Exotic vs. Native: Global and urban investigations of leaf litter decay in streams

by

Kimberly Theresa May Kennedy
B.NRSc, Thompson Rivers University, 2009

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Supervisory Committee

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Abstract

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Exotic species alter the streamside plant community by changing the resources available to the stream food web, causing cascading changes throughout the entire aquatic ecosystem. To better understand the impacts of exotic litter species on stream communities, investigations were made at global and local levels. A meta-analysis was performed to understand which environmental and litter quality factors impact native and exotic litter decay rates on the global scale. It was found that exotic species are likely to decay faster than native species at larger mesh sizes, and in warm temperature environments because high quality exotic leaves have a lower C:N ratio than native leaves. An urban litter decay experiment in Victoria, B.C. streams contrasting *Alnus rubra*, *Salix sitchensis*, *Hedera* sp., *Rubus armeniacus* and plastic trash found that trash decays more slowly than leaf litter, but leaf species all decay at the same rate, and stream invertebrates colonize all litter types equally. Significant differences in litter decay rates and invertebrate community alpha and Shannon diversities were also observed across the four different streams. The more that is learned about the impacts of exotic leaf litter, the better we are able to respond to keep streams as healthy and as biodiverse as possible.

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If you are in the middle of your own study:

Start working on whatever makes you hesitate, because there is an ending to every beginning. When you make it to the end, you will realize the hesitation was a waste of time. - David Wong

Being a good writer is 3% talent, 97% not being distracted by the internet. - Unknown

Chapter 1 : Introduction

Streams are important freshwater ecosystems that are rich in biodiversity. Streams are home to a diverse range of organisms from bacteria and algae to invertebrates, fish, reptiles and amphibians, mammals and birds (Dudgeon et al. 2006, Meyer et al. 2007). Streams provide many environmental goods and services, including nutrient transport and cycling, flood control, and habitat (Paul and Meyer 2008, Baron et al. 2002). Humans also use streams for food (fishing), recreation, transportation, waste disposal, flood control (stormwater), industrial processing and hydroelectric power generation (Postel et al. 1996).

Aquatic detritivores

The aquatic biota that live in the stream are often dependent on allochthonous subsidies that come from the stream banks (Vannote et al. 1980, Allan and Castillo 2007). The stream food web is based on leaf litter inputs that provide both essential nutrition and shelter to several trophic levels of the aquatic community (Vannote et al. 1980, Davies and Boulton 2009, Tank et al. 2010). When leaf litter falls into the stream, it is quickly colonized by algal, fungal and bacterial microbes that begin to decay the leaf and condition it for consumption by other creatures (Webster and Benfield 1986, Gulis and Suberkropp 2003, Tank et al. 2010). Shredders are stream invertebrates like freshwater shrimp and stoneflies that feed on the conditioned leaf litter, tearing and chewing it into small pieces and consuming it (Cummins and Klug 1979, Wallace and Webster 1996). Shredders tend to be chiefly responsible for the physical disintegration of litter materials, and vary considerably by region, with insect shredders playing a key role in temperate stream ecosystems, whereas macrodecomposer shredders such as crabs, shrimp, tadpoles and fish are present in tropical systems, and resilient gastropod shredders are more common in degraded urban stream ecosystems (Wantzen and Wagner 2006, Moulton et al. 2009, Yule et al. 2015). Shredders, microbial detritivores and their by-products support all the other trophic guilds in the stream including scrapers, collectors, predators and omnivores which form the higher levels of the aquatic food web (Cummins and Klug 1979, Wallace and Webster 1996). It follows that shifts in shredder populations due to changes in leaf litter composition, quality, and decay rate can have a defining impact on the stream ecosystem (Wantzen et al. 2002, Boyero et al. 2012, Leite-Rossi et al. 2015).

Leaf litter quality

Leaf litter has species-specific attributes that impact its processing rate and palatability for stream invertebrates including leaf toughness, leaf density, and leaf carbon, nitrogen, and phosphorus content (Quinn et al. 2000a, 2000b, Graça and Cressa 2010). Tough or dense leaves are often avoided by invertebrates in favor of softer, thinner leaves and thus decay more slowly (Li et al. 2009, García-Palacios et al. 2015). Leaf chemistry, specifically the carbon to nitrogen ratio (C:N) or carbon to phosphorus ratio (C:P) of the leaf litter is also an important determinant of leaf litter decay (Ostrofsky 1997, García-Palacios et al. 2015). High C:N and high C:P leaves tend to be tougher and of low nutritional quality and thus avoided by invertebrates, while the opposite is true of low C:N or C:P leaves (Lecerf and Chauvet 2008, Marquis et al. 2012, Martínez et al. 2013, Bruder et al. 2014). Leaf chemistry can also affect microbial and fungal colonization and conditioning, which in turn plays role in leaf palatability and processing by invertebrates (Graça and Cressa 2010, Jabiol and Chauvet 2012, Graça et al. 2016).

Physical factors impacting litter decay

Physical factors including temperature and latitude can impact biological processes and influence leaf litter decomposition (Irons et al. 1994, Allan and Castillo 2007). Decay rates increase at higher temperatures because leaf litter leaches higher concentrations of nutrients more quickly, and microbial and fungal activity increases (Park and Cho 2003, Ferreira et al. 2014, Graça et al. 2016). Temperature increase is also associated with changes in invertebrate abundance, growth, emergence, and sex ratios, which impact invertebrate-mediated litter decay rates (Hogg and Williams 1996, Durance and Ormerod 2007, Friberg et al. 2009). Latitude has a significant positive impact on leaf litter decay rates even after temperature differences have been accounted for (Irons et al. 1994, Graça et al. 2015). Latitude affects litter decay rates through its impact on detritivore species diversity and trophic specialization (Pearson and Boyero 2009, Boyero et al. 2011, Jabiol et al. 2013). Latitude also governs the biogeochemical processes that affect leaf litter N:P and leaf palatability for aquatic invertebrates (Reich and Oleksyn 2004, Hladyz et al. 2009).

Chemical factors impacting litter decay

Three chemical properties of water that impact biological processes are pH, conductivity and dissolved oxygen (Allan and Castillo 2007). Low pH decreases litter decay rates by decreasing microbial colonization and inhibiting microbial metabolism and diversity (Mulholland et al. 1987 Jenkins and Suberkropp 1995, Clivot et al. 2013). Low pH also tends to decrease or exclude pH-sensitive invertebrates and detritivores (Dangles and Chauvet 2003, Dangles et al. 2004, Herbst et al. 2008). Higher conductivity due to alkalinity has been linked with optimal enzyme activity in hyphomycetes, and increased zoobenthos biomass (especially shredders and scrapers), which all lead to higher litter decay rates (Kok and Van Der Velde 1994, Imbert and Stanford 1996, Royer and Minshall 2001). Low dissolved oxygen reduces litter decay rates by reducing fungal biomass and depressing microbial respiration (Canhoto et al. 2013). Low oxygen also reduces invertebrate activity and emergence, and leads to insect exodus (i.e. drift) or mortality, especially among more sensitive taxa such as mayflies and beetles (Kolar and Rahel 1993, Connolly et al. 2004). Because leaf litter decay is influenced by different factors, it is difficult to achieve consensus on general trends. Yet over time a large body of knowledge about leaf litter decay rates has accrued, so a meta-analysis approach would be useful for achieving consensus on the drivers of leaf litter decay and their potential impacts on the wider ecosystem (Castro-Díez et al. 2014, Ferreira et al. 2016, McCary et al. 2016). However, few of these studies have been done for litter decay in the aquatic environment.

Urban impacts on stream ecosystems

Urbanization of a stream ecosystem can have additional effects on the physical and chemical properties of the stream (Allan and Castillo 2007). As flowing water can be a highly destructive natural force, typically humans will re-engineer watercourses to prevent stormwater and other high flow events, from changing the course of streams, causing erosion, or damaging human infrastructure (Walsh et al. 2005b, Paul and Meyer 2008, Kaushal and Belt 2012). As human development of the land progresses, impervious surfaces tend to increase due to the construction of roads and paved areas. Buildings with impervious roofs and any other impacts that prevent natural infiltration of rainwater and runoff into the land completely alter urban hydrology (Walsh et al. 2005b, Paul and Meyer 2008). In systems with natural infiltration through soil or vegetation, when rain falls, slow percolation into natural surfaces allows stormwater to enter streams through gradual sub-surface flow from a wide geographic area, resulting in a gradual increase and then gradual decrease of stream depth and flow volume (Allan and Castillo 2007). Alternatively, in urban areas rainfall is channelled across impervious surfaces and quickly aggregated into substantial surface flows that funnel into stormwater systems (Walsh et al. 2005a, 2005b, Allan and Castillo 2007, Paul and Meyer 2008). These stormwater systems are often directly linked to urban streams, causing sudden high flows wherein stream depth and flow volume increase and decrease rapidly in sudden contrast to the base flow regime (Walsh et al. 2005a, 2005b, Allan and Castillo 2007, Paul and Meyer 2008). The net result of the increase in impervious surfaces in urban areas is a drastic change to the stream hydrograph (the depth and flow of the stream over time) (Walsh et al. 2005b, Paul and Meyer 2008, Kaushal and Belt 2012). Flashy stream flow and larger total flow volume can impact stream ecosystem processes like litter decay through physical fragmentation by increasing physical abrasion forces due to increased water flow (Ferreira et al. 2006, MacKenzie et al. 2013).

Urban streams are also exposed to anthropogenic contaminants such as excess nutrients, heavy metals, hydrocarbons, salt and litter, which reduce water quality and impact stream ecosystem processes (Walsh et al. 2005b, Paul and Meyer 2008, Kaushal and Belt 2012). Eutrophication can cause stream ecosystem processing to increase due to increased microbial metabolism and biomass, as well as increased invertebrate biomass, and increased leaf litter decay rates (Pascoal et al. 2003, Woodcock and Huryn 2005, Paul et al. 2006, Young et al. 2008).

However, very high levels of nutrient–rich pollution (such as sewage) cause a reduction in stream metabolism. Initial increases in biological oxygen demand from microbial detritivore consumption of waterborne nutrients leads to dissolved oxygen depletion. These anoxic conditions then restrict further microbial metabolism and constrain invertebrate populations, ultimately reducing litter decay rates (Kolar and Rahel 1993, Daniel et al. 2002, Pascoal and Cássio 2004, Dodds 2006). Understanding leaf litter decay rates is an important part of understanding basic ecosystem functions in urban streams. However, studies in urban streams disagree on which factors are the most important in driving stream litter decay, so further research is necessary (see chapter 3 for more discussion).

Urbanization and trash in streams

Humans also have a long history of using rivers and streams as disposal services, from Ancient Rome's Cloaca Maxima draining into the Tiber River to London's use of the Thames as a key part of its sewer system (Burian and Edwards 2002, Lofrano and Brown 2010). Trash in streams is still a problem to this day, particularly plastic trash, which is resistant to biodegradation, travels easily and quickly throughout aquatic environments worldwide, and can impact aquatic biota at all levels of the food chain by entanglement, ingestion, smothering, and as a vector for additional persistent organic chemicals (Barnes et al. 2009, Gregory 2009, Hoellein et al. 2014, Wagner et al. 2014). Though it may provide additional habitat for some enterprising species (Adams 2014), trash in streams is ultimately carried towards the ocean where it is degraded into toxic microplastic particles. These plastic particles can collect and carry persistent organic pollutants along with them up the aquatic food web leading to the impairment, illness, and possibly the death of their consumers (Wright et al. 2013, Eerkes-Medrano et al. 2015, Galloway 2015).

Exotic species in urban riparian zones

Altered flows, stream chemistry, and trash are not the only impact humans have on urban streams however, as humans facilitate the invasion by exotic species as well (McKinney and Lockwood 1999, Allan and Castillo 2007). Humans translocate desired species whenever they settle a new environment (Hulme 2009). As a result, urban areas are hot-spots of exotic invasion due to the intentional and accidental import of exotic species from other locations and the invasion-enabling conditions of human disturbance (Knapp et al. 2008, Pickett et al. 2008, Kowarik 2011). This is particularly true of exotic plants that have agricultural and horticultural value (Reichard and White 2001). Exotic plant invasion of riparian areas can alter the stream in a number of ways: it can cause the riparian canopy cover to close or open, leading to a more heterotrophic (closed canopy) or autotrophic (open canopy) mode of production as the base of the stream ecosystem (Kominoski et al. 2013, McInerney et al. 2016). A shift in riparian plant cover can make the stream bank more or less prone to erosion, thus indirectly changing the geomorphology of the stream (Gordon 1998, Cremer 2003, Kominoski et al. 2013).

Riparian plant community changes can also change what leaf litter subsidies are available to the stream, and how long those subsidies persist in the stream before decaying (Quinn et al. 2000a, Davies and Boulton 2009, Kominoski et al. 2013). Leaf litter provides both food and shelter to the in–stream biota, so changes in litter decay rates can have severe consequences that cascade up the riparian food chain (Wallace et al. 1997, Reinhart and VandeVoort 2006, Davies and Boulton 2009, Jabiol et al. 2014). If essential habitat structure is lost, then invertebrates vulnerable to predation have nowhere to hide (Jabiol et al. 2014). In addition, leaf litter provides essential nutrition to several levels of the aquatic food web and if the nutritional properties of the leaf litter shift, then their consumers could be adversely impacted (Davies and Boulton 2009, Hladyz et al. 2009, Hladyz et al. 2011).

Two Pacific Coast riparian invaders

Changes to riparian plant communities due to exotic species invasion often happens unintentionally when exotic plants escape human oversight (Reichard and White 2001, Clarke et al. 2006). Two particularly prominent invaders that are found in many areas on the Pacific coast of North America from California to Alaska (hereafter Pacific Coast) that have the potential to impact leaf litter subsidies in urban streams are English ivy (*Hedera helix, Hedera hibernica,* and their hybrid, hereafter *Hedera* sp.) and Himalayan blackberry (*Rubus armeniacus*) (Ingham and Borman 2010, Green et al. 2013, Gaire et al. 2015). English ivy has long been appreciated on the Pacific Coast as a horticultural plant (Bailey 1910, Green et al. 2013) and it has been observed blooming in Victoria, BC gardens since at least 1891 (Fraser 1891). Beginning in the 1930s ivy was noted to have started to naturalize in the areas surrounding human settlements on the Pacific Coast and it has spread rapidly ever since (Green et al. 2013). English ivy tends to be a shade-specialist and an efficient water user that shades-out and out-competes the surrounding plants with mild allelopathy (Biggerstaff and Beck, 2007, Copp 2014). It engineers its own ecosystem with its smothering vines and tree-strangling lianas, creating beautifully lush but bio-uniform ivy deserts (Okerman 2000).

Likewise the Pacific Coast is also invaded by another smothering vine with a similar history and ecological strategy, the English Ivy’s sun loving counter-part the Himalayan blackberry. Himalayan blackberry was first introduced in 1885 to gardens along the Pacific Coast by the renowned botanist and agricultural entrepreneur Luther Burbank and sold as a hardy and highly-productive garden berry (Hummer 1996, Ceska 1999). Himalayan blackberry can out-compete almost any plant due to superior water efficiency and storage, photosynthetic capability and leaf resource allocation (McDowell 2002, Caplan and Yeakley 2006, Caplan and Yeakley 2013, Gaire et al. 2015). Himalayan blackberry produces large, abundant and tasty fruits that are full of seeds and are widely dispersed by anything that eats berries (e.g. humans, bears, deer, slugs, birds, rats) (Gervais et al. 1998, Gaire et al. 2015). Himalayan blackberry is so ubiquitous on the Pacific Coast that many people do not realize that it is an exotic invasive species, and its naturalization is becoming entrenched more firmly as it readily hybridizes with local Pacific Coast blackberry species (Hummer 1996, Gaire et al. 2015). Blackberry is so successful that in certain areas, it too has created its own exotic ecosystem of vast expanses of land covered in impenetrable blackberry thickets (Gaire et al. 2015). On the Pacific Coast ivy and blackberry are the most ubiquitous invasive vines in the urban riparian zone (Ringold et al. 2008, Green et al. 2013, Gaire et al. 2015), but almost nothing is known about their impact on stream systems, especially leaf litter decomposition.

Restoration willows

Changes to riparian plant communities are not always due to invasion by chance. Sometimes exotic species are introduced to riparian environments intentionally. Willows (*Salix* spp.) have long been appreciated by people for their beauty and their usefulness. Since their recommendation by Leonardo Da Vinci, in the 1500s, willows have been a mainstay of stream restoration and have been used to revegetate denuded or exotic invaded stream banks, to stabilize eroding stream banks, and to improve riparian plant cover (Evette et al. 2009). Willows are an ideal plant for riparian plant cover because they grow quickly, have thick root mats that dissipate the erosive kinetic energy of stream flow, flourish in wet and flood-prone environments, and have deep roots that are very good at anchoring the plant and holding together the surrounding soil (Kuzovkina and Quigley 2005, Pezeshki et al. 2007). Willows can also serve as nurse species to inhibit understory competition and facilitate the establishment of taller and longer-lived tree species (Dulohery et al. 2000, McLeod et al. 2001). Some species of willows are invasive and can have a negative effect on stream ecosystems (McInerney et al. 2016). In the past any commercially available willow species was used for stream bank stabilization, regardless of its origin, but more recently, removal of invasive willows and replacement with native willows has been favored (Kuzovkina and Quigley 2005, The Bowker Creek Initiative 2012). Given the potential tradeoffs that could accompany their benefits, further investigation on the impact of native willow species on stream ecosystems is necessary for informed environmental decision-making.

Understanding the impacts of riparian vegetation change in the global and urban context

Plant community shifts in urban systems from native to exotic species, and potentially from exotic species to restoration species, can impact the leaf litter subsidies available to urban streams and the wider food web that relies upon them. The consequences of community shifts due to exotic species invasion, particularly in urban ecosystems, are not well understood and require further investigation (Rosenzweig 2001, Wenger et al. 2009, Strayer 2012). We are beginning to understand the factors that impact aquatic litter decay from a global perspective (Boyero et al. 2012, Boyero et al. 2016) but we do not yet have a global consensus on whether native and exotic litter decays differently in streams (Wenger et al. 2009). In addition, climate change has the potential to increase and accelerate invasion by exotic species and alter riparian plant communities, so now more than ever, it is important to understand the potential impacts of exotic species on sensitive aquatic ecosystems (Meyer et al. 1999, Hellmann et al. 2008). On a more local scale, both restoration with willows and invasion by exotic English ivy and Himalayan blackberry are quite common throughout the Pacific Coast, particularly in urban ecosystems (Kauffman et al. 1997, Green et al. 2013, Gaire et al. 2015), and as of yet we do not know what impact they may have on urban streams, or even what their relative decay rates might be in relation to native litter species. In addition, though it is a very common subsidy in urban streams, very little is known about the decay rate of plastic trash relative to natural litter materials, and the impact it has on freshwater stream environments (Hoellein et al. 2014, Wagner et al. 2014).

Research objectives

To investigate the impact of exotic species on the stream ecosystem at both the global and local level and the potential impact of exotic species, restoration willow, and trash on urban streams, the objectives of this thesis are as follows:

In Chapter 2, I conduct a meta-analysis to identify whether there are differences between exotic and native leaf litter decay rates on a global scale. Using linear modeling I examine which of the extrinsic decay factors of latitude, temperature, pH, conductivity, and mesh size (via the exclusion of invertebrates) contribute to differences between exotic and native leaf litter decay rates on a global scale. Additionally, using multivariate statistics I test if the intrinsic factors of leaf litter quality (C:N, C:P, toughness and leaf mass area (LMA)) are related to differences between native and exotic leaf litter decay rates.

In Chapter 3, I conduct an urban leaf litter decay experiment to: 1) determine whether exotic Himalayan blackberry and English ivy leaves decay more slowly than native leaves in urban streams; 2) examine whether exotic blackberry and ivy leaves attract fewer and less diverse stream invertebrates than native leaves in urban streams; 3) investigate whether plastic trash decays more slowly than leaves in urban streams; and 4) verify whether plastic trash attracts fewer and less diverse stream invertebrates than leaves in urban streams.

Chapter 2 : Do exotic leaves decay faster than native leaves in streams? A global meta-analysis

Abstract

Streams are reliant on streamside plants for allochthonous inputs that form the base of the stream food web. The impact of exotic leaves on stream ecosystems has been investigated regionally, but not assessed globally. In this study I conducted a global meta-analysis contrasting native and exotic aquatic litter decay. A linear mixed effects model was used to identify how the environmental factors of latitude, temperature, pH, conductivity, and the exclusion of invertebrates (via mesh size) cause relative differences in exotic and native decay rates. Subsequently, the intrinsic factors of leaf litter quality (C:N, C:P, toughness and leaf mass area (LMA)) were assessed using analysis of variance (ANOVA), Kruskal-Wallis, and Tukey or Nemenyi post hoc tests to assess their contribution to differences in native and exotic litter decay rates.

The averaged model that best described the relative response ratio of exotic to native decay rates included temperature, mesh size, conductivity, pH, as fixed effects and study site as a random factor. The model intercept was not significant indicating that exotic leaves do not decay faster than native leaves on a global scale. However, temperature and mesh size were significant covariates indicating that only at higher temperatures and larger mesh sizes exotic leaves tend to decay faster than native leaves, yet those differences disappeared at lower temperatures and finer mesh sizes. Post hoc analysis suggested that differences between native and exotic species in their C:N ratios might explain differences in decomposition rates observed at high temperature. However, leaf quality differences did not explain the broader patterns of exotic and native litter decay at coarse mesh sizes. I conclude that exotic leaf litter is likely to have the most impact in high-temperature stream ecosystems and that the nature of the impact is potentially related to the C:N ratio differences in native and exotic leaves. I recommend that future leaf litter decay studies include stream discharge measurements and leaf litter quality information so that both intrinsic and extrinsic factors that impact litter decay can be fully accounted for when assessing the factors that drive differences in leaf litter decay rates.

Introduction

Exotic species affect the environment (Vitousek 1990, Ehrenfeld 2010, Simberloff 2011). The severity of those impacts and the necessity of human intervention, however, is hotly contested (MacDougall and Turkington 2005, Davis et al. 2011, Simberloff et al. 2013). Central to this debate is our ability to detect and measure the impacts of exotic species (Simberloff 2011, Davidson and Hewitt 2014, Jeschke et al. 2014). Our ability to detect impacts is lacking due to past focus on a few easily measurable invasion metrics (e.g. nutritional and chemical impacts of a few select species like cheatgrass or Japanese knotweed) (Hulme et al. 2013). As a consequence there has been a call for testing hypotheses on specific questions with well-defined datasets to broaden our understanding of the impacts that exotic species can have on a grand scale (Kueffer et al. 2013, Strayer 2012).

Stream ecosystems have a high exotic species invasion rate because they tend to be nutrient rich, disturbance rich environments that are highly susceptible to anthropogenic intervention (Hood and Naiman 2000, Schnitzler et al. 2007, Chytrý et al. 2008). In turn, stream ecosystems can act as invasion corridors to upland and marsh habitats (Stohlgren et al. 1998, Zedler and Kercher 2004). When riparian areas are invaded by exotic plants there are direct impacts on the endemic plant community including changes in community structure, environmental alteration and allelopathy (Gould and Gorchov 2000, Levine et al. 2003, Cappuccino and Arnason 2006). Exotic plants also change terrestrial nutrient and moisture regimes (Kourtev et al. 2003, Cushman and Gaffney 2010). In addition, the soil biota and both the terrestrial and aerial arthropod communities experience negative impacts from exotic plant invasions (Herrera and Dudley 2003, Burghardt and Tallamy 2013, Lekberg et al. 2013).

As stream ecosystems are often reliant on streamside plants for litter inputs that form the base of the stream food web (Vannote et al. 1980,Tank et al. 2010), riparian invasion by exotic plants can have impacts on the stream ecosystem (Kominoski et al. 2013). Leaf litter is an important source of nutrients for microbial detritivores and hosts a complex community of aquatic invertebrates that both live in and feed on the leaf litter that accumulates in the stream (Webster and Benfield 1986, Abelho 2001, Findlay 2010). If the plant species that contribute the leaf litter change, then the properties of the new leaves may alter leaf litter decay rates, severely impacting the aquatic community dependant on them (Clapcott and Bunn 2003, Davies and Boulton 2009, Boyero et al. 2012).

One area of exotic species impact that has been investigated regionally, but not assessed globally is the impact of exotic leaves on stream ecosystems (Sampaio et al. 2001, Albariño and Balseiro 2002, Bärlocher and Graça 2002). The impacts of exotic leaves on stream ecosystems can be studied by looking at differences in a widely reported metric: leaf litter decay rates and how they differ between native and exotic species. Many individual studies on the relative decay rates of native and exotic leaf litter have been done at discrete locations across the globe, and their collective assessment of the impacts of exotic and native leaf litter decay has yielded mixed results (Table 2.1). For example, many studies have concluded that exotic species decay faster than native species, that the opposite was true, or that there was no difference between the speed at which native and exotic species decay (Table 2.1). Some studies have suggested that decay rates are governed by leaf litter quality rather than origin (Table 2.1). Still other studies have determined that leaf litter origin does play a role in relative decay rates, but only in specific conditions that vary by location or with water quality attributes (Table 2.1).

Differences among studies could be due to no consistent differences among exotic and native leaf litter decay rates. Alternatively, differences in leaf decay study apparatus such as mesh size, or local abiotic factors such as temperature, could mask a global native vs. exotic trend in leaf decay. If leaf litter decay rate data are aggregated from enough studies and the effects of decay-moderating factors including location, mesh size, and water quality attributes can be accounted for, then a central decay tendency by leaf origin can be unmasked and the impacts of exotic litter on stream ecosystems can be quantified.

Invasive exotic species tend to have more labile litter traits (*e.g.* softer leaves with higher nitrogen and phosphorous, lower carbon, and higher specific leaf area) than native species owing to a carbon capture strategy optimized for rapid growth (Leishman et al. 2007, Van Kleunen et al. 2010). Exotic species also tend to decay faster in terrestrial environments (Ashton et al. 2005). Thus, I expect that exotic litter species in streams will have more labile litter traits that will make them decay faster in aquatic environments. I also expect that environmental factors known to contribute to faster decay (i.e. higher temperature (Richardson 1992b, Lecerf et al. 2007b), lower pH (Webster and Benfield 1986, Young et al. 2008), increased conductivity (Young et al. 2008), increased latitude (Irons et al. 1994, Graça et al. 2015) and increased mesh size (Taylor and Chauvet 2013, Ágoston-Szabó et al. 2015)) will interact synergistically with litter quality resulting in an overall trend of exotic litter decaying faster than native litter on a global scale.

In this study I conduct a meta-analysis of published aquatic leaf litter decay rates to identify the impacts of exotic species on relative decay rates. A linear mixed effects model is used to determine whether there are systematic differences in the relative decay rates of native and exotic species, and identify potential drivers of those differences. The model assesses how extrinsic environmental factors such as latitude, temperature, pH, conductivity, and the exclusion of invertebrates (via mesh size) affects exotic decay rates differently than native decay rates. Subsequently, the intrinsic factors of leaf litter quality (C:N, C:P, toughness and leaf mass area (LMA)) of native and exotic species are assessed using analysis of variance (ANOVA), Kruskal-Wallis, and post hoc tests will be used to identify which differences in litter quality are associated with the modeled differences between native and exotic leaf litter decay rates, completing a comprehensive analysis of the factors that affect differences in native and exotic litter decay rates on a global scale.

Methods

Collecting the databases:

I searched for primary leaf decay studies that featured both native (endemic) and exotic (non-endemic) leaf litter in a natural aquatic environment. The literature review was conducted between February 2014 and January 2016 and included published journal articles, theses and reports accessed via the online journal article databases JSTOR, BioOne, Google Scholar, and Web of Science. Article searches were conducted using systematic combinations of the search terms “exotic” and/or “allochthonous” and/or (“leaf” or “leaf pack” or “litter”) and/or “decomp*” and/or “stream”. Also included in this meta-analysis are data from my own unpublished leaf decay study (Chapter 3).

To be included in the analyses, each primary study had to satisfy the following criteria: 1) the study had to compare at least one endemic (native) and one non-endemic (exotic) leaf species; 2) the study had be a leaf pack experiment conducted in a natural aquatic environment, or a mesocosm continuously supplied by unfiltered water and invertebrates flowing directly from an adjacent natural aquatic ecosystem; 3) the study had to report decay rates (k day^{-1}), percent mass loss, or percent ash free dry mass for the leaf species; and, 4) the leaf pack study also had to report measurements for leaf pack mesh size, mean temperature, conductivity and pH of the study stream. A total of 44 studies that satisfied the above inclusion criteria were included in the final database (see Figure 2.1, Figure 2.2, and Table 2.2).

In cases where the decay rate was not reported by the investigators, the decay rate was calculated from the final percent mass loss or final percent ash free dry mass reported (Ferreira et al. 2015). Data Thief graph analysis software (Tummers et al. 2010) was used to extract the decay rate, percent mass loss or percent ash free dry mass for a study when the information was only provided in the form of a figure (after Waring, 2012). Decay rates in k day^{-1} for the Boyero et al. (2015) study were kindly supplied by Dr. Boyero. In cases where the leaf decay experiment featured manipulation of the decay environment, by chemical or hydrological means, only the decay rates for the control group were included. In cases where the leaf decay experiment was conducted across multiple study sites or times, all natural or control group decay rates were included.

Calculation of response ratios

The effect size of the difference between native and exotic leaf decay rates was assessed using the ln-transformed response ratio method after Darling and Côté (2008), a robust approach for answering ecological questions (Hedges et al. 1999, Elser et al. 2007). For each treatment (defined by a unique combination of study date, sub-site, and mesh-size reported within each study), the decay rate of the exotic species was divided by the decay rate of the native species, and the natural log of this response ratio was taken to ensure the data followed an approximation of the normal distribution and to ensure that the impact of both the numerator and the denominator decay rates were weighted equally within the response ratio.

In cases where decay rates for several native and exotic species were reported, separate response ratios were calculated for each possible native-exotic combination as a unique comparison (after Ferreira et al. 2015). In cases where ten or more native-exotic response ratios were calculated for a single treatment (Quinn et al. 2000a, López et al. 2001, Bottollier-Curtet et al. 2011, Blanco and Gutiérrez-Isaza 2014, and Raposeiro et al. 2014), only the highest, lowest, and mean response ratio for the treatment were included to prevent disproportionate weighting of individual sub-sites. The potential non-independence resulting from including multiple response ratios per study was addressed by including study as a potential random effect during the linear model selection process. The variance for each response ratio was calculated from the reported standard deviation and sample size for each leaf pack decay rate used in the ratio according to Hedges et al. (1999). If the standard deviation for the decay rate was not reported directly, it was calculated from the reported standard error, or confidence interval (Koricheva et al. 2013, Ferreira et al. 2015). For 179 of the 495 leaf decay rates, the study failed to report standard deviation, standard error, or confidence intervals, so standard error was approximated from the p value for the decay rate reported by the study (Higgins and Green 2011). The aggregated dataset for the linear model was composed of the ln-response ratio of the exotic and native decay rates, the study site and sub-site, latitude, pH, conductivity, and mean temperature of the treatment stream, and leaf pack mesh size. This dataset consisted of 273 response ratios from 118 sub-sites examined by 44 studies.

Publication bias

To investigate potential issues of publication bias affecting the outcome of the overall effect size modled, the effect sizes were examined using both a funnel plot of effect size vs. standard error and by comparison with failsafe numbers (Koricheva et al. 2013) as calculated by the metafor package in R (Viechtbauer 2015). Both Rosenberg and Rosenthal failsafe numbers were calculated to determine how many additional studies with non-significant results would be necessary to negate any overall effect found to be significant in this dataset (Rosenberg 2005).

Analysis

Model construction

The dataset was analyzed using R statistical software (R Core Team 2016). First, each variable in the dataset was evaluated visually for normality and homogeneity of variance using box plots, histograms correlation plots and Q-Q plots. The conductivity data were found to be skewed and were ln transformed for further analysis in a normalized condition. The data were also examined for correlation between the covariates. Absolute latitude and temperature exhibited a slight negative correlation, and pH and conductivity exhibited a slight positive correlation on diagnostic correlation plots (Figure 2.3). Potential exclusion from the model due to collinearity was determined by analysing the variance inflation factor (VIF) as recommended by Zuur et al.

(2010), and dismissed as the covariates did not have VIFs greater than 3. VIFs were calculated using the ‘car’ package in R (Fox et al. 2016).

Linear modeling

Overall trends in the leaf decay response ratio were evaluated using a mixed linear model approach as outlined by Zuur et al. (2009). First, a “beyond optimal” linear model was fit using latitude, pH, conductivity and temperature as covariates, and mesh size as a categorical fixed factor, and all permutations of paired covariate interactions were included (Zuur et al. 2009). Then, the paired covariate interactions were sequentially removed by backwards step-wise selection if any interaction had a VIF greater than 3 (Zuur et al. 2009, Zuur et al. 2010). The reduced “optimal” model was evaluated for significant collinearity, which was ruled out by low VIF values (Table 2.3).

Then, the “optimal” model was re-formed as a generalized least squares (GLS) model (Pinheiro et al. 2016), using restricted maximum likelihood (REML). Refitting the model with REML was necessary to enable analysis of variance (ANOVA) verification of improvement in the Akaike information criterion (AIC) in competing models during the random effects fitting process. The residuals of the reduced “optimal” model were checked for signs of heteroscedasticity and nonlinearity.

The random effects of study site and sub-site were checked for fit to the “optimal” model using ANOVA once again to confirm that the addition of random effects improved the AIC with the ‘AICcmodavg’ package (Mazerolle 2016). The random effect of site was retained as it significantly improved the fit of the model, yielding the “optimal random effects” global model (Table 2.4).

The residuals of the “optimal random effects” global model were checked for signs of heteroscedasticity and nonlinearity. To identify the top model candidates, the optimal fixed effects structure was derived from the “optimal random effects” model (re-fit again with GLS as necessary) using the dredge function of the ‘MuMIn’ package (Bartoń 2016). As the highest-ranked top model identified by the dredge function did not have an Akaike weigh greater than 0.9 (corresponding to <90% certainty of it being the best model), a selection criterion of ΔAICc < 2, and was used to determine which of several top models should be averaged (Symonds and Moussalli 2010, Grueber et al. 2011). The top model candidates selected for averaging had a combined Akaike weight of >0.95 corresponding to >95% certainty of encompassing the best model (Symonds and Moussalli 2010). The selected top model candidates were averaged to produce the final weights for the coefficients of the linear model (Symonds and Moussalli 2010, Grueber et al. 2011). The model averaging approach also permitted the retention of more biologically relevant covariates than would have been included in a non-averaged model, allowing for a more comprehensive approximation of the stream environment. Model averaged coefficients with confidence intervals that excluded zero were identified as significant (Burnham and Anderson 2002). As the model predictors were on different scales, interpreting their relative strength visually was challenging, so I standardized the input variable to a mean = 0 and a SD = 0.5, and the resultant coefficients were plotted on a common scale with 95% confidence intervals for visual interpretation (Grueber et al. 2011). To infer the goodness-of-fit of the averaged model, the adjusted R^2 was calculated for the global model as per Symonds and Moussalli (2011).

The study site map was drawn using the 'PBSmapping' package (Schnute et al. 2015), and the modeling results were graphed using the 'ggplot2' package (Wickham et al. 2016) and the 'visreg' package (Breheny and Burchett 2016).

Post hoc leaf quality testing

I also tested whether differences in decay rates observed in the meta-analysis were associated with differences in leaf litter quality. Due to the limited amount of published litter quality data available for the 122 leaf species studied, leaf quality data could not be included as covariates in the mixed effects model. As a result the litter quality data that were available for a subset of the species from the mixed model were analysed separately in the context of a post hoc test to better understand how the intrinsic factors of leaf litter quality contributed to the results of the mixed effects model.

Leaf litter quality metrics, specifically the carbon to nitrogen ratio (C:N) carbon to phosphorus ratio (C:P), leaf toughness as measured by penetrometry, and leaf mass area (LMA), were queried separately for each species using the species name and the search terms "C:N" and/or "C/N" or "C:P" and/or "C/P" and/or "%" and/or "carbon" and/or "nitrogen" and/or "phosphorous" for leaf element ratios, "lma" and /or "sla" and/or "lsm" and/or "leaf" and/or "specific" and/or "mass" and/or "area" for leaf mass/area measurements, and "toughness" and/or "hardness" and/or "penetrometer", for leaf toughness measurements. C:N ratio data were available for 96/122 species, C:P data were available for 92/122 species, LMA data were available for 94/122 species and leaf toughness data were available for 73/122 species.

Leaf elemental ratios were transcribed directly or calculated as necessary from elemental amounts or proportions listed for the species in one or more studies. Leaf mass area was transcribed directly or converted to common units (mg/cm^2) as necessary. Leaf toughness as measured by penetrometry was transcribed directly or calculated and/or converted to common units (g/mm^2) as necessary (see Table 2.5). In cases where multiple values were reported for a leaf quality metric, the values of the control group were selected, or an average of the reported values was used if no control group was specified.

The litter quality dataset was composed of the natural log (ln) of litter decay rate, ln C:N ratio, ln C:P ratio, ln LMA and ln leaf toughness for as many of the litter species as could be found in the literature. The litter quality dataset was built to reflect the species frequencies present in the larger linear modeling dataset and as such, a replicate of the species litter qualities was present for each separate decay rate available for that species.

To investigate whether leaf quality was associated with decay rate differences indicated by the significant covariates in the model, the database of individual leaf litter decay rates and other leaf quality metrics (C:N, C:P, toughness, and LMA) for each species was evenly divided into four groups for comparison based on the results of the model.

All metrics were then ln transformed to normalize their distributions, and the dataset was evaluated for normality and homogeneity of variance. Comparisons between groups were tested using ANOVA and a Tukey post hoc test or a Kruskal-Wallis test and a Nemenyi post hoc test from the R package 'PMCMR' (Pohlert 2016) as appropriate. The post hoc results were graphed using the 'ggplot2' package (Wickham et al. 2016).

ANOVA or a Kruskal-Wallis test and post-hoc test approach was used to investigate significant correlations between groups. My data did not meet the assumption of ANCOVA because some of the covariates and their residuals were non-normal, and because the covariates did not show homogeneity of regression slopes at all factor levels.

Results

Linear modeling results

The model selection procedure identified three model candidates (Table 2.6), which were then averaged to produce the final model.

The model that best describes the relative response ratio (lnRR) of exotic to native decay rates is: lnRR~ (0.026 * mesh size) + (0.051* temperature) + (-0.016* pH)+ (-0.005* conductivity) - (0.613) ~1 | study

The intercept for the averaged model was not significant (z=1.469, P=0.142), which indicates there was no unified tendency of exotic leaves to decay faster than native leaves on a global scale. However, temperature (z=4.293, **P < 0.001**) and mesh size (z=2.237, **P=0.025**) were significant covariates identified by the model as key drivers in the difference between native and exotic decay rates (Table 2.7, Table 2.8, Figure 2.4, Figure 2.5, and Figure 2.6).

The model indicated that at higher temperatures exotic leaves tended to decay faster than native leaves, yet those differences disappeared as water temperatures decreased. In coarse mesh sizes (≥3 mm), exotic species decayed significantly faster relative to native species, but this difference disappeared in fine mesh sizes (<3 mm) (Figure 2.5).

Although the averaged model retained pH (z=0.333, P=0.739) and conductivity (z=0.197, P=0.844), both were non-significant, fixed covariates of low variable importance whose presence marginally improved parsimony in the model. Latitude was completely omitted from the averaged model as a non-significant covariate, likely because it appeared somewhat correlated with temperature (Figure 2.3). Finally, study was found to be a significant random effect, the retention of which both improved the model and addressed independence issues associated with using multiple data points from each study. The global model had an adjusted R^2 of 0.4195 which indicates that approximately 42% of the variation in relative native-exotic response ratios is explained by mesh size and the environmental covariates in my model (Figure 2.7). Due to the considerable amount of variation and noise inherent in ecological data an adjusted R^2 of approximately 42% represents a ‘large’ ecological effect (Møller and Jennions 2002, Symonds and Moussalli 2011).

Data validation results

Publication bias was not present in this study. Visual inspection of the funnel plot did not show any asymmetry or gaps in the data points indicative of publication bias (Figure 2.11). The study also was well below the failsafe and Rosenberg thresholds. The threshold failsafe number calculated for my effect sizes was 5n+10 or 5*(273) +10 = 1375, the Rosenthal value calculated was 4,564,225,492 and the Rosenberg value calculated was 857,725,641,821. Both Rosenthal and Rosenberg numbers were well beyond the failsafe minimum of 1375, which ruled out any likelihood of publication bias.

Post hoc analysis of leaf quality variation by stream temperature

To conduct post hoc analysis, the leaf quality database was split according to the following covariate groups: it was bisected evenly into high and low temperature groups with water temperatures of 1.13-14.6°C in the low temperature group (n=237), and water temperatures of 14.7-30.5°C in the high temperature group (n=238). The studies were assigned to the high and low temperature groups to allow for an approximately even number of studies in each group and these temperatures were chosen for convenience and are not associated with any specific known biological threshold. The leaf quality database was also split by invertebrate exclusionary function into coarse and fine mesh categories with mesh sizes <3 mm in the fine mesh group which excluded macroinvertebrate decomposers (n=132), and mesh sizes ≥3 mm in the coarse mesh group which permitted macroinvertebrate decomposers(n=343) (Table 2.9).

Post hoc analysis showed that there were significant differences in exotic and native leaf quality at different stream temperatures and mesh sizes. Exotic leaves decayed faster than native leaves in the high temperature category (ANOVA $F_{3, 471} = 8.16$, **P<0.001**) (Tukey HSD = -0.596, **P<0.001**) (Figure 2.8, Table 2.10, and Table 2.). Re-examination of the effects of mesh size showed that exotic leaves decayed faster than native leaves in the coarse mesh category (ANOVA $F_{3,471} = 4.221$, **P=0.006**) (Tukey HSD = -0.345, **P=0.004**) (Figure 2.8, Table 2.10, and Table 2.).

When the leaf quality data were divided into temperature groups, significant contrasts were observed in C:N ratios (Kruskal-Wallis $H_{3, 363} = 36.461$, **P<0.001),** C:P ratios (Kruskal-Wallis $H_{3, 346} = 27.097$, **P<0.001**), leaf toughness (Kruskal-Wallis $H_{3, 280} = 21.033$, **P<0.001**), and LMA (Kruskal-Wallis $H_{3, 368} = 22.096$, **P<0.001**) (Figure 2.9 and Table 2.10).

Tukey tests revealed the source of differences in C:N ratios observed at both high and low temperatures. At high temperatures, exotic leaves had lower C:N ratios than native leaves (Nemenyi H = 12.503, **P=0.006**), and at low temperatures exotic leaves had higher C:N ratios than native leaves (Nemenyi H = 21.529, **P<0.001**), (Figure 2.9 and Table 2.11).

Differences in C:P ratios, leaf toughness and LMA were only observed at low temperatures. Exotic species had higher C:P ratios (Nemenyi H = 19.333, **P<0.001**), higher LMA (Nemenyi H = 18.063, **P<0.001**) and tougher leaves (Nemenyi H = 12.208, **P=0.007**) than native species (Figure 2.9 and Table 2.11).

As a group, exotic species had different leaf properties at different temperatures. Exotic leaves at high temperatures had lower C:N ratios (Nemenyi H = 25.904, **P<0.001**), lower LMA (Nemenyi H = 15.388, **P=0.002**), and lower leaf toughness (Nemenyi H = 14.433, **P=0.002**) than exotic leaves at low temperatures (Figure 2.9 and Table 2.11).

In contrast, only the C:P ratio was different between natives and exotics when the decay was divided by mesh size. At fine mesh sizes, exotic leaves had higher C:P ratios than native leaves (Nemenyi H = 39.574, **P<0.001**), and exotic leaves in fine mesh also had higher C:P ratios than exotic leaves in coarse mesh (Nemenyi H = 12.747, **P=0.005**) (Figure 2.10 and Table 2.11). However these C:P ratio differences did not explain the broader patterns of exotic and native litter decay at larger mesh sizes.

Discussion

Leaf litter subsidies are an essential energy source for streams and a key determinant of the nature and structure of the invertebrate and microbial community within the stream (Webster and Benfield 1986, Moore et al. 2004). Changes to leaf litter subsidies through the invasion by exotic species have the potential to impact the stream in many different ways. Litter increases through increased influx, increased litter diversity, or reduced decay rate have been shown to cause increases in microbial richness, invertebrate density, richness and biomass, and shifts in the invertebrate community composition (Richardson 1991, Lecerf et al. 2005, Serra et al. 2013).

My meta-analysis revealed that there is no consistent unified global trend of exotic leaves decaying faster or slower than native leaves. This implies that the impacts of exotic leaves do not have the same effect in every stream ecosystem, but rather the impacts of exotic leaves differ depending on the attributes of the leaves and on the attributes of the stream ecosystem. However, my model also showed that exotic leaf decay does appear to be significantly more temperature sensitive than native leaf decay, and exotic leaves decay faster than native leaves at higher temperatures. Most of the low temperature studies were from temperate streams (low temperature: 1 tropical site, 55 temperate sites), while the majority of my high temperature studies were tropical (high temperature: 38 tropical sites, 17 temperate sites), (See Table 2.12). My results therefore imply that higher temperature stream ecosystems, such as those in the tropics are more likely to experience changes in the detrital food web if the watershed is home to exotic species.

Increases in temperature elevate aquatic litter decay rates (Lecerf et al. 2007b, Ferreira and Chauvet 2011), in part by enabling quicker microbial decomposition of lignin at higher temperatures (Fernandes et al. 2012). It follows that temperature-mediated increases in leaf litter decay rates tend to vary according to leaf species (Irons et al. 1994, Fierer et al. 2005, Lecerf et al. 2007b) likely due to differences in litter quality (Fernandes et al. 2012). Thus to fully understand the differences in decay associated with differences in temperature, we must also look at the leaf litter qualities of the species themselves.

Indeed, interesting patterns emerged when I examined leaf litter qualities associated with native and exotic leaves at high and low temperatures. It seems that in high temperature ecosystems, exotic leaves have a lower C:N ratio than native leaves (Figure 2.9). High leaf litter nitrogen content has long been associated with an increased rate of decay (Webster and Benfield 1986), particularly if the nitrogen content is high relative to the carbon content of the leaf (Enriquez et al. 1993, Ostrofsky 1997, Mathuriau and Chauvet 2002). Low quality (i.e. high C:N) leaves have less diverse bacterial communities (Kominoski et al. 2009), and are avoided by shredders (Rosemond et al. 2010), collector-browsers (Quinn et al. 2000b), and chironomids (Ágoston-Szabó et al. 2015). Marcarelli et al. (2011) found that freshwater animals select for high-quality food resources disproportionately relative to all food resources available. This invertebrate selectivity could, in turn, cause disproportionate shifts in ecosystem processes and the food web if there is a change in the types or quality of food resources available. Therefore it is possible that higher temperature ecosystems are particularly vulnerable to food web shifts due to higher nitrogen in exotic leaf litter and faster decay rates as identified by my model.

However, significant differences in leaf quality metrics (C:N, C:P, leaf toughness, and LMA) emerged at lower temperatures, without necessarily corresponding to differences in litter decay rate. Therefore more studies are needed to fully understand the effects of litter quality on decay rates at different temperatures. One possible explanation for this discrepancy was identified by Swan and Palmer (2004), who found that their summer litter mixture decay rates were much faster and more unpredictable than those in a cooler fall trial of the same experiment. They propose that lower fall temperatures reduces decomposer activity and decay rates so much that the litter identity effects on decomposition are masked because the litter quality differences have such a small impact on decay rates at low temperature (Swan and Palmer 2004).

My model also indicated that mesh size changes the outcome of exotic vs. native decay rates. Mesh size is used by many studies as a way of differentiating microbial vs. invertebrate mediated leaf litter decay (Pascoal et al. 2005, Ribas et al. 2006, Taylor and Chauvet 2013). A larger mesh size allows more invertebrate access. One way to interpret my findings is that when mesh size (and therefore access for invertebrates) increases, exotic leaves tend to decay more quickly relative to native leaves. This suggests that stream systems where litter decomposition is largely invertebrate-driven, (e.g. most temperate streams (Gonçalves et al. 2006, Lecerf et al. 2007a)), and tropical streams with high shredder abundances or crayfish (Graça et al. 2001, Boulton et al. 2008) are more likely to experience accelerated exotic litter decay compared to stream systems where litter decay is dominated by microbial processes (e.g. tropical systems with low shredder abundance (Mathuriau and Chauvet 2002)) as proposed by Boyero et al. (2012).

However, although I found significant differences among native and exotic decay (and therefore, possibly shredding) at coarse mesh sizes, no consistent differences in leaf litter quality associated with the coarse mesh sizes emerged. Therefore more research is necessary to fully understand the effects of leaf identity and leaf litter quality on both invertebrate and microbial mediated litter decay.

Despite the fact that pH and conductivity have been shown to affect microbial decay rates and litter decay processes (Webster and Benfield 1986, Mulholland et al. 1987, Suberkropp 1995, Young et al. 2008, Jenkins and Clivot et al. 2013), my model did not indicate that they were important for explaining large scale differences between native and exotic leaf litter decay rates. These covariates were retained during the model averaging process however, as both pH and conductivity are highly relevant to understanding biological decay rates, and they improved parsimony in the linear model. Likewise latitude was excluded from the model, likely because the chief attribute associated with latitude change is the accompanying shift in ambient temperature, which is explained separately by the temperature covariate.

Study was retained as an essential random effect. Study as a random effect addressed both the independence issues inherent in the dataset, and also likely accounted for abiotic decay factors such as varying levels of dry-leaf cuticle damage (allowing swift fungal ingress), and stream-flow abrasion (Canhoto and Graça 1996, dos Santos Fonseca et al. 2013). My meta-analysis was not able to capture the impacts of discharge or stream flow due to the paucity of such information in the literature. Likewise my leaf litter quality database was limited by the scarcity of published values for leaf litter properties.

Other potential impacts of exotic leaves in streams

My study focused on one metric of leaf litter (decay rate), which is widely reported. However, shifts in the species of leaf litter present can also have unpredictable impacts on the invertebrates and microbes in the stream. Different litter mixtures can have both synergistic and antagonistic effects on stream decomposer taxon richness, abundance, and biomass (Swan and Palmer 2006a, 2006b, Kominoski et al. 2007, Kominoski et al. 2009, Kominoski and Pringle 2009). Jabiol et al. (2014) observed that the litter quality of species present in leaf mixtures plays a key role in invertebrate trophic interactions. In highly labile (soft, high-quality) litter mixes, shredder biomass is high, litter decay rates are high, and predation is also high due to the reduced habitat structural complexity of softer leaves (Jabiol et al. 2014). Conversely in highly refractory (recalcitrant, tough, low quality) litter, shredder biomass is low, litter decay rates are low, and predation is low because tough leaves provide greater habitat structural complexity so shredders have more refugia to hide from predators (Jabiol et al. 2014). In mixes of labile and refractory litter, shredder biomass is high because shredders feed selectively on the labile litter, but decay rate and predation rate are lower because of the time shredders spend hiding from predators in refugia provided by the refractory component of the litter (Jabiol et al. 2014). Therefore it is possible that differences in quality between native and exotic leaves that I observed can affect important ecosystem processes beyond decomposition. The addition of exotic subsidies to the native leaf pack may have unpredictable impacts that cascade across the wider food web.

Exotic leaves likely enter streams because exotic species have invaded the riparian zone. Therefore it is also important to characterize how exotic riparian species might affect stream ecosystems by changing total litter input, a decrease in total influx of litter into the system has been shown to decrease microbial richness, invertebrate density, richness and biomass, and to shift invertebrate community composition (Stout et al. 1993, Hall et al. 2000, Fernandes et al. 2013, Wallace et al. 2015). Changes in canopy cover due to vegetation change can cause stream ecosystems to become more reliant on autochthonous production. For example, leaf litter is a major direct carbon source for shaded stream invertebrates, and a reduction in streamside canopy cover shifts stream invertebrates to rely more heavily on carbon from algal sources within the stream (Pettit et al. 2012). Changes to leaf litter subsidies can also have wide ranging impacts on downstream ecosystems, as streams are connected to larger fluvial networks and provide important subsidies to downstream networks across the landscape (Wipfli et al. 2007).

Conclusion

Although no overarching global impact of exotic leaf litter was found by my meta-analysis, I did find that exotic leaf litter is likely to have the most impact in high-temperature stream ecosystems with invertebrate stream detritivores, and the nature of the impact is potentially related to the C:N ratio of the leaves (low C:N exotic leaf litter decay more quickly than high C:N native leaf litter). Likewise exotic species decay faster than native species in coarse mesh sizes that permit the ingress of invertebrate detritivores. The addition of exotic leaf litter to stream ecosystems may also have other effects on detritivore interactions, allochthonous primary production, and other ecosystem processes. The impacts of exotic litter invasion can cascade through the food web and widely throughout the interconnected stream landscape.

I recommend that in addition to the standard measurements of temperature, pH and conductivity, future leaf litter decay studies include stream discharge measurements and leaf litter quality information so that both intrinsic and extrinsic factors that impact litter decay can be fully accounted for when assessing the factors that drive differences in leaf litter decay rates. Future meta-analyses should expand the leaf decay model to include both hydrological and litter quality attributes as covariates in the base model. The impacts of exotic species on stream ecosystems are highly dependent on both environmental and intrinsic factors, but as we amass knowledge stream by stream, a few broad patterns begin to emerge that clarify the impacts of exotic species and provide focus for the nature of human intervention.

Tables

Table 2.1 Outcomes of aquatic leaf litter decay studies based on relative decay rates of native and exotic species.

Decay tendency	*Study*
Exotic species decay faster than native species	Schulze and Walker 1997, Bailey et al. 2001, Black 2005, Wantzen and Wagner 2006, Imberger et al. 2008, Swan et al. 2008, Rezende et al. 2010, Roon 2011, Walpola et al. 2011, McNeish et al. 2012, Freund et al. 2013, MacKenzie et al. 2013, Marano et al. 2013, Aragón et al. 2014, Blanco and Gutiérrez-Isaza 2014, Rezende et al. 2014, Roon et al. 2014, Fargen et al. 2015
Exotic species decay slower than native species	Baldy et al. 1995, Pozo et al. 1998, Casas and Gessner 1999, Albariño and Balseiro 2002, Hladyz et al. 2011, Serra et al. 2013, García et al. 2014, Larrañaga et al. 2014, Masese et al. 2014, Pérez et al. 2014, Correa-Araneda et al. 2015, Lidman 2015, Leite-Rossi et al. 2016
There is no significant difference between the decay rates of exotic and native species	Abelho and Graça 1996, Canhoto and Graça 1996, Molinero et al. 1996, López et al. 1997, Parkyn and Winterbourn 1997, Bärlocher and Graça 2002, Reinhart and VandeVoort 2006, Braatne et al. 2007, Kates 2007, Carvalho and Uieda 2009, Harner et al. 2009, Hladyz et al. 2009, Alonso et al. 2010, Laćan et al. 2010, Gonçalves Jr et al. 2012, Remor et al. 2013, Bo et al. 2014, Claeson et al. 2014, Bruder et al. 2015, Kennedy (Chapter 3)
Litter decay rates are determined by leaf quality rather than leaf origin	Pidgeon and Cairns 1981, Pomeroy et al. 2000, Quinn et al. 2000a, López et al. 2001, Sampaio et al. 2001, Kennedy and Hobbie 2004, Bottollier-Curtet et al. 2011, Martínez et al. 2013, Blanco and Gutiérrez-Isaza 2014, Faccin 2014, König et al. 2014, Raposeiro et al. 2014, Bottollier-Curtet et al. 2015, Boyero et al. 2015
Leaf litter origin impacts relative decay rates under specific conditions	Royer et al. 1999, Graca et al. 2002, Lecerf et al. 2007a, Cabrini et al. 2013, Casas et al. 2013, Bruder et al. 2014, Pérez et al. 2014

Table 2.2 The location and litter species of the 44 studies used in the mixed effects model. The studies marked * were subject to response ratio reduction due to a high number of species contrasts, as noted in the methods.

#	*Study*	*Location*	*Latitude*	*Longitude*	*Exotic species*	*Native species*
1	Abelho and Graça 1996	Serra do Acor and Serra do Caramulo, Portugal	40.5861	-8.1663	*Eucalyptus globulus*	*Castanea sativa*
2	Albariño and Balseiro 2002	Nireco catchment, Patagonian Andes, Argentina	-41.0799	-71.17	*Pinus ponderosa*	*Nothofagus pumilio*
3	Alonso et al. 2010	Madrid, Spain	40.3	-3.2	*Ailanthus altissima* *Robinia pseudoacacia*	*Ulmus minor* *Fraxinus angustifolia*
4	Baldy et al. 1995	Garonne River, France	43.5307	1.4287	*Platanus × acerifolia*	*Salix alba* *Populus nigra*
5	Bärlocher and Graça 2002	Coimbra, Portugal	40.1975	7.7994	*Eucalyptus globulus*	*Castanea sativa*
6	Black 1995	Mill Creek, Lycoming Pennsylvania, USA	41.2698	-76.9215	*Fallopia japonica*	*Acer saccharum*
7*	Blanco and Gutiérrez-Isaza 2014	Quebrada Piedras, Río Cauca, San Roque, Antioquia State, Colombia	6.4872	76.0225	*Magnifera indica* *Schefflera actinophylla* *Araucaria* sp. *Terminalia catappa* *Bauhinia picta* *Hibiscus* sp. *Artocarpus altilis* *Ficus benjamina* *Ficus elastica* *Ficus lyrata* *Ficus* sp. *Eucalyptus* sp. *Eugenia malaccensis* *Syzygium jambos* *Fraxinus chinensis* *Tectona grandis*	*Campnosperma panamensis* *Pachira insignis* *Theobroma cacao* *Sapium* sp. *Inga* sp. *Guadua angustifolia* *Persea americana* *Cecropia* sp. *Ficus* sp. *Psidium guajava* *Cespedesia macrophylla*

Table 2.2 Continued

#	*Study*	*Location*	*Latitude*	*Longitude*	*Exotic species*	*Native species*
8	Bo et al. 2014	Pellice River, Luserna and Villar Pellice, Italy	44.808	7.1556	*Fallopia japonica* *Robinia pseudoacacia*	*Alnus incana* *Populus alba* *Quercus robur*
9*	Bottollier-Curtet et al. 2011	Toulouse, France	43.5267	-1.4271	*Paspalum distichum* *Fallopia japonica* *Buddleja davidii* *Impatiens glandulifera* *Acer negundo*	*Agrostis stolonifera* *Rubus caesius* *Populus nigra* *Urtica dioica* *Salix alba*
10	Boyero et al. 2015	Serra do Cipó, Brazil	19.27	4.52	*Alnus glutinosa*	Native mix
		La Selva Biological Station, Costa Rica	10.43	84.03	*Alnus glutinosa*	Native mix
		Tiputini Biodiversity Station, Ecuador	0.74	76.38	*Alnus glutinosa*	Native mix
		Kourou, French Guiana	5.07	53.01	*Alnus glutinosa*	Native mix
		Tai Po Kau Forest, Hong Kong	22.43	114.15	*Alnus glutinosa*	Native mix
		Southwestern Ghats, India	8.8	77.32	*Alnus glutinosa*	Native mix
		Nakuru, Kenya	0.37	35.93	*Alnus glutinosa*	Native mix
		Borneo, Malaysia	3.15	113.94	*Alnus glutinosa*	Native mix
		Michoacán, Mexico	19.73	100.66	*Alnus glutinosa*	Native mix
		Soberanía National Park, Panama	9.09	79.44	*Alnus glutinosa*	Native mix
		Luquillo Mountains, Puerto Rico	18.32	65.82	*Alnus glutinosa*	Native mix
		Paluma Range National Park, Queensland, Australia	18.98	146.17	*Alnus glutinosa*	Native mix
		Northern Range, Trinidad	10.69	62.29	*Alnus glutinosa*	Native mix
11	Braatne et al. 2007	Clear Creek, Idaho, USA	46.75	-115.7599	*Fallopia japonica*	*Alnus incana* *Populus trichocarpa*

Table 2.2 Continued

#	*Study*	*Location*	*Latitude*	*Longitude*	*Exotic species*	*Native species*
12	Bruder et al. 2014	Petit Saut, French Guyana	5.681	-53.0077	*Alnus glutinosa*	*Eperua falcata* *Vochysia densiflora* *Qualea rosea*
13	Bruder et al. 2015	Kauru River, New Zealand	-45.1111	170.775	*Betula pendula*	*Melicytus ramiflorus*
14	Cabrini et al. 2013	Piedmmont, Lombardy, Italy	45.6675	9.1519	*Prunus laurocerasus* *Robinia pseudoacacia*	Mix of *Alnus glutinosa, Quercus robur, Carpinus betulus*
15	Carvalho and Uieda 2009	Ribeirão da Quinta, São Paulo, Brazil	-23.1131	-48.4961	*Pycreus decumbens*	*Cabralea canjerana*
16	Casas and Gessner 1999	Rio Vicario, Andalucia, Spain	36.8485	-3.8655	*Platanus orientalis*	*Populus nigra* *Salix atrocinerea* *Rubus ulmifolius*
17	Claeson et al. 2014	Porter, Stony and Wildcat Creek, Chehalis River, Washington State, USA	47.0271	-123.3504	*Fallopia polygonum* × *bohemicum*	*Alnus rubra* *Populus trichocarpa*
18	Faccin 2014	Riacho Cachoeira Grande, Florianópolis, Brazil	-27.7	-48.5166	*Eucalyptus grandis*	*Ficus adhatodifolia* *Alchornea glandulosa*
19	Ferreira et al. 2012	Estero Numa, Tiputini River watershed, Ecuador	-0.6443	-76.1585	*Alnus glutinosa*	*Inga punctata* *Triplaris dugandi* *Zygia cataractae*
20	García et al. 2014	Galicia, Spain Vancouver, BC, Canada	42.5902 49.16	-7.3799 -122.339	*Eucalyptus nitens* *Eucalyptus globulus*	*Alnus glutinosa* *Alnus rubra*
21	Gonçalves Jr et al. 2012	Zé Adão stream, Brazil	-19.5728	-42.6318	*Eucalyptus camaldulensis* *Protium heptaphyllum*	*Erythrina verna*
22	Imberger et al. 2008	Melbourne, Victoria, Australia	-37.7933	145.3288	*Pittosporum undulatum*	*Eucalyptus obliqua*
23	Kennedy (Chapter 3)	Bowker, Cecelia, Swan and Francis-King Crk. Victoria, BC, Canada	48.4222	-123.3657	*Hedera* sp. *Rubus armeniacus*	*Alnus rubra* *Salix sitchensis*

Table 2.2 Continued

#	*Study*	*Location*	*Latitude*	*Longitude*	*Exotic species*	*Native species*
24	König et al. 2014	Rio Cravo, Brazil	-27.7163	-52.2455	*Hovenia dulcis* *Platanus × acerifolia*	*Sebastiania brasiliensis* *Campomanesia xanthocarpa*
25	Laćan et al. 2010	Alameda and Contra Costa counties, California, USA	37.8837	-122.183	*Eucalyptus globulus*	Native mix
26	Lecerf et al. 2007a	Piedmont of the Pyrenees, France	42.8	0.35	*Fallopia japonica*	*Quercus robur*
		The Pennines, England	53.3667	-1.8166	*Fallopia japonica*	*Quercus robur*
27	Lidman 2015	Västerbotten and Ångermanland, Sweden	65	17.5	*Pinus contorta*	*Alnus glutinosa* *Betula pubescens* *Picea abies*
28	López et al. 1997	Mera, River Miño, Galicia, Spain	42.9534	-7.6813	*Eucalyptus globulus*	*Alnus glutinosa*
29*	López et al. 2001	Mera headwaters, Galicia, Spain	42.9534	-7.6813	*Populus × canadensis* *Pinus radiata* *Eucalyptus nitens*	*Alnus glutinosa* *Betula pubescens* *Castanea sativa* *Quercus robur* *Lolium perenne*
30	MacKenzie et al. 2013	Wailuku River Hawaii, Hawaii, USA.	19.7097	-155.1609	*Falcataria moluccana*	*Metrosideros polymorpha*
31	Masese et al. 2014	Mara river, Mau escarpment, Kenya	-0.6666	30.0333	*Eucalyptus globulus*	*Croton macrostachyus* *Syzygium cordatum*
32	Molinero et al. 1996	Agüera stream, Spain	43.3029	-3.2701	*Eucalyptus globulus*	*Castanea sativa* *Quercus robur*
33	Pérez et al. 2014	Agüera river headwaters, Spain	43.3114	-3.2645	*Eucalyptus globulus*	*Alnus glutinosa*
34	Pozo et al. 1998	Agüera stream, Spain	43.3029	-3.2701	*Eucalyptus globulus*	*Alnus glutinosa*
35*	Quinn et al. 2000a	Mangaotama Stream, New Zealand	-37.9096	175.1626	*Eucalyptus regnans* *Juglans nigra* *Lolium perenne* *Pinus radiata* *Populus × canadensis*	*Aristotelia serrata* *Beilschmiedia tawa* *Hoheria populnea* *Knightia excelsa* *Melicytus ramiflorus*

Table 2.2 Continued

#	*Study*	*Location*	*Latitude*	*Longitude*	*Exotic species*	*Native species*
36*	Raposeiro et al. 2014	Ribeira da Praia and Ribeira das Lombadas, São Miguel Island, Azores, Portugal	37.7687	-25.4731	*Solanum mauritianum* *Acacia melanoxylon* *Eucalyptus globulus* *Pittosporum undulatum* *Clethra arborea*	*Picconia azorica* *Morella faya* *Ilex perado* *Viburnum treleasei* *Laurus azorica*
37	Rezende et al. 2010	Aguapé and Barra lakes, Rio Doce State Park, Brazil	-19.7957	-42.6146	*Eucalyptus grandis*	*Hirtella glandulosa*
38	Rezende et al. 2014	Gama-Cabeca do Veado, Brazil	-15.9181	-47.9167	*Eucalyptus cloeziana*	*Inga laurina*
39	Roon 2001, Roon et al. 2014	Anchorage, Campbell and Chester Creeks, Alaska, USA	61.1668	-149.7499	*Prunus padus*	*Alnus tenuifolia* *Betula neoalaskana* *Populus trichocarpa*
40	Royer et al. 1999	Big Wood River and Mink Creek, Idaho, USA	42.9451	-114.7954	*Elaeagnus angustifolia*	*Populus tremuloides* *Populus trichocarpa* *Cornus stolonifera*
41	Schulze and Walker 1997	River Murray, Blanchetown, South Australia	-34.3978	139.6122	*Salix babylonica*	*Eucalyptus camaldulensis*
42	Tonin et al. 2014	Araucaria Rainforest, Brazil	-27.7180	-52.3078	*Eucalyptus grandis*	*Campomanesia xanthocarpa* *Cupania vernalis*
43	Walpola et al. 2011	Eswathu Oya,Sri Lanka	6.8876	80.1939	*Alstonia macrophylla* *Hevea brasiliensis*	*Ochlandra stridula*
44	Wantzen and Wagner 2006	Corrego Tenente Amaral Mato Grosso, Brazil	-15.54	-55.1	*Alnus glutinosa* *Fagus sylvatica*	*Brosimum lactescens*

Table 2.3 Stepwise rejection of fixed factor interactions using the variance inflation factor (VIF) cut-off value of VIF >3.

Interaction	*VIF*
Temperature:pH	365.412
Conductivity:pH	143.644
Mesh size:pH	136.599
pH:Latitude	107.855
Conductivity:Latitude	83.178
Mesh size:Temperature	35.261
Temperature:Conductivity	27.017
Mesh size:Conductivity	18.817
Mesh size:Latitude	7.143
Temperature:Latitude	6.159

Table 2.4 Random effects selection by Akaike information criterion (AIC) and ANOVA tests against the null model. Also shown are the degrees of freedom (df), corrected Akaike information criterion (AICc), Bayesian information criterion, log-likelihood relative support, and the significance of the test (*P*).

Random effect	*df*	*AIC*	*AICc*	*BIC*	*Log-likelihood*	*P*	*Status*
Null	**7**	659.054	659.519	683.505	-322.527	>0.05	Rejected
~1|study	8	632.435	633.035	660.380	-308.218	**<0.0001**	**Retained**
~1|subsite	8	649.679	650.279	677.623	-316.840	>0.05	Rejected
study|subsite	-	-	-	-	-	-	Incalculable

Table 2.5 Leaf quality properties (C:N, C:P, penetrometer toughness (g/mm^2), and leaf mass area (LMA (mg/cm^2)) for native and exotic leaf litter species from published sources.

#	*Species, Alternate names*	*C:N ratio*	*C:P ratio*	*Leaf chemistry study*	*Toughness (g/mm^2)*	*Toughness study*	*LMA (mg/cm^2)*	*LMA study*
1	*Acacia melanoxylon*	26.9	952.0	Wetterburn and Carter 1999, Campbell et al. 1992	13.41	Read and Sanson 2003	4.03	Atkin et al. 1998
2	*Acer negundo*	18.8	221.8	Bottollier-Curtet et al. 2011	649.68	Ostrofsky 1997	2.53	Porté et al. 2011
3	*Acer saccharum*	65.1	1115.7	King et al. 2001, Adams and Angradi 1996	1060.00	Ostrofsky 1997	4.23	Hagen and Chabot 1986
4	*Agrostis stolonifera*	21.9	111.3	Bottollier-Curtet et al. 2011	-	-	4.55	Goverde and Erhardt 2003
5	*Ailanthus altissima*	32.7	546.3	Godoy et al. 2010	6.92	Swan et al. 2008	5.14	Grotkopp and Rejmánek 2007
6	*Alchornea glandulosa*	-	-	-	-	-	-	-
7	*Alnus glutinosa*	15.6	998.1	Casas et al. 2013	100.11	Ferreira et al. 2012	4.69	Cornelissen 1996
8	*Alnus incana*	23.1	697.0	Myrold and Huss-Danell 2003, Claeson et al. 2014	714.95	Ostrofsky 1997 incan ssp rugosa	7.84	Uri et al. 2009
9	*Alnus rubra*	31.5	694.2	Edmonds 1980	-	-	9.40	Compton et al. 1997
10	*Alnus tenuifolia*	23.1	697.0	Myrold and Huss-Danell 2003, Claeson et al. 2014	20.70	Kenzo et al. 2016	5.36	Anderson et al. 2004
11	*Alstonia macrophylla*	31.3	1324.0	Walpola et al. 2011, Kueffer et al. 2008	-	-	9.22	Dietz et al. 2004

Table 2.5 Continued

#	*Species, Alternate names*	*C:N ratio*	*C:P ratio*	*Leaf chemistry study*	*Toughness (g/mm^2)*	*Toughness study*	*LMA (mg/cm^2)*	*LMA study*
12	*Aristotelia serrata*	54.2	677.8	Quinn et al. 2000a, Wardle et al. 2006	691.18	Quinn et al. 2000a	5.31	Jackson et al. 2013
13	*Artocarpus altilis*	29.1	340.2	Blanco and Gutiérrez-Isaza 2014	60.83	Blanco and Gutiérrez-Isaza 2014	-	-
14	*Beilschmiedia tawa*	53.1	250.0	Quinn et al. 2000a, Enright and Ogden 1987	398.07	Quinn et al. 2000a	9.70	Lusk et al. 2013
15	*Betula neoalaskana*	30.4	235.2	Poteri et al. 1997, Melvin et al. 2015	27.43	Kenzo et al. 2016	5.90	Kenzo et al. 2016
16	*Betula pendula*	63.4	563.3	Bruder et al. 2015	74.70	Bruder et al. 2015	6.21	Cornelissen 1996
17	*Betula pubescens, Betula alba*	28.7	210.8	Berglund et al. 2013, Berg and Ekbohm 1991	12.72	Riipi et al. 2002	4.00	Kramer and Mohren 1996
18	*Brosimum lactescens*	25.1	717.3	Campos 2009, Scott et al. 1992	-	-	5.24	Selaya and Anten 2010
19	*Buddleja davidii*	18.9	241.9	Bottollier-Curtet et al. 2011	1.51	Read and Sanson 2003	8.77	Cornelissen 1996
20	*Cabralea canjerana*	-	-	-	-	-	5.76	Gliesch Silva 2015
21	*Campomanesia xanthocarpa*	22.6	1174.2	Biasi et al. 2013	-	-	-	-
22	*Castanea sativa*	63.2	243.6	Anderson 1973, Lopez et al. 2001	128.46	Ferreira et al. 2012	3.53	Cornelissen 1996
23	*Cecropia* sp.	40.1	526.9	Blanco and Gutiérrez-Isaza 2014	115.93	Blanco and Gutiérrez-Isaza 2014	4.61	Selaya and Anten 2010
24	*Cespedesia macrophylla*	40.2	1025.5	Blanco and Gutiérrez-Isaza 2014	146.23	Blanco and Gutiérrez-Isaza 2014	-	-

Table 2.5 Continued

#	*Species, Alternate names*	*C:N ratio*	*C:P ratio*	*Leaf chemistry study*	*Toughness (g/mm²)*	*Toughness study*	*LMA (mg/cm²)*	*LMA study*
25	*Clethra arborea*	-	-	-	-	-	-	-
26	*Cornus stolonifera, Cornus sericea*	65.0	288.5	Royer and Minshall 2001, Ostrofsky 1997	568.85	Ostrofsky 1997	5.80	Kenzo et al. 2016
27	*Croton macrostachyus*	37.9	169.4	Mahari 2014	-	-	4.36	Gindaba 2004
28	*Cupania vernalis*	16.2	2349.0	Tonello et al. 2014, Tonin et al. 2014	-	-	7.96	Gliesch Silva 2015
29	*Elaeagnus angustifolia*	25.5	204.3	Godoy et al. 2010	-	-	7.90	Alonso et al. 2010
30	*Eperua falcata*	49.4	1571.0	Hattenschwiler and Jorgensen 2010	112.88	Bruder et al. 2014	11.60	Guehl et al. 1998
31	*Erythrina verna, Erythrina mulungu*	17.7	324.5	Duart 2007	-	-	8.66	Campoe et al. 2014
32	*Eucalyptus camaldulensis*	37.8	41.6	Glazebrook and Robertson 1999	170.59	Moretti et al. 2009	3.17	Grotkopp and Rejmánek 2007
33	*Eucalyptus cloeziana*	-	-	-	-	-	6.34	Ngugi et al. 2003
34	*Eucalyptus globulus*	83.8	2807.5	Godoy et al. 2010	575.10	Ratnarajah and Barmuta 2009	13.09	Close et al. 2004
35	*Eucalyptus grandis*	56.4	1421.2	Garay et al. 2004, Turner and Lambert 1983	-	-	3.83	Grassi et al. 2002
36	*Eucalyptus nitens*	77.7	641.3	Wetterburn andCarter 1999, Lopez et al. 2001	129.50	Loney et al. 2006	15.02	Close et al. 2004
37	*Eucalyptus obliqua*	37.5	2781.3	Snowdon et al. 2005, Attiwill 1968	591.50	Ratnarajah and Barmuta 2009	4.03	Merchant et al. 2007
38	*Eucalyptus regnans*	29.0	906.7	Quinn et al. 2000a, Ashton 1975	510.82	Quinn et al. 2000a	16.89	England and Attiwill 2006

Table 2.5 Continued

#	*Species, Alternate names*	*C:N ratio*	*C:P ratio*	*Leaf chemistry study*	*Toughness (g/mm^2)*	*Toughness study*	*LMA (mg/cm^2)*	*LMA study*
39	*Eucalyptus* sp.	57.1	637.3	Blanco and Gutiérrez-Isaza 2014	124.68	Blanco and Gutiérrez-Isaza 2014	-	-
40	*Eugenia malaccensis, Syzygium malaccense*	-	-	-	76.54	Blanco and Gutiérrez-Isaza 2014	5.06	Dawson et al. 2011
41	*Fagus sylvatica*	46.6	543.0	Vos et al. 2011, Jacob et al. 2010	90.62	Bruder et al. 2014	10.99	Cornelissen 1996
42	*Falcataria moluccana*	33.0	1383.0	Hughes and Uowolo 2006	151.95	MacKenzie et al. 2013	7.14	Hughes and Uowolo 2006
43	*Fallopia japonica, Reynoutria japonica, Polygonum Cuspidatum*	21.2	270.7	Bottollier-Curtet et al. 2011	39.92	Miura and Ohsaki 2004	6.67	Herpigny et al. 2011
44	*Fallopia polygonum × bohemicum*	63.2	893.3	Claeson et al. 2014	-	-	5.26	Herpigny et al. 2011
45	*Ficus adhatodifolia*	9.8	707.8	Faccin 2014	-	-	-	-
46	*Ficus benjamina*	52.3	365.2	Hirschel et al. 1997, Cokuysal et al. 2006	10.93	Blanco and Gutiérrez-Isaza 2014	3.46	Veneklaas et al. 2002
47	*Ficus elastica*	58.1	564.7	Blanco and Gutiérrez-Isaza 2014	30.46	Blanco and Gutiérrez-Isaza 2014	15.63	Choong et al. 1992
48	*Ficus lyrata*	-	-	-	220.06	Blanco and Gutiérrez-Isaza 2014	1.64	Ceulemans et al. 1985, Jackson et al. 1991

Table 2.5 Continued

#	*Species, Alternate names*	*C:N ratio*	*C:P ratio*	*Leaf chemistry study*	*Toughness (g/mm^2)*	*Toughness study*	*LMA (mg/cm^2)*	*LMA study*
49	*Ficus* sp.	-	-	-	-	Blanco and Gutiérrez-Isaza 2014	-	-
50	*Fraxinus angustifolia*	52.6	917.4	Alonso et al 2010, Gallardo and Merino 1993	23.73	Gallardo and Merino 1993	8.70	Alonso et al. 2010
51	*Fraxinus chinensis, Fraxinus rhynchophylla*	29.1	167.3	Yang and Zhu 2014	112.84	Blanco and Gutiérrez-Isaza 2014	6.72	Cho et al. 2008
52	*Guadua angustifolia*	-	-	-	70.43	Blanco and Gutiérrez-Isaza 2014	5.21	Márquez de Hernández and Marín Ch 2011
53	*Hedera helix*	-	-	-	-	-	6.94	Cornelissen 1996
54	*Hevea brasiliensis*	23.3	431.3	Walpola et al. 2011, Martinelli et al. 2000	-	-	5.81	Kositsup et al. 2008
55	*Hibiscus* sp.	39.7	569.3	Blanco and Gutiérrez-Isaza 2014	88.46	Blanco and Gutiérrez-Isaza 2014	-	-
56	*Hirtella glandulosa*	-	-	-	-	-	-	-
57	*Hoheria populnea*	51.8		Quinn et al. 2000a	384.26	Quinn et al. 2000a		
58	*Hovenia dulcis*	12.4	187.6	König et al. 2014, Dawson et al. 2011	-	-	2.82	Dawson et al. 2011
59	*Ilex perado*	-	-	-	-	-	-	-
60	*Impatiens glandulifera*	14.0	138.7	Bottollier-Curtet et al. 2011	-	-	1.25	Andrews et al. 2009
61	*Inga laurina*	32.6	1009.4	Francis 2000, Rezende et al. 2014	-	-	11.16	Martins et al. 2015
62	*Inga punctata*	27.8	941.0	Batterman et al. 2013	241.10	Ferreira et al. 2012	11.19	Zotz et al. 1998

Table 2.5 Continued

#	*Species, Alternate names*	*C:N ratio*	*C:P ratio*	*Leaf chemistry study*	*Toughness (g/mm^2)*	*Toughness study*	*LMA (mg/cm^2)*	*LMA study*
63	*Inga* sp.	-	-	-	72.78	Blanco and Gutiérrez-Isaza 2014	-	-
64	*Juglans nigra*	23.2	154.8	Quinn et al. 2000a, Ostrofsky 1997	668.33	Ostrofsky 1997	9.13	Cook and Saunders 2013
65	*Justicia americana*	25.0	393.8	Edmonds 2011, Twilley et al. 1985	-	-	-	-
66	*Knightia excelsa*	129.1	850.0	Quinn et al. 2000a, Enright and Ogden 1987	1021.95	Quinn et al. 2000a	7.58	Lusk et al. 2013
67	*Laurus azorica, Laurus novocanariensis*	-	-	-	-	-	12.89	Villar and Merino 2001
68	*Lolium perenne*	10.4	146.8	Quinn et al. 2000a, Lopez et al. 2001	196.85	Quinn et al. 2000a	4.48	Cornelissen 1996
69	*Lonicera maackii*	30.0	496.2	Poulette and Arthur 2012, Demars and Boerner 1997	-	-	4.20	Luken et al. 1997
70	*Magnifera indica*	76.6	531.3	Mubarak et al. 2008	111.71	Blanco and Gutiérrez-Isaza 2014	12.75	Holder 2011
71	*Melicytus ramiflorus*	16.3	337.7	Bruder et al. 2015	99.80	Bruder et al. 2015	5.17	Jackson et al. 2013
72	*Metrosideros polymorpha*	157.0	566.3	Hughes and Uowolo 2006, Matson 1990	375.73	MacKenzie et al. 2013	19.23	Hughes and Uowolo 2006
73	*Morella faya, Myrica faya*	27.0	6383.3	Matson 1990	-	-	17.48	Asner et al. 2008

Table 2.5 Continued

#	*Species, Alternate names*	*C:N ratio*	*C:P ratio*	*Leaf chemistry study*	*Toughness (g/mm^2)*	*Toughness study*	*LMA (mg/cm^2)*	*LMA study*
74	*Nothofagus pumilio*	90.6	7888.2	Satti et al. 2003, Caldenty et al. 2001	84.20	Albariño and Balseiro 2001	5.46	Villar and Merino 2001
75	*Ochlandra stridula*	33.5	-	Walpola et al. 2011	-	-	-	-
76	*Pachira insignis*	-	-	-	140.90	Blanco and Gutiérrez-Isaza 2014	4.60	Bracho-Nunez et al. 2013
77	*Paspalum distichum*	39.5	422.9	Bottollier-Curtet et al. 2011	-	-	-	-
78	*Persea americana*	41.6	59.0	Murovhi et al. 2012	81.20	Blanco and Gutiérrez-Isaza 2014	8.26	Okubo et al. 2012
79	*Picconia azorica*	-	-	-	-	-	-	-
80	*Picea abies*	44.4	644.4	Berglund et al. 2013, Lundmark-Thelin and Johansson 1997	292.70	Hatcher 1990	9.80	Košvancová et al. 2009
81	*Pinus contorta*	167.0	1250.0	Yavitt and Fahey 1986	-	-	25.32	Gower et al. 1987
82	*Pinus ponderosa*	77.1	538.0	Hart et al. 1991, Monleon and Cromack 1996	1146.50	Albariño and Balseiro 2001	6.06	Shipley 2002
83	*Pinus radiata*	81.3	4657.3	Casas et al. 2013	386.58	Casas et al. 2013	21.28	Warren and Adams 2000
84	*Pittosporum undulatum*	55.4	-	Moselhy et al. 2014	-	-	5.08	Wright and Westoby 2000
85	*Platanus orientalis*	89.0	1297.3	Casas and Gessner 2001	51.28	Rumbos et al. 2010	-	-

Table 2.5 Continued

#	*Species, Alternate names*	*C:N ratio*	*C:P ratio*	*Leaf chemistry study*	*Toughness (g/mm^2)*	*Toughness study*	*LMA (mg/cm^2)*	*LMA study*
86	*Platanus × acerifolia, Platanus hispanica, Platanus hybrid*	63.0	4092.5	Casas et al. 2013	249.21	Casas et al. 2013	11.36	Khavaninzadeh et al. 2015
87	*Populus alba*	46.0	595.3	Cotrufo et al. 2005, Kopinga and Van den Burg 1995	14.40	Akanil and Middleton 1997	8.53	Villar and Merino 2001
88	*Populus nigra*	27.9	176.6	Bottollier-Curtet et al. 2011	38.95	Pabst et al. 2008	7.46	Cornelissen 1996
89	*Populus tremuloides*	79.9	950.4	Taylor et al. 1989	1529.38	Ostrofsky 1997	8.13	Villar and Merino 2001
90	*Populus trichocarpa*	68.1	953.0	Royer et al 1999, Claeson et al. 2014	-	-	10.60	McKown et al. 2012
91	*Populus × canadensis*	60.3	1858.3	Casas et al. 2013	215.53	Casas et al. 2013	8.33	Fernàndez-Martínez et al. 2013
92	*Protium heptaphyllum*	53.7	1878.7	Silva et al. 2013, Moretti et al. 2007	-	-	8.20	Paine et al. 2015
93	*Prunus laurocerasus*	81.8	1738.6	Hladyz et al. 2009	-	-	11.49	Cornelissen 1996
94	*Prunus padus*	23.0	160.9	Pott and Hüppe 2008, Yu et al. 2014	82.77	Mąderek et al. 2015	8.07	Liu et al. 2012
95	*Psidium guajava*	46.5	307.5	Mubarak et al. 2008	15.48	Holder 2011	13.88	Holder 2011
96	*Pycreus decumbens*	-	-	-	-	-	-	-
97	*Qualea rosea*	48.1	1899.0	Brechet et al. 2009	174.89	Bruder et al. 2014	4.44	Baraloto et al. 2006
98	*Quercus pyrenaica*	55.6	1844.4	Casas et al. 2013	174.47	Casas et al. 2013	5.34	Rodríguez-Calcerrada et al. 2007

Table 2.5 Continued

#	*Species, Alternate names*	*C:N ratio*	*C:P ratio*	*Leaf chemistry study*	*Toughness (g/mm^2)*	*Toughness study*	*LMA (mg/cm^2)*	*LMA study*
99	*Quercus robur*	37.4	1121.8	Muller and Malthesius 1999, Hladyz et al. 2009	196.32	Ferreira et al. 2012	6.37	Cornelissen 1996
100	*Robinia pseudoacacia*	29.5	741.9	Godoy et al. 2010	1255.83	Ostrofsky 1997	7.30	Alonso et al. 2010
101	*Rubus armeniacus*	-	-	-	-	-	3.39	Grotkopp and Rejmánek 2007
102	*Rubus caesius*	17.9	201.6	Bottollier-Curtet et al. 2011	-	-	-	-
103	*Rubus ulmifolius*	62.0	982.0	Casas and Gessner 2001	-	-	10.20	Raevel et al. 2012
104	*Salix alba*	19.1	245.0	Bottollier-Curtet et al. 2011	6.88	Akanil and Middleton 1997	6.71	Cornelissen 1996
105	*Salix atrocinerea*	68.0	786.5	Casas and Gessner 2001	67.31	Gallardo and Merino 1993	10.20	Mediavilla and Escudero 2003
106	*Salix babylonica*	17.9	128.3	Burns and Walker 2000, Pidgeon and Cairns 1981	-	-	10.23	Roderick et al. 1999
107	*Salix sitchensis*	15.3	78.9	Che-Castaldo et al. 2015	-	-	-	-
108	*Sapium* sp.	-	-	-	-	-	-	-
109	*Schefflera actinophylla*	55.6	244.7	Blanco and Gutiérrez-Isaza 2014	107.65	Blanco and Gutiérrez-Isaza 2014	20.53	Asner et al. 2008
110	*Sebastiania brasiliensis*	16.7	1566.0	Biasi et al. 2013	-	-	7.93	Gliesch Silva 2015
111	*Solanum mauritianum, Solanum verbascifolium*	51.0	-	Bini et al 2013	-	-	-	-

Table 2.5 Continued

#	*Species, Alternate names*	*C:N ratio*	*C:P ratio*	*Leaf chemistry study*	*Toughness (g/mm^2)*	*Toughness study*	*LMA (mg/cm^2)*	*LMA study*
112	*Syzygium cordatum*	-	-	-	332.95	Mwanake 2010	9.98	Greenberg et al. 2004
113	*Syzygium jambos*	43.3	431.5	Ostertag et al. 2008, Dawson et al. 2011	114.32	Blanco and Gutiérrez-Isaza 2014	10.28	Dawson et al. 2011
114	*Tectona grandis*	28.5	3.7	Cernusak et al. 2010	96.77	Blanco and Gutiérrez-Isaza 2014	8.06	Okubo et al. 2012
115	*Terminalia catappa*	18.0	227.5	Blanco and Gutiérrez-Isaza 2014	52.46	Blanco and Gutiérrez-Isaza 2014	7.42	Turner and Tan 1991
116	*Theobroma cacao*	47.2	793.5	Isaac et al. 2005, Hartemink 2005	111.36	Blanco and Gutiérrez-Isaza 2014	7.30	Miyaji et al. 1997
117	*Triplaris dugandi*	-	-	-	103.50	Ferreira et al. 2012	-	-
118	*Ulmus minor*	48.3	1081.4	Godoy et al. 2010	-	-	11.80	Alonso et al. 2010
119	*Urtica dioica*	11.4	133.0	Bottollier-Curtet et al. 2011	-	-	5.03	Cornelissen 1996
120	*Viburnum treleasei*	-	-	-	-	-	-	-
121	*Vochysia densiflora*	48.5	1979.1	García-Palacios et al. 2015, Bruder et al. 2014	131.96	Bruder et al. 2014	4.79	García-Palacios et al. 2015
122	*Zygia cataractae*	-	-	-	307.66	Ferreira et al. 2012	-	-

Table 2.6 Top mixed effects model candidates and their degrees of freedom (df), log-likelihood relative support, corrected Akaike information criterion (AICc), the difference from the lowest AICc (ΔAICc), and the model candidate's Akaike weight in the averaged model (AICcw).

Mixed effects model candidates	*df*	*Log-likelihood*	*AICc*	*ΔAICc*	*AICcw*
Mesh + Temperature +~1|study	5	-292.50	595.25	0.00	0.53
Mesh + pH + Temperature + ~1|study	6	-292.18	596.70	1.45	0.26
Conductivity + Mesh + Temperature + ~1|study	6	-292.39	597.13	1.88	0.21

Table 2.7 Estimated coefficients and their standard errors (SE), adjusted standard errors, Z values and their significance (*P*) in the regression model for lnRR.

Coefficients	*Estimate*	*SE*	*Adjusted SE*	*Z value*	*P*
Intercept	-0.613	0.415	0.417	1.469	0.142
Latitude	-	-	-	-	-
Mesh	0.026	0.012	0.012	2.237	**0.025**
Temperature	0.051	0.012	0.012	4.293	**< 0.001**
pH	-0.016	0.048	0.048	0.333	0.739
Conductivity	-0.005	0.028	0.028	0.197	0.844

Table 2.8 Model averaged coefficients, confidence intervals (CI), and their relative variable importance to the model.

Coefficients	*Model averaged coefficients*	*2.5% CI*	*97.5% CI*	*Relative variable importance*
Intercept	-0.613	-1.430	0.205	-
Latitude	-	-	-	-
Mesh	0.026	0.003	0.049	1.00
Temperature	0.051	0.027	0.074	1.00
pH	-0.016	-0.110	0.078	0.26
Conductivity	-0.005	-0.060	0.049	0.21

Table 2.9 Mean values, standard errors (SE), and sample sizes (n) for leaf quality properties (decay rate (k), C:N, C:P, penetrometer toughness (g/mm^2), and leaf mass area (LMA (mg/cm^2)) by temperature or mesh size and origin.

Temperature-Origin	*High-Exotic*	*High-Native*	*Low-Exotic*	*Low-Native*
mean k	0.031	0.017	0.022	0.023
SE k	0.003	0.001	0.002	0.002
n k	118	120	107	130
mean C:N	37.71	60.87	57.75	38.34
SE C:N	2.3	6.02	2.97	2.09
n C:N	103	64	95	105
mean C:P	1083.12	876.33	1641.76	931.6
SE C:P	69.75	100.22	140.39	134.76
n C:P	98	62	86	104
Mean Toughness	215.57	242.04	413.45	214.09
SE Toughness	33.02	20.8	39.43	30.88
n Toughness	76	57	75	76
mean LMA	7.243	8.963	9.602	7.102
SE LMA	0.356	0.707	0.467	0.323
n LMA	104	65	97	106
Mesh size-Origin	*Coarse-Exotic*	*Coarse-Native*	*Fine-Exotic*	*Fine-Native*
mean k	0.028	0.02	0.022	0.021
SE k	0.002	0.001	0.003	0.003
n k	165	178	60	72
mean C:N	47.17	44.54	47.79	53.72
SE C:N	2.14	2.83	4.72	6.86
n C:N	148	126	50	43
mean C:P	1230.83	955.47	1684.4	779.55
SE C:P	91.2	101.56	139.48	207.79
n C:P	138	124	46	42
Mean Toughness	322.11	231.26	290.15	208.98
SE Toughness	33.87	24.89	37	21.96
n Toughness	112	102	39	31
mean LMA	8.522	7.408	8.017	9.042
SE LMA	0.353	0.348	0.586	0.869
n LMA	145	129	56	42

Table 2.10 Results of post hoc leaf quality testing by temperature or mesh size and origin including the sample sizes (n), degrees of freedom (df), the statistical test used, the test statistic calculated, and the significance of the test (*P*) for leaf quality properties (decay rate (k), C:N, C:P, penetrometer toughness, and leaf mass area (LMA)) by temperature or mesh size and origin.

Group	*Quality*	*n*	*df*	*Statistical test*	*Test statistic*	*P*
Temperature group	k	471	3	ANOVA	F = 8.160	**<0.001**
Temperature group	C:N	363	3	Kruskal-Wallis	H = 36.461	**<0.001**
Temperature group	C:P	346	3	Kruskal-Wallis	H = 27.097	**<0.001**
Temperature group	Toughness	280	3	Kruskal-Wallis	H = 21.033	**<0.001**
Temperature group	LMA	368	3	Kruskal-Wallis	H = 22.096	**<0.001**
Mesh group	k	471	3	ANOVA	F = 4.221	**0.006**
Mesh group	C:N	363	3	Kruskal-Wallis	H = 1.337	0.720
Mesh group	C:P	346	3	Kruskal-Wallis	H = 45.360	**<0.001**
Mesh group	Toughness	280	3	Kruskal-Wallis	H = 1.714	0.634
Mesh group	LMA	368	3	Kruskal-Wallis	H = 7.428	0.059

Table 2.11 Post hoc test results of leaf quality differences for leaf quality properties (decay rate (k), C:N, C:P, penetrometer toughness, and leaf mass area (LMA)) by temperature or mesh size and origin. Included are the post hoc test used, the test statistic calculated, and the significance of the test (*P*). Comparison key: H= high temperature, L= low temperature, C= coarse mesh, F=fine mesh, E = exotic species, N= native species.

Quality	*Group*	*Comparison*	*Statistical test*	*Test statistic*	*P*
k	Temperature group	HE-HN	Tukey HSD	-0.596	**<0.001**
k	Temperature group	HE-LE	Tukey HSD	-0.348	**0.028**
k	Temperature group	HE-LN	Tukey HSD	-0.323	**0.034**
C:N	Temperature group	HE-HN	Nemenyi H	12.503	**0.006**
C:N	Temperature group	HE-LE	Nemenyi H	25.904	**<0.001**
C:N	Temperature group	HN-LN	Nemenyi H	9.775	**0.021**
C:N	Temperature group	LE-LN	Nemenyi H	21.529	**<0.001**
C:P	Temperature group	HE-LN	Nemenyi H	12.928	**0.005**
C:P	Temperature group	HN-LE	Nemenyi H	12.212	**0.007**
C:P	Temperature group	LE-LN	Nemenyi H	19.333	**<0.001**
Toughness	Temperature group	LE-HE	Nemenyi H	14.433	**0.002**
Toughness	Temperature group	LE-LN	Nemenyi H	12.208	**0.007**
LMA	Temperature group	LE-HE	Nemenyi H	15.388	**0.002**
LMA	Temperature group	LE-LN	Nemenyi H	18.063	**<0.001**
Quality	*Group*	*Comparison*	*Statistical test*	*Test statistic*	*P*
k	Mesh group	CE-CN	Tukey HSD	-0.345	**0.004**
C:N	Mesh group	not different	Kruskal-Wallis	1.337	0.720
C:P	Mesh group	FE-CE	Nemenyi H	12.747	**0.005**
C:P	Mesh group	FN-CE	Nemenyi H	17.383	**0.001**
C:P	Mesh group	FE-CN	Nemenyi H	26.466	**<0.001**
C:P	Mesh group	FE-FN	Nemenyi H	39.574	**<0.001**
Toughness	Mesh group	not different	Kruskal-Wallis	1.714	0.634
LMA	Mesh group	not different	Kruskal-Wallis	7.428	0.059

Table 2.12 Study locations by temperature group including the study site, latitudinal zone, latitude, and stream temperature.

Low temperature studies	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*	*High temperature studies*	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*
Royer et al. 1999	Big Wood River, Idaho, USA	Temperate	42.228	1.1	Faccin 2014	Riacho Cachoeira Grande, Florianópolis, Brazil	Temperate	-27.7	14.9
Bo et al. 2014	Pellice River, Luserna and Villar Pellice, Italy	Temperate	44.8071	3.0	Bärlocher and Graça 2002	Coimbra, Portugal	Temperate	40.585	15.0
Albariño and Balseiro 2002	Nireco catchment, Patagonian Andes, Argentina	Temperate	-41.08	3.4	Wantzen and Wagner 2006	Corrego Tenente Amaral Mato Grosso, Brazil	Tropic	-15.54	15.0
Royer et al. 1999	Mink Creek, Idaho, USA	Temperate	42.228	3.6	Imberger et al. 2008	Melbourne, Victoria, Australia	Temperate	-37.793	15.2
Lidman 2015	Västerbotten and Ångermanland, Sweden	Temperate	65	4.2	Imberger et al. 2008	Melbourne, Victoria, Australia	Temperate	-37.793	15.4
Bo et al. 2014	Pellice River, Luserna and Villar Pellice, Italy	Temperate	44.808	4.8	Bärlocher and Graça 2002	Coimbra, Portugal	Temperate	40.587	15.4
Claeson et al. 2014	Chehalis River, Washington State, USA	Temperate	47.0271	6.0	Boyero et al. 2015	Tai Po Kau Forest, Hong Kong	Tropic	22.43	15.4
Lecerf et al. 2007a	Piedmont of the Pyrenees, France	Temperate	42.8	6.1	Boyero et al. 2015	Paluma Range National Park, Queensland AUS	Tropic	18.98	15.5

Table 2.12 Continued

Low temperature studies	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*	*High temperature studies*	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*
Lecerf et al. 2007a	Piedmont of the Pyrenees, France	Temperate	42.8	6.2	Boyero et al. 2015	Michoacán, Mexico	Tropic	19.73	15.6
Roon 2001, Roon et al. 2014	Anchorage, Campbell and Chester Creeks, Alaska, USA	Temperate	61.1668	6.2	Cabrini et al. 2013	Piedmmont, Lombardy, Italy	Temperate	45.6675	15.8
Claeson et al. 2014	Chehalis River, Washington State, USA	Temperate	47.0272	6.4	Casas and Gessner 1999	Rio Vicario, Andalucia, Spain	Temperate	36.8484	15.8
Claeson et al. 2014	Chehalis River, Washington State, USA	Temperate	47.027	6.5	Schulze and Walker 1997	River Murray, Blanchetown, South Australia	Temperate	-34.398	15.9
Lecerf et al. 2007a	The Pennines, England	Temperate	53.3667	6.7	Rezende et al. 2014	Gama-Cabeca do Veado watershed, Brazil	Tropic	-15.918	15.9
Braatne et al. 2007	Clear Creek, Idaho, USA	Temperate	46.75	7.0	Schulze and Walker 1997	River Murray, Blanchetown, South Australia	Temperate	-34.398	16.0
Lecerf et al. 2007a	The Pennines, England	Temperate	53.3667	7.0	Boyero et al. 2015	Nakuru, Kenya	Tropic	0.37	16.5
López et al. 1997	Mera, River Miño, Galicia, Spain	Temperate	42.9534	8.0	Rezende et al. 2014	Gama-Cabeca do Veado watershed, Brazil	Tropic	-15.918	16.8
Molinero et al. 1996	Agüera stream, Spain	Temperate	43.3029	8.4	Carvalho and Uieda 2009	Ribeirão da Quinta, São Paulo, Brazil	Tropic	-23.113	16.9
Roon 2001, Roon et al. 2014	Anchorage, Campbell and Chester Creeks, Alaska, USA	Temperate	61.1668	8.7	MacKenzie et al. 2013	Wailuku River Hawaii, Hawaii, USA.	Tropic	19.7098	16.9

Table 2.12 Continued

Low temperature studies	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*	*High temperature studies*	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*
Pozo et al. 1998	Agüera river, Spain	Temperate	43.3029	8.8	Boyero et al. 2015	Serra do Cipó, Brazil	Tropic	19.27	17.3
Molinero et al. 1996	Agüera stream, Spain	Temperate	43.3029	8.9	Cabrini et al. 2013	Piedmmont, Lombardy, Italy	Temperate	45.6675	17.4
López et al. 2001	Mera headwaters, Galicia, Spain	Temperate	42.9534	9.0	Rezende et al. 2014	Gama-Cabeca do Veado watershed, Brazil	Tropic	-15.918	17.4
Black 1995	Mill Creek, Lycoming Pennsylvania, USA	Temperate	41.2698	9.4	Carvalho and Uieda 2009	Ribeirão da Quinta, São Paulo, Brazil	Tropic	-23.113	17.5
Bottollier-Curtet et al. 2011	Toulouse, France	Temperate	43.5267	9.5	Imberger et al. 2008	Melbourne, Victoria, Australia	Temperate	-37.793	17.7
Baldy et al. 1995	Garonne River, France	Temperate	43.5307	9.5	Tonin et al. 2014	Araucaria Rainforest, Brazil	Temperate	-27.718	17.8
Kennedy (Chapter 3)	Victoria, BC, Canada	Temperate	48.4222	9.7	Imberger et al. 2008	Melbourne, Victoria, Australia	Temperate	-37.793	17.9
Alonso et al. 2010	Madrid, Spain	Temperate	40.3	9.7	Rezende et al. 2014	Gama-Cabeca do Veado watershed, Brazil	Tropic	-15.918	17.9
Pérez et al. 2014	Agüera river headwaters, Spain	Temperate	43.2094	9.7	Boyero et al. 2015	Southwestern Ghats, India	Tropic	8.08	18.0

Table 2.12 Continued

Low temperature studies	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*	*High temperature studies*	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*
Roon 2001, Roon et al. 2014	Anchorage, Campbell and Chester Creeks, Alaska, USA	Temperate	61.1668	10.1	Masese et al. 2014	Mara river, Mau escarpment, Kenya	Tropic	-0.6666	18.7
Bruder et al. 2015	Kauru River, New Zealand	Temperate	-45.111	10.5	Cabrini et al. 2013	Piedmmont, Lombardy, Italy	Temperate	45.6675	19.5
Cabrini et al. 2013	Piedmmont, Lombardy, Italy	Temperate	45.6675	10.5	MacKenzie et al. 2013	Wailuku River Hawaii, Hawaii, USA	Tropic	19.7097	19.5
García et al. 2014	Galicia, Spain	Temperate	42.5902	10.5	Imberger et al. 2008	Melbourne, Victoria, Australia	Temperate	-37.793	19.6
Pozo et al. 1998	Agüera stream, Spain	Temperate	43.3029	10.5	MacKenzie et al. 2013	Wailuku River Hawaii, Hawaii, USA	Tropic	19.7097	19.7
Kennedy (Chapter 3)	Victoria, BC, Canada	Temperate	48.4222	10.7	Cabrini et al. 2013	Piedmmont, Lombardy, Italy	Temperate	45.6675	20.1
Molinero et al. 1996	Agüera stream, Spain	Temperate	43.3029	10.8	MacKenzie et al. 2013	Wailuku River Hawaii, Hawaii, USA	Tropic	19.7097	20.1
Abelho and Graça 1996	Serra do Acor and Serra do Caramulo, Portugal	Temperate	40.5861	10.9	Gonçalves Jr et al. 2012	Zé Adão stream, Brazil	Tropic	-19.573	20.2
Pozo et al. 1998	Agüera stream, Spain	Temperate	43.3029	10.9	Carvalho and Uieda 2009	Ribeirão da Quinta, São Paulo, Brazil	Tropic	-23.113	21.7
Pérez et al. 2014	Agüera river headwaters, Spain	Temperate	43.2094	11.2	MacKenzie et al. 2013	Wailuku River Hawaii, Hawaii, USA	Tropic	19.7097	21.7

Table 2.12 Continued

Low temperature studies	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*	*High temperature studies*	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*
García et al. 2014	Vancouver, BC, Canada	Temperate	49.16	11.9	Boyero et al. 2015	Luquillo Mountains, Puerto Rico	Tropic	18.32	21.8
Abelho and Graça 1996	Serra do Acor and Serra do Caramulo, Portugal	Temperate	40.5861	12.0	Carvalho and Uieda 2009	Ribeirão da Quinta, São Paulo, Brazil	Tropic	-23.113	22.0
López et al. 2001	Mera headwaters Galicia, Spain	Temperate	42.9534	12.0	Faccin 2014	Riacho Cachoeira Grande, Florianópolis, Brazil	Temperate	-27.7	22.1
Roon 2001, Roon et al. 2014	Anchorage, Campbell and Chester Creeks, Alaska, USA	Temperate	61.1668	12.4	Blanco and Gutiérrez-Isaza 2014	Quebrada Piedras, Río Cauca, San Roque, Antioquia State, Colombia	Tropic	6.4872	22.5
Kennedy (Chapter 3)	Victoria, BC, Canada	Temperate	48.4222	12.5	MacKenzie et al. 2013	Wailuku River Hawaii, Hawaii, USA	Tropic	19.7097	22.7
Casas and Gessner 1999	Rio Vicario, Andalucia, Spain	Temperate	36.8485	12.6	Boyero et al. 2015	Borneo, Malaysia	Tropic	3.15	23.7
Bärlocher and Graça 2002	Coimbra, Portugal	Temperate	40.1976	12.7	Boyero et al. 2015	Soberanía National Park, Panama	Tropic	9.09	24.1
Bärlocher and Graça 2002	Coimbra, Portugal	Temperate	40.1975	12.8	Ferreira et al. 2012	Estero Numa, Tiputini River watershed, Ecuador	Tropic	-0.6443	24.1

Table 2.12 Continued

Low temperature studies	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*	*High temperature studies*	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*
Abelho and Graça 1996	Serra do Acor and Serra do Caramulo, Portugal	Temperate	40.5861	13.1	Boyero et al. 2015	Tiputini Biodiversity Station, Ecuador	Tropic	0.74	24.3
Lacan et al. 2010	Alameda and Contra Costa counties, California, USA	Temperate	37.8837	13.1	Boyero et al. 2015	Kourou, French Guiana	Tropic	5.07	24.4
Imberger et al. 2008	Melbourne, Victoria, Australia	Temperate	-37.793	14.1	Bruder et al. 2014	Petit Saut, French Guyana	Tropic	5.681	24.4
König et al. 2014	Rio Cravo, Brazil	Temperate	-27.716	14.2	Boyero et al. 2015	Northern Range, Trinidad	Tropic	10.69	24.7
Kennedy (Chapter 3)	Victoria, BC, Canada	Temperate	48.4222	14.3	Rezende et al. 2010	Aguapé and Barra lakes, Rio Doce State Park, Brazil	Tropic	-19.796	25.0
Raposeiro et al. 2014	São Miguel Island, Azores, Portugal	Temperate	37.7687	14.3	Rezende et al. 2010	Aguapé and Barra lakes, Rio Doce State Park, Brazil	Tropic	-19.796	25.5
Masese et al. 2014	Mara river, Mau escarpment, Kenya	Tropic	-0.6666	14.4	Walpola et al. 2011	Eswathu Oya,Sri Lanka	Tropic	6.8876	25.6
Quinn et al. 2000a	Mangaotama Stream, New Zealand	Temperate	-37.91	14.5	Boyero et al. 2015	La Selva Biological Station, Costa Rica	Tropic	10.43	26.0

Table 2.12 Continued

Low temperature studies	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*	*High temperature studies*	*Site*	*Latitude zone*	*Latitude*	*Stream temp (°C)*
Raposeiro et al. 2014	São Miguel Island, Azores, Portugal	Temperate	37.7687	14.5	Rezende et al. 2010	Aguapé and Barra lakes, Rio Doce State Park, Brazil	Tropic	-19.796	27.5
Bärlocher and Graça 2002	Coimbra, Portugal	Temperate	40.586	14.6	Rezende et al. 2010	Aguapé and Barra lakes, Rio Doce State Park,	Tropic	-19.796	30.5
Cabrini et al. 2013	Piedmmont, Lombardy, Italy	Temperate	45.6676	14.6					

Figures

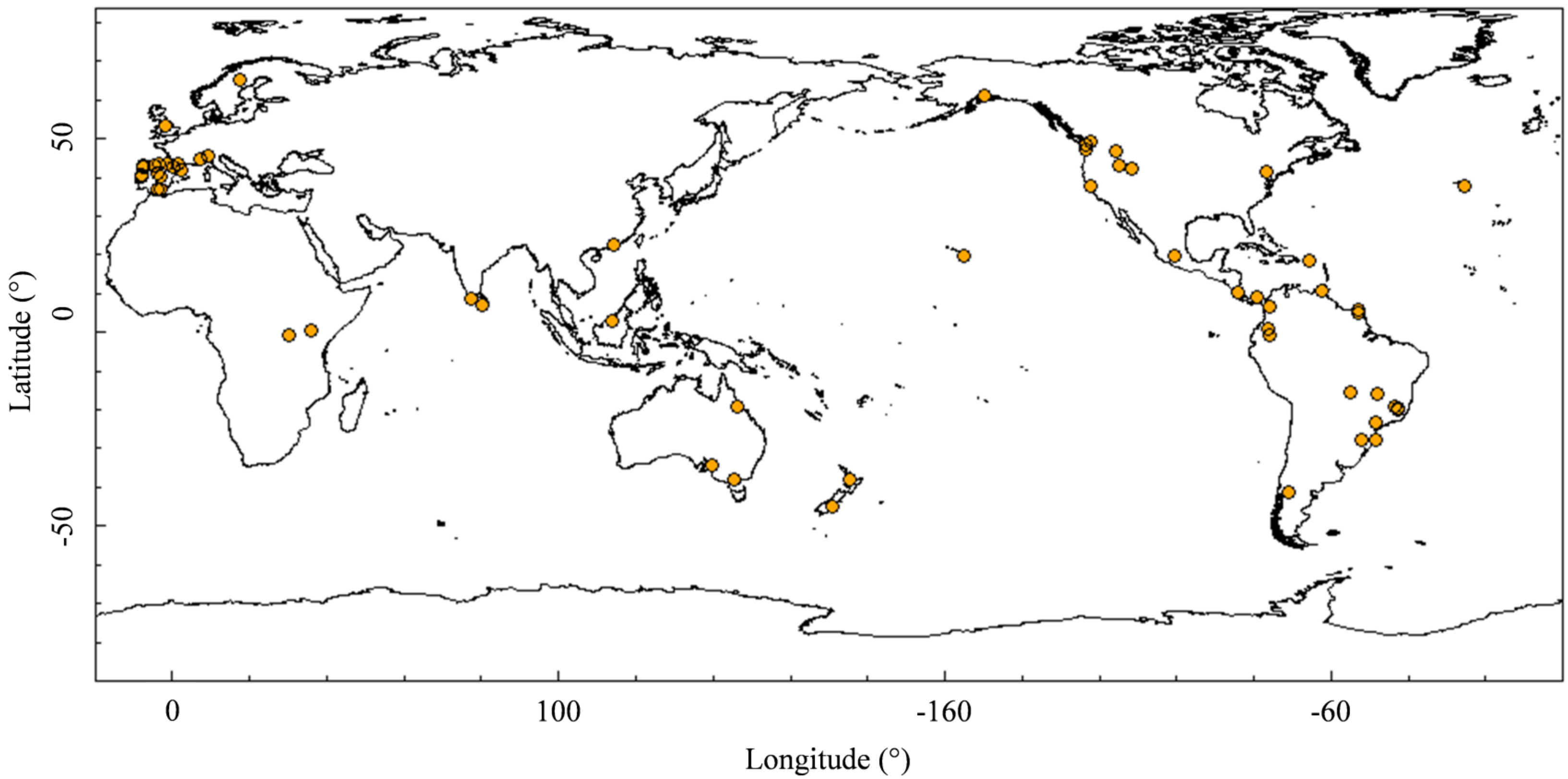

Figure 2.1 Global distribution of the 44 leaf litter decay study sites included in this meta-analysis. The study site map was drawn using the PBSmapping package (Schnute et al. 2015).

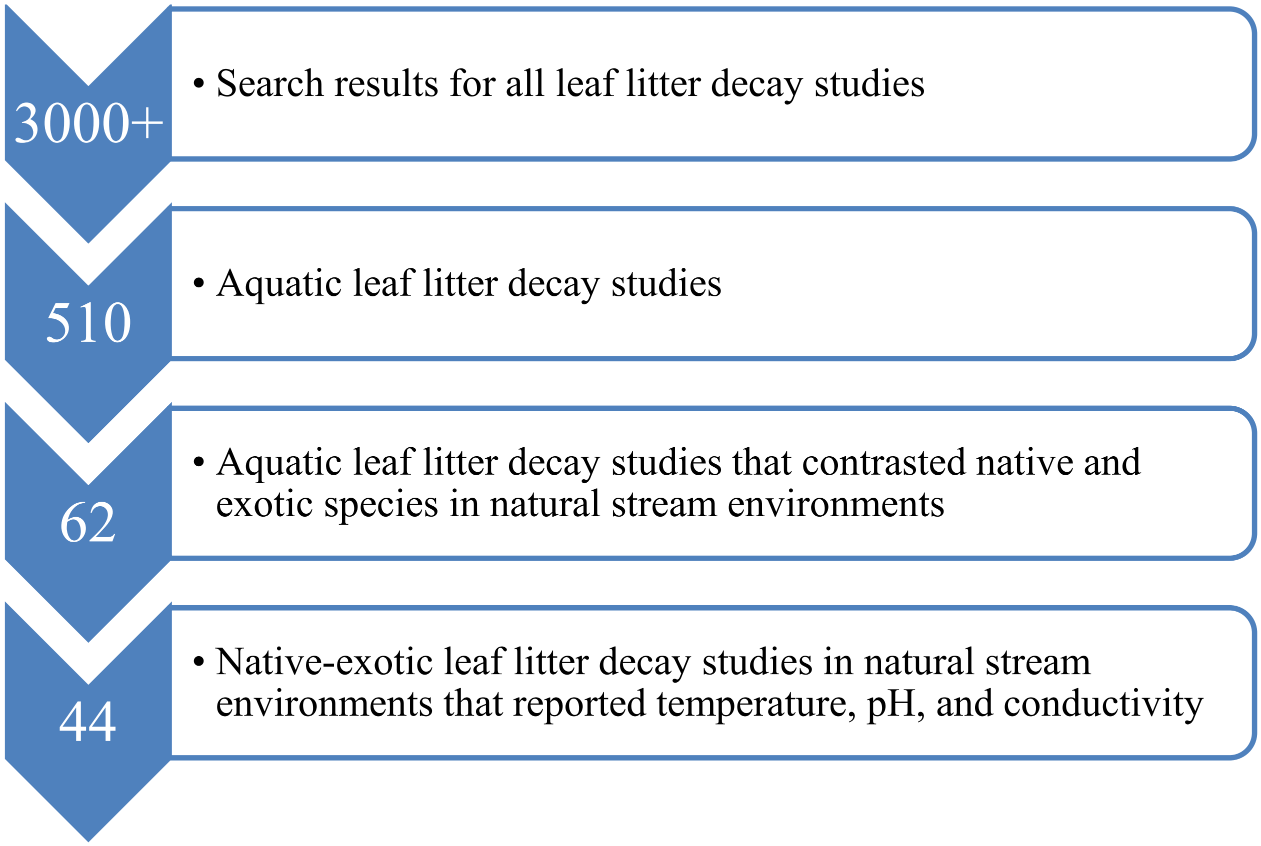

Figure 2.2 Metaanalysis literature review and study selection process.

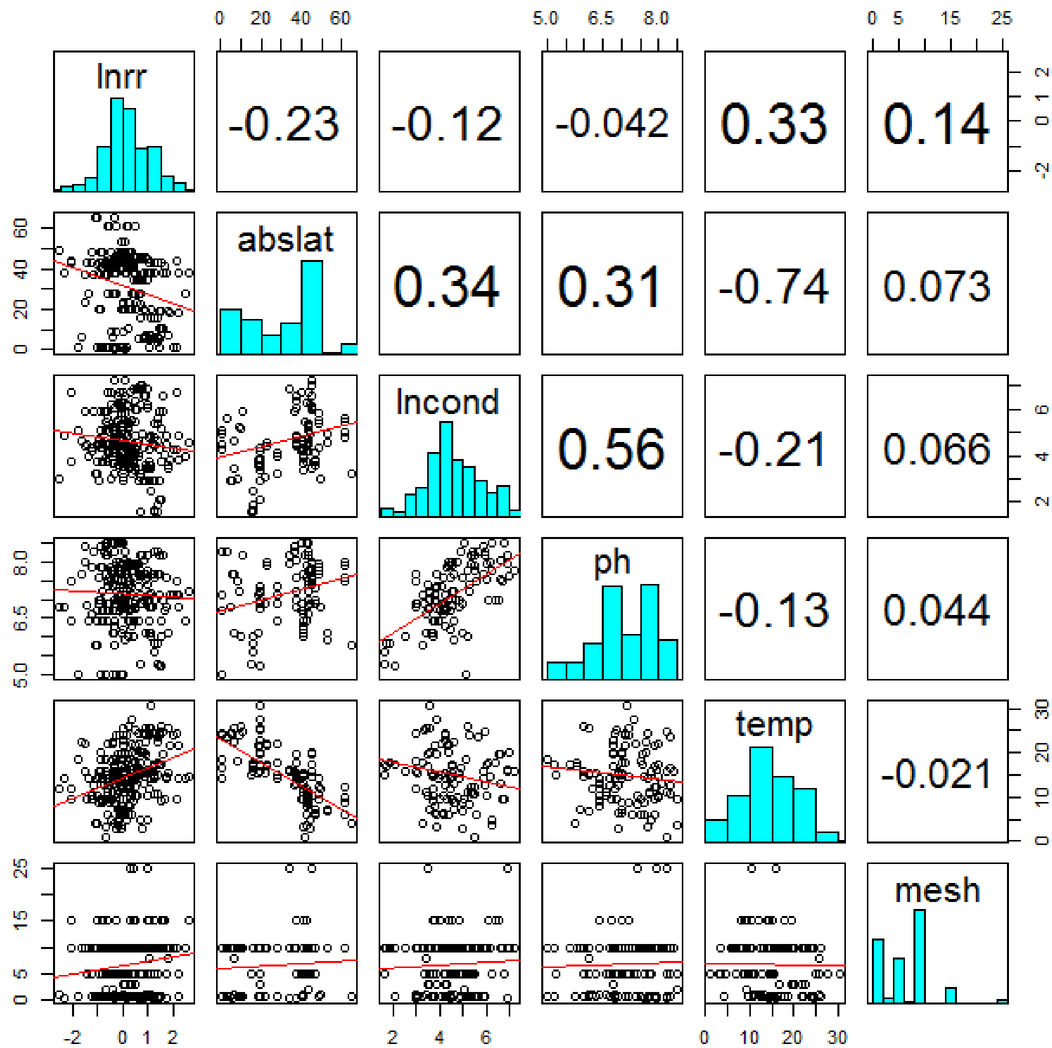

Figure 2.3 Diagnostic correlation plot of the fixed effects used in the mixed effects linear model. The lower left section contains x-y scatterplots of the fixed effects plotted against one another, the middle diagonal shows histograms for each fixed effect, and the upper right section lists the Pearson's r correlation values for the relationship between the fixed factors. The values contrasted are listed as follows: native-exotic response ratio (lnrr), latitude (abslat), conductivity (lncond), pH (ph), temperature (temp), and mesh size (mesh).

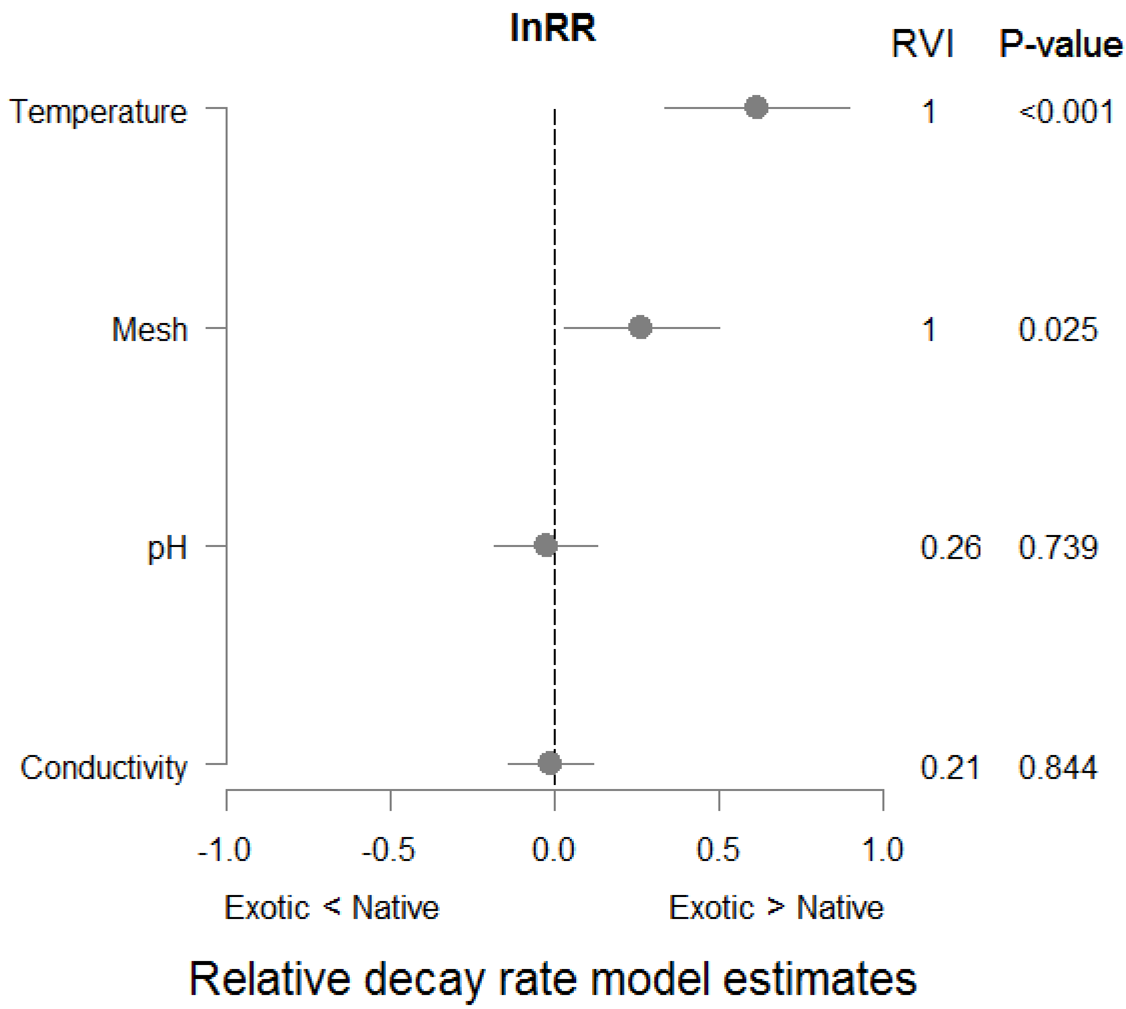

Figure 2.4 Mean effect sizes of the scaled model averaged coefficients (± 95% CI) and their relative variable importance (RVI) and significant impact (P-value) on the decay rate of exotic species relative to native species (lnRR).

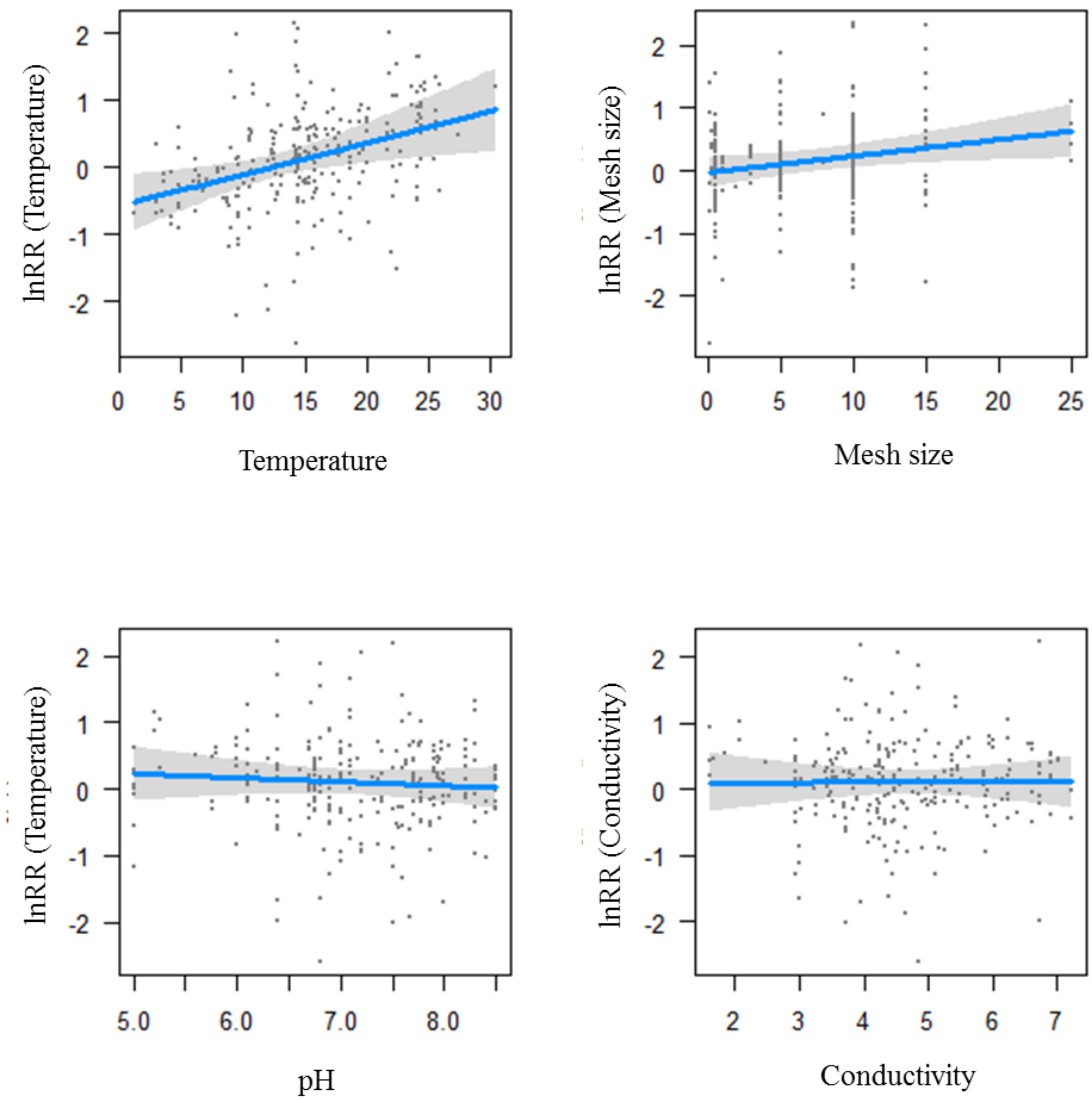

Figure 2.5 The mixed effects model's fit of the native-exotic response ratio to each coefficient (temperature, mesh size, pH, conductivity) with a P=0.05 confidence band.

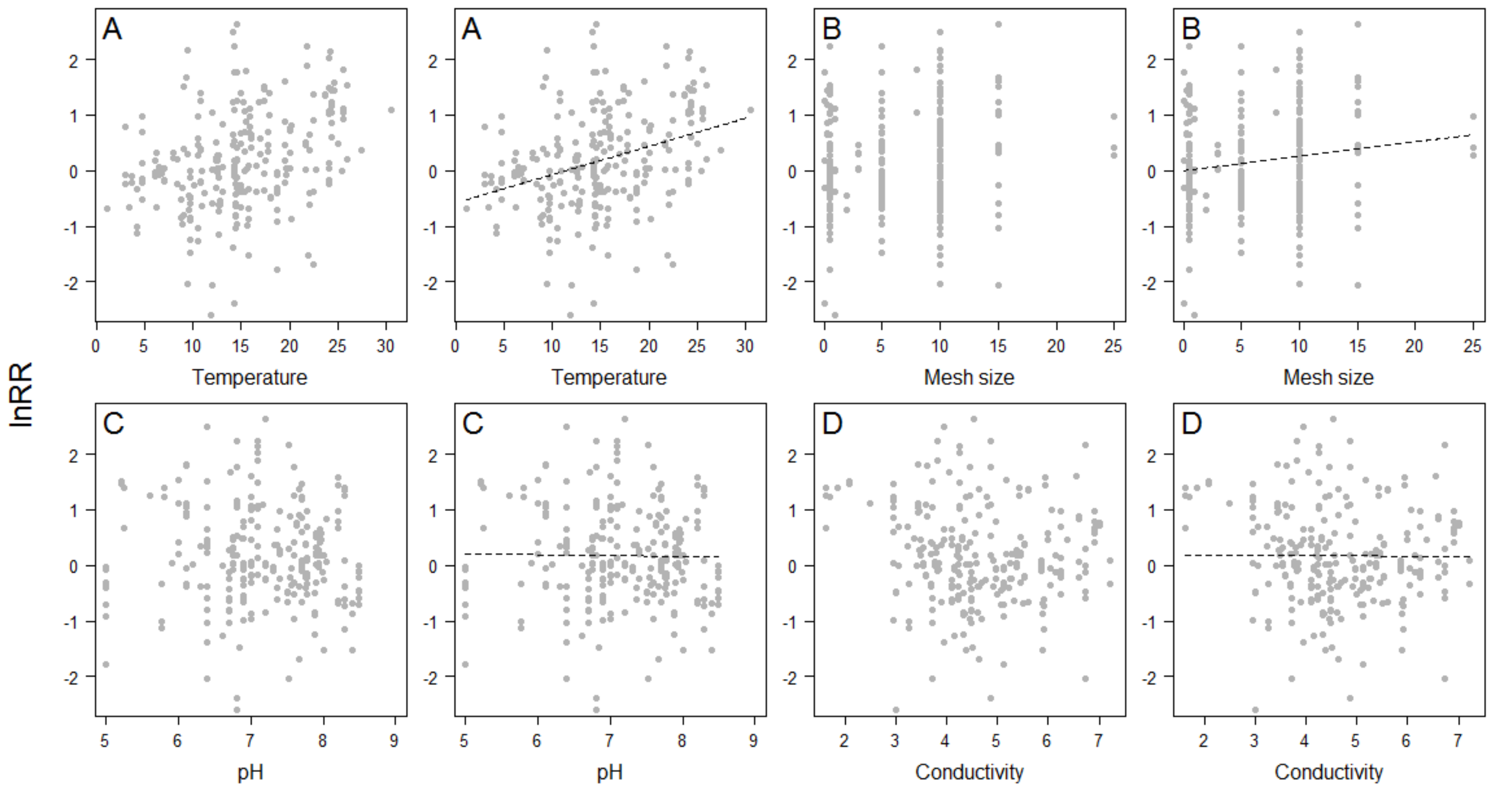

Figure 2.6 Paired plots of the native-exotic response ratio (lnRR) and each coefficient (A = temperature, B = mesh size, C = pH, D = conductivity) with (right) and without (left) the mixed effects model's line of best fit.

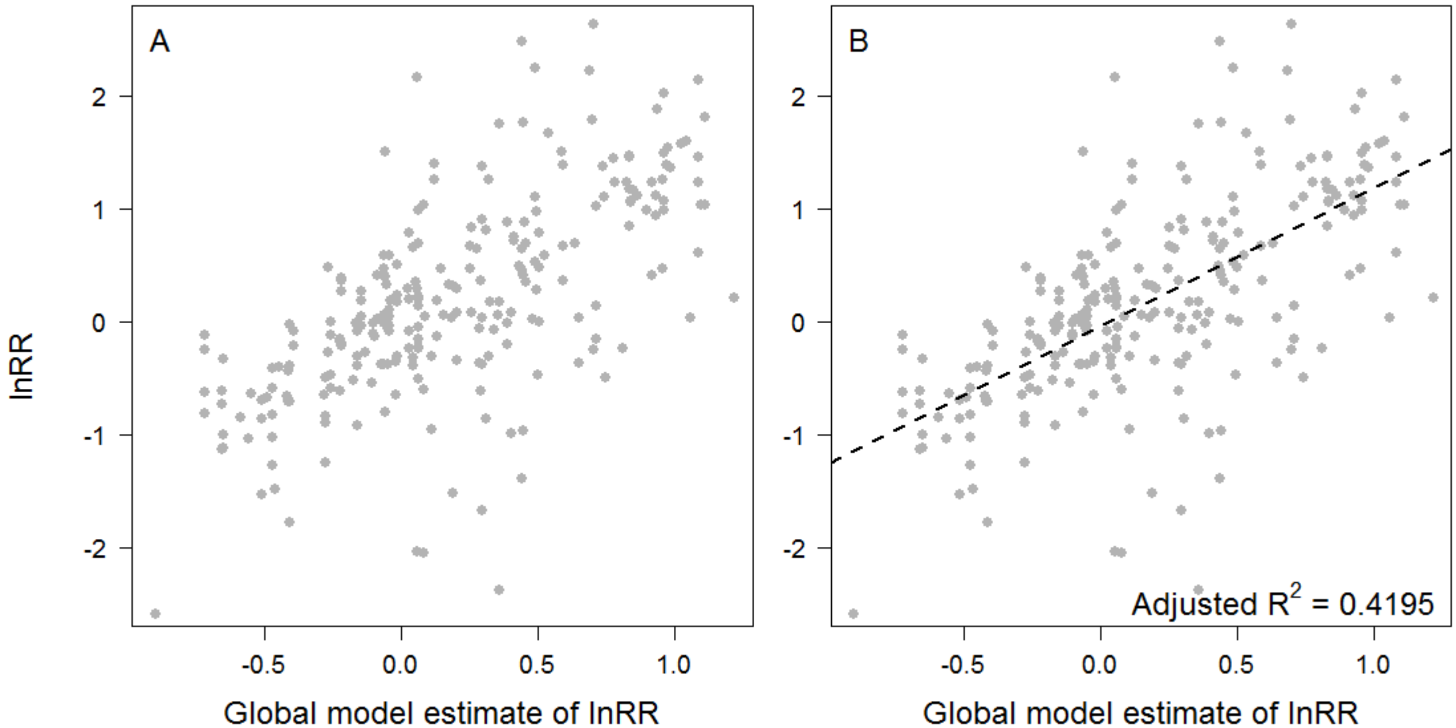

Figure 2.7 The "optimal random effects" global model's estimate of the native-exotic response ratio (lnRR) and the native-exotic response ratio (lnRR) with (B) and without (A) the line of best fit corresponding to the goodness-of-fit of the model.

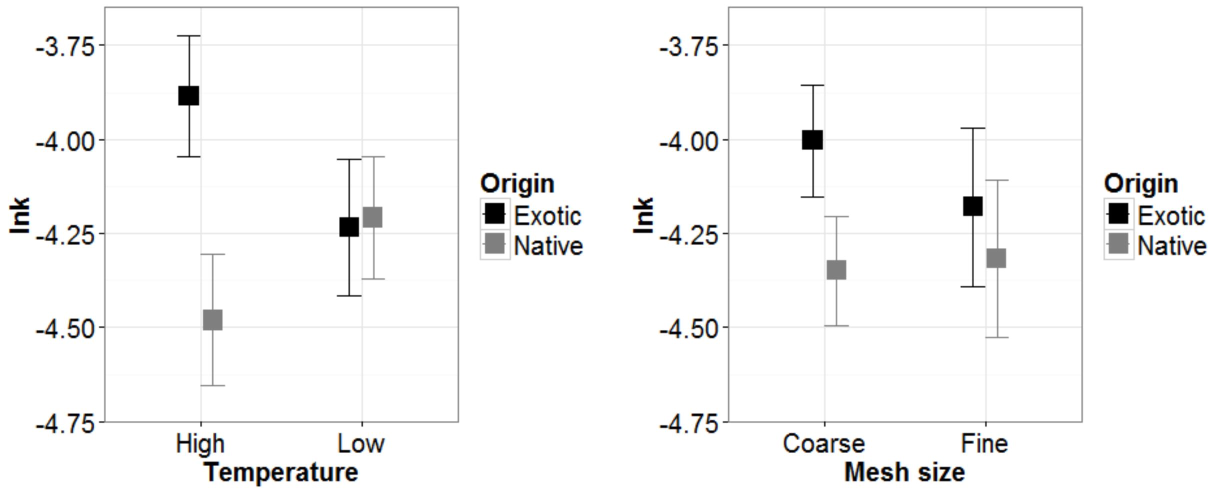

Figure 2.8 Mean litter decay rate (lnk) (± 95% CI) of leaf litter of different origins by high (14.7-30.5°C) and low (1.13-14.6°C) temperature groups, and by coarse (<3 mm) and fine (≥3 mm) mesh sizes.

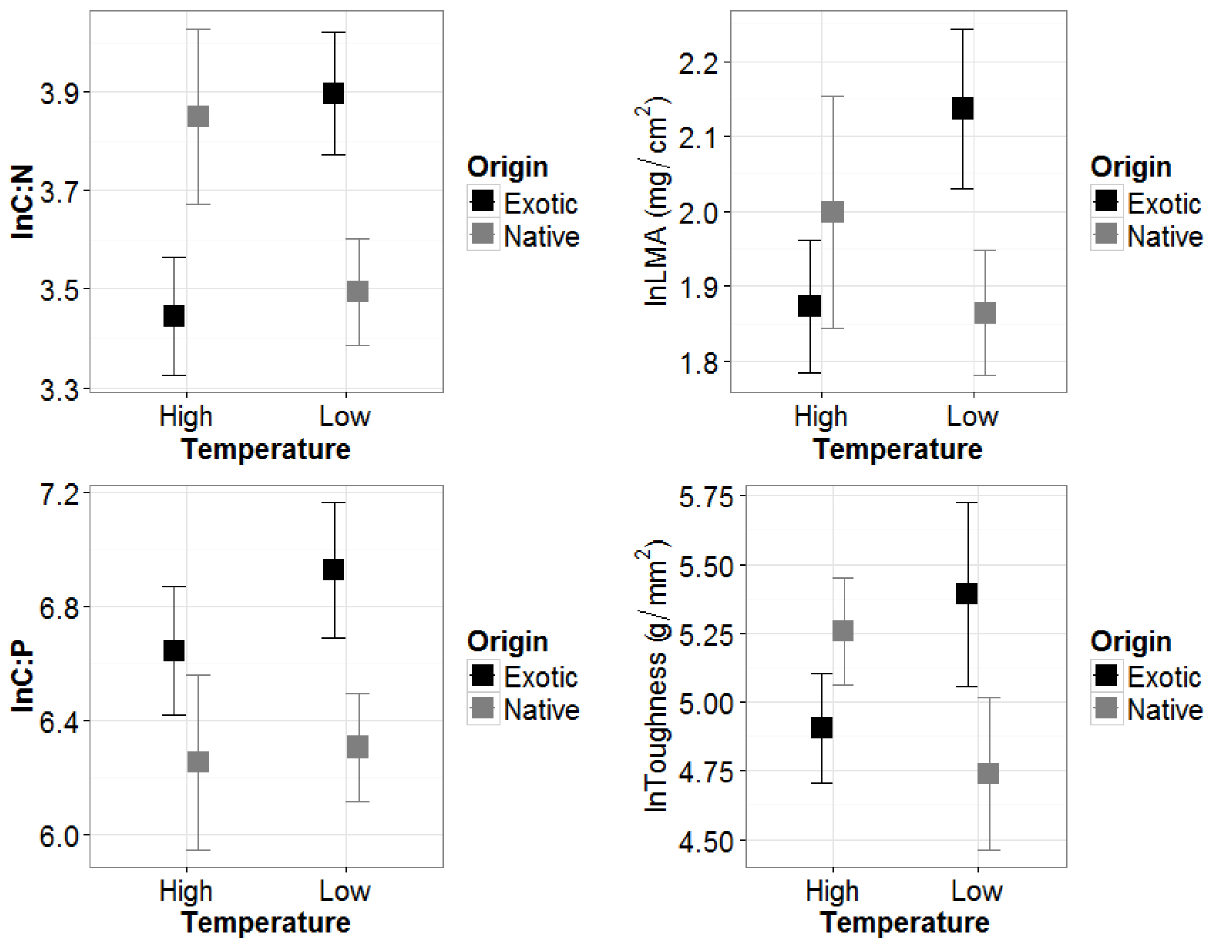

Figure 2.9 Mean litter quality values (ln C:N ratio, ln C:P ratio, ln LMA, and ln toughness) ± 95% C.I. of leaf litter of different origins by high (14.7-30.5°C) and low (1.13-14.6°C) temperature groups.

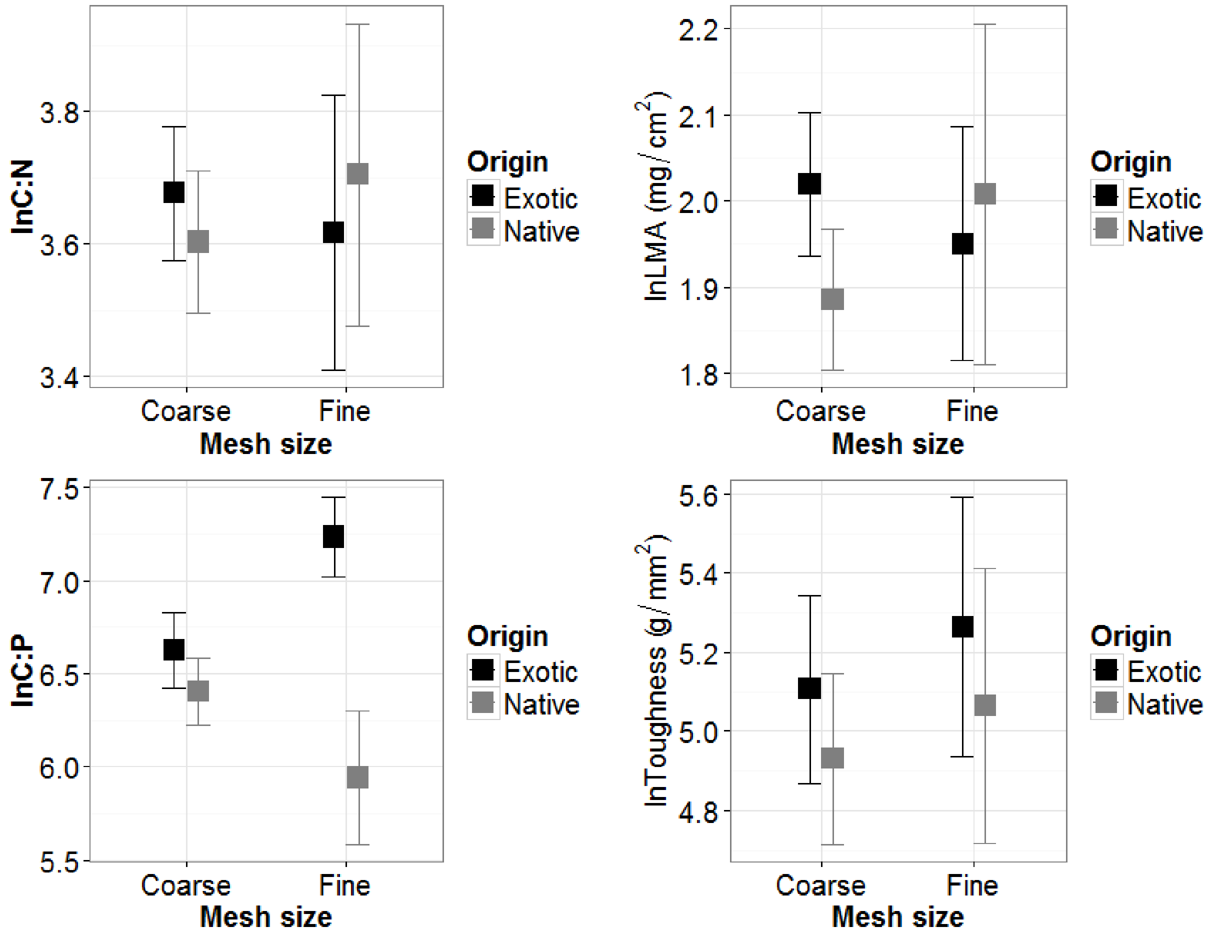

Figure 2.10 Mean litter quality values (ln C:N ratio, ln C:P ratio, ln LMA, and ln toughness) ± 95% C.I. of leaf litter of different origins by by coarse (<3 mm) and fine (≥3 mm) mesh sizes.

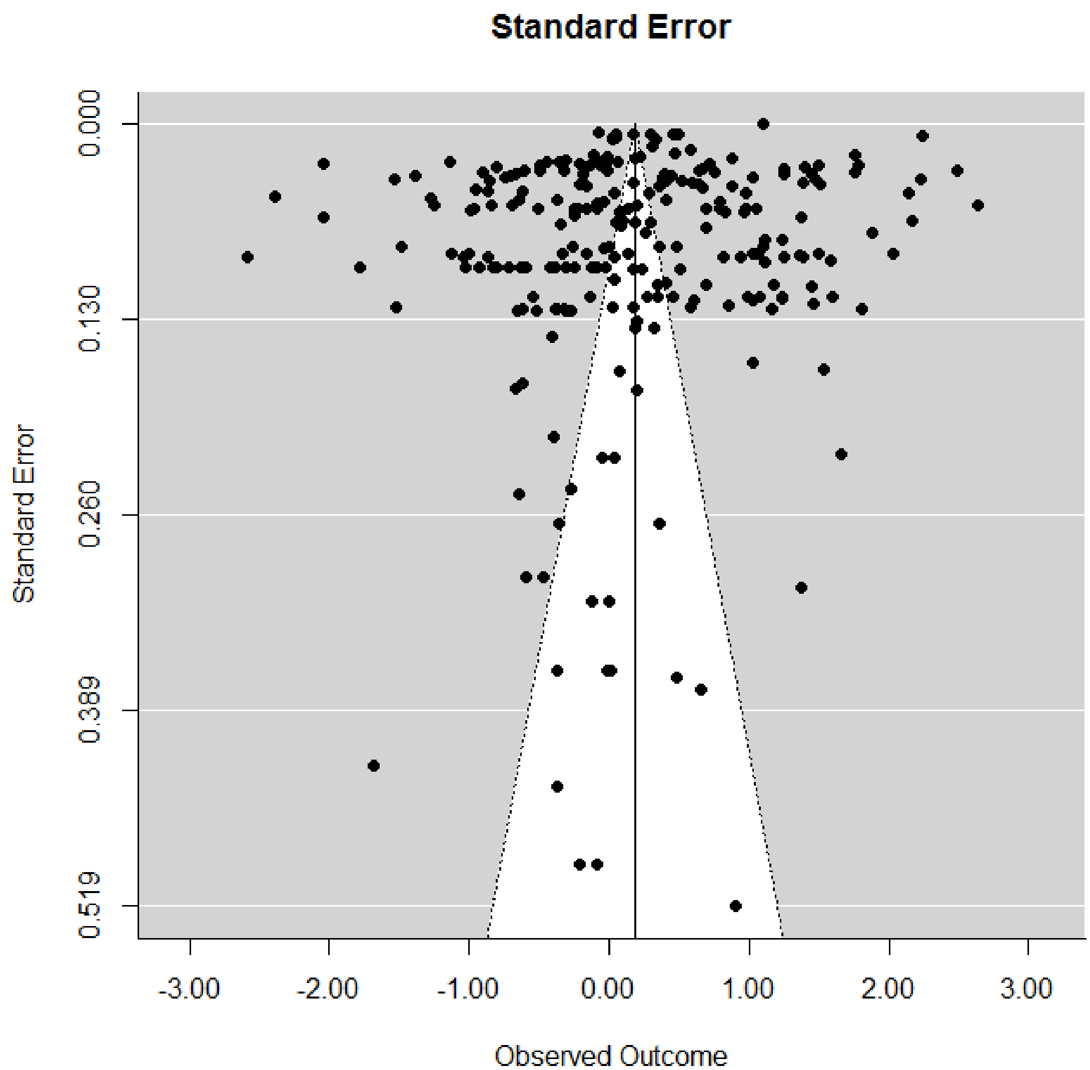

Figure 2.11 Funnel plot of all the native-exotic response ratios (Observed Outcome) and their respective standard errors (Standard Error), for the relative leaf litter decay rates of exotic and native species included in this meta-analysis.

Chapter 3 : Trash and invasive litter decay in urban streams

Abstract

Urban streams have been altered from their natural state through impacts such as hydrological, chemical, and biotic changes. Two less well-studied impacts on urban streams are plastic trash, and stream-side invasion by exotic plants, which alter in-stream litter subsidies, and cause changes that cascade up the aquatic food web.

I compared the decay rates and invertebrate colonizers of five types of litter packs in four urban streams in Victoria, B.C.: Native Red alder (*Alnus rubra*) and Sitka willow (*Salix sitchensis*), invasive English ivy (*Hedera* sp.) and Himalayan blackberry (*Rubus armeniacus*) and trash (styrofoam, plastic bag and Mylar). Four initial hypotheses were tested: 1) exotic leaves decay more slowly than native leaves; 2) exotic leaves attract fewer and less diverse stream invertebrates than native leaves; 3) plastic trash decays more slowly than leaves; and, 4) plastic trash attracts fewer and less diverse stream invertebrates than leaves.

Plastic trash decayed more slowly than leaf litter, but there was no difference between the decay rates of native and invasive litter species. Stream invertebrates colonized all pack types and were equally abundant and diverse in all litter materials. The invertebrate communities in the litter packs were reflective of the stream as a whole rather than the specific litter material. Significant differences in litter decay rates and invertebrate community alpha and Shannon diversities were also observed across the four different streams and these differences are likely related to differences in the environmental attributes of the streams.

My results indicate that urban stream invertebrate community similarity and stream invertebrate response to environmental change is difficult to predict based on geographic proximity, as even streams in the same or adjacent watersheds have very different litter decay regimes and biotic communities. Based on my results I recommend that stream trash removal should be a top priority, as plastic trash does not follow a natural decay rate and fragments to join the aquatic and marine food chains as toxic microplastic.

Introduction

Urban streams are highly valued both for recreation and because they allow urban populations to connect with nature, which is essential for human health and well-being (Bolund and

Hunhammar 1999, Asakawa et al. 2004, Grinde and Patil 2009, Shafer et al. 2013). However, through the process of human settlement and the encroachment of the built environment, urban streams have been substantially transformed from their origin as natural ecosystems. Urban streams are impacted by many hydrological, chemical, and biotic processes that can alter litter decay rates (Paul and Meyer 2001, Walsh et al. 2005b, Young et al. 2008). Leaf litter forms the base of the stream food web, is the main source of energy for the stream ecosystem and particularly in allochthonous streams, leaf litter decay rates ultimately determine whether stream biota starve or flourish (Abelho 2001, Tank et al. 2010, Wallace et al. 2015).

Urban streams have been structurally altered from their natural state and their waterways feature a high proportion of impervious infrastructure to manage erosion, floods and stormwater (Walsh et al. 2005a, Vietz et al. 2014, Booth et al. 2016). Alteration of the natural watershed to be covered by as little as 2% impervious surface adversely impacts stream biota including fish, invertebrates and microbes and negatively impacts stream health (Morse et al. 2003, Walsh et al. 2005b, Wenger et al. 2008, Vietz et al. 2014). Increased stream flow due to imperviousness and stormwater infrastructure causes litter decay through hydraulic abrasion and physical fragmentation; which can be an even stronger driver of decay than microbial or invertebrate processing (Miller and Boulton 2005, Chadwick et al. 2006, Paul et al. 2006, Yule et al. 2015).

Urbanization derived changes in water quality (e.g. increases in temperature, conductivity, acidification, heavy metal and hydrocarbon pollution, eutrophication, sediment, and anoxic conditions) impact the microbial and invertebrate stream communities, which in turn, impact litter decay rates (Maltby et al. 1995, Pascoal et al. 2005, Woodcock and Huryn 2005, Chadwick et al. 2006, Baldy et al. 2007, Imberger et al. 2008). Due to the adverse impacts of suboptimal water quality and hydrology, urban streams tend to exhibit a decline in members of the shredder functional feeding group, which are important invertebrate drivers of litter decay in natural systems (Miller and Boulton 2005, Pascoal et al. 2005, Martins et al. 2015). In some urban systems the role of shredder is assumed by alternate macrodecomposers such as crabs, shrimp, tadpoles and fish, and increasingly snails are being recognized as resilient facultative shredders in the reduced urban stream food web (Chadwick et al. 2006, Moulton et al. 2009, Yule et al. 2015).

Urban areas are also hotspots for exotic plant invasion facilitated through human intervention and anthropogenic impacts (Godefroid and Koedam 2007, Pickett et al. 2008, Kowarik

2011).The presence of exotic species can impact the structure and function of urban aquatic ecosystems and food webs (Rahel 2002, Riley et al. 2005, Ehrenfeld 2008). Allochthonous leaf litter from riparian plants forms the base of the urban stream food web (Vannote et al. 1980, Tank et al. 2010). Exotic plants and their partial or total replacement of endemic leaf litter subsidies can severely impact stream ecosystems by altering leaf litter decay regimes and causing shifts in the aquatic invertebrate community and trophic cascades up the food web (Swan et al. 2008, Boyero et al. 2012, Kominoski et al. 2013, McInerney et al. 2016). However, the impacts that foreign leaf litter could have on the urban stream ecosystem are difficult to predict and are less well understood than hydrologic and chemical impacts (Kominoski et al. 2007, Swan et al. 2008, Wenger et al. 2009, Rosemond et al. 2010).

Two common streamside invasive species on the Pacific Coast are English ivy (*Hedera helix, Hedera hibernica,* and their hybrid, hereafter *Hedera* sp.) and Himalayan blackberry (*Rubus armeniacus*); rogue horticultural plants that if unchecked, completely replace native species and impose novel ecosystems (Ingham and Borman 2010, Green et al. 2013, Gaire et al. 2015). Though these invaders are commonly found around streams in British Columbia, Washington, Oregon and California, their impact on aquatic litter decay rates and stream invertebrate communities has not yet been investigated. In addition, both exotic and native willows are often used during stream restoration to stabilize the stream bank and facilitate the establishment of taller and longer lived tree species (McLeod et al. 2001, Kuzovkina and Quigley 2005, Pezeshki et al. 2007). However, there is growing evidence that willows can also have a detrimental impact on in-stream fungal, algal and macroinvertebrate species, reduce stream biotic integrity, and drastically alter the structure of the invertebrate food web (Read and Barmuta 1999, McInerney et al. 2015, McInerney et al. 2016). There is also debate on whether the presence of willows increases or decreases litter decay rates (Schulze and Walker 1997, Serra et al. 2013, McInerney et al. 2015).

In this litter decay study I contrast the leaf litter decay rates of exotic English ivy and Himalayan blackberry with those of native Red alder (*Alnus rubra*) and a local native restoration species, Sitka willow (*Salix sitchensis*). I also compare the stream invertebrate communities that colonize the litter packs to see if stream invertebrate communities differ between the various litter materials. I predict that exotic leaf litter packs will degrade more slowly than native leaf litter because exotic leaves tend to be tougher and of lower nutritional quality than native leaves

(Casas et al. 2013, Larrañaga et al. 2014, Leite-Rossi et al. 2016). I also predict that exotic leaf litter will host a distinct and less diverse invertebrate community than native leaf litter, as invertebrates tend to colonize exotic leaves less abundantly and in different communities than those in native leaves (Serra et al. 2013, García et al. 2014, Leite-Rossi et al. 2016).

Plastic trash is the most ubiquitous anthropogenic litter material found in urban riparian areas, yet limited research has been done to investigate its impact on freshwater ecosystems (Hoellein et al. 2014, Wagner et al. 2014, Eerkes-Medrano et al. 2015). Plastic strips have been incorporated in previous litter pack decay studies as controls for invertebrate habitat, but have not yet been studied as a riparian subsidy in their own right (Bird and Kaushik 1992, Quinn et al. 2000b, Valdovinos 2001). As such, I also incorporate trash packs (*i.e.* styrofoam, plastic bag and Mylar) in my urban stream study to examine both their decay rate (a known contributor to aquatic microplastic) and their capacity as refugia for invertebrates. I predict that plastic trash packs degrade more slowly than natural leaf litter due to their non-water soluble properties, and very low observed rate of biodegradation in other environments (Mueller 2006, Shah et al. 2008, O'Brine and Thompson 2010). I also predict that plastic trash composed of hydrophobic, unnaturally smooth materials host a distinct and less diverse invertebrate community than natural leaf litter materials as invertebrates have had a very short time to adapt to these novel materials.

Methods

Study sites

The litter decay study was conducted between October 1st and November 28th 2014 in the Capital Regional District around Victoria, BC. The leaf litter decay experiment was carried out in four urban streams in the greater Victoria, BC area: Bowker Creek, Cecelia Creek, Francis King Creek and Swan Creek (Figure 3.1, Figure 3.2, Figure 3.3, Figure 3.4, and Figure 3.5). The leaf decay experiment was deployed from October 1st to November 26th 2014 at Cecelia Creek and Bowker Creek and from October 3rd to November 28th 2014 at Swan Creek and Francis King Creek in Francis King Regional Park.

All four urban streams are small and have relatively similar temperature, and pH profiles, although they have vastly different flow rates (Table 3.1). Bowker Creek, Cecelia Creek, and Swan Creek are all located in highly urbanized residential and industrial areas and have greater than 2% impervious cover across their watersheds; which is the threshold value associated with detrimental urban impacts on stream biota (Morse et al. 2003, Walsh et al. 2005b, Wenger et al. 2008, Vietz et al. 2014, Capital Regional District Integrated Watershed Management Program 2015) (See Table 3.1). Swan Creek has the largest watershed and discharge but has lower impervious cover, is approximately 20% piped, and is fed by Blenkinsop Creek and Swan Lake, and urban stormwater (Buchanan et al. 2009). Bowker Creek has the second largest watershed, a relatively high degree of impervious cover, is piped approximately 50% if its reach length, and is fed by urban stormwater (Capital Regional District 2011a, The Bowker Creek Initiative 2012, Capital Regional District Integrated Watershed Management Program 2015). Cecelia Creek is extremely urbanized as it has a relatively small watershed, has the greatest amount of impervious cover and is approximately 90% piped, and is fed by urban stormwater (Capital Regional District 2011b, Capital Regional District Integrated Watershed Management Program 2015). Francis King Creek is the smallest watershed in this study and is a forested watershed with less than 2% impervious cover, un-piped, and sourced through groundwater and the natural infiltration of rainwater (Pottinger Gaherty Environmental Consultants Ltd. and Northwest Hydraulic Consultants Ltd. 2000, Buchanan et al. 2009). Although found in a natural park environment, Francis King Creek faces ongoing human impacts including heavy recreational use and a history of homesteading and selective logging prior to 1967 (Crocker 1999, Buchanan et al. 2009), so it too is considered an urban impacted stream.

Each litter pack installation site in this study was situated in a stream reach that featured second-growth (Francis King Creek) or restored (Bowker, Cecelia, and Swan Creeks) canopy cover and a natural stream-bed in order to compare decay rates in similar environments and maximize the potential for invertebrate colonization. Stream temperature measurements were logged once an hour for the duration of the experiment using HOBO Pendant temperature loggers attached to the leaf pack apparatus. Stream chemistry was assessed prior to leaf pack collection on days 0, 6, 14, 27, and 56. Dissolved oxygen and conductivity were measured using a YSI Pro 2030 oxygen and conductivity probe. Stream pH was measured using a Hannah Instruments HI 98128 pH meter. Stream flow for each stream in the study was assessed at every collection date at five points between the upper and lower leaf pack sites using a Hatch FH950 flowmeter. Stream width was measured using a meter tape, and stream depth was measured using a meter stick. Discharge for each stream was measured and calculated once according to the midsection method (Gore 2007) (Table 3.1). Watershed size, % impervious cover, and %

watershed piped were collated from existing watershed documentation (Pottinger Gaherty Environmental Consultants Ltd. and Northwest Hydraulic Consultants Ltd. 2000, Buchanan et al. 2009, Capital Regional District 2011a,b, The Bowker Creek Initiative 2012, Capital Regional District Integrated Watershed Management Program 2015). Total impervious area was calculated as the watershed size multiplied by the % impervious cover.

Prior to litter pack installation or collection, baseline benthic invertebrates were collected from areas of the natural streambed approximately 2 m downstream of the litter pack installation sites, in each stream on each sampling date using a Wildco 0.086 m^2 Hess sampler following Taylor et al. (2001). Invertebrates from the Hess samples were processed in the same manner as the invertebrates from the litter packs, as described below.

Leaf pack preparation

Freshly-senesced leaves were collected September 2014 from several locations in Victoria, BC. English ivy (*Hedera* sp.) and Himalayan blackberry (*Rubus armeniacus*) leaves were collected when yellowed, but still attached to the plant. Red alder (*Alnus rubra*) and Sitka willow (*Salix sitchensis*) leaves were collected by shaking freshly senesced leaves from the tree. All leaves were air dried for two weeks and then oven-dried at 60°C for 72 hours prior to weighing. Leaves of each species were weighed out to 3.000 g ± 0.100 g (2.900 g - 3.100 g). Trash pack composition was based on the most common types of litter observed in Victoria B.C. streams. Each trash pack contained one 12 cm x 30 cm strip of plastic shopping bag (QuickMate-EZ High-density polyethylene (HDPE)), one 258 ml styrofoam (polystyrene (PS)) cup cut into eight even pieces and one 12 cm by 43 cm strip of Mylar (polyethylene terephthalate (PET)) to 3.000 g ± 0.100 g (2.900g- 3.100g) of material. The mass of styrofoam and plastic does not fluctuate with ambient humidity, and these materials tend to burn or melt when exposed to heat, thus the trash materials were not oven dried prior to weighing.

Litter packs of leaf litter or trash mix were contained in rigid 1 pint plastic strawberry baskets, zip tied within in a 10 mm green mesh bag (MasterNet H-62). The ridged baskets ensured that the mesh remained at 10 mm aperture size independent of the litter pack contents and decay state. Blank control packs (after Richardson et al. 2004) consisted of empty strawberry baskets zip tied within green mesh and were included in the study to control for the fact that simply placing apparatus in the stream creates habitat and attracts invertebrates. All packs (hereafter litter packs) were identified by zip tying 8.5 cm x 1 cm numbered metal tags (Universal Field Supplies) within each pack. Litter packs were randomized and zip tied to 122 cm lengths of rebar (24 leaf packs per bar, 10 bars per stream). In total there were six pack types, eight replicates of each pack type per collection date, collected across five time periods, at four streams locations, for a total of 960 packs (Figure 3.6).

Stream deployment

The litter pack-bearing rebar was installed at the stream sites by zip tying it lengthwise along nylon boat rope that was anchored to large trees at either end of the study site. The lengths of rebar were then arranged in a line parallel to the stream flow in the deepest part of the stream and weighed-down with zip tied bags of rocks at each end of the bar. Leaf packs were allowed to decay in the natural stream environment and eight of each pack type per stream were collected on days 0, 6, 14, 27, and 56. Collected leaf packs were kept chilled and returned to the lab for processing.

Pack processing

In the lab litter pack material was rinsed free of invertebrates and non-litter debris (silt and sediment) with tap water over a 250 μm sieve. Litter material was retained and oven-dried at 60°C for 72 hours prior to weighing. Then to correct for inorganic sediment accrual, litter material was ashed at 550°C for 40 minutes according to the protocol set out by Benfield (2007). As trash materials were unable to be safely ashed, they were instead cleaned by a three-minute cycle of an ultrasonic cleaner filled with tap water to dislodge any inorganic debris. Then the trash was air-dried for two weeks prior to final weighing. Organic sediment accrual, though minimal, could not be accounted for through ashing or ultrasonic cleaning and as a result actual litter decay rates could be marginally higher than those reported here. Hess samples were rinsed with tap water over a 250 μm sieve and the invertebrates were picked out of the particulate matter, preserved and identified as described below.

All invertebrates collected on the 250 um sieve were preserved in 70% ethanol and all invertebrates from the day 14 collection period were identified to family or lowest practical taxonomic level (i.e. Oligochaeta, Hirudinea, Copepoda, and Nemetoda), and were assigned to a functional feeding group (Barbour et al. 1999, Chadwick et al. 2006, Merritt and Cummins 2007). Day 14 was chosen because sufficient time had passed to allow a wide-range of invertebrates and microbial detritivores to colonize the litter packs, yet all litter types were still available in sufficient quantity to provide a full range of options for habitat choice.

Data analysis

Statistical analysis of all data was performed using R (R Core Team 2016). A handling loss correction was applied to the final litter pack mass loss data based on mass losses during the day 0 collection period. Decay rates per day (k) and per degree-day (kdd^{-1}) were calculated for each litter pack according to the exponential decay formula (Benfield 2007), using the average daily stream temperature as appropriate. The per-day and per degree day decay rates displayed the same trends, so only the per day decay rate data were focused on. Litter decay data were tested for normality and homogeneity of variance. As the litter decay rates were not normal, comparisons of decay rates across pack types and stream types were tested using Kruskal-Wallis tests and Nemenyi post hoc tests from the R package 'PMCMR' (Pohlert 2016) as appropriate. The post hoc results were graphed using the 'ggplot2' package (Wickham et al. 2016).

The invertebrate community data were examined in two ways: first, the invertebrate species count data from the litter packs were analysed using unconstrained ordination (indirect gradient analysis) (Lepš and Šmilauer 2003). The Hellinger transformation was applied to the community count data due to the high count variation and the large number of zeros present (Legendre and Legendre 1998). Then, species making up less than 2% of the dataset were omitted to prevent the disproportionate influence of rare species on the community ordination (McCune and Grace 2002). The unimodal ordination approach of detrended correspondence analysis (DCA) was chosen due to the heterogeneity of the data (Lepš and Šmilauer 2003). To identify community similarity across stream types or pack types the DCA was performed in R (R Core Team 2016) using the 'vegan' package (Oksanen et al. 2016) and Bayesian clustering was performed using the 'Mclust' package (Fraley et al. 2016). The resultant ordination plot was graphed using 'ggplot2' (Wickham et al. 2016). A similar ordination procedure was performed on the Hess invertebrate samples.

For each day 14 litter pack alpha diversity, and a Shannon diversity index score was calculated based on the number of individuals and families present. The alpha diversities and Shannon diversity index scores were both compared across pack types and stream types using analysis of variance (ANOVA) or Kruskal-Wallis tests if the assumptions of ANOVA were not met. If a significant difference was detected, then Tukey post-hoc tests or Nemenyi post hoc-tests were performed to detect the specific differences between pack types or stream sites. The post hoc results were graphed using the ‘ggplot2’ (Wickham et al. 2016).

Results

Litter decay results

Analysis of litter decay results showed that leaf litter decayed significantly differently depending on the litter pack material (Kruskal-Wallis $H_{4,631} = 175.75$, $P<0.001$) (Figure 3.7, Table 3.2, and Table 3.3), and the stream site (Kruskal-Wallis $H_{3,631} = 68.49$, $P<0.001$) (Figure 3.7, Table 3.3, and Table 3.4).

Differences in the decay rates of different litter types were as follows: trash decayed significantly more slowly than alder (Nemenyi H = 143.672, P<0.001), blackberry (Nemenyi H = 91.564, P<0.001), ivy (Nemenyi H = 82.111, P<0.001), and willow (Nemenyi H = 105.819, P<0.001), (Figure 3.7, Table 3.4, and Table 3.5). However, there were no significant differences between the decay rates of the different leaf litter types, and analysis of degree-day decay rates corrected for temperature differences yielded the same results (Table 3.5).

Significant differences in all litter decay rates combined by stream site were also observed: Litter packs in Bowker Creek decayed significantly more quickly than Cecelia Creek (Nemenyi H = 23.549, P<0.001), Francis King Creek (Nemenyi H = 66.070.162, P<0.001), and Swan Creek (Nemenyi H = 11.000, P=0.012). Also, litter packs in Francis King Creek decayed more slowly than those in Cecelia Creek (Nemenyi H = 10.770, P= 0.013) and Swan Creek (Nemenyi H = 23.480, P<0.001) (Figure 3.7 and Table 3.4). The analysis of stream site degree-day decay rates yielded similar results, except the decay rates at Bowker and Swan Creeks were only marginally significantly different (Nemenyi H = 7.813, P=0.050) and the decay rate differences at Francis King Creek and Cecelia Creek were no longer statistically significant when the temperature correction was made (Table 3.5 and Figure 3.8). In addition, positive correlations were noted between decay rates and pH, stream flow, and total impervious area (Figure 3.9, Figure 3.10, and Figure 3.11).

Invertebrate community results

Each stream hosted a unique community of invertebrates, and had aproximately the same number of taxa present in each functional feeding group (Table 3.6). However the abundance of individuals in each functional feeding group differed for each stream (Table 3.6 and Figure 3.12). Bowker Creek was dominated by gathering collectors, with predators, shredders, snails, and filtering collectors and other groups also fairly prevalent. The top four taxa present in Bowker Creek, representing 87% of the invertebrates present were Oligochaeta, Chironomidae, Crangonyctidae, and Sphaeriidae. The most common groups in Cecelia Creek were gathering collectors and predators, with a few omnivores and other taxa also present. The top three taxa present in Ceclia Creek, representing 98% of the invertebrates present were Oligochaeta, Chironomidae, Hirudinea, and Dugesiidae. Francis King Creek was dominated by gathering collectors and shredders, with a few predators, filtering collectors, omnivores and other groups. The top three taxa present in Francis King Creek, representing 71% of the invertebrates present, were Lepidostomatidae, Chironomidae, Dixidae, and Sphaeriidae. Swan Creek was predominantely represented by gathering collectors with a few predators shredders and snails and other groups present. The top three taxa present in Swan Creek, representing 97% of the invertebrates present, were Chironomidae, Oligochaeta, Copepoda, and Crangonyctidae. Shredders were found in relatively low numbers at all streams except for Francis King, and shredder numbers do not seem to reflect the leaf litter decay rates measured for each stream. Bowker Creek and Swan Creek were also home to crayfish (Astacidae), which may play an important role in leaf litter processing (Huryn and Wallace 1987, Schofield et al. 2001).

Earthworms (Oligochaeta) were present in large numbers but were omitted from further analysis for all streams due to count uncertainty and because they likely did not impact leaf decay rates. The earthworms in the samples were exceptionally prone to fragmentation and as such, earthworm counts could be overestimated by a factor of five. Earthworms are terrestrial taxa that tend to use streams as dispersal corridors (Costello et al. 2010). It is also unlikely that they were feeding on leaf litter; Ward's 1976 study on earthworms in streams concluded that epilithic bacteria and diatoms were their main sources of food based on gut contents of sand grains, fine detritus and diatoms, which seem consistent with geophage feeding ecology (Curry and Schmidt 2007). The biomass of earthworms ranged from 0.03-1.15X the biomass of aquatic invertebrates and the percentage of individual oligochaetes present appeared to be directly proportional to the percent of the stream watershed that was piped, which supports an earthworm dispersal vector of transportation via the stormwater system (Table 3.6 and Table 3.7).

The DCA ordination plot of litter pack invertebrates by community similarity (Axis 1 length = 2.718, Eigenvalue =0.4349; Axis 2 length =2.580, Eigenvalue =0.2768) showed that the litter pack communities were generally clustered and more ecologically similar according to stream site rather than pack type (Figure 3.13).

In quantitative confirmation of trends observed in the DCA plot, four litter pack community clusters were identified by Bayesian cluster analysis, with the three main clusters centered on the Francis King packs, the Swan Creek packs and the Cecelia Creek packs (n=174, df=17, log likelihood = -149.123, BIC = -385.950, Integrated Classification Likelihood (ICL) = -409.653) (Figure 3.14 and Figure 3.15). The Bowker Creek packs were distributed across the Swan Creek and Cecelia Creek clusters. A DCA ordination plot and Bayesian clustering of litter pack invertebrates and background invertebrates (i.e. those collected by Hess samples) by community similarity, and DCA ordination plot and Bayesian clustering the background invertebrates (Hess samples) alone showed similar trends of clustering by stream, and indicated that the invertebrates found in the litter packs were representative of the invertebrate community in the stream as a whole (Figure 3.16 and Figure 3.17).

Analysis of invertebrate diversity within the week two litter packs showed that alpha diversities were not significantly different across litter pack type (ANOVA $F_{5,181} = 0.861$, P=0.508), but were significantly different across stream site (Kruskal-Wallis $H_{3,181} = 88.544$, P<0.001) (Figure 3.18, Table 3.8, Table 3.9, and Table 3.10). The alpha diversity of Bowker Creek was significantly lower than that of Cecelia Creek (Nemyeni H = 11.384, P=0.010), Francis King Creek (Nemyeni H = 84.233, P<0.001), and Swan Creek (Nemyeni H = 19.358, P<0.001). In addition, the alpha diversity of Francis King Creek was significantly higher than Cecelia Creek (Nemyeni H = 38.277, P<0.001) and Swan Creek (Nemyeni H = 26.025, P<0.001) (Figure 3.18, Table 3.9, and Table 3.10).

Similarly, analysis of invertebrate diversity within the week two litter packs showed that the Shannon diversity index score was not significantly different across litter pack type (ANOVA $F_{5,181} = 1.944$, P=0.0894), but was significantly different across stream site (Kruskal-Wallis $H_{3,181} = 88.866$, P<0.001) (Figure 3.18, Table 3.8, Table 3.9, and Table 3.10). The Shannon diversity index score of Francis King Creek was significantly higher than that of Bowker Creek

(Nemyeni H = 57.437, P<0.001), Cecelia Creek (Nemyeni H = 34.577, P<0.001), and Swan Creek (Nemyeni H = 72.322, P<0.001) (Figure 3.18, Table 3.9, and Table 3.11). In addition, negative correlations were noted between invertebrate diversity and most stream attributes examined in this study (Figure 3.19, Figure 3.20, and Figure 3.21).

Discussion

My study found that invasive English ivy and Himalayan blackberry leaves decayed at rates similar to those of native Red alder and Sitka willow leaves in all four urban streams, which refutes my hypothesis that that exotic leaf litter packs would degrade more slowly than native leaf litter (Figure 3.7).

My results are the first to show that the two most important invaders in Pacific Coast streams English ivy and Himalayan blackberry as well as the restoration species Sitka willow all decay similarly to the native Red alder. Similarly, in heavily impacted urban stream ecosystems, Harner et al. (2009) found that native cottonwood (*Populus deltoides* ssp. *wislizeni*), and exotic Russian olive (*Elaeagnus angustifolia*) decayed at similar rate, and Pérez et al. (2014) found that native European alder (*Alnus glutinosa*) and exotic Eucalyptus (*Eucalyptus globulus*) had similar decay rates. Predicting species specific litter decay rates in urban streams is difficult because exotic species can decay faster, slower, or at the same rate as native species, depending on the litter species and their leaf litter qualities (Table 3.12). Litter decay experiments in pristine conditions can be a poor predictor of relative decay rates in urban streams because native and exotic species can show significantly different litter decay rates at natural and urban sites, as eutrophication and elevated stream flow in urban streams will cause exotic litter decay to accelerate relative to native litter decay, or vice versa (Molinero et al. 1996, MacKenzie et al. 2013 Pérez et al. 2014).

The major differences in litter decay rates of all materials seemed to be due to differences at the stream sites (Figure 3.7 and Table 3.1). These differences are particularly striking as the watersheds are either adjacent to each other (Bowker Creek, Cecelia Creek, and Swan Creek) or are smaller watersheds within in the same urban river system (Francis King Creek and Swan Creek). My study highlights how differences in the extent of urban impacts and discontinuities within a watershed can result in considerable variation among the streams. Relative decay rates in my streams are likely governed by three drivers - two hydrologic factors: 1) flashiness due to watershed total impervious area (TIA) (Allan 2004, Walsh et al. 2005a, 2005b, Kaushal and Belt 2012); 2) baseline discharge (Ferreira et al. 2006, MacKenzie et al. 2013); and, also by 3) biologically mediated decay factors (including the presence of shredders, crayfish, and elevated dissolved oxygen (DO) levels that permit biological activity) (Graça 2001, Schofield et al. 2001, Pascoal and Cássio 2004). The highest mean decay rates were observed at Bowker Creek, which had the largest TIA and a relatively high discharge, low shredders, crayfish, and the second highest DO.

Flashiness is highly correlated with total impervious area in urban streams because rainfall funnels into the stream across impervious surface cover (a defining feature of urban landscapes) (Allan 2004). Flashiness is a chief contributor to the characteristic degradation of urbanized waterways known as the “urban stream syndrome” (Walsh et al. 2005b, Kaushal and Belt 2012). Bowker and Cecelia Creeks have been identified as flashy streams based on their sudden depth and flow increases in response to rainstorms (Capital Regional District and Green, personal communication, 2016). In my study the degradation of trash relative to that of natural leaf litter materials in each stream can be used as a proxy measure to isolate the effects of stream flow abrasion vs. those of biological litter decay processes, as trash can be quickly fragmented by abrasion, but not through microbial and invertebrate degradation. In both Bowker Creek and Cecelia Creek trash packs exhibited a sudden and substantial mass loss around day 22, which corresponds to a large rainstorm event (17.8 mm) on October 25, 2014 (Environment Canada 2016) (Figure 3.22). Swan Creek and Francis King Creek received the same rainstorm, but their trash packs remained unaffected. Analysis of trash-only decay results by stream site showed that leaf litter decayed significantly differently depending on the stream (Kruskal-Wallis $H_{3,94}$ = 33.578, P<0.001), with faster decay rates noted in Bowker Creek and Cecelia Creek ((Table 3.13, Table 3.14, and Table 3.15). This suggests that Bowker Creek and Cecelia Creek are more susceptible to physical abrasion from sudden high flows, whereas perhaps microbial and invertebrate degradation are more important drivers of decay in Swan Creek and Francis King Creek.

Higher discharge has been associated with elevated litter decay rates through the abrasive action of stream flow (Ferreira et al. 2006, MacKenzie et al. 2013), and the presence of shredders, crayfish, and elevated microbial processing at higher levels of DO, are all correlated with increased litter decay rates (Graça 2001, Schofield et al. 2001, Pascoal and Cássio 2004). It is likely that any of these factors or the interaction of more than one factor causes the decay rate in Bowker Creek to be higher. However, specific tests need to be conducted to isolate and confirm the effects of each specific driver. My study clearly indicates that urban streams are not homogenous systems and they can show wide variation in litter decay rates and invertebrate communities, even when they are located within relatively close proximity to one another, and even when they are above the 2% impervious cover threshold. Future studies designed to control for variation in urban gradient may be able to tease apart the interconnected drivers of litter decay left uninvestigated in this preliminary study.

I also found that trash decays at about half the speed of leaf litter in urban streams, which supports my hypothesis that trash would decay slower than natural litter materials in urban streams (Figure 3.7). O'Brine and Thompson (2010) reported a 2% decay after 40 weeks for plastic bags submerged in a marine environment, which is equivalent to a decay rate (k) of 7.22×10^{-4} per day, and is quite a bit slower than my observed mean decay rate (k) of 0.0101 per day. One reason for the relatively high mean trash decay rates I observed was that in two streams, physical abrasion by stormwater caused scouring and caused pack materials to be swept away (Figure 3.22). In streams that are not susceptible to stormwater scouring, I expect plastic trash decay rates to be much lower.

Contrary to my hypothesis that exotic leaf litter would host a distinct and less diverse invertebrate community than native leaf litter, I found that in each stream, the stream determined the invertebrate community, which colonized all litter packs with equal abundance and diversity (Figure 3.13 and Figure 3.18). Other studies have also found that invertebrates colonized native and exotic litter materials equally despite differences in leaf litter origin (Laćan et al. 2010, Bottollier-Curtet et al. 2011, Gonçalves Jr et al. 2012). My study shows that the same pattern holds for two widespread exotic invaders (Himalayan blackberry and English Ivy) and for an important restoration species (Sitka willow). My observations of invertebrate colonization confirms the prospect that in urban streams invertebrates do not differentiate by leaf origin, and that native and exotic leaf litter are of equal availability as primary subsidies for the urban stream food web (Braatne et al. 2007). Based on my results, the presence of Himalayan blackberry and English ivy does not seem to be altering the natural aquatic litter decay regime or the stream invertebrate community. I also found that native Sitka willow followed the natural litter decay regime and attracted a diverse community of invertebrates. My litter decay results suggest that urban stream invertebrate communities may be able to colonize the full spectrum of exotic litter materials that grow in the increasingly globalized urban ecosystem.

I also found evidence that the stream invertebrate community in the litter packs tends to reflect the stream community as a whole, irrespective of pack material type, as shown by diversity metrics and ordination of invertebrate community data (Figure 3.13). I show that urban streams with the same or adjacent watersheds have distinct invertebrate communities that each show a unified and rapid response to novel litter materials (Figure 3.13 and Figure 3.18). This trend of the stream rather than litter material being the chief determinant of invertebrate community composition is also supported by other studies (Leroy and Marks 2006, Bo et al. 2014, Rezende et al. 2014), and I show this trend continues even at very close proximity in the urban environment. Despite having similar diversity of functional feeding group taxa, the abundances of each functional feeding group varied widely between streams. Quite striking were the very low numbers of shredders at three of the four streams. Only Francis King Creek hosted a large number of sensitive taxa like mayflies, stoneflies and caddisflies, which shows that even a small parkland with a substantial history of human use can be an oasis of biodiversity as long as it is not impacted by impervious cover. Stepenuck et al. (2002) observed that as watershed imperviousness increases, collectors and gatherers increase, while scrapers, shredders and filterers, Shannon diversity, % Ephemeropteran, Plecopteran, and Trichopteran taxa, and taxa richness all decrease. Likewise Miserendino and Masi (2010) found that as human land use and urbanization increased collector gatherers tended to increase, while shredders, collector filterers, scrapers/grazers and predators all tended to decrease. I observed a similar increase in collector gatherers and a general decrease in shredders and scrapers, but other shifts in functional feeding groups did not seem to follow the urbanization gradient in a predictable way.

Surprisingly, trash packs and empty control packs in urban streams attracted the same diversity and abundance of invertebrates as the natural leaf packs (Figure 3.13 and Figure 3.18). Although invertebrates often prefer natural substrates (Richardson 1992a, Negishi and Richardson 2006, Hofer and Richardson 2007), plastic leaf litter substitutes have also been observed by other studies to support invertebrate communities similar to those of natural leaf litter materials (Bird and Kaushik 1992,Quinn et al. 2000b, Valdovinos 2001), this shows that habitat structure is very important to stream invertebrates and confirms that even though a substrate is not of nutritional value it is still attractive as an invertebrate habitat. Pomeroy et al. (2000) observed that invertebrates found in litter packs were not necessarily using the litter pack material as a food source. My observation of the trash and blank control packs was that they readily collected stream sediment and grew a substantial periphyton cover quite quickly. My trash and blank control packs also contained the same abundance and diversity of stream invertebrates that my natural litter packs did, which is contrary to previous observations of empty control packs and artificial leaf packs showing lower invertebrate abundance and diversity than natural leaf packs in forested stream ecosystems (Richardson 1992a, Richardson et al. 2004, Hofer and Richardson 2007). My observation of similar colonization of blank and control packs suggests that urban stream biota may be attracted by the intrinsic properties of the plastic mesh itself. This has uncertain implications for any mesh litter bag study focusing on the invertebrate community, and should be investigated further. My blank control packs demonstrate that in eutrophic urban streams artificial substrates can quickly accumulate sufficient sediments and primary trophic biomass to support an invertebrate community similar to that found in natural leaf litter. This has promising implications for the use of anchored synthetic refugia as a restoration technique to increase stream invertebrate habitat in areas where heterogeneous habitat structure is lacking, provided necessary trophic resources are also available.

One clear trend that I observed is that the trash mix of Styrofoam, Mylar and shopping bag plastic does not tend to decay very quickly in streams (Figure 3.22). I recommend frequent stream clean up and trash removal to prevent plastic garbage from accumulating faster than natural litter materials and changing the nature of resources and refugia available to the invertebrates and the wider stream ecosystem. Stream flow carries plastic trash to the ocean where the plastic is fragmented through environmental forces into fine microplastic particles which rapidly accumulate hydrocarbons and other persistent organic pollutants (Wright et al. 2013, Eerkes-Medrano et al. 2015). Toxic microplastic particles are then consumed at all levels of marine and freshwater food webs, (including seafood for human consumption), leading to illness and death (Wright et al. 2013, Galloway 2015). If we do not remove trash from urban streams, that trash is eventually swept downstream and into lakes or the ocean, where it is much harder to remove and has much graver ecological impacts.

Conclusion

In conclusion, I found that both native and exotic leaf litter species decay at similar rates and that trash decays at much slower rates than natural leaf litter materials in urban streams. I also found that that both trash and litter materials attract similarly diverse and abundant stream invertebrate communities. In urban areas, the stream itself is the chief driver of differences in litter decay rates and the type of invertebrate community present and this is likely due to hydrologic factors unique to each urban stream, including total impervious area, and the community of microbial and invertebrate decomposers present. Geographic proximity may not be a good predictor of stream similarity, and response to environmental changes as even streams in the same or adjacent watersheds have very different biotic communities and litter decay regimes.

My research shows that urban stream invertebrate communities are highly responsive to novel materials, and take full advantage of any subsidies that they receive. Future research on the role of earthworms in urban streams, and the impact of blackberry, ivy and Sitka willow on microbial communities and stream chemistry would help complete our understanding of urban streams and the impact of novel litter on the urban stream ecosystem. Urban streams, no matter how small, are oases of biodiversity and host very different communities even when they are located within close proximity to one another and face similar urban impacts. Urban streams are an important place for people to connect with nature and we should treasure them and care for them by keeping them clear of trash.

Tables

Table 3.1 Physical and hydrological attributes for each stream.

Stream	*Bowker*	*Cecelia*	*Francis King*	*Swan*
Latitude	48.47194	48.443764	48.482607	48.466874
Longitude	-123.308844	-123.378910	-123.445833	-123.400317
Stream width (m)	3.03	2.99	0.61	2.99
	(1.01 - 4.85)	(2.25 - 4.11)	(0.26 - 1.20)	(0.54 - 5.08)
Stream depth (m)	0.24	0.30	0.04	0.28
	(0.07 - 0.54)	(0.12 - 0.56)	(0.03 - 0.09)	(0.06 -0.70)
Stream flow (m/s)	0.26	0.09	0.08	0.24
	(0.02 - 0.74)	(0.02 - 0.24)	(0.02 - 0.16)	(0.00 - 0.94)
Discharge (L/s)	43.7	14.8	0.6	148.9
Dissolved oxygen (%/L)	89.9	66.4	96.2	71.3
	(84.7 - 98.0)	(39.3 - 95.7)	(95.3 - 97.8)	(69.6 - 73.0)
Conductivity (µs/cm)	206.8	351.6	74.9	251.1
	(139.3 - 269.2)	(262.6 - 481.2)	(66.2 - 80.7)	(186.8 - 294.8)
Specific conductance (µs/cm)	262.1	429.7	104.3	337.5
	(181.3 - 333.3)	(331.1 - 586.1)	(91.8 - 111.8)	(269.5 - 387.8)
pH	7.94	7.70	7.87	7.76
	(7.72 - 8.21)	(7.29 - 8.03)	(7.39 - 8.25)	(7.43 - 7.98)
Temperature (°C)	12.46	14.28	9.69	10.72
	(6.67 - 15.86)	(8.28 - 18.43)	(5.96 - 11.82)	(3.89 - 14.61)
% Impervious cover	47.5%	61.4%	<2%	24.1%
% Watershed piped	~50%	~90%	0%	~20%
Watershed size (ha)	1028	360	110	1200
Total Impervious Area (ha)	488.3	221.04	<2.2	289.2

Table 3.2 Mean values, standard errors (SE) and sample sizes (n) for the litter decay rates by day (k) and by degree day (kdd^{-1}) according to litter pack type.

Pack type	*Alnus rubra*	*Hedera* sp.	*Rubus armeniacus*	*Salix sitchensis*	*Trash*
mean k	0.0405	0.0359	0.0455	0.0373	0.0101
SE k	0.0067	0.0094	0.0090	0.0078	0.0037
n k	125	127	128	128	123
mean kdd^{-1}	0.0031	0.0027	0.0034	0.0028	0.0008
SE kdd^{-1}	0.0005	0.0007	0.0007	0.0006	0.0003
n kdd^{-1}	125	127	128	128	123

Table 3.3 Comparison of the litter decay rates by day (k) and by degree day (kdd^{-1}) according to differences by litter pack type and by stream, including the sample size (n), degrees of freedom (df), the statistical test used, the test statistic calculated, and the significance of the test (*P*).

Group	*Decay rate*	*n*	*df*	*Statistical test*	*Test statistic*	*P*
Pack type	k	631	4	Kruskal-Wallis	H = 175.75	**<0.001**
Pack type	kdd^{-1}	631	4	Kruskal-Wallis	H = 178.32	**<0.001**
Stream	k	631	3	Kruskal-Wallis	H = 68.49	**<0.001**
Stream	kdd^{-1}	631	3	Kruskal-Wallis	H = 50.066	**<0.001**

Table 3.4 Mean values, standard errors (SE) and sample sizes (n) for the litter decay rates by day (k) and by degree day (kdd^{-1}) according to stream.

Stream	*Bowker Creek*	*Cecelia Creek*	*Francis King Creek*	*Swan Creek*
mean k	0.0896	0.0185	0.0088	0.0210
SE k	0.0127	0.0022	0.0008	0.0019
n k	154	158	160	159
mean kdd^{-1}	0.0067	0.0012	0.0008	0.0018
SE kdd^{-1}	0.0009	0.0002	0.0001	0.0002
n kdd^{-1}	154	158	160	159

Table 3.5 Post hoc test results of litter pack decay rate comparisons by day (k) and by degree day (kdd^{-1}) according to differences by stream and by type including the statistical test used, the test statistic calculated, and the significance of the test (*P*). Comparison key: Stream B=Bowker Creek, C= Cecelia Creek, FK = Francis King Creek, S= Swan Creek. Pack type: A= Alder B= Blackberry, C= Control, I – Ivy, T = Trash, W = Willow.

Group	*Decay rate*	*Comparison*	*Statistical test*	*Test statistic*	*P*
Pack type	k	T-A	Nemenyi H	143.672	**<0.001**
Pack type	k	T-B	Nemenyi H	91.564	**<0.001**
Pack type	k	T-I	Nemenyi H	82.111	**<0.001**
Pack type	k	T-W	Nemenyi H	105.819	**<0.001**
Pack type	kdd^{-1}	T-A	Nemenyi H	144.708	**<0.001**
Pack type	kdd^{-1}	T-B	Nemenyi H	90.485	**<0.001**
Pack type	kdd^{-1}	T-I	Nemenyi H	82.661	**<0.001**
Pack type	kdd^{-1}	T-W	Nemenyi H	110.835	**<0.001**
Stream	k	B-C	Nemenyi H	23.549	**<0.001**
Stream	k	B-FK	Nemenyi H	66.070	**<0.001**
Stream	k	B-S	Nemenyi H	11.000	**0.012**
Stream	k	FK-C	Nemenyi H	10.770	**0.013**
Stream	k	FK-S	Nemenyi H	23.480	**<0.001**
Stream	kdd^{-1}	B-C	Nemenyi H	30.815	**<0.001**
Stream	kdd^{-1}	B-FK	Nemenyi H	46.303	**<0.001**
Stream	kdd^{-1}	B-S	Nemenyi H	7.813	**0.050**
Stream	kdd^{-1}	S-FK	Nemenyi H	16.302	**<0.001**

Table 3.6 Counts of all invertebrates in day 14 leaf litter packs and Hess samples identified to the lowest practical taxonomic level and categorized by functional feeding group (FFG). Functional feeding groups are abbreviated: EW=Earthworm, FC=Filterer collector, GC=Gatherer collector, OM = Omnivore, PA=Parasite, PR=Predator, SC = Scraper, SH = Shredder.

Class	*Order*	*Taxon/Family*	*FFG*	*Bowker*	*Cecelia*	*Francis King*	*Swan*
Bivalvia	Veneroida	Sphaeriidae	FC	67	1	402	16
Branchipoda	Cladocera	Daphniidae	FC	0	0	0	35
-	-	Oligochaeta	EW	847	10764	151	2361
Clitellata	-	Hirudinea	PR	11	470	0	1
Gastropoda	Basommatophora	Ancylidae	SC-SH	21	6	0	49
Gastropoda	Basommatophora	Planorbidae	SC-SH	17	33	5	28
Gastropoda	Heterostropha	Valvatidae	SC-SH	0	0	3	0
Gastropoda	Hygrophila	Lymnaeidae	SC-SH	0	0	0	3
Gastropoda	Hygrophila	Physidae	SC-SH	19	13	0	115
Gastropoda	Littorinimorpha	Hydrobiidae	SC-SH	0	2	2	0
Hydrozoa	Anthoathecata	Hydridae	PR	4	0	3	53
Insecta	Coleoptera	Elmidae	GC	1	0	3	1
Insecta	Diptera	Athericidae	PR	0	0	2	0
Insecta	Diptera	Ceratopogonidae	PR	3	3	23	6
Insecta	Diptera	Chironomidae	GC/PR	328/37	800/89	1318/147	7069/785
Insecta	Diptera	Dixidae	GC	1	0	709	5
Insecta	Diptera	Dolichopodidae	PR	23	0	28	7
Insecta	Diptera	Empididae	PR	5	0	0	0
Insecta	Diptera	Psychodidae	GC	12	64	65	0
Insecta	Diptera	Ptychopteridae	GC	0	0	1	0
Insecta	Diptera	Simuliidae	FC	22	0	9	4
Insecta	Diptera	Stratiomyidae	GC	3	2	0	0
Insecta	Diptera	Tabanidae	PR	1	0	0	0

Table 3.6 Continued

Class	*Order*	*Taxon/Family*	*FFG*	*Bowker*	*Cecelia*	*Francis King*	*Swan*
Insecta	Diptera	Tipulidae	SH	4	3	9	19
Insecta	Ephemeroptera	Heptageniidae	SC	0	0	248	0
Insecta	Megaloptera	Sialidae	PR	0	0	0	9
Insecta	Odonata	Aeshnidae	PR	0	4	0	0
Insecta	Odonata	Coenagrionidae	PR	0	7	0	0
Insecta	Plecoptera	Chloroperlidae	PR	0	0	225	0
Insecta	Plecoptera	Nemouridae	SH	0	0	239	0
Insecta	Trichoptera	Lepidostomatidae	SH	0	1	1826	0
Insecta	Trichoptera	Limnephilidae	SH	0	0	0	2
Insecta	Trichoptera	Phryganeidae	SH	0	1	0	0
Insecta	Trichoptera	Rhyacophilidae	PR	1	0	36	1
Malacostraca	Amphipoda	Crangonyctidae	SH	76	68	158	520
Malacostraca	Decapoda	Astacidae	SH	2	0	0	2
Maxillopoda	-	Copepoda	GC	14	43	204	547
Turbellaria	Tricladida	Dugesiidae	OM	23	113	315	1
-	-	Nemetoda	PA	11	47	61	11
			Total	1553	12534	6192	11650

Table 3.7 Invertebrate and earthworm counts, masses and proportions for day 14 litter pack and Hess samples by stream site.

Stream	*Bowker*	*Cecelia*	*Francis King*	*Swan*
Invertebrates	706	1770	6041	9289
Worms	847	10764	151	2361
Total individuals	1553	12534	6192	11650
% Invertebrates	45.46	14.12	97.56	79.73
% Worms	54.54	85.88	2.44	20.27
Worms: Invertebrates	1.20:1	6.08:1	0.02:1	0.25:1
Invertebrates (g)	1.631	5.168	7.270	7.487
Worms (g)	1.676	5.937	0.191	1.476
Total mass (g)	3.307	11.104	7.461	8.964
% Invertebrates (g)	49.32	46.54	97.44	83.53
% Worms (g)	50.68	53.46	2.56	16.47
Worms: Invertebrates (g)	1.03:1	1.15:1	0.03:1	0.20:1

Table 3.8 Mean values, standard errors (SE) and sample sizes (n) for alpha diversities and Shannon diversity index scores by litter pack type.

Pack type	*Alnus rubra*	*Hedera* sp.	*Rubus armeniacus*	*Salix sitchensis*	*Trash*	*Control*
mean alpha diversity	5.906	5.500	6.839	5.862	5.563	5.185
SE alpha diversity	0.662	0.548	0.656	0.621	0.546	0.616
n alpha diversity	32	30	31	29	32	27
mean Shannon diversity	0.911	0.892	1.157	0.893	1.136	0.834
SE Shannon diversity	0.099	0.106	0.098	0.102	0.082	0.114
n Shannon diversity	32	30	31	29	32	27

Table 3.9 Mean values, standard errors (SE) and sample sizes (n) for alpha diversities and Shannon diversity index scores by stream.

Stream	*Bowker Creek*	*Cecelia Creek*	*Francis King Creek*	*Swan Creek*
mean alpha diversity	2.842	4.875	9.574	5.458
SE alpha diversity	0.374	0.279	0.448	0.271
n alpha diversity	38	48	47	48
mean Shannon diversity	0.665	0.927	1.605	0.653
SE Shannon diversity	0.084	0.061	0.045	0.049
n Shannon diversity	38	48	47	48

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Table 3.10 Comparison of litter pack alpha diversity and Shannon diversity index score differences by stream and by type, including the sample size (n), degrees of freedom (df), the statistical test used, the test statistic calculated, and the significance of the test (*P*).

Group	*Index*	*n*	*df*	*Statistical test*	*Test statistic*	*P*
Pack type	Alpha diversity	181	5	ANOVA	F = 0.861	0.508
Stream	Alpha diversity	181	3	Kruskal-Wallis	H = 88.544	**<0.001**
Pack type	Shannon diversity	181	5	ANOVA	F = 1.944	0.0894
Stream	Shannon diversity	181	3	Kruskal-Wallis	H = 88.866	**<0.001**

Table 3.11 Post hoc test results of litter pack alpha diversity and Shannon diversity index score differences by stream and by type, including the statistical test used, the test statistic calculated, and the significance of the test (*P*). Comparison key: B=Bowker Creek, C=Cecelia Creek, FK=Francis King Creek, S=Swan Creek.

Group	*Index*	*Comparison*	*Statistical test*	*Test statistic*	*P*
Pack type	Alpha diversity	not different	ANOVA	0.861	0.508
Stream	Alpha diversity	B-C	Nemenyi H	11.384	**0.00982**
Stream	Alpha diversity	B-FK	Nemenyi H	84.233	**<0.001**
Stream	Alpha diversity	B-S	Nemenyi H	19.358	**<0.001**
Stream	Alpha diversity	C-FK	Nemenyi H	38.277	**<0.001**
Stream	Alpha diversity	FK-S	Nemenyi H	26.025	**<0.001**
Pack type	Shannon Diversity	not different	ANOVA	1.944	0.0894
Stream	Shannon Diversity	B-FK	Nemenyi H	57.437	**<0.001**
Stream	Shannon Diversity	C-FK	Nemenyi H	34.577	**<0.001**
Stream	Shannon Diversity	S-FK	Nemenyi H	72.323	**<0.001**

Table 3.12 Outcomes of aquatic leaf litter decay studies in urban streams based on relative decay rates of native and exotic species.

Decay tendency	*Study*
Exotic species decay faster than native species	Molinero et al. 1996, Schulze and Walker 1997, Imberger et al. 2008, Swan et al. 2008, McNeish et al. 2012, MacKenzie et al. 2013, Roon et al. 2014, Fargen et al. 2015
Exotic species decay slower than native species	Baldy et al. 1995, Pozo et al. 1998
There is no significant difference between the decay rates of exotic and native species	Harner et al. 2009, Pérez et al. 2014, Roon et al. 2014, Bottollier-Curtet et al. 2015
Litter decay rates are determined by leaf quality or stream attributes rather than leaf origin.	Pomeroy et al. 2000, Bo et al. 2014, Bottollier-Curtet et al. 2015

Table 3.13 Comparison of the trash decay rates by day (k) and by degree day (kdd^{-1}) according to differences by stream, including the sample size (n), degrees of freedom (df), the statistical test used, the test statistic calculated, and the significance of the test (*P*).

Group	*Decay rate*	*df*	*n*	*Statistical test*	*Test statistic*	*P*
Stream - Trash	k	3	94	Kruskal-Wallis	H = 33.578	**<0.001**
Stream - Trash	kdd^{-1}	3	94	Kruskal-Wallis	H = 34.009	**<0.001**

Table 3.14 Mean values, standard errors (SE), and sample sizes (n) for trash decay rates by day (k) and by degree day (kdd^{-1}) according to stream.

Stream - Trash	*Bowker Creek*	*Cecelia Creek*	*Francis King Creek*	*Swan Creek*
mean k	0.0399	0.0019	0.0007	0.0003
SE k	0.0144	0.0009	0.0001	0.0003
n k	29	30	32	32
mean kdd^{-1}	0.0032	0.0001	<0.0001	<0.0001
SE kdd^{-1}	0.0012	<0.0001	<0.0001	<0.0001
n kdd^{-1}	29	30	32	32

Table 3.15 Post hoc test results of trash pack decay rate comparisons by day (k) and by degree day (kdd^{-1}) according to differences by stream, including the statistical test used, the test statistic calculated, and the significance of the test (*P*). Comparison key: Stream B=Bowker Creek, C= Cecelia Creek, FK = Francis King Creek, S= Swan Creek.

Group	*Decay rate*	*Comparison*	*Statistical test*	*Test statistic*	*P*
Stream - Trash	k	B-C	Nemenyi H	23.548	**<0.001**
Stream - Trash	k	B-FK	Nemenyi H	66.070	**<0.001**
Stream - Trash	k	B-S	Nemenyi H	11.000	**0.012**
Stream - Trash	k	FK-C	Nemenyi H	10.770	**0.013**
Stream - Trash	k	FK-S	Nemenyi H	23.480	**<0.001**
Stream - Trash	kdd^{-1}	B-C	Nemenyi H	30.815	**<0.001**
Stream - Trash	kdd^{-1}	B-FK	Nemenyi H	46.303	**<0.001**
Stream - Trash	kdd^{-1}	B-S	Nemenyi H	7.813	**0.050**
Stream - Trash	kdd^{-1}	S-FK	Nemenyi H	16.302	**<0.001**

Figures

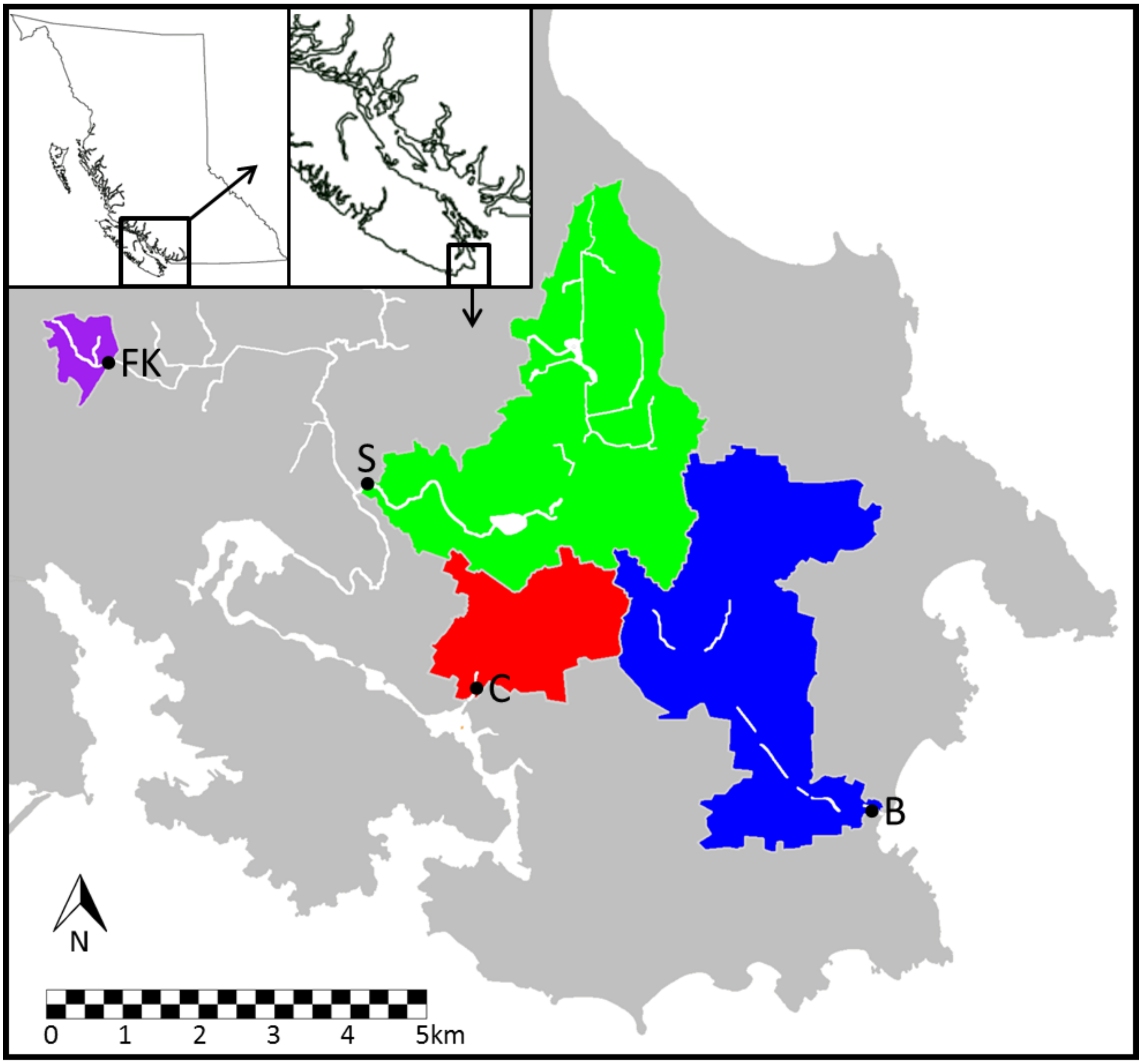

Figure 3.1 The four urban watersheds of the streams in this study located in the greater Victoria, BC area. The black dots show the locations of the study sites. Key: Stream B=Bowker Creek, C= Cecelia Creek, FK = Francis King Creek, S= Swan Creek. Only the above-ground portions of the streams are visible. This map is based on data from the CRD Regional Map (Capital Regional District 2016).

Figure 3.2 Bowker Creek litter decay study site, Oak Bay, BC**.**

Figure 3.3 Cecelia Creek litter decay study site, Victoria, BC.

Figure 3.4 Francis King Creek litter decay study site, Saanich, BC.

Figure 3.5 Swan Creek litter decay study site, Saanich, BC.

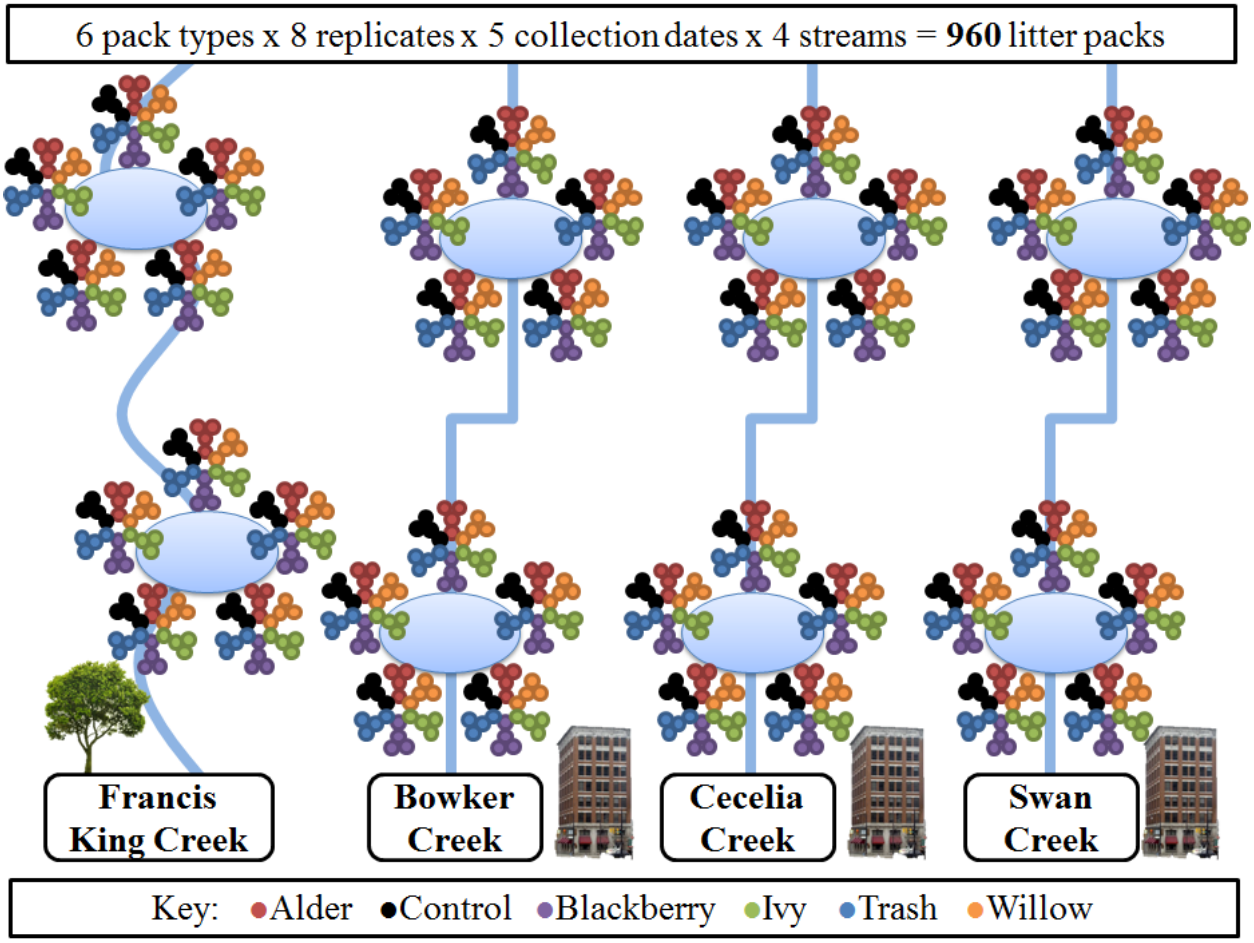

Figure 3.6 The study design of the litter decay experiment conducted in four streams in the greater Victoria, BC area between October 1st and November 28th 2014.

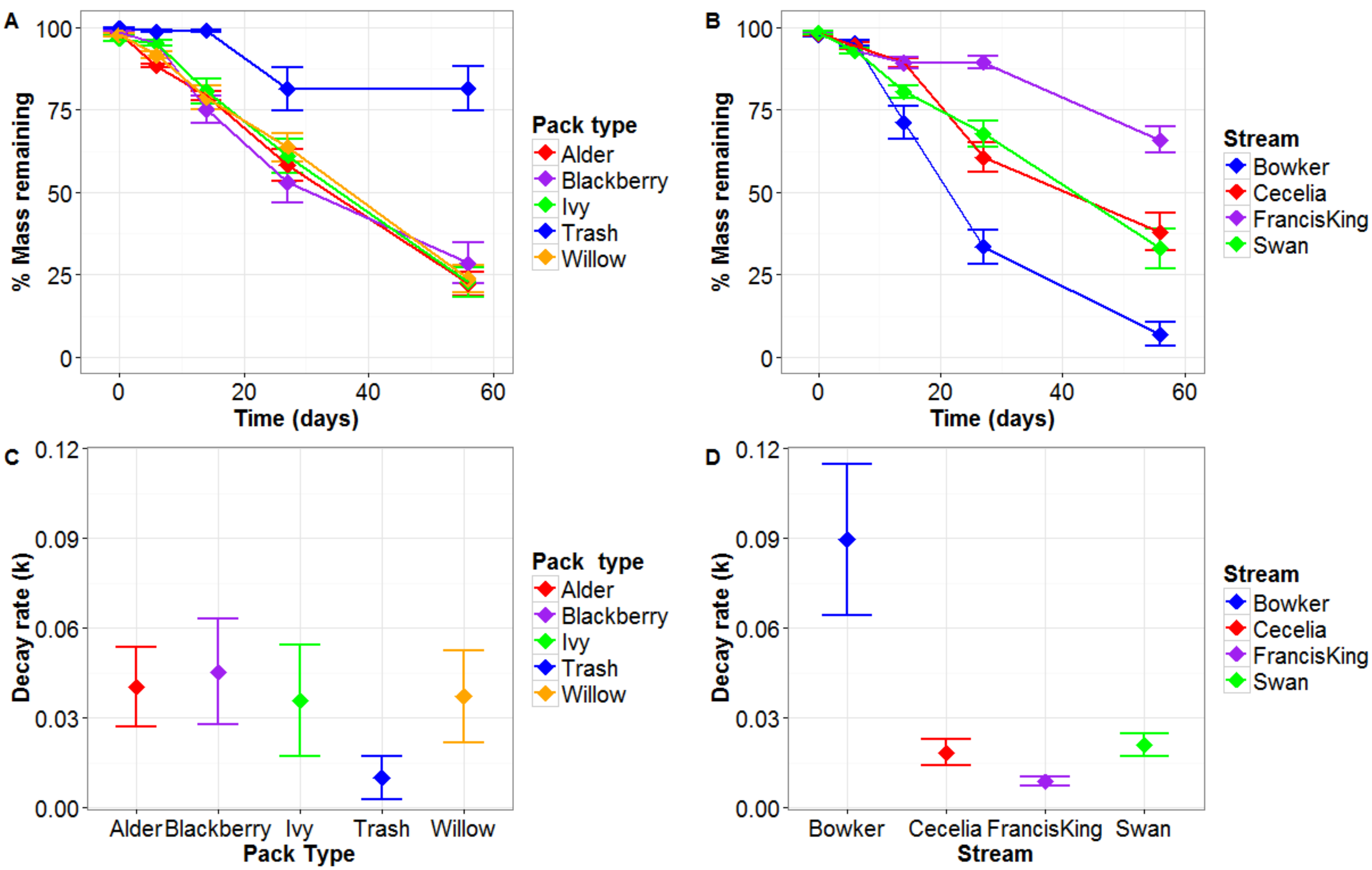

Figure 3.7 Litter pack decay rate (k) comparisons by pack type (alder, blackberry, ivy, trash and willow) and by stream (Bowker, Cecelia, Francis King, and Swan Creeks). (A) Mean litter pack percent mass remaining ± S.E. over time by litter pack type. (B) Mean litter pack percent mass remaining ± S.E. over time by stream site. (C) Mean decay rate (k) ± 95% C.I. by litter pack type. (D) Mean decay rate (k) ± 95% C.I. by stream.

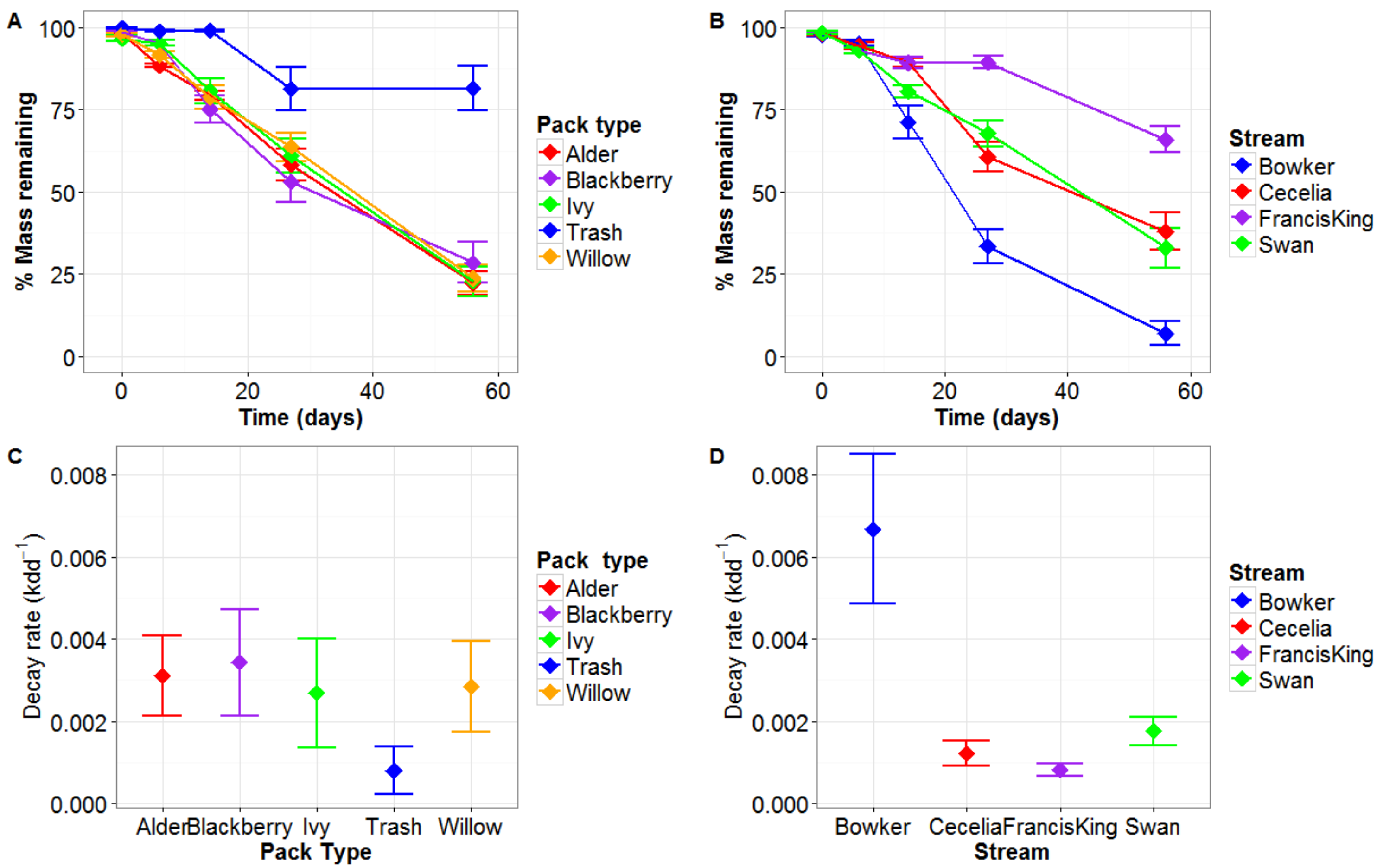

Figure 3.8 Litter pack degree-day decay rate (kdd^{-1}) comparisons by pack type (alder, blackberry, ivy, trash and willow) and by stream (Bowker, Cecelia, Francis King, and Swan Creeks). (A) Mean litter pack percent mass remaining ± S.E. over time by litter pack type. (B) Mean litter pack percent mass remaining ± S.E. over time by stream site. (C) Mean degree-day decay rate (kdd-1) ± 95% C.I. by litter pack type. (D) Mean degree-day decay rate (kdd-1) ± 95% C.I. by stream

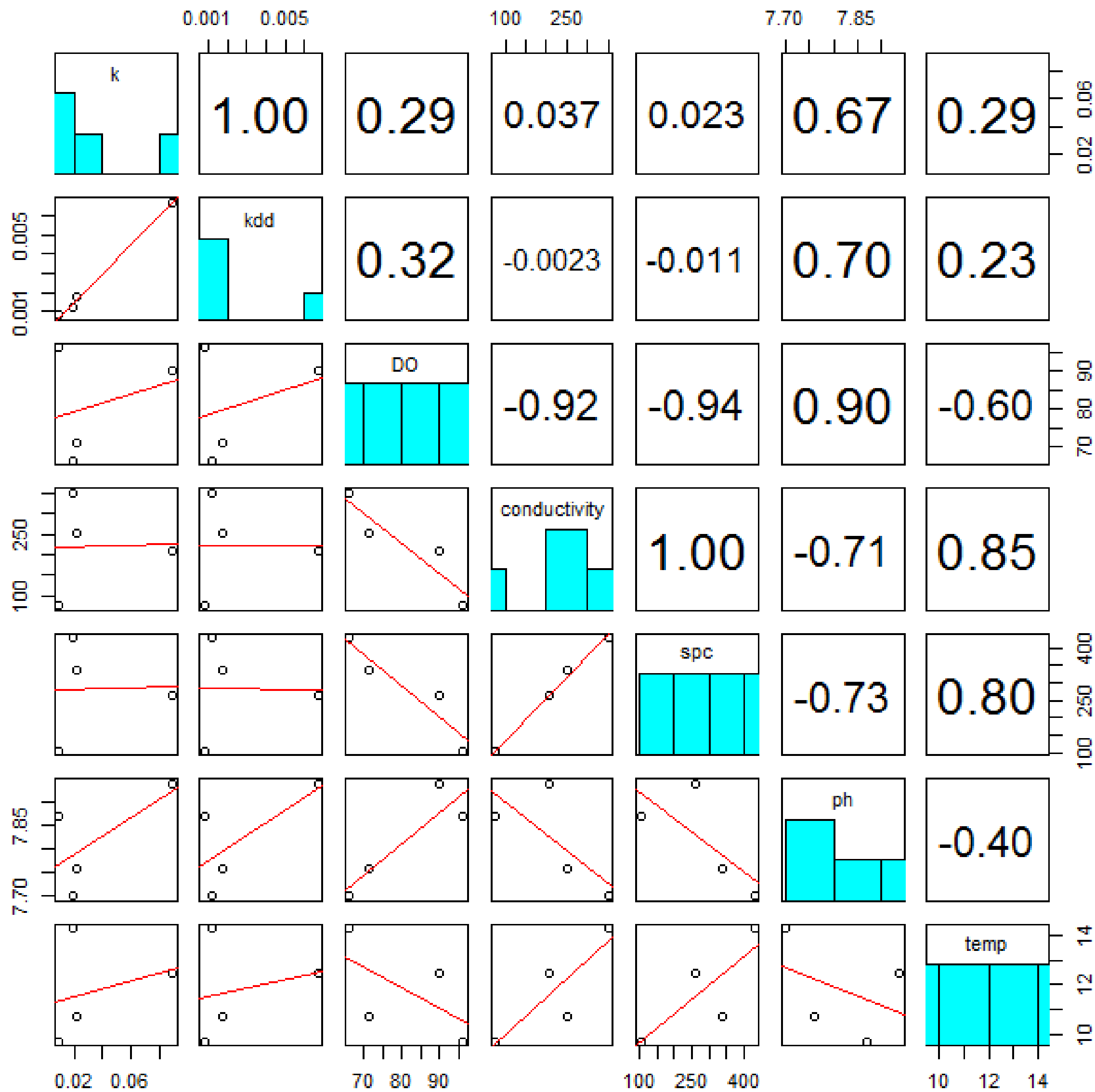

Figure 3.9 Correlation plot of the mean litter decay rates and stream attributes examined in the litter decay study at Bowker, Cecelia, Francis King, and Swan Creeks. The lower left section contains x-y scatterplots of the mean decay rates and stream attributes plotted against one another, the middle diagonal shows histograms for each value, and the upper right section lists the Pearson's r correlation values for the relationship between the values. The values contrasted are listed as follows: mean decay rate (k), mean decay rate by degree-day (kdd), Dissolved oxygen (%/L) (DO), Conductivity (µs/cm) (conductivity), Specific conductance (µs/cm)(spc), pH(ph), and stream temperature (°C) (temp).

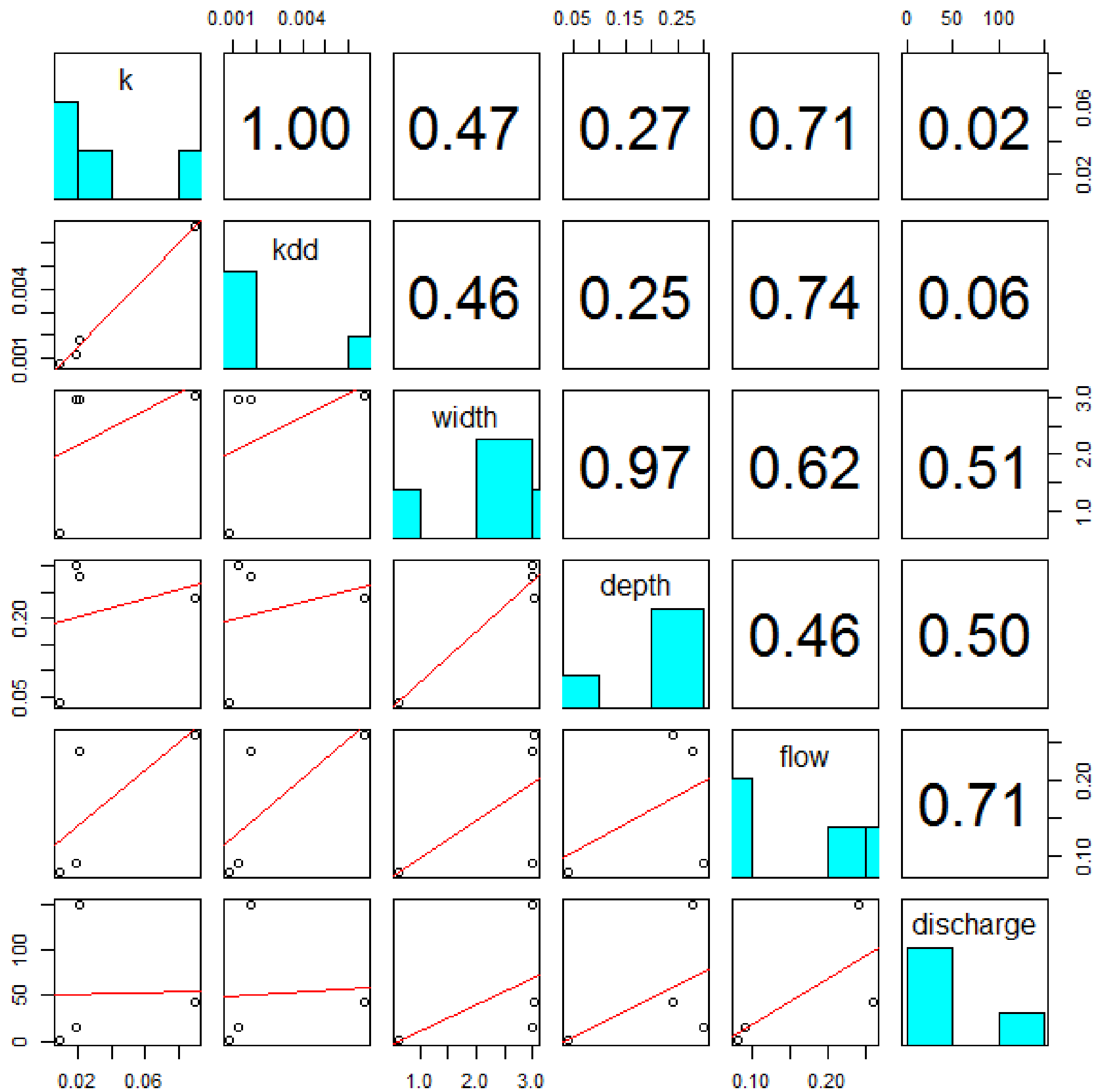

Figure 3.10 Correlation plot of the mean litter decay rates and stream attributes examined in the litter decay study at Bowker, Cecelia, Francis King, and Swan Creeks. The lower left section contains x-y scatterplots of the mean decay rates and stream attributes plotted against one another, the middle diagonal shows histograms for each value, and the upper right section lists the Pearson's r correlation values for the relationship between the values. The values contrasted are listed as follows: mean decay rate (k), mean decay rate by degree-day (kdd), stream width (m) (width), stream depth (m) (depth), stream flow (m/s) (flow), and discharge (L/s) (discharge).

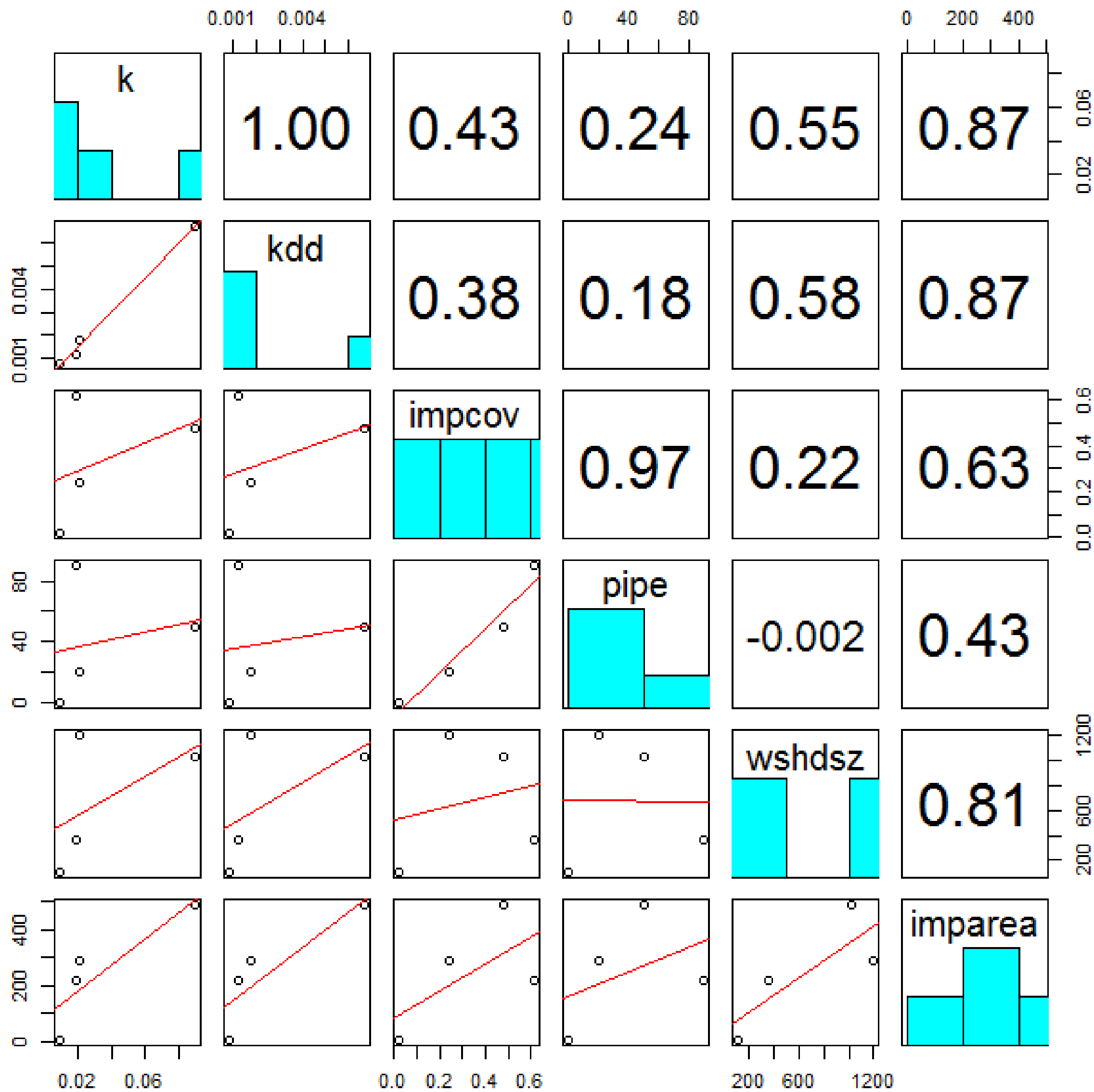

Figure 3.11 Correlation plot of the mean litter decay rates and stream attributes examined in the litter decay study at Bowker, Cecelia, Francis King, and Swan Creeks. The lower left section contains x-y scatterplots of the mean decay rates and stream attributes plotted against one another, the middle diagonal shows histograms for each value, and the upper right section lists the Pearson's r correlation values for the relationship between the values. The values contrasted are listed as follows: mean decay rate (k), mean decay rate by degree-day (kdd), % impervious cover (impcov), % watershed piped (pipe), watershed size (ha) (wshdsz), and total impervious area (ha) (imparea).

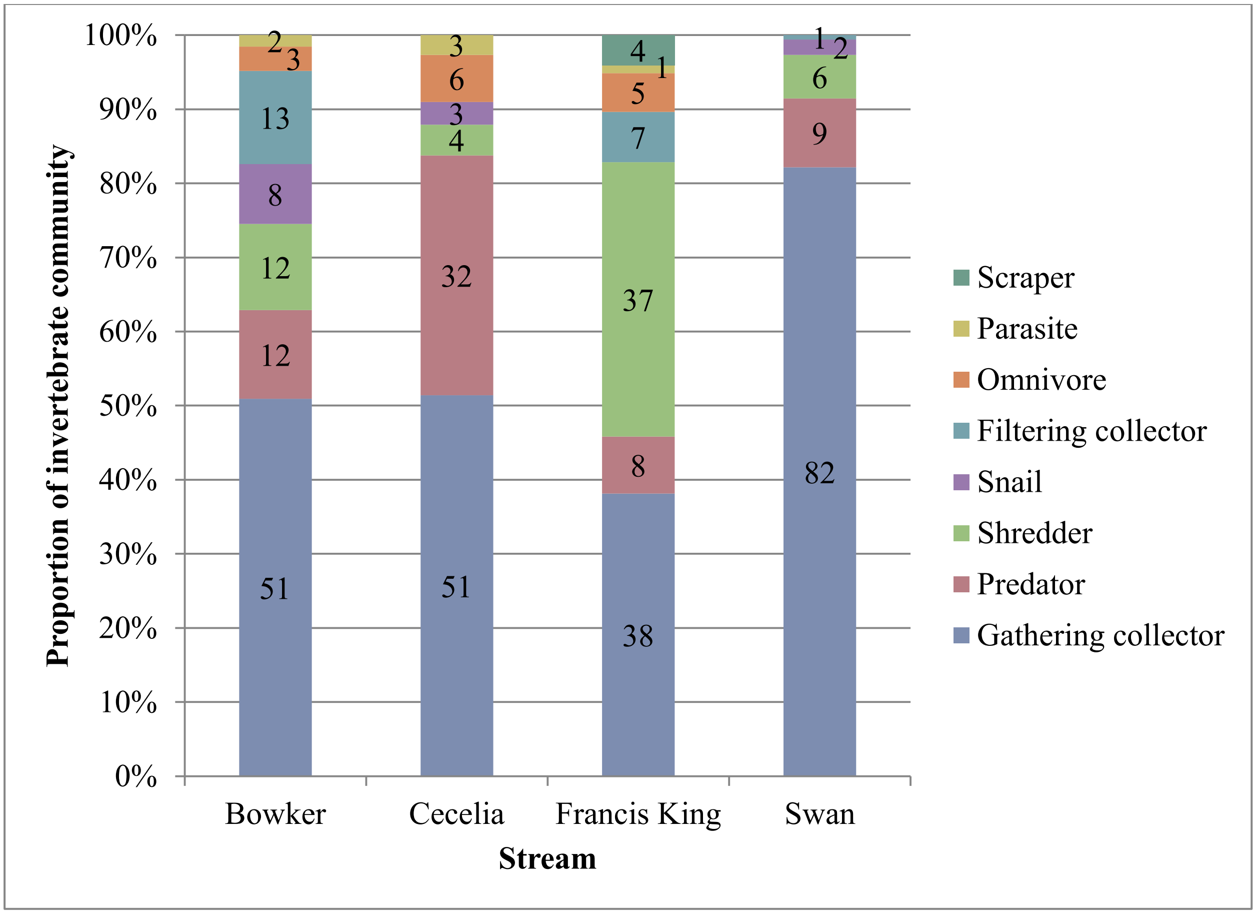

Figure 3.12 Invertebrate community functional feeding groups as a proportion of total aquatic invertebrates present in each stream (rounded to the nearest percent) from all day 14 Hess samples and litter packs.

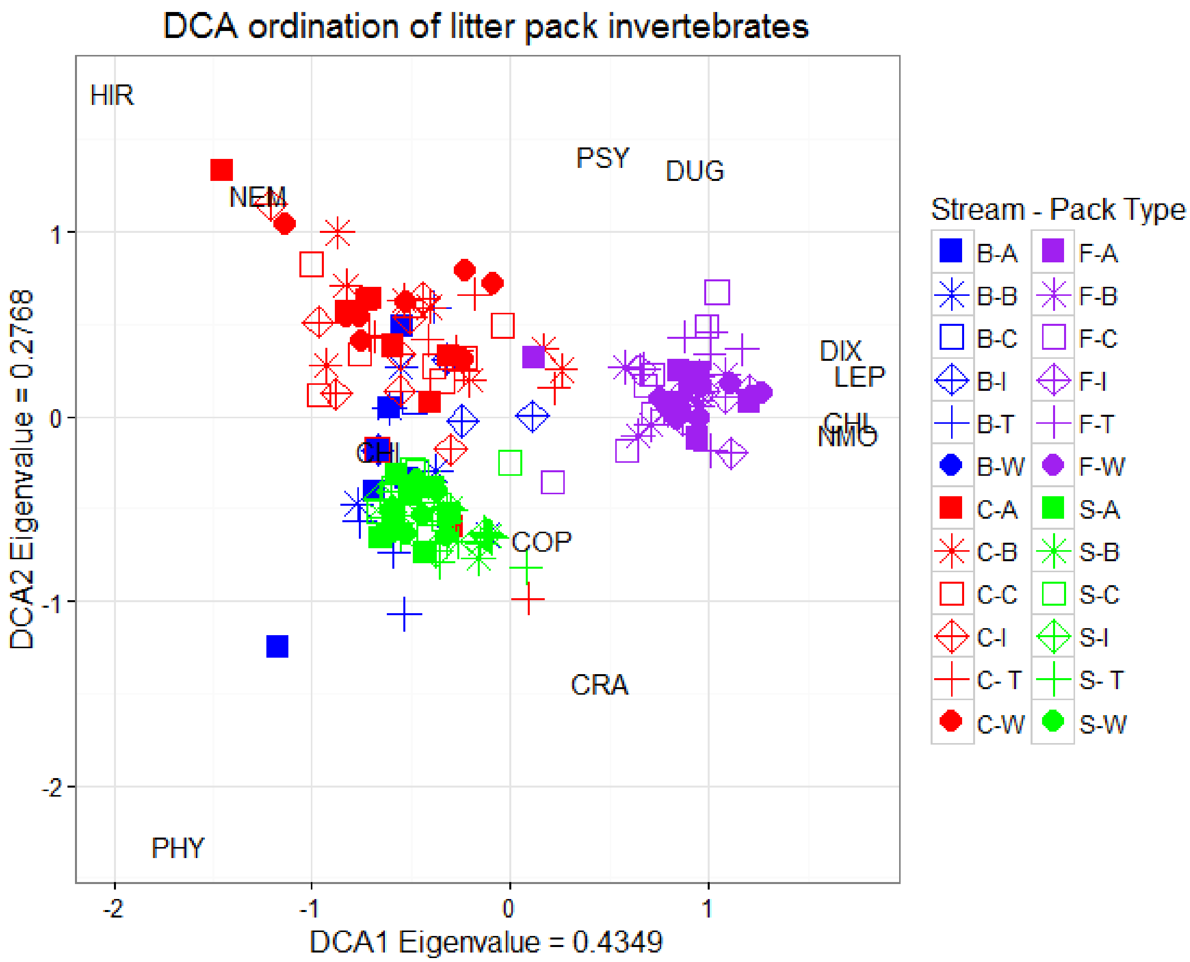

Figure 3.13 DCA ordination plot of litter pack invertebrates in which color denotes stream and shape denotes packtype. Key: Stream B=Bowker Creek, C= Cecelia Creek, FK = Francis King Creek, S= Swan Creek. Pack type: A= Alder, B= Blackberry, C= Control, I – Ivy, T = Trash, W = Willow. Invertebrate vectors are as follows: Chironomidae = CHI, Dugesiidae = DUG, Hirudinea = HIR, Psychodidae = PSY, Crangonyctidae = CRA, Nemetoda = NEM, Lepidostomatidae = LEP, Nemouridae = NMO, Chloroperlidae = CHL, Copepoda = COP, Dixidae = DIX, Physidae = PHY.

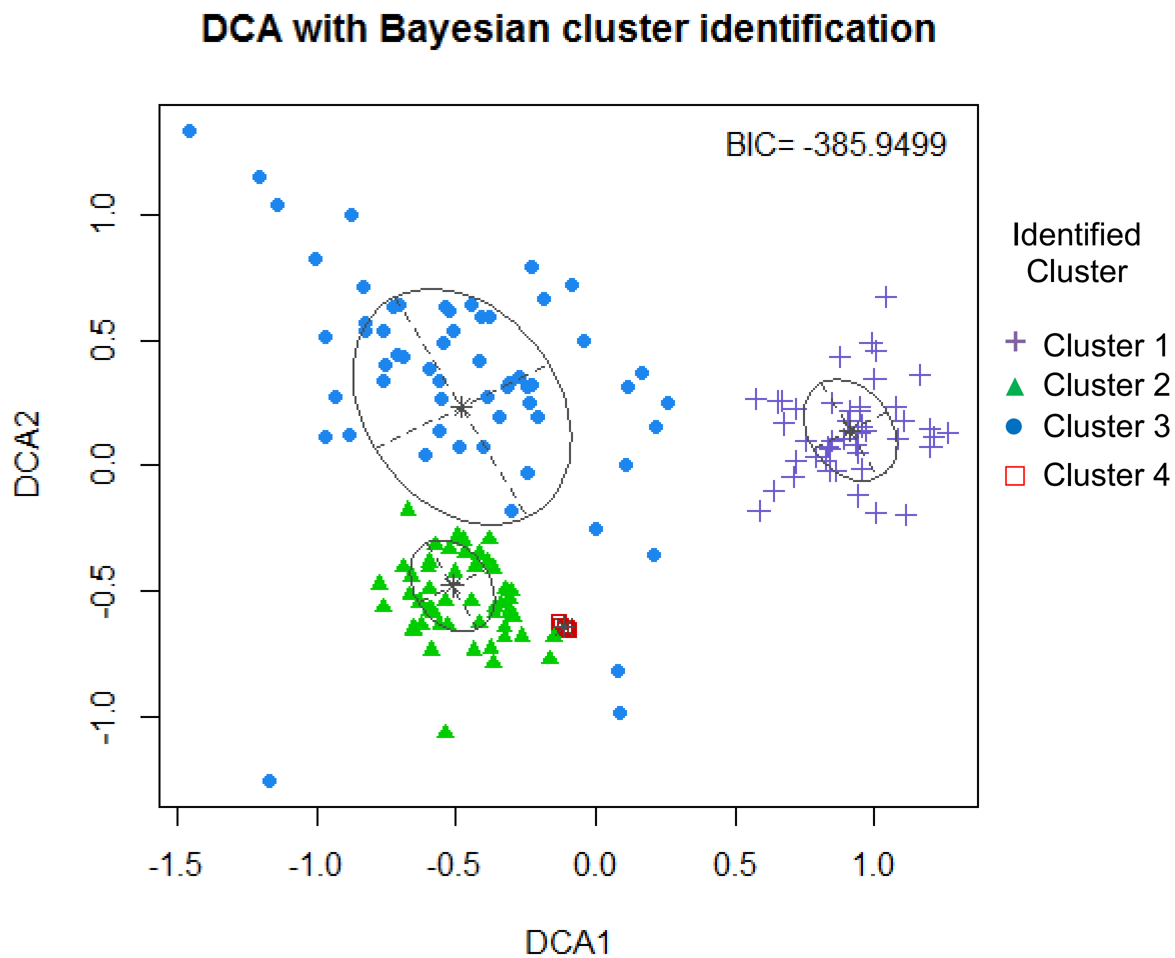

Figure 3.14 Bayesian clustering applied to the DCA ordination plot of litter pack invertebrates, with four clusters identified. The three main clusters centered on the Francis King packs (right), the Swan Creek packs (lower left) and the Cecelia Creek packs (upper left). The Bowker Creek packs are distributed across the Swan Creek and Cecelia Creek clusters.

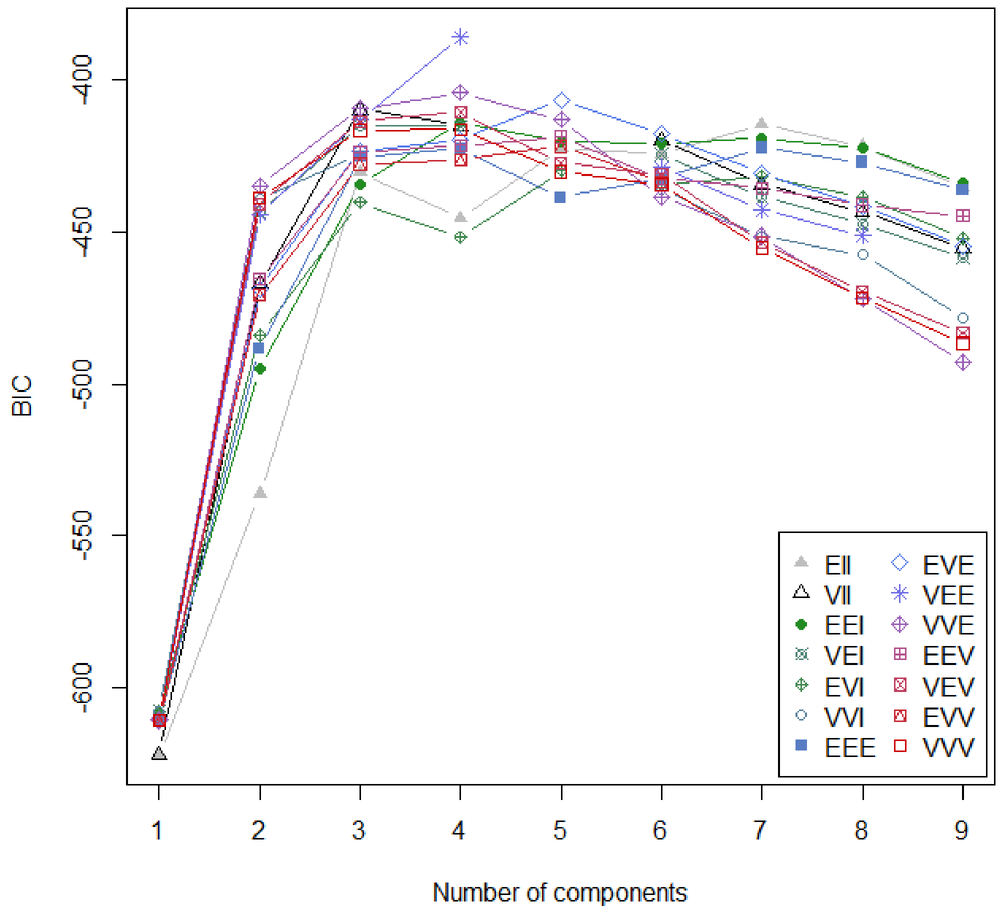

Figure 3.15 Bayesian clustering results for the optimal numbers of components (clusters) and cluster shape according to the Bayesian Information Criterion (BIC) calculated for each component-cluster shape combination applied to the DCA ordination plot of litter pack invertebrates. The optimal cluster arrangement was identified (top blue asterisk) as having four components that were ellipsoidal with equal shape and orientation. Cluster shape key: EII = spherical, equal volume; VII = spherical, unequal volume; EEI = diagonal, equal volume and shape; VEI = diagonal, varying volume, equal shape; EVI = diagonal, equal volume, varying shape; VVI = diagonal, varying volume and shape; EEE = ellipsoidal, equal volume, shape, and orientation; EVE = ellipsoidal, equal volume and orientation; VEE = ellipsoidal, equal shape and orientation; VVE = ellipsoidal, equal orientation; EEV = ellipsoidal, equal volume and equal shape; VEV = ellipsoidal, equal shape; EVV = ellipsoidal, equal volume; VVV = ellipsoidal, varying volume, shape, and orientation.

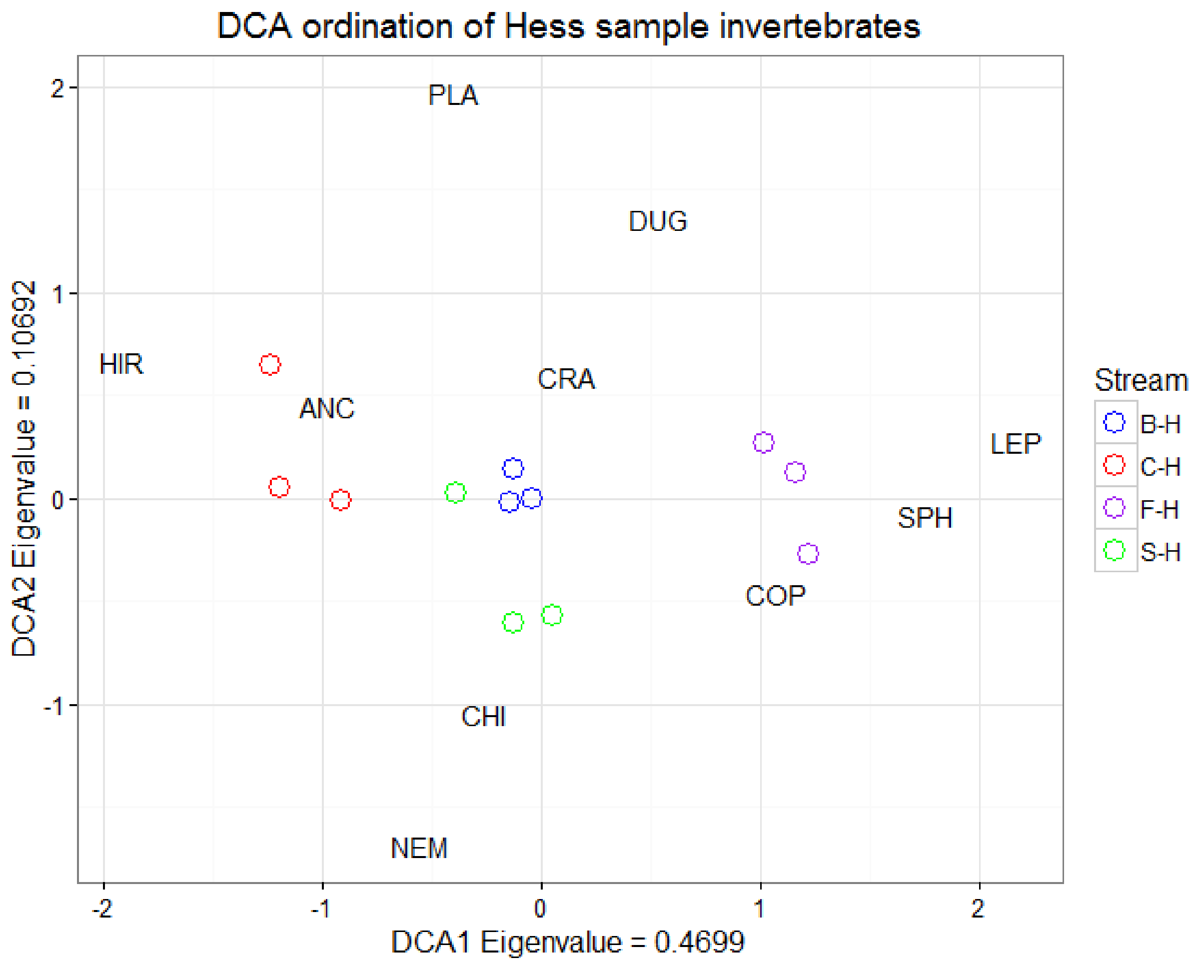

Figure 3.16 DCA ordination plot of Hess sample invertebrates in which color denotes stream and shape denotes pack type. Key: Stream B=Bowker Creek, C= Cecelia Creek, FK = Francis King Creek, S= Swan Creek, H= Hess sample. Invertebrate vectors are as follows: Ancylidae = ANC, Chironomidae = CHI, Dugesiidae = DUG, Hirudinea = HIR, Crangonyctidae = CRA, Nemetoda = NEM, Lepidostomatidae = LEP, Copepoda = COP, Planorbidae = PLA, Sphaeriidae = SPH.

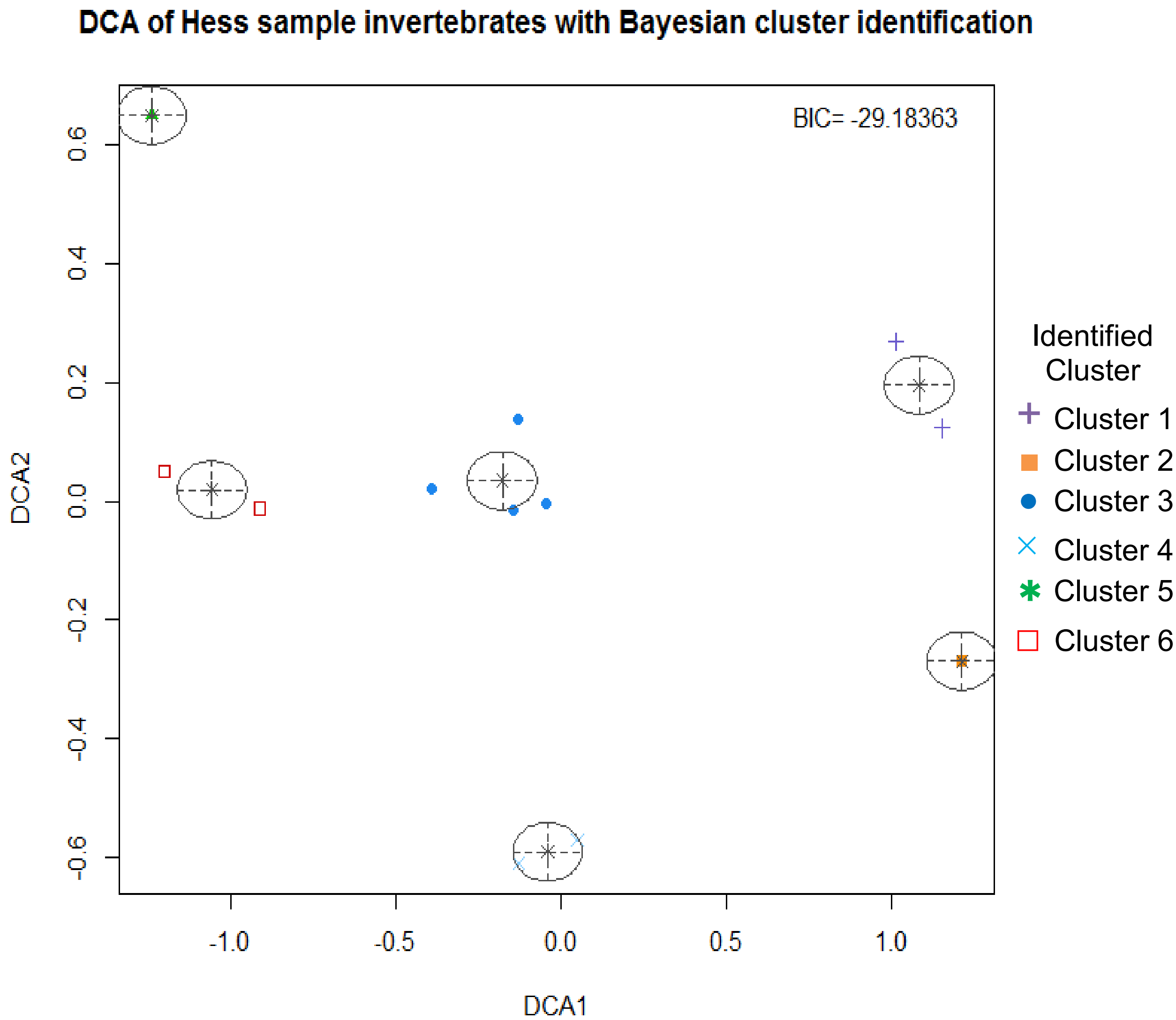

Figure 3.17 Bayesian clustering applied to the DCA ordination plot of Hess sample invertebrates, with six clusters identified. The clusters are centered on the Francis King samples (right), the Swan Creek samples (center) and the Cecelia Creek samples (left). The Bowker Creek samples are in the upper center cluster.

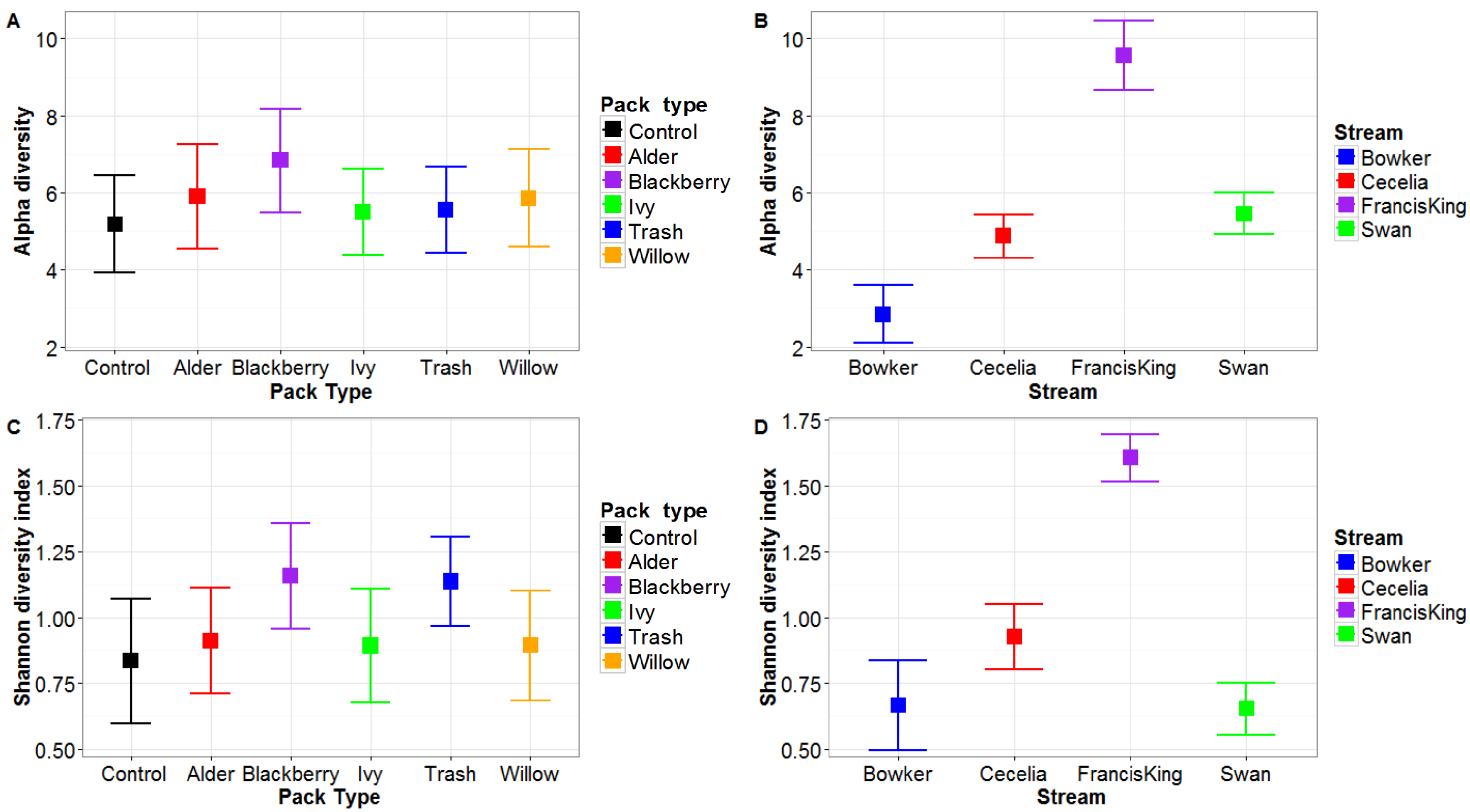

Figure 3.18 Day 14 litter pack invertebrate diversity comparisons by pack type (control, alder, blackberry, ivy, trash and willow) and by stream (Bowker, Cecelia, Francis King, and Swan Creeks). (A) Litter pack alpha diversity ± 95% C.I. by pack type. (B) Litter pack alpha diversity ± 95% C.I. by stream. (C) Litter pack Shannon diversity ± 95% C.I. by pack type. (D)Litter pack Shannon diversity ± 95% C.I. by stream.

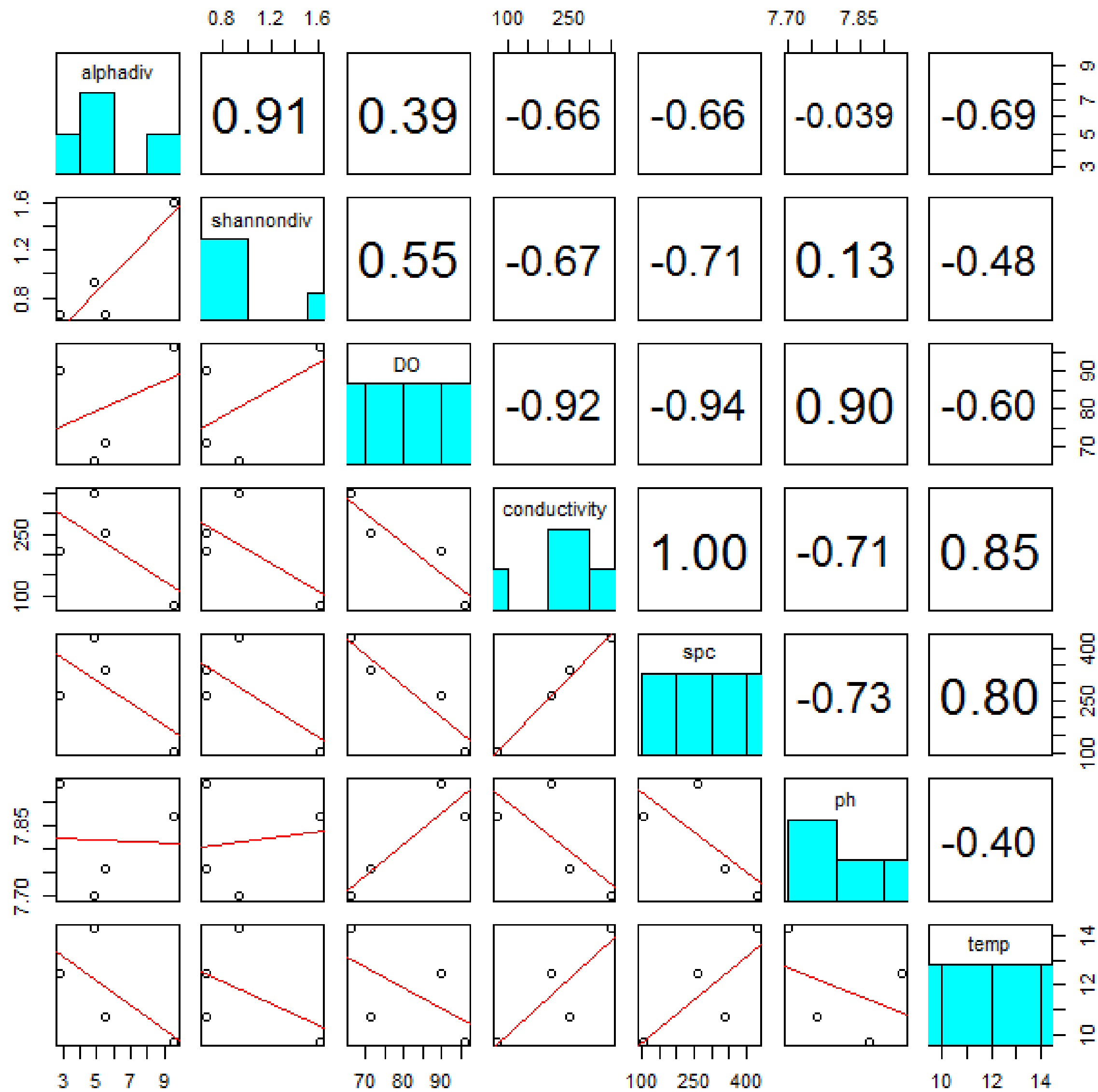

Figure 3.19 Correlation plot of the stream invertebrate mean alpha diversity, stream invertebrate mean Shannon diversity and stream attributes examined in the litter decay study at Bowker, Cecelia, Francis King, and Swan Creeks. The lower left section contains x-y scatterplots of the mean diversities and stream attributes plotted against one another, the middle diagonal shows histograms for each value, and the upper right section lists the Pearson's r correlation values for the relationship between the values. The values contrasted are listed as follows: mean alpha diversity (alphadiv), mean Shannon diversity (shannondiv), Dissolved oxygen (%/L) (DO), Conductivity (µs/cm) (conductivity), Specific conductance (µs/cm)(spc), pH(ph), and stream temperature (°C) (temp).

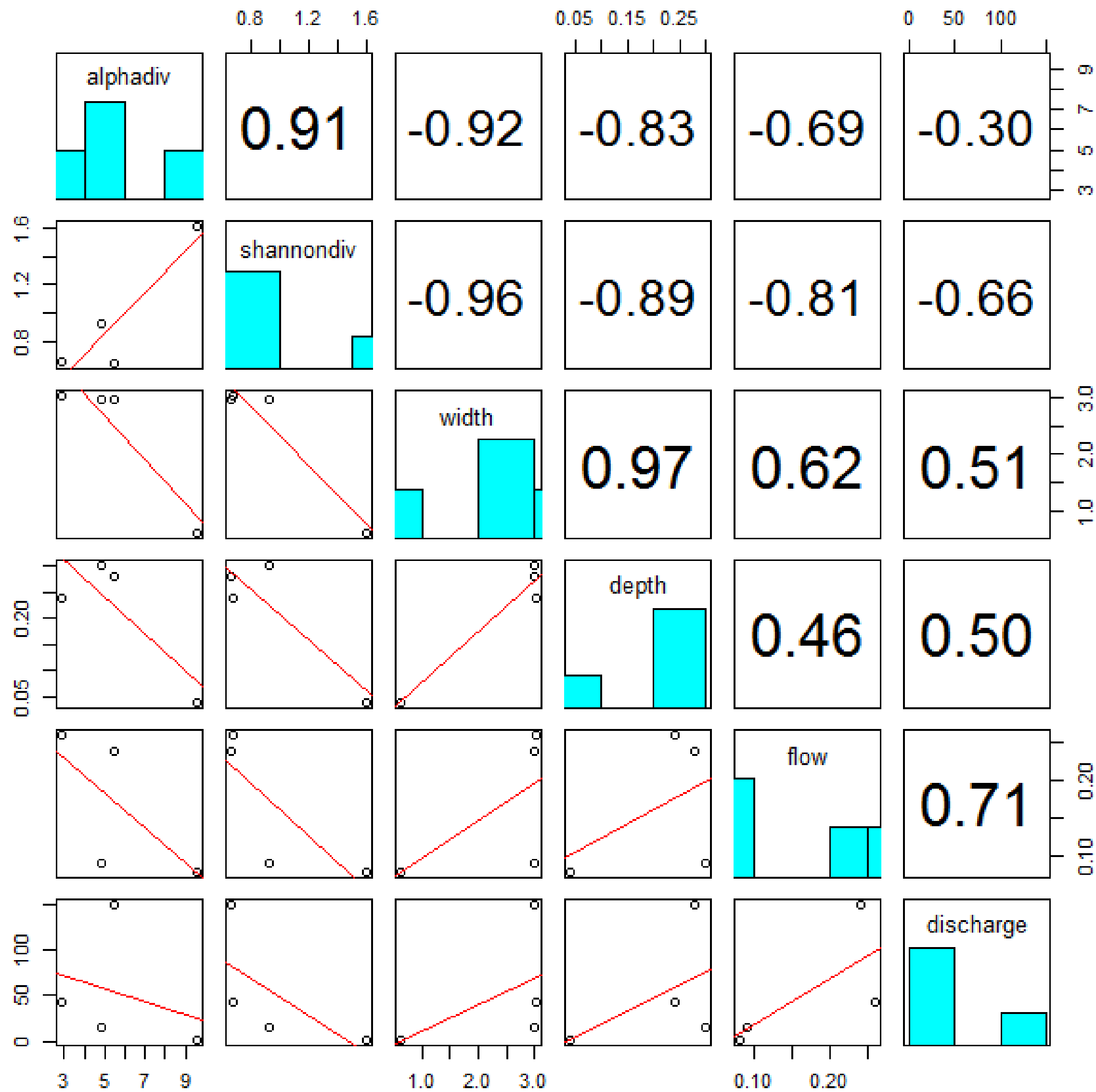

Figure 3.20 Correlation plot of the stream invertebrate mean alpha diversity, stream invertebrate mean Shannon diversity and stream attributes examined in the litter decay study at Bowker, Cecelia, Francis King, and Swan Creeks. The lower left section contains x-y scatterplots of the mean diversities and stream attributes plotted against one another, the middle diagonal shows histograms for each value, and the upper right section lists the Pearson's r correlation values for the relationship between the values. The values contrasted are listed as follows: mean alpha diversity (alphadiv), mean Shannon diversity (shannondiv), stream width (m) (width), stream depth (m) (depth), stream flow (m/s) (flow), and discharge (L/s) (discharge).

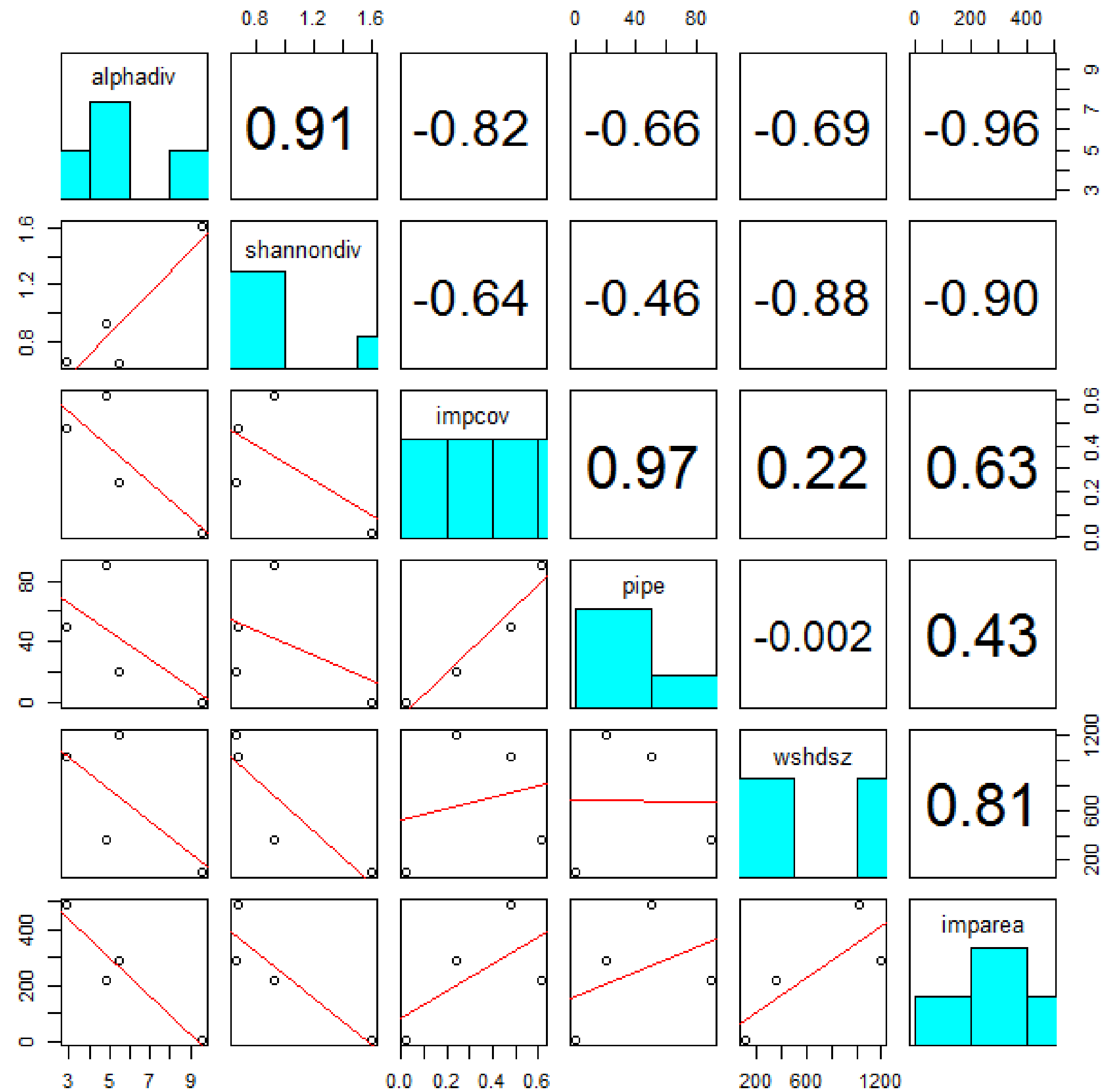

Figure 3.21 Correlation plot of the stream invertebrate mean alpha diversity, stream invertebrate mean Shannon diversity and stream attributes examined in the litter decay study at Bowker, Cecelia, Francis King, and Swan Creeks. The lower left section contains x-y scatterplots of the mean diversities and stream attributes plotted against one another, the middle diagonal shows histograms for each value, and the upper right section lists the Pearson's r correlation values for the relationship between the values. The values contrasted are listed as follows: mean alpha diversity (alphadiv), mean Shannon diversity (shannondiv), % impervious cover (impcov), % watershed piped (pipe), watershed size (ha) (wshdsz), and total impervious area (ha) (imparea).

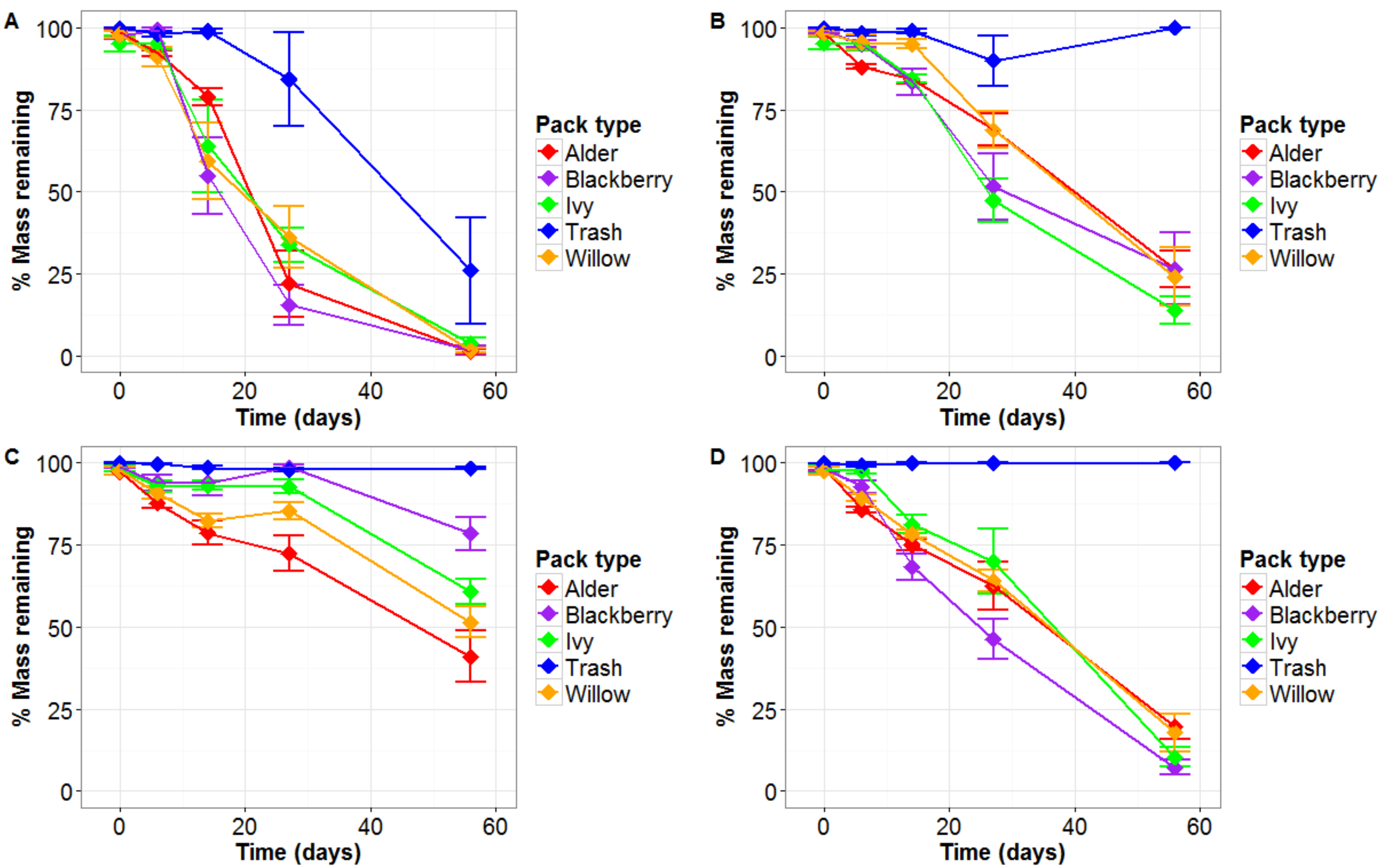

Figure 3.22 Litter pack mass loss comparisons by pack type (alder, blackberry, ivy, trash and willow) for each stream studied. (A) Bowker Creek mean litter pack percent mass remaining ± S.E. over time by litter pack type. (B) Cecelia Creek mean litter pack percent mass remaining ± S.E. over time by litter pack type. (C) Francis King Creek mean litter pack percent mass remaining ± S.E. over time by litter pack type. (D) Swan Creek mean litter pack percent mass remaining ± S.E. over time by litter pack type.

Chapter 4 : Conclusion

Exotic leaf litter has the potential to impact all levels of the stream ecosystem by changing the base resources available to the stream and thus shaping the biotic community. The results of my global meta-analysis investigating the factors that impact native and exotic litter decay rates indicated that exotic litter is unlikely to have the same impact in all ecosystems, and that high temperature ecosystems are more likely to experience exotic leaf litter decaying faster than native leaf litter. A potential driver for the exotic decay rate difference in high temperature ecosystems is the change in leaf litter quality from low quality, high C:N leaf native litter to high quality, low C:N exotic leaf litter.

The next logical step is to field-test these results in a multi-ecosystem litter decay experiment across several similar natural stream ecosystems in low and high temperature areas, contrasting four types of litter: low and high C:N native species and low and high C:N exotic species. Such a field experiment would effectively test the trends I have observed in the meta-analysis and post-hoc analysis, and extend their application from the database model to the wider world.

A limitation of the meta-analysis and post hoc testing method was the incomplete nature of the litter quality information available for each species. A future step could be measuring leaf litter quality for every leaf species in the initial litter decay dataset. This would allow me to include leaf litter quality information in the main linear model to truly understand how much intrinsic litter quality differences impact litter decay rates relative to extrinsic environmental decay drivers. A more complete model would ultimately allow us to understand whether environment or leaf species plays the largest role in the differences between native and exotic litter decay rates.

A complete understanding of where and when exotic leaf litter is likely to cause the most disruption to stream ecosystems will help us predict the most troublesome invaders and target prevention and restoration efforts on the most vulnerable areas. As resources for conducting research are limited, more information about the mechanisms responsible for the negative impacts of invasive riparian plants will allow us to maximize our ability to safeguard the systems that are at the highest risk of degradation.

My trash and invasive species litter decay experiment in urban streams yielded results that were congruent with the outcome of the linear model in Chapter 2. In the low temperature

Pacific Coast ecosystem, exotic leaf litter did not decay significantly differently than native leaf litter, nor did the aquatic macroinvertebrates preferentially colonize either litter material. In addition, plastic trash decayed much more slowly than natural litter materials and macroinvertebrates swiftly colonized trash to the same extent that they colonized natural litter materials.

My urban stream litter decay experiment showed that the stream itself was a far stronger driver of aquatic community and litter processing than the allochthonous inputs to the stream system and that a wide diversity in flow regime and aquatic invertebrate community can exist over a relatively small area. This experiment confirmed the homogenizing effect that urban impact has on litter decay rates, and yet in other ways (e.g. biotic community, flow regime, % impervious cover) the streams were quite different. Clearly urban streams are not as similar as they are assumed to be (Booth et al. 2016, Parr et al. 2016), and studies gauging impacts in urban watersheds should examine shifts in the stream invertebrate communities themselves rather than variation in litter decay rates, as the invertebrate community exhibits far more variation.

A limitation of the invertebrate analysis portion of my urban litter decay experiment was both the abundance and fragility of the earthworm population, which made them difficult to enumerate. Although it is unlikely they play a role in litter decay regimes, their abundant biomass must be an important resource in the urban stream ecosystem and it would be fascinating to further explore the role of earthworms in urban streams through food web analysis or ecological stoichiometry.

Additionally, although my study found no significant impact of invasive species and trash on litter decay rates and stream invertebrate colonization, this does not fully encompass the extent of impacts these materials could be having on the urban stream ecosystem. Further study examining the impact of trash and invasive species on the microbial community to see if these materials impact the bacterial, fungal or algal constituents of the stream would give a more complete understanding of the ecosystem impacts of these materials. Also a study of the relative frequency and volume of litter inputs by ivy and blackberry as compared to alder and willow would shed further light on whether these subsidies are truly interchangeable.

Further investigation of trash in urban streams is an area ripe for discovery. Assessment of trash accumulation and exodus rates, as well as individual decay rates by plastic type would be interesting areas of inquiry, as would a study of benthic samples to quantify local amounts and types of microplastic in the stream bed, and whether it is present in the gut contents of urban stream invertebrates.

Based on the colonization rates of both trash and blank control packs, it seems that stream invertebrates are quite capable of occupying artificial refugia. It would be interesting to see if artificially increasing habitat heterogeneity in structurally uniform urban streams would open up more niche space to a potentially more diverse stream invertebrate community. Ocean restoration work employing artificial reef structures is a growing common practice (Baine 2001, Cresson et al. 2014), and I believe there is potential for similar enrichment to enhance degraded freshwater ecosystems.

Both in urban ecosystems and in the natural environment, exotic species and trash have the potential to cause severe ecological impacts. The more we learn about these threats to our streams, the better we are able to intervene as needed to keep streams of all types as healthy and as biodiverse as possible. High biodiversity stabilizes ecosystem processes and enhances the capacity of ecosystems to perform multiple functions (Maestre et al. 2012, Loreau and de Mazancourt 2013). Conservation of stream biodiversity can help alleviate the impacts of ecological disturbance and preserve ecosystem values (Moore and Palmer 2005). Humans and many other creatures are dependent on streams for water, food, energy, habitat, and travel, and we should preserve these shared resources for all through careful stewardship.

> “In the confrontation between the stream and the rock, the stream always wins, not through strength but by perseverance.” ― H. Jackson Brown Jr.

May the stream always win.

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