

Uptake of salmon-derived nitrogen by mosses and liverworts in coastal British Columbia

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Throughout forested watersheds bordering the North Pacific, anadromous salmon (*Oncorhynchus* spp.) are transferred into coastal forests by numerous predators and scavengers with remnants providing an important nutrient subsidy to riparian zones. The contribution of these nutrients to mosses and liverworts, which are the dominant ground cover of coastal forests, has not been investigated. We examine here $\delta^{15}\text{N}$ isotope signatures and foliar percent N of eight moss and liverwort species, as well as moss and liverwort community structure, in multiple habitat blocks that vary in access to salmon nutrients from two watersheds on the central coast of British Columbia. For the most common moss *Rhytidiadelphus loreus*, we also examine $\delta^{15}\text{N}$ values and foliar percent N among salmon carcass micro-sites and along wildlife trails. Overall, $\delta^{15}\text{N}$ signatures ranged from 2‰ to 7‰ higher below the falls near the salmon stream than above the small falls that are impassable to salmon, or at the adjacent control watershed that had no salmon. Among micro-sites, $\delta^{15}\text{N}$ and %N values were highest near bony carcass remnants from transfer during previous years and high adjacent to wildlife trails indicating spatial heterogeneity in the salmon nutrient pools of these forests. Species richness and prevalence of nitrogen-rich soil indicators were also highest in forests adjacent to the salmon stream. These data suggest an important contribution of salmon-derived nutrients to the non-vascular plants of the riparian zone of old-growth forests throughout the Pacific Rim.

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Introduction

Throughout the Pacific Rim, anadromous salmon (*Oncorhynchus* spp.) constitute an important seasonal pulse of nutrients for diverse taxa of marine, freshwater and terrestrial organisms (summarized by Cederholm et al. 2000). As well as subsidizing lake and stream food webs (Kline et al. 1990, 1993, Bilby et al. 1996, Wipfli et al. 1998, Chaloner et al. 2002), salmon nutrients also act as an important nutrient source for riparian vegetation (Ben-David et al. 1998, Helfield and Naiman 2001, Mathewson et al. 2003) and for multiple trophic levels in forest food webs adjacent to salmon streams (Hocking and Reimchen 2002, Reimchen et al. 2003).

Salmon-derived fertilization of coastal riparian zones can have multiple sources. Bears (*Ursus arctos* and *U. americanus*), which are abundant and widespread throughout the distribution of salmon, are major vectors through which salmon nutrients are transferred to the forest floor, either from direct carcass transfer (Reimchen 1994, 2000) or from urine and faeces deposition (Hilderbrand et al. 1999). Other predators such as wolves (*Canis lupus*) and river otters (*Lutra canadensis*) can have important local influences (Ben-David et al. 1997, Cederholm et al. 2000, Darimont et al. 2003). In addition, when there is a low gradient between the stream and riparian zones, flooding events and hyporheic flow can lead to input of salmon-derived

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nutrients (Ben-David et al. 1998, O'Keefe and Edwards 2003).

Mosses and liverworts comprise the dominant surface and ground cover throughout temperate rainforest ecosystems in the Pacific northwest. These constitute a minor contribution to overall biomass within forest ecosystems, yet are essential to nutrient dynamics, temperature regulation, and moisture retention of soils (Oechel and Van Cleve 1986). They occupy a significant portion of the landscape and use a variety of substrata such as humus, rock, woody debris, shrubs and standing trees (Jonsson 1997). Bryophytes lack true roots and absorb nutrients mainly throughout the leaf surface (Héban 1977, Bates 1992). Typical sources of nutrients include atmospheric deposition (Soares and Pearson 1997, Williams et al. 1999, Aldous 2002), precipitation and canopy throughfall (Tamm 1953, Oechel and Van Cleve 1986, Eckstein 2000), litterfall decomposition (Oechel and Van Cleve 1986), underlying soils (Bates 1992), N-fixing symbioses (Deluca et al. 2002), as well as coarse woody debris and periodic flooding of stream terraces (Jonsson 1997). Bryophytes have efficient absorption (Weber and Van Cleve 1984, Oechel and Van Cleve 1986, Bates 1992) and extensive internal recycling (Rydin and Clymo 1989, Brown and Bates 1990, Wells and Brown 1996, Eckstein and Karlsson 1999, Eckstein 2000) and those occupying soil and humus substrata can act as autogenic ecosystem engineers (Jones et al. 1994).

In this study, we investigate the contribution of salmon-derived nitrogen to common moss and liverwort species at three representative watersheds on the central coast of British Columbia, Canada. Using nitrogen isotopes ($\delta^{15}\text{N}$), we examine the extent of uptake of salmon-derived nitrogen in eight species of mosses and liverworts above and below waterfalls that are barriers to salmon migration. Within areas of high salmon transfer, we further assessed the nitrogen signature on wildlife trails and at salmon-carcass sites predicting that trails and feeding micro-sites act as major source pools of nitrogen in these riparian areas. Our findings build on previous studies at these watersheds that have investigated isotope signatures in invertebrate and vascular plant communities (Hocking and Reimchen 2002, Mathewson et al. 2003).

We also investigate variation in percent nitrogen in moss and liverworts across the gradient of salmon-nutrient access, and use this as a potential proxy for productivity. Nitrogen is an essential macronutrient to all plants (Raven et al. 1992) and is generally considered to be the principal limiting nutrient in temperate forest ecosystems (Chabot and Mooney 1985, Chapin et al. 1986). Mosses and liverworts readily assimilate dissolved inorganic nitrogen, including NO_3^- and NH_4^+ (Weber and Van Cleve 1981, Williams et al. 1999, Eckstein 2000). Variation in %N and $\delta^{15}\text{N}$ within and among

species and habitats can provide insight into the contribution of Pacific salmon and its effect on productivity within the moss and liverwort community. Additionally, we examine community structure of these taxa across salmon nutrient gradients and compare richness, Shannon diversity and prevalence of nitrogen-rich versus nitrogen-poor soil indicators in multiple sites.

Methods

Study site

This study was conducted on three watersheds on the mid-coast of British Columbia, Canada: Clatse ($52^\circ 20.6'\text{N}$; $127^\circ 50.3'\text{W}$), Ripley Bay ($52^\circ 25.5'\text{N}$; $127^\circ 53.1'\text{W}$) and Neekas ($52^\circ 28.4'\text{N}$; $128^\circ 8.0'\text{W}$). Most of our data is derived from Clatse. All watersheds occur on the mainland in the Coastal Western Hemlock Biogeoclimatic Zone, with a mean annual temperature of approximately 8°C , and mean annual precipitation in excess of 4000 mm (Green and Klinka 1994). General site descriptions are given in several previous studies (Hocking and Reimchen 2002, Mathewson et al. 2003). Briefly, the riparian community is dominated by stands of western hemlock (*Tsuga heterophylla*), western red cedar, (*Thuja plicata*), amabilis fir (*Abies amabilis*), sitka spruce (*Picea sitchensis*) and red alder (*Alnus rubra*). Understory shrub species include false azalea (*Menziesia ferruginea*), Alaskan blueberry (*Vaccinium alaskaense*), oval-leaved blueberry (*V. ovalifolium*), red huckleberry (*V. parvifolium*), devil's club (*Oplopanax horridus*), and salmonberry (*Rubus spectabilis*). Common herb layer species among all sites include false lily-of-the-valley (*Maianthemum dilatatum*), foamflower (*Tiarella trifoliata*), creeping raspberry (*Rubus pedatus*), dwarf dogwood (*Cornus canadensis*), deer fern (*Blechnum spicant*), lanky moss (*Rhytidiadelphus loreus*), step moss (*Hylocomium splendens*) and common green sphagnum (*Sphagnum girgensohnii*).

The Clatse and Neekas watersheds support autumn spawning populations of pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon, with modest runs of coho (*O. kisutch*) and infrequent sockeye (*O. nerka*) (Manzon and Marshall 1981). Recent salmon returns average 17000 pink and 5000 chum salmon, and 18000 pink and 30000 chum salmon, on the Clatse and Neekas respectively (Dept of Fisheries and Oceans Escapement data: 1990–1999). Spawning occurs from late August to early November to the base of a five-meter waterfall one km upstream from the estuary on the Clatse and a ten-meter waterfall 2.1 km upstream on the Neekas. Bears (mainly *Ursus americanus*, but, occasional *U. arctos*) and wolves (*Canis lupus*) are active vectors of salmon carcasses. The Ripley Bay watershed serves as a control watershed due to the presence of a 20 m waterfall at the

mouth of the river that prevents entrance by Pacific salmon to the stream.

Experimental design

In late June 2001, we examined moss and liverwort nitrogen nutrition and community structure from multiple habitat blocks on the Clatse and Ripley Bay rivers that differed in access to salmon nutrients. At Clatse River, we sampled from two blocks below the waterfall, 500–600 m upstream from the estuary, the first situated 5–20 m from the stream (CR-below/near), with access to salmon nutrients, and the second situated 90–110 m into the forest where there was minimal salmon transfer (CR-below/far). We also sampled two blocks above the waterfall, the first situated 200–250 m above the falls and 5–20 m from the stream (CR- above/near) and a second situated 350–400 m above the falls and 100–120 m into the forest (CR- above/far). Although the waterfall prevents upstream movement of salmon, upstream movement of vertebrate predators may result in some nutrient transfer above the falls. These sampling sites coincide with habitat blocks used in previous studies in this watershed investigating isotope signatures in invertebrates (Hocking and Reimchen 2002) and vascular plant community structure (Mathewson et al. 2003), and were chosen based on similarity in forest structure, canopy cover and slope. We also sampled mosses and liverworts at the control watershed, Ripley Bay. Two habitats blocks were established 450–500 m upstream from the Ripley Bay estuary, the first situated 5–20 m from the stream (RB-near) and the second situated 100–120 m from the stream (RB-far). In total, six habitat blocks were established between these two watersheds.

For each habitat block, we designated three sequential 10×10 m plots parallel to the stream. Within each plot, we sampled three 10×1 m belt transects (0 m, 5 m and 10 m) perpendicular to the stream to collect representative specimens off the underlying humus layer for $\delta^{15}\text{N}$ and %N analysis. For each of the most common moss species, *Rhytidiadelphus loreus*, *Hylocomium splendens* and *Sphagnum girgensohnii*, one sample was taken on every transect in all habitat blocks ($n=9$ per species per habitat block). The only exception occurred in CR-below/near, where *H. splendens* and *S. girgensohnii* were absent from one and two transects respectively ($n=8$ and $n=7$). The liverwort *Pellia neesiana* was also sampled but was less abundant in most plots. Four additional species, *Rhizomnium glabrescens*, *Kindbergia oregana*, *Conocephalum conicum* and *Sphagnum squarrosum* were collected on the Clatse River only. *R. glabrescens* and *K. oregana* were collected along transects in plots in the two habitat blocks below the falls (CR- below/near and CR- below/far), while *C. conicum*

and *S. squarrosum* were collected in the two habitat blocks within 20 m of the stream above and below the falls (CR- below/near and CR- above/near). *R. glabrescens* typically occurred as epiphytic and was sampled off the underlying woody substratum. Sample sizes within blocks varied among species (range 4–9).

Due to the non-random distribution of salmon carcasses and nutrients in the riparian zone by vertebrate predators, we further investigated the micro-spatial influence of salmon nutrients on mosses and liverworts on the Clatse River. We compared $\delta^{15}\text{N}$ and %N values in the dominant moss *R. loreus* collected immediately adjacent to and 2 m away from wildlife trails and vertebrate feeding micro-sites. Two wildlife trail sections were chosen, one above and one below the falls. Trails were positioned roughly parallel to the stream at a distance that varied from 5–30 m. We made paired samples every 10 m along the wildlife trail from below and above the waterfalls ($n=13$ pairs below; $n=12$ pairs above). At each site we sampled *R. loreus* from the edge of the trail as well as a second sample 2 m perpendicular off the trail towards the stream. We also sampled mosses adjacent to vertebrate feeding micro-sites below falls on the Clatse (CR- below/near). Feeding sites were identified by the presence of bony carcass remnants abandoned during the previous autumn spawning season. For each micro-site we took paired samples of *R. loreus*, one from directly on the site and a second from 2 m away in the downstream direction ($n=23$ pairs).

Finally, we assessed moss community structure in all three plots within each habitat block from both watersheds. Belt transects within plots were reduced to line transects perpendicular to the stream (0 m, 5 m and 10 m), and % cover of each moss and liverwort species along each transect was measured using the line intercept method (Bauer 1943). Percent cover is indicated as the fraction of each 10 m transect covered by a particular species. We used percent cover values found along transects to determine shifts in community structure corresponding to varying degrees of salmon transfer. We calculated species richness (S) using:

$$S = \sum s_n \quad (1)$$

where s is the number of species found on the n th transect. A Shannon index of diversity (H') was also calculated using:

$$H' = -[\sum p_i(\ln p_i)] \quad (2)$$

where p_i is the relative abundance of the i th species on each transect within each habitat block.

We also investigated the proportionate representation of mosses and liverworts based on their soil-nitrogen indicator status according to Klinka et al. (1989) and Mathewson et al. (2003), to compare the percent cover of both nitrogen-poor and nitrogen-rich soil-indicator species among blocks. Plants can act as indicators of

specific soil conditions from nutrient poor to rich soils, and may even prefer certain concentrations of a specific nutrient such as nitrogen, phosphorus, calcium or magnesium (Klinka et al. 1989). Although nutrient-rich and nutrient-poor indicators can co-occur, total cover of plants from different indicator categories within a defined area can provide insight into specific site properties within different biogeoclimatic subzones (Green and Klinka 1994).

In middle to late August 2000, a small number of collections were made from above and below the waterfall at Neekas River in plots that were used in previous studies on invertebrates and vascular plants from this watershed (Hocking and Reimchen 2002, Mathewson et al. 2003). Lanky moss (*R. loreus*) (n = 4 above falls, n = 3 below falls) and snake liverwort (*C. conicum*) (n = 3 above falls, n = 4 below falls) were collected at random within 15 m from the stream and within 200 m of either side of the waterfall.

Isotope analysis

All samples were oven-dried at 60°C for 7 days. We clipped the apical segments (<1 cm) of each moss sample, pulverized these in Wig-L-Bug grinder (Crescent Dental Co., Chicago, Illinois). Samples (1 mg) were processed for continuous-flow isotope ratio mass spectrometry (CF-IRMS) analysis of nitrogen (Europa Scientific ANCA NT gas/solid/liquid preparation module coupled to a Europa Scientific Tracer/20 mass spectrometer). We follow the convention for isotopic characterization (Peterson and Fry 1987):

$$\delta^{15}\text{N}(\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (3)$$

where R_{sample} is the ratio of the two isotopes of nitrogen ($^{15}\text{N}/^{14}\text{N}$) for any moss or liverwort sample and R_{standard} is the standard atmospheric ratio of $^{15}\text{N}/^{14}\text{N}$ ($R = 0.0036765$; $\delta^{15}\text{N} = 0\text{‰}$). In comparison, the $\delta^{15}\text{N}$ isotope signature of salmon tissue has been reported to range from 11.2‰ (Mathisen et al. 1988) to 13.01‰ (Ben-David et al. 1997).

Statistical analyses

We examined the effects of habitat block and plots within blocks on $\delta^{15}\text{N}$ and %N for each of the four common species (ANOVA's), and further evaluated the effect among blocks using Tukey's multiple comparison tests. In cases where variances were not equal we performed Dunnett's T3 tests of multiple comparisons. Individual sample sets of each habitat and species were tested for normality and all were normally distributed (one-sample Kolmogorov-Smirnov tests). For the less common species, including the small collection from the

Neekas River and those for comparisons between carcass micro-sites and wildlife trails, we compared $\delta^{15}\text{N}$ and %N using independent and paired t-tests (two-tailed). To examine the variance of $\delta^{15}\text{N}$ and %N among species, we used ANOVA and Tukey tests within a subset of available habitat blocks (Clatse- below/near; Clatse- above/near). The community structure data, including species richness (S), Shannon diversity (H'), and soil-nitrogen indicator status, were also analyzed using ANOVA and Tukey's multiple comparison tests. All statistical analyses were performed using SPSS (ver. 10, SPSS, Inc, Chicago, IL).

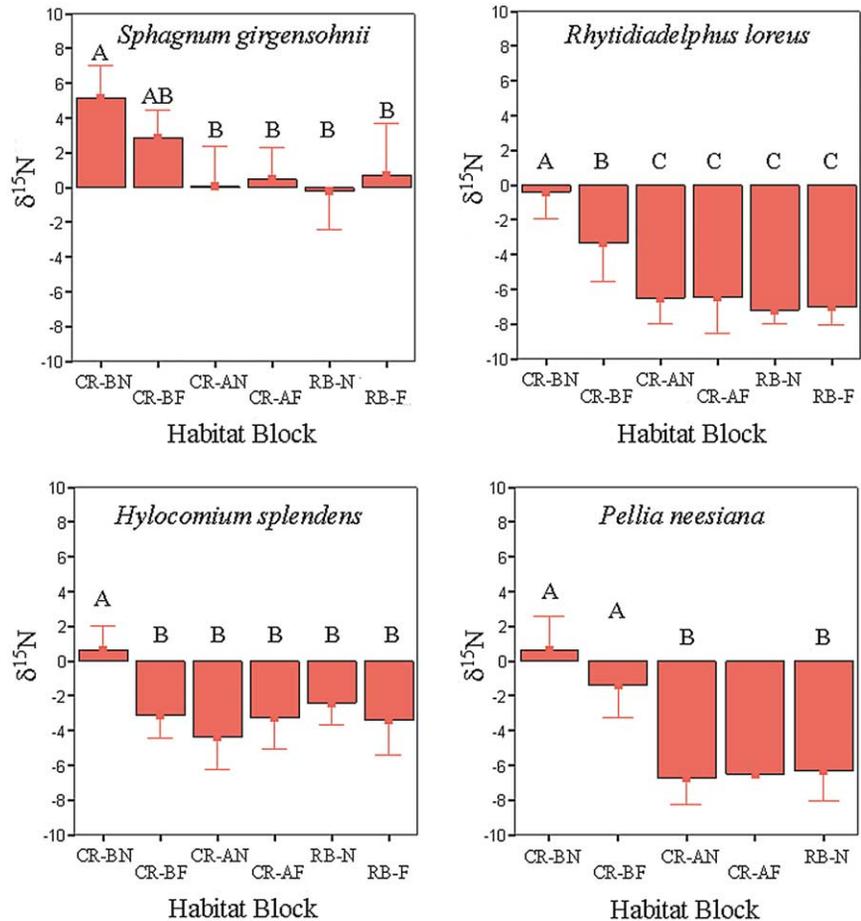
Results

$\delta^{15}\text{N}$ values

There were major differences in the nitrogen signatures of mosses and liverworts among the sampling sites. In all of the four common species, $\delta^{15}\text{N}$ signatures varied significantly among habitat blocks on Clatse and Ripley: *Rhytidiadelphus loreus* ($F_5 = 15.43$, $P < 0.001$), *Hylocomium splendens* ($F_5 = 5.78$, $P < 0.001$), *Sphagnum girgensohnii* ($F_5 = 4.40$, $P = 0.002$), and *Pellia neesiana* ($F_4 = 18.42$, $P < 0.001$). The $\delta^{15}\text{N}$ signatures ranged from 2‰ to 7‰ higher below the falls near the salmon stream than at each of the other sites (Fig. 1). In all species there was a reduction in $\delta^{15}\text{N}$ with increased distance into the forest (significant for *R. loreus* and *H. splendens*), but this did not occur in riparian zones without salmon such as above the falls or at Ripley River. Signatures above the falls at Clatse River were not significantly different than at Ripley River where salmon were absent. For *Kindbergia oregana* and *Rhizomnium glabrescens*, which were only sampled on blocks below the falls at Clatse River, the former showed significantly higher values near the stream (mean diff. = 3.5‰, $t_{13} = -2.38$, $P = 0.033$) while the latter showed no significant difference between sites (mean diff. = 0.5‰, $t_{16} = -0.62$, $P = 0.54$). For *Conocephalum conicum* and *Sphagnum squarrosum*, which were only sampled on blocks near the stream at Clatse River, both showed significant increase in $\delta^{15}\text{N}$ below the falls compared to above falls (*C. conicum* mean diff. = 6‰, $t_8 = -3.29$, $P = 0.011$; *S. squarrosum* mean diff. = 4.5‰; $t_{10} = -4.68$, $P = 0.001$).

We also examined $\delta^{15}\text{N}$ signatures in *Rhytidiadelphus loreus* among feeding micro-sites and along wildlife trails on the Clatse River (Fig. 2). We observed a significant difference of 2.3‰ in *R. loreus* collected from feeding micro-sites relative to samples collected 2 m away ($t_{22} = 3.80$, $P = 0.001$). The signatures for *R. loreus* on feeding micro-sites were higher than all other areas sampled, but were only marginally higher than samples collected at random from the same habitat block with high salmon transfer.

Fig. 1. $\delta^{15}\text{N}$ isotope signatures in three common mosses (*S. girgensohnii*, *R. loreus*, *H. splendens*) and one common liverwort (*P. neesiana*) from two watersheds on the central coast of British Columbia, Canada. Samples were collected on transects in six habitat blocks that vary in access to salmon nutrients. Habitat blocks consist of: CR-BN – Clatsse River-below falls, near stream (highest salmon nutrient transfer); CR-BF – Clatsse River-below falls, far from stream (minor salmon transfer); CR-AN – Clatsse River-above falls, near stream (within watershed control); CR-AF – Clatsse River-above falls, far from stream (within watershed control); RB-N – Ripley Bay-near stream (control); RB-F – Ripley Bay, far from stream (control). Letters (A, B, C) refer to homogeneous subsets derived from Tukey's multiple comparison tests.



For *R. loreus* collected below the falls on trails, there was a non-significant decrease of 1.5‰ between adjacent sites on and off the wildlife trail ($t_{12} = 1.61$, $P = 0.13$) while above the falls, there was no effect (mean diff. = 0.21‰, $t_{11} = -0.31$, $P = 0.76$). *R. loreus* on trails below falls had higher signatures compared to those collected on trails above the falls (mean diff. = 3.55‰, $t_{23} = 4.40$, $P < 0.001$). Above the falls, the nitrogen signatures on and adjacent to the bear trails were both higher than *R. loreus* collected from sites distant from bear trails. However, this pattern was not observed below the falls, as $\delta^{15}\text{N}$ values from trails were similar or marginally lower than samples collected at random (Fig. 2).

Mosses and liverworts also differed in their $\delta^{15}\text{N}$ signatures within sites (Clatsse- below/near: $F_7 = 4.60$, $P < 0.001$; Clatsse- above/near: $F_5 = 12.11$, $P < 0.001$; Fig. 3). *Sphagnum girgensohnii*, and to a lesser extent *S. squarrosum*, had higher $\delta^{15}\text{N}$ signatures than all other species sampled. In the case of *S. girgensohnii*, this constituted a mean difference of 4.5‰ to 5.8‰ below the falls and 4.5‰ to 6.8‰ above the falls compared to the non-*Sphagnum* species.

On the Neekas River, we measured substantial enrichment in $\delta^{15}\text{N}$ in both species sampled below the falls compared to above the falls (*R. loreus*: mean diff. = 7.25‰, $t_5 = 4.01$, $P = 0.01$; *C. conicum*: mean diff. = 5.08‰, $t_5 = 3.26$, $P = 0.023$), supplementing the results observed along the spawning channel at Clatsse.

Percent nitrogen

Percent N differed among species and among habitat blocks (Fig. 4). Significant differences were found in *Rhytidiadelphus loreus*, which had highest values below the falls near the stream ($F_5 = 3.08$, $P = 0.017$) and in *Pellia neesiana*, which had the highest values below the falls far from the stream ($F_4 = 9.05$, $P < 0.001$) but not in *Hylocomium splendens* ($F_5 = 2.23$, $P = 0.066$) or *Sphagnum girgensohnii* ($F_5 = 1.53$, $P = 0.20$). Below the falls, *Rhizomnium glabrescens* had significantly higher values in the block away from the stream ($t_{16} = 3.79$, $P = 0.002$), but this did not occur for *Kindbergia oregana* ($t_{13} = 1.51$, $P = 0.16$). The comparison of %N on near-stream blocks on either side of the falls at Clatsse

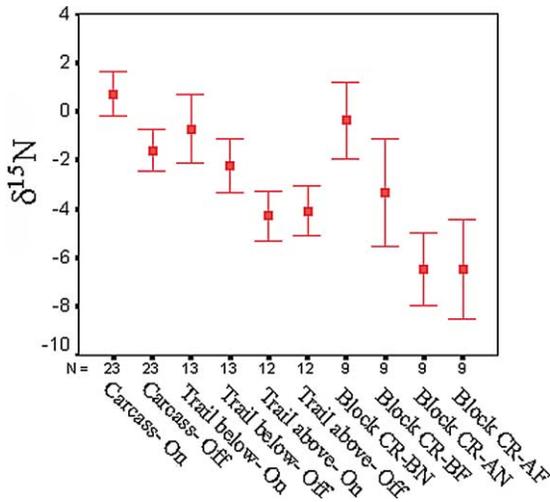


Fig. 2. $\delta^{15}\text{N}$ isotope signatures in the common moss *Rhytidiadelphus loreus* from multiple micro-sites on the Clatse River, on the central coast of British Columbia, Canada. Paired samples were taken immediately adjacent to and 2 m away from salmon carcass sites below the falls (carcass-on; carcass-off), and wildlife trails below and above the falls (trail below-on; trail below-off; trail above-on; trail above-off). For comparison, $\delta^{15}\text{N}$ signatures in *R. loreus* from the random collection in the four habitat blocks at Clatse are also shown (block BN; block BF; block AN; block AF; Fig. 1).

River did not show significant differences for either *Conicephalum conicum* ($t_8 = -1.04$, $P = 0.33$) or *Sphagnum squarrosum* ($t_{4,1} = -1.50$, $P = 0.21$), though both exhibited marginally higher mean values along the salmon spawning channel.

For *R. loreus*, there were regular differences in $\%N$ among micro-sites (Fig. 5). At Clatse River below the falls, $\%N$ values on feeding micro-sites showed highly significant differences compared to those collected 2 m away ($t_{22} = -4.38$, $P < 0.001$). Similarly to $\delta^{15}\text{N}$, mean $\%N$ was highest on feeding micro-sites compared to any other areas sampled. $\%N$ on wildlife trails did not differ from adjacent sites 2 m off the trails above falls (mean

diff. = 0.02%, $t_{11} = 0.21$, $P = 0.84$) or below falls (mean diff. = 0.01%, $t_{11} = -0.34$, $P = 0.91$). However, there was a significant difference between samples collected on trails below and above the falls (mean diff. = 0.36%, $t_{23} = 4.46$, $P < 0.001$). Overall, $\%N$ values were higher on trails and carcass micro-sites than samples collected at random from the same area, contrary to the pattern observed for $\delta^{15}\text{N}$ (Fig. 5).

Within each habitat block, $\%N$ values varied among species and were highest in the liverworts *P. neesiana* and *C. conicum* compared to the mosses (Clatse- below/near: $F_7 = 8.29$, $P < 0.001$; Clatse- above/near: $F_5 = 22.62$, $P < 0.001$; Fig. 6). This constituted a mean difference varying from 0.5% to 1.2% depending on species and habitat block.

On the Neekas River, we observed higher $\%N$ values in both species below the falls compared to above the falls (*R. loreus*: mean diff. = 0.61%, $t_5 = 4.73$, $P = 0.005$; *C. conicum*: mean diff. = 0.43, $t_5 = 3.83$, $P = 0.012$).

Community structure

Overall, the most dominant species in all habitat blocks was *R. loreus*, followed by *H. splendens* and *S. girgensohnii*, which dominated in moist nutrient poor areas such as Ripley Bay and Clatse above the falls (Fig. 7). On Clatse below the falls close to the stream, where there was highest access to salmon nutrients, we observed the most number of species. This included increased coverage of the liverworts *C. conicum* and *P. neesiana*, which are nitrogen- and calcium-rich soil-indicators.

Moss and liverwort community structure differed among habitats. Species richness (S) was highest in the block below the falls, near the stream on Clatse (CR-below/near) and the lowest in the block far from the stream on Ripley (RB-far) (ANOVA: $F_5 = 25.35$, $P < 0.001$; Fig. 8). The Shannon diversity index (H') was also highest below falls, near the stream on the Clatse, but did not differ from the other sites close to stream on

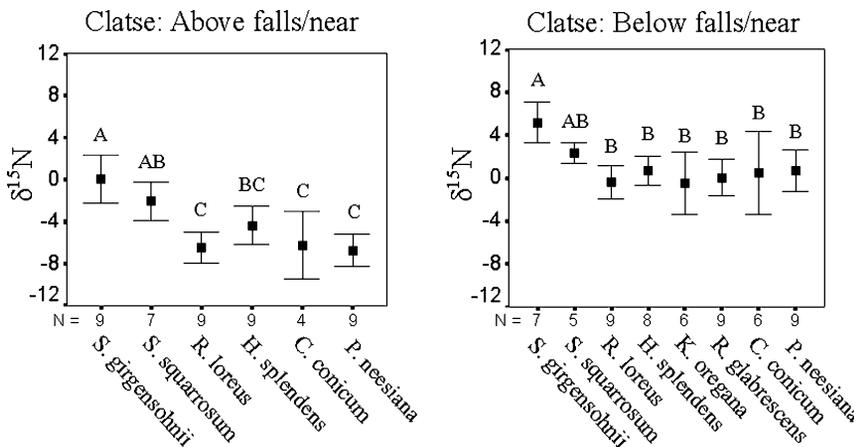
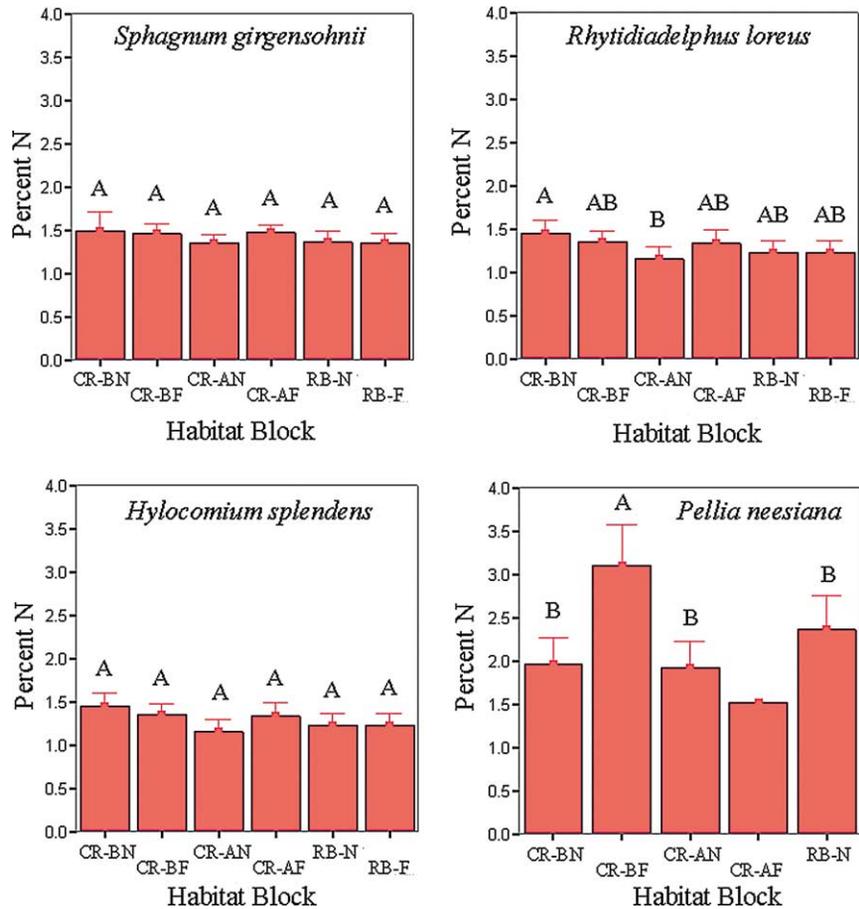


Fig. 3. $\delta^{15}\text{N}$ isotope signatures in all moss and liverwort species collected from two representative habitat blocks on the Clatse River, on the central coast of British Columbia, Canada. Letters (A, B, C) refer to homogeneous subsets derived from Tukey's multiple comparison tests.

Fig. 4. Foliar percent N in three common mosses (*S. girgensohnii*, *R. loreus*, *H. splendens*) and one common liverwort (*P. neesiana*) from two watersheds on the central coast of British Columbia, Canada. Samples were collected on transects in six habitat blocks that vary in access to salmon nutrients. Habitat blocks consist of: CR-BN – Clatse River-below falls, near stream (highest salmon nutrient transfer); CR-BF – Clatse River-below falls, far from stream (minor salmon transfer); CR-AN – Clatse River-above falls, near stream (within watershed control); CR-AF – Clatse River-above falls, far from stream (within watershed control); RB-N – Ripley Bay-near stream (control); RB-F – Ripley Bay, far from stream (control). Letters (A, B) refer to homogeneous subsets derived from Tukey's multiple comparison tests.



Ripley and Clatse above the falls (ANOVA: $F_5 = 7.17$, $P < 0.001$; Fig. 8). Mean percent cover of N-rich soil-indicator species on the Clatse-below/near was 8% higher than below/far at Clatse and at least 11% higher than all other blocks ($F_5 = 6.58$, $P < 0.001$; Fig. 9). In comparison, percent cover of N-poor soil-indicator species varied from 12% to 35% lower below/near at Clatse compared to all other blocks ($F_5 = 7.21$, $P < 0.001$; Fig. 9).

Discussion

$\delta^{15}\text{N}$ values

Our results indicate that mosses and liverworts, which comprise the dominant ground cover in temperate forests of the Pacific northwest, exhibit substantive uptake of salmon-derived nitrogen primarily extending from predator foraging activity on *Oncorhynchus* spp. We observe enrichment of 2‰ to 7‰ in $\delta^{15}\text{N}$ in all common species collected on transects 0–20 m from the Clatse River spawning channel compared to all other habitat blocks on the same watershed and two blocks on

an adjacent control watershed. The pattern of $\delta^{15}\text{N}$ signatures across habitat blocks is consistent among the seven humus-dwelling species sampled, and concordant with the diverse assemblage of taxa that demonstrate uptake of salmon nutrients by primary and secondary consumers (Bilby et al. 1996, Ben-David et al. 1998, Cederholm et al. 2000, Naiman et al. 2002, Gende et al. 2002, Hocking and Reimchen 2002, Reimchen et al. 2003). Our analyses of isotopic signatures in mosses above and below waterfalls, which acts as a sharp ecological gradient of salmon density, often demonstrated larger differences between sites than over equivalent distances within the riparian zone perpendicular to the stream. This indicates that the signature of salmon can be detected in mosses and liverworts to distances of 100 m into the riparian zone, a pattern that has been observed previously in vascular plants and invertebrates (Ben-David et al. 1998, Hilderbrand et al. 1999, Hocking and Reimchen 2002). The observed $\delta^{15}\text{N}$ enrichment in lanky moss (*R. loreus*) and snake liverwort (*C. conicum*) collected adjacent to the spawning channel at the Neekas River supplements the results observed at Clatse and suggests that this pattern may be wide-

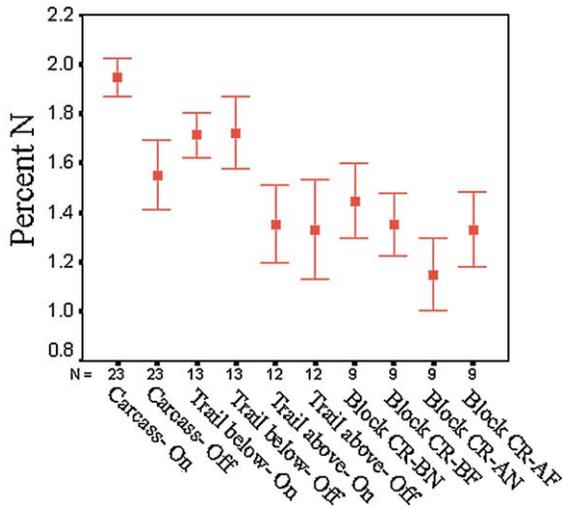


Fig. 5. Foliar percent N in the common moss *Rhytidiadelphus loreus* from multiple micro-sites on the Clats River, on the central coast of British Columbia, Canada. Paired samples were taken immediately adjacent to and 2 m away from salmon carcass sites below the falls (carcass- on; carcass- off), and wildlife trails below and above the falls (trail below- on; trail below- off; trail above- on; trail above- off). For comparison, $\delta^{15}\text{N}$ signatures in *R. loreus* from the random collection in the four habitat blocks at Clats are also shown (block BN; block BF; block AN; block AF; Fig. 4).

spread along salmon streams throughout the Pacific Northwest.

The only exception to the trend of reduced $\delta^{15}\text{N}$ signatures with increased distance from the spawning region on Clats was observed in *R. glabrescens*, the only species collected directly off a woody substratum. Since all other species were collected from the humus layer, this may suggest that salmon-derived nitrogen is not as accessible to epiphytic species, and is only available via N in humus. Epiphytic mosses have a high capacity to absorb atmospheric NO_3^- and NH_4^+ (Clark et al. 1998, Hietz et al. 2002), and may not access the limited total nitrogen from decaying wood, which itself may also be

enriched in salmon nitrogen (Reimchen et al. 2003). However, high fractionation during ammonia volatilization from the abundant decaying salmon carcasses in the stream channel and in the forest could lead to a depleted atmospheric N source for *R. glabrescens* (Robinson 2001) throughout the riparian zone. As a consequence, we cannot exclude salmon-derived atmospheric N as a partial source for *R. glabrescens* within 100 m from the stream given the absence in our data of a completely non-salmon comparison for this species.

For lowland and mid-elevation rainforest ecosystems of coastal British Columbia, *Rhytidiadelphus loreus* is often the dominant ground cover (Pojar and MacKinnon 1994). Our data on isotopic signatures in this species demonstrated high localized spatial heterogeneity concordant with the distribution of salmon carcasses abandoned by bears and wolves (Reimchen 1994, 2000, Darimont et al. 2003), and to a lesser extent, associated with the use of trails established by wildlife. Hilderbrand et al. (1999) report 96% of the salmon-derived N consumed by adult female brown bears is excreted as urine and 3% excreted as faeces, much of which is distributed along trails. Because urine is depleted in $\delta^{15}\text{N}$ relative to diet (Gannes et al. 1997), this may partly explain why $\delta^{15}\text{N}$ gradients off trails are not as pronounced as off carcass sites. It is also likely that fractionation from ammonia volatilization from decaying salmon carcasses results in a very locally enriched signature of NH_4^+ (Cocks et al. 1998) compared to more evenly distributed signatures along trails. Enrichment in *R. loreus* along trails compared to random transects was particularly evident above the falls at Clats, demonstrating the importance of trails as vectors of salmon-derived N over longer distances. Overall, the combination of carcass deposition by predators and trail corridor use by bears and other wildlife enhances the external nitrogen source pools on the forest floor and creates a non-uniform and clumped distribution of nutrients. Such a heterogeneous nutrient

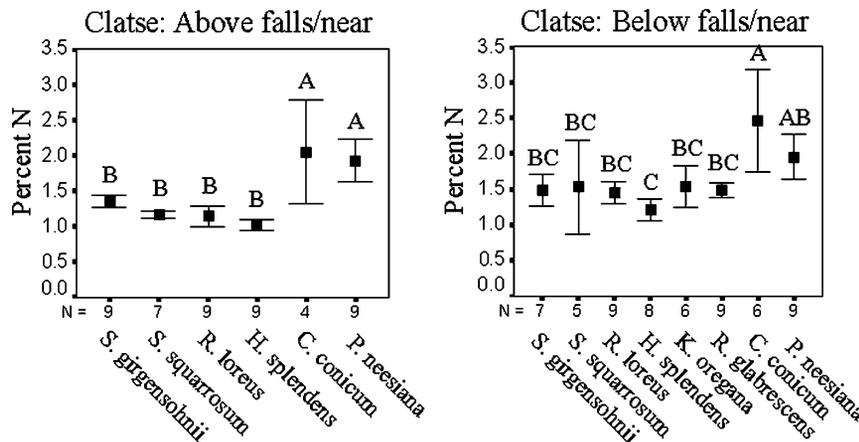


Fig. 6. Foliar percent N in all moss and liverwort species collected from two representative habitat blocks on the Clats River, on the central coast of British Columbia, Canada. Letters (A, B, C) refer to homogeneous subsets derived from Tukey's multiple comparison tests.

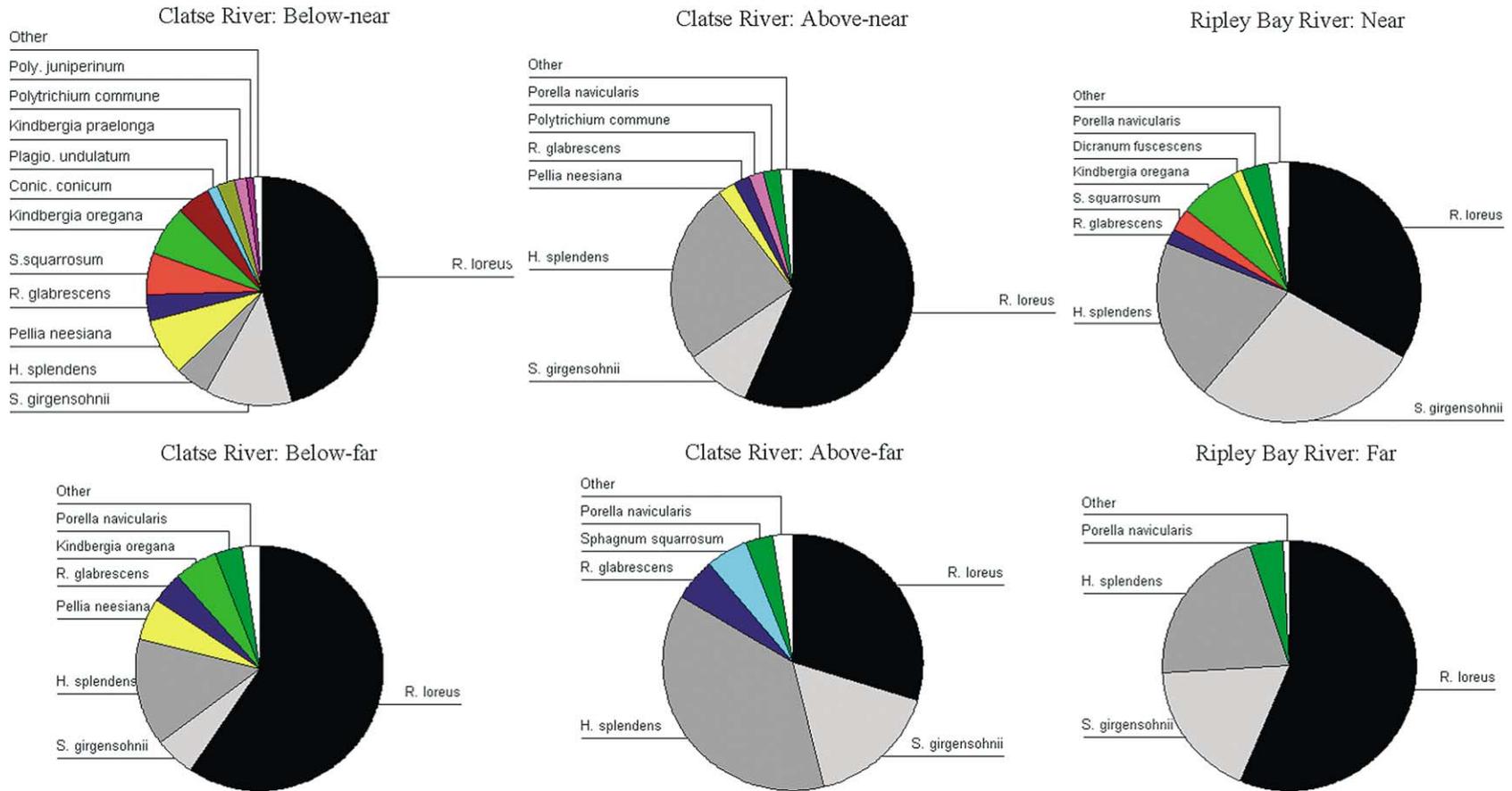


Fig. 7. Mean percent cover of all moss and liverwort species in six habitat blocks on the Clatse and Ripley Bay watersheds that vary in access to salmon nutrients, on the central coast of British Columbia, Canada. Habitat block 'Clatse River-below-near' is immediately adjacent to the salmon spawning channel with highest access to salmon nutrients, followed by 'Clatse River-below-far'. Other sites are control sites with little to no salmon nutrient input. Species of less than 1% total cover were summed and placed in the category 'other'.

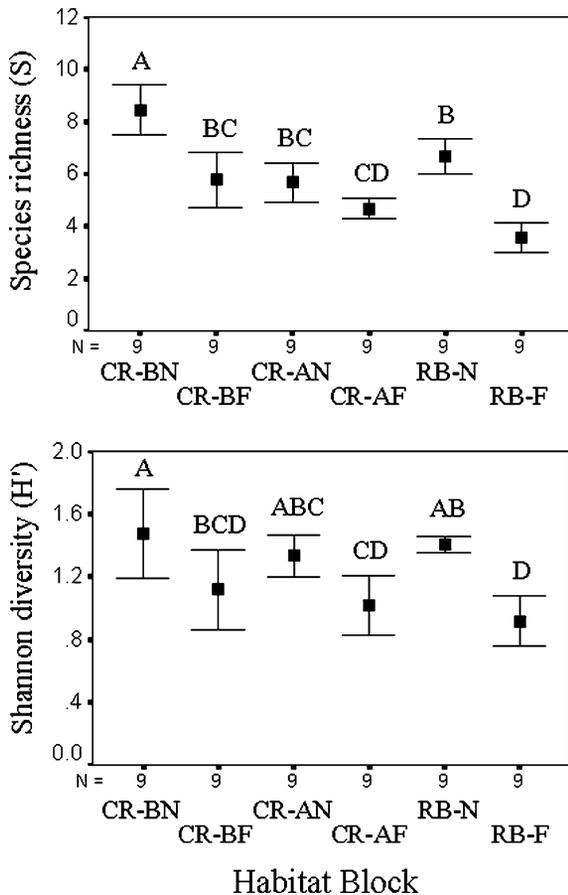


Fig. 8. Species richness (S) and Shannon diversity (H') of the moss and liverwort community in six habitat blocks on the Clatse and Ripley Bay watersheds that vary in access to salmon nutrients, on the central coast of British Columbia, Canada. Habitat block 'Clatse River-below-near' is immediately adjacent to the salmon spawning channel with highest access to salmon nutrients, followed by 'Clatse River-below-far'. Other sites are control sites with little to no salmon nutrient input. Letters (A, B, C, D) refer to homogeneous subsets derived from Tukey's multiple comparison tests.

distribution may have implications for niche partitioning among bryophyte species.

$\delta^{15}\text{N}$ signatures varied among moss and liverwort species, with the highest signatures observed in *Sphagnum* spp, particularly *S. girgensohnii*. Variation in $\delta^{15}\text{N}$ signatures in vascular plants within habitats is often attributed to differences in the predominant N source (NH_4^+ , NO_3^- , organic N, or fixed N), differences in fractionation during N uptake, and variable plant-mycorrhizal interactions (Nadelhoffer and Fry 1994, Schulze et al. 1994, Michelsen et al. 1998, Hobbie et al. 2000, Evans 2001). Species in nutrient poor habitats are often more depleted in foliar $\delta^{15}\text{N}$ than species found in nutrient rich habitats (Hobbie et al. 2000, Mathewson et al. 2003), yet we observe in bryophytes an opposite pattern with high signatures in the nutrient-poor *Sphag-*

num spp. and relatively low signatures in the nutrient-rich liverworts. Hyaline cells in *Sphagnum* are known to exhibit high retention of water and surplus nutrients (Daniels and Eddy 1990), and as a result leave the surrounding water nutrient-depleted (Anderson and Ammann 1991). Nitrogen losses from these cells may be highly fractionated leaving foliar tissue comparatively enriched. Other possibilities include N-fixing symbioses such as that observed in mosses of the boreal forest (Deluca et al. 2002), or partitioning of the nitrogen niche (ie-N source) among moss and liverwort species. *Sphagnum* assimilates NO_3^- and NH_4^+ , with no preference being displayed between these two forms (Williams et al. 1999). In comparison, recent studies on mosses in heath ecosystems reveal the importance of organic N from free amino acids to nitrogen budget of multiple species (Kielland 1997, Michelsen et al. 1998, Näsholm et al. 1998). The inter-specific pattern of $\delta^{15}\text{N}$ signatures among mosses and liverworts from our data remains very similar in all habitat blocks despite an upwards shift of $\sim 5\text{‰}$ below the falls on Clatse in all species, and suggests that many forms of nitrogen may be enriched in salmon N along the spawning channel.

Percent nitrogen

Temperate rainforests subject to the annual pulse of salmon nutrients show elevated foliar percent N in vascular plant communities (Helfield and Naiman 2001, Naiman et al. 2002, Mathewson et al. 2003), which suggests enhanced primary productivity in riparian zones with access to salmon-derived nitrogen. Our data show some instances of increased %N in mosses and liverworts collected at random along salmon streams compared to other sites, particularly on the Neekas River, though many comparisons revealed similar values between salmon and non-salmon habitats. The most striking pattern we observe is high %N values for the most abundant moss *R. loreus* among carcass feeding sites, followed by samples along wildlife trails, in comparison to samples collected from the transects below the falls at Clatse. These data are consistent with the importance of carcass transfer and excretion by secondary consumers as sources of salmon-derived nitrogen within habitats adjacent to spawning beds and indicate the coarse grain or patchiness of the nutrient pools within these habitats. The variability in %N among carcass sites, trails and the random collection within the Clatse-below/near habitat exceeded that of the $\delta^{15}\text{N}$ signatures themselves indicating the degree of competition for available nitrogen among non-vascular and vascular plants in these temperate rainforests. Furthermore, these data demonstrate the widespread enrichment in $\delta^{15}\text{N}$ throughout this riparian zone

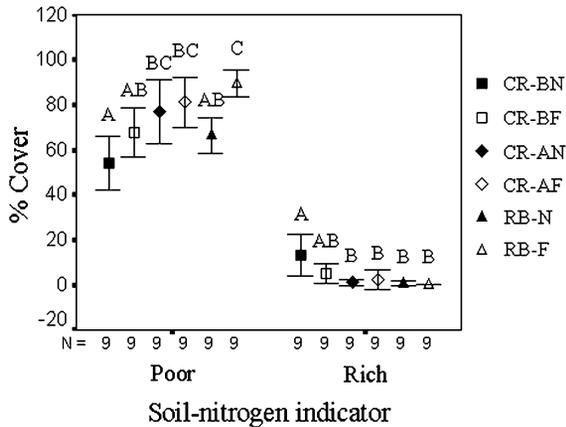


Fig. 9. Percent cover of nitrogen-rich and nitrogen-poor soil indicator species (based on Klinka et al. 1989) in six habitat blocks on the Clatse and Ripley Bay watersheds that vary in access to salmon nutrients, on the central coast of British Columbia, Canada. Habitat block 'Clatse River-below-near' is immediately adjacent to the salmon spawning channel with highest access to salmon nutrients, followed by 'Clatse River-below-far'. Other sites are control sites with little to no salmon nutrient input. Letters (A, B, C) refer to homogeneous subsets derived from Tukey's multiple comparison tests.

(Hocking and Reimchen 2002, Mathewson et al. 2003), which presumably reflects thousands of years of the salmon–bear–forest association. Overall, increased foliar N concentrations are correlated to increased rates of photosynthesis and higher turnover (Reich et al. 1997, Hikosaka and Hirose 2000), and areas with high salmon carcass transfer and/or high wildlife activity may promote increased primary productivity of the moss layer.

Plants with higher foliar concentrations of a particular nutrient may be more competitive for that specific nutrient (Mamolos and Veresoglou 2000). In riparian zones of the Pacific northwest, vascular plants that indicate nitrogen-rich soil conditions tend to have higher foliar %N than nitrogen-poor soil indicators, and are more prevalent along salmon spawning channels of the Clatse and Neekas rivers (Mathewson et al. 2003). This pattern is also shown in the current study, as was evident in the high %N values in the liverwort species *P. neesiana* and *C. conicum* in all habitat blocks and lower values in the remaining moss species that we investigated, which are nitrogen-poor indicators (Klinka et al. 1989). This is consistent with previous evidence of elevated nitrogen levels in thallose liverworts (Shaw and Goffinet 2000) and suggests that these liverworts may have increased competitive ability in nutrient-rich habitats along salmon streams.

Community response

Among mosses and liverworts, we observed greater species richness and increased prevalence of nitrogen-rich soil indicators on transects along the spawning

channel at Clatse compared to all other habitat blocks. Comparisons with the Shannon diversity index also demonstrated highest mean values in this region although the trends were more marginal, reflecting increased evenness as a component to the diversity index. Our results are concordant with global patterns of richness and productivity in vascular plants (Currie 1991).

The increased richness observed below/near on Clatse occurred partly due to the increased prevalence of nitrogen-rich soil indicators including the liverworts *P. neesiana* and *C. conicum* (Klinka et al. 1989). Rich-soil indicator plants occur in soils that have six times the mineralizable nitrogen, double the total soil N, and available Ca, Mg and K than soils dominated by poor-soil indicators, and occur in areas with reduced forest floor pH and C/N ratios (Klinka et al. 1989). *C. conicum* was only evident on transects of the salmon-bearing watershed, and was dramatically reduced above the falls. As well, *P. neesiana* was evident in far higher abundance below the falls on Clatse, indicating that thallose liverworts interspersed with mosses in the humus substratum may be exploiting a unique niche available through wildlife activity and transfer of salmon carcasses. The spatial heterogeneity of both $\delta^{15}\text{N}$ signatures and %N among species and microhabitats likely reflects a variety of localized nutrient source pools and a coarse-grained distribution of available niches. Although we emphasize nitrogen as a predictor for community diversity, other nutrients such as calcium, phosphorus and magnesium may be equally important in determining community structure. This may be particularly true for the liverworts *C. conicum* and *P. neesiana*, which are indicators of calcium-rich soils. Overall, salmon-rich habitats display the greatest variation among transects in presence and percent coverage of nitrogen indicator species, suggesting that increased community richness and niche partitioning among mosses and liverworts is an outcome of increased nutrient heterogeneity (McKane et al. 2002).

Implications on nutrient dynamics in temperate forest ecosystems

The flow of salmon-derived nutrients through riparian ecosystems comprises multiple levels, from initial transference from streams to the forest floor through surface layers, to soils, to root systems of the vascular plant community and through successive higher trophic levels. The moss and liverwort layer on the forest floor has ecosystem-level effects as these regulate soil temperature and retain soil moisture levels (Oechel and Van Cleve 1986). Additionally, bryophytes are known to be effective competitors with vascular plants for incoming nutrients (Oechel and Van Cleve 1986). Weber and Van

Cleve (1981) have shown that bryophyte layers including *Hylocomium splendens* effectively capture over 90% of dissolved N. Efficient nutrient uptake, recycling and slow decomposition rates may allow the bryophyte layer to control nutrient availability to vascular plants, and potentially act as an autogenic ecosystem engineer (Jones et al. 1994). This may contribute to the observations of enhanced primary productivity in vascular plants where salmon-derived nutrients are available (Helfield and Naiman 2001, Naiman et al. 2002, Mathewson et al. 2003).

Conclusion

Assessment of $\delta^{15}\text{N}$, percent N and community structure in mosses and liverworts among multiple habitat blocks in coastal temperate rainforests of British Columbia provides strong evidence for a community wide response to marine-derived nutrients provided by Pacific salmon spawning events. *Rhytidiadelphus loreus*, the most abundant moss species, exhibits elevated nitrogen levels on bear trails and feeding-micro-sites where salmon nutrients are available and suggests coarse-grained distribution of nutrient source pools. Such spatial heterogeneity of nutrient availability may provide a broader range of niches that consequently enhances biodiversity in such habitats. Our data provide further evidence for the major contribution of salmon-derived nutrients to terrestrial ecosystems in watersheds of the North Pacific (Willson et al. 1998, Stockner 2003).

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