 30:1 (Table 2).

Mean exchangeable N varied among ecosystem types, but this relationship was only significant for NO_3^--N (Table 2). The inorganic N pool was dominated by NH_4^+-N (both area and mass; Table 2), and TIN was highest in PFO followed by U sites (Table 2). Exchangeable NH_4^+-N was similar in PEM, PSS, and U sites but two to three times higher on PFO sites (Table 2). The contribution of NO_3^--N to the inorganic N pool was low compared with NH_4^+-N in PFO sites, and inputs of NO_3^--N to TIN were highest in PEM and PSS sites (Table 2).

Mineralized N was recovered primarily as ammonium at most sites (Table 2). Net rates of N mineralization were nearly all negative (Table 2), indicating immobilization of N during the incubation. The greatest N immobilization occurred in two of the PFO sites (Tee Harbor and Fish Creek; Table 2), and the degree of immobilization corresponded with the initial TIN concentration across all sites (Fig. 2a). Immobilization was lower in PSS and U sites, and these ecosystem types contained the only net positive mineralization rates (Eagle PSS, Water Tower PSS, and Peterson U; Table 2).

Relationship between initial nitrogen and water table depth

Concentrations of TIN were closely associated with net mineralization rates (Fig. 2a; *F* = 72.4, *p* < 0.001). The concentration of NH_4^+-N tended to increase as depth to water decreased in all ecosystem types (Fig. 2b). The relationship between NH_4^+-N and water table depth was significant only after stratifying the data among ecosystem types. In PFO and U ecosystems, NH_4^+-N corresponded to water table depth (Fig. 2b; *F* = 52.5, *p* = 0.002), but this relationship was not significant in the saturated PEM and PSS ecosystems (Fig. 2b; *F* = 6.2, *p* = 0.07). There was a trend toward increasing

Table 2. Total concentration of carbon (C), nitrogen (N), ratio of C to N (C:N), and nutrient concentrations from initial extractions and rates of N turnover within nitrogen mineralization experimental sites near Juneau in the southeast Alaska perhumid coastal temperate rainforest.

Site name	Ecosystem type	C (%)	N (%)	C:N (%)	NH$_4^+$ (g·m^{-2})	NO$_3^-$ (g·m^{-2})	TIN (g·m^{-2})	NH$_4^+$ (µg·g^{-1})	NO$_3^-$ (µg·g^{-1})	TIN (µg·g^{-1})	Nitrification (µg·g^{-1}·day^{-1})	Ammonification (µg·g^{-1}·day^{-1})	Net mineralization (µg·g^{-1}·day^{-1})
FAA Bog	PEM	44.51±0.63	0.50±0.63	92±5	17.64±1.30	13.16±1.85	30.84±2.69	14.71±1.20	10.82±1.28	25.58±1.97	0.04±0.07	−0.20±0.05	−0.17±0.10
Water Tower PEM	PEM	43.56±1.65	1.64±0.17	29±3	64.15±21.95	37.27±25.87	101.42±41.28	28.81±10.76	12.99±7.00	41.81±12.72	−0.26±0.18	−0.93±0.39	−1.19±0.41
Ski Area Fen	PEM	42.84±0.30	0.99±0.12	47±5	23.71±3.12	21.82±5.14	45.53±8.04	16.53±2.32	15.14±3.61	33.02±4.71	−0.22±0.15	−0.01±0.11	−0.23±0.24
					35.17±9.14	**24.09±8.52**	**59.26±15.67**	**20.02±3.84**	**13.01±2.46**	**33.02±4.71**	**−0.15±0.08**	**−0.38±0.17**	**−0.53±0.20**
Eagle River PSS	PSS	42.73±0.71	0.52±0.05	86±7	19.13±7.16	25.98±6.99	45.12±13.91	17.61±6.54	23.89±6.03	41.51±12.36	−0.50±0.21	0.20±0.21	−0.29±0.38
Water Tower PSS	PSS	42.81±0.57	1.59±0.20	31±4	16.17±2.66	20.47±5.20	36.64±7.28	10.58±2.73	13.05±3.86	23.63±6.30	−0.10±0.15	1.15±00.41	1.04±0.53
Mt Jumbo Bog	PSS	43.08±0.91	0.83±0.12	58±6	61.92±2.67	15.32±2.39	77.24±5.10	42.19±2.51	10.47±1.79	52.67±4.24	−0.22±0.04	−1.38±0.06	−1.61±0.09
					32.41±6.76	**20.59±3.02**	**52.99±7.25**	**23.46±4.67**	**15.80±2.83**	**39.27±5.67**	**−0.28±0.09**	**−0.01±0.35**	**−0.29±0.38**
Tee Harbor PFO	PFO	47.58±0.60	0.82±0.04	59±2	140.16±65.73	9.25±0.97	149.41±66.34	72.46±29.11	5.20±0.32	77.67±29.10	−0.08±0.02	−2.04±1.08	−2.12±1.09
Fish Creek PFO	PFO	43.85±2.51	1.26±0.15	38±4	169.28±48.68	9.06±1.04	178.34±48.48	95.53±26.59	5.05±0.89	100.58±26.99	−0.06±0.05	−3.17±0.89	−3.23±0.90
Ski Area PFO	PFO	39.47±4.43	1.00±0.14	42±6	38.22±14.89	10.30±4.59	48.52±18.51	12.49±3.82	3.22±0.46	15.71±3.87	−0.02±0.02	−0.50±0.17	−0.07±0.17
					115.89±30.25	**9.54±1.46**	**125.42±30.44**	**60.16±15.94**	**4.49±0.42**	**64.65±16.17**	**−0.05±0.02**	**−1.75±00.58**	**−1.81±0.58**
Eagle River U	U	38.80±4.45	1.01±0.09	38±3	49.64±13.51	9.02±1.63	58.67±14.74	23.49±8.39	4.04±0.95	27.54±9.21	−0.04±0.02	−0.27±0.29	−0.30±0.31
Peterson U	U	48.29±0.81	1.20±0.07	41±3	15.69±2.13	8.89±1.38	24.58±3.01	8.05±1.15	4.55±0.73	12.59±1.65	−0.05±0.03	0.53±0.09	0.48±0.12
Sheep Creek U	U	31.04±6.12	1.06±0.20	29±3	100.70±51.85	32.65±9.69	133.36±56.15	38.42±26.21	9.39±3.22	47.81±29.30	−0.26±0.12	−0.81±0.99	−1.08±1.11
					55.35±19.29	**16.86±4.51**	**72.20±22.24**	**23.32±9.11**	**5.99±1.27**	**29.32±7.09**	**−0.12±0.05**	**−0.18±0.36**	**−0.29±0.40**

Note: Values are mean ± SE at individual sites averaged from four locations within the site. Bold values represent mean ± SE of ecosystem type. Percent C and N samples were subsampled at 0–10 cm depth for consistency across sites. See Table 1 for abbreviations. Total inorganic nitrogen is presented as TIN. C, N, C:N, and NO$_3^-$ (µg·g^{-1}) are significantly different among ecosystem types at $p < 0.05$.
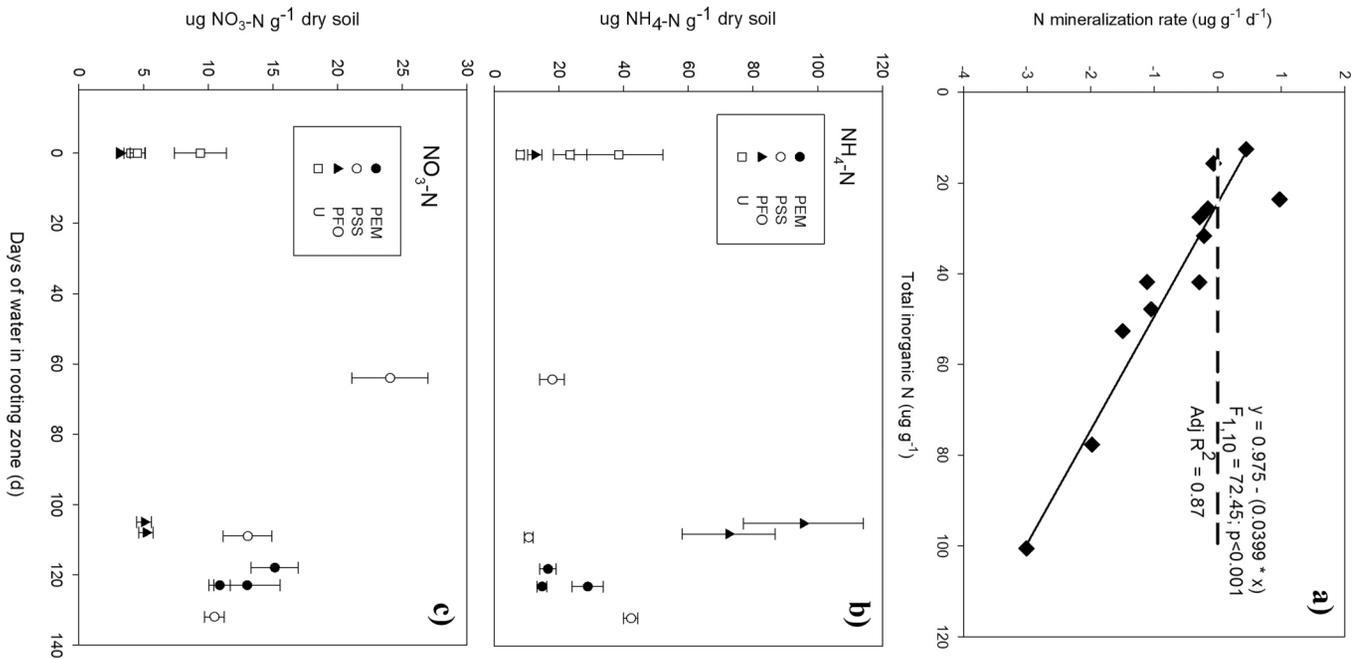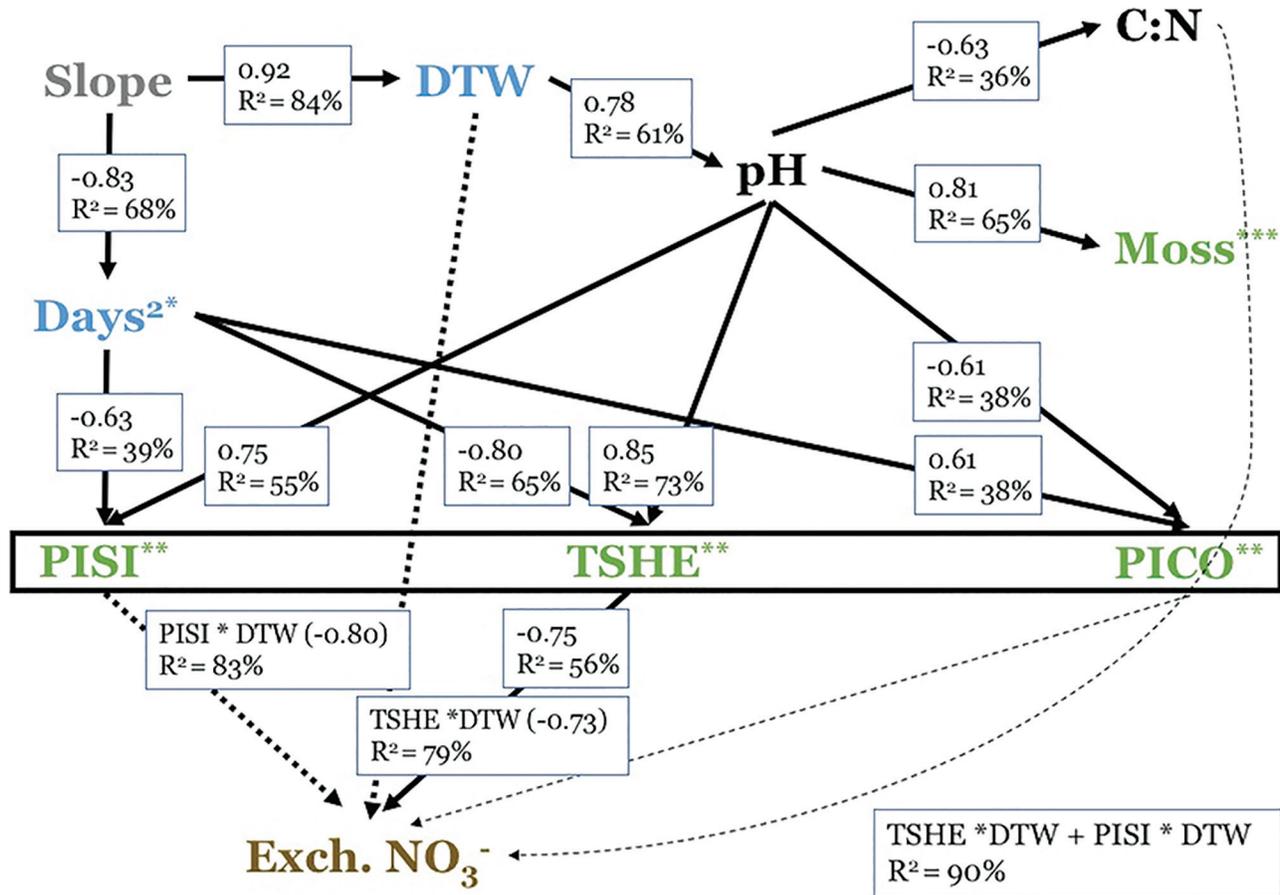

Fig. 2. (*a*) Relationship between average nitrogen (N) mineralization rate and total exchangeable inorganic nitrogen across all ecosystem types near Juneau, Alaska. Dashed line represents no net mineralization. Values above the line represent net N gain in the incubation, while below the line is immobilization of N. The equation represents a model of N mineralization across all sites as a function of total inorganic N. (*b*) NH$_4^+$-N and (*c*) NO$_3^-$-N (mean ± SE) of initial exchangeable N in all ecosystem types near Juneau, Alaska, as a function of average water table depth (cm) for the sample period. Ecosystem types are classified as palustrine emergent (PEM), palustrine scrub–shrub (PSS), palustrine forested wetland (PFO), and forested upland (U).

y = 0.975 − (0.0399 * x)
F$_{1,10}$ = 72.45; p<0.001
Adj R^2 = 0.87

Fig. 3. Complete path diagram of relationships between landscape, hydrologic, and ecological characteristics and exchangeable (Exch.) NO_3^--N tested using structural equation modeling (SEM). Path analysis of each nitrogen (N) variable (exchangeable and mineralized TIN, NH_4^+-N, and NO_3^--N) was identical from slope to conifer species' biomass, so the full model is only presented for this response variable. The black box around species denotes this separation. Lines between variables represent relationships tested in the final model. Solid lines indicate path significance ($p > 0.05$, indicating good model fit), dark dashed lines are not significant ($p < 0.05$), and light dashed lines represent relationships significant in interactions alone. Standardized coefficients and R^2 values are presented for each path as are full models if multiple pathways influenced N. All N data were log-transformed to fit a Gaussian distribution. Tree biomasses ($Mg \cdot ha^{-1}$) of *Pinus contorta* (PICO), *Picea sitchensis* (PISI), and *Tsuga heterophylla* (TSHE) were modeled as potential direct effects. Moss data represent site productivity ($Mg \cdot ha^{-1} \cdot year^{-1}$). Days^2 is a quadratic term of days when water was in the rooting zone. Depth to water (DTW) corresponds to the reading on the dates of the incubation study on day 1 and on day 30. TIME represents change over the incubation period. [Colour online.]

NO_3^--N with decreasing depth to water, but there was a great deal of variability at the most saturated sites (PEM and PSS; Fig. 2c). There was clear dominance of NH_4^+-N compared with NO_3^--N in the PFO ecosystems (Figs. 2b and 2c).

Linkages between landscape and N dynamics

Plant–soil–water model

Structural equation modeling identified significant direct and indirect linkages between landscape, hydrologic, and ecosystem characteristics (Fig. 3). Models presented here include standardized path coefficients and met the SEM criteria of $p > 0.05$, indicating no major discrepancies between the model and the data (Grace and Keeley 2006). Additional relationships were tested (e.g., moss and C:N paths to conifer biomass) but are not presented due to poor model fit (model $p < 0.05$) and lack of significance in driving responses (variable $p > 0.05$).
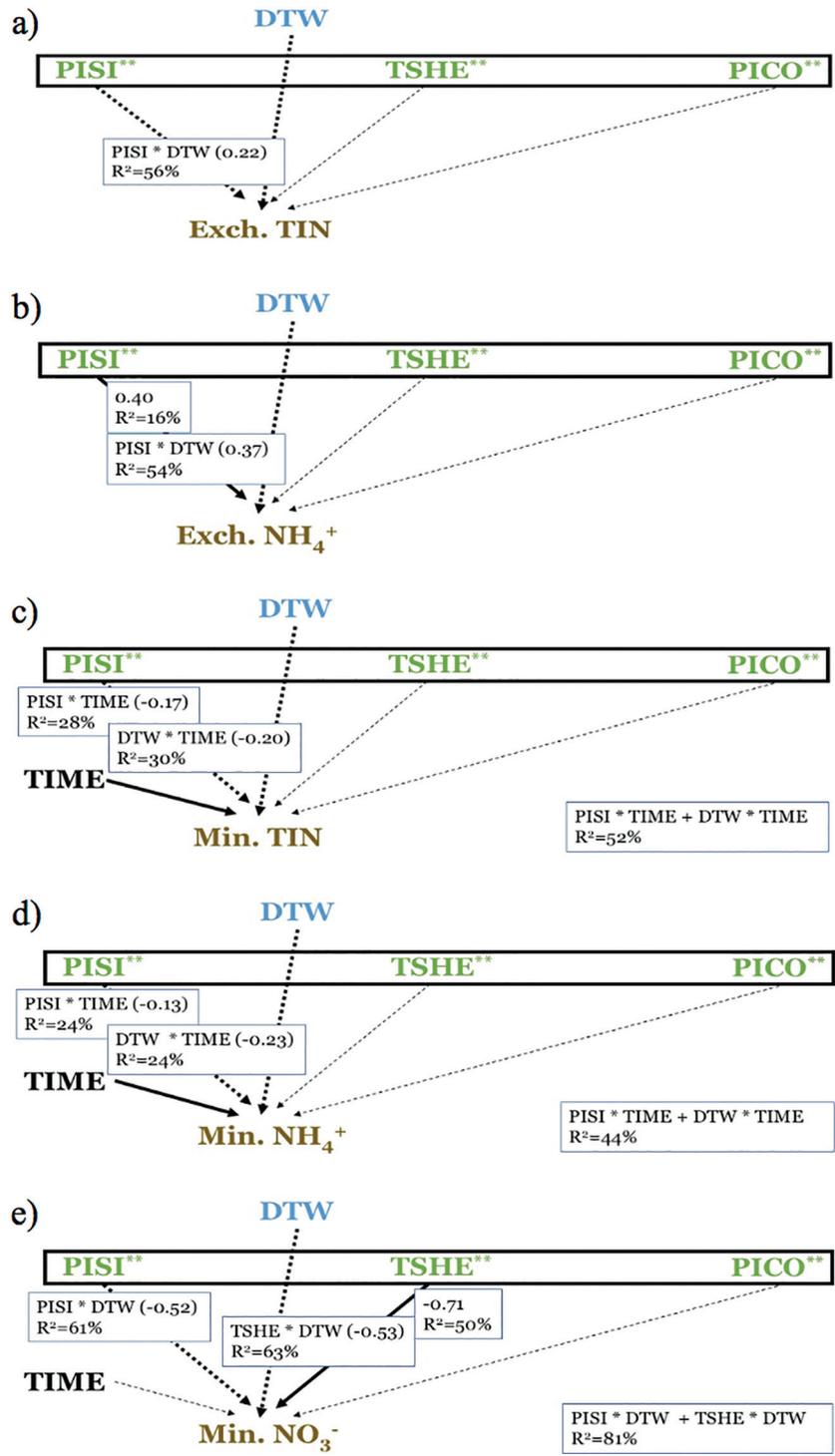
All models evaluating initial exchangeable and mineralized N (NH_4^+-N, NO_3^--N, and TIN) followed the same paths from slope to species' conifer biomass (Fig. 3), only diverging after this point in the path analysis (black box in Fig. 3). The full model is presented only for NO_3^--N (Fig. 3), although relationships were identical up to species' biomass for all exchangeable and mineralized N mod-

els (Figs. 4a–4e). The slope of the landscape positively influenced DTW (Fig. 3; standardized coefficient = 0.92, $R^2 = 84\%$) and negatively influenced Days^2 (-0.83, $R^2 = 68\%$). *Pinus contorta* biomass was then directly, positively related to Days^2 (0.61, $R^2 = 38\%$), while PISI and TSHE had direct, negative associations (-0.63, $R^2 = 39\%$, and -0.80, $R^2 = 65\%$, respectively). The DTW directly, positively influenced pH (0.78, $R^2 = 61\%$) and indirectly affected a number of ecosystem and species' characteristics through its influence on pH. The pH of a site had a direct, positive effect on moss productivity (0.81, $R^2 = 65\%$), PISI biomass (0.75, $R^2 = 55\%$), and TSHE biomass (0.85, $R^2 = 73\%$); conversely, pH had a direct, negative effect on soil C:N (-0.63, $R^2 = 36\%$) and PICO biomass (-0.61, $R^2 = 38\%$). The soil C:N path to N was not significant in any model but is displayed (Fig. 3) due to its hypothesized direct effect on N.

Exchangeable N model

Initial TIN was directly, positively affected by the interaction between PISI biomass and DTW (0.22, $R^2 = 56\%$; Fig. 4a). Initial exchangeable NH_4^+-N was directly, positively influenced by PISI (0.40, $R^2 = 16\%$) but more strongly affected by the interaction between PISI biomass and DTW (0.37, $R^2 = 54\%$; Fig. 4b). Initial exchangeable NO_3^--N was directly, negatively impacted by TSHE

Fig. 4. Diagrams of final nodes in path analysis of relationships between landscape, hydrologic, and ecological characteristics and each nitrogen (N) variable: (*a*) exchangeable (Exch.) TIN, (*b*) exchangeable NH_4^+-N, (*c*) mineralized (Min.) TIN, (*d*) mineralized NH_4^+-N, and (*e*) mineralized NO_3^--N. The complete model is presented in Fig. 2. Paths presented represent the direct effects of conifer species' biomass, hydrologic regime, and incubation time on N dynamics tested using structural equation modeling (SEM). Lines between variables represent relationships tested in the final model. Solid lines indicate path significance ($p > 0.05$, indicating good model fit), dark dashed lines are not significant ($p < 0.05$), and light dashed lines represent relationships significant in interactions alone. Standardized coefficients and R^2 values are presented for each path as are full models if multiple pathways influenced N. All N data were log-transformed to fit a Gaussian distribution. Tree biomasses ($Mg \cdot ha^{-1}$) of *Pinus contorta* (PICO), *Picea sitchensis* (PISI), and *Tsuga heterophylla* (TSHE) were modeled as potential direct effects. Moss data represent site productivity ($Mg \cdot ha^{-1} \cdot year^{-1}$). $Days^2$ is a quadratic term of days when water was in the rooting zone. Depth to water (DTW) corresponds to the reading on the dates of the incubation study on day 1 and on day 30. TIME represents change over the incubation period. [Colour online.]

biomass (-0.75, $R^2 = 56\%$), the interaction between TSHE and DTW (-0.73, $R^2 = 79\%$), and the interaction between PISI and DTW (-0.80, $R^2 = 83\%$; Figs. 3 and 4). Exchangeable NO_3^--N was best explained by a model including all of these factors (TSHE × DTW + PISI × DTW, $R^2 = 90\%$; Fig. 3).

Mineralized N model

Mineralized TIN was negatively influenced by the interactions between PISI × TIME (-0.17, $R^2 = 28\%$) and DTW × TIME (-0.20, $R^2 = 30\%$; Fig. 4c). The TIN mineralized was best explained by a model including all of these factors (PISI × TIME + DTW × TIME, $R^2 = 52\%$; Fig. 4c). The rate of NH_4^+-N mineralized was directly, negatively influenced by interactions between PISI × TIME (-0.13, $R^2 = 24\%$) and DTW × TIME (-0.23, $R^2 = 24\%$; Fig. 4d). Mineralized NH_4^+-N was best explained by a model including all of these factors (PISI × TIME + DTW × TIME, $R^2 = 44\%$; Fig. 4d). The rate of NO_3^--N mineralized was directly, negatively affected by TSHE biomass (-0.71, $R^2 = 50\%$) and interactions between PISI × DTW (-0.52, $R^2 = 61\%$) and TSHE × DTW (-0.53, $R^2 = 63\%$; Fig. 4e). Mineralized NO_3^--N was best explained by a model including all of these factors (PISI × DTW + TSHE × DTW, $R^2 = 81\%$; Fig. 4e).

Discussion

Models for nutrient dynamics across complex landscapes are needed to guide research into existing patterns of N cycling and design experiments for prediction of the future fate on ecosystem function. Our conceptual model of plant–soil–water interactions was based on the strong influence of landscape, in particular slope, on local hydrology (Fig. 1; D'Amore et al. 2015a), the role of hydrologic regime and soil nutrients in determining conifer distributions (Bisbing et al. 2016), and a hypothesized effect of hydrologic regime and conifer distributions on N cycling. Our test of this conceptual model across a natural hydrologic gradient (Fig. 3) introduces pathways of connectivity from landscape characteristics to coupled hydrologic and biological interactions and their effects on initial exchangeable and mineralized N, providing a framework in which resources co-vary coincident with the local environment and as a function of the forest community. Our study findings (i) support the concept that hydrologic and biological interactions shape N cycling and (ii) indicate that N concentration and mineralization are closely linked to tree species, forest biomass, and water table indicators regardless of ecosystem type. In particular, the emergence of forest community composition as an indicator of N cycling highlights the effect that species have on nutrient dynamics, while the trend of increasing inorganic N with increasing soil saturation points to the physical influence of saturation on N. The interaction of these two factors must therefore be considered to adequately model N relationships.

Influence of soil saturation on N cycling

Consistent with our conceptual model (Fig. 1), our results clearly establish the influence of soil saturation on patterns of N concentration and cycling, with DTW identified as a primary driver of N in our complex models of initial exchangeable and mineralized N (Figs. 3 and 4). Across the wetness gradient tested here, the change in DTW over time directly affected exchangeable N and capacity to mineralize N through interactions with conifer biomass (Figs. 3 and 4a–4e). Nitrate mineralization occurred as a function of linked hydrologic and biological interactions (e.g., PISI × DTW; Fig. 4e), while TIN and NH_4^+-N mineralization were driven primarily by change in the water table over time (e.g., TIN, DTW × TIME; Fig. 4c). Although nitrification occurred under saturated conditions (PEM and PSS sites; Table 2 and Fig. 3), increasing depth to groundwater and associated increases in PISI biomass led to ammonification (Fig. 4b) and increases in total inorganic N mineralization (Fig. 4a) at the driest end of the hydrologic gradient (PFO and U sites; Table 2). Soil moisture and DTW have previously been

identified as prime determinants of N form and cycling in other pine-dominated wetlands (Yu and Ehrenfeld 2009) and along riparian wetland gradients (Hefting et al. 2004). Mineralization rates may differ by aeration status, with increased mineralization and ammonification under aerobic conditions in peatlands (Bridgham et al. 1998) and forested wetlands (Yu and Ehrenfeld 2009) but variable responses under fluctuating soil moisture conditions (Yu and Ehrenfeld 2009). Nitrification may also increase under drier conditions in certain soils (Hefting et al. 2004), but increased rates of denitrification may reduce this pool over time (Pinay et al. 2007).

In our study, the increase in exchangeable N from NH_4^+-N to NO_3^--N associated with increased soil saturation (Table 2) is consistent with the reduced capacity for N mineralization and decreased denitrification in hydric soils (Williams and Wheatley 1988). Denitrification is generally facilitated by alternating wet and dry conditions (Pinay et al. 2007). The PEM and PSS sites had consistent water tables that did not fluctuate, therefore poising the system at a state of anoxic conditions that were usually out of the range of denitrification (D'Amore et al. 2015a). In addition, low pH may inhibit nitrification leading to accumulation of dissolved organic nitrogen that is neither mineralized nor nitrified but leaves the soil matrix through lateral flow (Fellman et al. 2009). Shifts from NH_4^+-N in better drained PFO and U sites to NO_3^--N in saturated PEM and PSS sites (Table 2) can occur through accumulation of NO_3^--N by suppression of denitrification and lack of export via groundwater flow (Pinay et al. 2007). The low NO_3^--N to NH_4^+-N yield in PFO and U sites is also consistent with lower nitrification in acidic (De Boer and Kowalchuk 2001) and anaerobic (Sajedi et al. 2012) forest soils.

Our methodological approach to N assays controlled for potential disturbance effects and facilitated comparisons of soil saturation with N cycling in the context of the study. This method may have introduced constraints on N turnover and yield, as the core was open to the environment and subject to potential leaching or gaseous loss of N over the course of the experiment (Robertson et al. 1999a). Our results, however, are consistent with regional data (Fellman and D'Amore 2007; Prescott et al. 1993) and add another line of empirical evidence supporting the role of hydrologic regime in shaping N dynamics.

Role of conifers in N cycling

Our findings in intact, natural PCTR ecosystems concur with recent experimental studies (e.g., Prescott and Vesterdal 2013; Ribbons et al. 2016) in identifying tree species as influential in shaping N cycling. Interacting with hydrologic regime, tree species' biomass corresponded to N availability and cycling (Table 2; Figs. 3 and 4), suggesting that conifers generate species-specific effects on nutrient cycling. In particular, the strong signal of *P. sitchensis* on the concentration and mineralization of NH_4^+-N and NO_3^--N (Figs. 3 and 4) indicates that forest community composition shapes N dynamics in the PCTR. Soil saturation exerts a clear influence on soil N, but the forest community directly affects nutrient input, use, and limitation (Hobbie et al. 2006).

Species-specific impacts to N cycling likely occur via return of varying quality and amount of litter to the forest floor, which is recycled through decomposition (Gurmesa et al. 2013). Foliar litter quality can be more important than decomposition rates (Prescott 2002), with forest composition directly influencing the amount and type of litterfall N input. The close association of exchangeable TIN and the mineralization rate (Fig. 2) can be linked to species-specific litter foliage. In this study, the lower TIN associated with saturated sites (Table 2), which are characterized by low overstory biomass of *P. contorta* (Table 1), may be explained by reduced litterfall input and subsequent lower N turnover. High nutrient concentrations in *Picea* foliar litter compared with *Pinus* (Johansson 1995) and *Tsuga* (Turner and Franz 1985) may be key to the influence of tree species on N availability, and our results support the concept that conifer litter quality influences N.

Other potential explanations for the significance of tree species in this study may be variation in site quality driven by parent material type (Kranabetter et al. 2005) or shifts in microbial uptake of N across ecosystem types. Although parent material can influence forest composition, feedbacks from tree species further shape microbial community composition (Ushio et al. 2008; Prescott and Grayston 2013), which in turn drives N turnover (Prescott and Vesterdal 2005). The significance of the interaction between incubation time and species (e.g., TIME × PISI) on N mineralization (Figs. 3 and 4) suggests that N pools are additionally influenced by site factors associated with specific tree species and by unmeasured ecosystem processes such as microbial activity.

Soil nutrient dynamics

The immobilization of N in our study (Table 2), while not uncommon (e.g., Lewis and Kaye 2012), is notable for its consistency across sites, as well as for its high magnitude in the PFO sites. Immobilization of N in our wettest sites indicates an assimilation of both NH_4^+-N and NO_3^--N. The presence of NH_4^+-N may also facilitate N immobilization and increase inaccessibility of N by forest trees, as microbial immobilization is more effective with NH_4^+-N than with NO_3^--N (Kaye and Hart 1997). Immobilization of N may also be enhanced by the availability of labile C for use in microbial assimilation of N. The large carbon stocks at the sites (Table 2) may not be as important as the C quality. Support for labile C as a driver of N cycling was identified by Bengtsson et al. (2003), where respiration rate and ATP were more closely associated with N cycling than C:N. There is also evidence that some ecosystems have flexible responses to substrate availability, as plant stoichiometric traits may alter ecosystem-level N cycling due to food web response to different substrate functional groups (Carrillo et al. 2016) or vary with ecosystem age (Kaye et al. 2003). Biogeochemistry studies in the Alaskan PCTR support the assertion that there is labile organic matter present in the soil solution that is exported to associated headwater streams (Fellman et al. 2009). Microbial assimilation of N may be facilitated through access to this labile carbon pool in sites with conditions that constrain N turnover, limit biomass assimilation, and accumulate labile soluble carbon such as the PFO sites.

Conclusions

The concentrations of N, magnitude of N mineralization, and relationship with the landscape described in this research expands the scope of plant–soil–water interactions in temperate forest ecosystems. We have outlined a model that captures the integrative impact of soil saturation, tree biomass concentration and type, and unexplained site variation on the form and availability of N. While complex, reducing the trajectory of N cycling to major factors establishes a foundation to outline both the present and the future fates of N in temperate forest ecosystems. This foundation is important given the prediction for an altered precipitation regime, reduction in snowpack, and overall increase in precipitation with climate change, which may shift some mesic temperate systems into similar humid conditions with concomitant alterations of the N cycle. Nutrient cycling is complex and thus rarely assessed in a single study, but our findings provide a clear linkage between tree species' biomass, the degree of soil saturation, and N dynamics in temperate forests.

Acknowledgements

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Appendix A

Table A1. Correlation matrix of all response and potential predictor variables from exploratory data analysis.

Variable	Slope_Avg	NH4_ugg	NO3_ugg	TIN_ugg	DTW	Days_.20	PICO_mass	PISI_mass	TSHE_mass	Overstory	C	N	C.N	pH	Moss_Mghayr
Slope_Avg	1.00	−0.12	−0.62	−0.27	−0.92	−0.82	−0.50	0.67	0.82	0.84	−0.45	0.21	−0.59	0.77	−0.71
NH4_ugg	−0.12	1.00	−0.32	0.98	0.09	0.30	−0.23	0.36	0.13	0.19	0.09	0.04	−0.11	0.40	−0.26
NO3_ugg	−0.62	−0.32	1.00	−0.10	0.62	0.40	0.32	−0.47	−0.70	−0.69	−0.01	−0.21	0.44	−0.64	0.60
TIN_ugg	−0.27	0.98	−0.10	1.00	0.24	0.40	−0.16	0.27	−0.03	0.04	0.09	−0.01	−0.02	0.27	−0.14
DTW	−0.92	0.09	0.62	0.24	1.00	0.86	0.56	−0.71	−0.90	−0.90	0.36	−0.04	0.38	−0.78	0.68
Days_.20	−0.82	0.30	0.40	0.40	0.86	1.00	0.60	−0.63	−0.81	−0.80	0.48	0.02	0.30	−0.60	0.61
PICO_mass	−0.50	−0.23	0.32	−0.16	0.56	0.60	1.00	−0.56	−0.65	−0.63	0.14	0.37	−0.07	−0.61	0.42
PISI_mass	0.67	0.36	−0.47	0.27	−0.71	−0.63	−0.56	1.00	0.70	0.81	−0.72	0.04	−0.42	0.75	−0.65
TSHE_mass	0.82	0.13	−0.70	−0.03	−0.90	−0.81	−0.65	0.70	1.00	0.98	−0.19	0.11	−0.41	0.85	−0.74
Overstory	0.84	0.19	−0.69	0.04	−0.90	−0.80	−0.63	0.81	0.98	1.00	−0.34	0.13	−0.46	0.87	−0.77
C	−0.45	0.09	−0.01	0.09	0.36	0.48	0.14	−0.72	−0.19	−0.34	1.00	−0.02	0.34	−0.24	0.25
N	0.21	0.04	−0.21	−0.01	−0.04	0.02	0.37	0.04	0.11	0.13	−0.02	1.00	−0.87	0.34	−0.42
C.N	−0.59	−0.11	0.44	−0.02	0.38	0.30	−0.07	−0.42	−0.41	−0.46	0.34	−0.87	1.00	−0.63	0.69
pH	0.77	0.40	−0.64	0.27	−0.78	−0.60	−0.61	0.75	0.85	0.87	−0.24	0.34	−0.63	1.00	−0.81
Moss_Mghayr	−0.71	−0.26	0.60	−0.14	0.68	0.61	0.42	−0.65	−0.74	−0.77	0.25	−0.42	0.69	−0.81	1.00

Note: Shaded cells indicate high correlation (>0.65) between variables. Days is the number of days when water was in the rooting zone (<−20 cm). Depth to water (DTW) corresponds to the reading on the dates of the incubation study on day 1 and on day 30. Total tree biomass (Mg·ha^{-1}) is presented for *Pinus contorta* (PICO), *Picea sitchensis* (PISI), and *Tsuga heterophylla* (TSHE).