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**Invasive European bird cherry (*Prunus padus*) reduces
terrestrial prey subsidies to urban Alaskan salmon streams**

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1 **Invasive European bird cherry (*Prunus padus*) reduces terrestrial prey subsidies to urban Alaskan**
2 **salmon streams**

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Abstract

The spread of invasive species in riparian forests has the potential to affect both terrestrial and aquatic organisms linked through cross-ecosystem resource subsidies. However, this potential had not been examined in regards to terrestrial prey subsidies for stream fishes. To address this, we looked at the effects of an invasive riparian tree, European bird cherry (*Prunus padus*; EBC), spreading along urban Alaskan salmon streams, by collecting terrestrial invertebrates present on the foliage of riparian trees, their subsidies to streams, and their consumption by juvenile Coho Salmon (*Oncorhynchus kisutch*). Riparian EBC had 4-6 times less terrestrial invertebrate biomass on its foliage and 2-3 times lower subsidies relative to native deciduous trees. This reduction in terrestrial invertebrate biomass was consistent between two watersheds over two years. In spite of this reduction in terrestrial prey resource input, juvenile Coho Salmon consumed similar levels of terrestrial invertebrates in stream reaches bordered by EBC. Although we did not see ecological effects extending to stream salmonids, reduced terrestrial prey subsidies to streams are likely to have negative consequences as EBC continues to spread.

Introduction

Stream and riparian ecosystems are linked through resource subsidies that extend beyond ecosystem boundaries, supporting adjacent species and food webs (Polis et al. 1997; Nakano and Murakami 2001; Power 2001; Baxter et al. 2005). Examples of these cross-ecosystem resource subsidies include the inputs of allochthonous leaf litter from riparian plants to streams that support aquatic invertebrates (Cummins et al. 1989; Wallace et al. 1997); the emergence of adult life stages of aquatic insects to feed riparian spiders, birds, and bats (Murakami and Nakano 2002; Paetzold et al. 2005; Fukui et al. 2006); and the inputs of terrestrial invertebrates from riparian plants to stream fishes (Wipfli 1997; Nakano et al. 1999; Kawaguchi et al. 2003). As predicted by the river continuum concept (Vannote et al. 1980), these cross-ecosystem subsidies are especially important for aquatic species in headwater and small streams where heavy riparian canopy cover shades the stream channel and limits aquatic productivity (Baxter et al. 2005). Much research has been dedicated to the importance of these cross-ecosystem resource subsidies for aquatic species across multiple trophic levels including macroinvertebrates and fish (Wallace et al. 1997; Nakano et al. 1999; Baxter et al. 2005).

Riparian forests are highly susceptible to the spread of invasive plants due to floods that disturb riparian soils and to the extensive habitat connectivity along stream networks (Gregory et al. 1991; Hood and Naiman 2000; Friedman et al. 2005). As a result, riparian forests often support a higher number of invasive plants than upland habitats (Planty-Tabacchi et al. 1996; Hood and Naiman 2000). Because riparian zones connect terrestrial and aquatic ecosystems, the spread of invasive plants in riparian forests has the potential to impact aquatic organisms and food webs linked through cross-ecosystem resource subsidies (Gregory et al. 1991; Hood and Naiman 2000; Baxter et al. 2005). This has been studied extensively in regards to the effects of invasive plants on leaf litter inputs and the aquatic invertebrate communities that depend on them (Lecerf et al. 2007; Mineau et al. 2012; Claeson et al. 2014; Roon et al. 2014). However, less is known about the effects of invasive riparian plants on terrestrial invertebrate prey subsidies.

Terrestrial invertebrate abundance can vary widely among plant species (Mason and MacDonald 1982), and according to the resource quality hypothesis, terrestrial invertebrates are more likely to feed on vegetation types that are higher in quality (Schowalter et al. 1986; Ober and Hays 2008). Therefore, if an

invasive plant differs in quality from native species through the presence of secondary compounds or lower nutrient content, then the spread of invasive plants in riparian forests could affect terrestrial invertebrate communities, and consequently their subsidies to streams (Mason and MacDonald 1982; Ober and Hays 2008). Previous research documented declines in terrestrial invertebrate abundance and species richness associated with invasive plants relative to native vegetation with invasive willows in Australia (Greenwood et al. 2004), giant reed in California (Herrera and Dudley 2003), Japanese knotweed in Europe (Gerber et al. 2008), tamarisk in the American southwest (Wiesenborn 2005), and a mix of invasive species in Chile (Hagen et al. 2010). While Greenwood et al. (2004) documented that invasive willow reduced the abundance of terrestrial invertebrate inputs to streams, little research has specifically addressed the effects of invasive riparian plants on terrestrial invertebrate subsidies and the potential effects on upper trophic level consumers like stream fishes that depend on these terrestrial prey resources. To our knowledge, this topic remains largely unknown and merits further study.

The subsidy of terrestrial invertebrates from riparian vegetation to aquatic ecosystems can be especially important for stream fishes (Wipfli 1997; Nakano et al. 1999; Allan et al. 2003; Baxter et al. 2005). Terrestrial invertebrates act as important seasonal supplemental prey resources during summer and fall – a critical period for growth and survival (Edwards and Huryn 1995; Wipfli 1997; Nakano and Murakami 2001; Allan et al. 2003; Romero et al. 2005). Terrestrial invertebrates often have higher energy content than aquatic taxa, and fish have been documented to selectively feed on them (Nakano et al. 1999b; Utz and Hartman 2007). Experimental reductions of terrestrial prey subsidies to streams have resulted in decreased abundance, density, and growth of stream fishes (Kawaguchi et al. 2003; Eros et al. 2012; Gillette 2012). Considering that juvenile Coho Salmon (*Oncorhynchus kisutch*) in coastal Alaska spend one to two years rearing in freshwater before migrating to the ocean as smolt, terrestrial prey subsidies are especially important resources for growth and survival (Wipfli 1997; Allan et al. 2003; Wipfli and Baxter 2010).

European bird cherry (*Prunus padus*; EBC) is an invasive, ornamental tree frequently planted in Alaska because it is one of the few flowering trees that is able to survive Alaska's winters (Alaska Natural Heritage Program 2006). Birds feed on the cherries, transporting the seeds from source trees to adjacent natural areas, allowing for wild populations to spread over time. Able to tolerate a wide range of climates

and habitat types in its native Europe, EBC thrives in cold climates and wet soils, making it well suited for Alaskan riparian forests (Leather 1996). EBC has spread rapidly in the last decade and appears to be displacing native trees in riparian forests along streams in the urban centers of Alaska (Roon et al. 2015). EBC is able to form dense monotypic stands and is ranked as ‘highly invasive’ (Carlson et al. 2008). This shift in vegetation from native trees and shrubs to invasive EBC raises the question of whether EBC may be affecting terrestrial invertebrate prey subsidies important for rearing juvenile Coho Salmon.

The objective of this study was to determine if riparian EBC along urban streams affects the abundance and composition of terrestrial invertebrate communities that are prey for juvenile Coho Salmon. We hypothesized that invasive EBC supports a different community composition and a lower biomass of terrestrial invertebrates relative to native trees. Such a reduction in biomass on the riparian foliage would then result in reduced terrestrial invertebrate subsidies to streams. We further hypothesized that a reduction in subsidies associated with invasive EBC stands would reduce terrestrial invertebrate consumption by juvenile Coho Salmon versus that of native trees in adjacent stream reaches. This study was conducted in Anchorage, Alaska, an urban center with largest tracts of established EBC stands. Knowledge of how the spread of invasive EBC in riparian forests affects terrestrial prey resources important for juvenile Coho Salmon will increase our understanding of the ecological effects associated with invasive riparian plant species, important information for natural resource managers in Alaska.

Methods

Study streams

This study focused on two streams located in Anchorage, Alaska, Campbell and Chester creeks. Chester Creek is a third-order stream with a watershed draining 78 km² and Campbell Creek is a fourth-order stream draining 202 km² (Fig. 1). Located in the southcentral part of the state, the Anchorage area has a coastal climate and is considered to be a transitional zone between boreal and temperate rainforest biomes (Milner and Oswood 2000). Originating in the Chugach Mountains, these streams flow west through the urbanized lowlands of the Anchorage bowl before ultimately reaching the saltwater of Cook Inlet (Fig. 1). Greenbelt corridors of municipal parkland parallel the lower portions of both streams, protecting riparian forests as they flow through Alaska’s largest city (Ourso and Frenzel 2003). Riparian forests lining these

streams are composed of a mix of broadleaf deciduous and conifer tree species including thin-leaf alder (*Alnus tenuifolia*), Sitka alder (*Alnus viridis*), Alaska paper birch (*Betula neoalaskana*), black cottonwood (*Populus trichocarpa*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and various species of willow (*Salix* spp.). Invasive EBC is widespread along the lower, urbanized portions of these watersheds, completely displacing native riparian vegetation in places (Roon et al. 2015).

Although the lower portions of these watersheds are urbanized, they still support high quality spawning and rearing habitat for wild runs of Pacific salmon (*Oncorhynchus* spp.). While we focused our sampling on juvenile Coho Salmon in this study, other fish species present at low densities in these streams included: juvenile Chinook Salmon (*Oncorhynchus tshawytscha*), Dolly Varden char (*Salvelinus malma*), rainbow trout (*Oncorhynchus mykiss*), sculpin (*Cottus* sp.), and three-spined stickleback (*Gasterosteus aculeatus*).

To capture seasonal patterns in terrestrial prey subsidies, sampling was conducted monthly during summer months, June through October in 2009 ($n = 5$) and June through September in 2010 ($n = 4$). Spatial replication was limited due to the gradient in urbanization that occurs within these watersheds (Milner and Oswood 2000; Ourso and Frenzel 2003). To avoid confounding the effects of invasive EBC with the effects of urbanization, two study reaches were selected nearby one another that varied in riparian vegetation composition. As a result, sampling took place at two study reaches within each watershed delineated by riparian vegetation type: a ~150 m reach dominated by invasive EBC and a second ~150 m reach approximately 200 m upstream dominated by native riparian trees and shrubs.

Study reach characterization

Riparian forest and instream conditions of each study reach were characterized every 15 m for a total $n=10$ /reach. This was repeated monthly June through September in 2009 and 2010 with the results averaged together in Table 1. Riparian forest canopy cover and composition was measured using a hand-held densiometer at the center of the channel. Stream flow was measured with a Marsh-McBirney flow meter (Flo-Mate 2000, Marsh-McBirney® Inc., Hach, CO) and was combined with channel width and depth measurements to calculate discharge. Dissolved oxygen and conductivity was measured with a YSI multimeter (YSI 556 MPS, YSI® Incorporated, Yellow Springs, OH), while stream temperature was

recorded hourly with Tidbit digital temperature sensors (StowAway Tidbit Temperature Data Logger, Onset Computer Corp., Bourne, MA) deployed through the field season.

Terrestrial invertebrates on riparian tree foliage

To determine if terrestrial invertebrate communities associated with riparian trees differed between invasive EBC and native species, we sampled the foliage of riparian trees following the methods described by Allan et al. (2003). Careful not to disturb insects present, we clipped branches containing foliage overhanging or within 1 m of the stream channel, placing them into a plastic garbage bag with a small piece of insecticide (i.e. Pyrethrin[®] strip). This was repeated for EBC and the three dominant native riparian tree species: thin-leaf alder (*Alnus tenuifolia*), Alaska paper birch (*Betula neoalaskana*), and spruce (*Picea* spp.). Three replicate samples were collected from each species from each study reach June through October in 2009 and June through September in 2010. In October of 2009, only spruce and EBC were sampled because they were the only species with foliage still present. This resulted in a total sample size of $n=204$ in 2009 and $n=192$ in 2010.

Terrestrial invertebrate subsidies to streams

To determine whether riparian EBC affected terrestrial invertebrate prey subsidies to streams relative to native riparian trees, we collected the inputs of terrestrial invertebrate to streams using floating pan traps following the methods outlined in Wipfli (1997) and Allan et al. (2003). Pan traps were constructed out of plastic dishpans (~1000 cm² surface area) supported by a foam square that floated on the stream surface and was tethered to the streambank. Dishpans were filled with ~ 5L stream water and a small amount of unscented dish soap to break the surface tension ensuring that insects would not escape. Five replicate pan traps were placed underneath overhanging patches of riparian EBC and mixed native riparian trees for three days each month June through September in 2010 in both Campbell and Chester creeks. In native vegetation study reaches, effort was made to place pan traps under a mix of deciduous and coniferous trees. Due to the interference of curious humans and bears, 1-2 pan traps were disturbed per site each month. This resulted in a final sample size of $n=68$ of the 80 pan traps originally set. Contents for each

pan were screened through a 250-um mesh sieve, stored in Whirl-pak[®] bags (Nasco, Fort Atkinson, WI), and preserved with 90% ethanol until processed in the laboratory.

Juvenile Coho Salmon consumption of terrestrial invertebrates

To determine whether riparian EBC affected prey consumption of terrestrial invertebrates by stream salmonids, we collected diet samples from juvenile Coho Salmon in stream reaches lined by EBC and by native riparian trees. Juvenile Coho Salmon (fork length 60 – 120 mm) were captured with Gee minnow traps baited with salmon roe deployed in pool habitats. At each study reach, juvenile Coho Salmon were anaesthetized with MS-222[®] (Argent Chemical Laboratories Inc., Redmond, WA), mass and fork length measured, and then the stomach contents were flushed via gastric lavage from the fish with a soft-tipped 10 ml plastic syringe filled with water. Stomach contents were stored in Whirl-paks[®] and preserved with 95% ethanol. All fish were returned to the same location where they were originally caught following complete recovery from the anesthetic. Fifteen fish were sampled from each study reach in both Campbell Creek and Chester Creek June through October in 2009 and June through September in 2010. In 2009, high flows prevented sampling in Campbell Creek in June and in Chester Creek in October, resulting in a final sample size of $n=240$ fish. In 2010, low densities of fish in Chester Creek made it difficult to achieve the designated sample size. Sample sizes in Chester Creek ranged 8-10 per study reach each month, resulting in a total sample size of $n=189$. To help ensure invertebrates in Coho Salmon diets reflected terrestrial invertebrates available in the environment we collected diet contents from juvenile Coho Salmon within one to two days of riparian foliage and pan trap sampling in the same locations.

Invertebrate sample processing

All invertebrate samples collected in the field were stored in ethanol until processed in the laboratory. All invertebrates were identified to family in order to distinguish aquatic or terrestrial origin, enumerated, and their length measured to estimate biomass using length weight regressions (Sample et al. 1993, Sabo et al. 2002, Wipfli lab unpublished). While adult life stages of aquatically-derived taxa were also found in invertebrate samples, we focused exclusively on taxa that we could confidently identify as terrestrially-derived. This excluded some dipteran families. To standardize differences in foliar mass

between branch samples, terrestrial invertebrate mass was divided by the leaf dry mass of each sample. To do this all foliage was removed from the branch stem and dried at 60 °C for 24 hours and weighed.

Statistical analysis

To understand how invasive EBC affected the composition of terrestrial invertebrate communities relative to native riparian trees, we compared the community structure of terrestrial invertebrates on riparian foliage, their subsidies to streams, and consumption by juvenile Coho Salmon. To do this, terrestrial invertebrate communities were broken down by family and percent composition was calculated by mean biomass. While aquatic taxa and understory terrestrial taxa were present in diet samples, we only considered terrestrially-derived taxa present on riparian trees. After applying a square root transformation to the data, we ran a non-metric multidimensional scaling (NMDS) ordination with a Bray-Curtis similarity matrix at repeated iterations ($n = 999$) to look for natural groupings among these categories. Similarity of terrestrial invertebrate communities were assessed by how closely communities grouped together within 2-d ordination space and circles indicating 95% confidence intervals were added to show natural groupings. Stress <0.2 is considered to be acceptable within an ordination. Vectors representing taxonomic groups were overlaid on the NMDS ordination to determine how individual taxa influenced the composition and structure of terrestrial invertebrate communities. All community analyses were run in Primer version 7.0 (PRIMER, Plymouth, UK, 2006).

We compared the biomass of terrestrial invertebrates between EBC and native riparian tree foliage via a repeated measures (RM) 2-way ANOVA where riparian vegetation type (EBC vs. native) and date were used as predictor variables. To account for differences between streams we used a nested design, where study reaches (EBC vs. native vegetation) were nested within streams and samples were nested within study reaches. This model was used with all three datasets: the biomass of terrestrial invertebrates associated with riparian foliage, their subsidies to streams, and their consumption by juvenile Coho Salmon. To determine statistical significance, an α value of 0.05 was used for the primary effects and then Bonferroni-corrected values were used for multiple comparisons described in Table 2. Because biomass data did not initially meet assumptions of normality or equal variance, we applied a $\log(x + 1)$

transformation. While figures show pre-transformed data, all statistical analysis used transformed data. ANOVAs were run using PROC-MIXED in SAS[®] (SAS Institute Inc., version 9.2).

Results

Study reach characteristics

Riparian forests differed substantially in composition between EBC and native vegetation study reaches. Invasive EBC dominated the riparian canopy along EBC reaches, comprising 70.6% of the canopy cover along Campbell Creek and 68.3% of the cover along Chester Creek (Table 1). Thin-leaf alder, birch, cottonwood, and spruce were all present within EBC reaches of both streams but only accounted for 29.4% and 31.7% of the total canopy cover along Campbell and Chester Creeks respectively. A mix of native riparian tree species dominated the canopy along native vegetation study reaches and included thin-leaf alder, birch, spruce, and cottonwood (Table 1). EBC was present within study reaches bordered with native vegetation but contributed little cover (<10%). Overall canopy cover of the riparian forest was higher in EBC forests versus native forests along both streams but this difference was more dramatic along Chester Creek (53.9% vs. 26.5%) (Table 1).

Chester Creek study reaches were narrower in width than Campbell Creek reaches and while similar in flow velocity, Chester Creek had a lower discharge than Campbell Creek reaches (Table 1). Water quality measurements indicated that stream temperature, dissolved oxygen, and conductivity were similar between EBC and Native reaches within each watershed, but were all slightly higher in Chester Creek than in Campbell Creek reaches (Table 1).

Composition and structure of terrestrial invertebrate communities

Fifteen orders and 32 families of terrestrial invertebrates were identified as part of this study. On the foliage of riparian trees, wasps (Hymenoptera), true bugs (Homoptera), spiders (Arachnida), and moths (Lepidoptera) were the most common taxa by biomass. Taxa in the sawfly family Tenthredinidae (Hymenoptera) were the most abundant family for native deciduous trees, alder and birch. Sawflies were especially abundant on alder branches accounting for 53% of the biomass in 2009 and 63% in 2010. Sawflies were also abundant on birch branches, accounting for 13% in 2009 and 33% of the biomass in

2010. EBC branches supported mostly true bugs including aphids and hoppers, spiders, and adult wasps. Spruce branches supported mostly spiders and adult wasps. Terrestrial invertebrate prey subsidies consisted mostly of wasps, terrestrial flies (Diptera), and spiders. Subsidies from EBC reaches contributed more aphids but fewer moths and wasps than subsidies from native vegetation reaches in both streams. Sawfly larvae (Tenthredinidae) were the most abundant taxa captured in mixed native vegetation reaches, accounting for 45% of total biomass at Campbell Creek and 35% of total biomass at Chester Creek. Juvenile Coho Salmon diets were composed mostly of adult wasps, beetles, and spiders. Juvenile Coho Salmon also consumed a large number of terrestrial slugs, but these were not associated with riparian trees.

The structure of terrestrial invertebrate communities varied between years and between vegetation types as evident in the NMDS ordination (Fig.5). First, terrestrial invertebrate communities separated along Axis 1 with two distinct groupings between 2009 and 2010, indicating that the communities differed between years (Fig. 5). Second, there was also divergence along Axis 2 with communities associated with native deciduous trees grouping separately in both 2009 and 2010. In 2010, terrestrial invertebrate communities were similar between the foliage of native deciduous trees and the pan traps, indicating these species were contributing most of the subsidies collected by the pan traps (Fig. 5). Terrestrial invertebrate subsidies in EBC study reaches were closely associated with EBC foliage in 2010 (Fig. 5). The foliage of EBC and native spruce grouped separately from native deciduous trees, but overlapped more closely to the communities consumed by juvenile Coho Salmon in both 2009 and 2010 (Fig. 5). Terrestrial invertebrates in juvenile Coho Salmon diets were similar in composition between EBC and native vegetation study reaches and grouped more closely by year than by vegetation type (EBC vs. native vegetation) (Fig. 5).

Terrestrial invertebrates on riparian tree foliage

Terrestrial invertebrate biomass present on the foliage of riparian trees did not vary between watersheds (RM 2-way ANOVA: $F_{1,137} = 0.23$, $p = 0.63$) or by study reach nested within each watershed (RM 2-way ANOVA: $F_{1,137} = 1.04$, $p = 0.31$) (Table 2). However, there was a significant interaction between species and month (RM 2-way ANOVA: $F_{51,137} = 2.74$, $p < 0.001$), indicating that terrestrial invertebrate biomass depended on both riparian tree species (RM 2-way ANOVA: $F_{6,137} = 27.2$, $p < 0.001$) and season (RM 2-way ANOVA: $F_{7,137} = 3.27$, $p = 0.003$) (Table 2). Terrestrial invertebrate biomass

peaked mid-summer in July and August on native deciduous trees in both years, while invasive EBC and spruce supported a consistent low level of biomass all summer long (Fig. 2). Native deciduous trees, alder and birch, supported significantly more biomass of terrestrial invertebrates than EBC in 2009 and 2010 (RM 2-way ANOVA: $p < 0.001$ for both species in both years), while EBC supported a significantly higher biomass than spruce in 2009 and 2010 (RM 2-way ANOVA: $p < 0.001$ for both years) (Table 2). Alder supported the highest mean biomass of all species sampled, supporting an average terrestrial invertebrate biomass of $2.7 \text{ mg} \cdot \text{g}^{-1}$ leaf mass in 2009 and $3.6 \text{ mg} \cdot \text{g}^{-1}$ leaf mass in 2010 (Fig. 2). Birch supported the second highest mean biomass of terrestrial invertebrates with an average of $1.3 \text{ mg} \cdot \text{g}^{-1}$ leaf mass in 2009 and $2.9 \text{ mg} \cdot \text{g}^{-1}$ leaf mass (Fig. 2). EBC supported less biomass compared to the native deciduous trees, with $0.3 \text{ mg} \cdot \text{g}^{-1}$ leaf mass in 2009 and $0.6 \text{ mg} \cdot \text{g}^{-1}$ leaf mass in 2010 (Fig. 2). Spruce supported the lowest biomass of terrestrial invertebrates of any species sampled, with an average biomass of $0.2 \text{ mg} \cdot \text{g}^{-1}$ leaf mass in 2009 and $0.3 \text{ mg} \cdot \text{g}^{-1}$ leaf mass in 2010 (Fig. 2).

Terrestrial invertebrate subsidies to streams

Terrestrial invertebrate biomass collected by floating pan traps did not vary between watershed (RM 2-way ANOVA: $F_{1,52} = 1.06$, $p = 0.309$), but there was a significant interaction between study reach and date (RM 2-way ANOVA: $F_{6,52} = 2.09$, $p = 0.009$) (Table 2). This indicates that terrestrial invertebrate subsidies varied both between EBC and native vegetation (RM 2-way ANOVA: $F_{2,52} = 5.65$, $p = 0.006$), and season (RM 2-way ANOVA: $F_{6,52} = 4.21$, $p = 0.002$) (Table 2). Native riparian trees contributed significantly more terrestrial invertebrate biomass to streams than EBC in both Campbell Creek ($26.7 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ vs. $11.2 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, $p < 0.001$) and Chester Creek ($35.5 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ vs. $12.0 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, $p < 0.001$) (Table 2, Fig.3). Biomass of terrestrial invertebrate subsidies peaked in study reaches lined by native riparian trees in July, while biomass was consistently lower in study reaches lined by EBC (Fig. 3).

Juvenile Coho Salmon consumption of terrestrial invertebrates

Terrestrial invertebrates associated with riparian trees composed between 10 and 28% of juvenile Coho Salmon diets in 2009 and 11 and 34% in 2010 (Fig. 4). There were no clear differences in the proportion of terrestrial invertebrates in juvenile Coho Salmon diets between EBC and native vegetation study reaches in 2009 or 2010 (Fig. 4). The proportion of juvenile Coho Salmon diets composed of

terrestrial invertebrates increased through the summer in 2009 July through September and decreased again in October (Fig. 4). In 2010, terrestrial invertebrates started high and decreased slightly over the summer (Fig. 4). Juvenile Coho Salmon also consumed terrestrial slugs (Gastropoda), which were a large component of diets in 2010 but were not associated with riparian trees (Fig. 4)

Mean terrestrial invertebrate biomass in juvenile Coho Salmon diets did not vary between watersheds (RM 2-way ANOVA: 2009 - $F_{1,224} = 4.90$, $p = 0.270$, 2010 - $F_{1,175} = 0.15$, $p = 0.698$), EBC or native vegetation study reaches (RM 2-way ANOVA: 2009 - $F_{2,224} = 1.25$, $p = 0.289$, 2010 - $F_{2,175} = 0.51$, $p = 0.600$), or date in 2009 (RM 2-way ANOVA: 2009 - $F_{6,224} = 2.59$, $p = 0.443$). Although there was a significant effect of date in 2010 (RM 2-way ANOVA: 2010 - $F_{5,175} = 7.74$, $p < 0.001$), there was no interaction between study reach and date in either year (RM 2-way ANOVA: 2009 - $F_{6,224} = 0.99$, $p = 0.433$, 2010 - $F_{5,175} = 0.76$, $p = 0.576$) (Table 2). In 2009, juvenile Coho Salmon consumed slightly more terrestrial invertebrate biomass later in the summer (August and September) in the EBC study reaches than the native vegetation reaches, but these differences were not statistically significant (Fig. 4). In 2010, juvenile Coho Salmon consumed similar amounts of terrestrial invertebrate biomass between EBC and native vegetation study reaches that peaked at the beginning of the summer and decreased as the summer continued (Fig. 4).

Discussion

As invasive species spread within riparian forests they have the potential to not only affect terrestrial organisms but also aquatic organisms and ecological processes that are linked through stream-riparian food webs (Baxter et al. 2005). In this study, we documented that invasive EBC negatively affected the abundance of terrestrial invertebrates associated with riparian foliage and their subsidies to streams, but did not affect consumption by juvenile Coho Salmon. These data demonstrate that while the riparian invasion of EBC reduced the abundance of terrestrial invertebrates present in riparian forests and their subsidies to streams, this reduction was not great enough to extend to terrestrial prey consumption by these stream fishes.

Our results supported our first hypothesis that invasive EBC would support a significantly lower biomass of terrestrial invertebrates on the foliage of riparian branches than native deciduous trees. In both

years, native deciduous alder and birch supported a higher level of terrestrial invertebrate biomass that peaked mid-summer, while in contrast invasive EBC supported a consistently lower level throughout the season more similar to trends in native spruce. Our results coincide with previous studies documenting that terrestrial invertebrate biomass varies between conifer and deciduous trees and native and invasive trees (Mason and MacDonald 1982; Allan et al. 2003; Ober and Hayes 2008). While our study confirmed the findings of Allan et al. (2003) that native deciduous trees supported higher levels of terrestrial invertebrates than conifers in Southeast Alaska, our finding that invasive EBC functioned more like a conifer, supporting a similar level of terrestrial invertebrate biomass to spruce, was unexpected.

One explanation for why EBC supported a lower biomass of terrestrial invertebrates could be that the foliage was of lower quality relative to the native deciduous trees in this study (Mason and MacDonald 1982; Ober and Hayes 2008). For example, alder is known to have a high concentration of foliar nitrogen, and as a result may be more digestible for herbivorous invertebrates (Helfield and Naiman 2002; Wipfli and Musslewhite 2004). EBC leaves contain cyanogenic glycosides, a cyanide derivative and strong secondary compound that could reduce herbivory (Leather 1996; Sargison et al. 1996). Leather (1985) determined that even in its native range EBC supported fewer phytophagous insect pests like aphids than expected, supporting our results. While we did not see a difference in aquatic invertebrate shredder communities associated with the leaf litter of invasive EBC and native species in a previous study (Roon et al. 2014), Gleadow and Woodrow (2000) indicate that trees often take back secondary compounds before leaf senescence.

Another explanation for the lower biomass associated with EBC is the enemy release hypothesis (Keane and Crawley 2002; Cincotta et al. 2008). The enemy release hypothesis suggests that invasive plants often support fewer invertebrates because as novel resources, fewer local herbivores have adapted to feed on them. Our results align with previous studies documenting that invasive riparian plants often support a lower biomass of terrestrial invertebrates compared to native trees (Herrera and Dudley 2003; Greenwood et al. 2004; Wiesenborn 2005; Gerber et al. 2008; Hagen et al. 2010). Aphids are documented as the primary invertebrate pest in EBC's native range (Leather 1996), and while they did not account for much biomass, were the most common taxa present on EBC foliage in this study. In contrast, invertebrate biomass on alder and birch was dominated by larval sawflies (Hymenoptera, Tenthredinidae); these were

largely absent from both invasive EBC and spruce. Terrestrial invertebrate biomass on these native deciduous trees peaked mid-summer when larval sawflies were most abundant. In contrast, the terrestrial invertebrate community on EBC and native spruce supported a consistently lower biomass over the summer.

Our results demonstrated that invasive EBC contributed significantly lower terrestrial invertebrate subsidies to streams. Although effort was made to place pan traps in areas of mixed native vegetation (a combination of deciduous and conifer trees), subsidies from native trees were two to three times higher than invasive EBC. This is confirmed by our community analysis that showed that communities associated with the foliage of native deciduous trees grouped closely with subsidies collected in native vegetation study reaches (Fig. 5). These results are supported by previous research, which also determined that changes in riparian vegetation composition can influence the abundance of terrestrial prey subsidies to streams (Allan et al. 2003; Kawaguchi et al. 2003; Saunders and Fausch 2012). Although few studies have specifically examined the influence of riparian invasive plants on riparian subsidies to streams, Greenwood et al. (2004) found that invasive willow reduced subsidies to streams relative to native vegetation, consistent with our results. While spatial replication was limited in this study due to sampling constraints, the fact that identical patterns were detected between years in regards to riparian foliage and between watersheds for both riparian foliage and terrestrial subsidies provide strong evidence that EBC supported significantly less terrestrial invertebrate biomass than native deciduous trees.

Terrestrial invertebrates comprised a substantial portion of juvenile Coho Salmon diet in our study, accounting for an average of 20-25% of their diet by biomass in 2009 and 2010. However, there was no significant difference in the biomass of terrestrial invertebrates consumed by juvenile Coho Salmon between reaches lined by EBC and native trees. Instead we found juvenile Coho Salmon consumed similar levels of terrestrial invertebrates between riparian forest types. Seasonal patterns in terrestrial invertebrate biomass associated with native deciduous tree foliage and subsidies to streams were not reflected by juvenile Coho Salmon diets. Collectively, these results suggest that the magnitude of reduction in terrestrial invertebrates associated with the current distribution of invasive EBC on riparian foliage and as subsidies to streams was not enough to extend to juvenile Coho Salmon. The disconnect between the availability of terrestrial prey in riparian forests and actualized prey consumption by stream fishes has been documented

previously (Wipfli 1997; Kawaguchi and Nakano 2001; Allan et al. 2003; Romero et al. 2005), indicating that variation in terrestrial prey availability between vegetation types on smaller, reach-level scales may not be a large driver of terrestrial prey consumption by stream fishes.

One explanation for why EBC did not negatively affect terrestrial prey consumption by juvenile Coho Salmon in this study is that food in general and terrestrial prey resources more specifically may not be limiting in this system. Second, juvenile Coho Salmon like many other stream salmonids are primarily drift feeders and as a result feed on a mix of drifting prey items that are comprised by local subsidies and resources drifting from further upstream (Wipfli 1997; Allan et al. 2003). In addition to this mixing occurring within the stream channel, prey mixing may also occur in the terrestrial environment via wind or insect dispersal obscuring the effect of riparian EBC on terrestrial prey resources for fish (Mason and MacDonald 1982; Ober and Hayes 2008). Thus, even though juvenile Coho Salmon were sampled in a reach of stream lined by EBC, their stomach contents could be reflecting patterns that extend beyond the boundaries of a study reach. A follow-up study utilizing a more experimental approach may be necessary to better understand the extent that juvenile Coho Salmon may respond to local reductions in terrestrial prey subsidies (Gillette 2012).

Not only did EBC reduce the biomass of terrestrial invertebrates relative to native deciduous trees, it also shifted the community composition and structure. NMDS ordination revealed that invasive EBC and native forests supported unique communities on riparian foliage and their subsidies to streams. Terrestrial invertebrate communities overlapped more closely between the foliage of native deciduous trees with subsidies from native forests, while communities associated with EBC foliage overlapped closely with the subsidies collected from EBC forests. However, due to the absence of sawfly larvae present on native deciduous trees, diets from juvenile Coho Salmon overlapped more closely with communities associated with EBC and spruce. These results are supported by Hagen et al. (2010) who documented shifts in community structure of terrestrial invertebrates between native and invasive forests. We also observed differences in terrestrial invertebrate community structure between years. These shifts could be due to interannual variation in environmental conditions (Schowalter et al. 1986). In 2009, the summer was warmer and drier (June – September 2009: 16.6 °C mean air temperature, 17.2 cm of precipitation, National Weather Service, Anchorage, AK). In contrast, the summer of 2010 was slightly cooler and wetter (May –

September 2010: 15.5 °C mean air temperature, 22.7 cm of precipitation, National Weather Service, Anchorage, AK).

Although not included in the analysis, we documented that juvenile Coho Salmon extensively fed on terrestrial prey items not associated with riparian trees. Terrestrial slugs (Gastropoda) were especially abundant in juvenile Coho Salmon diets in August 2010 when heavy precipitation likely led to increased discharge that flushed these invertebrates into streams from understory vegetation. These terrestrial taxa associated with understory plants may provide another important terrestrial subsidy for stream fishes that should be considered in future studies.

At this point, it does not appear that EBC is affecting terrestrial prey resources for juvenile Coho Salmon in these systems, however this may change in the future. This could be due to a threshold effect where the current distribution of EBC is not yet high enough to have a measureable effect on terrestrial prey resources for juvenile Coho Salmon (Groffman et al. 2006). Systematic vegetation surveys documented EBC to be widespread in the lower portions of these watersheds, but the upper portions were still dominated by native vegetation (Roon et al. 2015). Native forests in the upper portions of these watersheds could provide a sufficient source of terrestrial prey for fish located further downstream (Wipfli and Musslewhite 2004). However, this could change over time as EBC continues to spread and displace native trees in these watersheds. Synergistic effects could also occur if the future spread of EBC interacts with the current decline of native deciduous species like thin-leaf alder (*Alnus tenuifolia*) that is currently occurring across southcentral Alaska (Ruess et al. 2009; Kruse et al. 2010). Continued monitoring of these watersheds and adjacent watersheds for the future spread of invasive EBC into upstream habitats will be important to evaluate the potential for this ecological threshold to be crossed (Groffman et al. 2006).

As invasive species continue to spread to more remote places such as Alaska (Carlson and Shephard 2007), it is important to evaluate their potential to displace native species and disrupt ecological processes (Spellman and Wurtz 2011; Greene 2014). This is especially true with invasive riparian plants that can cross ecosystem boundaries and impact both terrestrial and aquatic organisms linked through stream-riparian food webs (Baxter et al. 2005). While previous studies have examined the effects of riparian plants on leaf litter processing by aquatic invertebrate shredders (Mineau et al. 2012) or aquatic invasive species on stream-riparian food webs (Baxter et al. 2004; Baxter et al. 2007; Benjamin et al. 2013)

or riparian invaders on aquatic insects (Burkle et al. 2012), this is the first attempt of which we are aware to document how the spread of an invasive riparian tree can affect stream fishes through a reduction in their terrestrial prey. While we documented that invasive EBC strongly affected terrestrial invertebrate communities in riparian forests, we did not see the reductions of terrestrial prey subsidies from invasive EBC extend to juvenile Coho Salmon. Although we did not detect a negative effect of invasive EBC on stream fishes in this study, reduced prey subsidies may have long-term consequences across broader spatial scales if EBC continues to spread along these urban Alaskan salmon streams over time.

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Figure Legends

Fig. 1. Invasive European bird cherry (EBC) and native vegetation study reaches along Campbell and Chester creeks, Anchorage, Alaska.

Fig. 2. Mean terrestrial invertebrate biomass associated with the foliage of riparian tree branches in (a) 2009 and (b) 2010. Error bars represent standard errors.

Fig. 3. Mean biomass of terrestrial invertebrate subsidies collected by floating pan traps set underneath invasive European bird cherry (EBC) and mixed native vegetation in Campbell and Chester creeks in 2010. Error bars represent standard errors.

Fig. 4. Seasonal patterns in terrestrial prey consumption by juvenile Coho Salmon expressed as (A) mean terrestrial biomass and (B) proportion of total biomass in EBC and native vegetation study reaches in 2009 and 2010. Only includes terrestrial taxa associated with riparian trees. Error bars represent standard errors.

Fig. 5. NMDS ordination of terrestrial invertebrate communities associated with the foliage of riparian trees, their subsidies to streams, and the diet of juvenile Coho Salmon in 2009 and 2010. Terrestrial invertebrate communities associated with native vegetation are open while communities associated with invasive European bird cherry (EBC) are bordered by black boxes. Vectors indicate the taxonomic groups that influenced community structure.

Table 1. Characteristics of invasive European bird cherry (EBC) and native vegetation study reaches in Campbell and Chester creeks. Physical parameters of stream conditions were measured monthly ($n=4$) in 2009 and 2010. All mean values shown with ± 1 SE.

Parameters	Campbell Creek		Chester Creek	
	EBC	Native Vegetation	EBC	Native Vegetation
Study Reach Length (m)	139	143	166	162
Wetted Width (m)	9.8 (± 1.4)	9.6 (± 1.6)	4.7 (± 0.9)	3.8 (± 0.6)
Discharge ($\text{m}^3 \cdot \text{s}^{-1}$) 2009	3.15 (± 0.44)	2.90 (± 0.39)	0.63 (± 0.18)	0.57 (± 0.16)
Discharge ($\text{m}^3 \cdot \text{s}^{-1}$) 2010	3.81 (± 0.54)	3.50 (± 0.49)	0.60 (± 0.14)	0.55 (± 0.13)
Stream Temperature ($^{\circ}\text{C}$) 2009	11.1 (± 0.9)	11.3 (± 1.2)	12.1 (± 0.8)	12.3 (± 0.9)
Stream Temperature ($^{\circ}\text{C}$) 2010	10.6 (± 0.7)	10.7 (± 0.7)	11.8 (± 0.9)	11.9 (± 0.9)
Conductivity ($\mu\text{S} \cdot \text{cm}^{-1}$) 2009	118 (± 13)	122 (± 14)	256 (± 21)	258 (± 10)
Conductivity ($\mu\text{S} \cdot \text{cm}^{-1}$) 2010	109 (± 12)	111 (± 15)	219 (± 27)	224 (± 21)
Dissolved Oxygen ($\text{mg} \cdot \text{L}^{-1}$) 2009	10.4 (± 0.8)	10.6 (± 0.9)	11.4 (± 1.2)	11.4 (± 1.1)
Dissolved Oxygen ($\text{mg} \cdot \text{L}^{-1}$) 2010	10.1 (± 0.9)	10.8 (± 1.2)	10.9 (± 0.9)	11.1 (± 1.2)
Riparian Canopy Cover (%)	30.7 (± 4.8)	21.4 (± 3.6)	53.9 (± 8.7)	26.5 (± 5.1)
Alder (%)	8.2	33.7	10.1	25.6
Birch (%)	4.1	30.3	2.0	24.1
Cottonwood (%)	0	0	10.3	4.4
Spruce (%)	8.1	25.4	10.3	40.1
EBC (%)	70.6	9.2	68.3	5.8
Estimated Terrestrial Prey Subsidy ($\text{mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$)*	11.2 (± 4.9)	26.7 (± 12.2)	12.0 (± 5.2)	35.5 (± 10.1)
Coho Density (CPUT) in 2009	12.4 (± 3.3)	10.0 (± 3.3)	2.7 (± 0.7)	3.1 (± 0.9)
Coho Density (CPUT) in 2010	7.5 (± 2.5)	7.9 (± 2.4)	1.5 (± 0.4)	0.9 (± 0.3)
Coho Fork Length (mm)	89.5 (± 1.5)	87.3 (± 1.4)	73.6 (± 0.4)	78.0 (± 0.3)
Coho Biomass (g)	8.6 (± 0.4)	8.0 (± 0.4)	4.9 (± 0.3)	5.9 (± 0.3)

* Mean summer biomass of terrestrial prey subsidies calculated using data from floating pan traps and the composition of riparian vegetation within each study reach.

Table 2. Results of ANOVA on the effect of invasive EBC on terrestrial invertebrate biomass associated with riparian foliage, riparian subsidies to streams, and in the diet of juvenile Coho Salmon in 2009 and 2010.

Factor	d.f.	F	p	d.f.	F	p
<u>Riparian Foliage</u>	2009			2010		
Watershed	1, 137	0.23	0.630	1, 128	1.39	0.240
Study Reach (EBC vs. Native)	1, 137	1.04	0.309	1, 128	1.08	0.376
Date	7, 137	3.27	0.003*	7, 128	3.33	0.007*
Vegetation Type	6, 137	27.23	<0.001*	6, 128	21.96	<0.001*
Vegetation x Date Interaction	51, 137	2.74	<0.001*	48, 128	2.15	<0.001*
Bonferroni-corrected <i>P</i> values ($\alpha = 0.015$)						
Alder vs. EBC			<0.001*			<0.001*
Birch vs. EBC			<0.001*			<0.001*
Spruce vs. EBC			<0.001*			<0.001*
<u>Riparian Subsidies</u>						
Watershed				1, 52	1.06	0.309
Study Reach (EBC vs. Native)				2, 52	5.65	0.006*
Date				6, 52	4.21	0.002*
Study Reach x Date Interaction				6, 52	2.09	0.009*
Bonferroni-corrected <i>P</i> values ($\alpha = 0.025$)						
Chester Creek (EBC vs. native)						<0.001*
Campbell Creek (EBC vs. native)						<0.001*
<u>Juvenile Coho Salmon Diet</u>						
Stream	1, 224	4.90	0.270	1, 175	0.15	0.698
Study Reach (EBC vs. Native)	2, 224	1.25	0.289	2, 175	0.51	0.600
Date	6, 224	2.59	0.443	5, 175	7.74	<0.001*
Study Reach x Date Interaction	6, 224	0.99	0.433	5, 175	0.76	0.576

Fig. 1. Invasive European bird cherry (EBC) and native vegetation study reaches along Campbell and Chester creeks, Anchorage, Alaska.

Fig. 2. Mean terrestrial invertebrate biomass associated with the foliage of riparian tree branches in (a) 2009 and (b) 2010. Error bars represent standard errors.

Fig. 3. Mean biomass of terrestrial invertebrate subsidies collected by floating pan traps set underneath invasive European Bird cherry (EBC) and mixed native vegetation in Campbell and Chester creeks in 2010. Error bars represent standard errors.

Fig. 4. Seasonal patterns in terrestrial prey consumption by juvenile Coho Salmon expressed as (A) mean terrestrial biomass and (B) proportion of total biomass in EBC and native vegetation study reaches in 2009 and 2010. Only includes terrestrial taxa associated with riparian trees. Error bars represent standard errors.

Fig. 5. NMDS ordination of terrestrial invertebrate communities associated with the foliage of riparian trees, their subsidies to streams, and the diet of juvenile Coho Salmon in 2009 and 2010. Terrestrial invertebrate communities associated with native vegetation are open while communities associated with invasive European bird cherry (EBC) are bordered by black boxes. Vectors indicate the taxonomic groups that influenced community structure.

Appendix 1. Community composition of terrestrial invertebrates associated with the foliage of riparian tree branches along Campbell and Chester Creeks in 2009 and 2010. Mean dry mass (mg) standardized per gram of leaf mass $\pm$ 1 SE of terrestrial invertebrate taxa present ($n = 204$ in 2009; $n = 192$ in 2010).

Taxon	2009				2010			
	Alder	Birch	EBC	Spruce	Alder	Birch	EBC	Spruce
Acari	<0.01 (± 0.00)	0.01 (± 0.01)	<0.01 (± 0.00)	<0.01 (± 0.00)	<0.01 (± 0.00)	<0.01 (± 0.00)	<0.01 (± 0.00)	<0.01 (± 0.00)
Arachnida	0.06 (± 0.02)	0.20 (± 0.08)	0.05 (± 0.02)	0.07 (± 0.02)	0.26 (± 0.06)	0.26 (± 0.08)	0.14 (± 0.04)	0.10 (± 0.02)
Coleoptera	0.20 (± 0.13)	0.04 (± 0.02)	0.02 (± 0.02)	0.02 (± 0.02)	0.02 (± 0.01)	0.03 (± 0.01)	<0.01 (± 0.01)	<0.01 (± 0.01)
Collembola	<0.01 (± 0.00)	<0.01 (± 0.00)	<0.01 (± 0.00)	<0.01 (± 0.00)	0.01 (± 0.01)	0.01 (± 0.01)	0.01 (± 0.01)	<0.01 (± 0.01)
Diptera	0.01 (± 0.01)	0.01 (± 0.01)	<0.01 (± 0.01)	<0.01 (± 0.01)	0.08 (± 0.03)	0.08 (± 0.04)	0.13 (± 0.05)	0.02 (± 0.01)
Heteroptera	0.06 (± 0.04)	0.11 (± 0.08)	0	0.01 (± 0.01)	0.02 (± 0.01)	0.01 (± 0.01)	<0.01 (± 0.01)	0.01 (± 0.01)
Homoptera	0.69 (± 0.16)	0.32 (± 0.11)	0.11 (± 0.02)	0.01 (± 0.01)	0.47 (± 0.10)	0.46 (± 0.11)	0.09 (± 0.01)	<0.01 (± 0.00)
Hymenoptera	1.55 (± 0.49)	0.54 (± 0.19)	0.05 (± 0.03)	0.03 (± 0.02)	2.45 (± 0.53)	1.81 (± 0.66)	0.14 (± 0.04)	0.12 (± 0.04)
Lepidoptera	0.11 (± 0.03)	0.06 (± 0.02)	0.05 (± 0.01)	<0.01 (± 0.01)	0.19 (± 0.07)	0.19 (± 0.17)	0.06 (± 0.03)	<0.01 (± 0.00)
Neuroptera	0	0.01 (± 0.01)	0	0	<0.01 (± 0.01)	<0.01 (± 0.00)	0.01 (± 0.01)	<0.01 (± 0.00)
Psocoptera	0.01 (± 0.01)	0.01 (± 0.01)	0.02 (± 0.01)	0.01 (± 0.01)	0.06 (± 0.03)	0.04 (± 0.02)	0.01 (± 0.01)	0.04 (± 0.01)
Thysanoptera	0.01 (± 0.01)	0.01 (± 0.01)	0.01 (± 0.01)	<0.01 (± 0.01)	<0.01 (± 0.00)	<0.01 (± 0.00)	0.01 (± 0.01)	<0.01 (± 0.00)
Total	2.72 (± 0.54)	1.31 (± 0.33)	0.32 (± 0.06)	0.16 (± 0.03)	3.56 (± 0.59)	2.89 (± 0.77)	0.61 (± 0.10)	0.29 (± 0.05)

Appendix 2. Community composition of terrestrial invertebrate subsidies collected by floating pan traps set on Campbell and Chester creeks in 2010. Mean dry mass (mg) per m² per day $\pm$ 1 SE of terrestrial taxa present ($n = 68$).

Taxon	Campbell Creek		Chester Creek	
	EBC	Native Vegetation	EBC	Native Vegetation
Acari	<0.1 ($\pm$ 0.1)	<0.1 ($\pm$ 0.1)	0.1 ($\pm$ 0.1)	0
Arachnida	2.0 ($\pm$ 1.5)	1.7 ($\pm$ 1.1)	0.6 ($\pm$ 0.2)	0.1 ($\pm$ 0.1)
Archaeognatha	<0.1 ($\pm$ 0.1)	0	0.1 ($\pm$ 0.1)	0
Chilopoda	1.1 ($\pm$ 1.0)	0	0	0
Coleoptera	1.2 ($\pm$ 0.8)	2.9 ($\pm$ 1.9)	0	0
Collembola	0.1 ($\pm$ 0.1)	0.1 ($\pm$ 0.1)	0.2 ($\pm$ 0.1)	0.1 ($\pm$ 0.1)
Diptera	0.9 ($\pm$ 0.2)	2.3 ($\pm$ 1.1)	1.8 ($\pm$ 0.5)	9.9 ($\pm$ 4.8)
Heteroptera	0.3 ($\pm$ 0.1)	2.6 ($\pm$ 1.8)	0.5 ($\pm$ 0.1)	4.8 ($\pm$ 1.2)
Homoptera	1.1 ($\pm$ 0.4)	3.1 ($\pm$ 0.9)	1.5 ($\pm$ 0.7)	3.8 ($\pm$ 1.4)
Hymenoptera	3.3 ($\pm$ 1.3)	13.1 ($\pm$ 5.7)	6.2 ($\pm$ 2.3)	12.4 ($\pm$ 6.3)
Lepidoptera	0.4 ($\pm$ 0.1)	3.8 ($\pm$ 1.9)	0.6 ($\pm$ 0.1)	3.9 ($\pm$ 1.8)
Neuroptera	0.2 ($\pm$ 0.1)	0.3 ($\pm$ 0.2)	0	0
Psocoptera	0.7 ($\pm$ 0.2)	1.8 ($\pm$ 0.6)	0.3 ($\pm$ 0.1)	0.4 ($\pm$ 0.2)
Thysanoptera	0.1 ($\pm$ 0.1)	0.1 ($\pm$ 0.1)	0.1 ($\pm$ 0.1)	<0.1 ($\pm$ 0.1)
Total	11.2 ($\pm$ 3.5)	26.7 ($\pm$ 6.8)	12.0 ($\pm$ 3.9)	35.5 ($\pm$ 8.1)

Appendix 3. Community composition of terrestrial invertebrates consumed by juvenile Coho salmon in Campbell and Chester Creeks in 2009 and 2010. Mean dry mass (mg) per fish $\pm$ 1 SE of terrestrial taxa present ($n = 240$ in 2009, $n = 189$ in 2010).

Taxon	2009 EBC	Native Vegetation	2010 EBC	Native Vegetation
Acari	0.01 (± 0.01)	0.01 (± 0.01)	0.01 (± 0.01)	0.01 (± 0.01)
Arachnida	0.61 (± 0.24)	0.26 (± 0.09)	0.34 (± 0.10)	0.47 (± 0.15)
Coleoptera	0.40 (± 0.14)	0.37 (± 0.17)	0.56 (± 0.23)	0.28 (± 0.10)
Collembola	0.04 (± 0.01)	0.02 (± 0.01)	0.04 (± 0.01)	0.03 (± 0.01)
Diptera	0.32 (± 0.17)	0.05 (± 0.02)	0.62 (± 0.23)	0.39 (± 0.11)
Gastropoda*	0.68 (± 0.43)	0.28 (± 0.13)	4.37 (± 1.42)	4.21 (± 1.31)
Heteroptera	0.02 (± 0.01)	0	<0.01 (± 0.00)	0.01 (± 0.01)
Homoptera	0.23 (± 0.06)	0.20 (± 0.04)	0.36 (± 0.10)	0.64 (± 0.15)
Hymenoptera	1.16 (± 0.47)	0.69 (± 0.39)	0.49 (± 0.20)	0.62 (± 0.36)
Lepidoptera	0.06 (± 0.06)	0.01 (± 0.01)	0.07 (± 0.04)	0.26 (± 0.11)
Neuroptera	0	0	0.03 (± 0.01)	0.01 (± 0.01)
Psocoptera	0.09 (± 0.05)	0.09 (± 0.05)	0.02 (± 0.01)	0.05 (± 0.02)
Thysanoptera	<0.01 (± 0.00)	<0.01 (± 0.00)	0.01 (± 0.01)	0.02 (± 0.01)
Total Terrestrial – Only Riparian Trees	2.83 (± 0.67)	1.60 (± 0.38)	2.85 (± 0.71)	3.02 (± 0.82)
Total Aquatic	13.87 (± 4.19)	5.69 (± 0.79)	5.18 (± 0.59)	7.09 (± 0.74)
Total All Taxa	17.38 (± 4.35)	7.57 (± 0.90)	12.40 (± 1.64)	14.32 (± 1.87)
Percent Terrestrial – Only Riparian Trees	16.3%	21.1%	23.0%	21.1%
Percent Terrestrial – All taxa	20.2%	24.8%	58.0%	50.4%

* Gastropoda not associated with riparian trees, but accounted for a large portion of terrestrially-derived diet.