

# Riparian defoliation by the invasive green alder sawfly influences terrestrial prey subsidies to salmon streams

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## Abstract

Invasive species in riparian forests are unique as their effects can transcend ecosystem boundaries via stream-riparian linkages. The green alder sawfly (*Monsoma pulveratum*) is an invasive wasp whose larvae are defoliating riparian thin-leaf alder (*Alnus tenuifolia*) stands across southcentral Alaska. To test the hypothesis that riparian defoliation by this invasive sawfly negatively affects the flow of terrestrial prey resources to stream fishes, we sampled terrestrial invertebrates on riparian alder foliage, their subsidies to streams and their consumption by juvenile coho salmon (*Oncorhynchus kisutch*). Invasive sawflies altered the composition of terrestrial invertebrates on riparian alder foliage and as terrestrial prey subsidies to streams. Community analyses supported these findings revealing that invasive sawflies shifted the community structure of terrestrial invertebrates between seasons and levels of energy flow (riparian foliage, streams and fish). Invasive sawfly biomass peaked mid-summer, altering the timing and magnitude of terrestrial prey subsidies to streams. Contrary to our hypothesis, invasive sawflies had no effect on the biomass of native taxa on riparian alder foliage, as terrestrial prey subsidies, or in juvenile coho salmon diets. Juvenile coho salmon consumed invasive sawflies when most abundant, but relied more on other prey types selecting against sawflies relative to their availability. Although we did not find effects of invasive sawflies extending to juvenile coho salmon in this study, these results could change as the distribution of invasive sawflies expands or as defoliation intensifies. Nevertheless, riparian defoliation by these invasive sawflies is likely having other ecological effects that merits further investigation.

## KEYWORDS

insect outbreaks, invasive species, juvenile coho salmon, *Monsoma pulveratum*, riparian alder, stream-riparian food webs

## 1 | INTRODUCTION

Stream-riparian ecosystems are dynamic interfaces linked by the exchange of cross-ecosystem resource subsidies (Baxter, Fausch, & Saunders, 2005; Gregory, Swanson, McKee, & Cummins, 1991; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). For example, riparian forests contribute inputs of terrestrial leaf litter and insects

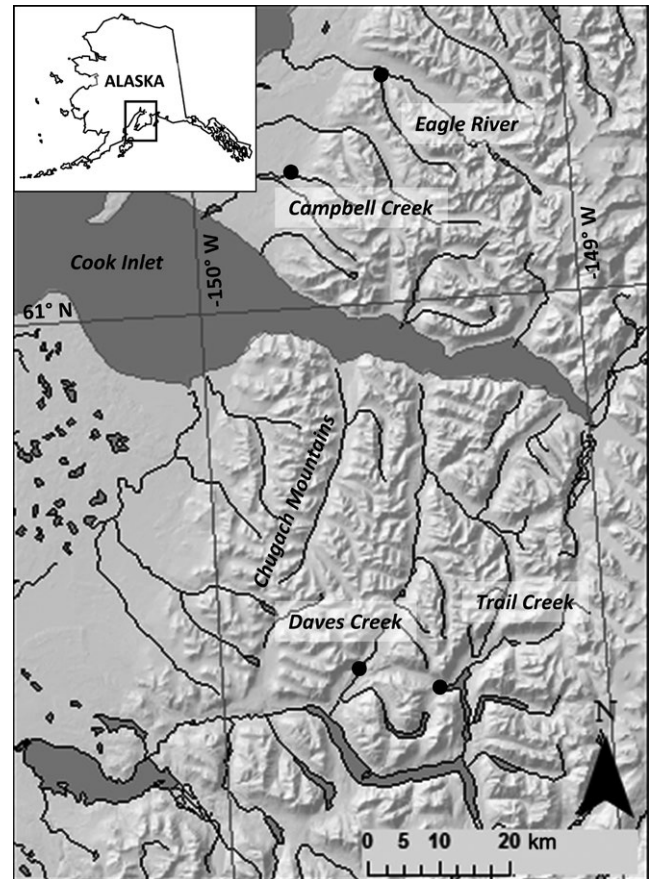
to streams, and in turn, the emergence of aquatic insects supports riparian consumers such as birds and bats (Baxter et al., 2005; Nakano & Murakami, 2001; Vannote et al., 1980). However, field experiments have demonstrated that interrupting the exchange of these reciprocal resource subsidies can negatively affect both aquatic and terrestrial species through these stream-riparian linkages (Baxter, Fausch, Murakami, & Chapman, 2004; Nakano, Miyasaka, & Kuhara,

1999a; Nakano & Murakami, 2001). Therefore, changes in the environment that disrupt these cross-ecosystem resource subsidies have the potential to transcend ecosystem boundaries and can have implications for both streams and riparian forests (Larsen, Muehlbauer, & Marti, 2016; Warren et al., 2016).

The spread of invasive species is one such mechanism that can alter stream-riparian food webs. To date, previous examples have focused on the effects of invasive riparian plants (Greenwood, O'Dowd, & Lake, 2004; Hladyz, Abjornsson, Giller, & Woodward, 2011; Mineau, Baxter, Marcarelli, & Minshall, 2012; Roon, Wipfli, Wurtz, & Blanchard, 2016) and the effects of aquatic invasive species such as invertebrates (Larson, Busack, Anderson, & Olden, 2010) and fish (Baxter et al., 2004; Benjamin, Lepori, Baxter, & Fausch, 2013; Epanchin, Knapp, & Lawler, 2010). However, little is known about the potential effects surrounding invasive riparian invertebrates. Given that outbreaks of invasive insects can result in widespread defoliation and dieback of terrestrial vegetation (Adkins & Rieske, 2013; Gandhi & Herms, 2010; Hutchens & Benfield, 2000), these outbreaks have the potential to influence streams whenever they occur in riparian forests. As a result, the direct and indirect effects associated with outbreaks of invasive insects in riparian forests warrants further investigation in these linked systems.

Along the northern Pacific coast of North America, riparian alder (*Alnus* spp.) provides a myriad of ecological functions for adjacent freshwater ecosystems (Allan, Wipfli, Caouette, Prussian, & Rodgers, 2003; Helfield & Naiman, 2002; Shaftel, King, & Back, 2012; Wipfli & Musslewhite, 2004). Due to its symbiotic relationship with a nitrogen-fixing bacteria, riparian alder is an important source of nitrogen for both riparian and freshwater ecosystems (Helfield & Naiman, 2002; Ruess, McFarland, Trummer, & Rohrs-Richey, 2009; Shaftel et al., 2012). Alder contributes nitrogen-rich inputs via senesced leaf litter in the fall, supporting shredding taxa of aquatic invertebrates (Irons, Oswood, & Bryant, 1988; Wipfli & Musslewhite, 2004). Riparian alder supports terrestrial invertebrates on its foliage, which can fall into streams (Allan et al., 2003; Roon et al., 2016; Wipfli, 1997). Previous studies have documented that riparian alder contributes higher inputs of terrestrial invertebrates to streams relative to coniferous forests (Allan et al., 2003; Kawaguchi, Taniguchi, & Nakano, 2003; Nakano & Murakami, 2001; Romero, Gresswell, & Li, 2005; Roon et al., 2016; Wipfli, 1997). Some stream fishes, such as salmonids, are adapted to feed on these subsidies of terrestrial invertebrates and can account for over half of prey biomass mid-summer and fall when they are most abundant (Allan et al., 2003; Nakano & Murakami, 2001; Romero et al., 2005; Wipfli, 1997). Given that stream salmonids such as juvenile coho salmon (*Oncorhynchus kisutch*) occupy freshwater habitats for their first 1–2 years, terrestrial prey subsidies are important resources that can influence fish growth, production and survival (Dineen, Harrison, & Giller, 2007; Rosenfeld & Raeburn, 2009; Wipfli, 1997; Wipfli & Baxter, 2010).

Across southcentral Alaska riparian thin-leaf alder (*Alnus tenuifolia*), stands are declining from the interaction between a native canker and the defoliation by the invasive green alder sawfly (Adams, Catal, & Trummer, 2010; Kruse, Smith, & Schiff, 2010; Kruse et al.,



**FIGURE 1** Study watersheds, southcentral Alaska

2015; Ruess et al., 2009), resulting in widespread dieback along streams in this region (Kruse et al., 2010, 2015). Invasive green alder sawflies are native to Eastern Europe and are thought to have arrived in North America via imported firewood or dunnage. Sawflies overwinter as prepupae, pupate and emerge in spring as adults, lay eggs on riparian alder foliage upon leaf-out, and larvae develop during summer. Sawfly larvae are voracious herbivores, defoliating riparian alder stands where present. First records of invasive sawflies are from Newfoundland in the 1990s (Smith & Goulet, 2000), and are currently distributed across southcentral Alaska and the Pacific Northwest (Kruse et al., 2010; Looney et al., 2012). Although the full distribution is currently unknown, invasive sawflies may present a threat in a wide range of habitats. Defoliation of riparian alder due to the invasive sawflies has the potential to cause a variety of ecological effects in both riparian and stream ecosystems (Bjelke, Boberg, Oliva, Tattersdill, & McKie, 2016; Lecerf, Dobson, Dang, & Chauvet, 2005). Considering the importance of riparian alder as a source of terrestrial invertebrate prey resources for juvenile coho salmon, managers are concerned that the defoliation of riparian alder by this invasive sawfly may negatively affect terrestrial prey resources for these stream fishes.

The objective of this study was to determine how riparian alder defoliation by invasive green alder sawfly larvae affects terrestrial prey resources for juvenile coho salmon. We hypothesised that

**TABLE 1** Characteristics of study reaches in southcentral Alaska

Parameter	Anchorage Bowl streams				Kenai Peninsula streams			
	North Fork of		South Fork of		Dave's Creek		Trail Creek	
	Campbell Creek		Eagle River					
	Reach 1	Reach 2	Reach 1	Reach 2	Reach 1	Reach 2	Reach 1	Reach 2
Elevation (m)	82	62	242	236	143	142	156	155
Wetted width (m)	5.7 (±1.1)	4.9 (±1.0)	10.2 (±1.8)	9.4 (±0.8)	8.9 (±1.8)	7.9 (±1.1)	6.6 (±1.5)	5.9 (±1.2)
Discharge (m <sup>3</sup> /s)	0.8 (±0.3)	0.7 (±0.2)	3.1 (±0.8)	2.9 (±0.7)	1.5 (±0.1)	1.7 (±0.2)	0.7 (±0.1)	0.7 (±0.1)
Air temperature (°C)	13.3 (±5.1)	13.0 (±4.3)	11.9 (±3.5)	12.4 (±4.4)	12.6 (±5.5)	12.6 (±5.5)	12.3 (±4.3)	11.9 (±4.2)
Stream temperature (°C)	9.7 (±1.6)	9.7 (±1.6)	9.9 (±1.5)	–	10.3 (±1.4)	10.3 (±1.4)	11.4 (±1.7)	9.2 (±1.5)
Total canopy cover (%)	25.4 (±21.6)	16.6 (±11.3)	39.6 (±18.0)	13.7 (±8.8)	17.8 (±19.3)	15.6 (±8.3)	17.8 (±19.3)	15.6 (±8.3)
Riparian alder (%)	58.0	66.4	47.2	61.9	55.7	54.9	67.4	68.2
Riparian defoliation (%)	13.7 (±4.3)	29.9 (±14.7)	22.4 (±6.6)	38.2 (±15.6)	15.5 (±3.4)	25.2 (±4.5)	24.6 (±9.1)	30.4 (±12.9)

Table contains mean and standard deviations of monthly measurements June–August 2011. Riparian vegetation measurements (total canopy cover, riparian alder, and riparian defoliation) were made in July during peak sawfly abundance.

defoliation by invasive sawfly larvae would negatively affect native terrestrial invertebrate communities via competition for shared resources (in this case riparian foliage). We predicted that this in turn would negatively affect subsidies of native terrestrial invertebrates to streams, and ultimately, the consumption of those native terrestrial invertebrates by juvenile coho salmon. We hypothesised that this would be evident as shifts in community composition and reductions in biomass of native terrestrial invertebrates. Due to the emergence of larval sawflies mid-summer, we hypothesised that terrestrial invertebrate communities would also vary seasonally and that the impacts of invasive sawflies would be greatest during and after emergence.

## 2 | METHODS

### 2.1 | Study design

In the summer of 2011, we sampled four watersheds in southcentral Alaska where invasive sawflies have defoliated riparian thin-leaf alder stands (Figure 1, Table 1). Due to the widespread distribution of invasive sawflies across this region, no control sites in these study watersheds were possible. In each watershed, we sampled two stream reaches across four watersheds for a total of eight total stream reaches that varied in sawfly density. Study reaches were 150–200 m in length and were spaced at least 200 m apart. This sampling was repeated once a month in June, July and August. Due to the phenology of larval sawflies, the timing of this sampling corresponded to before, during and after larval sawfly emergence and riparian defoliation.

Riparian plant communities consisted primarily of thin-leaf alder (*Alnus tenuifolia*), but also included a variety of broadleaf deciduous and conifer tree species including the following: Sitka alder (*Alnus viridis*), Alaska paper birch (*Betula neoalaskana*), black cottonwood (*Populus trichocarpa*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), invasive European bird cherry in

urban areas (*Prunus padus*) and various species of willow (*Salix* spp.). Riparian vegetation was measured with a hand-held densiometer and characterised as total canopy cover and per cent alder. Riparian alder defoliation was estimated visually after sawfly emergence in July on three randomly selected branches of 10 alder patches systematically distributed every 15 m within each study reach. Stream flow was measured each month with a Flo-Mate 2000 (Marsh-McBirney Inc., Hach, CO) along channel cross-sections to calculate discharge. Air and stream temperature were recorded hourly throughout the summer with StowAway Tidbit Temperature data loggers<sup>®</sup> (Onset Computer Corporation, Pocasset, MA).

### 2.2 | Terrestrial invertebrate sampling

To determine whether riparian defoliation by this invasive sawfly affected the flow of terrestrial prey resources from riparian vegetation to juvenile coho salmon, we collected terrestrial invertebrates monthly at three different levels described by Allan et al. (2003). First, we sampled terrestrial invertebrates present on riparian alder foliage. To do this, we clipped an alder branch growing within 1 m of the stream channel and 1–2 m above the ground into a plastic garbage bag containing insecticide (Pyrethrin<sup>®</sup> strip). Five replicate samples were collected from each study reach from all watersheds each month during the summer for a total sample size of 120.

Second, we collected terrestrial invertebrate subsidies to streams using floating pan traps placed underneath patches of riparian alder. Pan traps were constructed out of plastic dishpans (~1,000 cm<sup>2</sup> surface area) supported by an inflatable rubber ring that floated on the stream surface and was tethered to the stream-bank. Dishpans were filled with ~ 5 L stream water and a small amount of dish soap to break the water tension and ensure that collected invertebrates would not escape. After 3 days, contents of

each pan were sieved through 250  $\mu\text{m}$  mesh and stored in 90% ethanol. Five replicate pan traps were initially set in each study reach, but only a portion was recovered due to the interference by curious grizzly bears, resulting in a final sample size of 97 of the 120 pan traps originally deployed.

Third, we collected terrestrial invertebrates consumed by juvenile coho salmon via nonlethal gastric lavage. Juvenile coho salmon (fork length 60–120 mm) were captured with Gee<sup>®</sup> minnow traps baited with salmon roe placed in pool habitats. At each study reach, fish were anaesthetised with MS-222<sup>®</sup> (Argent Chemical Laboratories Inc., Redmond, WA), mass and fork length measured, and stomach contents flushed via gastric lavage with a soft-tipped 10 ml plastic syringe filled with water. Stomach contents were stored in 90% ethanol. All fish were returned to the same location where they were originally caught once the effects of the anaesthetic had worn off. Diet samples were collected from 10 fish at each study reach, and sampling was repeated monthly for a total sample size of 240 fish. To ensure invertebrates in juvenile coho salmon, diets were likely to reflect the invertebrates available in the environment, and we collected diets within a day of riparian foliage and pan trap sampling.

All invertebrate samples collected in the field were identified to family, enumerated and their length measured to estimate biomass using length–weight regressions (Sample, Cooper, Greer, & Whitmore, 1993; Sabo, Bastow, & Power, 2002; Wipfli lab, unpublished). To standardise terrestrial invertebrate biomass between foliage samples, all foliage was dried at 60°C for 24 hr and total invertebrate biomass was divided per gram of leaf mass.

## 2.3 | Statistical analysis

### 2.3.1 | Riparian alder defoliation

To determine the effect of sawfly biomass on riparian alder defoliation, we used a linear mixed-effects model to test the fixed effect of sawfly biomass on riparian defoliation with a random effect of watershed (Pinheiro & Bates, 2000). Residuals were checked graphically and did not initially meet model assumptions of equal variance or normality, so we applied a  $\log(x + 1)$  transformation for each response and explanatory variable. Statistical significance was determined with  $\alpha = .05$ .

### 2.3.2 | Terrestrial invertebrate community composition and structure

To visualise how terrestrial invertebrate communities varied in composition and structure, we used nonmetric multidimensional scaling (NMS) ordination. We decided to use NMS ordination due to the prevalence of 0s in the data set and because it has no underlying assumption on the distribution of the data, making it suitable for community data which are often nonlinear (McCune & Grace, 2002). In PC-ORD, we ran a NMS of medium thoroughness on autopilot mode using a Sorensen distance measure (McCune & Medford,

2016). We compared the data to a randomisation test and determined the results were better than expected by chance ( $p < .05$ ). We overlaid the ordination of sample units in species space with convex hulls (boxes that encompass points) to show the amount of overlap between groups of sample units. To determine the role of sawfly biomass and riparian defoliation on terrestrial invertebrate community structure, we then overlaid these continuous variables as vectors to see how they were associated with the distribution of sample units. To determine how terrestrial invertebrate community structure varied between seasons (before, during and after sawfly emergence) and between level of energy flow (riparian foliage, streams, and fish), NMS ordinations were repeated for each categorical variable.

We applied permutational multivariate analysis of variance (perMANOVA) to test whether terrestrial invertebrate community structure differed between the categorical variables of month and level of energy flow (riparian foliage, streams and fish) (Anderson, 2001; McCune & Grace, 2002). In PC-ORD, we applied a one-way perMANOVA to test the effect of each categorical variable on terrestrial invertebrate community structure (McCune & Medford, 2016). Statistically significant differences for all tests were determined with  $\alpha = .05$ .

### 2.3.3 | Terrestrial invertebrate biomass

To test the effects of invasive sawflies on terrestrial invertebrate biomass, we used linear mixed-effects models (Pinheiro & Bates, 2000). In the first model, to determine whether terrestrial invertebrate biomass differed seasonally (before, during and after sawfly emergence), we tested the fixed effect of month and random effect of watershed. This model was repeated for invasive sawflies and for native taxa. In the second model, to determine the effect of sawfly biomass on the biomass of native taxa, we tested the fixed effect of sawfly biomass with a random effect of watershed. These models were tested separately for each level of energy flow (riparian alder foliage, terrestrial prey subsidies to streams and juvenile coho salmon diet). Residuals were checked graphically and did not initially meet model assumptions of equal variance or normality, so we applied a  $\log(x + 1)$  transformation for each response and explanatory variable to correct for this. While figures show pretransformed data unless specified, all statistical analyses used transformed data. Statistical significance was determined with  $\alpha = .05$ . All linear mixed-effects models were conducted in the *nlme* package (Pinheiro, Bates, DebRoy, & Sarkar, 2017) of R version 3.2.3 (2015).

### 2.3.4 | Selectivity index

To determine the selectivity of juvenile coho salmon for different terrestrial prey items including invasive sawflies, we used Jacob's selectivity index (Jacobs, 1974). Prey selectivity ( $D$ ) was calculated using the formula:

$$D = r - p/r + p - 2rp$$



where  $r$  is the proportion of a given prey taxa in the diet (% frequency of occurrence) and  $p$  is the proportion available of that taxa in the environment. The index provides an indication of whether a prey taxa is selected for more or less than its availability in the environment. We compared terrestrial prey taxa including invasive sawflies consumed by juvenile coho salmon to their availability entering streams as terrestrial prey subsidies. Index values range between  $-1$  and  $1$  where values greater than  $0$  indicate positive selection relative to availability in the environment, while values less than  $0$  indicate negative selection relative to availability in the environment.

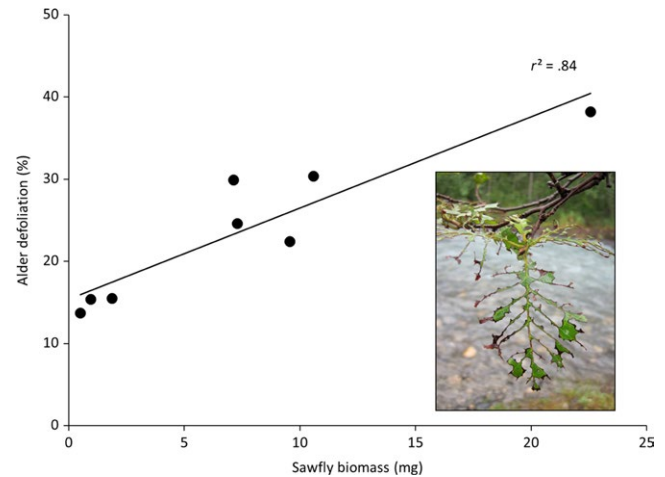
### 3 | RESULTS

#### 3.1 | Riparian alder defoliation

Riparian alder defoliation by invasive sawfly larvae occurred in July with the emergence of larval sawflies and was highly correlated with sawfly biomass ( $r^2 = .84$ ) (Figure 2). Sawfly biomass was determined to have a significant effect on riparian alder defoliation ( $F_{1,19} = 10.88, p = .004$ ) (Table 2).

#### 3.2 | Terrestrial invertebrate community composition and structure

Invasive sawflies influenced the composition of terrestrial invertebrate communities resulting in variation between seasons and levels of energy flow (riparian alder foliage, subsidies to streams and juvenile coho salmon diets). Terrestrial invertebrate communities were similar in composition between riparian alder foliage and terrestrial prey subsidies, especially in June and July (Figure 3). In June, communities were composed primarily by native terrestrial taxa (Figure 3, Table 2), accounting for 77.8% of the biomass on riparian alder foliage, 67.2% of terrestrial prey subsidies (Table 2). Once invasive sawfly larvae emerged in July, terrestrial invertebrate communities shifted in composition and became dominated by invasive sawflies (Figure 3, Table 2). Invasive sawflies accounted for 90.8% of the biomass on riparian alder foliage and 68.9% of terrestrial prey subsidies (Table 2). After sawfly emergence peaked, the composition of terrestrial invertebrate communities in August shifted back towards native taxa, but sawflies remained abundant accounting for 57.5% of the biomass on riparian alder foliage and 17.4% of terrestrial prey subsidies (Figure 3, Table 2). Understory terrestrial slugs (Gastropoda) were absent from riparian alder foliage but were abundant in terrestrial prey subsidies, accounting for 55.1% of the biomass (Table 2). Juvenile coho salmon diets diverged from riparian alder foliage and terrestrial prey subsidies, relying more on aquatic invertebrates throughout the summer, especially early in the season (Figure 3). Juvenile coho salmon consumed invasive sawflies when most abundant in July, but only accounted for 11.3% of the biomass in July (Table 2). Later in the summer, juvenile coho salmon primarily fed on understory terrestrial slugs in August, accounting for 84.5% of terrestrial taxa consumed and 65.3% of overall biomass (Figure 3).



**FIGURE 2** Relationship between mean biomass of invasive sawfly larvae and mean per cent defoliation of riparian alder. Defoliation was assessed along stream reaches during peak defoliation, July 2011

Nonmetric multidimensional scaling ordinations reflected patterns in community composition demonstrating that invasive sawflies influenced terrestrial invertebrate community structure resulting in variation both seasonally and between levels of energy flow (riparian foliage, streams and fish). First, NMS ordinations showed that terrestrial invertebrate structure varied between months along Axis 2 (Figure 4). Convex hulls indicated community structure shifted between months and was associated with riparian defoliation and sawfly density causing communities in July to be more distinct than in June and August (Figure 4). Seasonal patterns observed in the NMS ordination were supported by a perMANOVA test, which determined terrestrial invertebrate community structure differed significantly between months ( $F_{2,71} = 5.44, p < .001$ ) (Table 3). NMS ordinations also determined that terrestrial invertebrate community structure varied between levels of energy flow (riparian alder foliage, terrestrial prey subsidies to streams and juvenile coho salmon diets) along Axis 1 (Figure 4). Convex hulls indicated community structure was most distinct on riparian alder foliage and in juvenile coho salmon diets, and both were overlapped by terrestrial prey subsidies (Figure 4). These shifts along Axis 1 especially for communities on riparian alder foliage were associated with riparian alder defoliation and sawfly density (Figure 4). Divergence in community structure between sampling levels was supported by a perMANOVA test, which determined community structure differed significantly between level of energy flow ( $F_{2,71} = 4.42, p < .001$ ) (Table 3).

#### 3.3 | Terrestrial invertebrate biomass

Biomass of invasive sawflies and native taxa varied seasonally and between levels of energy flow (Figure 5). Invasive sawfly biomass differed significantly between months, peaking in July for all three levels of energy flow including on riparian alder foliage ( $F_{2,18} = 16.13, p < .001$ ), as terrestrial prey subsidies ( $F_{2,18} = 16.13, p < .001$ ) and in juvenile coho salmon diets ( $F_{2,18} = 5.73, p = .012$ ) (Figure 5, Table 3). Invasive sawfly biomass was substantially higher than native terrestrial

**TABLE 2** Composition of terrestrial invertebrate communities and Jacob's Index of prey selectivity

Taxa	Riparian Alder Foliage			Terrestrial Prey Subsidies			Juvenile Coho Salmon Diet			Jacob's Selectivity Index		
	June	July	August	June	July	August	June	July	August	June	July	August
Acari	0.2	<0.1	0.1	0.1	<0.1	0.2	<0.1	0.2	<0.1	-0.30	-0.70	-0.72
Arachnida	4.7	0.4	4.4	6.9	2.6	2.9	6.7	1.5	1.0	-0.02	-0.26	-0.51
Coleoptera	5.3	1.2	1.2	4.9	3.9	0.9	38.2	2.4	1.7	0.85	-0.24	0.36
Collembola	0.0	0.0	<0.1	0.1	<0.1	0.6	0.2	0.3	0.3	0.31	0.71	-0.29
Diptera	0.5	0.1	0.5	1.7	1.4	2.8	7.7	4.3	6.1	0.65	0.53	0.38
Gastropoda	17.8	0.0	8.0	0.0	0.0	55.1	0.0	15.5	84.5	0.00	1.00	0.63
Hemiptera	0.3	0.2	0.0	8.3	0.4	0.4	0.0	0.3	0.4	-1.00	-0.04	0.00
Homoptera	18.9	3.4	5.2	2.3	4.6	4.1	5.0	7.5	3.2	0.39	0.25	-0.13
Hymenoptera	1.2	0.8	2.8	47.2	6.2	3.2	23.8	43.3	0.9	-0.48	0.84	-0.54
Lepidoptera	38.7	1.8	4.7	18.9	7.4	5.7	10.7	0.0	1.1	-0.32	-1.00	-0.68
<i>Monsoma pulveratum</i>	8.6	91.8	72.2	0.6	72.3	21.3	0.8	23.0	0.0	0.14	-0.79	-1.00
Neuroptera	3.8	0.2	0.9	7.7	0.1	0.7	4.1	0.6	0.6	-0.33	0.75	-0.06
Psocoptera	0.2	<0.1	0.0	0.1	1.2	1.4	2.7	0.9	0.1	0.91	-0.14	-0.87
Thysanoptera	0.0	<0.1	<0.1	0.1	<0.1	<0.1	0.1	0.2	<0.1	0.12	0.82	-0.22
Total Aquatic Taxa	13.4	0.5	20.1	30.7	3.5	17.2	72.7	42.4	18.9			
Native Terrestrial Taxa	77.8	8.1	22.1	67.2	26.4	64.4	24.7	38.2	78.2			
Invasive Sawfly Larvae	7.3	90.8	57.5	0.4	68.9	17.4	0.2	11.3	0.0			
Other	1.6	0.6	0.3	1.6	1.2	1.0	2.3	8.1	2.9			

Percent composition by biomass of terrestrial invertebrate communities on riparian alder foliage, terrestrial prey subsidies and juvenile coho salmon diets during 3 months in the summer 2011. Jacob's Index of prey selectivity to determine whether juvenile coho salmon were selecting for or against terrestrial prey taxa relative to availability as terrestrial prey subsidies. Jacob's Index values ( $D$ ) greater than 0 indicate positive selection relative to availability in the environment while values less than 0 indicate negative selection relative to availability in the environment.

invertebrate biomass when at its peak in July, supporting 9x greater biomass on riparian alder foliage and contributing 3x greater biomass as terrestrial prey subsidies (Figure 5). Juvenile coho salmon consumed invasive sawflies in July, but sawflies only accounted for 11% of overall diets and less than half the biomass of native terrestrial taxa (Figure 5). The biomass of native terrestrial invertebrate taxa differed significantly between months on riparian alder foliage ( $F_{2,18} = 6.94, p = .006$ ), peaking in June before sawfly emergence and declining as the summer continued (Figure 5, Table 3). In contrast, native terrestrial invertebrate biomass did not differ between months as terrestrial prey subsidies ( $F_{2,18} = 1.53, p = .244$ ) or in juvenile coho salmon diets ( $F_{2,18} = 0.51, p = .611$ ), remaining stable through the summer (Figure 5, Table 3).

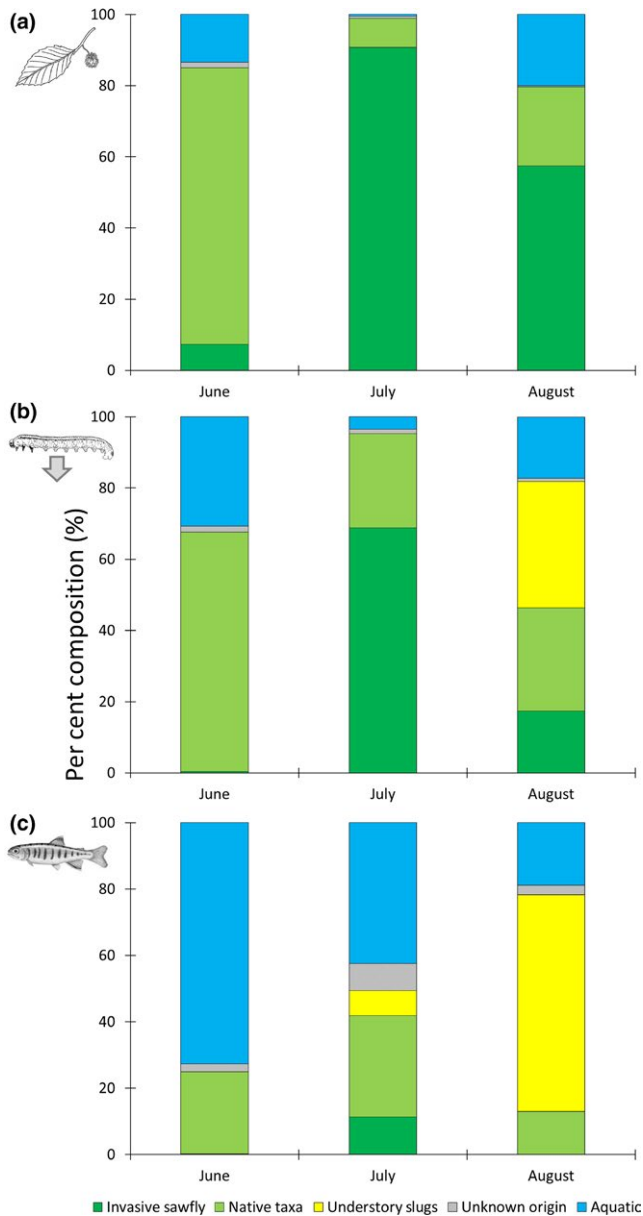
Invasive sawflies had no effect on the biomass of native taxa. There was no relationship between invasive sawfly biomass and the biomass of native taxa on riparian alder foliage ( $r^2 = .05$ ), as terrestrial prey subsidies ( $r^2 = .13$ ) and in juvenile coho salmon diets ( $r^2 = .02$ ) (Figure 6). These relationships were determined not to be significantly related on riparian alder ( $F_{1,19} = 0.54, p = .473$ ), as terrestrial prey subsidies ( $F_{1,19} = 2.61, p = .122$ ), or in juvenile coho salmon diets ( $F_{1,19} = 0.29, p = .596$ ) (Table 3).

### 3.4 | Selectivity index

Using Jacob's selectivity index to determine prey selection patterns of terrestrial invertebrates by juvenile coho salmon relative to their availability in the environment as terrestrial prey subsidies, we see that juvenile coho salmon exhibited positive selection for several terrestrial invertebrate taxa including the following: Coleoptera, Diptera, Homoptera, and Psocoptera in June; Collembola, Diptera, Gastropoda, Hemiptera, Hymenoptera and Neuroptera in July; and Coleoptera, Diptera, Gastropoda in August (Table 2). Juvenile coho salmon exhibited slight positive selection for invasive sawflies in June, but selected against invasive sawflies relative to their availability in July and August (Table 2).

## 4 | DISCUSSION

Terrestrial invertebrates are important trophic resources for stream salmonids, linking riparian forests to stream food webs. Juvenile coho salmon relied on terrestrial invertebrates for a major portion

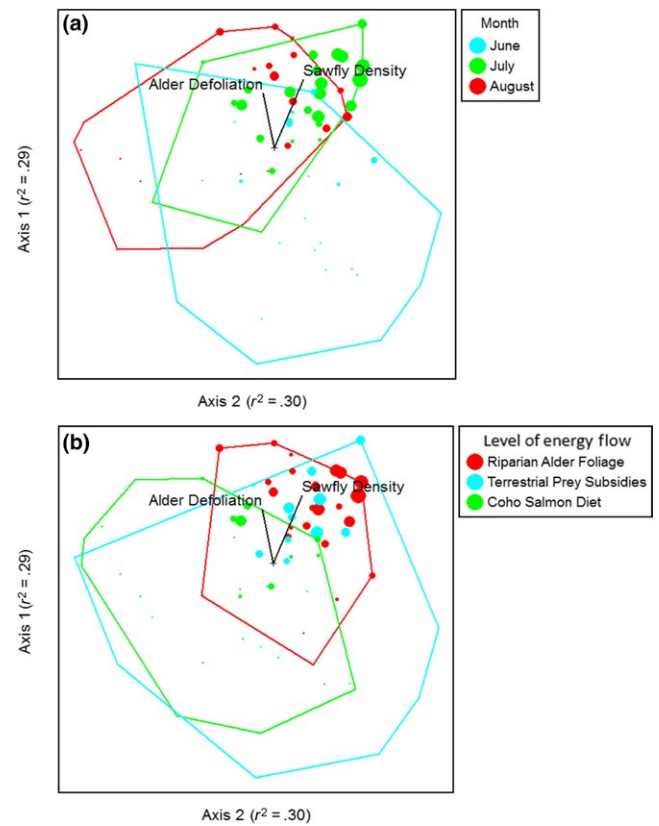


**FIGURE 3** Per cent composition by biomass of invertebrate communities present: (a) on riparian alder foliage, (b) as terrestrial prey subsidies and (c) in diets of juvenile coho salmon. Categories are invasive sawfly larvae, native riparian invertebrate taxa, understory slugs, taxa of unknown origin and aquatic invertebrates

of their diet, accounting for 25%–78% of overall prey biomass. Therefore, the loss of riparian vegetation via the defoliation of riparian alder by the invasive green alder sawfly has the potential to disrupt these linkages. In this study, we documented that riparian defoliation by invasive sawflies influenced terrestrial prey subsidies to these southcentral Alaskan salmon streams.

#### 4.1 | Terrestrial invertebrate community composition and structure

Invasive sawflies were an important driver in structuring terrestrial invertebrate communities, supporting our hypothesis that they



**FIGURE 4** Nonmetric multidimensional scaling ordinations of terrestrial invertebrate communities in relation to alder defoliation (%) and sawfly biomass broken down by (a) month and (b) level of energy flow. Points are sample units in species space with the size of point indicating sawfly abundance

would shift the composition of terrestrial invertebrate communities. Once invasive sawfly larvae emerged in July, they dominated the composition of terrestrial invertebrate communities on riparian alder foliage and as terrestrial prey subsidies. NMS ordinations supported these observations showing riparian defoliation and sawfly biomass to be major drivers of terrestrial invertebrate community structure. These shifts in community composition and structure associated with invasive sawflies help to explain the variation we see between seasons and levels of energy flow. These results are supported by previous research that has documented that invasive species can be responsible for shifts in terrestrial invertebrate community composition and structure (Adkins & Rieske, 2013; Greenwood et al., 2004; Hladyz et al., 2011; Roon et al., 2016). Relative to the patterns observed on riparian alder foliage and terrestrial prey subsidies to streams, invasive sawflies had little influence on the composition of terrestrial invertebrates consumed by juvenile coho salmon. Although juvenile coho salmon consumed invasive sawflies in July, they only accounted for a small portion of their overall diet. Instead, juvenile coho salmon relied more on aquatic invertebrates and other native terrestrial taxa such as adult beetles, adult wasps and understory terrestrial slugs.

Terrestrial invertebrate communities exhibited substantial seasonal variation, supporting our original hypothesis that terrestrial

**TABLE 3** Output of statistical models

Linear mixed-effects model 1: Effect of sawfly biomass on riparian alder defoliation ( $\alpha = .05$ )						
				<i>df</i>	<i>F</i>	<i>p</i>
Riparian defoliation				1, 19	10.88	.004*
Linear mixed-effects model 2: Effect of month (before, during, after) on biomass of invasive sawfly larvae and on native taxa ( $\alpha = .05$ )						
	Invasive Sawfly Larvae			Native Taxa		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Riparian alder foliage	2, 18	16.13	<.001*	2, 18	6.94	.006*
Terrestrial prey subsidies	2, 18	16.13	<.001*	2, 18	1.53	.244
Juvenile coho salmon diet	2, 18	5.73	.012*	2, 18	0.51	.611
Linear mixed-effects model 3: Effect of sawfly biomass on biomass of native taxa ( $\alpha = .05$ )						
	<i>df</i>	<i>F</i>	<i>p</i>			
Riparian alder foliage	1, 19	0.54	.473			
Terrestrial prey subsidies	1, 19	2.61	.122			
Juvenile coho salmon diet	1, 19	0.29	.596			
PerMANOVA model: Effect of environmental variables month and level of energy flow (riparian foliage, subsidies to streams, and juvenile coho salmon) on terrestrial invertebrate community structure ( $\alpha = .05$ )						
	<i>df</i>	<i>F</i>	<i>p</i>			
Month	2, 71	5.44	<.001*			
Level of energy flow	2, 71	4.42	<.001*			

\*Statistically significant differences ( $p < .05$ ).

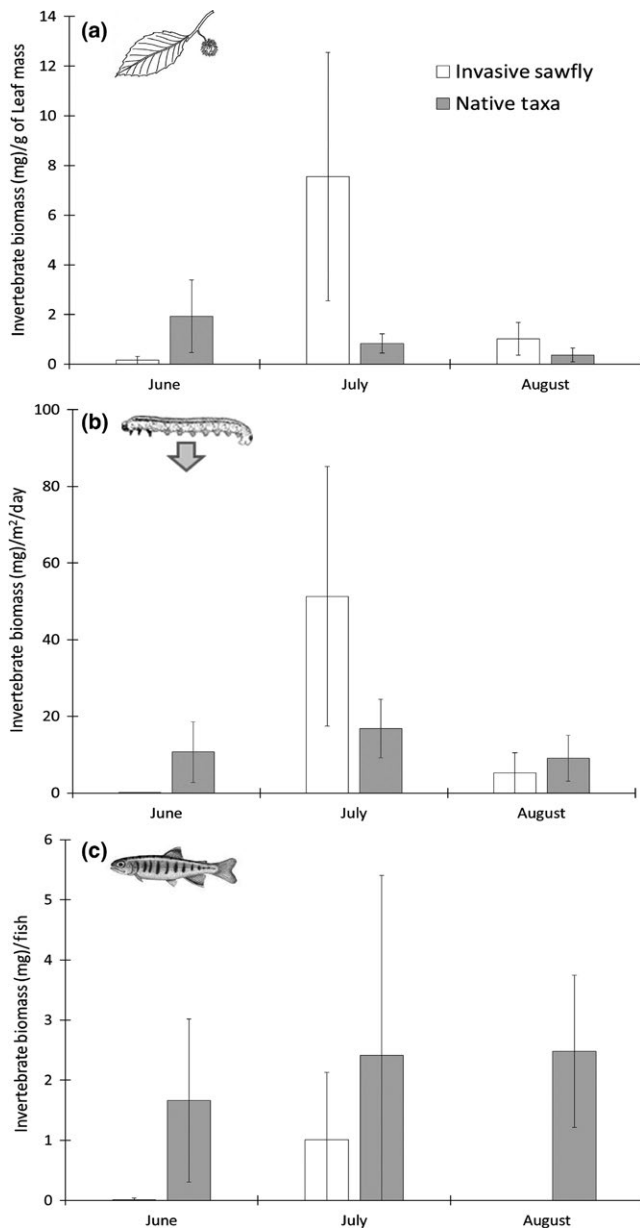
invertebrate communities would vary between seasons. This seasonal variation was likely driven in part by the prevalence of sawflies mid-summer causing July sample units to group separately from June to August. Sawflies were also present in June and August (although less frequently so) causing some overlap between terrestrial invertebrate communities between the three sampling months. These seasonal patterns could also be driven by the phenology of other taxonomic groups such as native terrestrial invertebrates (e.g. beetles, moth larvae and adult wasps) early in the season, and understory terrestrial slugs later in the summer. These patterns are supported by the results from our perMANOVA in which we were able to reject the null hypothesis.

Terrestrial invertebrate communities varied between riparian foliage, terrestrial prey subsidies to streams and juvenile coho salmon. To capture the flow of terrestrial invertebrates from riparian vegetation to juvenile coho salmon, we sampled terrestrial invertebrates at different levels. Although we documented a high degree of overlap between these levels of energy flow, the results from our NMS ordinations and perMANOVA tests also indicated substantial variation. NMS ordinations demonstrated that terrestrial invertebrate communities sampled on the foliage of riparian alder branches were most distinct from the terrestrial invertebrates consumed by juvenile

coho salmon. Terrestrial invertebrate subsidies to streams collected by floating pan traps tended to overlap with both, suggesting that it was an integration between riparian vegetation and fish.

Results from our community analyses indicate that terrestrial invertebrate communities present on the riparian vegetation were not always closely associated with what the juvenile coho salmon consumed in a given location. This observation has been documented by previous research finding that there is not always concordance between resource availability and prey consumption possibly due to prey mixing in the environment and selective foraging by stream fishes (Allan et al., 2003; Romero et al., 2005; Roon et al., 2016). This was exemplified by the fact that the sawflies were highly abundant on riparian alder foliage and as terrestrial prey subsidies to streams but occurred only occasionally in juvenile coho salmon diets. This indicates that even though sawflies may be highly abundant in the riparian vegetation and are falling into streams, they do not appear to be important prey items for juvenile coho salmon. This observation was supported by the results from the Jacob's selectivity index, finding that juvenile coho salmon selected against invasive sawflies relative to the availability in the environment. The fact that communities associated with riparian foliage continued to be more distinct than as terrestrial prey subsidies and juvenile coho salmon diets suggests that other vegetation types



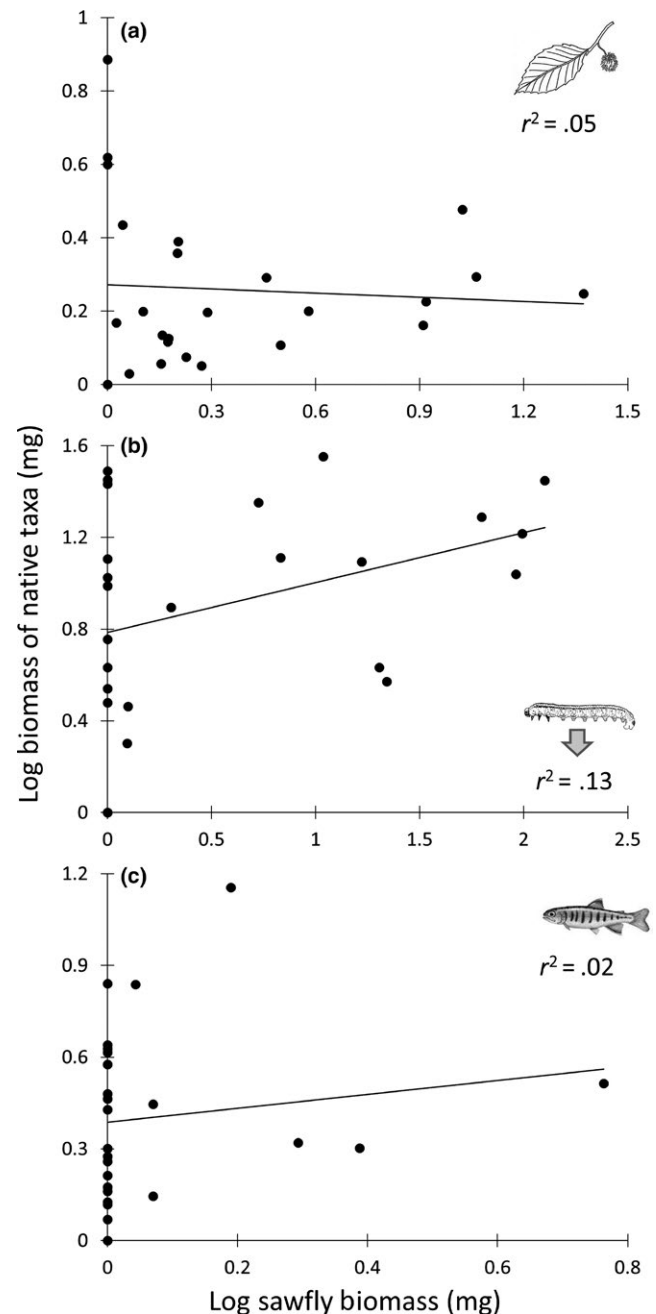


**FIGURE 5** Seasonal patterns of mean biomass (mg) of invasive sawfly larvae and native terrestrial invertebrate taxa for all streams in the summer of 2011. Invertebrate biomass present: (a) on riparian alder foliage, (b) as terrestrial prey subsidies, and (c) in diets of juvenile coho salmon. Error bars indicate 95% Confidence Intervals

beyond riparian alder are also likely contributing terrestrial prey items to streams and juvenile coho salmon (e.g. understory terrestrial slugs).

#### 4.2 | Terrestrial invertebrate biomass

Invasive sawfly biomass was highly seasonal, peaking mid-summer on riparian foliage, as subsidies to streams and in juvenile coho salmon diets. This seasonality reflected the phenology of larval sawflies, which emerge mid-summer (Kruse et al., 2010). At least on the riparian alder foliage and as terrestrial prey subsidies to streams, this pulse in biomass mid-summer was substantially higher than all native



**FIGURE 6** Relationships between biomass of invasive sawfly larvae and the biomass of native terrestrial invertebrate taxa present: (a) on riparian alder foliage, (b) as terrestrial prey subsidies and (c) in diets of juvenile coho salmon. Biomass was characterised as mean log biomass

terrestrial invertebrate taxa combined, increasing overall terrestrial prey subsidies to streams, and altering the timing and magnitude of these inputs to streams. In contrast to our hypothesis, the biomass of native terrestrial invertebrate taxa associated with riparian alder did not consistently decline during or after sawfly emergence. While the biomass of native terrestrial invertebrate taxa declined slightly over the summer on riparian alder foliage, the biomass of native taxa remained stable as terrestrial prey subsidies and in juvenile coho salmon diets.

When we directly related sawfly biomass to the biomass of native taxa, we found no negative effect of invasive sawflies on native terrestrial invertebrate biomass. This result did not support our original hypothesis that invasive sawflies would negatively affect the biomass of native terrestrial invertebrates. These results contrast with previous studies that have documented that invasive riparian plant species support less biomass of terrestrial invertebrates on their foliage, reducing the biomass of terrestrial prey subsidies to streams (Greenwood et al., 2004; Roon et al., 2016). It is important to consider that this study took place relatively early in the invasion of sawflies and defoliation values of riparian alder stands ranged between 13 and 38%. Thus, the effects of invasive sawflies on terrestrial invertebrates could change as defoliation intensifies and follow-up studies are needed to evaluate the effects under a broader gradient of defoliation conditions.

In contrast to their abundance in the riparian vegetation and as terrestrial prey subsidies to streams, invasive sawflies were not especially important prey items for juvenile coho salmon. Even when sawfly abundance was at its peak, juvenile coho salmon consumed a similar amount of sawfly biomass relative to native invertebrate taxa. The results of the selectivity index suggest that despite the abundance of sawflies, juvenile coho salmon appear to prefer other prey items. This selection against invasive sawflies is surprising considering soft-bodied terrestrial invertebrates are often preferred prey items by stream fishes (Nakano et al., 1999b; Syrjanen, Korsu, Louhi, Raavola, & Muotka, 2011; Utz, Ratcliffe, Moore, & Hartman, 2007). As mentioned above, prey availability and prey consumption do not always overlap possibly due to the mediating roles of prey mixing in the environment and selective foraging behaviour. However, this limited consumption by coho could also be due to the novelty of sawflies as a prey source (Carlsson, Sarnelle, & Strayer, 2009). If coho prey preferences change over time, invasive sawflies could act as a high-quality prey resource for juvenile coho salmon mid-summer (Marcarelli, Baxter, Mineau, & Hall, 2011). This in turn could have implications for the growth and energetics of these stream fishes if the invasion of sawflies persists (Rosenfeld & Raeburn, 2009; Wipfli, 1997; Wipfli & Baxter, 2010).

When all taxonomic groups were considered (both aquatic and terrestrial), juvenile coho salmon diets exhibited extensive seasonal variation (Li, Gerth, VanDriesche, Bateman, & Herlihy, 2016; Rundio & Lindley, 2008). Juvenile coho salmon consumed terrestrial invertebrate taxa associated with riparian alder primarily in mid-summer, instead relying more on aquatic invertebrates early in the summer and terrestrial taxa likely associated with understory vegetation (e.g. terrestrial slugs, ground beetles and collembolans) late in the summer. This extensive seasonality in prey consumption suggests that invasive sawflies have a limited window in which they could negatively affect terrestrial prey resources for juvenile coho salmon, potentially buffering these stream fishes from impact if sawflies continue to spread.

#### 4.3 | Future directions

As riparian forest conditions continue to change, it is essential to understand how cross-ecosystem resource subsidies that link riparian

forests to streams may also be changing (Larsen et al., 2016; Warren et al., 2016). The effects of invasive riparian species are unique in that they can transcend ecosystem boundaries via stream-riparian linkages (Hladyz et al., 2011). While previous studies have examined the role of invasive species in aquatic-terrestrial food webs (Baxter et al., 2004; Benjamin et al., 2013; Burkle, Mihaljevic, & Smith, 2012; Epanchin et al., 2010; Greenwood et al., 2004; Mineau et al., 2012; Roon et al., 2016), none to our knowledge have specifically examined the effect of an invasive riparian invertebrate on terrestrial prey subsidies for stream fishes. Given that widespread defoliation has been documented with the outbreaks of invasive and native insect herbivores such as the gypsy moth, emerald ash borer, spruce budworm and hemlock woolly adelgid (Adkins & Rieske, 2013, 2015; Candau & Fleming, 2005; Gandhi & Herms, 2010; Hutchens & Benfield, 2000; Nisbet, Kreutzweiser, Sibley, & Scarr, 2015), there are implications for terrestrial prey subsidies whenever this defoliation occurs in riparian forests near streams. This ecological process merits further investigation with other species and other systems to strengthen our understanding of the effects associated with riparian defoliation by insect herbivores on terrestrial prey subsidies to stream fishes.

In this study, we considered a single pathway (terrestrial prey subsidies for stream fishes) in which invasive sawflies could influence stream food webs. However, as there are multiple mechanisms and processes that link stream and riparian ecosystems, the loss of riparian alder could have a myriad of effects and further studies are needed (Bjelke et al., 2016; Lecerf et al., 2005). Considering riparian alder is a major source of nitrogen for riparian and stream ecosystems (Helfield & Naiman, 2002; Ruess et al., 2009; Shaftel et al., 2012; Wipfli & Musslewhite, 2004), its loss has implications for nitrogen inputs and nutrient dynamics in these linked systems (Bjelke et al., 2016; Lecerf et al., 2005). Riparian alder contributes large inputs of leaf litter that are important sources of allochthonous energy for aquatic invertebrates (Irons et al., 1988). Future studies should consider how the loss of riparian alder may alter these leaf litter inputs and the associated aquatic macroinvertebrate communities that depend on them (Adkins & Rieske, 2015; Bjelke et al., 2016; Hladyz et al., 2011; Hutchens & Benfield, 2000; Lecerf et al., 2005). The potential reduction in leaf litter inputs could alter the trophic dynamics of these streams and switch them from allochthonous to autochthonous production akin to impacts associated with other riparian forest disturbances such as timber harvest (Bilby & Bisson, 1992; Bjelke et al., 2016). Stable isotopes or whole-stream ecosystem metabolism could be useful approaches to understand how the relative pathways of energy flow may be shifting. The addition of these studies would provide a more comprehensive understanding of how riparian alder defoliation by invasive sawflies may be affecting these stream-riparian food webs.

## 5 | CONCLUSIONS

The defoliation of riparian alder by the invasive green alder sawfly has the potential to alter fluxes of energy and organic matter to

adjacent river ecosystems via multiple pathways. In this study, we focused on the effects of this invader on allochthonous inputs of terrestrial invertebrates to river ecosystems which are an important prey resource for riverine fishes. We observed that invasive sawflies shifted the composition and structure of terrestrial invertebrate communities and altered the timing and magnitude of terrestrial prey subsidies to streams. Our findings illustrate that invasive sawflies can represent a substantial pulse of terrestrial invertebrates to streams that can exceed the input of all other native taxa combined. Thus, outbreaks of invasive sawfly larvae may have the potential to influence the dynamics of adjacent stream food webs, particularly in situations where dense invasions occur across entire watersheds and overlap with aquatic consumers that are able to usurp this novel subsidy. Although we did not find that effects associated with invasive sawflies extended to juvenile coho salmon, it is important to consider that this study occurred early in the invasion. Follow-up studies are needed to see if these patterns persist as sawflies continue to spread or as riparian defoliation intensifies. In this context, these data provide important initial observations to further our understanding of the effects of invasive riparian species in stream-riparian food webs and for resource managers involved with managing invasive species both in Alaska and worldwide.

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