The impacts of biotic and abiotic factors on resource subsidy processes - leaf litter breakdown in freshwaters

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Abstract

Freshwaters are closely linked with adjacent terrestrial ecosystems through reciprocal resource subsidies, which are fluxes of nutrients, organisms, and materials between ecosystems. Terrestrial ecosystems provide many resource subsidies to freshwaters including leaf litter, one of the most prevalent terrestrial-derived subsidies. Inputs of leaf litter fuel detritivores food web, as food resources and refuges, and affect nutrients cycling in freshwaters. The decomposition of leaf litter is subjected to many biotic and abiotic factors, which makes it a good indicator of freshwater ecosystem functioning. Yet, this ecosystem process has been affected by anthropogenic disturbances that alter abiotic and biotic factors in the nature. Therefore, this thesis aimed to investigate some previously under-investigated or unclear but important factors that may affect the decomposition of leaf litter in streams.

First, I reviewed the importance of resource subsidy fluxes between riparian zones and freshwaters and how these subsidies can influence recipient ecosystems. Then, I conducted a field experiment exploring the effects of anthropogenic carrion subsidy (chicken meat) and environmental-relevant concentration of glyphosate (the most widely applied herbicides worldwide) on leaf litter decomposition and invertebrate communities colonizing in the leaf-litter bags deploying in streams with different types of land use. Next, I conducted a mesocosm experiment nearby an urban stream to investigate the effects of water temperature (~ 8 °C above *vs* ambient), consumer - snails (presence *vs* absence), and leaf-litter quality (intact *vs* >40 % leaf area was consumed by terrestrial insects) on litter decomposition. Finally, I explored the global patterns of riparian leaf litter C, N, P, and their stoichiometric ratios to gradients of climatic (mean annual temperature and precipitation) and geographic (absolute latitude and altitude) factors, and the differences between biotic factors (phylogeny, leaf habit, N-fixing function, invasion status, and life form).

The results of field experiment indicated that: in coarse mesh bags, glyphosate, carrion subsidy, and the addition of both decreased litter breakdown rates by 6.3 %, 22.6 %, and 24.3 % respectively; in fine mesh bags, glyphosate and the addition of both retarded litter breakdown rates by 8.3 % and 12.5 % respectively. Litter decomposition also differed among streams, with the highest breakdown rates in village streams and lowest in urban/suburban streams. Invertebrates were significantly different among streams, with biodiversity index and total taxon richness were highest in village streams and lowest in suburban stream. However, overall effects of carrion subsidy and glyphosate on macroinvertebrates were not significant.

The results of mesocosm experiment indicated that warming and the presence of snails accelerated litter decomposition by 60.2 % and 34.9 % respectively, while litter breakdown rates of terrestrial insect damaged leaves were 5.1 % slower than intact leaves because of lower leaf litter quality.

The results of meta-analysis study demonstrated that global riparian leaf litter had higher N and P, while lower C, C:N, and C:P ratios than terrestrial leaf litter in general. Riparian leaf litter quality changed with gradients of climatic and geographic predictors, and these patterns differed between leaf habits (evergreen or deciduous) and climate zones (tropical or non-tropical area).

In general, my research provides important information on resource subsidy processes, which will benefit freshwater ecosystem management to support biodiversity and maintain ecosystem services.

Keywords: Stream, Ecosystem functioning, Leaf quality, Climate change, Land use change, Macroinvertebrate

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Chapter 1 General Introduction

1.1 Definition and characters of subsidy

Ecologists have long noticed that there are movements of energy and organisms across ecosystem boundaries which can influence recipient ecosystems (Lindeman 1942, Likens and Bormann 1974, Polis et al. 1997, Montagano et al. 2019). In the first formally publication, Polis et al (1997) defined spatial subsidies as “a donor-controlled resource (prey, detritus, nutrients) from one habitat to a recipient (plant or consumer) from a second habitat which increases population productivity of the recipient, potentially altering consumer–resource dynamics in the recipient ecosystem”. However, the term “subsidy” was first brought into ecological theory by Odum et al (1979). In the explanation of subsidy-stress gradient: “*subsidy* is derived from the Latin *subsidium*, implying "enhancement," "assistance," or "reserve support." If input into the ecosystem reduces maintenance cost or otherwise enhances overall function, then the system can be considered to be "subsidized," even though certain species may be stressed” (Odum et al. 1979).

The remarkable paper (Polis et al. 1997) attracted many researchers’ interest in this area. Over the past half century, the study of subsidy in ecology is becoming popular and demonstrating the importance of cross-ecosystem subsidies in recipient ecosystems (Likens and Bormann 1974, Polis et al. 1997, Subalusky and Post 2019). By now, we know that spatial subsidies are an important feature to many ecosystems, and these subsidies have strong and complex effects on recipient ecosystems at levels range from individual to ecosystem (Baxter et al. 2005, Brett et al. 2017, Gounand et al. 2018). For example, exogenous subsidy inputs usually directly benefit consumers in recipient ecosystems due to the increased abundance of food resources (Chan et al. 2007), or indirectly through enhanced habitat heterogeneity (Pilotto 2015). All of which can induce higher abundance (either by migrating, higher reproduction or both), larger individual body size, and faster growth rate of consumers in recipient ecosystems (Wright et al. 2013, Jonsson et al. 2015). Since the original definition of subsidy proposed by Polis et al (1997), researchers have modified and added information on the definition of subsidy. Anderson et al (2008) modified that subsidies can influence the dynamics of recipient populations and communities, which means subsidies could either enhance or inhibit recipient consumer production (Anderson et al. 2008). Richardson et al (2010) defined resource subsidies “are flows of biologically fixed energy and nutrients from one ecosystem to another, i.e. allochthonous resources produced outside of the recipient system”. The definition by Richardson et al (2010) was further proposed in a recently published paper (Larsen et al. 2016). In a newly published paper, Subalusky and Post (2019) defined a resource subsidy “is a resource that originates from production in a donor ecosystem, moves into a recipient ecosystem, and alters the dynamics of a consumer in that recipient ecosystem”.

Most researchers admitted the following characters of subsidies: donor-controlled; the transfer of materials, organisms, and nutrients across systems; and have impact on consumers in recipient systems. However, there are still some argument about the definition of subsidy. Firstly, the delineation of the boundaries between donor and recipient ecosystems (Ballinger and Lake 2006). Some use “habitat” (e.g. Polis et al 1997) while others use “ecosystem” (e.g. Subalusky and Post 2019). In addition, the edges of the boundaries may be diffuse (e.g. forest edges) or abrupt (e.g. terrestrial–aquatic boundaries) which means the width of boundaries can be tens of meters to several kilometers (Giling et al. 2015). Secondly, the effects of subsidies on recipient ecosystems may be positive or negative. The first one is especially important because if we have different delineation of the boundaries, we can include more subsidies (Subalusky and Post 2019). In this thesis, I agreed with the opinion of Richardson et al (2010), i.e. the boundaries between donor and recipient systems should be ecosystems, and subsidies should alter consumers in recipient ecosystems (i.e. consumers can be either enhanced or inhibited).

Subsidies have some specific characters to distinguish from other relevant concepts (Richardson and Sato 2015, Subalusky and Post 2019). Subsidies are donor-controlled and do not fit a fully coupled predator-prey system, i.e. consumers in recipient ecosystems can not directly influence the inputs of subsidies (e.g. invertebrates can not directly affect the inputs of terrestrial leaf litter to streams) (Richardson et al. 2010). Another character of subsidy is that it is usually available for short periods, i.e. subsidies are pulsed resources that can be characterized by their duration, magnitude and other aspects, and their rates can be scaled relative to the life cycles of recipient consumers (Richardson and Sato 2015, Subalusky and Post 2019).

Many researchers have contributed to the classification of subsidies. Polis et al (1997) summarized the movement of nutrient, detritus, prey, and consumers. Each type of subsidy was further classified according to the direction of subsidy movement, i.e. water to water, land to water, water to land, and land to land (Polis et al. 1997). Allen and Wesner (2016) further developed this classification system, they first classified subsidies according to the flux type: i.e. nutrient, detritus, producer, prey, and predator. Then, these subsides were further grouped according to the differences in donor-recipient ecosystems: freshwater-freshwater, freshwater-marine, freshwater-terrestrial, terrestrial-freshwater, terrestrial-marine, terrestrial-terrestrial marine-freshwater, marine-marine, and marine-terrestrial (Allen and Wesner 2016). Richardson et al (2010) classified the subsidies between land and freshwater ecosystems into: leaf litter and other terrestrial inputs to aquatic ecosystems, terrestrial invertebrate inputs to streams, flows from streams to terrestrial areas, flows from upstream to downstream (or from downstream to upstream), lake outlets, benthic-pelagic coupling in lentic systems, and linkages at the community level. Subsidies can also be simply grouped into two categories: passive and active (Subalusky and Post 2019). Passive subsidies (e.g. leaf litter) are mainly caused by natural forces such as wind, atmospheric deposition, gravity, and riverine flow, while active subsidies mainly refer to the transfer of organisms across ecosystems including adult aquatic insects and salmon. In terrestrial-aquatic ecosystems, subsidies can be considered at four dimensions due to the hydrological connectivity (Ward 1989, Kaushal and Belt 2012, Giling et al. 2015): lateral (e.g. leaf litter and adult aquatic insects), longitudinal (e.g. downstream drifting of invertebrates), vertical (e.g. nutrients transported between groundwater and hyporheic zones), and temporal (time).

1.2 Current and future research topics of subsidy

I used the term “subsidy” and “ecology” in Web of Science (data updated on 21 July 2019) result in 3,144 articles. Most of the studies focused on environmental sciences ecology, zoology, marine freshwater biology, and biodiversity conservation (Fig. 1.1). In addition, most of these studies were conducted during the last 10 years. Since 2007, more than 100 articles published every year, and this number increased to over 200 since the year 2014 (Fig. 1.2). These results indicated that the study of subsidy is attracting the interests of more and more researchers. For example, the effects of urbanization on the movement of aquatic organisms and nutrients is among the 26 key research questions in urban stream ecology (Wenger et al. 2009). In terms of the subsidy types, salmon carcasses, leaf litter, terrestrial and aquatic insects, and terrestrial organic matter are among the most studied subsidies across terrestrial and freshwater ecosystems. These subsidies were further discussed in Chapter 2.

Many researchers have proposed the potential directions for future study of subsidy. Richardson et al (2010) showed two main future directions, i.e. coupling ecosystem dynamics through complex life cycles and behavior, and investigating the dynamical consequences of certain types and rates of subsidies to recipient ecosystems. Richardson and Sato (2015) further developed more key questions for future study: (1) how do the duration, magnitude and predictability of resource subsidy pulses affect consumer populations ?; (2) quality varies, so are the resources still substitutable ?; (3) can we make quantitative predictions about the rates and form of consumer population responses to subsidy inputs?; (4) can resource subsidies strengthen (or weaken) trophic cascades?; (5) do resource subsidies lead to higher or lower system stability?; and (6) how do the temporal and spatial scales of subsidies affect system responses and co-evolution. Larsen et al (2016) suggested that under global changes, future studies of subsidies between stream and terrestrial ecosystems should focus on the following topics: agriculture and land-use conversion, water resource use, biotic homogenization and species losses, multiple stressors, and tropical and arctic ecosystems (Larsen et al. 2016). Subalusky and Post (2019) recommened five research topics for future study: (1) measuring and reporting the magnitude and stoichiometry of subsidies, i.e. the quantity and quality of subsidies; (2) developing new study designs that can measure the effects of subsidies at spatial and temporal scales to capture relevant environmental variability; (3) investigating how animals can affect food webs and ecosystems; (4) using the conceptual framework to guid subsidy research in general; (5) following the more general definition of resource subsidies to include more case studies. Montagano et al (2019) advocated to foucs on tropical and high latitute areas, they also suggested to expand the scope of studing subsidies at a macroecological scale (Montagano et al. 2019). This thesis aimed to adding more information on the following areas which are among the above projected topics: the quality of subsides; multiple stressors; land use; and climate change.

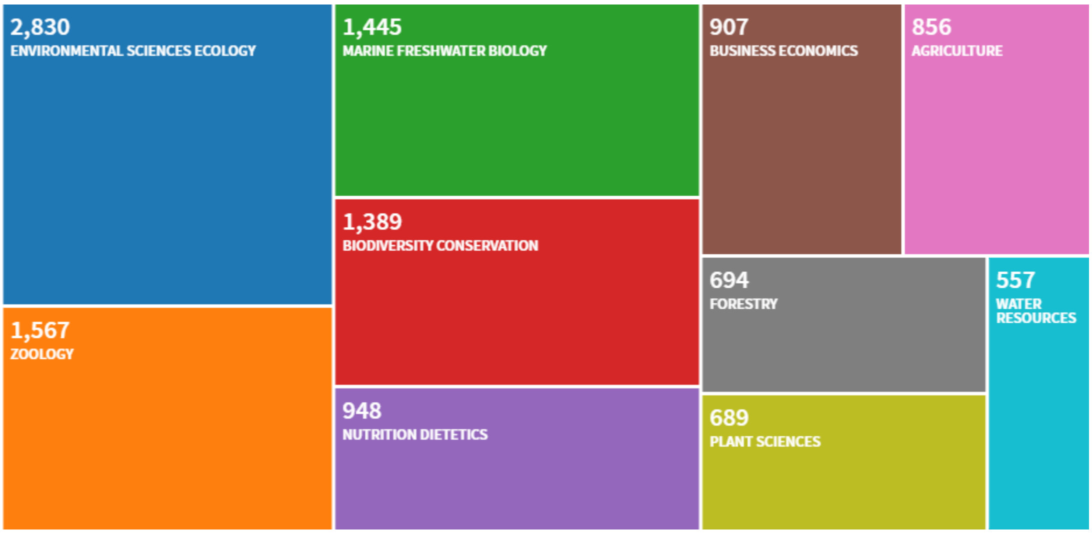

Figure 1.1 Searching result of the top 10 study areas (classified according to the number of articles) in Web of Science. Data were updated on 21 July 2019 using the searching theme “subsidy” AND “ecology”.

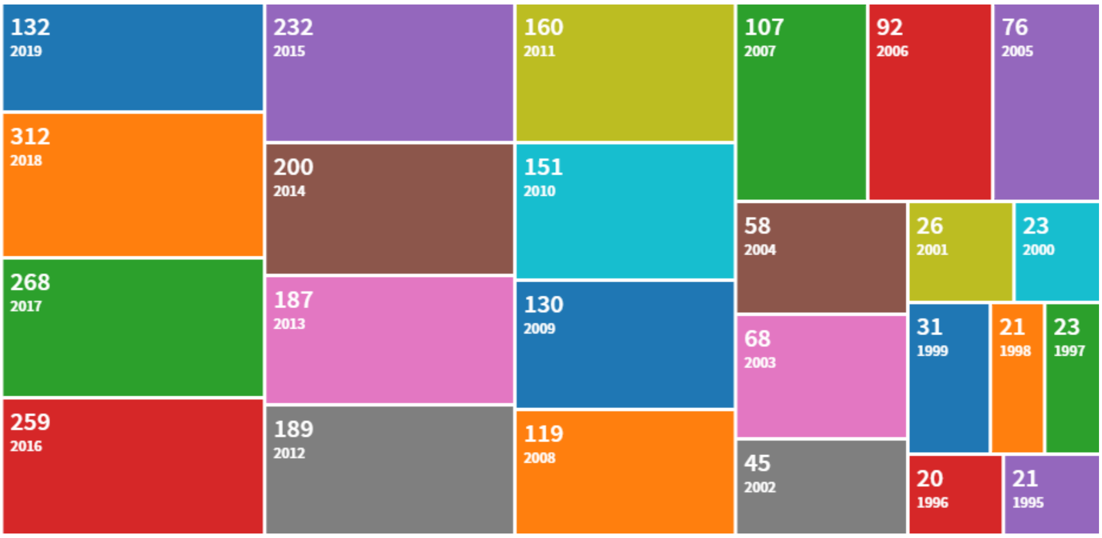

Figure 1.2 Searching result of the number of articles published during the past 25 years (1995 - 2019) in Web of Science. Data were updated on 21 July 2019 using the searching theme “subsidy” AND “ecology”.

1.3 Reciprocal subsidies between linked ecosystems

Freshwaters and adjacent terrestrial ecosystems are closely linked by numerous reciprocal subsidies (Polis et al. 1997, Richardson et al. 2010, Gounand et al. 2018). These allochthonous subsidies can affect recipient ecosystems at levels ranging from individuals to ecosystems (Baxter et al. 2005, Richardson and Sato 2015, Subalusky and Post 2019). For example, more than half of the annual energy consumption of drift-feeding fishes were composed by terrestrial invertebrates, and adult aquatic insects provide 25-100 % of the annual energy or carbon to terrestrial birds, bats and spiders (Baxter et al. 2005). The strength of subsidies on recipient ecosystems depending on the types of subsidies, quantity, quality, and the time when it enters ecosystems (Tiegs et al. 2008, Allen and Wesner 2016, Kreutzweiser et al. 2019). Many organisms have evolved to capture the dynamic of subsidies to enjoy the feast (Schindler et al. 2013, Shardlow and Hyatt 2013). One representative example is salmon, the key stone species in many northern temperate streams, that provide energy to numerous aquatic and terrestrial species such as invertebrates, fish, bears, birds, and plants (Hocking and Reynolds 2011, Kiffney et al. 2018).

However, these subsidies have been changed by many factors such as land use change, climate change, and invasive species (Kautza and Sullivan 2015, Larsen et al. 2016). These disturbances can alter the quality, quantity, and timing of subsidies and cascade to recipient ecosystems (Micael Jonsson and Canhoto 2016). For example, warmer water temperature advanced adult mayfly emergence by 19 days and prolonged the emergence period. Consequently, riparian spiders benefited from the prolonged aquatic subsidy result in higher growth rate and female fecundity (Uno 2016). In addition, as up to 30-40 % of all food produced in Earth is wasted (Oro et al. 2013), ecological consequences of anthropogenic subsidies have been reported in both terrestrial (Newsome et al. 2015) and freshwater ecosystems (Johnson et al. 2018).

1.4 Importance of leaf litter decomposition in streams

Leaf litter is one of the most important terrestrial-derived subsidies to freshwaters (Wallace et al. 1997). Numerous studies have investigated the role of leaf litter in streams, rivers, lakes, and other freshwater bodies (LeRoy 2005, Kominoski and Pringle 2009, Migliorini et al. 2018). Generally, leaf litter is recognized to fueling detritivores food webs, providing food resources and refuges to invertebrates, amphibians, and fish, increasing growth surface area for microbes, and influencing nutrients (e.g. carbon and nitrogen) cycling (Anderson and Sedell 1979, Boyero et al. 2011b, Márquez et al. 2017). Leaf litter inputs are especially important in headwater streams because these ecosystems have dense canopy that can restrict primary production. It is estimated that global terrestrial plants produce *ca* 122 billion tonnes of organic carbon annually (Beer et al. 2010), with only 10 % of which are directly consumed by herbivores and the rest of these carbon follow into dead organic matter pool (Cebrian 1999), and 70 % of which are leaf litter (Benfield 1997). Part of these leaf litter flow into streams because of the lower position of freshwaters than terrestrial ecosystems (Leroux and Loreau 2008), making freshwaters a hotspot in controlling global C cycling (Raymond et al. 2013). Microbes and invertebrates are the two dominate contributors driving leaf litter decomposition in streams (Hieber and Gessner 2002). However, these two ways generate different forms of carbon that can influence nutrients (e.g. C and N) cycling (Fig. 1.3). The process of leaf litter by invertebrates generate fine organic particles while the work of microbes generate gaseous form of C (i.e. CO_2) (Boyero et al. 2011b). Therefore, how leaf litter were processed in freshwaters can affect global nutrients cycling. Whereas, the dominant role controlling leaf litter decomposition may shift under different physicochemical conditions, with the contribution of invertebrates to litter decomposition decreased in tropical than in non-tropical areas, and lower in polluted and urban streams than forest streams (Mathuriau and Chauvet 2002, Pascoal et al. 2005, Iñiguez-Armijos et al. 2016).

1.5 Leaf litter decomposition under anthropogenic and natural disturbances

Many environmental factors can result in the change of overall litter decomposition and the relative role of invertebrates and microbes in driving litter decomposition (Iñiguez-Armijos et al. 2016, Tiegs et al. 2019). Land use change exert one of the predominant changes in the last century and are likely to have serious consequences for ecosystem functioning at local, regional and global scales (Matson et al. 1997). Freshwaters are affected by land use in many ways, including geomorphology, hydrology, water quality, riparian plant communities, invertebrate communities, and many other factors (Allan 2004, He et al. 2015, Little and Altermatt 2018), all of which can directly or indirectly affect leaf litter decomposition in streams. Global changes are predicted to alter riparian plant communities in three main ways: shifts in the dominant role between deciduous and coniferous plants; favoring drought-tolerant species; and the global expanding of plantation and crop species (Kominoski et al. 2013). In addition, global leaf litter quality (Yuan and Chen 2009, Boyero et al. 2017), macroinvertebrates (Boyero et al. 2011a, Boyero et al. 2012), and fungi (Seena et al. 2019) all showed response to the gradients of mean annual temperature (MAT), mean annual precipitation (MAP), latitude, or altitude. These factors may locally or globally affect leaf litter decomposition in freshwaters.

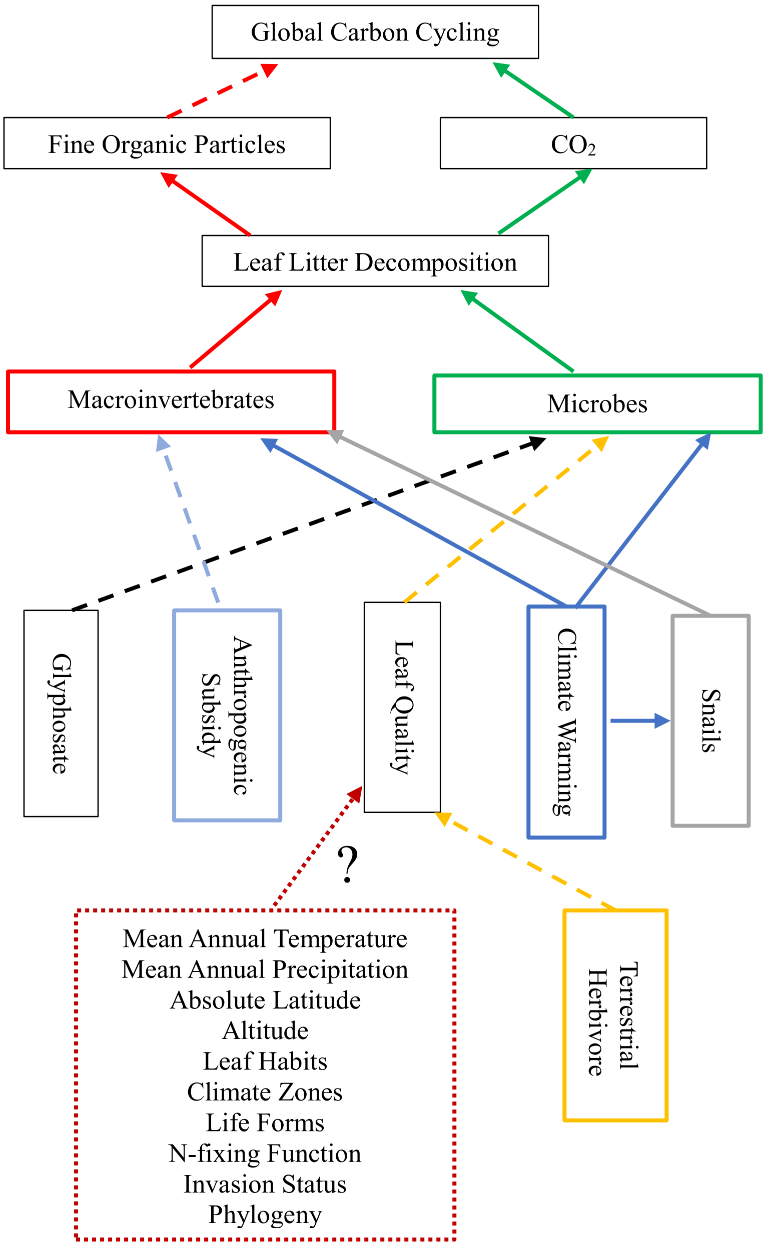

Figure 1.3 A diagram showing the structure of this thesis. Leaf litter processed by macroinvertebrates generate fine organic particles which slowing carbon cycling, while the process by microbes generate CO_2 which accelerate carbon cycling. I focused on how leaf litter decomposition was affected by abiotic and biotic factors. I hypothesized that: (1) environmental relevant concentration of glyphosate would retard microbial-mediated litter decomposition; (2) anthropogenic carrion subsidy (chicken meat) would reduce macroinvertebrate-mediated litter decomposition; (3) terrestrial insect herbivore would decrease leaf litter quality and depress microbial-mediated litter decomposition; (4) climate warming would stimulate both snail-mediated and microbial-mediated litter decomposition; (5) the presence of snails would increase leaf litter decomposition; and (6) global riparian leaf litter quality (C, N, P, and stoichiometric ratios) would response to the gradients of climatic (mean annual temperature and precipitation), geographic (absolute latitude and altitude), and also would differ between climate zones, leaf habits, life forms, N-fixing functions, invasion status, and phylogeny. Solid and dashed lines indicate positive and negative effects respectively. The same color indicates the same factor.

1.5.1 Glyphosate Modern development of agriculture induced many new stressors such as pesticides to aquatic ecosystems. One of the biggest problems is glyphosate, the most widely used herbicides worldwide (Annett et al. 2014), which can enter freshwaters through run-off. Detectable concentration of glyphosate were found in many waterbodies worldwide (Glozier et al. 2012, Annett et al. 2014), and the concentrations are dynamically changed with season and the occurrence of rainfall (Pérez et al. 2017). Field and ecotoxicological experiments demonstrated that microbes (Pérez et al. 2007), algae (Magbanua et al. 2013a), zooplankton (Baker et al. 2016), invertebrates (Puertolas et al. 2010, Cuhra et al. 2013), fish (Cavalcante et al. 2008, Kelly et al. 2010), and amphibians (Howe et al. 2004, Relyea et al. 2005) were likely to be affected by glyphosate. Consequently, leaf litter decomposition was potentially to be influenced by glyphosate through both invertebrate-mediated and microbial-mediated ways (Magbanua et al. 2010, Magbanua et al. 2013b). However, whether environmental relevant concentration of glyphosate would affect streams remains unclear, as some studies showed no or low impacts (Giesy et al. 2000, Solomon and Thompson 2003, Cerdeira and Duke 2006) while others revealed significant effects on microbes (Sura et al. 2012, Muturi et al. 2013, Shaw and Mibbayad 2016). Therefore, it is important to investigate whether and how environmental relevant concentration of glyphosate can affect leaf litter decomposition in streams for ecosystem management and policy making.

1.5.2 Anthropogenic subsidies which derived from human activities (e.g. recreational fishing and livestock farming), are increasingly entering streams (Lecerf and Chauvet 2008, Rasmussen et al. 2012). These newly emerged subsidies can influence leaf litter decomposition through the impacts on macroinvertebrates (e.g. detritivores and predators), fish, and microbes (Singer and Battin 2007, Jean-Marc et al. 2018). These subsidies (e.g. wastewater subsidy) are projected to increase because of the positive relationship with urbanization (Townsend-Small et al. 2013) which is predicted to increase in the future (Seto et al. 2012). How these subsidies would affect streams and litter decomposition is not fully understood. In addition, anthropogenic subsides such as wastewater subsidy contains not only nutrients but also contaminants which may obscure their effects on microbes and invertebrates (Bunzel et al. 2013, Aristi et al. 2015, Berger et al. 2016).

1.5.3 Climate warming Global air temperature is predicted to increase 2.0 – 4.9 °C by the end of this century (Raftery et al. 2017) and the shift of thermal condition can influence almost all levels of stream ecosystems (Daufresne et al. 2009, Woodward et al. 2010). Increasing water temperature can stimulate microbial activities while hamper the activities of stenothermic species in streams (Fernandes et al. 2014, Domingos et al. 2015, Martins et al. 2017). Therefore, microbial-mediated litter decomposition may be increased while invertebrate-mediated litter decomposition is likely to be reduced (Boyero et al. 2011b). However, eurythermal invertebrates seem to benefit from increasing water temperature as temperature sensitive species were restricted (Daufresne et al. 2009, Shah et al. 2017). If the “winners” of climate warming species contributed the same or even larger to litter decomposition, overall litter decomposition would be unchanged or enhanced (Wenisch et al. 2017). Consequently, the effects of warming on leaf litter decomposition depend on local organism communities. At global scale, shredders are scarce in tropical areas and urban streams (Boyero et al. 2011a). Thus, the rising water temperature may stimulate microbial-mediated litter decomposition while have no significant effects on invertebrate-mediated litter decomposition in shredders scarce streams.

1.5.4 Leaf litter quality has long been acknowledged as a fundamental factor driving the process of litter decomposition in streams (Schindler and Gessner 2009, Jackrel et al. 2016, LeRoy and Fischer 2019). High quality leaf litter are preferentially selected by invertebrates and microbes result in faster decomposition rate than low quality litter (Schindler and Gessner 2009). At global scale, leaf litter N and P were closely correlated with the gradients of mean annual temperature (MAT) and precipitation (MAP), with leaf litter quality indicated by litter N increased from the equator to the poles (Yuan and Chen 2009). This pattern is hypothesized to be induced by low soil P (Hou et al. 2018), and the higher pressure of terrestrial insect herbivore in tropical areas than non-tropical areas (Marquis et al. 2012). However, the distribution range of pest insects is estimated to moving at higher altitude and latitude areas, and expanding at urban areas (Chen et al. 2009, Meineke et al. 2013, Ramsfield et al. 2016). These changes may influence overall quality of riparian leaf litter, especially for headwater streams which are located at high altitude and are highly depend on the inputs of leaf litter. Moreover, leaf litter quality can also be influenced by increasing concentration of CO_2 and elevated air temperature (Tuchman et al. 2002). These changes have been captured by the decreasing leaf litter quality in urban areas (Meineke et al. 2018). Thus, it is urgent to investigate how these changes would influence litter decomposition in streams and their consequences on nutrients cycling.

1.5.5 Snails Urban streams are subjected to many human activities including channelization, water intake, wastewater effluent, concrete banks, and habitat homogenization (Carpenter et al. 2011), which depressed diversity of macroinvertebrates (Urban et al. 2006), and benefit tolerant species (e.g. snails and Oligochaeta) in these streams (Gray 2004, Ramírez et al. 2009). The lack of shredders in these waterbodies making microbes dominate in the decomposition of leaf litter and a negligible role of invertebrates. However, this viewpoint has been challenged by other findings that illustrated the importance of snails in driving litter decomposition in shredders scarce urban streams (Suren and McMurtrie 2005, Chadwick et al. 2006, Yule et al. 2015). Moreover, as tolerant species such as snails have different traits with shredders, they may also vary in the response to warming and other stressors (Baumgartner and Robinson 2015).

1.5.6 Global patterns of riparian leaf litter quality Global terrestrial leaf litter quality changed along the gradients of climatic (MAT and MAP), geographic (altitude and absolute latitude) factors, as well as among biotic (e.g. life forms and leaf habits) factors. Generally, leaf litter N increased while P decreased with increasing MAP and MAT (Yuan and Chen 2009). However, most leaf litter entering streams come from riparian forests which differ from other terrestrial forests such as soil moisture, with higher soil moisture in riparian forests even during dry season (Uria-Diez and Ibáñez 2014). This difference may induce the variation of leaf litter quality as soil moisture correlated with soil nutrients content and nutrients uptake by plants (Yuan and Li 2007). A recently published global field experiment revealed that global riparian leaf litter N and N:P ratio increased with MAP and MAT respectively, while litter P decreased with MAT (Boyero et al. 2017). These results only partly supported the results of global terrestrial leaf litter quality trends (Yuan and Chen 2009), indicating that the global trends of riparian leaf litter quality may have different patterns with terrestrial leaf litter. Therefore, the estimated global leaf litter decomposition rates based on terrestrial leaf litter quality may be biased, with consequences on the prediction of global nutrient cycling.

1.6 Thesis structure and aims

The central aim of this thesis focuses on the biotic and abiotic factors, which are previously ignored or unclear, driving leaf litter decomposition in streams (Fig. 1.3). To address this aim, I conducted a literature review, a field and mesocosm experiment, followed by a meta-analysis, resulting in five chapters. The five chapters are all formatted in the way ready for journal submission. Therefore, there is some information repeated in the two chapters related to field experiment, especially in the introduction and method parts.

Chapter 2 – Streams and adjacent terrestrial ecosystems are closely coupled by numerous subsidies, influencing recipient ecosystems at levels from individuals to ecosystems. In this chapter, I summarized how these reciprocal subsidies were affected by anthropogenic disturbances (land use change, climate change, and invasive species) and the ecological consequences of recipient ecosystems.

Chapter 3 – Streams and rivers receive glyphosate, the most widely used herbicides worldwide, from surrounding terrestrial ecosystems through runoff. Despite the widely acknowledged adverse effects of glyphosate on freshwaters, studies on the impacts of low concentrations or environmental relevant concentrations of glyphosate may come out to be low, negative, or even positive on organisms in freshwaters. In addition, intensive human disturbances introduced large quantity of subsidies to freshwaters, while the effects of these newly emerged subsidies are limited. In this chapter, I used leaf litter bags containing only leaves, leaves with either anthropogenic carrion subsidy (chicken meat) or glyphosate (glyphosate contaminated agar to simulate the continuous releasing of glyphosate during the experimental period), and leaves with both carrion subsidy and glyphosate, deploying in five streams (forest, 50 m downstream of a village, 1000 m downstream of village, suburban, and urban) with different land use. I investigated whether leaf litter decomposition was affected by stream types, and the effects of carrion subsidy and glyphosate on litter decomposition.

Chapter 4 – In this chapter, I used the data (excluded the data of urban stream) of macroinvertebrates from the experiment conducted in chapter 3. I aimed to investigate how macroinvertebrates differed among streams, and were affected by carrion subsidy and glyphosate. To our knowledge, we are the first to use glyphosate contaminated agar and chicken meat (agent of anthropogenic subsidy) to study their impacts on leaf litter decomposition and macroinvertebrates in streams.

Chapter 5 – In this chapter, I conducted a mesocosm experiment to explore three individual and combined factors on leaf litter decomposition in urban streams. Firstly, I manipulated water temperature at two levels, i.e. ambient and an average of 8 ºC above ambient, to investigate the effects on microbial-mediated and snail-mediated litter decomposition. Secondly, I controlled the presence and absence of snails in mesocosm to test whether snails can accelerate litter decomposition. Thirdly, I used leaf litter without obvious damage (i.e. intact leaves) and leaves that had > 40 % area were consumed by terrestrial insects to investigate whether litter quality was changed by terrestrial insect herbivore, and to assess whether these changes can cascade to aquatic ecosystems to influence litter decomposition. In addition, I examined the interactions of these three factors to investigate the possibility of predicting litter decomposition and management of streams facing these problems.

Chapter 6 – In this chapter, I conducted a meta-analysis trying to find out the global trends of riparian leaf litter quality response to the gradients of climatic (MAT and MAP) and geographic (absolute latitude and altitude) predictors, as well as the differences of leaf litter quality between climate zones (tropic and non-tropic areas), phylogeny (broadleaf and conifer), leaf habits (deciduous and evergreen), invasion status (native and exotic), N-fixing function (N-fixing and non-nitrogen fixing), and life forms (tree and not tree). I also compared the results of this meta-analysis with a global field experiment investigating the global trends of riparian leaf litter quality, and another study that examined global terrestrial leaf litter quality patterns.

Chapter 7 – A briefly summary of the major findings throughout the above five chapters.

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Chapter 2 Importance of riparian zone: effects of resource availability at the land-water interface

2.1 Abstract

Riparian zone provides a variety of resources to freshwaters, including availability of water and subsidies. Water availability in riparian areas influences species distribution and trophic interaction of terrestrial food webs. Cross-ecosystem subsidies as resource flux of additional energy, nutrients, and materials benefit riparian populations and communities (e.g. plants, spiders, lizards, birds and mammals). However, aquatic ecosystems and riparian zones are prone to anthropogenic disturbances, which interrupt and change water availability and the flux dynamics of cross-system subsidies. Yet, we still lack sufficiently empirical studies on the impacts of land use, climate change, and invasive species on subsidies and the ecological consequences on recipient ecosystems. In filling this knowledge gap, we need to make more effective efforts to protect and conserve riparian biodiversity, and maintain riparian ecosystem functioning and services.

Keywords: cross-system subsidy, water resource, climate change, land use, invasive species

2.2 Introduction

Cross-ecosystem resource subsidies is an important ecological concept for scientists and managers that coupled terrestrial and aquatic systems (Polis et al. 1997, Richardson et al. 2010, Gounand et al. 2018). Understanding the importance of subsidies is crucial while restoring and managing aquatic and terrestrial ecosystems (McInturf et al. 2019), because aquatic ecosystems and riparian zones are closely linked (Moon and Silva 2013, Soininen et al. 2015, Wallace et al. 2015). Subsidies are donor controlled allochthonous resource flux (Likens and Bormann 1974, Polis et al. 1997) and can benefit recipient ecosystems in multiple ways such as increasing reproduction and survival of consumers (Sabo and Power 2002a, Chan et al. 2007, Butler and Wahl 2010). Ecological responses in riparian zones to allochthonous resources often present an “edge effect” along aquatic habitats, with higher population density and diversity as compared to other habitats (Sabo and Power 2002b). Riparian zones benefit from their proximity to river ecosystems, deriving food resources from the river in the form of subsidies of algae, emerging arthropods (Polis et al. 1997, Marczak and Richardson 2007, Bartrons et al. 2013) and anadromous fish (Flecker et al. 2010, Wheeler et al. 2015, Harding et al. 2019).

Allochthonous resource inputs across riparian and aquatic ecosystems are often shown to go in both directions (Baxter et al. 2005, Earl et al. 2014, Larsen et al. 2016), with each ecosystem receiving a resource pulse during its least productive season (Nakano and Murakami 2001). Subsidies transferred across riparian zones are not only beneficial for terrestrial species (Sabo and Power 2002b, Marczak and Richardson 2007), but also provide multiple necessary services for aquatic ecosystems (Pusey and Arthington 2003, Wipfli and Baxter 2010). These services include the provision of dissolved organic carbon (DOC) for energy, leaf litter and woody debris for habitat, and food in the form of terrestrial invertebrates (Nakano et al. 1999, Pusey and Arthington 2003). The effects of subsidies can be altered by predators (Baxter et al. 2004, Burdon and Harding 2008, Wesner 2012). As typical, asymmetrical or one-sided dynamics can occur in habitats with higher trophic level consumers including lizards and birds, they merely consume the aquatic subsidy, yet provide little benefit back to the freshwater ecosystem (Burdon and Harding 2008).

When assessing the relationship between freshwater and terrestrial ecosystems, it is important to take hydrology into consideration (Zalewski 2000, Jackson et al. 2009, Petkovska and Urbanic 2015). Riparian hydrology can be considered from four aspects of spatial variability: lateral across the riparian zone, longitudinal down the river continuum, vertical from groundwater to atmospheric interactions, and temporal (Ekness and Randhir 2007). Stream and river ecosystems provide necessary freshwater resources for riparian organisms to consume in its free-form, which eventually flows up the trophic system from primary producers such as riparian plants or lower order consumers to higher order consumers. To track these relationships, previous studies have formulated the idea of a water web in riparian ecosystems to look to the map of the flow of water throughout trophic systems (Bastow et al. 2002, Sabo et al. 2008, Ramey and Richardson 2017).

Theoretical studies postulate the potential impacts of subsidies on food web, the consequences to differing quantity (Cottingham and Narayan 2013) and quality (Marcarelli et al. 2011) of inputs, and at which level of the trophic system the resource enters (Jardine et al. 2009). Low levels of resource input can stabilize food webs, while may potentially cause detrimental effects if allochthonous inputs are too large (Huxel and McCann 1998). The strength of the effects of subsidy depends not only on its quantity, but also its quality (Stoler and Relyea 2013). For example, mesocosms with grass litter addition had highest treefrog biomass export, while it was lowest in white oak litter addition treatments, because of the differences in litter quality (Earl et al. 2014). While resources move from areas of high to low productivity, as the amount of input increases, the systems (e.g. caves, headwater streams, and some small marine islands) might become unstable due to increased predators (Huxel and McCann 1998, Huxel et al. 2002). The duration and magnitude of resource subsidy flux pulse, together with generation times and biomass of consumers and predators of those consumers, can determine community stability and possible dynamics (Holt 2008, Takimoto et al. 2009, Yang et al. 2010).

Trophic cascades, a potential consequence of subsidies, vary in strength and are commonly thought to be influenced by consumer body size (Lisi et al. 2014), quantity of subsidy input (Klemmer and Richardson 2013), general system productivity, diversity of primary producers (Allen et al. 2012), and predator traits (Shurin et al. 2002, Leroux and Loreau 2008), as well as habitat heterogeneity level (Zhang and Richardson 2011). In addition, attributes of each ecosystem (aquatic or terrestrial) can give insight into the strength of potential trophic cascades following a particular amount of allochthonous resources they receive (Klemmer and Richardson 2013). Generally, aquatic ecosystems experience stronger trophic cascades than terrestrial ecosystems (Halaj and Wise 2001, Shurin et al. 2006, Schlacher and Cronin 2007) for numerous reasons, including their low level and concave structure naturally attracts a greater rate of input, in comparison with mountain areas or even flat terrestrial areas (Leroux and Loreau 2008).

Allochthonous resource pulses can be viewed in two ways: as singular events and then as recurrent environmental events (Holt 2008). With recurrent resource pulses, local persistence of an organism can be threatened due to destabilizing adaptive habitat choice of consumers, which is because many consumers can aggregate in a habitat having resource subsidy pulses, and then disperse to adjacent habitats when those subsidies are disappeared. However, resource subsidy pulses can sustain species diversity at community level, whereas alter community structure through complex interactions by influencing coexistence mechanisms such as hampering predator coexistence, resource partitioning, and keystone predation (Shurin et al. 2002, Holt 2008, Yang et al. 2010).

The distribution of necessary resources in a riparian zone has been shown to impact the method of resource acquisition of consumers, particularly in predatory terrestrial taxa. We present a review of literature concerning the acquisition of food and water by riparian populations and communities, and include a case study involving lizards. We will take the spatial variability into account, in terms of lateral across the riparian zone, longitudinal down the river continuum, and vertical which connects groundwater to atmospheric interactions. These factors are important to consider going forward as humans continue to deplete water resources and the effects of climate change increase. The aims of this review are to show: i) the importance of resources, including water and subsidies, in supporting and maintaining consumer populations along the riparian zone, ii) how land use, climate change and invasive species can influence water and subsidies to riparian consumers, iii) how riparian consumers are influenced by the altered water availability and subsidies, iv) the dynamic interactions of consumers, hydrological regime, and subsidies within their ecosystems. Figure 2.1 presents a full framework of the relationships discussed in this review.

2.3 Impact of aquatic resource subsidies on specific terrestrial organisms

Aquatic ecosystems often transfer large quantity of resource subsidies to terrestrial ecosystems, such as adult aquatic insects (Bartrons et al. 2013, Dreyer et al. 2015). The majority of aquatic insects deposited in riparian area because aquatic insect deposition rate decreased with the distance to water edge (Gratton and Vander Zanden 2009). These inputs are especially important for consumers during certain periods (Fukui et al. 2006). The flow of food resources from freshwater to terrestrial ecosystems can stimulate high abundance of consumers along the edge of aquatic habitats (Chan et al. 2007, Hoekman et al. 2011). In fact, studies indicated that dominant predators in the riparian area at the time when insects emerge from the river determine specific predation effect in the riparian habitats (Fukui et al. 2006, Burdon and Harding 2008, Gonsalves et al. 2013). Since aquatic insect emergence is an important subsidy for many terrestrial consumers including spiders, birds and bats (Sabo and Power 2002b, Marczak and Richardson 2007), the management of aquatic and riparian habitats should consider trophic linkage of aquatic resource and terrestrial organisms (Chan et al. 2007, Gratton et al. 2008, Butler and Wahl 2010). This section will focus on studies in the field of subsidies and their impact on specific riparian taxa, including: spiders, birds, reptiles, mammals, plants, as well as a small section on aquatic predators and their influence on riparian zone trophic dynamics.

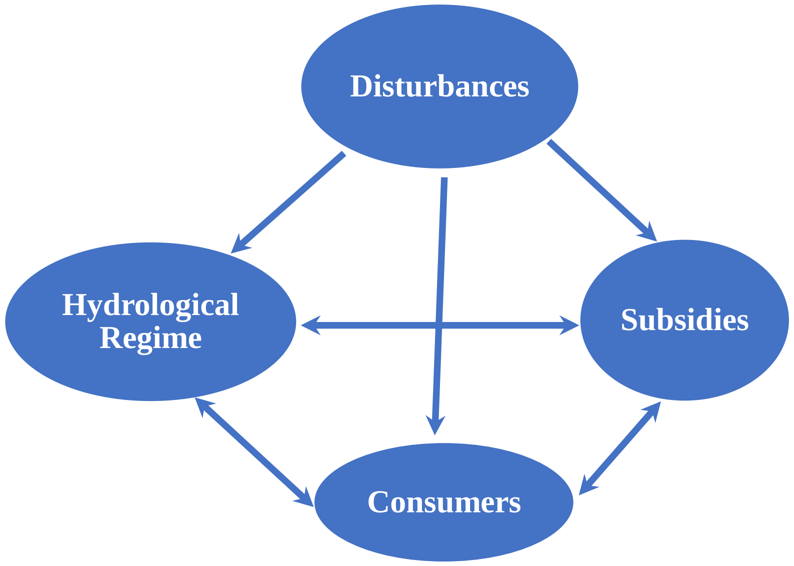

Figure 2.1 A diagram of relationships among disturbances, hydrological regime, subsidies, and consumers.

2.3.1 Spiders – Spiders living in riparian zones receive large proportion of food resources from freshwaters in the form of emerging aquatic insects (Kato et al. 2003, Chan et al. 2009, Benjamin et al. 2011, Kelly et al. 2019). Over 40% of the diet of spiders, which live adjacent to the stream, comprised by adult aquatic insects, and this proportion decreased to < 1% at 20 m from the stream (Briers et al. 2005). Higher aquatic insect abundance caused higher overall density of spiders (Marczak and Richardson 2007), but this distribution model was species dependent, and was strongest for horizontal orb weavers (Tetragnathidae) which mainly feed on emerging aquatic insects (Kato et al. 2003, Marczak and Richardson 2007, Chan et al. 2009, Wesner 2012). Therefore, factors that can reduce the flux of emerging aquatic insects, such as the presence of predatory fish, may limit the abundance of terrestrial spiders (Wesner 2012). However, the distributional models of web-building spiders is closely linked to the temporal dynamics of aquatic insect subsidy (Kato et al. 2003), the availability of web-building substrates can also influence the distribution of spiders (Chan et al. 2009). Moreover, through the aquatic-terrestrial linkage, riparian spiders can take a trophic bypass to directly consume emergent prey adults from aquatic habitats with toxic contaminant (e.g. polychlorinated biphenyls (PCBs), heavy metals, methylmercury - MeHg) (Walters et al. 2010). Whether spiders that consumed aquatic insects have higher or lower contaminant concentrations than those ate terrestrial insects may depend on the trophic level of aquatic prey insects and terrestrial insects, i.e. the food chain/web effects (Walters et al. 2010, Bartrons et al. 2015).

2.3.2 Bats – Riparian zones provide numerous benefits for insectivorous bats, including favorable open habitats in the middle of a wooded area, water availability, and emergent aquatic insects as food source (Vindigni et al. 2009, Yoshikura et al. 2011, Hagen and Sabo 2014, Salvarina 2016). Yoshikura *et al.* (2011) found that species richness and total abundance of two tree-roosting specialists and the Japanese large-footed bat were significantly higher in riparian habitats than in non-riparian habitats. This pattern is related to abundant emerging aquatic insects that are major food resources for bats. For instance, 62.4% of the diet of a long-fingered bat were aquatic insects (Almenar et al. 2008). Seasonal emergence of aquatic insects is a dominant factor affecting the distribution of riparian-foraging bats in Japan (Fukui et al. 2006). The foraging activity level of bats is correlated with aquatic insect emergence and the strongest peak in bat activity occurred with the peak in aquatic insect emergence in riparian forest (Hagen and Sabo 2014). During aquatic insects' peak emergence season, bat foraging activity in areas with natural aquatic insect emergence was nearly 34 times greater than treatment areas with limited insect emergence (Fukui et al. 2006). This resource-consumer relationship is also indicated by a case of bats benefiting from beavers (Nummi et al. 2011). Yet, prey abundance alone may not enough to explain the activity of insectivorous bats, because physical structure can also constrain the accessibility of aquatic insects to bats (Hagen and Sabo 2011). Foraging long-fingered bats showed a disproportionate use of river stretches with increased accessibility and detectability, i.e. open smooth water surfaces (Almenar et al. 2013). In addition, bats community structure were relate to riparian vegetation characteristics (Monadjem and Reside 2008). Moreover, freshwaters may be used by bats for providing their required drinking water resource for successful reproduction rather than the supply of both aquatic and terrestrial prey insects (Seibold et al. 2013).

2.3.3 Birds – Riparian habitats often have higher abundance and diversity of birds than in adjacent areas (Chan et al. 2008, Wagner and Reynolds 2019) because aquatic insects usually have higher quality (e.g. fatty acids) than terrestrial insects (Twining et al. 2018). Insectivorous birds rely on emerging insects in riparian zones for their food resource (Gray 1993), which can maintain their population size, especially when these subsidies were crucial for feeding their young (Epanchin et al. 2010). A study of insectivorous bird density found that bird density fluctuated based on seasonal events (Uesugi and Murakami 2007). During a resource pulse of insects (in spring) from the aquatic ecosystem, bird density significantly increased in the riparian zone (Uesugi and Murakami 2007). This was true for insectivorous birds that aggregate in habitats adjacent to streams where adult aquatic insects were more abundant, especially in spring when the biomass of terrestrial prey is low (Iwata et al. 2010). Habitat heterogeneous structure, stream geomorphology, and the density of stream channels can affect adult aquatic insect flux and insectivorous bird abundance in riparian areas (Iwata et al. 2003, Iwata et al. 2010). Longer and denser stream channels per unit area sustained high density of insectivorous birds due to greater adult aquatic insect abundance (Iwata et al. 2010) which was caused by increased length of stream edge, stream water surface, and suitable foraging sites for birds (Iwata et al. 2003) (Fig. 2.2 A). On the other hand, river-flow regulation disturbance by constructed dams can influence bird assemblages through altered aquatic insect emergence (Jonsson et al.

2012) (Fig. 2.2 B). Furthermore, invasive aquatic species also influenced bird foraging activity through indirect effect. Nonnative trout in five headwater lakes reduced 98% of mayflies than that in fishless lakes (Epanchin et al. 2010). Consequently, there were nearly 6 times more Rosy-Finches at fishless lakes than lakes with fish (Epanchin et al. 2010) (Fig. 2.2 C).

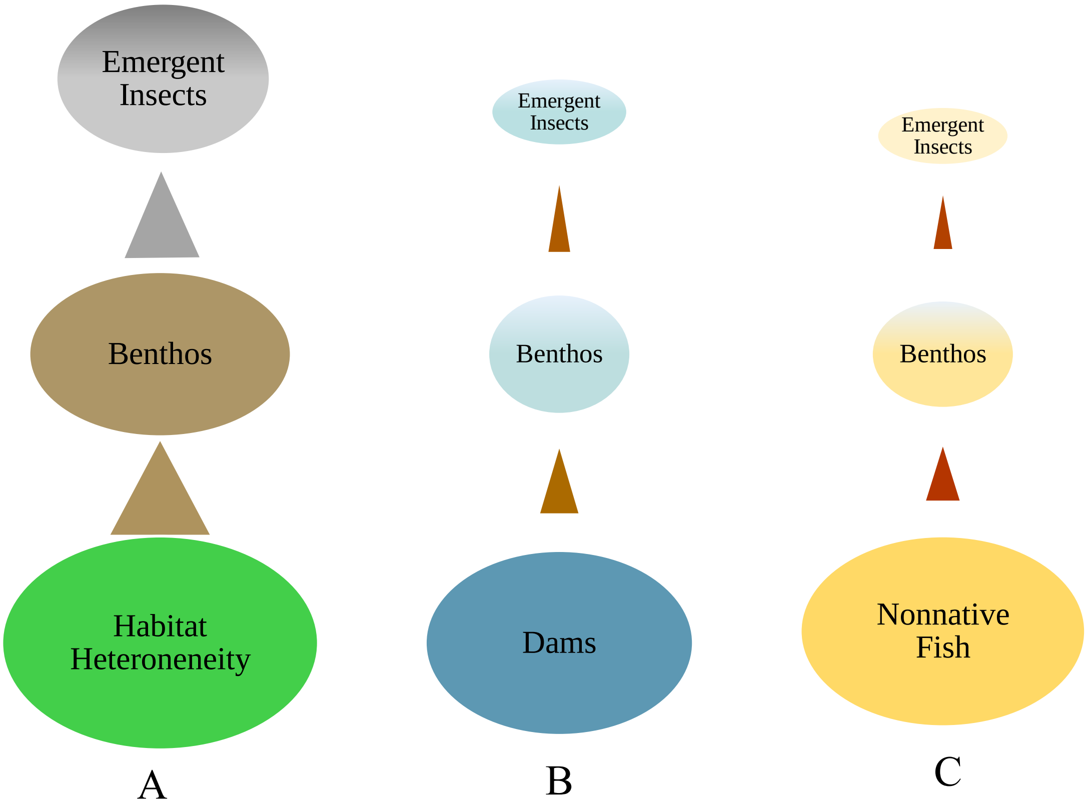

Figure 2.2 Conceptual model of the impacts of disturbances on invertebrates and adult aquatic insect emergence. A: Habitat heterogeneity enhances benthic communities and supports aquatic insects emerging from aquatic ecosystems, and thus, benefiting birds by supplementing their foods. B and C: Dams and non-native species have negative impacts on benthic communities and cause the reduction of aquatic insect emergence as the diet of birds, so that limiting the strength of cross-ecosystem trophic interactions.

2.3.4 Mammals – Even though mammals are highly mobile consumers, their presence exert large impact on the dynamics of riparian trophic systems and modify the structure and function of riparian zones (Naiman and Rogers 1997, Helfield and Naiman 2006, Beschta and Ripple 2012). Animal migrations often evolve to track seasonal variation of prey such as migration salmons (Sergeant et al. 2015). Many terrestrial mammals (e.g. bears, cougar, and wolverine) move among discrete habitats using environmental cues to time the arrival of seasonal peaks of salmons (Schindler et al. 2013, Shardlow and Hyatt 2013, Deacy et al. 2019). A suitable example of large mammal predators influencing nutrient dynamics along riparian zones is bears with their salmon prey (marine-derived nutrients, MDN) (Helfield and Naiman 2006, Koshino et al. 2013). It is reported that 49% of pink and chum salmon captured by bears were carried into riparian forests (Quinn et al. 2009). The consumption of salmon by bears varied widely among species, age class, sex, and location (Van Daele et al. 2013, Matsubayashi et al. 2014). Studies have shown that bears transport MDN to terrestrial systems through urine and faeces (Hilderbrand et al. 1999) and to riparian forests by physically moving salmon carcasses (Quinn et al. 2009) via foraging activities, with beneficial effects on plants, beetles, flies, and birds (Gende et al. 2002, Hocking and Reynolds 2011).

Further, there are other mammals that are not subsidy consumers but play an important role in terrestrial-aquatic subsidies (Stears et al. 2018, Subalusky et al. 2018). For instance, hippopotamus can act as ecosystem engineers to transport carbon and nutrients. It was estimated that *Hippopotamus amphibius* transported 8,563 kg dry matter, 3,499 kg C, 492 kg N and 48 kg P to Mara River every day, which equals to 670% of CPOM, 15% of DOC, 27% of TN and 29% of TP of loading from the upstream catchment (Subalusky et al. 2015). These nutrient subsidies benefited aquatic invertebrates and fish (McCauley et al. 2015). In addition, some small mammals themselves can be terrestrial subsidies for aquatic consumers. In the Wood River basin, Alaska, Arctic grayling (*Thymallus arcticus*) and rainbow trout (*Oncorhynchus mykiss*) contained 24% mammal (*Sorex* spp.) in their diet, although these predatory fish were gape-limited (Lisi et al. 2014). Moreover, the presence of beavers (*Castor canadensis*) enhanced cross-boundary resource subsidies by impounding streams which resulted in higher terrestrially derived organic material in habitats (Anderson and Rosemond 2010), or created suitable habitats for many other species such as bats through the habitat management (Nummi et al. 2011). Thus, mammals can enhance trophic and energetic aquatic-terrestrial linkage and affect ecosystem functioning in aquatic systems (Naiman and Rogers 1997, Wardle et al. 2011, Masese et al. 2015).

2.3.5 Plants – While most studies focused on the importance of riparian forests as donor ecosystems to transfer leaf litter, large wood, seeds, pollen and terrestrial insects to aquatic ecosystems (Atlas et al. 2013, Stoler and Relyea 2013, Richardson and Sato 2015, Correa and Winemiller 2018), or as recipient ecosystems for terrestrial consumers to enjoy the aquatic subsidy feast (Marczak et al. 2007, Dreyer et al. 2015), relative less ecologists investigated the effects of aquatic subsidies (e.g. organic matter, emerging aquatic insects, salmon carcasses) on riparian plants (Spiller et al. 2010, Hocking and Reynolds 2011, Bultman et al. 2014, Quinn et al. 2018). As most adult aquatic insects deposited within 100 m into the land (Bartrons et al. 2013), these nutrient subsidies significantly affected primary production in nutrient-limited ecosystems adjacent to freshwaters (Dreyer et al. 2015). In one study, midge deposition peaked at 12 kg $N \cdot ha^{-1} \cdot yr^{-1}$ near shore during a high midge-emergence year (Dreyer et al. 2015), and this N contribution from midges can be three to five times the level of background atmospheric deposition in the subarctic (Bobbink et al. 2010). Consequently, % N dry weight of willow leaves in high midge sites was 8-11% higher than low-midge sites, with further consequence on herbivorous insects which had 4-6 times higher density and 72% heavier individual biomass (Bultman et al. 2014). By comparing 50 rainforest watersheds of British Columbia's central coast in Canada, Hocking and Reynolds (2011) found that carcasses of Pacific salmon influenced nutrient loading to plants, and caused shifting plant community structure toward nutrient-rich species that in turn reduced plant diversity in riparian zones (Hocking and Reynolds 2011).

2.4 Cross-ecosystem trophic cascades: the role of aquatic predators on terrestrial trophic dynamics

Earlier statements discussed how a healthy terrestrial ecosystem provides an important source of allochthonous resources for aquatic consumers – with the top predator generally being fish species (Nakano and Murakami 2001, Pusey and Arthington 2003, Wipfli and Baxter 2010). Stream fishes, primarily in the low productivity of the headwaters, often heavily depend on terrestrial insects for prey items (Wipfli and Baxter 2010, Correa and Winemiller 2018, Roon et al. 2018). However, their linkage to the riparian food web can be tighter (Wesner 2010), as predators in streams have the potential to produce ecosystem effects on riparian trophic systems throughout aquatic-terrestrial food web linkages (Knight et al. 2005). Knight *et al.* (2005) found fish presence in ponds reduced dragonfly larval density, so that its adult densities surrounding ponds were low. Thus, visitation rates of pollinators normally preyed upon by adult dragonflies increased, and therefore increased plant reproduction in the adjacent riparian habitats. Such cross-ecosystem connectivity is crucial to assess anthropogenic impacts on the dynamics of meta-ecosystems (Walters et al. 2008, Piovia-Scott et al. 2011, Kraus et al. 2014).

2.5 Impacts of disturbances on cross-ecosystem subsidies and riparian consumers

Anthropogenic disturbances such as land use change, climate change and invasive species are leading forms of stressors for causing changes of ecological communities by losing species and influencing ecosystem structure and processes, with important implications for ecosystem management and biodiversity conservation (Wardle et al. 2011).

2.5.1 Land use – Almost all ecosystems suffer from some degradation of land use such as by agriculture, urbanization and deforestation or forest harvesting (Tiegs et al. 2008, Francis and Schindler 2009, Stenroth et al. 2015), and they are the predominant changes in the last century and are likely to have serious consequences for ecosystem functioning at local, regional and global scales (Matson et al. 1997). During the past 50 years, agricultural land use was and will continue to be the main reason of ecological changes in both aquatic and terrestrial ecosystems (Burdick and Hightower 2006). Aquatic ecosystems are particularly sensitive to land use. Regional habitat and biological diversity of streams and rivers are closely linked to landform and land use within watershed at multiple scales (Allan 2004). In addition, the consequences of land use are various, including effects on water quality, habitat change, altered canopy cover and sediment inputs (Zhang et al. 2010, Moore et al. 2014). The effects of land use can propagate to adjacent habitats through subsidies and influence adjacent ecosystems.

- Land use can changed the size structure of prey subsidy, for example, aquatic insects in streams which were subjected to agricultural land use were dominated by small body insects such as Nematocera, whereas larger-bodied aquatic insects (Plecoptera and Trichoptera) were more associated with forest land use, and this size change of prey subsidy is associated with the distribution of different types of terrestrial predators, causing a different terrestrial predator community structure (Stenroth et al. 2015).
- Land use can changed the magnitude of subsidies, Francis and Schindler (2009) found that at all geographical scales, shoreline development negatively influenced terrestrial invertebrate subsidies, with 100% of the diet of fish was terrestrial insects in undeveloped lakes, whereas it was only 2% in developed lakes (Francis and Schindler 2009).

- Land use can change nutrient concentration in subsidies. Boechat *et al*. (2014) found the total fatty acid (FA) concentrations in suspended particulate organic matter (SPOM) of urbanized tropical rivers were higher than undeveloped rivers, and the higher energy biochemical subsidies were beneficial to bacterial and suspension-feeders in river food webs (Boechat et al. 2014).
- The effects of land use may last for a long time, i.e. legacy effect. Historical logged streams transport more material subsidies to downstream compare to unlogged streams (Binckley et al. 2010).
- Land use can reverse the effects of subsidies to stress, for example, timber harvest altered stream sediment size to becoming smaller, and thus transform the dominant effect of salmon from nutrient enrichment to physical disturbance, thus modifying nutrient linkages between marine and freshwater ecosystems (Tiegs et al. 2008).

2.5.2 Climate change - Global climate change will have significant impacts on freshwaters all over the world (Heino et al. 2009, Jeremias et al. 2018). Climate warming can alter the size structure of emerging insect, an increase of 3 ºC above ambient temperatures caused an average of 57-58% fewer emerging Chironomidae, however, total aquatic insect emergence biomass was not influenced by warming, therefore, adult insects emerged from warm waterbodies had larger body size (Jonsson et al. 2015). Conversely, another study shows only the emerging Chironomidae were larger with raised temperature, while the emerging of both medium and large-sized insects were decreased, moreover, rising temperature decreased time to emergence (Piggott et al. 2015). Warming also increased 38% biomass of overall insect emergence, and advanced the spring pulses of aquatic emergence, and this effect was stronger in the presence of fish (Greig et al. 2012). Water temperature can influence the physiology of consumers to influence their consumption of subsidies. There is a size threshold for age-0 Coho salmon to consume salmon egg subsidy, which is regulated by water temperature (Armstrong et al. 2010). The temperatures in cooler streams constrained the potential for postemergence growth in age-0 Coho salmon, restricting their maximum size during a seasonal pulse of sockeye salmon eggs. Because gape size prevented smaller individuals from consuming eggs, cold temperatures indirectly prevented smaller fish from exploiting egg subsidies, severely reducing their growth potential (Armstrong et al. 2010). Climate change can induce phenological shifts of keystone species to influence population, evolutionary, and ecological dynamics, and this shift will further affect species that depend on salmon resource subsidy (Kovach et al. 2013).

Drought is another aspect of climate change and it will result in drying of streams, which has occurred at higher frequency and longer duration in many parts of the world. The earlier emerging aquatic insects can also be induced by drought. Leberfinger *et al.* (2010) found an earlier pupation for the caddisfly *Limnephilus flavicornis* in drought conditions, and this shift in timing of emergence may propagate to terrestrial food webs, where emerging aquatic insects are important food subsidy for terrestrial predators (Leberfinger et al. 2010). Furthermore, drought can reduce the fluxes of terrestrial organic matter subsidies transfer to streams, thus weaken the linkage between terrestrial and aquatic ecosystems (Kiffney et al. 2002). However, extreme drought can also enhance cross-system subsidies by causing large scale mortality of invasive bivalves, this unexpected resource subsidy may contribute remarkable amounts of nutrients and energy to the adjacent terrestrial ecosystem (Bódis et al. 2014).

2.5.3 Invasive species - As predators, invasive fish have the ability to reduce the efficiency of the food web as well as overall aquatic insects export (Epanchin et al. 2010) and terrestrial insects available to native species (Baxter et al. 2004), which can reduce the magnitude of a resource subsidy and the strength of the ecosystem linkages (Baxter et al. 2004, Epanchin et al. 2010, Rolla et al. 2017). The addition of invasive fish species to a linked stream-forest web in one study shows that an invasion of nonnative species were able to influence up to four levels of the trophic structure, indicating that the consequences of invasive species are comparable to cutting off prey subsidies between ecosystems (Baxter et al. 2004). Another study showed that organisms dependent on seasonally occurring subsidies are particularly sensitive to allochthonous resources if they occur during important life history events, including reproductive and young rearing phases, of the consumer (Epanchin et al. 2010). If there is a disruption in the flow of allochthonous resources due to landscape degradation, not only will the consumer be impacted, but the entire trophic system has the potential to be altered. The impacts of invasive species can propagate to adjacent ecosystems, for instance, the invasive brook trout reduced emergence rates of aquatic insects by 24%, which caused 6-20 % fewer spiders in the riparian zone (Benjamin et al. 2011).

While the invasive predators usually elicit top-down effects on recipient ecosystems, the invasive primary producers or invasive consumers at low trophic level usually cause bottom-up effects, and thus alter the exchange of subsidies between ecosystems (Roon et al. 2018). The invasive plant species *Rhododendron* had poor litter quality and densely shaded canopy that suppressed litter decomposition and algal production, and transports poorer quality detrital subsidies to stream consumer assemblages (Hladyz et al. 2011), which indicates that invasive species may reduce functional diversity (Kominoski et al. 2013). However, even if the invasive tree species has high litter quality, it may also become a stress to aquatic ecosystems for other reasons. For example, invasive Russian olive transport higher nutrient leaf litter subsidies to streams, and with 25-fold larger biomass of litter subsidies, but neither stream ecosystem respiration nor organic matter export was influenced. Thus, the estimated stream ecosystem efficiency (ratio of ecosystem respiration to organic matter input) decreased 14%, and it was a stress for the stream ecosystem (Mineau et al. 2011, Mineau et al. 2012). The effects of nonnative species on recipient ecosystems may be quantity dependent. For example, an invasive alga reduced total abundance and richness of subsidized macroinvertebrates relative to controls, and the adverse effects increased with higher detrital loading (Taylor et al. 2010). However, if the quantity of this subsidy was low (30 g / 0.25 m^2), the effects can be positive with a higher invertebrate richness (Bishop and Kelaher 2013). Some invasive species may be beneficial to native species, but they can interrupt important energetic subsidy flows into other ecosystems which may cause ecosystem-scale consequences (Boltovskoy and Correa 2015).

However, invasive species may have some positive effects on native species, which have been proved in a wide range of habitats (Rodriguez 2006). For example, greater terrestrial derived organic matter subsidies flow into stream food webs caused by the engineering activities of invasive beavers in the South American mainland (Anderson and Rosemond 2010). Moreover, if invasive species were prey for native species, they can become an important trophic subsidy for native predators. For instance, the invasive signal crayfish contributed up to 30% of population diet of a native omnivorous cyprinid fish (Bašic et al. 2015).

The linkage between aquatic and terrestrial ecosystems is crucial in the management of aquatic ecosystems (Likens and Bormann 1974). It is imperative for that new conservation strategies and forms of management are formulated, and ecosystems have a long enough frame to respond, as it may take a while before some effects of remediation can be seen (Likens and Bormann 1974). In addition, Epanchin *et al.* (2010) suggested that the goal of removing invasive fish species from lakes expand to include the restoration of linkages or subsidies between aquatic and terrestrial food webs. Human induced habitat destruction are increasing in rate and have cumulative effects on lakes, and the alteration of riparian forests can also affect lake population and food webs (Francis and Schindler 2009).

2.6 The role of water availability in influencing riparian trophic systems

2.6.1 Trophic effects of water limitation - Questions concerning the trophic system within habitat and the influence of hydrology on that system are not fully understood. Water is essential for organisms on Earth (Allen et al. 2014b) and may act as a trophic currency determining species interactions in terrestrial food webs (McCluney et al. 2012). A recent study shows that in riparian areas of reduced freshwater discharge, populations of tree species have leaves laden with groundwater and are consumed by primary consumers such as crickets (Sabo et al. 2008). Cricket body water content has been shown to be 25% higher near river habitats, so the further an organism's home territory is to the edge of an aquatic ecosystem, the more important these groundwater linkages may become as this consumption has the potential to "root animals in the regional water cycle" (Sabo et al. 2008). The water sources of riparian consumers can be traced through the trophic system by analyzing stable water isotopes, which assists researchers in determining a more exact source of water, whether it be from the groundwater or other local water features (McCluney and Sabo 2010).

In addition, environmental water conditions, usually categorized as wet or dry conditions, have the potential to impact the consumption habits of riparian consumers (McCluney and Sabo 2009, Soykan and Sabo 2009). Strikingly, the abundance of riparian organisms was greater where surface water and groundwater resources were added, regardless of the presence of a river, an abundant and natural water source (Allen et al. 2014b). When reviewing the interaction between two trophic levels, researchers found that predatory spiders altered their prey consumption; in dry conditions, crickets consumed more moist leaves than dry litter, and the spiders under the dry conditions consumed significantly more crickets under the same conditions

(McCluney and Sabo 2009). These preferences indicate that food consumption can vary across multiple levels of the trophic system depending upon water availability (Sabo et al. 2008, McCluney and Sabo 2009). Seasonal variation of water availability in a desert riparian habitat causes a shift in predator diet, with predators selecting to forage closer to the river during dry conditions and moving further out during wet conditions (Soykan and Sabo 2009). Studies show however, that the response to environmental conditions by an individual species, can be overshadowed over time by inter-species interactions, with the most significant results occurring during the wet spring season (Suttle et al. 2007).

2.6.2 Impact of water availability on the riparian community - Looking at the issue of water availability from a larger scale helps scientists understand the impact of water availability on an entire community. River drying in the United States has been shown to significantly decreased terrestrial arthropods in riparian zones (McCluney and Sabo 2012). Decreasing in terrestrial arthropod abundance is likely to impact all riparian zone consumers, including lizards. In this same vein, a general study of 36 American rivers shows that food chain length increases with drainage area and decreases with discharge variation (Sabo et al. 2010). While this study concerns only aquatic trophic systems, there is a potential for impact on the surrounding riparian zone, as it has already been clearly established how closely subsidies can connect riparian and aquatic systems. Finally, while the importance of available water is established, the quality of the water discharged should also be taken into consideration. Polluted river conditions can also have an impact on the riparian community, as it has been shown to decrease stream arthropod populations, thereby removing a subsidy for terrestrial consumers, who show clear preference for these aquatic insects (Paetzold et al. 2011).

Riparian zone inhabitants are not only benefit from easily get access to stream water, but also the large amount of water from uplands due to the low topographic position (Kuglerová et al. 2014). This higher influx of groundwater (GW) from upland areas caused a 15% - 20% higher Vascular plant species richness compared to non-discharge sites, and this pattern was best explained better soil conditions (e.g. higher soil pH, higher nitrogen availability, and lower soil C:N ratio) (Kuglerová et al. 2014). In addition, groundwater subsidy can affect plant root water uptake, habitats receive large GW subsidy are most prone to degradation by the low water table. Thus, ecosystems that strongly rely on groundwater will be affected by channel incision or climate-induced hydrologic changes (Lowry and Loheide 2010). Furthermore, riparian trees in arid zone may developed many strategies to adapt to high groundwater and soil water salinities (Costelloe et al. 2008).

2.6.3 Effects of hydrological regime on cross-system subsidies - Flow regime is a key factor to drive the exchanges of subsidies between linked ecosystems (Douglas et al. 2005). Floodplain is one of the most active habitats and they are prone to be affected by watershed hydrology. The percentage of floodplain inundated was strongly related to river discharge (Benke et al. 2000). And the short, stochastic floods stand for a strong environmental stressor which induced pronounced changes in the floodplain community, as well as dramatic change of plant assemblages (e.g. lower plant diversity) compared to the static wetlands (Drinkard et al. 2011). These influences may further affect stream consumers, as plant community in riparian zone/floodplain which is the source of leaf litter and other detritus are important food resources for stream consumers. In addition, anthropogenic disturbances, such as dredging, causing hydrological changes of lakes, may reduce algae and detritus inputs to midge habitats, with higher-amplitude fluctuations of midge populations. Consequently, fish and bird populations that feed on midges were negatively influenced (Ives et al. 2008). However, not only do subsidy flux is influenced by hydrological regime, riparian consumers are also driven by hydrological pressures of the stream because they are required to possess some specific traits. These traits either works through enhanced ability to process the aquatic subsidy, easier to move onto floodplain, or may only do so under low flow conditions. Riparian coleopteran species with rapid dispersal ability linked to highest abundance of aquatic prey. While less able consumers showed minimal dependence on aquatic subsidy and switched to a more terrestrial diet under medium inundation pressures. However, all trait groups shifted their diet to terrestrial prey in the early spring when inundation pressures were highest (O'Callaghan et al. 2013).

Longitudinally subsidy fluxes within streams and rivers can also be influenced by hydrological regime. Stream hydrological condition affects consumer excretion subsidies. As Wheeler *et al*. (2015) showed that the ratio of fish migrant biomass to system size which was measured by discharge, was related to spatiotemporal hydrologic variation, therefore, the excretion subsidies which were produced by potamodromous fishes was affected, with the maximum influence of consumer excretion occurred during periods of reduced flow (Wheeler et al. 2015). The downstream subsidy fluxes were another case that was driven by hydrology. For example, the drier conditions induced by climate events such as in-phase El Niño could decrease downstream organic matter flow, which reduced growth and survival of stream invertebrates, as well as vertebrates that rely on these resource subsidies in recipient systems (Kiffney et al. 2002).

Furthermore, the effects of hydrological regime usually combined with human impacts. Dams and weirs that impound streams and rivers could reduce flow velocities, and enhance nutrient retention, because water retention time was longer, this may further reduce downstream subsidy flux (Withers and Jarvie 2008). High flow events which may rapidly transport both storm inputs and organic matter retained at baseflow, were observed to increase in frequency and magnitude in human dominated freshwaters such as urban streams. Altering the magnitude, retention time, and the transport distance of organic matter subsidies (Imberger et al. 2011). All of these changed cross system subsidies that were due to hydrological variations, could further influence consumer communities in recipient systems. Interestingly, for a focal system, the subsidy donor systems can be changed due to the temporal hydrological variations. The estuarine consumers received particle organic matter (POM) subsidies from both river and ocean. However, river POM represented an important energy source for the estuarine benthos, especially in winter when river discharge was high. However, marine POM may be replaced by river POM to act as an important alternative food for the estuarine benthos during the rest time of the year when seawater intruded the bottom estuary (Antonio et al. 2012).

Seasonal hydrological change is a key driver of aquatic food web structure and ecosystem processes (Douglas et al. 2005). Whereas hydrological effects usually accompany with climate events, such as flooding, droughts and storms. Because flooding and droughts always associate with water level fluctuations, and influence hydrologic connectivity which is defined as the water-mediated transport of organisms, energy and materials within or between elements of the hydrologic cycle (Freeman et al. 2007), with flooding increase hydrologic connectivity and drought decrease hydrologic connectivity. However, the importance of aquatic subsidies for terrestrial consumers may not only be controlled by hydrological regime, but may also be influenced by other factors such as temperature (Kiffney et al. 2002, Adame and

Lovelock 2011). More aquatic subsidies were consumed in riparian zones of wet-dry tropical rivers in dry seasons in Australia (Douglas et al. 2005, Leigh et al. 2013). While riparian predators consume more aquatic insects in wet seasons (50%) than in dry seasons (21%) in Hong Kong (Chan et al. 2007). Therefore, while considering the importance of cross-system subsidies for freshwater conservation and restoration, we should take all the possible factors into consideration including hydrology.

2.7 Implications of resource subsidies for ecosystem conservation

Preserving freshwater ecosystems presents a unique challenge due to overall connectivity of each system, and due to the overall biodiversity, it is difficult to preserve a representative sample of freshwater diversity (Dudgeon et al. 2006). Décamps (2011) described the term “hotline” specifically for river networks in attempt to link their diversity as a more linear example of a biological hotspot and imply the necessity for their conservation (Décamps 2011). Freshwater ecosystems, diverse in species and benefits, are highly threatened and yet in high demand for their numerous ecosystem services (Allan and Flecker 1993). Threats to freshwater biodiversity are numerous, but can be categorized under the following general terms: anthropogenic disturbance, climate change, and invasive species (Allan and Flecker 1993). These changes can influence lotic and lentic systems alike. Human activities have cumulative effects on watersheds, and the modification of riparian forests likely has affected lake populations and food webs (Francis and Schindler 2009).

Pressure on ecosystems is increasing at an alarming rate and must also be taken into consideration when preserving biodiversity and hydrological cycles (Francis and Schindler 2009). However, cross-system subsidies were largely ignored while conducting ecosystem restoration. In fact, the structure and function of terrestrial and aquatic ecosystems cannot be understood without considering them simultaneously, even if the respective scientific communities may pretend to do so (Soininen et al. 2015). Fortunately, researchers have started to value the importance of cross-system subsidies while restoring or managing aquatic and terrestrial ecosystems (Inoue et al. 2013, Wallace et al. 2015). Saunders and Fausch (2012) compared the effects of three commonly used grazing systems on terrestrial invertebrate subsidy to streams and the consumption by trout in northern Colorado (Saunders and Fausch 2012). Their results show that rotational grazing management (either simple or intensive), lead to more riparian vegetation, higher terrestrial invertebrate inputs, greater terrestrial invertebrate consumption by trout. And rotational grazing systems can be effective for keeping terrestrial invertebrate inputs to streams necessary to support robust trout populations (Saunders and Fausch 2012). Marine subsidies from salmon spawning and salmon analogs are also important for stream restoration as they can increase lipid concentrations, production, and condition of resident and anadromous salmonids. This may further induce higher survival and reproduction, thereby enhance freshwater and marine salmonid production (Wipfli et al. 2004). Therefore, salmon analogs appear to have the possibility to restore nutrients and productivity in freshwater ecosystems which suffer from reduced salmon runs (Wipfli et al. 2004). However, this will need to balance between socio-economic barriers and salmon protection, because most salmon are highly commercially valuable fish (Schindler et al. 2005, Darimont et al. 2010). Yet, some restoration project that did not intend to restore cross-system linkage may do have unexpected effects. Some in-stream restoration projects such as rock weirs aimed to stabilize the channel do increase the abundance, species richness and diversity of emerging insects and higher larger bodied taxa, this change caused a higher total bird abundance, because birds showed a positive numerical response to large-bodied emerging insects, thus enhanced biological connectivity between the river and forest (Heinrich et al. 2014). Allochthonous material subsidies is especially important for estuarine ecosystems restoration, and the proportion of these subsidies entering estuarine marsh food webs did not likely to differ greatly across restoring marsh sites of vary ages, or between ancient (and centennial) reference sites and restoration sites (Howe and Simenstad 2011).

Results from a long-term experiment showed that physical structure alone failed to produce any noticeable changes in production, abundance, or biomass of invertebrates, this indicates that the addition of structures without concomitant changes in the energy base, i.e., addition of leaf subsidies, does not influence stream benthic assemblages (Wallace et al. 2015). The community structure of riparian trees is another factor that can influence terrestrial subsidies dynamics, mainly because of the variation in elemental stoichiometry (C:N:P) (Kominoski et al. 2012). Consequently, peak insect emergence was 1 month earlier and at 2-3 times higher density in coniferous forest streams than in mixed and deciduous-forest streams, but there was no significant difference of total biomass of emerging insects between forest types throughout the study period. In addition, community structure of emerging insects differed between deciduous and coniferous forest streams, and deciduous streams held nearly 2 times greater taxon richness and diversity than coniferous forest streams (Kominoski et al. 2012). Moreover, riparian forest community structure is associated with different magnitude of terrestrial prey inputs, for which streams bordered by conifer forests receive less terrestrial prey subsidies, which results in lower salmon abundance (Inoue et al. 2013).

The research presented in this review highlights the need for resource subsidies to be preserved as they can influence ecosystems across all scales, from an individual lizard species, to a riparian community, all the way up to an entire drainage basin. Ecohydrology touts the importance of increased riparian complexity due to its ability to amplify the self-purification process (Zalewski 2000). By ensuring that the resource requirements of riparian consumers are met, even in degraded areas, ecosystem complexity can be maintained. Future studies should work to show the importance of studying riparian ecosystems across all scales.

2.8 Dark sides of cross-system subsides

Not all cross-system subsidies are beneficial to recipient ecosystems, subsidies can also propagate pollutants (Walters et al. 2008, Paetzold et al. 2011, Kraus et al. 2014, Graf et al. 2019) and pathogen to consumers (Malmqvist et al. 2004), and lower ecosystem stability (Helmus et al. 2013). Contaminants in aquatic ecosystems such as heavy metals (Kotalik and Clements 2019) and polychlorinated biphenyls (PCBs) can be accumulated in terrestrial predators through directly feed on emerging aquatic insects. Total PCBs concentrations in riparian consumers (e.g. spiders) ranged from 180–2740 ng/g, with higher values approaching those of insectivorous fishes (2870 ng/g), while the total PCBs at the reference site were an order of magnitude lower for *Dolomedes* and *Tetragnatha* compared with contaminated sites (Walters et al. 2008). Walters *et al.* (2008) estimated the aquatic insect export of PCBs to the 25 km of Twelvemile Creek riparian zone they sampled is 6.13 g/yr, which is equivalent to the PCBs mass delivered by 50,000 returning Chinook salmon (Compton et al. 2006). This high levels of PCBs in terrestrial predators highlight the importance of emerging aquatic insects as ‘‘biotransporters’’ of contaminants to terrestrial ecosystems (Menzie 1980). In addition, total contaminants such as heavy metals exported by aquatic insects may depend on the metal concentrations in freshwaters. Kraus *et al.* (2014) found that although aquatic insect emergence declined 97% over the metal gradient, there was little change of metal concentrations in adult. Consequently, total metal transported by insects (flux) was least at the heaviest contaminated streams, declining 96% among sites. Therefore, spiders were influenced by the shrink of prey biomass (Paetzold et al. 2011), but not by metal exposure or metal flux to land in aquatic prey (Kraus et al. 2014). Interestingly, adult insect emergence may be better to reflect the impact of low metals concentrations on aquatic insect communities compared to larvae, mainly because adult insect emergence is co-limited by larval survival and other factors that limit successful emergence (Schmidt et al. 2013).

However, although many emerging aquatic insects are food resources for various terrestrial consumers, some of the adult insects (e.g. blackflies) are also pathogen vectors and can attack birds and mammals including human (Malmqvist et al. 2004). In August, at the peak of the rainy season, the biting-rate of a blackfly species was 9.5/man-hour at 10-1100 hours and was 12/man-hour at 14-1600 hours (White 1977). The blackfly (*Sitnulium innocens*) is considered as the prime vector in the transmission of a blood parasite (*Leucocytozoon simondi*) to Canada geese goslings, which caused the decrease of population size (Herman et al. 1975).

Even though we have been aware of some adverse impacts of cross-system subsidies, empirical studies were still limited. Most studies were focus on subsidies from aquatic to terrestrial (more specifically, the emerging aquatic insects), and their role as vectors of contaminants. The adverse effects of terrestrial subsidies were relatively less known. Additionally, due to the intensive human activities, aquatic invertebrate are heavily influenced by contaminants (e.g. heavy metals, PCBs, insecticide, antibiotics). This is a more serious problem in developing countries such as China, where many streams and lakes were polluted, and their consequences on cross-system subsidies and terrestrial ecosystems were largely unknown. Furthermore, the distribution ranges of many aquatic invertebrates have been altered because of climate warming. The shrinking distribution of many cold invertebrate species in high altitude and latitude areas may affect the community dynamic of terrestrial consumers due to the decreased insect flux. For others that expand their distribution ranges caused by climate warming, they may also expand the distribution area of pathogens. And this new introduced pathogen carried by emerging aquatic insects can threaten the health of many other organisms including human. Therefore, more studies should also be conducted to investigate the adverse effects of cross-system subsidies.

2.9 Conclusion

Riparian ecology and stream restoration must integrate into a broader scale to consider the importance of cross-system links such as subsidies and water currency (Soininen et al. 2015). Riparian zones and their adjacent aquatic ecosystems exchange various types of subsidies (e.g. terrestrial insects, leaf litter, aquatic emerging insects, salmon carcasses), and they are usually beneficial to both sides, with elevated population size, higher growth rate, and larger body size. However, ecosystems around the world are increasingly impacted by land use, climate change and invasive species, so that cross-ecosystem subsidies should be influenced by these changes (Jonsson et al. 2015, Stenroth et al. 2015). Understanding how ecological and physical processes respond to these changes needs interdisciplinary research approach, including ecohydrology and geomorphology (Allen et al. 2014a). In addition, land use, climate change and invasive species always interact with each other, and weaken or strengthen the effects on ecosystems and subsidy dynamics, thus complicate the situations. Moreover, we should also be concerned more about newly emerged cross-system subsidies (e.g. human-provided foods to predators, artificial light, and novel ecosystems) which are becoming more common and may have large impacts on aquatic and riparian ecosystems (Meyer and Sullivan 2013, Perkin et al. 2014, Bašic et al. 2015), and think more about the effects of subsidy quality, quantity, and fluctuation intensity (Marcarelli et al. 2011, Richardson and Sato 2015). Also, we should not ignore the dark side of cross-ecosystem subsidies (Walters et al. 2008, Paetzold et al. 2011), which may also influence riparian biodiversity and ecosystem functions through dynamic interactions of resource subsidy flux and consumer community and their ecological feedbacks (Allen and Wesner 2016). Future research should also focus on metacommunity framework (Massol et al. 2011) to understand cross-ecosystem dynamics influenced by food-web species traits through top-down and bottom-up control of local riparian and aquatic trophic dynamics and the subsidy flux of material and energy.

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Chapter 3 Effects of anthropogenic carrion subsidy and glyphosate on leaf decomposition in streams

3.1 Abstract

Terrestrial leaf litter closely links riparian ecosystems to adjacent freshwaters by providing food resources and refuges for aquatic organisms. Glyphosate (the most widely used herbicide worldwide) and anthropogenic carrion subsidy may influence litter decomposition in streams through the impacts on macroinvertebrates and microbes. However, these effects are not fully understood. Here, we investigated the effects of carrion subsidy (chicken meat) and environmentally concentration of glyphosate on the decomposition of *Cinnamomum camphora* leaf litter in streams with different land use (forest, village, suburban, and urban). Land use and experimental treatments significantly affected litter breakdown rates expressed by day (k d^{-1}) and degree-day (k dd^{-1}). In coarse mesh bags, glyphosate, carrion subsidy, and the addition of both glyphosate and carrion decreased litter breakdown rates by 6.3 %, 22.6 %, and 24.3 % respectively. In fine mesh bags, glyphosate and the addition of both glyphosate and carrion retarded litter breakdown rates by 8.3 % and 12.5 % respectively. Litter decomposition also differed among streams, with the highest breakdown rates in village streams and lowest in urban/suburban streams. These results imply that carrion subsidy reduced macroinvertebrate-mediated litter decomposition, whereas glyphosate depressed microbial-mediated litter decomposition, and these effects dependent on land use.

Key words: ecosystem functioning, herbicide, urbanization, land-water interaction, human disturbance

3.2 Introduction

Streams receive large quantity of leaf litter from surrounding terrestrial ecosystems which can fuel detrital food webs and influence freshwaters at multiple levels (Wallace et al. 1997, Kominoski et al. 2013, Datry et al. 2018). However, human activities (e.g. recreational fishing and livestock farming) also introduce large quantity of anthropogenic subsidies to streams (Lecerf and Chauvet 2008, Rasmussen et al. 2012), and can influence leaf litter decomposition through the impacts on macroinvertebrates (e.g. detritivores and predators), fish, and microbes (Singer and Battin 2007, Jean-

Marc et al. 2018). The ecological consequences of anthropogenic subsidies on freshwaters has only recently been noticed by researchers (Bašic et al. 2015, Burgin 2017, Roberts et al. 2017). Anthropogenic subsidies are capable to affect invertebrates by changing their diet (e.g. increase the diet contribution of anthropogenic subsidies to decrease trophic niche breadth of invertebrates) (Jean-Marc et al. 2018), increasing secondary production but reducing diversity and evenness (Singer and Battin 2007), and enhancing invertebrate abundance and richness (Ansah et al. 2012). Moreover, nutrient concentration may also be affected by anthropogenic subsidies (Ansah et al. 2012) which can lead to the change in microbial communities (White et al. 2017). Therefore, anthropogenic subsidies may affect leaf litter decomposition via both invertebrate and microbial mediated litter decomposition.

Along with anthropogenic subsidy, stream ecosystems are also threatened by other stressors such as pesticides (Relyea et al. 2005, Coors and De Meester 2008, Thompson et al. 2016). Glyphosate is the most popular and widely used herbicide in the world (Annett et al. 2014), and can enter freshwaters through run-off to affect water quality (Pizarro et al. 2016), microbes (Pérez et al. 2007), algae (Magbanua et al. 2013a), zooplankton (Baker et al. 2016), invertebrates (Puertolas et al. 2010, Cuhra et al. 2013), fish (Cavalcante et al. 2008, Kelly et al. 2010), amphibians (Howe et al. 2004, Relyea et al. 2005) and litter breakdown (Magbanua et al. 2010, Magbanua et al. 2013b). However, aquatic organisms may react differently to glyphosate, for example, low-dosage of glyphosate (1-300 $\mu g\ L^{-1}$) induced eutrophication and increase diatom biomass in oligotrophic waterbodies (Austin et al. 1991), while higher concentrations of glyphosate (700 $\mu g\ L^{-1}$) adversely affected growth and development of Chironomidae (Ferreira-Junior et al. 2017). Different responses may be related to the differences in organisms being tested, experimental duration, and glyphosate dosage (Pesce et al. 2009). Although, it is commonly accepted that aquatic organisms were negatively affected by high concentration of glyphosate. Some researchers suggested that the ecological effects of low-dosage and environmentally relevant concentration of glyphosate in freshwaters are low (Giesy et al. 2000, Cerdeira and Duke 2006). However, these studies may be underestimated the effects of environmentally relevant concentration of glyphosate on microbes which showed reaction at low concentration (Sura et al. 2012, Muturi et al. 2013). Therefore, microbial-mediated leaf litter decomposition is potentially to be reduced at environmentally relevant concentration of glyphosate.

Numerous studies indicated that land use can affect leaf litter decomposition (Chadwick et al. 2006, Iñiguez-Armijos et al. 2016, Malacarne et al. 2016). Land use change can alter both biotic and abiotic attributes of streams to influence leaf litter decomposition. For example, fungal biomass was highest in intermediate levels of impervious area (30 - 40 %) which was in accordance with the highest litter decomposition rates (Chadwick et al. 2006). Abundance and richness of shredders, which are mainly responsible for invertebrate-mediated litter decomposition, decreased from forest streams to pasture streams and almost disappeared in urban streams (Iñiguez-Armijos et al. 2016). The changed macroinvertebrate communities due to land use may influence their response to other stressors, streams with more sensitive macroinvertebrates are more sensitive to stressors (Baumgartner and Robinson 2015). Fungal assemblages in agricultural streams also showed limited response to fungicide exposure as they were dominated by tolerant species, while fungicide significantly depressed fungal diversity in forest streams where stress-intolerant species were dominated (Gardeström et al. 2016). Therefore, the effects of anthropogenic subsidy and glyphosate on leaf litter decomposition may differ among streams with different land use.

In this study, we aimed to investigate: 1) how anthropogenic carrion subsidy and glyphosate could affect leaf litter breakdown rate in freshwaters; and 2) whether these effects would change with land use. By using glyphosate as anthropogenic stressor and chicken meat as anthropogenic carrion subsidy, we tested their effects on litter breakdown rate in streams with different land use (i.e. forest, village, suburban, and urban area). We hypothesized that 1) the addition of carrion subsidy would retard macroinvertebrate-mediated litter decomposition; 2) glyphosate would depress microbial-mediated litter breakdown rate; and 3) these effects may be changed with land use with strongest effects in forest streams.

3.3 Materials and Methods

3.3.1 Study area

This study was conducted in four streams in Huangshan (area: 9807 km^2; population: 1.38 million) and one stream in Suzhou (area: 8488 km^2, population: 10.68 million), China (Fig. 3.1). The five subtropical streams were associated with a gradient of human disturbance. The stream in Suzhou (urban stream) was channelized with a concrete stream bank, and heavily disturbed by anthropogenic activities - being within the vicinity (< 1000 m) of several university campuses. Due to the lowland position (altitude, 4 m, but not affected by sea water) and relatively slow flow velocity of this urban stream, its benthic substrate was almost exclusively silt and mud. Mean flow velocity was estimated using float method. In addition, the urban riparian vegetation comprised planted species such as *Salix* and *Cinnamomum*. By contrast, streams in Huangshan had natural stream banks (e.g. stones and vegetation), high diversity of natural riparian vegetation (e.g. *Bambusoideae* and *Pterocarya stenoptera*), and various benthic substrates (mainly boulders, cobbles, and gravels) except for one stream that flowed through the suburban area of Huangshan District (suburban stream, downstream of the town), which had substrate similar to that of urban stream. Two streams were located ~50 m (V-50 stream) and ~1000 m (V-1000 stream) downstream of a small village respectively, and the last one located in the Jiulongfeng Nature Reserve (forest stream). Background water quality (water temperature, pH, dissolved oxygen (DO), conductivity, ammonium and nitrate) were measured using YSI (Pro Plus) in *situ* and physical characters were recorded at the beginning of the field experiment. Previous studies have demonstrated that macroinvertebrate taxon richness in urban streams (Suzhou area) was below 10 and Shannon-Wiener Diversity Index was usually less than 2, with the dominant taxa including Oligochaeta, leech, and mollusk, especially *Limnodrilus hoffmeisteri* (Cheng et al. 2009, Zhang et al. 2009). Taxon richness of macroinvertebrates in Huangshan area was more than 50, and communities were dominated by EPT taxa (i.e. Ephemeroptera, Plecoptera, and Trichoptera), Chironomidae and Coleoptera (Wang et al. 2005, Wang et al. 2015).

3.3.2 Field experimental set-up

A 2×2 full factorial design was used to investigate the effects of anthropogenic subsidy and glyphosate (two levels for each factor, i.e. with and without) on leaf litter decomposition in streams with different land use. Freshly fallen leaves of *Cinnamomum camphora*, an evergreen and widely distributed tree in Southern China, were collected daily around Xi'an-Jiaotong Liverpool University campus (31°16′28″ N, 120°44′17″ E) from 25th June to 15th July 2016. In the laboratory, intact leaves (i.e. no visually damage) were picked out, had attachments (e.g. small particles) gently removed and were then oven dried (48 h, 60 ºC) before being used. A total of 400 litter bags were used in this study (four treatments, five streams, two mesh sizes, two sampling dates, and five replicates). Coarse (mesh size: 8 mm) and fine (mesh size: 0.1 mm) mesh bag had 7.67 ± 0.02 g and 1.33 ± 0.01 g leaves respectively.

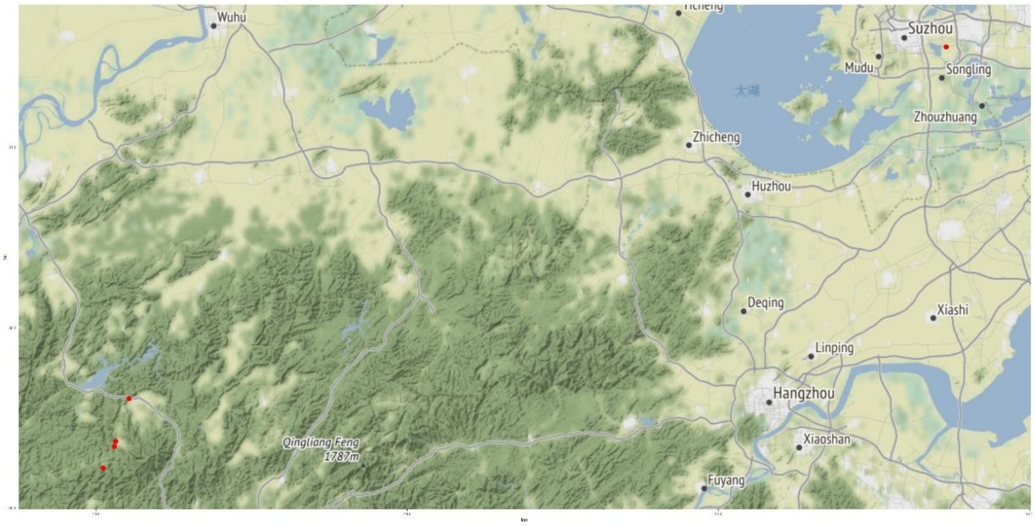

Figure 3.1 Locations (red points) of the five sampling streams. From top to bottom: urban, suburban, V-50 (50 m downstream of a village), V-1000 (1000 m downstream of a village), and forest stream respectively.

Experimental treatments were as follows:

1) Anthropogenic subsidy treatment: ~30 g and ~ 15 g fresh chicken meat was put in each coarse and fine mesh litter bag respectively. This proportion of litter : subsidy (0.26) for coarse mesh bag is similar to another study which used 0.4 g leaves (wet weight) and 1 g (wet weight) salmon carcasses (Ito 2003). Chicken meat was chosen to represent for anthropogenic carrion subsidy because (1) natural carrion subsidies are important in freshwaters but were largely ignored (Wenger et al. 2019); (2) anthropogenic carrion subsidies can be found in streams, for example - improper disposal of dead animals (e.g. pigs and chicken), which includes thousands of dead pigs reported floating in the Huangpu River in Shanghai in March 2013 (Hu et al. 2014); (3) carrion subsidy differs from other anthropogenic subsidies by remaining longer in the water (days to months) than fishing pellets (hours to days), and differs from wastewater subsidy because of its lack of contaminants; and (4) it is cheap and easy to manipulate.

2) Glyphosate treatment: we first diluted Roundup (30 % glyphosate) into tap water (concentration: 20 ml L^{-1}, a high concentration in the application of this product) and then added 2% agar to “immobilize” glyphosate. Before agar was solidified, PVC

pipes (1.5 cm in diameter, 8 cm in length) were immersed into the liquid. After the agar were solidified, we took out the PVC pipes for further use. For the glyphosate treatment, we inserted one PVC pipe per bag, which resulted in 85 μg glyphosate in each litter bag. In a field study investigating the effects of glyphosate on biofilms in a pond, authors showed that the diffusion rate of glyphosate from agar was non-linear, with a large pulse (>10%) being released in the first two days followed by decreasing concentrations released from agar within the following 20 days (Shaw and Mibbayad 2016). Therefore, we assume that this method can provide continuous diffusion of glyphosate to leaf litter exposed in bags in streams during the experimental period of our study of 30 days.

The field experiment was conducted from 24th July to 23rd August 2016 in Suzhou and from 29th July to 28th August 2016 in Huangshan. In each stream, we deposited litter bags that were treatment of controls (only leaf), with subsidy only (leaf + chicken meat), with subsidy + glyphosate (leaf + chicken meat + glyphosate), and with glyphosate only (leaf + glyphosate) from upstream to downstream. Each treatment was at least 20 m away from the others to reduce the influences of glyphosate on control and subsidy treatments. Five litter bags of the same treatment were tied to one nylon string, and litter bags on one string were at least 20 cm away from the others. Then, the nylon string was tied to a steel bar which was hammered into the streambed at a depth of at least 30 cm. On day 15 and 30, one string (i.e. five litter bags) of each treatment was retrieved from each stream. Each litter bag was put in a plastic zipper bag and then stored in a 4 ºC cool box immediately. Litter bags were taken back to the laboratory within 24 h and stored in a 4 ºC cold room. All litter bags were processed by gently washing and picking out invertebrates within 48 h, then invertebrates were preserved in 70% ethanol for further identification. The remaining leaf materials were oven dried (60 ºC, 48 h) and weighed again to calculate litter breakdown rates. The most of macroinvertebrates were identified to genus level, but when genus identification was not possible, the family name was recorded. Oligochaetes (dominated by Tubificidae) were not identified to a lower taxonomic level. We also recorded invertebrate abundance, taxon richness, and Shannon-Wiener Diversity Index.

3.3.3 Data analysis

Litter breakdown rate coefficient (k) was determined using the exponential decay model $W_t = W_I * e^{-kt}$, where W_t represents the final mass of leaf litter, W_I is the initial mass of leaf material, and t is incubation time (d) (Gonçalves et al. 2006). We also calculated litter breakdown rates per degree-days (k, dd^{-1}) through replacing time (t) in days in the equation above by the sum of average daily temperatures accumulated across the sampling period. We did not record temporal change of water temperature during the experimental period (i.e. August). Instead, we managed to get the weekly mean water temperature in another set of 28 streams in Suzhou (our urban stream was not included in this new set of streams) (mean ± SE, 31.95 ± 0.05 °C and 32.19 ± 0.06 °C for 15 days and 30 days respectively, Suzhou Environmental Protection Bureau official website) to represent the mean water temperature in the urban stream. In addition, we used water temperature data collected from 92 sites (surrounded by forest, forest-agriculture, or small villages) in August 2015 in Huangshan area to represent the mean water temperature in forest and village streams (mean ± SE, 25.62 ± 0.38 °C and 24.25 ± 0.23 °C for 15 days and 30 days respectively). For the suburban stream, we used the water temperature (mean ± SE, 27.48 ± 0.60 °C) measured on the day that the leaf litter bags were deployed to represent mean water temperature during 15 days and 30 days. One-way ANOVA (analysis of variation) was conducted to detect the effects of land use on water quality. Two-way ANOVA with repeated measures was used to determine the effects of experimental treatments (i.e. control, glyphosate, subsidy, subsidy + glyphosate) and land use (i.e. five streams) on litter decomposition and macroinvertebrate variables. The five streams were classified as forest, village (V-1000 and V-50, ~ 1 km and ~ 50 m downstream of a village respectively), suburban, and urban stream respectively. We separately conducted the two-way ANOVA with repeated measures for coarse and fine mesh bags, and did not compare litter breakdown rates between mesh sizes. For all analyses, if significant main effects were present, then Tukey's HSD was used for the post-hoc multiple comparison. In addition, regression analysis was conducted to test the response of litter breakdown rates (by days and degree-days) to macroinvertebrate abundance, richness, and Shannon-Wiener Diversity Index. All data were tested for the normality of residuals before conducting the ANOVAs, and data were transformed (e.g. log) if they deviated from normality. All data were analyzed using SPSS 22.0.

3.4 Results

3.4.1 Water quality At the beginning of the experiment, water temperature was higher in the urban stream (32.33 ºC) than the other four streams (26.33 – 27.48 ºC) ($F_{4,15}$ = 76.940, $P < 0.001$, Table 3.1). Dissolved oxygen concentrations (DO) were highest in V-50 stream (9.38 mg/L), reduced in suburban stream (5.28 mg/L) and lowest in the urban stream (2.40 mg/L) ($F_{4,15}$ = 878.052, $P < 0.001$, Table 3.1). Conductivity was lowest in forest stream (56.13 μs cm^{-1}), more than doubled in village streams, and was 7.75 and 10.90 times higher in suburban and urban stream respectively ($F_{4,15}$ = 9348.599, $P < 0.001$, Table 3.1). Ammonium did not differ between forest (0.13 mg L^{-1}) and village streams (0.14 – 0.25 mg L^{-1}), but were significantly lower than that in suburban (1.24 mg L^{-1}) and urban stream (1.28 mg L^{-1}) ($F_{4,15}$ = 179.737, $P < 0.001$, Table 3.1). The trend of nitrate concentration was similar to that of ammonium except that nitrate in the suburban stream (1.04 mg L^{-1}) was no different from that in the V-50 stream and was less than half of that in urban streams (2.28 mg L^{-1}) ($F_{4,15}$ = 190.325, $P < 0.001$, Table 1). The urban stream (pH: 8.70) was more alkaline than forest and village streams (pH: 7.64 – 7.82) and suburban stream (pH: 7.25) ($F_{4,15}$ = 574.864, $P < 0.001$, Table 3.1).

Table 3.1 Water quality of the five streams. Data were measured *in situ* at the beginning of the field experiment and are the mean values of four measurements. V-50 and V-1000 represent stream that was 50 m and 1000 m downstream of a village respectively. Data were shown as mean ± SE.

Parameter	$F_{4,15}$	Urban	Suburban	V-50	V-1000	Forest
Coordinate		31°16′30″ N, 120°43′59″ E	30°18′13″ N, 118°6′21″ E	30°11′5″ N, 118°3′45″ E	30°10′15″ N, 118°3′32″ E	30°6′39″ N, 118°1′21″ E
Elevation (m)		4	161	240	240	390
pH	574.864	8.70 ± 0.02^{a}	7.25 ± 0.00^{d}	7.64 ± 0.02^{c}	7.82 ± 0.02^{b}	7.81 ± 0.03^{b}
Water temperature (ºC)	76.940	32.33 ± 0.10^{a}	27.48 ± 0.60^{b}	27.35 ± 0.03^{b}	26.78 ± 0.06^{b}	26.33 ± 0.09^{b}
Dissolved oxygen (mg/L)	878.052	2.40 ± 0.10^{d}	5.28 ± 0.11^{c}	9.38 ± 0.05^{a}	8.63 ± 0.10^{b}	8.32 ± 0.12^{b}
Conductivity (μs/cm)	9348.599	612.0 ± 1.4^{a}	435.1 ± 5.3^{b}	120.4 ± 0.1^{d}	150.6 ± 0.1^{c}	56.1 ± 1.0^{f}
Ammonium	179.737	1.28 ± 0.01^{a}	1.24 ± 0.10^{a}	0.25 ± 0.00^{b}	0.14 ± 0.02^{b}	0.13 ± 0.01^{b}

(mg/L)						
Nitrate (mg/L)	190.325	2.28 ± 0.01^{a}	1.04 ± 0.09^{b}	0.93 ± 0.02^{b}	0.65 ± 0.06^{c}	0.54 ± 0.01^{c}
Flow velocity (m/s)	13.950	0.06 ± 0.005^{c}	0.19 ± 0.04^{b}	0.15 ± 0.03^{bc}	0.25 ± 0.03^{ab}	0.36 ± 0.04^{a}

Note: Superscript lowercase letters denote significant differences after one-way ANOVA and *post hoc* Tukey (parameters with same letter are not significantly different between streams).

3.4.2 Leaf breakdown rate Litter breakdown rates ranged from 0.011 to 0.047 d^{-1}, with mean values of 0.025 ± 0.001 d^{-1} and 0.023 ± 0.001 d^{-1} for coarse and fine mesh bags respectively. Experimental treatments significantly affected litter breakdown rates in coarse ($F_{3,80} = 23.624$, $P < 0.001$, Table 3.2, Fig. 3.2) and fine mesh bags ($F_{3,80} = 77.614$, $P < 0.001$, Table 3.2, Fig. 3.2). In coarse mesh bags, glyphosate and carrion subsidy decreased litter breakdown rates by 6.3 % and 22.6 % respectively, and the addition of both glyphosate and carrion subsidy also reduced litter breakdown rates by 24.3 %. Similarly, in fine mesh bags, glyphosate and the addition of both glyphosate and carrion subsidy retarded litter breakdown rates by 8.3 % and 12.5 % respectively, while carrion subsidy alone had no significant effect. Litter breakdown rates were also differed among streams regardless of the mesh size of litter bags (coarse mesh: $F_{4,80} = 23.624$, $P < 0.001$; fine mesh: $F_{4,80}=352.664$, $P < 0.001$, Table 3.2, Fig. 3.2). Litter breakdown rates in coarse mesh bags were highest in the slightly impacted village stream (1000 m downstream of a village, 0.035 ± 0.001 d^{-1}), followed by the medium impacted village stream (50 m downstream of a village, 0.034 ± 0.001 d^{-1}), forest stream (0.024 ± 0.001 d^{-1}), and then the statistically indistinguishable urban (0.017 ± 0.001 d^{-1}) and suburban stream (0.015 ± 0.001 d^{-1}). The effects of land use on litter breakdown rates in fine mesh bags were similar with that in coarse mesh bags except that the urban stream had 11.1 % faster breakdown rate than suburban stream. Experimental treatments also significantly interacted with land use to affect litter breakdown rates in coarse ($F_{12,80} = 12.688$, $P < 0.001$, Table 3.2) and fine mesh bags ($F_{12,80}=16.791$, $P < 0.001$, Table 3.2). For coarse mesh bags, our experimental treatments had greatest effects in the two village streams (range of litter breakdown rates: 0.025 – 0.043 d^{-1}), while the differences among experimental treatments were only ~ 0.005 d^{-1} in the other three stream types. The addition of glyphosate alone only decreased litter breakdown rates in the V-1000 stream, while the addition of carrion subsidy and the addition of both glyphosate and carrion subsidy decreased litter breakdown rates in all streams except for the forest stream. In fine mesh bags: glyphosate decreased litter breakdown rates in the V-50 and the suburban stream; carrion subsidy only retarded litter breakdown rates in the V-50 stream; and the addition of both glyphosate and carrion subsidy negatively affected litter breakdown rates in the V-50 and the V-1000 stream. The trend of litter breakdown rates across land uses, and their interactions with experimental treatments, when expressed per degree-day (k dd^{-1}), were similar with when rates were expressed per day (k d^{-1}) in both coarse and fine mesh bags (Fig. 3.2). The only exception was that, in fine mesh bags, rates (in degree-days) did not differ between urban and suburban streams.

Table 3.2 Summary results of two-way ANOVA with repeated measures for the effects of experimental treatments (Tre: control, subsidy, glyphosate, and subsidy + glyphosate) and land use (LS: forest, ~ 1 km and 50 m downstream of a village, suburb, and urban stream) on litter breakdown rates (k d^{-1}, days; and k dd^{-1}, degree-days), macroinvertebrate abundance (MA), richness (MR), and Shannon-Wiener Diversity (H) in the five streams. P-values < 0.05 are in bold print. Effect sizes (partial *eta* squared values; range 0-1) are shown in parentheses for all cases where $P < 0.1$.

Variations	df	k d^{-1} (coarse)		k d^{-1} (fine)		k dd^{-1} (Coarse)		k dd^{-1} (Fine)		MA		MR		H	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
LS	4	438.433	**<0.001** (0.956)	352.664	**<0.001** (0.946)	579.969	**<0.001** (0.967)	513.375	**<0.001** (0.963)	52.961	**<0.001** (0.726)	161.983	**<0.001** (0.890)	133.891	**<0.001** (0.870)
Tre	3	77.614	**<0.001** (0.744)	23.624	**<0.001** (0.470)	74.185	**<0.001** (0.736)	24.650	**<0.001** (0.480)	0.727	0.539	2.187	0.096 (0.076)	0.261	0.854
Tre × LS	12	12.688	**<0.001** (0.656)	16.791	**<0.001** (0.716)	14.036	**<0.001** (0.678)	17.500	**<0.001** (0.724)	3.731	**<0.001** (0.359)	3.931	**<0.001** (0.371)	3.920	**<0.001** (0.370)
Error	80														

Note: Data of macroinvertebrate abundance were log transformed to improve normality before conducting the analysis.

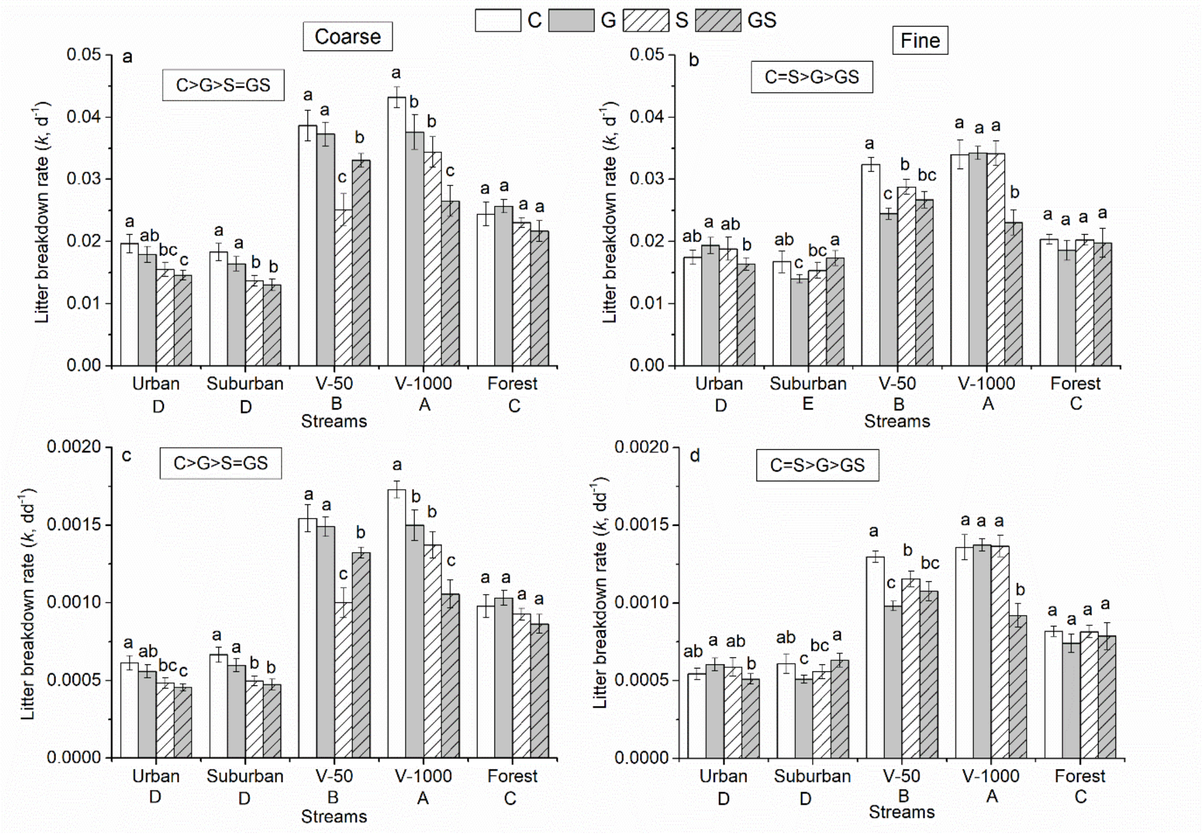

Figure 3.2 Averages of litter breakdown rates by days (k d^{-1}, a and b) and degree-days (k dd^{-1}, c and d) in coarse (a and c) and fine (b and d) mesh bags in the five streams with four treatments. V-50 and V-1000 was 50 m and 1 km downstream of a village respectively. The four treatments were: C, control, only leaf; G, leaf + glyphosate; S, leaf + anthropogenic subsidy (chicken meat); and GS, leaf + glyphosate + subsidy. Error bars (SEs) show the variation among replicates ($n = 5$ for each treatment). Capital letters under each stream indicate significant main effects of land use, and text in rectangle indicate the effects of experimental treatments. Lowercase letters above each bar indicate significant differences among treatments within each stream if land use significantly interacted with experimental treatments. Different letters indicate there was a significant effect between the two categories. Tukey's HSD test ($\alpha = 0.05$) was used for the post multiple comparison.

3.4.3 Macroinvertebrates Macroinvertebrate abundance, richness, and Shannon-Wiener Diversity Index varied between 11 – 259 ind. litter bag^{-1}, 2 – 17 taxa litter bag^{-1}, and 0.23 – 3.36 respectively, with mean values of 82 ± 6.39 ind. litter bag^{-1}, 9 ± 0.37 taxa litter bag^{-1}, and 2.14 ± 0.07 respectively. Experimental treatments did not have significant effects on invertebrate abundance, but land use did ($F_{4,80} = 52.961$, $P < 0.001$, Table 3.2, Fig. 3.3). Invertebrate abundance was lowest in the urban stream (22 ± 2.28 ind. litter bag^{-1}), was more than double in the forest stream (47 ± 8.36 ind. litter bag^{-1}), was almost five times higher in the suburban stream (104 ± 17.71 ind. litter bag^{-1}), and was around six times higher in village streams (115 – 121 ind. litter bag^{-1}). Invertebrate abundance was also significantly affected by the interaction between experimental treatments and land use ($F_{12,80} = 3.731$, $P < 0.001$, Table 3.2).

Experimental treatments had the lowest impacts on invertebrate abundance in the V-50 stream (~ 50 m downstream of a village). Invertebrate richness was significantly affected by land use ($F_{4,80} = 161.983$, $P < 0.001$, Table 3.2). The urban stream had the lowest invertebrate richness (4 taxa litter bag^{-1}), which increased by 41.9 % and 185.1 % in the suburban and forest stream respectively, and increased by more than three times in village streams. The effects of experimental treatments on macroinvertebrate richness differed depending on the land use ($F_{12,80} = 3.931$, $P < 0.001$, Table 3.2, Fig. 3.3). Shannon-Wiener Diversity of invertebrates was significantly affected by land use ($F_{4,80} = 133.891$, $P < 0.001$, Table 3.2, Fig. 3.3). Shannon-Wiener Diversity did not differ between the suburban (1.19 ± 0.13) and urban streams (1.27 ± 0.06), but was almost doubled in forest (2.50 ± 0.12) and V-50 stream (2.76 ± 0.08) and highest in the V-1000 stream (2.98 ± 0.05). The interaction between experimental treatments and land use also significantly affected Shannon-Wiener Diversity ($F_{12,80} = 3.920$, $P < 0.001$, Table 3.2). Regression analysis indicated that macroinvertebrate abundance, richness, and Shannon-Wiener Diversity Index all positively correlated with litter breakdown rates measured per day and per degree-day (Fig. 3.4). In addition, litter breakdown rates (k) were more related to total taxon richness than total abundance and Shannon-Wiener Diversity Index whether it was expressed by day (k d^{-1}) or degree day (k dd^{-1}). When data were grouped by stream ID, the results of regression analysis showed that there was no correlation between invertebrate characters and litter breakdown rates in most streams (Table 3.3).

Table 3. 3 Correlations between invertebrate characters and litter breakdown rates. Significant correlations are shown in bold ($P < 0.05$).

Variables	Stream ID	*n*	*k*, d^{-1}		*k*, dd^{-1}	
			R	*P*	*R*	*P*
Abundance (log)	All	200	0.408	**<0.001**	0.444	**<0.001**
	Forest	40	0.416	**0.008**	0.424	**0.006**
	V-1000	40	0.074	0.649	0.042	0.795
	V-50	40	-0.100	0.541	-0.065	0.689
	Suburban	40	0.213	0.187	0.213	0.187
	Urban	40	0.325	**0.041**	0.326	**0.040**
Richness	All	200	0.598	**<0.001**	0.662	**<0.001**

	Forest	40	0.208	0.197	0.283	0.076
	V-1000	40	-0.040	0.809	-0.067	0.682
	V-50	40	-0.318	**0.045**	-0.312	0.050
	Suburban	40	-0.258	0.107	-0.258	0.107
	Urban	40	0.194	0.231	0.194	0.230
Shannon-Wiener	All	200	0.543	**<0.001**	0.608	**<0.001**
	Forest	40	-0.001	0.993	0.105	0.517
	V-1000	40	-0.058	0.720	-0.037	0.820
	V-50	40	-0.265	0.098	-0.265	0.098
	Suburban	40	-0.380	**0.016**	-0.380	**0.016**
	Urban	40	0.088	0.588	0.088	0.590

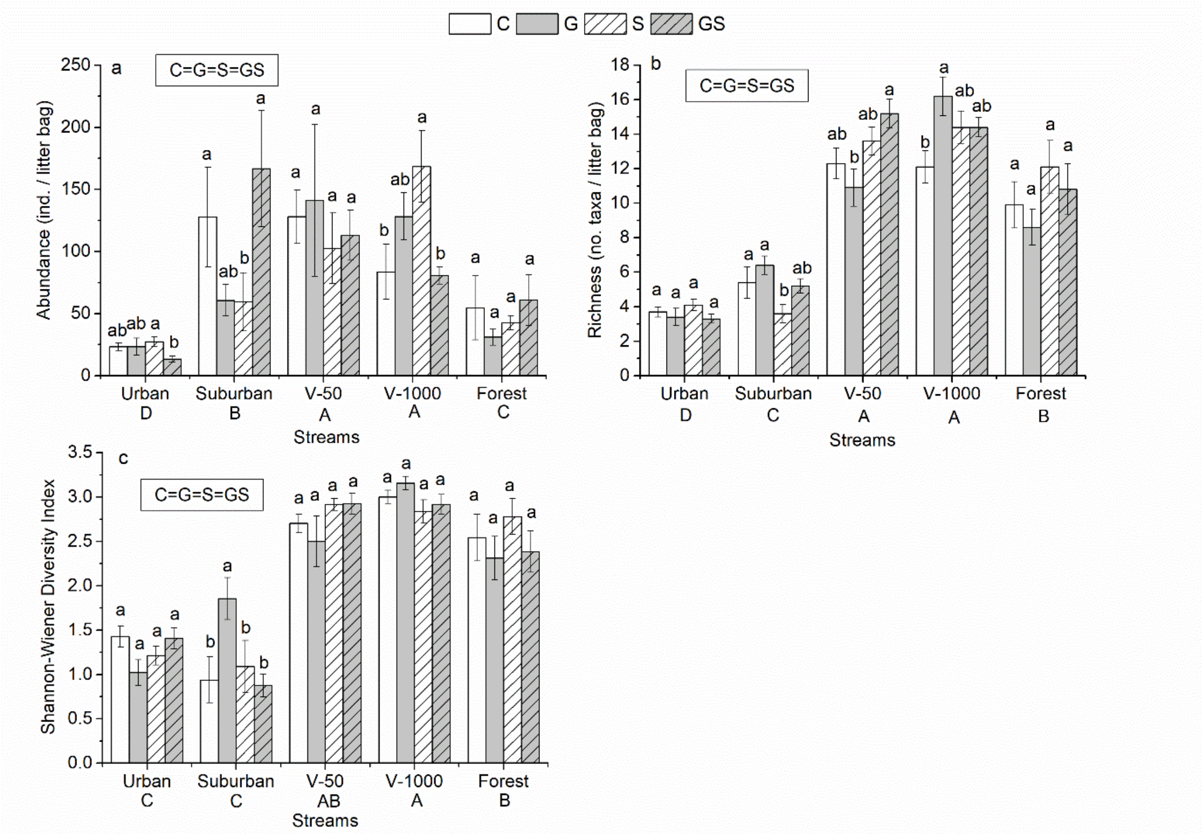

Figure 3.3 Averages of macroinvertebrate (a) abundance, (b) richness, and (c) Shannon-Wiener Diversity Index in coarse mesh bags in the five streams. V-50 and V-1000 was 50 m and 1 km downstream of a village respectively. The four treatments were: C, control, only leaf; G, leaf + glyphosate; S, leaf + anthropogenic subsidy (chicken meat); and GS, leaf + glyphosate + subsidy. Error bars (SEs) show the variation among replicates (*n* = 5 for each treatment). Capital letters under each stream indicate significant main effects of land use, and text in rectangle indicate the effects of

experimental treatments. Lowercase letters above each bar indicate significant differences among treatments within each stream if land use significantly interacted with experimental treatments. Different letters indicate there is significant effect between the two treatment. Tukey’s HSD test (α =0.05) was used for the post multiple comparison.

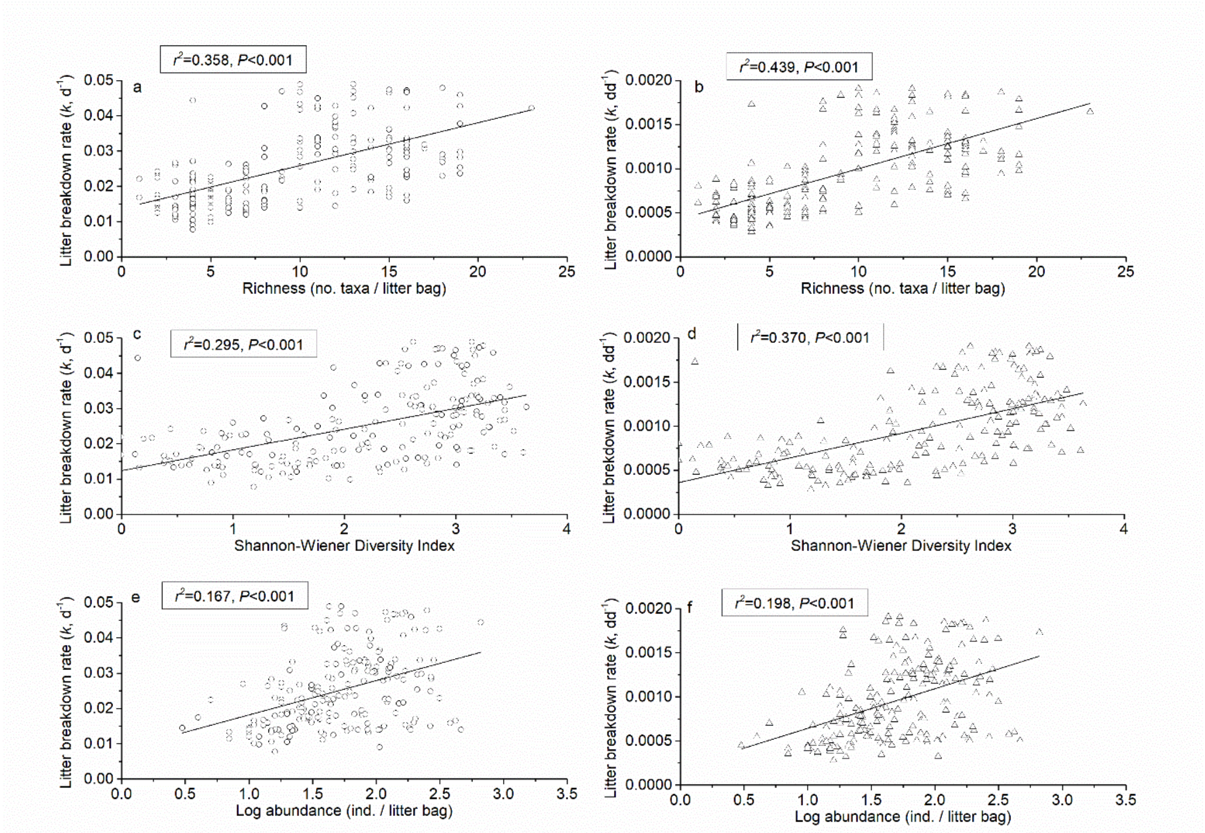

Figure 3.4 Leaf litter breakdown rates by days (k d^{-1}, left) and degree-days (k dd^{-1}, right) in relation to macroinvertebrate richness (above), Shannon-Wiener Diversity Index (below), and abundance (data were log-transformed, middle). The coefficients of determination (R^2) and P are shown in each panel. Each data point represents the mean value of each treatment in each stream at the two sampling dates.

3.5 Discussion

3.5.1 Effects of anthropogenic carrion subsidy on litter decomposition

We did find that carrion subsidy retarded litter decomposition in coarse mesh bags but not in fine mesh bags which support our first hypothesis that macroinvertebrate-mediated decomposition would be decreased by carrion subsidy. Invertebrate abundance and richness were not significantly affected by carrion subsidy except for a significant increase in the stream 1 km downstream of a village (i.e. V-1000 stream) and a significant decrease in suburban stream. Even though carrion subsidy affected macroinvertebrates differently among streams, litter breakdown rates were all reduced (except in the forest stream). Therefore, subsidy may influence leaf litter decomposition by different mechanisms in streams with different land use. In the suburban stream, we found increased abundance of Erpobdellidae in carrion subsidy treatment, whose predatory pressure may have reduced total abundance and richness of other macroinvertebrates, hence reduced litter breakdown rates. By contrast, in the village and forest streams, especially V-1000 stream, total abundance and richness were enhanced. In these streams, carrion subsidy probably caused a temporal diet change of invertebrates from leaf litter to subsidy, as found in other carrion subsidies (e.g. salmon carcasses) studies (Zhang et al. 2003, Bretherton et al. 2011). Specifically, Chironomidae, which dominated in these streams (% abundance were around 50%), can rapidly colonize carrion and directly consume it because of their rapid population growth rate, multivoltinism, propensity to drift, and opportunistic feeding behavior (Lessard and Merritt 2006, Cram et al. 2011).

The addition of carrion subsidy had a limited effect on microbially-mediated litter decomposition in this study. This result is contrary to that expected when the addition of carcass subsidy stimulates the production of biofilms through releasing nitrogen and phosphorus (Chaloner et al. 2007, Weaver et al. 2015). Claeson *et al.* (2006) suggested that the increased abundance and richness of invertebrates may increase the predation pressure on microbes, therefore, counteract the nutrient effect of subsidy on microbes (Claeson et al. 2006). However, these explanations may not apply to the present study because macroinvertebrates were excluded by fine mesh bags and litter breakdown rates in the V-50 stream (~ 50 m downstream of a village) were even reduced by subsidy.

3.5.2 Effects of glyphosate on litter decomposition

Litter breakdown rates were significantly decreased by the addition of glyphosate in both coarse and fine mesh bags which support our second hypothesis that the herbicide would inhibit microbial-mediated decomposition. Many studies have indicated that pesticides can affect litter breakdown in streams and rivers (Rasmussen et al. 2012, Schäfer et al. 2012, Fernández et al. 2015). Pesticides mainly function through their impacts on water quality, microbial communities (both fungi and bacteria), and macroinvertebrate communities to affect litter decomposition (Magbanua et al. 2013b, Talk et al. 2016, Thompson et al. 2016). Thus, overall effects of glyphosate on litter breakdown rate may depend on the combined effects of these factors. We did not find any significant effects of glyphosate on invertebrates which is in accordance with another study that glyphosate (0 – 0.37 mg/L) had low impacts on invertebrates (Magbanua et al. 2013b). In addition, the reduced litter breakdown rate by glyphosate in coarse and fine mesh bags were similar. Therefore, the decreased litter breakdown rate was likely to be triggered by the depressed microbial-mediated litter breakdown rates. Previous studies have found that bacterial abundance (e.g. *Alpha-proteobacteria*) (Muturi et al. 2013) and fungi (Tsui et al. 2001) can be negatively affected by the addition of glyphosate. However, these effects may be dosage-dependent, because low concentrations usually have no effects (Pérez et al. 2007, Magbanua et al. 2013b). According to Yang (2015), the range of glyphosate concentrations in several headwater streams and lakes were 0 – 28 μg L^{-1} (Yang 2015) which can reflect the background glyphosate concentrations in the village and forest streams in this study. Environmental glyphosate concentrations of urban stream in this study may be similar to those found by Fan (2013) (0 – 19 μg L^{-1}) in lake water in the same area (Fan 2013). Therefore, the concentration of glyphosate used in this study was environmentally relevant concentration. The environmentally relevant concentration of glyphosate was far less than the Canadian water quality guideline for long-term (800 μg L^{-1}) and short-term (27,000 μg L^{-1}) exposure for the protection of aquatic life in freshwaters (Canadian Council of Ministers of the Environment 2012), and below the reported range of projected worst-case scenarios for glyphosate concentrations (1.7 – 5.2 mg L^{-1}) in freshwaters (Annett et al. 2014). Thus, even though the concentration used in this study is well below national guidelines and those that cause severe harm, they nonetheless can affect aquatic ecosystems in this study and others (Magbanua et al. 2013a, Smedbol et al. 2018).

3.5.3 Effects of land use on litter decomposition

The forest stream and village streams are relatively natural, with better biochemical conditions (e.g. water quality and habitat diversity) than those in the suburban and urban streams. If nutrients (e.g. ammonium) were mainly responsible for enhancing litter decomposition, then leaves in the suburban and urban streams should decay faster than in forest and village streams because a medium level of eutrophication can stimulate leaf breakdown (Gulis et al. 2006, Woodward et al. 2012, Pereira et al. 2017). However, leaf litter in village and forest streams decomposed faster than those in urban and suburban streams. Similarly, water temperature was positively correlated with litter decomposition in streams (Ferreira and Chauvet 2011), litter breakdown rates should be higher in urban and suburban streams than in village and forest streams. However, both litter breakdown rates per day and per degree-day were lowest in suburban and urban streams. Therefore, other factors (e.g. flow velocity, invertebrate communities, and DO) may have overridden the effects of nutrients and water temperature on leaf decomposition in this study. For example, village streams had the highest invertebrate abundance and richness, which was correlated with highest litter breakdown rates, and was in accordance with other studies (Gonçalves et al. 2006).

In addition, land use changed the effects of carrion subsidy and glyphosate on litter breakdown rates. Carrion subsidy retarded litter breakdown rates in coarse mesh bags in all streams, except the forest stream, where it had no effect. This lack of effect in the forest stream - is contrary to our third hypothesis - that carrion subsidy would have greater impacts in forest stream than other streams. This result is contrary to one field study investigating the relationship between assimilation of terrestrial subsidies by invertebrates and stream size (i.e. primary production), the authors found that invertebrates assimilated more terrestrial subsidies in canopied headwater streams than in more open and productive streams (Collins et al. 2016). Therefore, the effect of carrion subsidy on recipient ecosystem functioning (litter decomposition) may depend not only on the primary production of recipient ecosystems but also other factors such as macroinvertebrate community structure. Because invertebrates response to subsidies differently (Kohler and Taki 2010). Also contrary to our third hypothesis, which is based on greater expected sensitivity of organisms from less human-influenced streams than in suburban and urban streams (Gardeström et al. 2016, Wagner et al. 2017), litter breakdown rates were unaffected by glyphosate in the forest stream, but were reduced in suburban and village streams. This result probably was associated with higher flow velocity in forest stream than other streams, because faster flow velocity may accelerate the diffusion rate of glyphosate from agar (Kreutzweiser et al. 1989, Pérez et al. 2017), result in a shorter time of glyphosate exposure in forest stream than other streams.

3.6 Conclusion

In conclusion, we found firstly that anthropogenic carrion subsidy retarded litter breakdown rate in coarse but not fine mesh bags, implying retardation of macroinvertebrate-mediated decomposition. Secondly, environmentally relevant concentration of glyphosate reduced litter breakdown rates mainly through its negative effects on microbes. Litter breakdown rates also differed among streams, with the fastest breakdown rate in village streams (slight-medium disturbed streams) and slowest in urban and suburban streams. In addition, the input of carrion subsidy and glyphosate had negligible impacts on litter breakdown rates in a forest stream but adversely affected litter decomposition in village, suburban, and urban streams, because of the differences in macroinvertebrate assemblages and biochemical characters. Given the wide application of glyphosate and increasing inputs of anthropogenic subsidy to freshwaters, these factors may interact with other factors including urbanization and climate change to affect aquatic organisms and ecosystem functioning.

3.7 Acknowledgments

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Chapter 4 Effects of anthropogenic carrion subsidy and glyphosate on macroinvertebrates in streams

4.1 Abstract

Streams and surrounding terrestrial ecosystems are closely linked by numerous resource subsidies including anthropogenic subsidies which are increasingly entering streams due to intensive human activities. Streams are also threatened by stressors such as glyphosate – the most widely used herbicide worldwide. However, ecological consequences of anthropogenic subsidies and glyphosate on freshwaters are not fully understood. Here, we aimed to investigate the individual and combined effects of anthropogenic carrion subsidy and environmentally relevant concentration of glyphosate on macroinvertebrates in streams with different land use (i.e. forest, village, and suburban). Macroinvertebrate communities significantly differed among streams, with biodiversity index and total taxon richness were highest in village streams and lowest in suburban stream. Overall effects of carrion subsidy and glyphosate on macroinvertebrates were not significant. However, several taxa were affected in some streams by the individual or combined effects of carrion subsidy and glyphosate, indicating the importance of local community structure and physical habitats in driving the response of macroinvertebrates to carrion subsidy and glyphosate. Collectively, these results imply that even though carrion subsidy and environmentally relevant concentration of glyphosate have no significant overall effects on macroinvertebrates, their impacts are probably overridden by land use which can change macroinvertebrate communities, therefore influence the response of macroinvertebrates to carrion subsidy and glyphosate.

Keywords: land-water interaction, herbicide, human disturbance, benthos community, urbanization, land use

4.2 Introduction

Fluxes of organisms, materials, and nutrients, i.e. resource subsidy, tightly link adjacent ecosystems (Polis et al. 1997, Richardson et al. 2010, Subalusky and Post 2019). Streams receive a bunch of subsidies such as leaf litter from surrounding terrestrial ecosystems (Wallace et al. 2015) affecting streams in a myriad of ways, include increasing benthic surface cover for the growth of biofilms, decreasing water clarity, providing refugia/habitats for invertebrates, and most importantly, fueling detrital food webs (Anderson and Sedell 1979, Stoler and Relyea 2013, Márquez et al. 2017). Numerous studies have investigated the responses of macroinvertebrates to inputs or exclusion of terrestrial leaf litter in freshwater ecosystems (Wallace et al. 1997, Andrushchenko et al. 2017). Macroinvertebrates play an important role in the decomposition of leaf litter, among which collector-gatherers, shredders, and grazers are especially crucial (Hax and Golladay 1993, Graça 2001). However, many environmental and ecological factors can influence invertebrates colonizing on leaf litter such as the co-existence of other subsidies (Bretherton et al. 2011, Leroy et al. 2016).

Streams receive many other natural (e.g. salmon carcasses) and anthropogenic subsidies (e.g. wastewater) which usually have higher nutrient concentration than leaves (Anderson and Cummins 1979, Brett et al. 2017). It is estimated that global urban area will increase by 1.2 million km^2 by 2030, which is three times of that in 2000 (Seto et al. 2012). Consequently, anthropogenic subsidies such as wastewater and sewage effluent (Singer and Battin 2007, Morrissey et al. 2013), and the widely occurred recreational fishing pellet subsidy (Bašic et al. 2015, Roberts et al. 2017) would increasingly entering streams. Therefore, it is important to understand how these anthropogenic subsidies would affect stream ecosystems. However, these studies may be constrained because wastewater effluent usually contains toxic pollutants which can obscure the subsidy effects on macroinvertebrates (Bunzel et al. 2013, Aristi et al. 2015, Berger et al. 2016), and most of the studies of anthropogenic carrion (e.g. pig) subsidies were focus on the area of Forensic Science (Hobischak and Anderson 2002, Chin et al. 2008, Barrios and Wolff 2011). According to studies on the ecological consequences of salmon carcasses (natural carrion subsidy) on stream consumers, macroinvertebrates were generally affected through two ways: 1) direct consumption of carcasses materials; and 2) indirect consumption of microbes and algae that were stimulated by nutrients leaching from decaying carcasses (Naiman et al. 2002). Consequently, macroinvertebrates can be influenced at levels of individual, population, and community, result in larger body size of some taxa (Lessard et al. 2009), shifting diet from leaves to salmon carcasses (Zhang et al. 2003), denser population (Kohler et al. 2012), and changed community structure (Fenoglio et al. 2010). The study of salmon carcasses subsidy may give us a clue to use animal carrion (e.g. chicken and pig) to mimic anthropogenic subsidies and investigating their effects on macroinvertebrates in streams from ecological perspective. A newly published study illustrated that natural animal carrion (except for salmon) subsidies are essential in nutrient cycling in streams but these subsidies were largely ignored (Wenger et al. 2019). Anthropogenic carrion subsidies have the following advantages: 1) they can be found in streams (Hu et al. 2014) and have high nutrient content as other anthropogenic subsidies do; 2) have no contaminants as wastewater subsidies do, and can stay in waterbodies for a longer time than fishing pellet subsidy; and 3) it is cheap and easy to manipulate.

In fact, freshwater ecosystems receive not only subsidies but also herbicides (stressors) from surrounding terrestrial ecosystems (Solomon and Thompson 2003, Kolpin et al. 2006, Masiol et al. 2018). Among all herbicides, glyphosate is the most widely used worldwide (Annett et al. 2014, van Straalen and Legler 2018). Previous studies showed that glyphosate or its formulated product (e.g. Roundup) can depress the growth rate of Chironomidae (Ferreira-Junior et al. 2017), enhance downstream drifting of *Gammarus sp*. and *Paraleptophlebia sp.* (Kreutzweiser et al. 1989) but not overall invertebrate drift propensity (Magbanua et al. 2016), decrease macroinvertebrate taxon richness, reduce densities of sensitive taxa while enhance tolerant ones (Magbanua et al. 2010), decline phytoplankton abundance and affect phytoplankton community structure (e.g. death of diatoms) (Pérez et al. 2007, Vera et al. 2010). These effects can affect invertebrates through directly influence on individual growth rate, decrease abundance and richness of sensitive taxa, or indirectly impact communities of phytoplankton and periphyton which are food resources for invertebrates. However, many researchers found the response of macroinvertebrates and microbes to glyphosate is dosage depend (Schäfer et al. 2012), and it is unclear whether environmentally relevant concentration and low-dosage glyphosate would adversely affect aquatic ecosystems. Some researchers hold the opinion that ecological risks of glyphosate used in freshwaters are low (Solomon and Thompson 2003, Tsui and Chu 2008). On the contrary, many other studies found negative effects of environmentally relevant concentration of glyphosate on microbes and macroinvertebrates (Relyea 2005, Muturi et al. 2013), but these effects may be masked by other factors and make it difficult to catch (Pesce et al. 2009, Talk et al. 2016). Therefore, it is important to understand whether and how environmentally relevant concentration of glyphosate can affect macroinvertebrates in streams for the protection of aquatic ecosystems and provide information on glyphosate relevant policy-making.

Numerous studies found significant effects of land use on macroinvertebrate assemblages in streams (Harding et al. 1998, Paul and Meyer 2001, Li et al. 2019). Macroinvertebrate communities in forest streams usually have high diversity and dominated by sensitive species, while diversity and evenness of macroinvertebrate decreased in agricultural and urban streams, and sensitive species may be totally disappear in urban streams (Urban et al. 2006, Iñiguez-Armijos et al. 2016, Burdon et al. 2019). The differences in macroinvertebrate communities could further influence their response to stressors (Baumgartner and Robinson 2015). Because macroinvertebrates in agricultural and urban streams are already subjected to some stressors (e.g. eutrophication and pesticides), then, the addition of another stressor such as glyphosate could induce different responses of macroinvertebrates between forest and agricultural/urban streams (Rasmussen et al. 2012, Arriagada et al. 2019). For example, macroinvertebrates from agricultural streams showed higher resistance to eutrophication than streams in conservation area because communities in agricultural streams were dominated by pollution-tolerant species (Burdon et al. 2016). Therefore, the effects of anthropogenic subsidies and glyphosate on macroinvertebrates may depend on land use.

In this study, we used coarse leaf litter bags (mesh size: 8 mm) containing only leaves (*Cinnamomum camphora*), leaves with either anthropogenic carrion subsidy (chicken meat) or glyphosate, and leaves with both carrion subsidy and glyphosate, deploying in four streams with different land use scenarios (i.e. forest, village, and suburban) to explore the effects of carrion subsidy and environmentally relevant concentration of glyphosate on macroinvertebrates. We hypothesized that (1) the addition of anthropogenic carrion subsidy would attract higher macroinvertebrate abundance and richness; (2) environmentally relevant concentration of glyphosate would have low impacts on the whole macroinvertebrate communities but may negatively affect pollution sensitive taxa; and (3) the effects of carrion subsidy and glyphosate would change with land use.

4.3 Materials and Methods

4.3.1 Study area

This study was conducted in four streams in Huangshan Anhui Province, China (Fig. 3.1). The four streams located in subtropical area and were associated with different land use. One stream (suburban stream) flowed through the suburban area of Huangshan District (downstream of the town). Two streams located in ~50 m and ~1000 m downstream of a village respectively (V-50 and V-1000). One stream (forest stream) was in the Jiulong Nature Reserve. Substrates of village and forest streams were mainly consisted of cobbles and pebbles, while silt and sand were the dominant substrates in suburban stream. Background water quality (water temperature, pH, dissolved oxygen (DO), conductivity, ammonia and nitrate) were measured using YSI (Pro Plus) in *situ* and physical characters were recorded at the beginning of field experiment. During the experimental period (i.e. August), mean water temperature was 24.2 ^{o}C (unpublished data, averaged from 92 stream sites in Huangshan in 2015). Annual air temperature and precipitation in the study area are 15.4 ^{o}C and 1500 – 1600 mm respectively. Macroinvertebrate richness in the study area is more than 50 and communities were dominated by EPT taxa (i.e. Ephemeroptera, Plecoptera, and Trichoptera), Chironomidae and Coleoptera (Wang et al. 2005, Wang et al. 2015).

4.3.2 Experiment setting up

A 2×2 full factorial design was used to investigate the effects of carrion subsidy and glyphosate (two levels for each factor, i.e. with and without) on macroinvertebrates colonizing in leaf litter bags in streams with different land use. Freshly fallen leaves of *Cinnamomum camphora*, an evergreen and widely distributed tree in Southern China, were collected daily around Xi'an-Jiaotong Liverpool University campus (31°16′28″ N, 120°44′17″ E) from 25th June to 15th July 2016. In the laboratory, intact leaves (i.e. no visually damage) were picked out, gently removed attachment (e.g. sand or other small particles) on the leaves, and oven dried (48 h, 60 ^{o}C) until use. A total of 160 litter bags were used in this study (four treatments, four streams, two sampling dates, and five replicates). Each coarse mesh bag had 7.67 ± 0.02 g leaves.

Experimental treatments were as follow:

1) Anthropogenic carrion subsidy treatment: ~30 g fresh chicken meat (only muscles) was put in each coarse mesh litter bag. This proportion of litter : subsidy (0.26) for coarse mesh bag is similar to another study which manipulated 0.4 g leaves (wet weight) and 1 g (wet weight) salmon carcasses (Ito 2003).

2) Glyphosate treatment: we first diluted Roundup (30% glyphosate) into tap water (concentration: 20 ml/L, a high concentration in the application of this product) and then added 2% agar to "immobilize" glyphosate. Before agar was solidified, PVC pipes (1.5 cm in diameter, 8 cm in length) were immersed into the liquid. After the agar were solidified, we took out the PVC pipes for further use. For the glyphosate treatment, we inserted one PVC pipe per litter bag which resulted in 85 μg glyphosate contained in each litter bag. According to a summary study, glyphosate concentrations in several headwater streams and lakes were < 30 μg/L, and it reached more than 1000 μg/L in waterbodies with high human impact (Yang 2015). Therefore, the glyphosate concentration applied in this study (85 μg/litter bag) can be considered as a low-dose and environmentally relevant concentration. In a field study investigating the effects of glyphosate on biofilms in a pond, authors illustrated that the diffusion rate of glyphosate from agar was non-linear, with a large pulse (>10%) being released in the first two days followed by decreasing concentrations released from agar within the following 20 days (Shaw and Mibbayad 2016). Therefore, we assume that this method can provide continuous diffusion of environmentally concentration of glyphosate to leaf litter bags deployed in streams during the experimental period of our study of 30 days.

4.3.3 Field experiment

The field experiment was conducted from 29th July to 28th August 2016. In each stream, we deployed litter bags of control (only leaf), carrion subsidy (leaf + chicken meat), carrion subsidy + glyphosate (leaf + chicken meat + glyphosate), and glyphosate treatment (leaf + glyphosate) from upstream to downstream. Each treatment was at least 20 m away from the others to reduce the influences of glyphosate on control and subsidy treatments. Five litter bags of the same treatment were tied to one nylon string, and litter bags on one string was at least 20 cm away from the others. Then, the nylon string was tied to a steel bar which was hammered into the streambed at a depth of at least 30 cm. On day 15 and 30, one string (i.e. five litter bags) of each treatment was retrieved from each stream. Each litter bag was put in one plastic zipper bag and then stored in a 4 ^{o}C cool box immediately. Litter bags were taken back to the laboratory within 24 h and stored in a 4 ^{o}C cold room. All litter bags were processed by gently washing and picking out invertebrates within 48 h, then invertebrates were preserved in 70% ethanol for further identification.

4.3.4 Macroinvertebrates

Most of macroinvertebrates were identified to genus level, but when genus identification was not possible, the family name was given. For organisms belonging to Oligochaete (dominated by Tubificidae) were not, we did not identify them to further level. Functional feeding groups of macroinvertebrates were determined according to previous study (Mandaville 2002). For data analysis, results were expressed as abundance, richness, and % abundance of the whole community and dominant taxa (i.e. insect, EPT, Chironomidae, collector-gatherer, scraper, and predator); and biodiversity index (i.e. Shannon-Wiener Diversity Index and Simpson's Diversity Index, the formula were given in (Mandaville 2002)). In order to investigate the potential effects of our treatments on aquatic insect emergence, we calculated Chironomidae (the dominate family found in all streams) emergence propensity by dividing the number of Chironomidae pupa and adult to total Chironomidae abundance in each litter bag.

4.3.5 Statistical analyses

One-way ANOVA was used for detecting the differences of water quality among the four streams. Two-way ANOVA with repeated measures (two time points) was conducted to check the individual and combined effects of anthropogenic carrion subsidy and glyphosate, and land use (stream type) was set as co-variable to test whether macroinvertebrates differ among streams. If significant effects of land use were shown, a further one-way ANOVA with repeated measures was conducted to show the multiple comparison among streams. The combined effects of herbicide and anthropogenic subsidy were classified into additive, directional antagonistic and synergistic effects according to a directional interaction classification system (Piggott et al. 2015). For each category of stream (i.e. suburban, village, and forest), we also conducted two-way ANOVA with repeated measures for families which had % abundance > 2%, and these results were present in supplementary material. Before conducting the analysis, all data were checked for normality. Data were transformed (e.g. $\log_{10} X$ or $\log_{10} (X +1)$ (when $X=0$)) if the data deviated from normality. All data were analyzed using SPSS 22.0 and the figures were produced using Origin 9.0.

4.4 Results

4.4.1 Water quality

Most water quality were differed among streams (Table 4.1). Conductivity was highest in suburban stream (435.13 mg/L) and was 3.16, 2.89, and 7.75 times of that in V-50 (50 m downstream of village), V-1000 (1000 m downstream of a village), and pristine stream correspondingly ($P < 0.001$); ammonia was highest in suburban stream (1.24 mg/L) and was 4.96, 8.86, and 8.27 times of that in V-50, V-1000, and forest stream respectively ($P < 0.001$); nitrate was significantly higher in suburban stream (1.04 mg/L) and V-50 (0.93 mg/L) than in V-1000 (0.65 mg/L) and forest stream (0.56 mg/L) ($P < 0.001$). By contrast, dissolved oxygen (DO) in suburban stream (5.28 mg/L) was only 56% - 64% of the other three streams ($P < 0.001$), even though water temperature did not differ among the four streams ($P = 0.071$); flow velocity in suburban stream (0.19 m/s) and V-50 (0.15 m/s) were significantly slower than that in forest stream (0.36 m/s) ($P = 0.004$); and pH was lowest in suburban and highest in V-1000 and forest stream ($P < 0.001$).

Table 4.1 Background water quality of the four streams. Values are mean ± SE of four measurements. Water quality data were compared by One-way ANOVA with the same letter do not significantly differ (Turkey HSD was chosen for Post multiple comparison except for conductivity and ammonia (Dunnett's T3) because equal variances were not assumed). $P < 0.05$ are in bold print. V-50 and V-1000 represent stream 50 m and 1000 m downstream of a village respectively.

Parameters	Suburban	V-50	V-1000	Forest	*P*
Coordinate	30°18′13″ N, 118°6′21″ E	30°11′5″ N, 118°3′45″ E	30°10′15″ N, 118°3′32″ E	30°6′39″ N, 118°1′21″ E	
Altitude (m)	161	240	240	390	
pH	7.25 ± 0.00^{a}	7.64 ± 0.02^{b}	7.82 ± 0.02^{c}	7.81 ± 0.03^{c}	**<0.001**
Water temperature (°C)	27.48 ± 0.60	27.35 ± 0.03	26.78 ± 0.06	26.33 ± 0.09	0.071
Dissolved oxygen (mg/L)	5.28 ± 0.11^{a}	9.38 ± 0.05^{c}	8.63 ± 0.10^{b}	8.32 ± 0.12^{b}	**<0.001**
Conductivity (μs/cm)	435.13 ± 5.29^{d}	120.38 ±	150.60 ±	56.13 ± 0.48^{a}	**<0.001**

		0.09^b	0.13^c		
Ammonia (mg/L)	1.24 ± 0.10^c	0.25 ± 0.00^b	0.14 ± 0.02^a	0.15 ± 0.02^a	**<0.001**
Nitrate (mg/L)	1.04 ± 0.09^b	0.93 ± 0.02^b	0.65 ± 0.06^a	0.56 ± 0.02^a	**<0.001**
Flow velocity (m/s)	0.19 ± 0.04^a	0.15 ± 0.06^a	0.25 ± 0.05^{ab}	0.36 ± 0.07^b	**0.004**

4.4.2 Macroinvertebrates

Land use A total of 15,490 specimen, belonging to 102 genus/species and 51 families, were collected from 160 litter bags, with an average of 97 individuals per litter bag. Most of the macroinvertebrate metrics differed among streams (Table 4.2, Fig. 4.1-4.4). Village streams had the highest total abundance, total richness, and Shannon-Wiener Index. Although, total abundance in suburban stream (104 ind. / litter bag) was comparable to that in village streams and was more than twice of that in forest stream (47 ind. / litter bag), total taxa richness (5 taxa / litter bag) and biodiversity index (Shannon-Wiener, 1.19; Simpson, 0.40) were only around half of that in forest and village streams. Insects dominated in village and forest streams (> 90 %), while they only contributed to ~20% of the individuals in suburban stream. In addition, more than half and 35-45 % of the individuals found in forest and village streams were Chironomidae and EPT taxa respectively. Regarding to functioning feeding groups (FFGs), Collector-gatherers dominated in all streams (> 65 %), and were higher in village streams than in suburban and forest streams. V-1000 stream had the highest % abundance of scrapers (23.7 %) and forest stream had the highest % abundance of predators (14.7 %). The effects of land use on taxon richness was similar with the results of % abundance. Insect richness were more than 10 in forest and village streams and was only 3 in suburban stream. Among these insects, EPT taxa were more than five in forest and village streams and was less than one in suburban stream. As to the FFGs, collector-gatherers were the dominant taxa in all streams.

Table 4.2 Summary (*P*-values) of two-way ANOVA with repeated measures comparing macroinvertebrate responses between experimental treatments (G, glyphosate; S, subsidy) in streams with different land use (L, i.e. forest, village, and suburban streams). Combined (C) glyphosate by subsidy interaction effects are shown and are classified directionally (+ or -) as antagonistic (A), synergistic (S), additive (AD; no interaction) or no significant effect of either stressor (O) according to the conceptual model proposed by Piggott *et. al.* (2015). $P < 0.05$ are in bold print. The symbol * indicate data were log transformed before conducting the analysis to improve normality.

Response variables	G	S	L	G × S
Total abundance*	0.823	0.690	**0.011**	0.242 (O)
Total richness	0.527	0.272	**<0.001**	0.941 (O)
Shannon-Wiener	0.921	0.810	**<0.001**	0.322 (O)
Simpson's Diversity	0.985	0.598	**<0.001**	0.209 (O)
Insect abundance*	0.819	0.989	**<0.001**	0.890 (O)
Insect richness	0.815	0.350	**<0.001**	0.725 (O)
% insect abundance	0.718	0.559	**<0.001**	0.379 (O)
Chironomidae abundance*	0.720	0.593	**0.005**	0.822 (O)
% Chironomidae abundance	0.813	0.833	**<0.001**	0.111 (O)
Chironomidae emergence propensity*	0.814	0.980	0.115	0.497 (O)
EPT abundance*	0.615	0.970	**<0.001**	0.999 (O)
% EPT abundance	0.912	0.351	**<0.001**	0.854 (O)
EPT richness	0.941	0.578	**<0.001**	0.941 (O)
Collector-gatherers abundance*	0.749	0.718	**<0.001**	0.170 (O)
% Collector-gatherers abundance	0.504	0.963	**<0.001**	0.081 (O)
Collector-gatherers richness	0.540	0.597	0.167	0.983 (O)
Scraper abundance*	0.875	0.890	**0.001**	0.855 (O)
% Scraper abundance*	0.502	0.864	**<0.001**	0.602 (O)
Scraper richness*	0.466	0.565	**<0.001**	0.742 (O)
Predator abundance*	0.983	0.502	0.382	0.713 (O)
% Predator abundance*	0.927	0.504	0.269	0.284 (O)
% Predator richness*	0.454	0.186	**0.009**	0.853 (O)

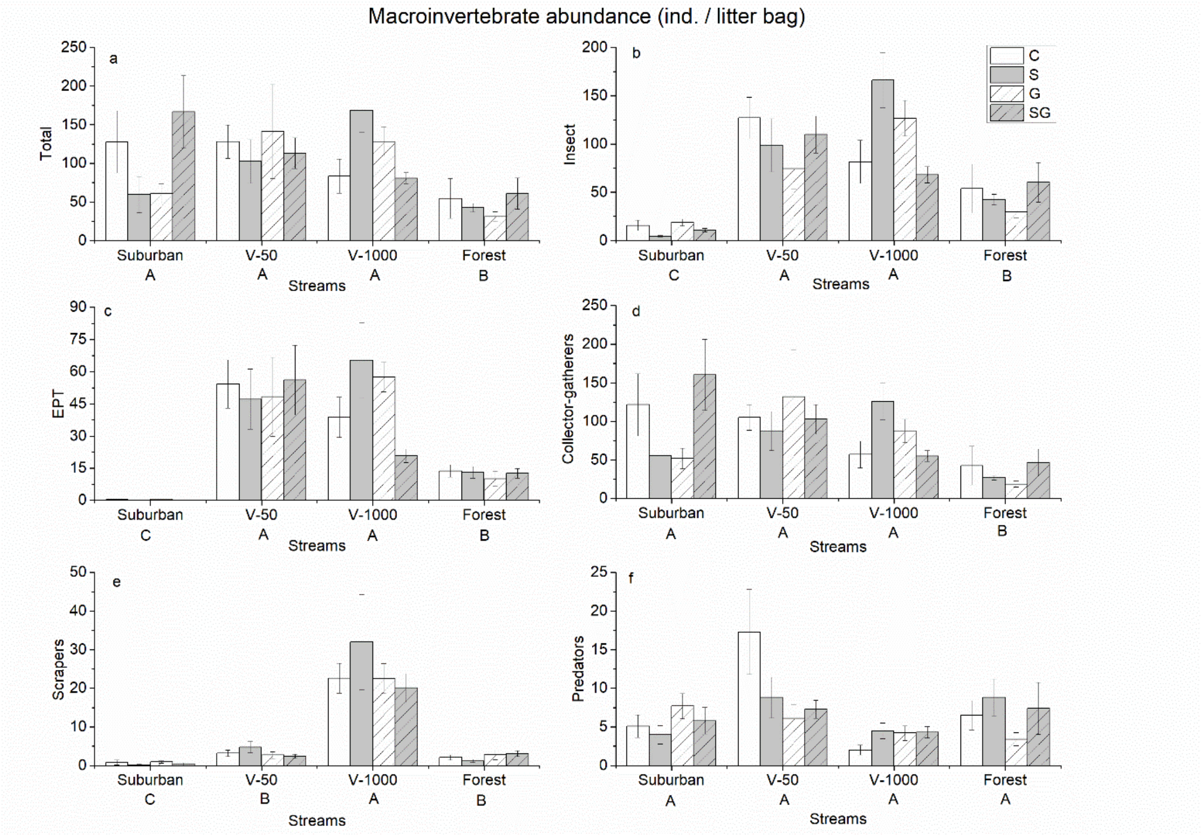

Figure 4.1 Averages of macroinvertebrate abundance (ind. / leaf litter bag) of (a) total, (b) insect, (c) EPT, (d) collector-gatherers, (e) scrapers, and (f) predators in the four streams. V-50 and V-1000 were streams 50 m and 1000 m downstream of a village respectively. Values are mean ± SE. Different capital letters below each stream indicate significant effects of land use (L) after one-way ANOVA with repeated measures and *post hoc* Tukey (parameters with same letter are not significantly different between treatments, $P > 0.05$) was used.

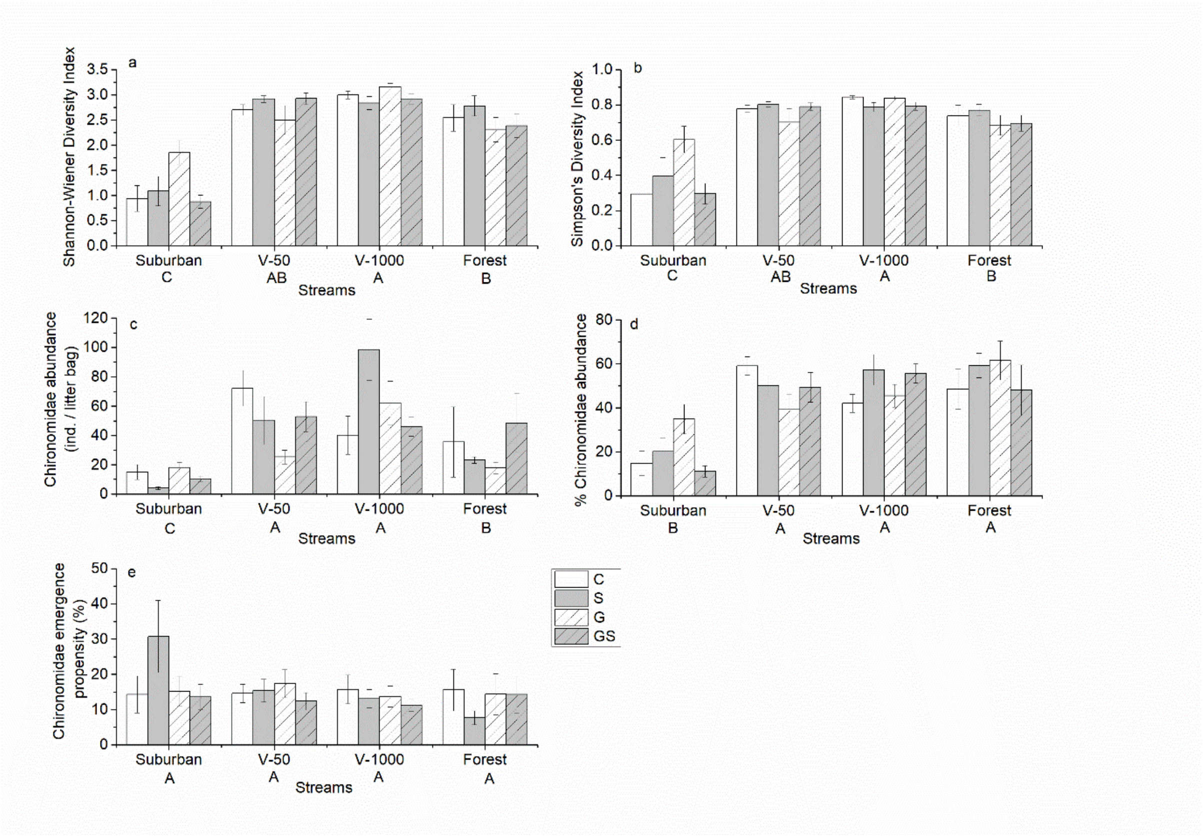

Figure 4.2 Averages of macroinvertebrate (a) Shannon-Wiener Diversity Index, (b) Simpson's Diversity Index, (c) Chironomidae abundance, (d) % Chironomidae abundance, and (e) Chironomidae emergence propensity in the four streams. V-50 and V-1000 were streams 50 m and 1000 m downstream of a village respectively. Values are mean ± SE. Different capital letters below each stream indicate significant effects of land use (L) after one-way ANOVA with repeated measures and *post hoc* Tukey (parameters with same letter are not significantly different between treatments, $P > 0.05$) was used.

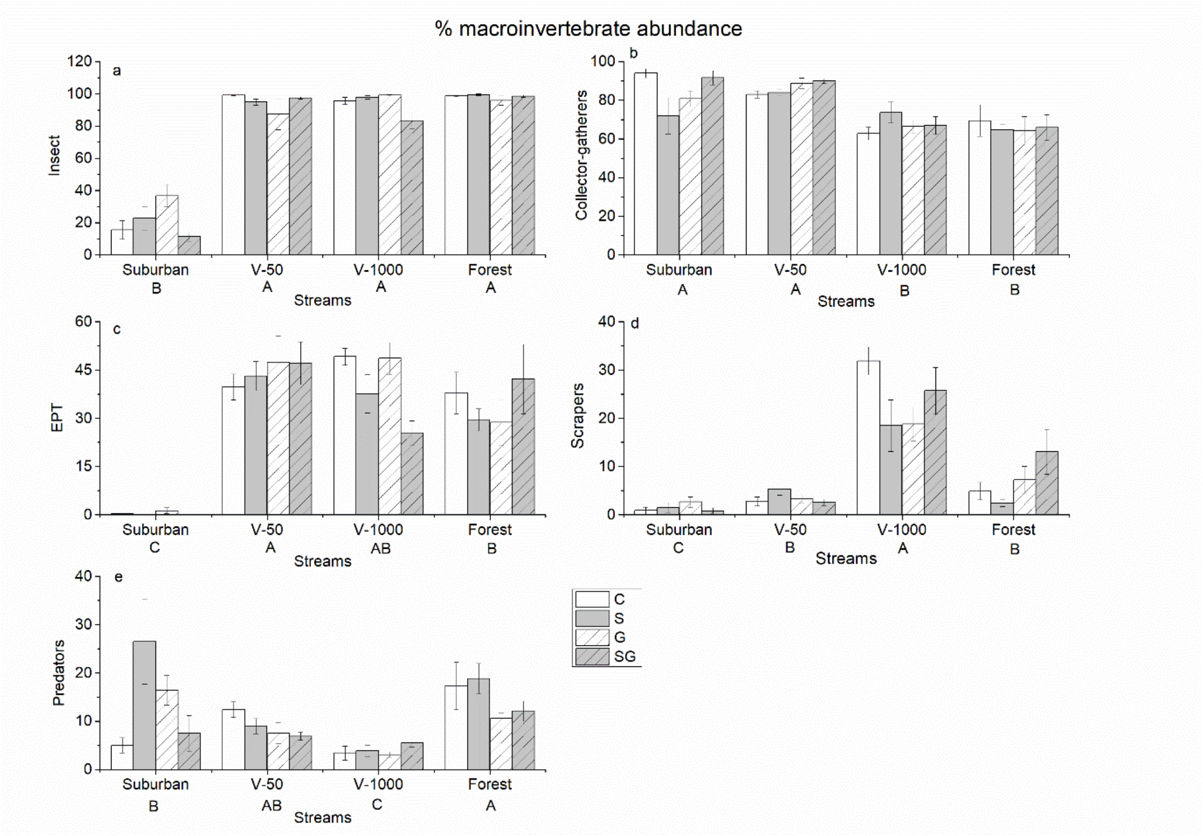

Figure 4.3 Averages of % macroinvertebrate abundance of (a) insect, (b) collector-gatherers, (c) EPT, (d) scrapers, and (e) predators in the four streams. V-50 and V-1000 were streams 50 m and 1000 m downstream of a village respectively. Values are mean ± SE. Different capital letters below each stream indicate significant effects of land use (L) after one-way ANOVA with repeated measures and *post hoc* Tukey (parameters with same letter are not significantly different between treatments, $P > 0.05$) was used.

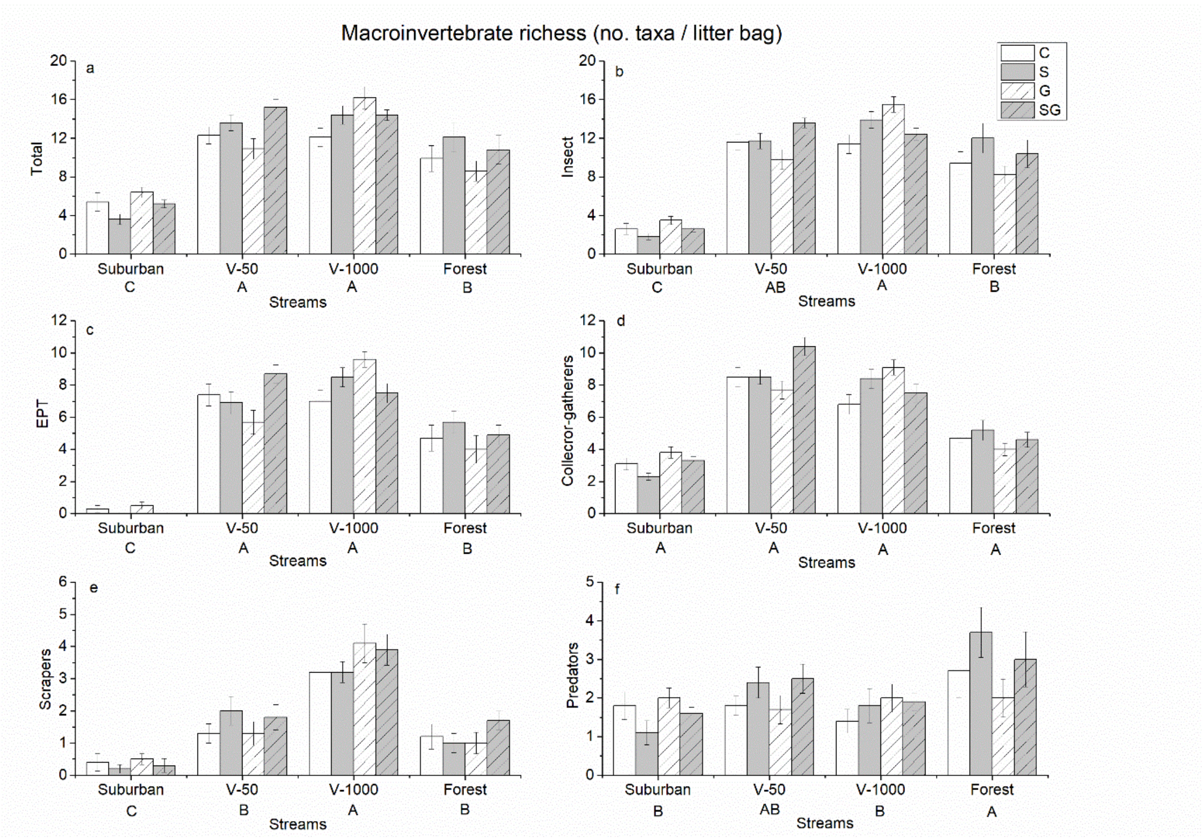

Figure 4.4 Averages of macroinvertebrate richness (no. taxa / leaf litter bag) of (a) total, (b) insect, (c) EPT, (d) collector-gatherers, (e) scrapers, and (f) predators in the four streams. V-50 and V-1000 were streams 50 m and 1000 m downstream of a village respectively. Values are mean ± SE. Different capital letters below each stream indicate significant effects of land use (L) after one-way ANOVA with repeated measures and *post hoc* Tukey (parameters with same letter are not significantly different between treatments, $P > 0.05$) was used.

Carrion subsidy and glyphosate None of anthropogenic carrion subsidy, environmentally relevant concentration of glyphosate, and their interactions showed significant effects on macroinvertebrates (Table 4.2). However, the effects of anthropogenic carrion subsidy and glyphosate depend on land use, with significant effects in some streams while not in others (Table S4.1). Glyphosate significantly decreased Ephemerellidae abundance in forest stream, and synergistically interacted with carrion subsidy to affect % abundance of Heptageniidae, Ephemerellidae, and Lepidostomatidae (Fig. S4.1). Carrion subsidy attracted higher abundance of Caenidae while negatively affected % abundance of Heptageniidae and Ephemerellidae in agricultural streams, and negatively synergistically interacted with glyphosate to affect abundance of Hydropsychidae and collector-gatherers (Fig. S4.2). Carrion subsidy also enhanced % abundance of Erpobdellidae, and the interaction between carrion subsidy and glyphosate showed positive synergistical effect on abundance of Oligochaeta (Fig. S4.3).

4.5 Discussion

Macroinvertebrate communities significantly differed among streams. While the addition of anthropogenic carrion subsidy and environmentally relevant concentration of glyphosate had no significant overall effects on macroinvertebrates. However, our treatments showed significant effects in some streams indicating that the response of macroinvertebrates to carrion subsidy and glyphosate depend on *in situ* community structure and physical habitats.

4.5.1 Effect of anthropogenic carrion subsidy on macroinvertebrates

We found no significant effects of anthropogenic carrion subsidy on macroinvertebrates which fails to support our first hypothesis that carrion subsidy would attract higher abundance and richness of invertebrates. This result differs from many previous studies that showed positive effects of carrion subsidy on stream macroinvertebrates (Zhang et al. 2003, Fenoglio et al. 2005, Kiffney et al. 2018). However, the significant effects of carrion subsidy on several taxa in village and suburban streams underscores the importance of fine-scale habitat variables, which is in accordance with other studies (Weaver et al. 2016). We found anthropogenic carrion subsidy significantly increased insect richness in forest stream, enhanced total taxa richness while decreased % EPT abundance in village streams, and had negative effects on some macroinvertebrate variables (e.g. total taxa richness and Shannon-Wiener Diversity Index) in suburban stream. These results indicate that the positive effects of anthropogenic carrion subsidy on macroinvertebrates could be reversed to negative due to land use change. Weaver et al. (2016) suggested that habitat characters such as shading could influence the response of macroinvertebrates to carrion subsidy (Weaver et al. 2016). In our study, village streams are relative open-canopy stream, thus nutrients leached from carrion subsidy may exert greater impact on periphyton production than in dense canopied forest stream (Kohler and Taki 2010). Therefore, macroinvertebrates that feed on biofilms should have higher abundance. However, % abundance of Heptageniidae and Ephemerellidae were reduced (despite an increased abundance of Caenidae) by the addition of anthropogenic subsidy in village streams, which is contrary to the results of other studies (Kohler et al. 2008, Verspoor et al.

2011, Weaver et al. 2016). One study also found the unexpected declining of % Heptageniidae abundance in salmon treatment reach and they had no clear explanation for this phenomenon (Kohler and Taki 2010). Another study suggested the reduction of heptageniid was due to the disturbance of salmon spawning activities (Lessard and Merritt 2006) which was not the case in this study. In our study, we assume the results could be attributed to: 1) marginally increased predator richness which induced top-down effect to reduce macroinvertebrate abundance and then counteract the positive bottom-up effect caused by carrion subsidy; 2) relative short experimental time, because the response time of macroinvertebrates to subsidy ranges from days to months (Rosario et al. 2002, Guyette et al. 2014), and the response time may be delayed for macroinvertebrates which are indirectly affected (i.e. benefit from enriched biofilms) by subsidy (Claeson et al. 2006). This could be supported by the higher abundance of Heptageniidae and Caenidae sampled on day 30 than on day 15 in treatments with anthropogenic subsidy; and 3) traits such as mouthparts morphology of Heptageniidae can limit them to benefit from subsidy (Merritt et al. 2017).

Even though Chironomids abundance was stimulated by anthropogenic carrion subsidy in forest and village streams, the differences were not significant which is only partially in accordance with other studies in which the authors found positive effects of salmon subsidy on Chironomidae abundance (Wipfli et al. 1999, Claeson et al. 2006, Cram et al. 2011). On the contrary, absolute and % abundance of Chironomidae were even negatively affected by anthropogenic carrion subsidy in suburban stream which was likely attributed to the higher predation pressure of Erpobdellidae. Chironomids can benefit from subsidy because they are capable of consuming salmon carcasses directly, and have traits (small body size, multivoltine, opportunistic feeding behavior, and propensity to drift) which can adapt to the new food resources (Lessard and Merritt 2006, Cram et al. 2011). We assume that the results of Chironomids may be relate to land use differences. Because anthropogenic carrion subsidy had no effect on Chironomids in forest stream, marginally increased its abundance in village streams, and declined its abundance in suburban stream. Furthermore, the negative effects of anthropogenic carrion subsidy on macroinvertebrates in suburban stream were likely to be facilitated by the fine sediments and higher concentration of nutrients (e.g. nitrate) (Collins et al. 2011, Janetski et al. 2013).

4.5.2 Effect of environmental relevant concentration of glyphosate on macroinvertebrates

Environmentally relevant concentration of glyphosate had no significant effects on macroinvertebrates which support our second hypothesis that glyphosate would have low impacts on macroinvertebrates. However, several taxa were negatively affected by glyphosate treatment in some streams. Glyphosate decreased Shannon-Wiener Diversity Index in forest stream, and positively affected some macroinvertebrates (e.g. enhanced total taxa richness and Shannon-Wiener Diversity Index) in suburban stream. The declined biodiversity in forest stream was caused by the depressed abundance of predators and sensitive taxa (e.g. Ephemerellidae), and marginally decreased richness of collector-gatherers. These results were in agreement with one field study that found glyphosate decreased total taxa richness (Magbanua et al. 2010). Negative effects of glyphosate on macroinvertebrates could be attribute to the direct toxicity effect on macroinvertebrates (Mercedes Iummato et al. 2013, Ferreira-Junior et al. 2017), or indirectly reduced food resources (e.g. algae and bacteria) (Pérez et al. 2007, Muturi et al. 2013, Baier et al. 2016). We did not find any significant effect of glyphosate on macroinvertebrates in village streams probably because 1) higher biodiversity and total taxa richness than the other two stream types, because a community with higher biodiversity are known to have higher resistance to stressors (Folke et al. 2004); 2) riparian zone of village stream were surrounded by some agricultural land which means macroinvertebrates in these streams can tolerate to some extend of toxic herbicide, therefore, glyphosate would not affect macroinvertebrate communities in these streams (Puertolas et al. 2010, Rasmussen et al. 2012). Unexpectedly, we found some positive effect of glyphosate on macroinvertebrates in suburban stream. This result is contrary to another study conducted in industrialized and urbanized Mediterranean stream, and they found no significant effect of glyphosate on macroinvertebrate communities (Puertolas et al. 2010). We assume the differences were related to macroinvertebrate community structure: both Baetidae and Chironomidae contributed >30% of individuals in Puertolas's study; while in our suburban stream, 64.7% and 20.3% of the individuals belonging to Oligochaeta and Chironomids respectively. In a mesocosm study where the macroinvertebrate communities (Oligochaeta and Chironomidae constitute 43.0% and 18.5% of the individuals respectively) (Magbanua et al. 2013) were similar to our study, they also found an increasing trend (but no significant difference) of Chironomidae abundance in concentration of 50 μg/L glyphosate (85 μg glyphosate per litter bag in our study) than control as we did. The enhanced richness of collector-gatherers and insect taxa were not likely result from increased food resources (e.g. higher cyanobacteria abundance) as proposed by some researchers (Pérez et al. 2007, Vera et al. 2010), because nutrient concentration in suburban stream was relative high and food resources for macroinvertebrates should be high enough. We are not sure what the hidden mechanisms of the increased taxa richness induced by glyphosate in suburban stream. One possible explanation may because the traits of dominant taxa (Oligochaeta, Chironomidae and Erpobdellidae) are: high dispersal (>1 km), multivoltine, and substrate preference for silt or mud, all of which are associated with high tolerance to stressors (Barnum et al. 2017, Berger et al. 2018). Consequently, glyphosate would not have toxicity effect on these macroinvertebrates, and it may indirectly benefit tolerant taxa by decreasing abundance and richness of sensitive taxa in suburban stream. The results indicate that even though the overall effects of low-dose glyphosate on macroinvertebrates were low, they still have significant effects on macroinvertebrates at population and community levels in forest streams where most organisms were glyphosate sensitive taxa.

4.5.3 Land use effect on macroinvertebrates

Macroinvertebrate communities differed among streams. Pollution sensitive species such as EPT taxa was almost disappeared in suburban stream, and pollution-tolerant species such as Oligochaete dominated (relative abundance > 50%) in suburban stream, these findings are similar with other studies (Walsh et al. 2007, Yule et al. 2015, Wang et al. 2018). The changed macroinvertebrate communities probably correlated with the percentage of impervious area (PIA). Even in streams with low PIA, other human activities such as the distance to a village (i.e. pollution source) could also influence macroinvertebrate communities by discharging domestic wastewater. We found that although total abundance and taxa richness were not differed between V-50 and V-1000 (50 m and 1000 m downstream of a village respectively), with longer distance from a village (i.e. decreasing human disturbance), macroinvertebrate communities switched to have lower abundance of collector-gatherers and predators, lower collector-gatherer richness, while had higher abundance of scrapers, more diverse insects, EPT taxa, and scrapers. These results support that pollution sensitive taxa (e.g.

Heptageniidae) recovered with decreasing human disturbance, which may be related to the declined nutrients (e.g. nitrate and ammonia) (Ortiz et al. 2005).

4.6 Conclusions

In conclusion, we found that (1) macroinvertebrate communities differed among streams, with the highest abundance and richness in village streams and lowest in suburban stream; (2) anthropogenic carrion subsidy, environmentally relevant concentration (low-dose) of glyphosate, and their interactions had no significant effects on any measured macroinvertebrate metrics when all data were combined; and (3) the response of macroinvertebrates to carrion subsidy and glyphosate differed among streams, indicating the importance of local community structure and habitat characters in driving the response of macroinvertebrates to stressors and subsidies. Therefore, as land use plays an important role in driving the effects of anthropogenic carrion subsidy and low-dose glyphosate (stressor) on macroinvertebrates, land use scenario should be taken into consideration when managing stream ecosystems.

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Chapter 5 Combined effects of water temperature, grazing snails and terrestrial herbivore on leaf decomposition in urban streams

5.1 Abstract

The decomposition of organic matter in freshwaters, such as leaf litter, can affect global nutrient (e.g. carbon) cycling. This process can be influenced by fast urbanization through increased water temperature, reduced aquatic diversity and changed leaf litter quality traits. In this study, we performed a mesocosm experiment to explore the individual and combined effects of warming (8 ºC higher and ambient), the presence *versus* absence of grazing snails (*Parafossarulus striatulus*), and intraspecific difference of leaf litter quality (intact *versus* > 40 % area of *Liriodendron chinense* leaves grazed by terrestrial insects) on litter decomposition in urban streams. Litter decomposition rates ranged from 0.019 d^{-1} to 0.058 d^{-1} with an average decomposition rate of 0.032 ± 0.002 d^{-1}. All the three factors had significant effects on litter decomposition rate. Warming and the presence of snails accelerated litter decomposition rates by 60 % and 35 % respectively. Litter decomposition rates of leaves damaged by terrestrial insects were 5 % slower than that of intact leaves, because litter quality of terrestrial insect-damaged leaves was lower (i.e. higher specific leaf weight) than intact leaves. For treatments with snails, warming stimulated microbial and snail mediated litter decomposition rates by 35 % and 167 %, respectively. All combinations of treatments showed additive effects on litter decomposition except for the interaction between warming and snails which showed positive synergistic effects. In addition, neither temperature nor litter quality affected snail growth rate. These results imply that higher water temperature and the presence of abundant snails in urban streams greatly enhanced litter decomposition. Moreover, the effect of pest outbreaks, which resulted in lower litter quality, can cascade to aquatic ecosystems by retarding microbe-mediated litter decomposition. When these factors co-occurred, warming could synergistically interact with snails to speed up the depletion of organic matter, while the effect of leaf quality on litter decomposition may be diminished at high water temperature. These effects could further influence stream food webs and nutrient cycling.

Key words: Leaf breakdown, Leaf quality, Snail, Cross-ecosystem subsidy,

Urbanization, Climate warming, Ecosystem functioning

5.2 Introduction

Global temperature is projected to increase 2.0 – 4.9 °C by the end of this century (Raftery et al. 2017), and the change in thermal conditions can influence almost all levels of stream ecosystems (Daufresne et al. 2009, Woodward et al. 2010). Numerous studies have indicated that warmer water can accelerate leaf litter (hereafter litter) decomposition in streams (Ferreira and Chauvet 2011, Ferreira and Canhoto 2015, Griffiths and Tiegs 2016, Martins et al. 2017). For example, from a synthesis of 1,025 records of litter decomposition, Follstad Shah et al. (2017) found that litter decomposition rates in freshwater ecosystems are expected to accelerate by 5–21 % when water temperature increases 1 – 4 °C. By contrast, in a global spatial field experiment, Boyero et al. (2011) found that warmer conditions stimulated microbe-mediated litter decomposition whereas invertebrate-mediated litter decomposition was decreased. Consequently, overall litter decomposition rate was unchanged. However, these results may not be suitable for the projection of warming effects on litter decomposition in urban streams, because data from these two global-scale studies were collected from streams with low human-impact intensity. Differences in invertebrate and microbial communities, physical conditions, and other factors were associated with different responses of litter decomposition to water temperature between urban and non-urban (e.g. forest) streams (Imberger et al. 2008, Iñiguez-Armijos et al. 2016, Wenisch et al. 2017). For instance, dominant invertebrates in urban streams have broader thermal breadth than invertebrates in mountain forest streams (Giersch et al. 2017). Consequently, warming results in reduced abundance and richness of warming-sensitive invertebrates in forest streams – which are mainly responsible for macroinvertebrate-mediated litter decomposition (Winterbourn et al. 2008, Griffiths and Tiegs 2016). By contrast, warming-induced reduction of abundance and richness of temperature-sensitive invertebrates in urban streams can benefit thermally tolerant invertebrates such as snails – the dominant contributor of macroinvertebrate-mediated litter decomposition (Yule et al. 2015). Therefore, results from most studies that have investigated warming effects on litter decomposition in non-urban streams may not be suitable for urban streams. Urban stream water temperature can be increased through various ways such as deforestation, water intake, discharging warmer effluent from domestic, industrial, and sewage-treatment sources (Lepori et al. 2015), runoff from hot impervious surfaces and stormwater (Somers et al. 2013). Furthermore, as natural stressors usually interact with each other, the effects of warming on litter decomposition are also subjected to seasonal change (Dossena et al. 2012, Ferreira and Canhoto 2014), nutrient concentration (Ferreira and Chauvet 2011), and the presence of shredders (Domingos et al. 2015, Moghadam and Zimmer 2016). Thus, predicting the consequences of warming on litter decomposition in urban streams needs to take account of other environmental stressors affecting consumer communities and litter quality.

In addition to abiotic factors (e.g. warming), biotic factors such as the presence of aquatic invertebrates (detritivores) can also affect litter decomposition (Jonsson et al. 2001, Gonçalves et al. 2006). Shredders are usually recognized as the dominant contributor to invertebrate-associated litter decomposition in streams (Bruder et al. 2014, Taylor and Andrushchenko 2014). In many tropical and urban streams where shredders were scarce, litter decomposition rates did not differ between coarse and fine mesh bags (i.e. when invertebrates excluded (Pascoal et al. 2005). However, these studies may underestimate the role of scrapers in litter decomposition, which shear off food, especially periphyton adhered to leaf surfaces (Cummins and Klug 1979). Specifically, many researchers have found a positive relationship between snail abundance and litter decomposition rate in streams where diversity and abundance of shredders are low (Suren and McMurtrie 2005, Chadwick et al. 2006, Yule et al. 2015). Snails can colonize litter rapidly even before microbes (e.g. fungi) can develop sufficient biomass or partially degrade the leaf tissues (Casas et al. 2011). Snails can completely eat the soft part of the leaves (Tanaka et al. 2006). The presence of snails is likely to affect the microbe-mediated litter decomposition through: 1) changing competition in microbial communities via direct consumption of some microbes such as bacteria; 2) altering microenvironments on the leaf surface due to feeding activities; and 3) stimulating fungal growth by excreting nutrients (e.g. higher ammonia) and labile carbon (Moghadam and Zimmer 2016) or decreasing turbidity which may influence the periphyton biomass (Hann et al. 2001, Li et al. 2008). Snails are abundant in urban streams due to their capability of tolerating high water temperatures and decreased water quality (Gray 2004, Ramírez et al. 2009). In addition, dams can transform upstream reaches from lotic to lentic habitats in rural streams, thereby altering water depth, flow velocity, sediment and water temperature regime (Stanley et al. 2002, Yan et al. 2011, Claeson and Coffin 2016). Although these changes may adversely affect sensitive invertebrates, other organisms including snails could benefit from these modified habitats (Cross et al. 2010, Gangloff et al. 2011). Therefore, snails may be an important factor influencing litter decomposition in these ecosystems and compensate for the loss of sensitive shredders (Chadwick et al. 2006, Casas et al. 2011).

Leaf quality has long been acknowledged as an important biotic factor influencing litter decomposition in streams (Leroy and Marks 2006, Hladyz et al. 2009). Generally, high quality leaves (e.g. high nitrogen concentration) are more preferred by invertebrates and microbes, thus making them decompose faster than low quality leaves (Schindler and Gessner 2009). Although numerous studies have investigated the effects of litter quality on its decomposition in freshwaters, most of them focused on interspecific differences in litter quality (Leroy and Marks 2006, Kominoski et al. 2007, Hladyz et al. 2009) rather than intraspecific differences (LeRoy et al. 2007, Jackrel et al. 2016). Environmental and anthropogenic stressors (e.g. insect herbivores, CO_2 concentrations, salt, and land use change) can decrease litter quality through various ways such as increasing concentrations of secondary chemicals (e.g. condensed tannins) (Frost et al. 2012, Rothman et al. 2015, Jackrel and Morton 2018). For example, plants in warmer urban areas are likely to suffer more serious insect pest outbreaks than in cooler areas (Meineke et al. 2013), and insect herbivores may continue to increase in the future due to global climate warming (Meineke et al. 2018). According to the nutrient acceleration hypothesis, insect damage enhances litter decomposition due to accelerated senescence, increased nutrient cycling, and improved litter quality (Chapman et al. 2003). By contrast, as per the nutrient deceleration hypothesis, insect attack can induce higher proportion of secondary defensive compounds which result in decreased nutrient cycling rates (Schweitzer et al. 2005), and thereby reduce litter decomposition rates. The changes in litter quality induced by insect herbivory can cascade to aquatic ecosystems (Jackrel and Wootton 2015, Jackrel and Morton 2018). Therefore, the effects of warming and other stressors associated with urbanization should be coupled with the effects of intraspecific litter quality to accurately estimate their individual and combined effects on ecosystem functioning and organism community structures (LeRoy et al. 2007, Lecerf and Chauvet 2008, Jackrel and Morton 2018). Such combinations of stressors are especially pertinent in urban and mountain areas (high elevation) where terrestrial insects are estimated to cause greater damage to plants, which could result in larger differences in intraspecific litter quality (Chen et al. 2009, Meineke et al. 2013, Ramsfield et al. 2016).

In this study, we used a mesocosm manipulative experiment to explore the effects of increased water temperature (~ 8 ºC) on the decomposition of intact and insect-damaged (> 40% leaf area were grazed by insects) tulip poplar (*Liriodendron chinense*), in the presence and absence of snails (*Parafossarulus striatulus*). Specifically, we aimed to test whether: 1) increasing water temperature would accelerate both microbe- and snail-mediated litter decomposition; 2) leaf damage caused by terrestrial herbivorous insects would reduce litter quality and result in retarded litter decomposition rate; and 3) the presence of snails would increase litter decomposition rate and partly compensate for the loss of shredders.

5.3 Materials and Methods

5.3.1 Leaf litter collection Freshly fallen *L. chinense* leaves were collected during the period 15th September to 1st October 2016 from a riparian forest in Jiulongfeng Nature Reserve (mean annual precipitation and air temperature are 1500 – 1600 mm and 15.4 ºC, respectively), Anhui Province, China (30°6′39″ N, 118°1′21″ E). This *ca* 30-year-old *L. chinense* woodland had suffered from pests (mainly Lepidoptera: moths, Fig. S5.1A-B) since 2009. Terrestrial pest outbreak occurred twice (June and September) every year. Consequently, the leaf-fall pattern had changed from once at the end of October to twice every year. In the laboratory, leaves were visually grouped into two categories (Fig. S5.1) according to the ratio of leaf area grazed by insects, i.e. intact-lightly damaged (0-5%) and heavily damaged (> 40%). Then, leaves were oven dried (60 ºC, 48 h) and weighed prior to use.

5.3.2 Experimental design Using ~60 L aquaria (50 × 30 × 40 cm), factorial combinations of manipulated water temperature (ambient *versus* 8 ºC above ambient), intraspecific leaf quality (intact *versus* insect-damaged) and scraper (snail) presence *versus* absence were each replicated five times (2 × 2 × 2 × 5 = 40 mesocosms). The experiment lasted for 25 days from 20th December 2016 to 14th January 2017. Mesocosms (Fig. S5.2) were installed on the riparian zone of a stream next to Xi'an-Jiaotong Liverpool University (31°16′30″ N, 120°43′59″ E), Suzhou, China. Water was pumped from the stream and circulated within the mesocosms to emulate the natural water quality, flow, and microbial supply. There was no substrate (e.g., rocks, gravel, sand) in the mesocosms. In each mesocosm, 10.01 ± 0.01 g of unconditioned litter (i.e. dry leaves) were added at the beginning of the experiment. One heating rod (LRB-210, 220 – 240 V, 100 W, SunSun Co. Ltd) was used to heat up the water in the warming treatment. The working temperature for the heating rod is 18 – 34 °C, as average annual air temperature in the study area (Suzhou, China) is 15 – 17 °C. We set the working temperature as 18 °C for each heater. In addition, warming usually induced a change of diel temperature oscillation, which can affect litter decomposition (Dang et al. 2009, Vyšná et al. 2014). Therefore, the diel temperature oscillation was also calculated. The average increased water temperature was 8 °C (Fig. 5.1 and Fig. S5.4), which is higher than the projected range of temperature increases by the end of this century globally (2.0 – 4.9 °C) (Raftery et al. 2017) and for China (3.9 – 6.0 °C) (Ding et al. 2006). This extreme high temperature may still be possible in urban areas where air temperature could be 1-3 °C warmer than rural areas, and the difference in air temperature between urban and rural areas can be as large as 10 °C under certain conditions (e.g. calm, cloudless nights in winter) (Grimmond 2007). In addition, for big cities such as Shanghai, China, the projected increase of mean temperature is estimated to be 2.5 times of that for global mean temperature (Chu et al. 2016). As water temperature in most streams would increase 0.6-0.8 °C for every 1 °C increase in air temperature (Morrill Jean et al. 2005), an 8 °C increase in water temperature would be realistic for streams in big cities. Moreover, an increase of 8 °C is not rare for laboratory microcosm studies (Ferreira and Chauvet 2011, Fernandes et al. 2012, Geraldes et al. 2012). Nine temperature loggers (ONSET, Stow Away TidbiT Temp Logger) were randomly placed into nine mesocosms (five warmed; four at ambient water temperature) to record water temperature once every hour during the experimental period (Fig. S5.3). Dissolved oxygen (DO), conductivity, and ammonia were measured using a YSI (Pro Plus), and pH and turbidity were measured using pH (CLEAN, PH30) and turbidity (HACH, 2100Q) meter, respectively, before conducting the experiment, and then on days 5, 14, and 24. On day 25, the litter (Fig. S5.5) was collected using a hand-held net, oven dried (60 °C, 48 h), and then weighed to calculate litter decomposition rate.

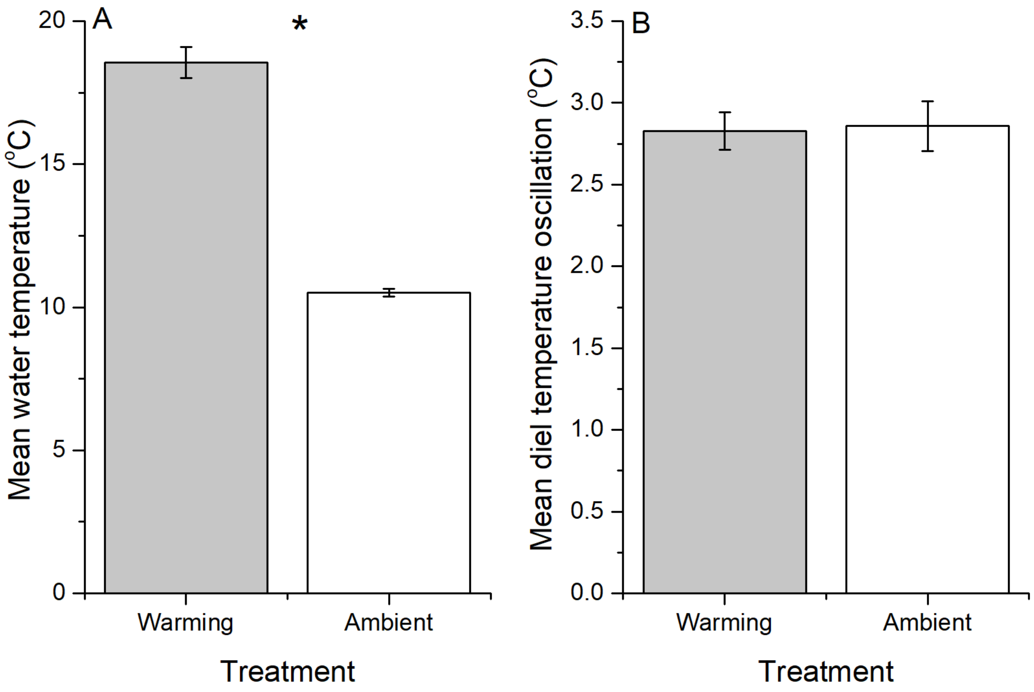

Figure 5.1 Averages of (A) water temperature and (B) diel temperature oscillation in treatments of warming and ambient temperature. Values are mean ± SE. The symbol * above the bar indicates a significant difference between the treatments.

5.3.3 Water quality Water temperature was successfully increased in mesocosms with the warming treatment (mean ± SE, 18.5 ± 0.54 °C) by an average of 8 °C above that in ambient treatment mesocosms (mean ± SE, 10.5 ± 0.14 °C) during the experimental period (t = 14.537, df = 4.502, P<0.001, Figure 5.1A). However, diel temperature oscillation did not differ between warming (2.83 ± 0.24 °C) and ambient (2.86 ± 0.10 °C) treatments (t = -0.124, df = 5.274, P=0.906, Fig. 5.1B).

Warming significantly affected all measured water quality variables (Table 5.1 and Table S5.1 Fig. 5.2), which was also found in other studies (Martínez et al. 2014, Domingos et al. 2015, Ferreira et al. 2015). Both pH and conductivity increased with increasing water temperature, while turbidity, dissolved oxygen (DO), and ammonia were reduced in warming treatments. The presence of snails decreased pH, turbidity, and DO. By contrast, snails increased ammonia and had no significant effect on conductivity. Litter quality only significantly affected pH by increasing pH in mesocosms containing insect-damaged litter. Most two-way interactions showed additive effects on water quality variables and only turbidity was affected by the three-way interaction.

Table 5.1 Summary results of three-way ANOVA with repeated measures for the effects of water temperature (T), snail (S), and litter quality (Q) on water quality in experimental mesocosms. Significant main effects are classified directionally as positive (+) or negative (-). Combined (C) two-way interaction effects are classified directionally (+ or -) as antagonistic (A), synergistic (S), additive (AD; no interaction) or no significant effect of either stressor (O) according to the conceptual model proposed by Piggott *et. al.* (2015). *P*-values < 0.05 are in bold print. Effect sizes (partial eta squared values; range 0-1) are shown in parentheses for all cases where *P* < 0.1.

Dependent variables	Litter quality	Q	Temperature	T	Snails	S	Q × T	C	Q × S	C	T × S	C	Q × T × S
pH	**0.003** (0.248)	+	**<0.001** (0.686)	+	**<0.001** (0.344)	-	0.149	AD	**<0.001** (0.402)	-S	0.2	AD	0.215
Turbidity (NTU)	0.313		**<0.001** (0.93)	-	**<0.001** (0.615)	-	0.394	AD	0.383	AD	**0.001** (0.318)	-A	**0.003** (0.244)
Conductivity (µs/cm)	0.422		**<0.001** (0.904)	+	0.356		0.315	AD	0.475	O	0.476	AD	0.996
DO (%)	0.163		**<0.001** (0.891)	-	**0.027** (0.143)	-	0.928	AD	0.227	AD	0.403	AD	0.092 (0.086)
DO (mg/L)	0.684		**<0.001** (0.941)	-	0.445		0.454	AD	0.383	O	0.827	AD	0.228
Ammonia (mg/L)	0.325		**<0.001** (0.887)	-	**<0.001** (0.492)	+	0.252	AD	**0.03** (0.14)	+S	**0.007** (0.206)	+A	0.7

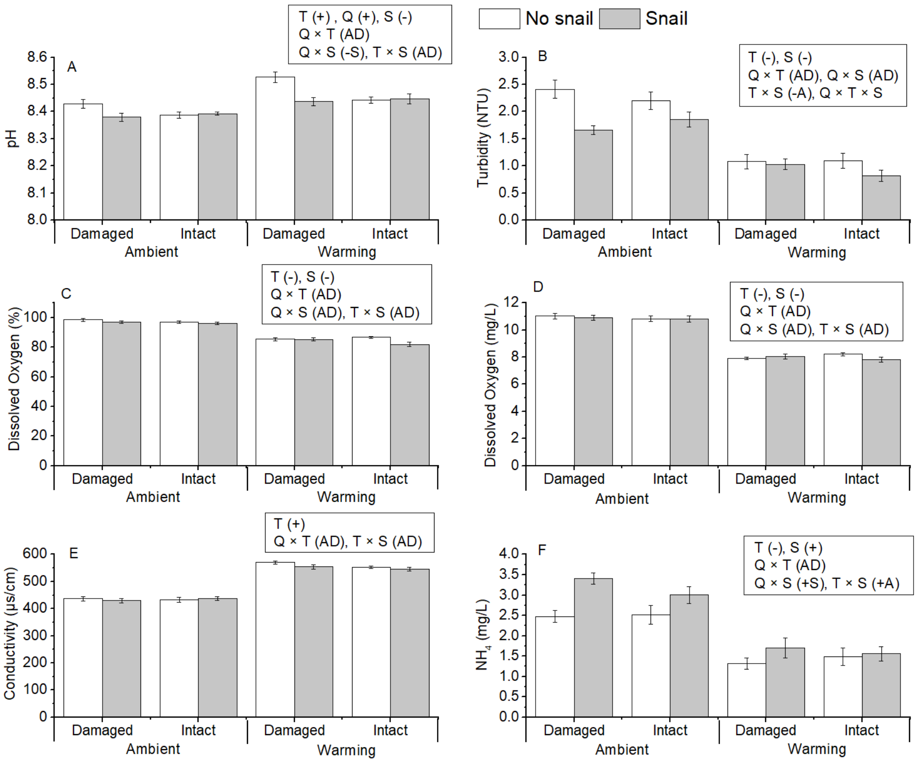

Figure 5.2 Averages of water quality across the experimental treatments (water temperature: ambient and warming, snails: presence/absence, litter quality: intact and insect damaged). Values are mean ± SE (data of three sampling dates are combined). Text in rectangles indicates significant directional main effects and two-way interaction effects (water temperature: T, Snails: S, litter quality: Q), with effect classifications (for abbreviations see Table 5.1) in parentheses.

5.3.4 Specific leaf weight Specific leaf weight (SLW, leaf dry weight per unit leaf area) can be regarded as an indicator of leaf toughness - an important litter quality trait (Steinbauer 2001). SLW was measured to test the potential physical structural quality differences between insect damaged and intact litter, because plants tend to have higher SLW when attacked by insects (Nabeshima et al. 2001, Sudderth and Bazzaz 2008). Thirty intact and insect-damaged leaves were randomly selected from the leaves collected for this study. For each focal leaf, one leaf disc (6 mm in diameter, avoiding leaf vein) was randomly cut out using a core borer. All leaf discs were oven dried (60 ^{o}C) to constant weight, which was recorded to the nearest 0.0001 g. Then, SLW was calculated by dividing the dry leaf mass to leaf disc area (Jackrel et al. 2016).

5.3.5 Snail Specimens of a common snail *P. striatulus* were collected from a stream to the north of Renmin University of China, Suzhou (31°16′54″N, 120°44′30″E). This stream is straight, ~ 15 m wide, with muddy sediment and concrete bank. Snails were kept in mesocosms for at least one week to acclimate to the new environment and were starved for three days before conducting the experiment. Before starting the experiment, each snail was blotted dry and weighed to the nearest 0.0001 g (mean ± S.E, 1.0744 ± 0.0322 g, n = 400). Twenty randomly selected snails were placed in each scraper treatment, giving a density of 133 ind/m^2, which was higher than the mean natural density (41-80 ind./m^2) but still within the natural range of population density (0-280 ind./m^2) in this area (Wang and Hong 2010, Hu et al. 2013). At the end of the experiment, snails were blotted dry and weighed again to determine the growth rate. Then, all snails were released to the stream where they were collected. Snail growth rates were calculated as $\mu = [\ln(W_t) - \ln(W_0)]/t$, where W_t and W_0 were blotted mean wet mass per treatment at the end of the experiment (day t) and before the experiment, respectively (Hill et al. 2010). In addition, snail tissue dry mass (TDM) and ash free dry mass (AFDM) were calculated using empirical equations in the study area (i.e. Suzhou, China), TDM=0.067W, and AFDM=0.286W, where W was blotted dry mass (Zhao et al. 2009).

5.3.6 Litter decomposition Litter decomposition rates were calculated assuming an exponential decay (k, d^{-1}), $W_t = W_I \times e^{-kt}$ (Eq. 1), where W_t represents the remaining leaf mass at the incubation time t (day) and W_I is the initial mass of leaf material (Ferreira and Chauvet 2011). In addition, we calculated the sensitivities of litter decomposition rates to temperature: $Q_{10\text{-}q} = (t_A/t_W)^{(10/(Tw-Ta)}$ (Eq. 2) (Conant et al. 2008), where t_A and t_W are the time (days) to decompose 50 % of initial dry leaf mass at the ambient and warming temperature respectively, *Ta* and *Tw* are the mean temperature during the experimental period in the ambient and warming mesocosms respectively.

Litter decomposition rates in the presence and absence of snails was total (k_{total}) and microbe-mediated ($k_{\text{microbial}}$) litter decomposition rates respectively. The contribution of snail-mediated litter decomposition rate was estimated by the difference in dry leaf mass remains between mesocosms in the presence and absence of snails, and then calculating a new k value (k_{snail}) (Magali et al. 2016, Mosele Tonin et al. 2018).

5.3.7 Data analysis Three-way ANOVA was used to test for differences in litter decomposition rates among treatments (warming, snail grazing, litter quality). In treatments with the presence of snails, two-way ANOVA was used to test the effects of warming and litter quality on litter decomposition rates, i.e., k_{total}, $k_{\text{microbial}}$, and k_{snail}. T-tests were used to test for differences in water temperature (daily mean water temperature and diel temperature oscillation) between warming and ambient treatments (Domingos et al. 2015, Ferreira et al. 2015). For each measured water quality variable, we used three-way ANOVA (analysis of variance) with repeated measures (RM ANOVA) to explore the effects of experimental treatments on water quality. A t-test was used to check for SLW differences between intact and insect-damaged leaves. One-way ANOVA was used to detect whether initial blotted dry mass differed among the four treatments with snails. If they differed among treatments, then, initial blotted dry mass was set as a co-variable when doing the two-way ANCOVA to test the potential effect of body size on snail growth rate and litter decomposition rate. As both TDM and AFDM are correlated with blotted dry mass, we only analyzed two-way ANOVA results of net blotted dry mass growth rates. To determine the interaction type of two-way interactions, we followed the methods proposed by (Piggott et al. 2015). After conducting normality tests for all data, the data were transformed (e.g. log) to improve the normality of data. All data were analyzed using SPSS 22.0.

5.4 Results

5.4.1 Leaf litter decomposition Litter decomposition rates varied between 0.019 d^{-1} and 0.058 d^{-1} (mean ± S.E, 0.032 ± 0.002 d^{-1}, Fig. 5.3, Fig. S5.3). Warming accelerated litter decomposition rates by 60 % (data were log-transformed, $F_{1,32} = 259.93$, $P<0.001$, Table 5.2). The presence of snails (0.037 ± 0.001 d^{-1}) also significantly increased litter decomposition rates by 35 % ($F_{1,32} = 90.21$, $P<0.001$, Table 5.2). However, litter decomposition rates of terrestrial insect-damaged leaves (0.031 ± 0.001 d^{-1}) were 5 % slower than those of intact leaves ($F_{1,32} = 4.687$, $P=0.038$, Table 5.2). The interaction of temperature and snail presence had positive synergistic effects on litter decomposition, i.e. warming increased the litter decomposition rates more in the presence of snails than in their absence. However, neither the rest of the two-way interactions nor the three-way interactions had significant effects on litter decomposition rates, i.e. the rest of the interactions all showed additive effects.

Table 5.2 Summary (*P*-values and effect sizes) of three-way ANOVA comparing litter decomposition rates (exponential model) among experimental treatments (Litter quality: Q, water temperature: T, snails: S). Main effects (M) are classified as positive (+) or negative (-). Combined two-way interaction effects (C) are classified directionally (+ or -) as antagonistic (A), synergistic (S), additive (AD; no interaction) or no significant effect of either stressor (O) according to the conceptual model proposed by Piggott *et. al.* (2015). $P < 0.05$ are in bold print. Effect sizes (partial eta squared values; range 0–1) are shown in parentheses for all cases where $P < 0.1$.

Treatments	df	Decomposition rate (k, d^{-1})		
		F	*P*	M/C
Q	1	4.687	**0.038** (0.128)	-
T	1	259.930	**<0.001** (0.890)	+
S	1	90.210	**<0.001** (0.738)	+
Q × T	1	1.595	0.216	AD
Q × S	1	0.588	0.449	AD
T × S	1	25.503	**<0.001** (0.444)	+S
Q × T × S	1	1.808	0.188	
Error	32			

Note: Data of litter decomposition rates were log transformed to improve normality before conducting the analysis.

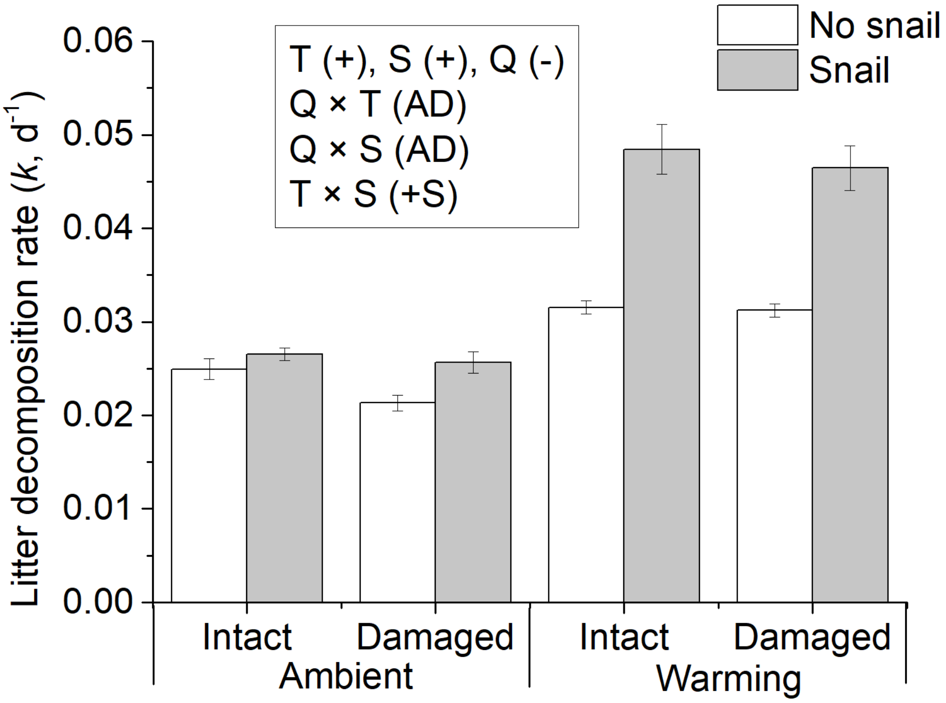

Figure 5.3 Averages of litter breakdown rate (k, d^{-1}) for intact (< 5%) and damaged leaves (> 40% leaf area were grazed by terrestrial insects) incubated in the absence (blank bar) and presence of snails (grey bar), at ambient and warming mesocosms for 25 days. Text in rectangles indicate significant directional main effects and two-way interaction effects (water temperature: T, Snails: S, litter quality: Q), with effect classifications (for abbreviations see Table 5.1) in parentheses. Values are mean ± SE.

The overall sensitivity of litter decomposition rates to temperature ($Q_{10\text{-}q}$) was low according to a classification system reported previously (Conant et al. 2008). When mean temperature increased from 10.5 ºC to 18.5 ºC, the litter decomposition was stimulated more in the presence of snails than in their absence for both intact leaves ($Q_{10\text{-}q} = 2.38$ vs. 1.66) and insect damaged leaves ($Q_{10\text{-}q} = 2.37$ vs. 1.61). However, the thermal sensitivity of litter decomposition rates showed no difference between the intact and insect-damaged leaves in the presence ($Q_{10\text{-}q} = 2.38$ vs. 2.37) and absence ($Q_{10\text{-}q} = 1.66$ vs. 1.61) of snails.

In treatments with snails, warming significantly increased total, microbial-, and snail-mediated litter decomposition rates by 81 %, 35 %, and 167 %, respectively ($P<0.001$, Table 5.3, Fig. 5.4). Microbe-mediated litter decomposition rates were also 7 % lower for damaged leaves than intact leaves ($F_{1,15} = 5.417$, $P=0.034$, Table 5.3). By contrast, neither total nor snail-mediated litter decomposition rates were affected by litter quality. Water temperature and litter quality showed additive effects on each of the three measures of litter decomposition rate (Table 5.3). In addition, in the presence of snails, even though initial blotted dry mass differed among the four treatments ($F_{3,16} = 3.893$, $P=0.029$, Fig. 5.5B), none of the litter decomposition rates were affected by initial dry mass of snails (Table 5.3).

Table 5.3 Summary (*P*-values and effect sizes) of two-way ANCOVA comparing the individual and combined effects of snail initial blotted dry mass (S), water temperature (T) and litter quality (Q) on total (k_{total}), microbe ($k_{microbe}$), and snail (k_{snail}) mediated litter decomposition rates. Main effects (M) are classified as positive (+) or negative (-). Combined two-way interaction effects (C) are classified directionally (+ or -) as antagonistic (A), synergistic (S), additive (AD; no interaction) or no significant effect of either stressor (O) according to the conceptual model proposed by Piggott *et. al.* (2015). $P < 0.05$ are in bold print. Effect sizes (partial eta squared values; range 0–1) are shown in parentheses for all cases where $P < 0.1$.

Treatments	df	k_{total}			$k_{microbe}$			k_{snail}		
		F	*P*	M/C	*F*	*P*	M/C	*F*	*P*	M/C
T	1	113.558	**<0.001** (0.883)	+	85.408	**<0.001** (0.851)	+	30.008	<0.001 (0.667)	+
Q	1	0.714	0.411		5.417	**0.034** (0.265)	-	1.170	0.296	
S	1	0.179	0.678		0.650	0.433		0.016	0.902	
T × Q	1	0.001	0.982	AD	4.194	0.058 (0.219)	AD	2.499	0.135	AD
Error	16									

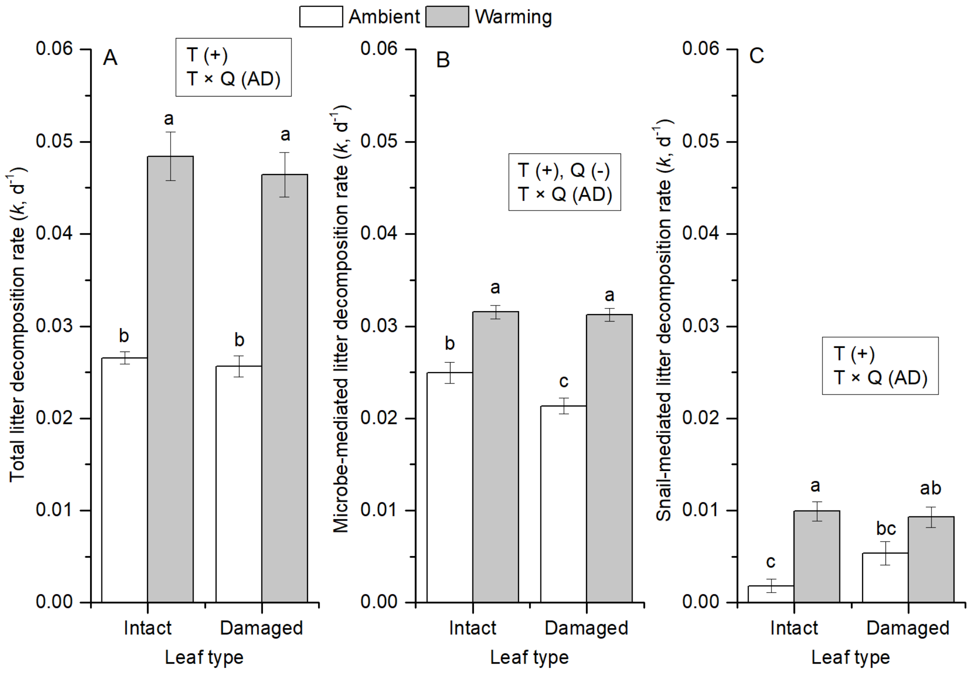

Figure 5.4 Averages of litter decomposition rates of (A) total, (B) microbe-mediated, and (C) snail-mediated for intact and insect-damaged leaf litter at ambient and warming (~ 8 °C higher) conditions. Different lowercase letters above each bar indicate significant differences after one-way ANOVA and *post hoc* Tukey (parameters with same letter are not significantly different between treatments). Text in rectangles indicate significant directional main effects and two-way interaction effects (water temperature: T, litter quality: Q), with effect classifications (for abbreviations see Table 5.1) in parentheses. Values are mean ± SE.

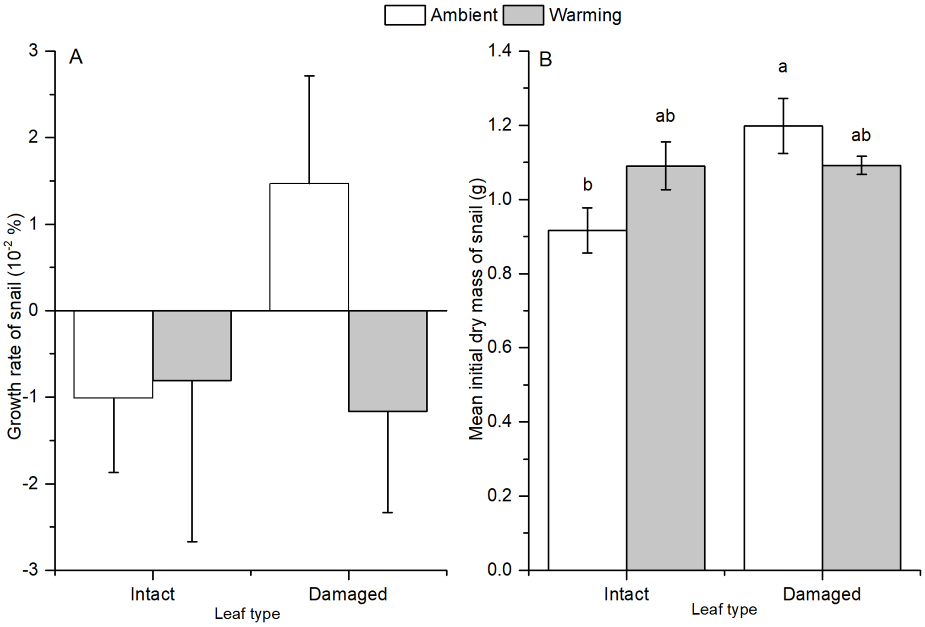

Figure 5.5 Averages of snail (A) growth rate and (B) initial blotted dry biomass in treatments of intact and insect-damaged litter at ambient and warming condition. Values are mean ± SE. Different lowercase letters above each bar indicate significant differences after one-way ANOVA and *post hoc* Tukey (parameters with same letter are not significantly different between treatments).

5.4.2 Specific leaf weight Mean (± S.E.) SLW of terrestrial insect-grazed leaves (7.9 ± 0.4 mg/cm^2) were 47 % higher than that of intact leaves (5.4 ± 0.4 mg/cm^2; $t = -4.872$, df = 58, $P<0.001$).

5.4.3 Snail growth There were no significant differences among treatments for snail growth rates (Table 5.4, Fig. 5.5A). Snail growth rates were negligible (close to 0, almost ceased growth) and net blotted dry biomass kept constant during the experiment (no significant difference was shown between initial and final blotted dry biomass).

Table 5.4 Summary (*P*-values and effect sizes) of two-way ANOVA comparing snail growth rates for the individual and combined effects of litter quality (Q) and water temperature (T). Main effects (M) are classified as positive (+) or negative (-). Combined two-way interaction effects (C) are classified directionally (+ or -) as antagonistic (A), synergistic (S), additive (AD; no interaction) or no significant effect of either stressor (O) according to the conceptual model proposed by Piggott *et. al.* (2015). $P < 0.05$ are in bold print. Effect sizes (partial eta squared values; range 0–1) are shown in parentheses for all cases where $P < 0.1$.

Treatments	df	Snail growth rate		
		F	*P*	M/C
T	1	0.881	0.363	
Q	1	0.187	0.671	
Initial biomass	1	0.201	0.66	
T × Q	1	0.434	0.52	O
Error	15			

5.5 Discussion

5.5.1 Warming enhanced litter decomposition

Litter decomposition rates were significantly increased in warming treatments, which agrees with previous findings (Martínez et al. 2014, Ferreira et al. 2015), increasing by 7.5 % per °C warming (mean $Q_{10\text{-}q}$ = 1.79). This acceleration is nearer to the estimated 10 % acceleration of litter decomposition rate per °C in the tropics rather than the 2.5 % in temperate biomes (Follstad Shah et al. 2017). Correa-Araneda et al. (2015) indicated that warmer conditions can depress abundance and species richness of macroinvertebrates with narrow thermal tolerance thereby reducing litter decomposition rate. However, if the depressed macroinvertebrate-mediated litter decomposition was compensated by stimulated microbe-mediated litter decomposition, then overall litter decomposition would be unchanged (Boyero et al. 2011) or even higher than under ambient conditions (Dossena et al. 2012). Our results indicated that warming can not only enhance microbe-mediated litter decomposition (Fernandes et al. 2012, Ferreira and Canhoto 2015), but also can accelerate snail-mediated litter decomposition (Friberg et al. 2009). Previous studies also found that microbe-mediated litter decomposition in urban streams was enhanced by the increased water temperature (Imberger et al. 2008, Yule et al. 2015). However, in urban streams with poor water quality (e.g. low DO and high ammonia), microbe-mediated litter decomposition would decrease, countering any increase with warmer water temperature (Martins et al. 2015, Iñiguez-Armijos et al. 2016). Therefore, it is important to take physicochemical factors into consideration when assessing the impact of increasing water temperature on litter decomposition in urban streams. For invertebrate-mediated litter decomposition, our result differs from that of Domingos et al. (2015) in which ~ 3 °C higher water temperature depressed the activity of *Allogamus laureatus* (Trichoptera, Limnephilidae), leading to a lack of thermal stimulation of litter decomposition in the presence of *A. laureatus*. Thus, we suggest that differences in the invertebrate community can influence the effects of warming on invertebrate-mediated litter decomposition.

In addition, along with increased mean water temperature, higher diel temperature oscillation, which is usually associated with climate warming, can also contribute to accelerated litter decomposition rate (Dang et al. 2009, Vyšná et al. 2014, Gonçalves et al. 2015). However, this was unlikely in this study, as diel temperature oscillation did not differ between warming and ambient treatments. Moreover, the effects of litter quality on both microbe- and snail-mediated litter decomposition rates diminished at higher water temperature, which accords with the suggestion of Fernandes et al. (2012) that warming (from 18 to 24 °C in their microcosms) could weaken the effects of litter quality on microbe-mediated (fungal) litter decomposition. Therefore, even though warming and other factors (e.g. increasing concentration of CO_2) associated with urbanization can alter litter quality (Tuchman et al. 2002, Meineke et al. 2013), these effects may be overridden by the effects of warming on litter decomposition in freshwaters.

5.5.2 The presence of snails accelerated litter decomposition

The presence of scrapers (snails) accelerated litter decomposition rates by 35 %. Our results suggest that the presence of snails in urban streams, where shredders are often scarce or absent, play an important role in litter decomposition, as also found by (Chadwick et al. 2006). We found that leaf morphology in treatments with snails differed from treatments without snails, indicating likely effects of grazing on the leaf surface. However, we could not ascertain whether leaf morphological changes arose from direct consumption of leaves by snails or from the indirect effects of grazing on algae attached to the leaf surface. The snails almost ceased growth in this study which was probably due to the overall low activities of snails in winter (Eleutheriadis and Lazaridou-Dimitriadou 2001), or because we used unconditioned leaves and 25 days may not be long enough for sufficient colonization by microbes (Wallace et al. 1970). Collectively, the presence of snails in urban streams can significantly accelerate litter decomposition in winter, even though snail growth rates were almost zero. Additionally, warming can synergistically enhance the effects of snails on litter decomposition. Due to the global increase of urban areas, we can anticipate that shredder-mediated litter decomposition would decrease while snail-mediated litter decomposition would be enhanced. In addition, water temperature would also likely increase as rural streams are transformed into urban streams, resulting in exaggerated snail-mediated litter decomposition.

5.5.3 Terrestrial insect herbivores retarded litter decomposition

Decomposition rates of terrestrial insect-grazed leaves were 5 % slower than those of intact leaves. The retarded litter decomposition was caused by lower litter quality, as indicated by (1) higher SLW of terrestrial insect-grazed litter (> 40% leaf area) than intact leaves (< 5% leaf area grazed), because a higher SLW has been associated with lower leaf N, P and N:P ratio (Wu et al. 2012), and (2) even though snail-mediated litter decomposition rates did not differ between intact and insect-damaged leaves, higher litter decomposition rates were found for insect-damaged leaves than for intact leaves under ambient conditions, because snails need to consume more insect-damaged leaves to compensate for the lower quality to meet their metabolic requirements (Flores et al. 2014). These results suggest that insect herbivores decreased litter quality (Peschiutta et al. 2018), thereby supporting the nutrient deceleration hypothesis. Another possible mechanism is that insect herbivory resulted in higher concentrations of secondary compounds in deciduous trees (Chapman et al. 2006). The lower litter quality had different effects on snails and microbes, with significantly slower microbe-mediated decomposition but faster (but not significant) snail-mediated decomposition in ambient conditions. This result is similar to that of LeRoy et al. (2007) in which aquatic fungi could discriminate intraspecific litter quality differences, whereas macroinvertebrates could not. LeRoy et al. (2007)

suggested that aquatic fungi may respond to quality differences in litter. Snail-mediated litter decomposition showed a weak relationship to intraspecific litter quality difference, possibly because: (1) the effects of litter quality diffused through trophic levels, and (2) large body size of snails enable them to tolerate many toxicant secondary compounds (Yule et al. 2009). In addition, the differences in litter decomposition rates between insect-damaged and intact *L. chinensis* leaves in this study (5 %) was much smaller than that of Jackrel and Wootton (2015) who observed 42 % faster decomposition of intact *Alnus rubra* leaves than of herbivory-treated leaves (Jackrel and Wootton 2015). The reason for this difference may be that litter quality of *L. chinensis* may be poorer than *Alnus rubra:* C:N stoichiometryof *L. tulipifera* (C:N, 36.69-56.3) (Kominoski et al. 2007, Ardón et al. 2009, Griffiths and Tiegs 2016), may reflect that of the congeneric *L. chinensis*, and is higher (i.e. suggesting poorer quality) than that of *A. rubra* (C:N were 21.11 and 18.73 for herbivory treated and control respectively). Therefore, a further herbivore-induced decline in the already less palatable *Liriodendron* might not make a big difference for consumers. Although we only found increased pH in treatments with damaged leaves, other water quality characters may also have been potentially influenced by the difference of intraspecific litter quality (Adams et al. 2003), and consequently affect litter decomposition. Our findings imply that when considering the importance of litter quality on decomposition in streams, we should consider not only interspecific differences but also intraspecific differences in litter, especially considering that future climate change, land use change, and other stressors can change intraspecific litter quality (Graça and Poquet 2014, Fey et al. 2015, Pincebourde et al. 2017).

5.5.4 The interactions of water temperature, snail, and litter quality on litter decomposition

Among all the two-way combinations, only that between snails and water temperature showed positive synergistic effects on litter decomposition rates, whereas all other combinations showed additive effects (i.e. no significant interaction). The macroinvertebrate-warming synergistic effects on litter decomposition rates, also observed by (Moghadam and Zimmer 2016), could be explained by enhanced consumption rates of litter by snails at higher temperature conditions because of higher metabolic demands of snails at these high temperatures (Seuffert et al. 2010, Gordon et al. 2018). Warming can increase the community-level energy demand with consequences for ecosystem functioning (Nelson et al. 2017). At higher water temperatures, snails often feed more selectively on higher quality food (Gordon et al. 2018). This could be the reason why snail-mediated litter decomposition was more sensitive to temperature for intact leaves than for insect-damaged leaves. In addition, litter quality would be increased (e.g. reduced toughness, fewer phenols and lower C:N ratios) when incubated at higher water temperature (Esther et al. 2015). Interactive effects of litter quality and water temperature on litter decomposition are difficult to predict because of conflicting types of interaction including warming either reinforcing poor litter-quality effects on decomposition (Correa-Araneda et al. 2015, Esther et al. 2015), dampening the effects of lignin-rich (i.e. poor quality) litter on decomposition (Fernandes et al. 2012), or additively interacting with litter quality to affect litter decomposition (Correa-Araneda et al. 2017). Our results supported a disappearance of the effects of litter quality on litter decomposition at high water temperatures. These results imply that even though the presence of snails can increase litter decomposition in urban streams, most of the carbon stored in litter is released by microbes and transformed into CO_2. Decomposition of lower quality litter is expected to be more stimulated by microbes than is higher quality litter at high water temperature condition. By contrast, snail-mediated litter decomposition may be more sensitive to the change of water temperature for high rather than low quality litter. Therefore, the effect of warming on nutrient cycling in urban streams depends on litter quality.

5.5.5 Implications for urban stream management and conservation

Our results indicate that reducing the impacts of warming should be the most important way to alter organic matter decomposition in urban streams, rather than the other two factors (intraspecific litter quality difference and the presence of snails). Warming can also induce a change of DO concentration, terrestrial subsidy input (quality, quantity, and input time of litter), and macroinvertebrate and microbial communities, which are among the 26 key research questions in urban stream ecology (Wenger et al. 2009), and consequently affect nutrient cycling (e.g. carbon) in these waterbodies. The effects of warming on nutrient (e.g. carbon) cycling through litter decomposition in streams depend on how much of this carbon goes into invertebrates (invertebrates converted litter to particulate and dissolved forms of carbon) or microbes (microbes released the carbon stored in litter to gaseous form) (Boyero et al. 2011, Follstad Shah et al. 2017).

This implies that CO_2 production via litter decomposition in urban streams might increase with warming, as well as the generation of particulate or dissolved carbon. However, this projection would be improved if we were able to know how future climate change would affect the quantity and quality of litter, and macroinvertebrate communities in freshwaters. Considering that urban streams are expected to suffer more serious stress from warming than rural streams, it is urgent to take actions to alleviate their negative effects on freshwaters. In particular, given the predicted increase in urban land cover of 1.2 million km^2 by 2030, , which is three times the global urban land area in 2000 (Seto et al. 2012), more streams will clearly be affected by this land-use change. Conservation actions to mitigate the effects of climate warming on urban ecosystems include: (1) increasing urban forest cover by sequestering CO_2 (Bowler et al. 2010, Blum 2016) and reducing storm water runoff (McPherson et al. 1997); (2) enhancing hyporheic exchange and adopting different wastewater treatment strategies through accelerated heat exchange with other media such as atmosphere and subsurface groundwater (Kaushal et al. 2010); (3) decreasing the quantity of water withdrawals by reducing the warming effects induced by impoundments (Webb and Nobilis 1995) and (4) increasing the reuse of treated wastewater (Kinouchi 2007).

5.6 Conclusions

In summary, we found that (1) litter decomposition rates were stimulated by increasing water temperature (~ 8 ºC higher than ambient) through increased activities of microbes and invertebrates (snails); (2) the presence of grazing snails (scrapers) accelerated litter decomposition rate through their direct consumption of leaf material or indirectly by scraping microbes attached to leaf surfaces, and these effects were stronger at raised water temperature than at ambient water temperature; and (3) terrestrial herbivorous insects retarded microbe-mediated litter decomposition by inducing higher SLW of litter (i.e. poorer litter quality), and the effects of litter quality on both microbial and snail mediated litter decomposition diminished at higher water temperature. Thus, although the increasing terrestrial insect herbivory could lead to lower litter quality that can retard litter decomposition (Adams et al. 2003, Meineke et al. 2018), warming is expected to stimulate both microbe- and snail-mediated litter decomposition in urban streams.

5.7 Acknowledgments

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Chapter 6 Global trends of leaf litter carbon, nitrogen, and phosphorus in riparian plants

6.1 Abstract

Decomposition of riparian leaf litter in freshwaters plays an important role in regulating global nutrients (e.g. carbon) cycling, which is partially controlled by leaf litter quality traits. Global terrestrial leaf litter N, P, and N:P ratio showed clear patterns along the gradients of mean annual temperature (MAT), mean annual precipitation (MAP), and absolute latitude. However, these patterns may not be true for riparian leaf litter because of differences in soil characters between riparian forests and non-riparian forests. Here we present the first global-scale analysis of riparian leaf litter quality by collecting data on senesced riparian leaf litter C, N, P, and their stoichiometry from 918 observations, 90 plant families in 159 studies, and the associated climatic and geographic information. We found that most mean nutrient concentrations in riparian leaf litter differed from those in global terrestrial leaf litter, as indicated by higher N and P, and lower C, C:N, and C:P ratios than terrestrial leaf litter in general, and no difference for N:P ratio. When all data of our data were pooled, leaf litter N and N:P increased while P and C:N decreased with MAP; C, P, and C:N decreased while N:P increased with MAT; C and P correlated positively while N:P correlated negatively with absolute latitude; C, N, and P decreased while C:N and C:P increased with altitude. However, these patterns were changed when data were analyzed using different leaf habits (evergreen or deciduous) or within different climate zones (tropical or non-tropical area). In addition, leaf litter quality traits also varied with climate zone, leaf habit, N-fixing functional category, invasion status, and life form. These results suggested that riparian leaf litter showed higher quality than overall terrestrial leaf litter, although the general responses of leaf litter quality to environmental factors were the same. Variation in riparian leaf-litter quality can be partially explained by environmental factors and these relationships change between leaf habits and between climate zones.

Keywords: Nutrient cycling; Litter quality; Senesced leaves; Stoichiometry; Freshwaters; Temperature and precipitation; Latitude and altitude

6.2 Introduction

Ecosystems are not isolated from each other but closely linked by numerous reciprocal subsidies (Polis et al. 1997, Richardson and Sato 2015, Gounand et al. 2018). Terrestrial leaf litter is one of the most important subsidies to freshwaters, fueling the detritus food web, providing refuges for aquatic organisms (e.g. invertebrates), increasing substrate surface for microbes, and influencing nutrient (e.g. C and N) cycling (Wallace et al. 1997, Tank et al. 2010, Tiegs et al. 2019). Annual organic carbon production derived from terrestrial plants is *ca* 122 billion tonnes (Beer et al. 2010), only 10 % of which are directly consumed by herbivores. The rest of this carbon flows into the dead organic matter pool (Cebrian 1999), 70 % of which is leaf litter (Benfield 1997). Freshwaters make a disproportionate contribution to global carbon cycling via the decomposition of leaf litter even though they only cover about 3 % of the Earth's area (Raymond et al. 2013, Follstad Shah et al. 2017, Datry et al. 2018). Therefore, rate of leaf-litter decomposition in freshwaters can exert a great impact on global nutrient cycling (Anderson and Sedell 1979, Lecerf et al. 2011, Bernabé et al. 2018).

Leaf-litter quality has long been acknowledged as an important factor driving its decomposition in freshwaters (Hladyz et al. 2009, Boyero et al. 2016, Stoler et al. 2016). High-quality leaf litter is preferentially selected by detritivores and microbes (Marcarelli et al. 2011), resulting in faster decomposition than for lower quality leaf litter (Kominoski et al. 2011, Jackrel et al. 2016). However, the importance of leaf-litter quality on litter decomposition in freshwaters is context-dependent, with many other factors such as temperature, precipitation, and soil characters influencing decomposition (Aerts 1997, Esther et al. 2015, Ferreira et al. 2015). Nonetheless, leaf-litter quality still explains large variation of litter decomposition in streams and rivers (Ardón et al. 2006, Quested et al. 2007, Kuglerová et al. 2017). In addition, leaf-litter quality can influence the relative contribution of invertebrates and microbes to litter decomposition, with the contribution of invertebrates to litter decomposition increased with increasing leaf-litter quality, which also resulted in faster litter decomposition (Lecerf et al. 2005, Kominoski et al. 2011, Raposeiro et al. 2018). At the global scale, the distribution pattern of detritivores may be related to global leaf-litter quality pattern, because leaf litter quality is lower in tropical than in temperate areas which perhaps partially induced lower abundance and diversity of shredders than in temperate freshwaters (Wantzen et al. 2002, Boyero et al. 2011a). Invertebrates mainly transform leaf litter into fine organic particles while microbes transform leaf litter into the gaseous form of C (i.e. CO_2) (Boyero et al. 2011b). Therefore, high flux of CO_2 emissions from tropical areas (Raymond et al. 2013) might be associated with the low leaf-litter quality and decomposition mainly by microbes. Therefore, it is essential to know how leaf-litter quality varies along climatic gradients and among functional groups for the prediction of future leaf-litter decomposition and their impacts on global nutrient cycling.

Large-scale comparisons of senesced riparian leaf litter quality are scarce. To our knowledge, only one global experimental study related global trends of leaf litter N, P, and several other litter quality traits to mean annual temperature (MAT), mean annual precipitation (MAP), and absolute latitude (Boyero et al. 2017). That study found that senesced riparian leaf litter tended to have higher N:P in tropical areas; N increased with MAP; while P decreased with MAT. These findings were partially in accordance with findings for global terrestrial leaf litter (Yuan and Chen 2009a) and green leaves (Reich and Oleksyn 2004). However, the study conducted by Boyero *et al.* (2017) only included 151 species from 24 regions which is relatively small compared to other large scale leaf litter studies (Yuan and Chen 2009a, Kang et al. 2010, Ge et al. 2017). Also, 60.1 % of the leaf litter were collected from tropical areas (Boyero et al. 2017), which may have biased the results because tropical leaf litter tended to have higher N but lower P concentrations compared with non-tropical leaf litter (Yuan and Chen 2009a, Kang et al. 2010). Knowledge from green leaves indicated that leaf quality decreases toward the equator because of higher mean temperature and longer growing season (Reich and Oleksyn 2004), or probably because these plants are better defended against terrestrial herbivores (Coley and Barone 1996). However, nutrients contents of senesced leaf litter differed from those of green leaves due to differences in nutrient resorption efficiency across latitude, MAP, and MAT (Yuan and Chen 2009b, Reed et al. 2012, Vergutz et al. 2012). Therefore, global relationships of MAP, MAT, and absolute latitude with senesced leaf-litter quality (Yuan and Chen 2009a) differed from those with quality of green leaves (Reich and Oleksyn 2004). However, among large-scale terrestrial leaf-litter studies, the relationship between leaf-litter quality traits and climatic and geographical factors were not always consistent, probably due to differences in study areas and plant functional traits (Yuan and Chen 2009a, Kang et al. 2010, Ge et al. 2017). Apart from the impacts of climatic and geographical factors on leaf litter quality, biotic factors such leaf habits, life forms, and invasion status can also affect leaf litter quality (Ge et al. 2017, Kennedy and El-Sabaawi 2017). Some of these factors are associated with climatic or geographical changes, for example, evergreen plants are more prevalent in tropical areas than in temperate areas because of low soil quality (Aerts 1995, Ge et al. 2017). However, riparian leaf-litter quality might differ from that in non-riparian areas due to the variation in soil characters (e.g. soil moisture). For example, riparian leaves have higher concentration of N but lower concentration of P than upland forest leaves because of the variation in environmental factors especially for water condition (Saha et al. 2010) which can influence nutrient uptakes by plants. By contrast, Tibbets and Molles (2005) found a contrary pattern: with leaf litter from flood riparian forest having significantly lower N:P ratio but higher P concentration than leaf litter collected from non-flood riparian forests (Tibbets and Molles JR 2005). In addition, riparian habitats harbor different species pools than upland forests which result in 50 % higher regional richness across the globe (Sabo et al. 2005). Even though, large-scale studies of riparian senesced leaf-litter quality are scarce, some regional studies are available. A study conducted in tropical riparian forests found that the concentration of lignin and P decreased while that of polyphenolics increased with increasing altitude (Jinggut and Yule 2015). In another study that compared leaf-litter quality in 15 species between tropical and temperate riparian forests, the concentrations of condensed tannins (which negatively affected litter decomposition) were significantly higher for temperate species than for tropical species (Ardón et al. 2009).

Riparian forests are predicted to be influenced by future global changes at levels from individual to community, consequently affecting leaf-litter quality, which can propagate to aquatic ecosystems (Kominoski et al. 2013, Jonsson and Canhoto 2016). Global changes are expected to change future plant communities of riparian forests, with likely increases in drought-tolerant, plantation, and crop species, and a shift in the dominance between deciduous and coniferous species (Kominoski et al. 2013). If future climate is warmer with reduced precipitation, coupled with changes of soil characteristics associated with aridification, deciduous plants would be negatively affected, while favoring the growth of giant graminoids (Salinas et al. 2018). If precipitation remains unchanged in wetter areas, climate warming would result in expanded distribution of evergreen plants and adversely affect deciduous plants

(Salinas et al. 2018). More specifically, the projected longer duration of flooding events is likely to reduce plant species richness in nutrient-rich flooded areas and sites that used to have relatively stable hydrographs (e.g. rain-fed lowland streams), while the increased species richness is expected in desert and semi-arid climate regions (e.g. intermittent streams) (Garssen et al. 2015). In addition, direct and indirect effects of climate change are likely to induce the change of plant community structure of riparian forests in arid and semiarid areas, with less abundance of dominant, native, early-successional tree species, while benefitting herbaceous species, drought-tolerant, and late-successional woody species (including many exotic species) (Perry et al. 2012). At the individual level, future increase of atmospheric CO_2 is predicted to decrease leaf-litter quality by increasing concentrations of structural compounds, reducing N concentrations (Tuchman et al. 2002), and reducing P concentrations (Ferreira et al. 2010, Martins et al. 2017). However, these effects may be species-specific responses (Sardans et al. 2012, Dray et al. 2014), for example the elevated CO_2 only decreased leaf litter quality for forb species but not for grass species (Monroy et al. 2016). The replacement of native species by plantation species may affect aquatic fungal communities to affect litter decomposition (Ferreira et al. 2017). Forest change induced by eucalyptus plantation (the most common type of forest change) can affect litter decomposition probably through the effects on detritivores, and the impacts are greater in streams receiving high quality leaf litter and where detritivores are abundant (Ferreira et al. 2016). Therefore, it is urgent to know the global leaf litter pattern in order to better protect the health of freshwaters and make efficient strategies to reduce the adverse effects of global change on freshwaters.

Here we present the first comprehensive study investigating global patterns of riparian leaf litter C, N, P, and their stoichiometry, including 331 – 793 cases for each leaf litter traits spanning 111° of latitude and large climatic (MAT and MAP) and geographical (altitude) gradients. We aimed to test: (1) whether global patterns of riparian leaf litter quality are similar to those for terrestrial leaf litter; (2) how leaf litter quality varies along the gradients of climatic and geographical factors and among plant functional groups (e.g. leaf habit, N-fixing function, invasion status, life form); (3) whether and how the responses of leaf-litter quality to climatic and geographical changes would differ between evergreen and deciduous plants, and between tropical and non-tropical areas.

6.3 Materials and Methods

6.3.1 Database compilation

We built the database (Fig. 6.1) through searching online databases and engine (ISI Web of Knowledge) with the following search terms: “(leaf OR litter) AND (stoichiometry OR C:N OR C:P OR N:P OR quality) AND (stream OR river OR riparian)”. We also added papers to the initial list of potential data sources from the reference lists of relevant reviews or meta-analysis studies (Follstad Shah et al. 2017, Kennedy and El-Sabaawi 2017) if these papers were not found in the literature search. In addition, I included the Chinese references by using the following searching terms “leaf litter (树叶)”, “quality (质量)”, and “decomposition (降解)” on CNKI. Papers included in the analysis had to satisfy the following criteria: (1) leaf litter had be naturally senesced to exclude data that were collected from fresh leaves or in-stream conditioned leaves; (2) leaf litter used in the study had to be used in a leaf pack experiment associated with natural aquatic ecosystems (most of them were lotic waterbodies) or aquatic mesocosms, we assumed that the authors collected leaf-litter from riparian forests or the species used belonging to riparian plants; (3) leaf litter had to be collected from the natural environment (most of them were associated with low level of anthropogenic disturbances) to avoid the data that were collected from pot experiment; (4) the study should include at least one of the following initial litter quality: carbon, nitrogen, phosphorus, C:N, N:P and C:P ratios. Information extracted from each paper included names of leaf collection site, year of the leaf collection, latitude, longitude, altitude, litter genus, family, and species, phylogeny (angiosperm *vs* gymnosperm or broadleaf *vs* conifer), functional type (nitrogen-fixing plants or not), phenology or leaf habit (deciduous *vs* evergreen), life form (i.e. tree, shrub, forb, grass), invasion status (native *vs* exotic), and leaf-quality traits. For life form, as one or two categories (e.g. forb and grass) had fewer than three cases for some leaf quality traits and most data were collected from tree species, we then classified them as tree or non-tree species. Latitude, longitude, or altitude data were determined by using Google Earth (version 7.1.8.3036) if these data were unavailable in the original paper. If leaf litter nutrients concentrations were present as mg g^{-1} in the original papers, these data were transformed into percentage. Mean annual air temperature (MAT) and precipitation (MAP) data were derived from WolframAlpha database (https://www.wolframalpha.com/) by inputting coordinate information if these data were not provided in the original studies. Leaf quality data that were shown in figures, these were obtained by manually calculating from the figures. The following criteria distinguish our datasets from previous studies (Yuan and Chen 2009a, Follstad Shah et al. 2017): (1) we only focus on riparian leaf-litter; (2) we simultaneously analyzed the relationships between leaf-litter quality and MAT, MAP, latitude, altitude, and we grouped leaf-litter into more categories such as invasion status and N-fixing functional types.

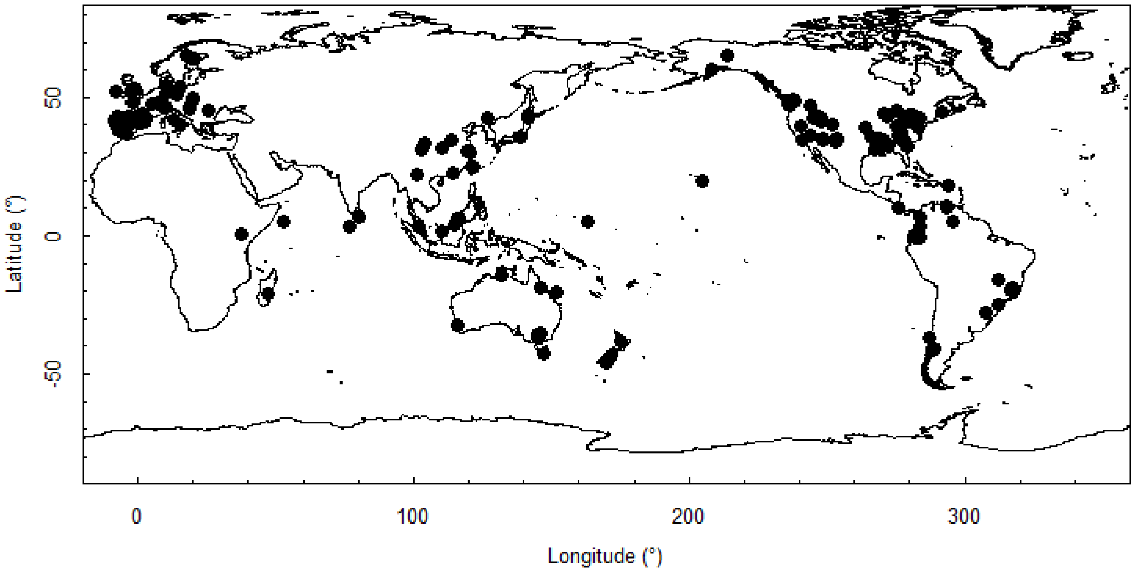

Figure 6.1 Geographic distribution of the sites contained in the database.

6.3.2 Data analysis

Leaf-litter nitrogen, phosphorus, carbon, and their stoichiometry were compared among phylogeny (broadleaf *vs* conifer), nitrogen-fixing function (N-fixing *vs* non-nitrogen fixing), phenology or leaf habit (deciduous *vs* evergreen), life form (tree *vs* not tree), and invasion status (exotic *vs* native) using t-tests. One-way ANOVA (Analysis of Variance) was conducted to test the differences of N, P, and N:P ratios between this study (including all the data from Boyero's study) and previous studies for global terrestrial leaf litter (Yuan and Chen 2009a) and riparian leaf litter (Boyero et al. 2017), and Tukey's HSD was used for the post-hoc multiple comparison. The differences in leaf-litter C, C:N, and C:P ratios between this study and the global terrestrial leaf litter study were compared using t-tests. Correlation tests were conducted between each pair of leaf litter quality traits and climatic (MAP and MAT) and geographical factors (absolute latitude and altitude). The correlation tests were conducted using four different data sets: (1) all data collected for each quality trait; (2) data were grouped by leaf habit (i.e. deciduous and evergreen); (3) grouped by climate zone (i.e. tropical and non-tropical areas); and (4) grouped by continental scale (Eurasia and North America). This kind of treatment on data was also used in previous studies of leaf litter quality at global (Yuan and Chen 2009a, Kang et al. 2010), continental (Liu et al. 2006), and country scales (Ge et al. 2017, Ge and Xie 2017). Each way of data treatment has its own bias and the combination of these treatments aimed to eliminate, obscure, and balance climatic and biotic variations of leaf litter quality (Reich and Oleksyn 2004). Stepwise multiple regression analysis was used to explore the associations of biotic and abiotic factors with each leaf litter trait to find out the best model to explain the variation in leaf quality traits. All data were checked for normality before conducting these analyses and were log-transformed to meet normality and homogeneity assumptions (Yuan and Chen 2009a). All statistical analyses were carried out using R 3.5.2 (R Core Team 2018).

6.4 Results

6.4.1 Comparison with previous studies Mean nitrogen concentration pooled for all data was 1.32 % (i.e. 13.2 mg g^{-1}, n=793) which was significantly higher than in the other study of riparian leaf litter (1.09 %) reported by Boyero *et al.* (2017) and global terrestrial leaf litter (1.00 %) reported by Yuan and Chen (2009a) (Table 6.1, Fig. 6.2). Leaf litter P concentration (0.1 %) was 38.9 % and 75.4 % higher than the concentrations reported by Yuan and Chen (2009a) and Boyero et al. (2007) respectively. Moreover, mean leaf litter C (45.02 %) was 3.7 % lower than global terrestrial leaf litter (Yuan and Chen 2009a). Mean leaf litter N:P ratio (20.56) was similar to global terrestrial leaf litter but was significantly lower than in the other riparian leaf litter study (Boyero et al. 2017). Ratios of C:N (46.84) and C:P (642.22) were 11.0 % and 45.1 % lower than that of the global terrestrial leaf litter respectively (Table 6.1).

Table 6.1 Comparisons of leaf litter concentrations (%) of C, N, P, and stoichiometric ratios (on a mass basis) in this study with previous studies. Data were shown as mean ± SE (*n*). Superscript lowercase letters denote significant differences after *t*-test (two studies) or one-way ANOVA (three studies) and *post hoc* Tukey (parameters with same letter are not significantly different between studies). All data were log-transformed to improve normality before doing the analysis except for leaf litter C.

Traits	*P*	*F*	This study	Boyero *et al.* (2017)	Yuan and Chen (2009a)
C	**<0.001**	751.202	45.02 ± 0.21^{b} (436)	-	46.74 ± 0.27^{a} (390)
N	**<0.001**	30.769	1.318 ± 0.027^{a} (793)	1.090 ± 0.053^{b} (793)	0.999 ± 0.013^{b} (1089)
P	**<0.001**	29.807	0.100 ± 0.004^{a} (599)	0.057 ± 0.003^{c} (168)	0. 072 ± 0.002^{b} (536)
C:N	**<0.001**	854.660	46.84 ± 1.29^{b} (556)	-	52.60 ± 1.27^{a} (321)
C:P	**<0.001**	269.089	642.22 ± 30.41^{b} (331)	-	1170.44 ± 70.07^{a} (129)
N:P	**<0.001**	12.000	20.56 ± 0.76^{b} (639)	26.28 ± 1.90^{a}(168)	19.45 ± 0.54^{b} (500)

This study and that of Boyero *et al.* (2017) collected data from riparian plants while Yuan and Chen's (2009a) study collected data from terrestrial plants, and this study included all data of Boyero et al.'s study.

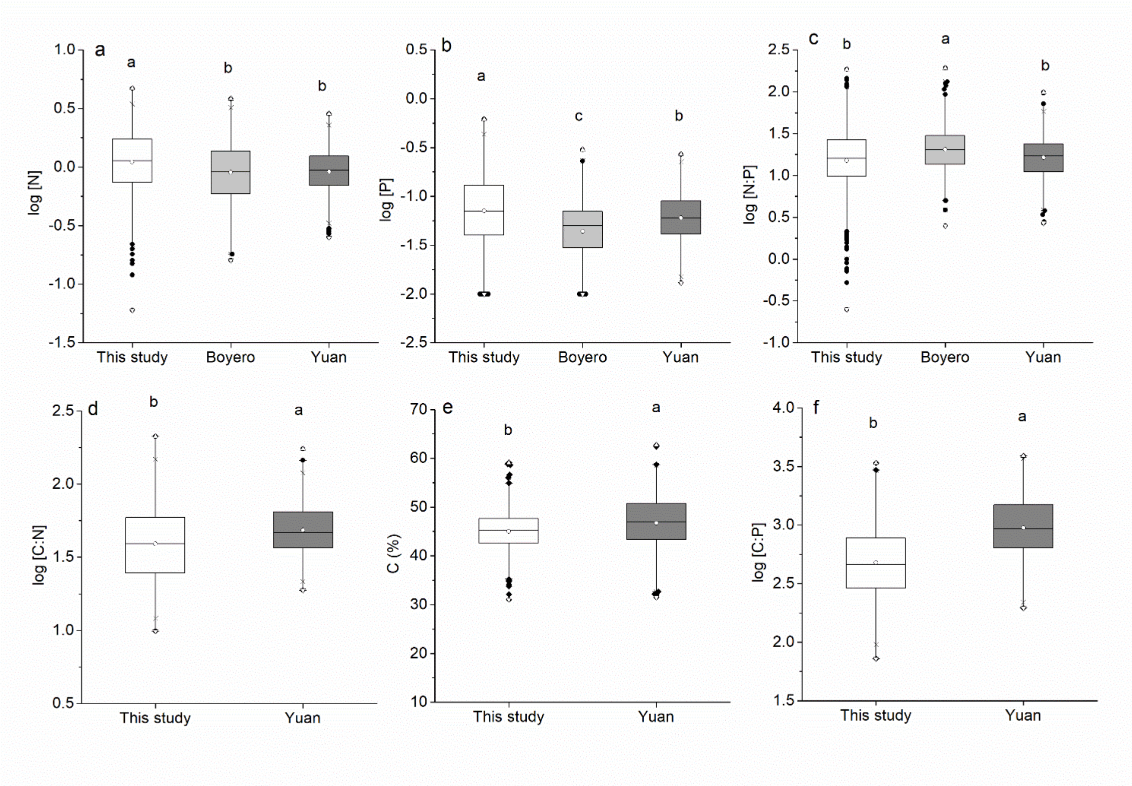

Figure 6.2 Box plot of leaf litter C, N, P, and their ratios for all collected data in this study and their comparisons with previous studies. The box plots summarize the distribution of all values for each study. Box plots indicated interquartile ranges (box part), medians (horizontal line in the box), 25th and 75th percentiles (lower and upper error bars), mean values (hollow circle in the box), and individuals in the lower 10th percentiles (solid circles). Different lowercase letters above each box indicated significant differences among (between) studies. For more information, please see Table 6.1.

6.4.2 Nitrogen Senesced-leaf litter N was 11.7 % higher in deciduous species than in evergreen species (*n*=793, *t*=2.137, *P*=0.033, Table 6.2, Fig. 6.3), and the concentration was more than twice for N-fixing species than for non-nitrogen fixing species (*n*=793, *t*=19.2, *P*<0.001, Table 6.2). When all data are pooled together, nitrogen concentration increased with MAP (*R*=0.115, *P*=0.001, Table 6.3, Fig. 6.4a) but decreased with altitude (*R*=-0.155, *P*<0.001, Table 6.3, Fig. 6.4j). These trends remained unchanged in non-tropical areas and for deciduous leaf litter but disappeared in tropical areas. For evergreen species, leaf litter N decreased with MAT and MAP while decreased with absolute latitude. The relationships between riparian litter N and environmental characters differed at continental scale. Riparian litter N decreased with MAP and MAT, while increased with absolute latitude in Eurasia (Table 6.3, Fig. S6.1). By contrast, riparian litter N increased with MAP and absolute latitude, while decreased with altitude in North America (Table 6.3, Fig. S6.1). Multiple regression models indicated that N-fixing function was the best single predictor for N concentration, and when combined with another seven factors, they explained 22.4 % of the variation in leaf litter N concentration (*R*=0.224, *P*<0.001, Table 6.4).

Table 6.2 Results of *t*-test of the effects of climatic zones, phylogeny, N-fixing function, leaf habits, invasion status, and life forms on senesced riparian leaf quality traits. *P* values < 0.05 were shown in bold. All data were log-transformed to improve normality before doing the analysis except for leaf litter C.

Traits	*n*	Climatic zone	Phylogeny	N-fixing	Leaf habit	Invasion status	Life form
C	436	**0.013**	0.060	**<0.001**	0.270	0.404	**<0.001**
N	793	0.196	0.921	**<0.001**	**0.033**	0.087	0.990
P	599	**<0.001**	**0.001**	0.091	**<0.001**	0.437	0.737
C:N	556	**<0.001**	0.062	**<0.001**	0.497	**0.002**	0.182
C:P	331	0.768	0.164	0.690	**0.004**	0.168	0.067
N:P	639	**<0.001**	**0.021**	**<0.001**	**<0.001**	0.933	0.656

Table 6.3 Results of linear models examining global-scale variation of riparian leaf litter quality traits (C, N, P, and stoichiometric ratios, on a mass basis) to climatic (MAP and MAT) and geographic (absolute latitude and altitude) predictors. Leaf litter data were analyzed in four ways: all data combined; grouped by leaf habit (deciduous and evergreen), climate zone (tropic and non-tropic), and continental

scale (Eurasia and North America). *P* values < 0.05 are shown in bold. All data were log-transformed to improve normality before doing the analysis except for leaf litter C.

Traits	Group	*n*	MAP		MAT		Absolute latitude		Altitude	
			R	*P*	*R*	*P*	*R*	*P*	*R*	*P*
C	all	436	-0.082	0.086	-0.115	**0.016**	0.175	**<0.001**	-0.102	**0.033**
	Tropic	67	-0.513	**<0.001**	0.058	0.639	0.150	0.226	0.147	0.235
	Non-tropic	369	0.342	**<0.001**	0.005	0.920	0.084	0.106	-0.179	**<0.001**
	Deciduous	330	0.109	**0.049**	-0.022	0.695	0.112	**0.043**	-0.222	**<0.001**
	Evergreen	106	-0.211	**0.030**	-0.187	0.055	0.236	**0.015**	0.063	0.521
	Eurasia	154	0.135	0.095	0.028	0.732	0.126	0.121	-0.190	**0.019**
	North America	199	0.367	**<0.001**	-0.062	0.385	0.071	0.316	-0.284	**<0.001**
N	all	793	0.115	**0.001**	0.061	0.085	0.004	0.914	-0.155	**<0.001**
	Tropic	226	0.124	0.062	0.096	0.151	-0.021	0.751	-0.051	0.441
	Non-tropic	567	0.126	**0.003**	0.022	0.598	0.171	**<0.001**	-0.210	**<0.001**
	Deciduous	514	0.202	**<0.001**	0.070	0.114	0.029	0.511	-0.250	**<0.001**
	Evergreen	279	0.191	**0.001**	0.216	**<0.001**	-0.164	**0.006**	-0.037	0.538
	Eurasia	331	-0.268	**<0.001**	-0.217	**<0.001**	0.299	**<0.001**	-0.023	0.681
	North America	248	0.212	**0.001**	-0.089	0.162	0.144	**0.023**	-0.353	**<0.001**
P	all	599	-0.088	**0.030**	-0.198	**<0.001**	0.193	**<0.001**	-0.133	**0.001**
	Tropic	190	0.290	**<0.001**	0.190	**0.009**	-0.194	**0.007**	-0.223	**0.002**
	Non-tropic	409	-0.114	**0.021**	-0.124	**0.012**	0.080	0.105	-0.046	0.351
	Deciduous	366	-0.098	0.061	-0.174	**<0.001**	0.188	**<0.001**	-0.178	**<0.001**
	Evergreen	233	0.157	**0.016**	0.021	0.749	-0.069	0.291	-0.070	0.290
	Eurasia	257	-0.141	**0.023**	-0.224	**<0.001**	0.174	**0.005**	-0.031	0.619
	North America	159	-0.139	0.081	-0.059	0.457	0.037	0.647	-0.289	**<0.001**
C:N	all	556	-0.225	**<0.001**	-0.156	**<0.001**	0.075	0.078	0.270	**<0.001**
	Tropic	75	-0.285	**0.013**	-0.210	0.070	0.087	0.460	0.309	**0.007**
	Non-tropic	481	-0.128	**0.005**	-0.005	0.918	-0.181	**<0.001**	0.268	**<0.001**
	Deciduous	417	-0.228	**<0.001**	-0.092	0.061	-0.059	0.229	0.318	**<0.001**

	Evergreen	139	-0.393	**<0.001**	-0.397	**<0.001**	0.379	**<0.001**	0.182	**0.032**
	Eurasia	183	0.089	0.233	-0.025	0.735	-0.112	0.132	0.141	0.056
	North America	253	-0.152	**0.016**	0.110	0.080	-0.251	**<0.001**	0.386	**<0.001**
C:P	all	331	0.028	0.614	0.104	0.059	-0.059	0.283	0.108	**0.049**
	Tropic	41	-0.173	0.279	-0.463	**0.002**	0.386	**0.013**	0.071	0.658
	Non-tropic	290	0.093	0.115	0.202	**<0.001**	-0.149	**0.011**	0.118	**0.046**
	Deciduous	253	0.025	0.697	0.085	0.176	-0.064	0.309	0.191	**0.002**
	Evergreen	78	-0.195	0.087	-0.059	0.607	0.214	0.059	-0.068	0.557
	Eurasia	123	0.192	**0.033**	0.211	**0.019**	-0.133	0.143	0.016	0.860
	North America	141	0.074	0.382	0.190	**0.024**	-0.196	**0.020**	0.389	**<0.001**
N:P	all	639	0.156	**<0.001**	0.226	**<0.001**	-0.170	**<0.001**	0.019	0.633
	Tropic	197	-0.169	**0.017**	-0.107	0.133	0.166	**0.020**	0.120	0.093
	Non-tropic	442	0.215	**<0.001**	0.174	**<0.001**	0.013	0.785	-0.117	**0.014**
	Deciduous	395	0.241	**<0.001**	0.221	**<0.001**	-0.160	**0.001**	-0.004	0.941
	Evergreen	244	-0.030	0.641	0.108	0.092	-0.020	0.759	0.018	0.783
	Eurasia	272	-0.074	0.226	0.042	0.487	0.049	0.419	0.036	0.550
	North America	173	0.360	**<0.001**	0.112	0.143	-0.040	0.600	-0.096	0.209

Table 6.4 Results of multiple regression examining global-scale variation of riparian leaf litter quality traits, depending on selected important predictors. These predictors including climatic (MAP and MAT), geographic (absolute latitude and altitude), biotic (phylogeny, N-fixing function, leaf habits, invasion status, life forms), and abiotic (climate zone) predictors. *P* values < 0.05 are shown in bold. All data were log-transformed to improve normality before doing the analysis except for leaf litter C.

Traits	Model	Factor	Estimate	Std. Error	*t*	*P*
C	R^2=0.140	Intercept	45.60	0.89	51.438	<0.001
	Adjusted R^2=0.130	**Life form**	-3.22	0.60	-5.329	**<0.001**
	P<0.001	**N-fixing**	-1.91	0.61	-3.116	**0.002**
	$F_{5,430}$=13.98	**Absolute latitude**	0.05	0.02	2.951	**0.003**
	Residual SE: 4.117	**Altitude**	-0.001	<0.001	-2.527	**0.011**

		Phylogeny	2.08	0.99	2.096	**0.037**
N	R^2=0.224	Intercept	0.430	0.048	8.884	<0.001
	Adjusted R^2=0.216	**N-fixing**	-0.344	0.027	-12.558	**<0.001**
	P<0.001	**Altitude**	-0.00005	0.00001	-3.130	**0.002**
	$F_{8,784}$=28.32	**MAP**	0.00003	0.00001	2.115	**0.035**
	Residual SE: 0.241	**Leaf habit**	-0.111	0.025	-4.405	**<0.001**
		Invasion status	0.060	0.029	2.050	**0.041**
		Climate zone	-0.091	0.031	-2.932	**0.003**
		Phylogeny	0.150	0.058	2.601	**0.009**
		Life form	0.043	0.027	1.600	0.110
P	R^2=0.118	Intercept	-0.517	0.168	-3.087	0.002
	Adjusted R^2=0.109	**Climate zone**	0.147	0.075	1.973	**0.049**
	P<0.001	**Altitude**	-0.0001	<0.001	-5.246	**<0.001**
	$F_{6,592}$=13.14	**Phylogeny**	0.368	0.097	3.790	**<0.001**
	Residual SE: 0.345	**Leaf habit**	-0.166	0.040	-4.111	**<0.001**
		Absolute latitude	-0.010	0.003	-3.653	**<0.001**
		MAT	-0.017	0.005	-3.049	**0.002**
C:N	R^2=0.294	Intercept	1.183	0.059	20.212	**<0.001**
	Adjusted R^2=0.284	**N-fixing**	0.310	0.030	10.265	**<0.001**
	P<0.001	**Altitude**	0.00007	0.00001	4.936	**<0.001**
	$F_{8,547}$=28.47	**Climate zone**	0.138	0.041	3.393	**<0.001**
	Residual SE: 0.219	**Leaf habit**	0.123	0.028	4.389	**<0.001**
		Life form	-0.080	0.029	-2.725	**0.007**
		Invasion status	-0.068	0.027	-2.514	**0.012**
		MAP	-0.00003	0.00001	-2.305	**0.022**
		Phylogeny	-0.094	0.051	-1.855	0.064
C:P	R^2=0.179	Intercept	0.801	0.308	2.604	0.010

	Adjusted R^2=0.158	**Leaf habit**	0.221	0.051	4.329	**<0.001**
	P<0.001	**Life form**	-0.165	0.050	-3.309	**0.001**
	$F_{8,322}$=8.766	**Phylogeny**	-0.284	0.098	-2.891	**0.004**
	Residual SE: 0.305	**Altitude**	0.0002	0.00004	6.023	**<0.001**
		Climate zone	0.351	0.107	3.272	**0.001**
		MAT	0.058	0.009	5.546	**<0.001**
		Absolute latitude	0.019	0.005	4.135	**<0.001**
		MAP	0.00005	0.00003	1.950	0.052
N:P	R^2=0.152	Intercept	0.890	0.167	5.321	<0.001
	Adjusted R^2=0.143	**N-fixing**	-0.319	0.044	-7.220	**<0.001**
	P<0.001	**MAT**	0.021	0.005	3.909	**<0.001**
	$F_{7,631}$=16.17	**Climate zone**	-0.172	0.072	-2.383	**0.017**
	Residual SE: 0.341	**Absolute latitude**	0.001	0.003	3.377	**<0.001**
		Altitude	0.00008	0.00003	2.993	**0.003**
		Leaf habit	0.077	0.038	2.013	**0.044**
		Phylogeny	-0.145	0.095	-1.522	0.129

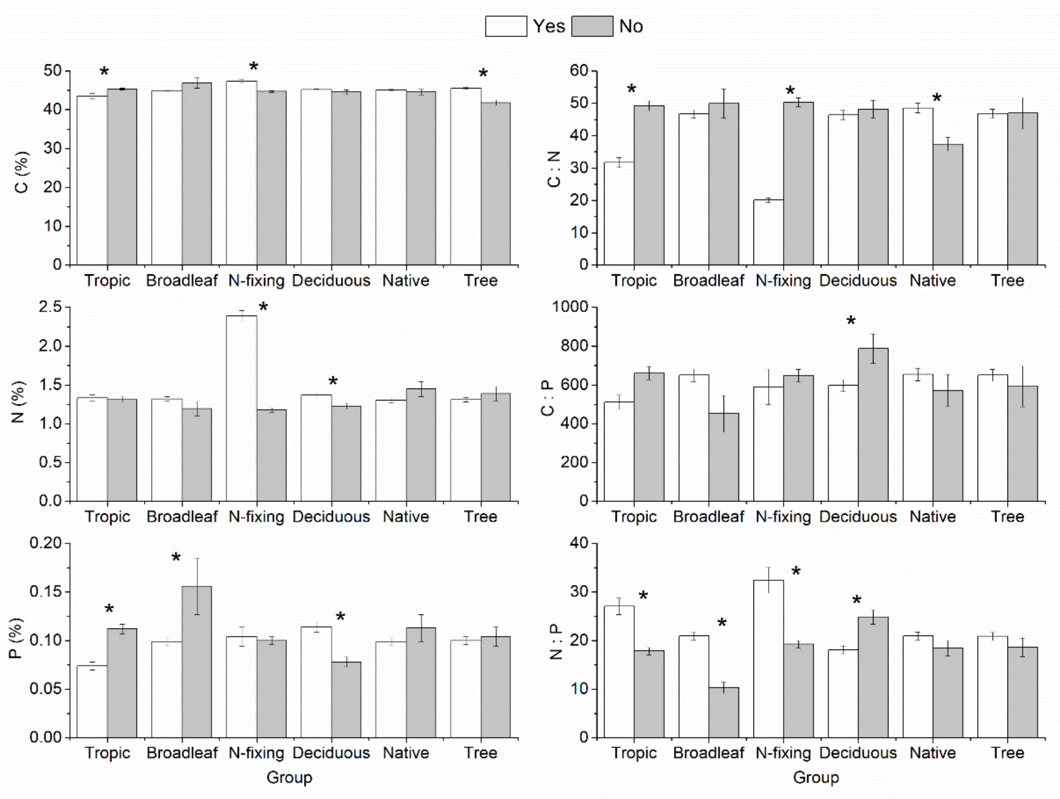

Figure 6.3 Mean values of riparian leaf litter C, N, P, and stoichiometric ratios by climate zones, phylogeny, N-fixing function, leaf habits, invasion status, and life-forms. Asterisks above bars indicated significant differences within categories. For more information, please see Table 6.2.

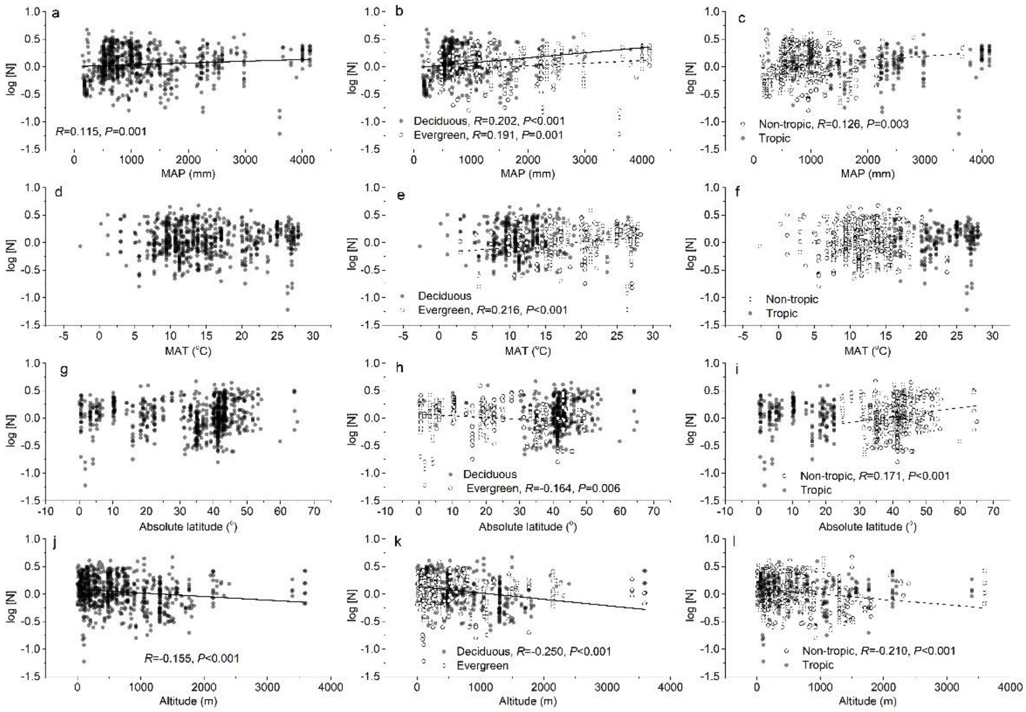

Figure 6.4 Senesced riparian leaf litter N in relation to mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), absolute latitude (°), and altitude (m), and their relationships by leaf habits and climate zones. Solid lines and solid circles represent deciduous plants and tropical area;

hollow circles and dashed lines represent evergreen plants and non-tropical area. Regression lines were plotted for relationships with $P<0.05$. The coefficients of determination (R) and P are shown in each panel if $P<0.05$.

6.4.3 Phosphorus Riparian leaf litter P was significantly higher in non-tropical than in tropical areas ($n=599$, $t=-5.577$, $P<0.001$, Table 6.2, Fig. 6.3), and was 57.6 % higher for conifers than for broadleaf plants ($n=599$, $t=-3.884$, $P=0.001$, Table 6.2, Fig. 6.3). Deciduous leaves had significantly higher concentration of P than evergreen leaf litter ($n=599$, $t=5.574$, $P<0.001$, Table 6.2, Fig. 6.3). When all data were pooled, leaf litter P decreased with increasing MAP, MAT, and altitude, while it positively correlated with absolute latitude (Table 6.3, Fig. 6.5). However, these patterns were changed within climate zones and leaf habits. In tropical areas, leaf litter P increased with MAP and MAT but decreased with absolute latitude and altitude. On the contrary, leaf litter P negatively correlated with MAP and MAT, which follows the overall trend. For deciduous leaf litter, P concentration was negatively associated with MAT and altitude while increased with absolute latitude. By contrast, leaf litter only increased with MAP for evergreen plants (Table 6.3, Fig. 6.5b). The relationships between riparian litter P with environmental characters in Eurasia were the same as when data were pooled together except that no significant relationship was shown for litter P and altitude (Table 6.3, Fig. S6.2). However, riparian litter P only decreased with altitude in North America ($R=-0.289$, $P<0.001$, Table 6.3, Fig. S6.2). Multiple regression models demonstrated that altitude explained most of the variation in leaf litter P, and the best model including six factors explained 11.8 % of the variation of P ($R^2=0.118$, $P<0.001$, Table 6.4).

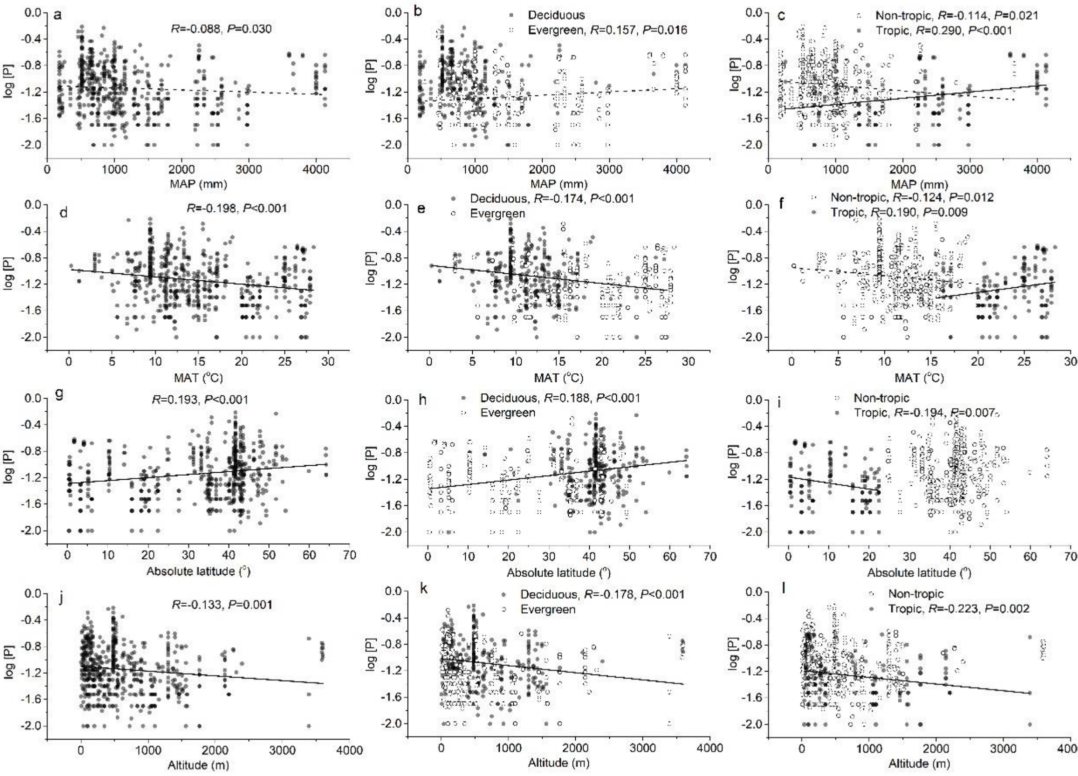

Figure 6.5 Senesced riparian leaf litter P in relation to mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), absolute latitude (°), and altitude (m), and their relationships by leaf habits and climate zones. Solid lines and solid circles represent deciduous plants and tropical area; hollow circles and dashed lines represent evergreen plants and non-tropical area. Regression lines were plotted for relationships with $P<0.05$. The coefficients of determination (R) and P are shown in each panel if $P<0.05$.

6.4.4 Carbon Riparian leaf-litter C concentration was significantly higher in tropical than in non-tropical areas (Table 6.2, Fig. 6.3). N-fixing plants had 5.8 % higher leaf litter C than non-nitrogen fixing plants (n=436, t=5.246, $P<0.001$, Table 6.2). Leaf litter from tree species had 8.9 % higher concentration of carbon than did non-tree species (Table 6.2). When all data were pooled, leaf litter C increased with absolute latitude (R=0.175, $P<0.001$, Table 6.3, Fig. 6.6) while decreased with MAT and altitude (Table 6.3, Fig. 6.6). These trends differed between climate zones and leaf habits. Leaf litter C decreased with MAP in tropical areas while it increased and decreased with MAP in non-tropical areas. For deciduous leaf litter, C concentrations positively correlated with MAP and absolute latitude while decreased with altitude. For evergreen species, leaf litter C decreased with MAP while increased with absolute latitude (Table 6.3, Fig. 6.6b). Riparian litter C decreased with altitude in both Eurasia and North America, while it only increased with MAP in North America (R=0.367, $P<0.001$, Table 6.3, Fig. S6.3). According to the result of multiple regression model, life form (i.e. whether plants are trees or not) explained the most in the variation of leaf litter C, and the best-fit model explained 14.0 % of the variation in C (R^2=0.140, P<0.001, Table 6.4).

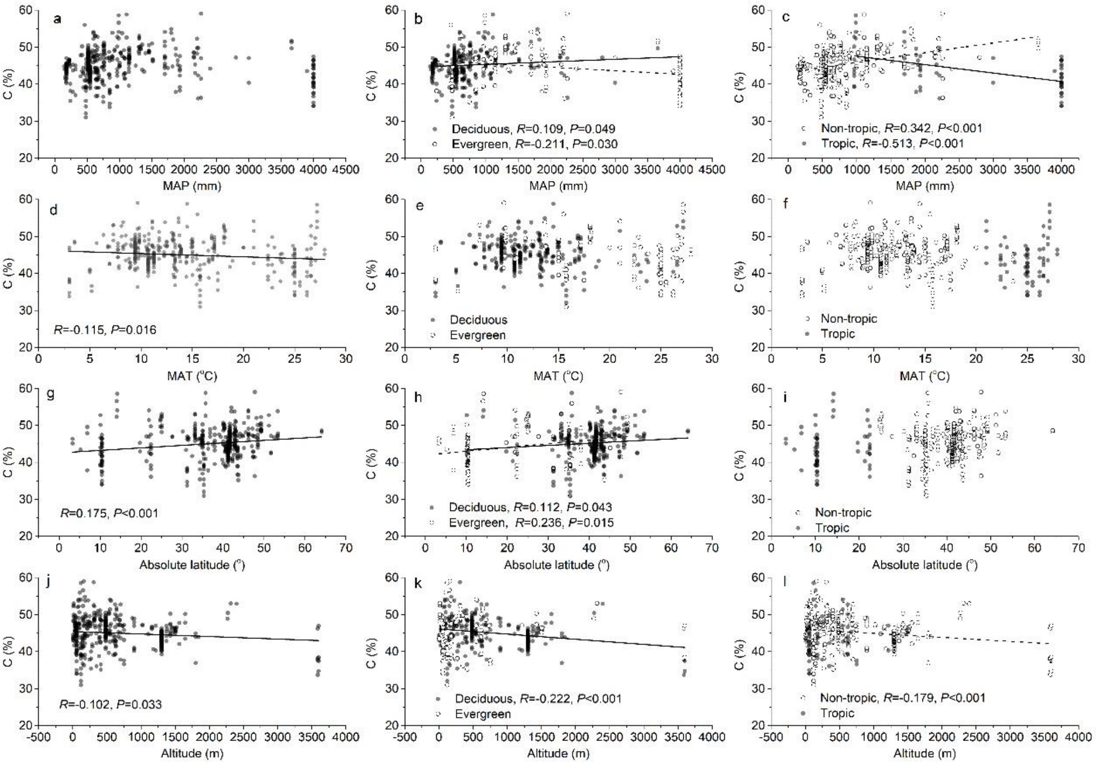

Figure 6.6 Senesced riparian leaf litter C in relation to mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), absolute latitude (°), and altitude (m), and their relationships by leaf habits and climate zones. Solid lines and solid circles represent deciduous plants and tropical area; hollow circles and dashed lines represent evergreen plants and non-tropical area. Regression lines were plotted for relationships with P<0.05. The coefficients of determination (R) and P are shown in each panel if P<0.05.

6.4.5 N:P ratio Riparian leaf litter N:P ratios were twice higher for broadleaf plants (20.93) than for conifer plants (10.27) (n=639, t=2.326, P=0.020, Table 6.2, Fig. 6.3). Leaf litter in tropical areas had 51.7 % higher N:P ratios than leaf litter in non-tropical areas (n=639, t=5.620, P<0.001, Table 6.2). N-fixing plants (32.42) showed 68.8 % higher N:P ratios than non-nitrogen fixing plants. Evergreen species (24.86) had 37.4 % higher N:P ratios than deciduous leaf litter. When all data pooled together, ratios of N:P were positively correlated with MAP and MAT while decreased with absolute latitude (Fig. 6.7). Patterns were changed if the data were split into different climate zones and leaf habits (Table 6.3). In tropical areas, N:P ratios showed opposite trends to the overall pattern, with negative correlation with MAP while positive correlation with absolute altitude. In non-tropical areas, the trends for MAP and MAT were similar with the overall patterns, and N:P ratios decreased with altitude. The patterns of N:P ratios for deciduous plants were the same as overall trends. However, none of MAP, MAT, absolute altitude, nor latitude significantly affected N:P ratios of leaf litter for evergreen plants. None of the environmental characters significantly correlated with riparian litter N:P in Eurasia (Table 6.3, Fig. S6.4). Whereas, riparian litter N:P positively correlated with MAP in North America (R=0.360, P<0.001, Table 6.3, Fig. S6.4). As indicated by the multiple regression model, plant function (i.e. nitrogen-fixing or not) contributed to the most variation in leaf litter N:P ratios and the best fitted model explained 15.2 % of the total variation in N:P ratios (R^2=0.152, P<0.001, Table 6.4).

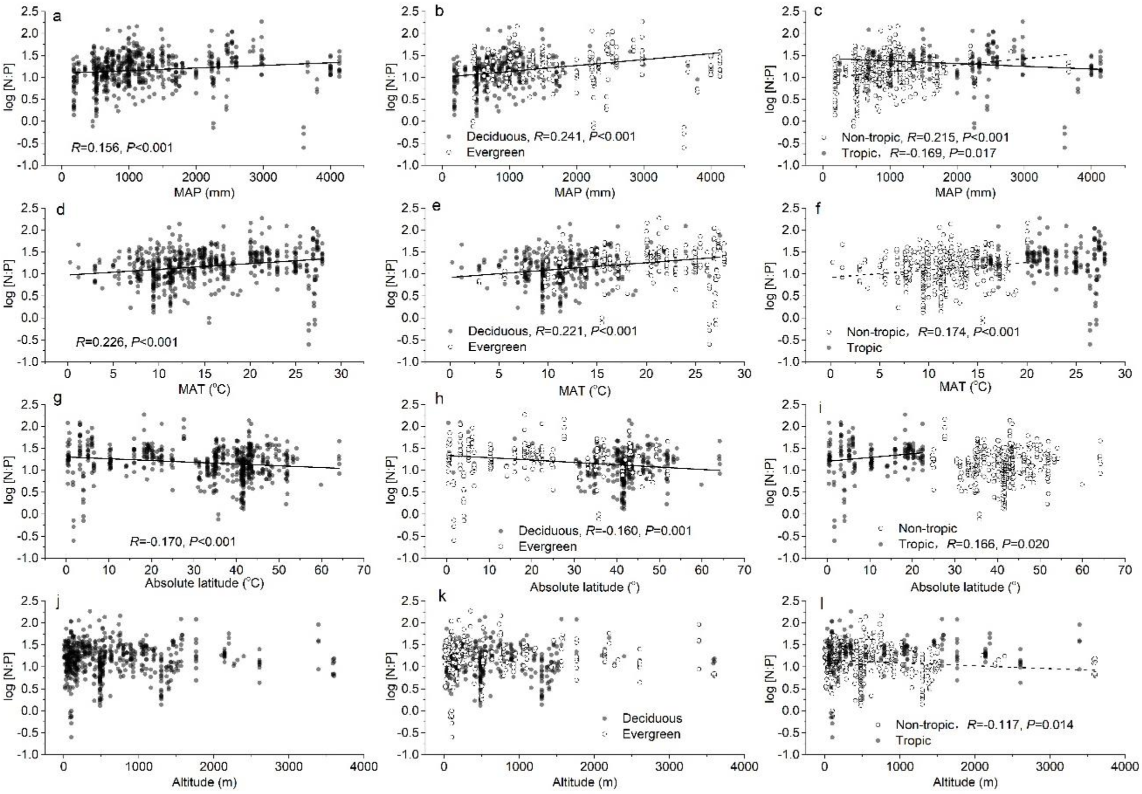

Figure 6.7 Senesced riparian leaf litter N:P in relation to mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), absolute latitude (°), and altitude (m), and their relationships by leaf habits and climate zones. Solid lines and solid circles represent deciduous plants and tropical area; hollow circles and dashed lines represent evergreen plants and non-tropical area. Regression lines were plotted for relationships with P<0.05. The coefficients of determination (R) and P are shown in each panel if P<0.05.

6.4.6 C:N ratio Leaf litter C:N ratios differed between climate zones, with tropical plants (31.67) were 35.6 % lower than non-tropical plants (n=556, t=-4.448, P<0.001, Table 6.2, Fig. 6.3). Ratios of C:N for non-nitrogen fixing plants (50.26) were 2.5 times of that for N-fixing plants (n=556, t=-19.061, P<0.001, Table 6.2). Exotic plants seemed to have higher leaf litter quality regarding to C:N ratios (i.e. lower C:N) than native plants (*n*=556, *t*=3.086, *P*=0.002, Table 6.2). When pooled all data, C:N ratios decreased with MAP and MAT while increased with altitude (Fig. 6.8). The relationship between C:N ratios and MAP and altitude were the same as overall trends regardless of climate zones and leaf habits. In addition, leaf litter C:N ratios negatively correlated with absolute latitude in non-tropical areas, and showed negative correlation with MAT while positive correlation with absolute latitude and altitude for evergreen species (Table 6.3). Riparian leaf litter C:N negatively correlated with MAP and absolute latitude, while positively correlated with altitude in North America (Table 6.3, Fig. S6.5). However, none of these trends were shown in Eurasia (Table 6.3, Fig. S6.5). N-fixing function contributed to the greatest variation in C:N ratios in the multiple regression analysis result, and the best fitted model explained 29.4 % of the variation in C:N ratios (R^2=0.294, *P*<0.001, Table 6.4).

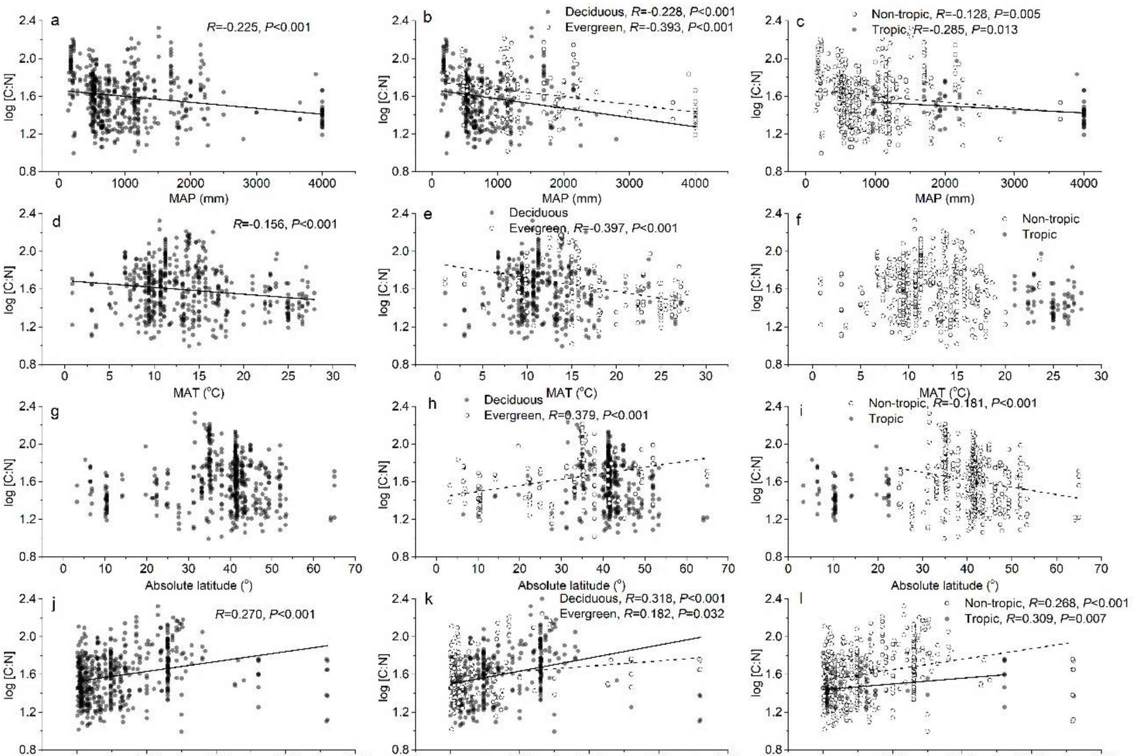

Figure 6.8 Senesced riparian leaf litter C:N in relation to mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), absolute latitude (°), and altitude (m), and their relationships by leaf habits and climate zones. Solid lines and solid circles represent deciduous plants and tropical area; hollow circles and dashed lines represent evergreen plants and non-tropical area. Regression lines were plotted for relationships with *P*<0.05. The coefficients of determination (*R*) and *P* are shown in each panel if *P*<0.05.

6.4.7 C:P ratio Leaf litter C:P ratios for evergreen species were 31.8 % higher than deciduous species (*n*=331, *t*=-2.884, *P*=0.004, Table 6.2, Fig. 6.3). Leaf litter C:P ratios were relative stable compared with N:P and C:N ratios, it only positively correlated with altitude when all data were combined (Table 6.3, Fig. 6.9). These patterns were the same and stronger for deciduous plants than for all plants pooled, while no significant correlations were found between C:P ratios and climatic and geographical factors for evergreen species. Leaf litter C:P ratios decreased while increased with MAT and absolute latitude respectively in tropical areas. However, the contrary patterns were found in non-tropical areas, and C:P ratios increased with altitude in non-tropical areas (Table 6.3, Fig. 6.9l). Riparian litter C:P increased with MAP and MAT in Eurasia (Table 6.3, Fig. S6.6). By contrast, riparian litter C:P increased with MAT and altitude, while decreased with absolute latitude in North America (Table 6.3, Fig. S6.6). Altitude and MAT explained most of the variation in leaf litter C:P ratios in the multiple regression model and the best fitted model explained 17.9 % of the variation (R^2=0.179, *P*<0.001, Table 6.4).

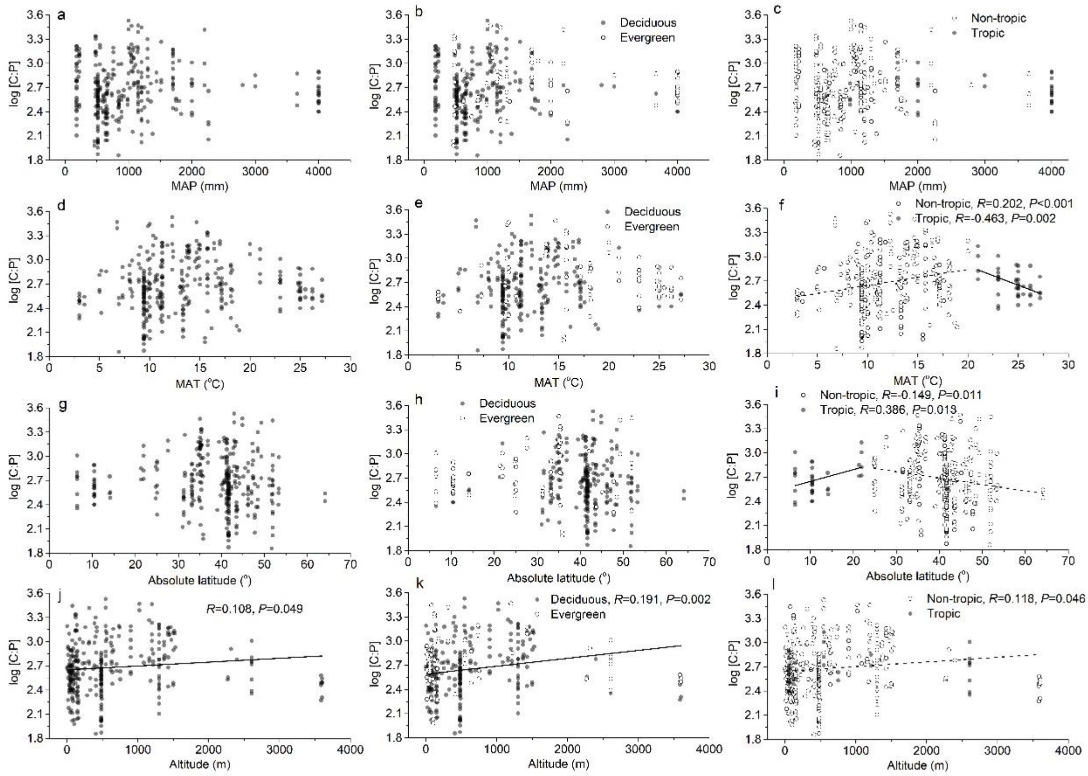

Figure 6.9 Senesced riparian leaf litter C:P in relation to mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), absolute latitude (°), and altitude (m), and their relationships by leaf habits and climate zones. Solid lines and solid circles represent deciduous plants and tropical area; hollow circles and dashed lines represent evergreen plants and non-tropical area. Regression lines were plotted for relationships with *P*<0.05. The coefficients of determination (*R*) and *P* are shown in each panel if *P*<0.05.

6.5 Discussion

6.5.1 Nitrogen

Our study demonstrated that riparian leaf-litter quality varied significantly across major climatic gradients and between plant functional groups. Mean leaf litter N concentrations in our study were higher than in a recently reported global experimental study on riparian leaf litter (Boyero et al. 2017) and in global terrestrial leaf litter in general (Yuan and Chen 2009a). The reason probably is that the proportion of conifers in our study (2.6 %) is lower than in Yuan and Chen's study (20.9 %), and conifer litter has lower N concentrations than broadleaf litter (Liu et al. 2006). In addition, grater topsoil moisture in riparian compared with other forests may have also contributed to the variation between our study and Yuan and Chen's study (Uria-Diez and Ibáñez 2014), as greater moisture results in high N-use efficiency by plants (Yuan and Li 2007). The differences of leaf-litter N between our study and that of Boyero et al. (2017) study are not likely to be caused by climatic factors because 60.1 % of the leaf litter were collected from tropical areas in Boyero et al.'s study (c.f. 35.2 % in our study), which should result in higher leaf-litter N, as tropical plants tended to have higher concentration of N than non-tropical plants (Yuan and Chen 2009a, Kang et al. 2010). Boyero et al. (2017) explained that less humid conditions in some sites and some species (e.g. *Nothofagus spp.* and *Eucalyptus spp.*) that are naturally low in N induced the low leaf litter N.

Overall leaf-litter N concentration increased with MAP, and did not show significant trends with MAT, as found previously on riparian leaf litter (Boyero et al. 2017). This lack of trend with MAT differed from the findings for senesced leaf-litter N in general (Yuan and Chen 2009a), for global woody plants (Kang et al. 2010), or for trends at a continental scale (Liu et al. 2006): these studies all reported increased leaf-litter N concentration with MAT. One possible explanation why leaf-litter N did not respond to MAT was because the effects of MAT on leaf litter N were larger in arid areas (low MAP) than humid areas (high MAP) which caused the insignificant effects of MAT in these humid areas (Zhang and Wang 2015). However, the relationship between leaf litter N and MAT differed between leaf habits, with a positive relationship found for evergreen species while no significant relationship was found for deciduous species. This pattern was also found for broadleaf litter in China (Ge et al. 2017), whereas, another two large scale studies found that both evergreen and deciduous leaf litter N increased with MAT (Liu et al. 2006, Kang et al. 2010). By contrast, green-leaf N decreased with MAT (Reich and Oleksyn 2004). The different relationships between litter N and MAT between evergreen and deciduous plants might be related to lower total N resorption and weaker response to MAT of N-resorption efficiency in evergreen than in deciduous plants (Yuan and Chen 2009b, Vergutz et al. 2012). Consequently, deciduous plants have smaller variation of N along the gradient of MAT. In addition, overall trend of leaf litter N to MAT may also be influenced by the large number of deciduous leaf litter examples (64.8 %) which showed no significant response to MAT. At continental scale, we found a negative relationship between MAT and riparian leaf litter N in Eurasia, which is contrary to the result found in one previous study for terrestrial leaf litter N in Eurasian forests (Liu et al. 2006).

High MAP can increase soil moisture which in turn positively affected soil N in water-limited ecosystems (Austin et al. 2004). Therefore, leaf-litter N may increase with MAP if soil N availability was an important influence on leaf N content (Yuan and Chen 2009a). The response of leaf litter N to MAP did not differ between evergreen and deciduous species, and both increased with MAP. These trends are in accordance with the finding for global terrestrial leaf litter (Yuan and Chen 2009a) and in Eurasian forests (Liu et al. 2006), and partly agrees with the study on leaf litter of global woody plants, which found positive relationship for evergreen plants while no relationship for deciduous plants (Kang et al. 2010). However, leaf litter N of Chinese broad-leaved trees decreased with MAP for deciduous species while no relationship were found for evergreen plants (Ge et al. 2017). This could also explain that we found negative relationship between MAP and riparian leaf litter N in Eurasia (74.9 % of the species were deciduous), even though overall terrestrial leaf litter N increased with MAP in Eurasian forests (Liu et al. 2006). It seems that the larger area sampled and the more diverse leaf litter included in this study, the more general a conclusion we can provide, i.e. leaf litter N increased with MAP for both evergreen and deciduous plants. In addition, a possible interaction between MAP and MAT in driving leaf litter N is suggested from the observed positive response of leaf litter N to MAP in non-tropical areas but no relationship in tropical areas.

Leaf-litter N declined from lowland areas to highland areas, a trend which was also found in the subtropics (He et al. 2016). Soil carbon, nitrogen, moisture, and other environmental factors such as the temperature and precipitation all changed with increasing altitude (Du et al. 2014a, Tashi et al. 2016), especially as temperature decrease with altitude and low temperature might inhibit uptake of N by plants (He et al. 2016). In addition, the negative relationship between altitude and leaf litter N disappeared in tropical areas and for evergreen species suggesting that geographical conditions and leaf habits adjusted the response of leaf litter N to altitude.

We did not find a significant linear relationship between leaf litter N and absolute latitude, which agrees with Boyero et al. (2017). However, the positive relationship between absolute latitude and riparian leaf litter N was found in both Eurasia and North America, which was consistent with the finding in Chinese broad-leaved tree species (Ge et al. 2017). Increasing absolute latitude is generally associated with decreasing MAT, and the change of plant communities (e.g. evergreen species are more common in tropical areas), which may induce a gradient of leaf litter quality from the equator to the poles (Kang et al. 2010, Ge et al. 2017). Therefore, leaf litter N should be higher when approaching the equator, because leaf litter N increased with MAT and MAP (Liu et al. 2006, Yuan and Chen 2009a). However, evergreen plants, which have lower leaf litter N than deciduous plants (Yuan and Chen 2009a, Ge et al. 2017), are more common in tropical areas, which should result in lower leaf litter N in tropical than in non-tropical areas. This contrast provides just one example of how opposing influences may lead to no overall significant response of leaf litter N to absolute latitude. Such combinations of either weak or opposing latitudinal trends was further supported by the variations of N response to absolute latitude between geographical areas and leaf habits, with leaf litter N positively responding to absolute latitude in non-tropical areas but decreasing across all (absolute) latitudes for evergreen species, and showing no trend in tropical areas or across all latitudes for deciduous plants. The positive relationship between evergreen but not deciduous leaf-litter N and absolute latitude were also found for global woody plants (Kang et al. 2010).

We also found significant higher leaf litter N for deciduous species than evergreen species and for N-fixing plants than non-nitrogen fixing plants, which agree with previous studies (Yuan and Chen 2009a, Kurokawa et al. 2010). Native leaf litter had marginally significant lower N than exotic species. However, invasive plants have traits such as rapid growth rates and elevated leaf nutrient concentrations to help them rapidly colonize new habitats (Allison and Vitousek 2004), which are likely to increase

N concentration. The differences of leaf litter N between exotic and native species might be species-specific, with exotic leaf litter showing higher (Kurokawa et al. 2010) or the same (Kuglerová et al. 2017) N concentrations compared with native species.

6.5.2 Phosphorus

Mean leaf-litter P concentration in our study was significantly higher than reported by Boyero *et al.* (2017) for riparian leaf litter and for terrestrial senesced leaf litter in general (Yuan and Chen 2009a). We assumed that this difference arose because more than half (60.1 %) of the leaf litter in Boyero et al.'s study were collected from tropical areas which usually have lower P concentration than non-tropical areas as shown in our study and by (Ge et al. 2017). Tibbets and Molles (2005) demonstrated that leaf litter P concentration were higher at flood sites than non-flood sites which was caused by the anaerobic conditions of riparian soils and the exchange of groundwater to increase mobilization of P. Therefore, differences in soil conditions (e.g. soil moisture) between riparian forests and other forests might induce the variation of leaf litter P between our study (with likely higher soil moisture) and the global terrestrial study (Yuan and Chen 2009a). Riparian leaf litter P declined with MAT and MAP while increasing with absolute latitude, which partially agrees with previous studies for riparian leaf litter (Boyero et al. 2017), woody plants (Kang et al. 2010), and terrestrial leaf litter in general (Yuan and Chen 2009a). The relationship between leaf litter P and MAT probably related to soil P availability (Yuan and Chen 2009a, Boyero et al. 2017), because terrestrial soil total P and available P decreased with MAT (Geng et al. 2017, Hou et al. 2018), which can lead to low P for plants in high MAT areas. Yuan and Chen (2009a) also suggested that the negative relationship between leaf litter P and MAT was likely attributed to the accelerated resorption of P by plants with MAT. The differences in soil P between geographical areas might also explain differential responses of leaf litter P to MAT, with a positive relationship in tropical areas but negative relationship in non-tropical areas. We also found that leaf litter P decreased with MAT for deciduous species, which is similar to the finding for global woody plants (Kang et al. 2010). These responses partially agree with the negative correlation with MAT for both deciduous and evergreen leaf litter from terrestrial species globally (Yuan and Chen 2009a), but is inconsistent with the positive relationship for evergreen species and no relationship for deciduous plants in a study of Chinese broadleaves tress (Ge et al. 2017). The relationships between riparian leaf litter P and environmental factors differed at continental scale. The trends in Eurasia were similar (positively correlated with absolute latitude and negatively correlated with MAP and MAT) with terrestrial broad-leaf litter in China (Ge et al. 2017), while these trends were no found in North American riparian leaf litter.

The impacts of MAP on leaf litter nutrients concentrations were likely influenced by the input from soil mineralization and output from leaching: in high MAP areas, soils are subjected to episodic saturation which result in more anoxia and reduced mineralization; leaching also increases with MAP (Zhang and Wang 2015). In addition, P-resorption also increased with MAP which can further decrease leaf litter P in high MAP areas (Yuan and Chen 2009b, Posada and Schuur 2011). Consequently, leaf litter P was lower in high MAP areas than low MAP areas. Increased leaf litter P concentrations with absolute latitude could be explained by the low soil P in tropical areas, because soil P is highly correlated with soil N concentrations which are low in tropical areas (Margalef et al. 2017). High altitude leaf-litter P was lower than in lowland areas which is probably attributed to the associated harsh environment such as low temperature, which may restrict the uptake of P by plants (Reich and Oleksyn 2004) and the changed freeze-thaw cycling (Tan and Wang 2016). If leaf litter P was primarily determined by soil P, it should increase with altitude as does soil P does (Tan and Wang 2016, Zhang et al. 2019). However, nutrient concentrations in soils and plants were decoupled along the altitude gradient (Tan and Wang 2016).

6.5.3 Carbon

Mean C concentrations in our study of riparian leaf litter were lower than those found for terrestrial leaf litter in general (Yuan and Chen 2009a), possibly because of higher soil moisture in riparian forests than upland forests. Although soil C has been found to increase with altitude (Du et al. 2014b, He et al. 2016, Tashi et al. 2016), litter C decreased with altitude in this study, which agrees with a previous study (Du et al. 2014b), but is inconsistent with another study which found an increase of 2.3 % of leaf litter C for every 1000 m (Tashi et al. 2016). Therefore, other factors such as decreasing temperature with altitude might explain the low leaf litter C at high altitudes, which can be supported by the decreasing leaf litter C with MAT as found in this study. Leaf litter C decreased with MAT and marginally significantly declined with MAP, in contrast to a previous study of broad-leaf litter in China, which found no significant relationship between leaf litter C and MAT while a positive correlation between leaf litter C and MAP (Ge et al. 2017). Riparian leaf litter C increased with absolute latitude, a trend also found for broad-leaf plants in China (Ge et al. 2017).

6.5.4 Stoichiometric ratios

Mean C:N and C:P ratios in this study were significantly lower than that reported for global terrestrial leaf litter, while N:P ratios showed no significant difference (Yuan and Chen 2009a), but both were lower than in another study for riparian leaf litter (Boyero et al. 2017). These differences were probably caused by the differences in plant species, because we included only a small number of conifers which are generally lower in N and P than broadleaf litter (Enright 2001), while the global study (Yuan and Chen 2009a) had more diverse plants. This difference between plant types also occurred in another study which found lower C:P ratios for broad-leaf litter than global terrestrial leaf litter (Ge and Xie 2017). Higher N:P ratios for riparian leaf litter in Boyero et al. (2017) than our study could be attributed to the larger number of evergreen species in their study than our study, because evergreen leaf litter tend to have higher N:P ratios than deciduous leaf litter as shown in this study and by (Ge and Xie 2017).

Our results showed that riparian leaf litter N:P ratios increased while C:N ratios decreased with MAT and MAP which were consistent with the pattern for terrestrial senesced leaf litter in general (Yuan and Chen 2009a), but we failed to find positive correlations for C:P ratios with MAT and MAP as in Yuan and Chen’s (2009a) study. Our results supported the viewpoint proposed by Yuan and Chen (2009a) that (1) plants in high-temperature and high-rainfall areas are more efficient to use P than N; (2) plants may adapt to different N use strategies with the change of MAT and MAP. Leaf litter N:P ratios negatively correlated with absolute latitude, which is consistent with the result found for another study of global riparian leaf litter (Boyero et al. 2017), for broad-leaf litter in China (Ge and Xie 2017), and for global green leaves (Reich and Oleksyn 2004), but differed from the concave quadratic response for woody plants at global scale (Kang et al. 2010). At continental scale, the relationships between stoichiometric ratios (C:N and C:P) and MAP, MAT, and absolute latitude in Eurasian riparian leaf litter were the same as found in Chinese broad-leaf trees (Ge and Xie 2017). However, we did not find any relationships between N:P and the other three predictors as Ge and Xie (2017) found, i.e. terrestrial leaf litter N:P increased with MAP and MAT while decreased with absolute latitude. In addition, we found more significant correlations between riparian leaf litter stoichiometric ratios with MAT, MAP, absolute latitude and altitude in North America than that in Eurasia. High leaf-litter N:P ratio in tropical areas may be related to the higher soil N:P ratios in tropical areas than non-tropical areas (Tian et al. 2010). This result adding evidence for the soil substrate age hypothesis which advocates that soil nutrients can explain the variation in leaf nutrient concentrations (Ordoñez et al. 2009, Zhang et al. 2019), and that tropical soils are lower in P than temperate areas (Tian et al. 2010, Hou et al. 2018). Therefore, tropical plants are more efficient at using P than N when compared to plants at higher latitudes (Hidaka and Kitayama 2009, Yuan and Chen 2009b). Neither litter C:P nor C:N ratios significantly responded to absolute latitude, which partly agrees with the finding for broad-leaf litter in China which found negative correlation between C:P and absolute latitude (Ge and Xie 2017). Tropical areas are usually recognized to have low P soils (Hou et al. 2018) which result in high soil N:P and C:P ratios (Tian et al. 2010). Therefore, soil nutrient stoichiometry may not be the reason for the insignificant relationship between leaf litter C:P and C:N ratios with absolute latitude. We found larger variation in C:P ratios than C:N ratios, which seems to advocate the hypothesis that plants are more efficient at using P than N (Hidaka and Kitayama 2009).

Litter C:N ratios were higher at high altitude than low altitude areas which was in accordance with other studies (He et al. 2016). N:P ratios were higher while C:N ratios were lower in tropical areas than in non-tropical areas which were in accordance with the results in Yuan and Chen's (2009a) study, but we did not find significant difference between tropical and non-tropical areas for C:P ratios. C:N ratio was lower for exotic leaf litter than native species as found in a recently published meta-analysis, while we did not find higher C:P ratio for exotic species than native species as found in that meta-analysis (Kennedy and El-Sabaawi 2017).

One important thing we should bear in mind is that the abiotic and biotic factors investigated in this study only explained 11 – 23 % of the variation in senesced riparian leaf litter N, P and N:P ratios, which is lower than the 22 -32 % reported for overall terrestrial leaf litter (Yuan and Chen 2009a). The low R^2 values in our study are probably because of the relatively small sample size, variation in plant functional types (e.g. extremely small number of gymnosperm and grass species), lack of information on soil nutrients, and plant age which can explain the variation of nutrients in leaf litter (Ordoñez et al. 2009, Yuan and Chen 2009a). For example, when soil characters (e.g. soil N) were included, the explained variation for riparian leaf litter N and P reached 34 -37 % (Boyero et al. 2017). In addition, intraspecific variation (e.g. geographic origin and genotypes) of leaf litter quality for one species can be as large as interspecific variation (Lecerf and Chauvet 2008, Compson et al. 2018), which may also contributed to the low R^2 values.

6.6 Conclusions

Overall, riparian leaf litter had higher N and P concentrations while lower C concentration, C:N, and C:P ratios than terrestrial leaf litter, indicating higher quality than general terrestrial leaf litter. Global patterns of leaf litter traits to environmental factors followed similar trends as terrestrial leaf litter. These patterns were different between evergreen and deciduous plants and between tropical and non-tropical areas, and some of these patterns for leaf habits and climate zones were not consistent with previous studies for terrestrial leaf litter. Riparian leaf litter quality traits were more associated with leaf habits, N-fixing function, MAT, absolute latitude, and altitude than other factors. The observed global patterns of riparian leaf-litter quality traits are useful for predicting nutrients cycling and has implications for freshwater management under global changes.

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Chapter 7 General Conclusions

This thesis aimed to investigate the factors that can influence leaf litter decomposition in streams. This was achieved by several studies that tested the individual and combined effects of factors that were not fully understood. Specifically, the following factors were included in this thesis: anthropogenic carrion subsidy, environmental relevant concentration of glyphosate, invertebrates, snails, warming, and leaf litter quality.

Chapter 3 Effects of anthropogenic carrion subsidy and glyphosate on leaf decomposition in streams

- The addition of anthropogenic carrion subsidy (chicken meat) and glyphosate alone or in combination affected leaf litter decomposition in both coarse and fine (excluded invertebrates) mesh bags.
- In coarse mesh bags, glyphosate and carrion subsidy decreased litter breakdown rates by 6.3 % and 22.6 % respectively, and the addition of both glyphosate and carrion subsidy also reduced litter breakdown rates by 24.3 %.
- In fine mesh bags, glyphosate and the addition of both glyphosate and carrion subsidy retarded litter breakdown rates by 8.3 % and 12.5 % respectively, while carrion subsidy alone had no significant effect.
- Leaf litter breakdown rates expressed by day (k d^{-1}) and degree-day (k dd^{-1}) varied among streams, with the fastest breakdown rates found in village streams and the slowest in urban and suburban streams.
- Total abundance, richness, and Shannon-Wiener diversity index of invertebrate positively correlated with litter breakdown rates measured per day and per degree-day.

Conclusions: (1) Anthropogenic carrion subsidy probably induced the shift of the diet of invertebrates from leaf litter to carrion which resulted in the decline of invertebrate-mediated litter decomposition; (2) environmental relevant concentration of glyphosate decreased microbial-mediated litter decomposition; (3) the lack of detritivores in suburban and urban streams decreased litter decomposition.

Chapter 4 Effects of anthropogenic carrion subsidy and glyphosate on macroinvertebrates in streams

- None of the anthropogenic carrion subsidy and environmentally relevant concentration of glyphosate, nor their interactions showed significant effects on macroinvertebrates. However, the effects of anthropogenic carrion subsidy and glyphosate depend on land use, with significant effects on macroinvertebrates in some streams while not in others.
- Most of the macroinvertebrate metrics differed among streams. Village streams had the highest total abundance, total richness, and Shannon-Wiener Index.
- Suburban stream had higher total abundance than forest stream, while total richness and Shannon-Wiener diversity index were significantly lower in suburban stream than forest stream.
- Insects (mostly Chironomidae) dominated in village and forest streams (> 90 %), while they only contributed to ~20% of the individuals in suburban stream.
- Collector-gatherers dominated in all streams (> 65 %), and were higher in village streams than in suburban and forest streams.

Conclusions: (1) overall effects of anthropogenic carrion subsidy and environmental relevant concentration of glyphosate on invertebrates were low while they showed site-specific effects on some taxa; (2) land use was the main driver influencing the changes in invertebrate communities, with lower richness and diversity in suburban stream (i.e. dense anthropogenic disturbance); (3) differences in invertebrate communities which associated with traits are likely to induce the site-specific responses of invertebrates to anthropogenic carrion subsidy and environmental relevant concentration of glyphosate.

Chapter 5 Combined effects of water temperature, grazing snails and terrestrial herbivore on leaf litter decomposition in urban streams

- Warming (average 8 ^{o}C higher than ambient) and the presence of snails accelerated litter decomposition by 60.2 % and 34.9 % respectively, while litter breakdown rates of terrestrial insect damaged leaves were 5.1 % slower than intact leaves because of lower leaf litter quality.

- Warming stimulated microbial and snail mediated litter decomposition by 34.8 % and 166.7 % respectively.
- All the two-way interactions showed additive effects on litter decomposition except for the interaction between warming and snails which showed positive synergistic effects.
- Neither temperature nor leaf quality affected snail growth rate.

Conclusions: (1) warming stimulates both microbial and snail mediated litter decomposition in urban streams; (2) the dominance of snails in urban streams could contribute to the decomposition of leaf litter decomposition and partly compensate the scarce of shredders in these waterbodies; (3) terrestrial insects are likely to induce the decrease of leaf litter quality, with cascade effects on its decomposition in freshwaters; (4) the co-occurrence of warming and higher abundance of snails in urban streams, which is likely to happen in the future, could synergistically speed up the depletion of organic matter, with further consequences on stream food webs and nutrient cycling.

Chapter 6 Global trends of leaf litter carbon, nitrogen, and phosphorus in riparian plants

- Riparian leaf litter had higher N and P, while lower C, C:N, and C:P ratios than terrestrial leaf litter in general, and showed no difference for N:P ratio.
- Riparian leaf litter N and N:P increased while P and C:N decreased with mean annual precipitation (MAP, mm).
- Riparian leaf litter C, P, and C:N decreased while N:P increased with mean annual temperature (MAT, ^{o}C).
- Riparian leaf litter C and P positively correlated while N:P negatively correlated with absolute latitude; C, N, and P decreased while C:N and C:P increased with altitude.
- These patterns were changed when data were analyzed using different leaf habits (evergreen and deciduous) or within different climate zones (tropical and non-tropical area).

- Riparian leaf litter quality traits also varied among climate zones, leaf habits, N-fixing function, invasion status (exotic and native), and life forms (tree and non-tree).

Conclusions: (1) riparian leaf litter showed higher quality (N and P) than overall terrestrial leaf litter; (2) riparian leaf litter quality generally showed linear relationship with the gradients of MAP, MAT, absolute latitude, and altitude, and these patterns differed between leaf habits (evergreen and deciduous) and between climatic zones (tropic and non-tropic areas); (3) riparian leaf litter quality traits were more associated with climatic zones, leaf habits, and N-fixing functions than phylogeny, invasion status, and life forms; (4) overall percentage of the variations in leaf litter quality can be explained by our predictors was low (i.e. low R^2).

In conclusion, this thesis revealed that leaf-litter decomposition in streams are subjected to many biotic and abiotic factors. To our knowledge, we are the first to use anthropogenic carrion subsidy (chicken meat) to investigate the effects on invertebrates and leaf litter decomposition in stream (Chapter 3 and 4). We are also the first to use glyphosate contaminated agar to test the effects of environmental relevant concentration of glyphosate, the most widely used herbicides worldwide, on leaf-litter decomposition (Chapter 3). These two methods can be improved by using different pesticides or agent of anthropogenic subsidies (e.g. fishing pellets) to advance our knowledge on how anthropogenic disturbances can affect leaf litter decomposition in freshwaters. We found that an average increasement of 8 °C in water temperature in winter can stimulate both snail and microbial-mediated litter decomposition (Chapter 5). As global urban area is increasing and urban waterbodies have higher water temperature than non-urban areas, consequently, urban waterbodies may release more CO_2 to atmosphere and affect global C cycling. We are the first to conduct a global meta-analysis to investigate the global patterns of riparian leaf litter quality (Chapter 6). Global riparian leaf litter had higher concentration of N and P than terrestrial leaf litter in general, and responded to the gradients of MAT, MAP, absolute latitude, and altitude. These findings are helpful for the prediction of global leaf litter decomposition in streams. However, more information such as soil nutrient concentrations should be included in future studies to get a better prediction of the variation of riparian leaf litter quality.

Appendices

Chapter 4

Table S4.1 Summary (*P*-values and effect sizes) of two-way ANOVA with repeated measures comparing macroinvertebrate responses (most are at the family level) between experimental treatments (G, glyphosate; S, subsidy) in forest, village (combined data of V-50 and V-1000, which was 50 m and 1000 m downstream of a village respectively), and suburban streams. Combined (C) glyphosate by subsidy interaction effects are classified directionally (+ or -) as antagonistic (A), synergistic (S), additive (AD; no interaction) or no significant effect of either stressor (O) according to the conceptual model proposed by Piggott *et. al.* (2015). $P < 0.05$ are in bold print. Effect sizes (partial eta squared values; range 0–1) are shown in parentheses for all cases where $P < 0.1$.

Response variables	Forest stream				Village streams					Suburban stream			
	G	S	G × S	C	G	S	Stream	G × S	C	G	S	G × S	C
Shredder abundance	0.805	0.805	0.097 (0.162)	O									
% shredder abundance	0.682	0.561	0.057 (0.209)	O									
c-f abundance					0.89	0.263	**0.001** (0.292)	**0.003** (0.220)	-S				
% c-f abundance					0.188	0.253	**0.039** (0.116)	0.981	O				
Oligochaeta abundance										0.347	0.655	**<0.001** (0.636)	+S
% Oligochaeta abundance										0.416	0.257	**<0.001**	+S

(0.803)

Heptageniidae abundance	0.672	0.935	0.078 (0.182)	O	0.303	0.129	**<0.001** (0.663)	0.968	O
% Heptageniidae abundance	0.137	0.664	**0.034** (0.251)	+S	0.051 (0.104)	**0.023** (0.139)	**<0.001** (0.633)	0.433	AD
Baetidae abundance	0.945	0.945	0.253	O	0.213	0.431	**0.039** (0.116)	0.796	O
% Baetidae abundance	0.769	0.828	0.446	O	0.385	0.095 (0.078)	**0.006** (0.198)	0.527	O
Caenidae abundance					0.105	**0.006** (0.195)	**<0.001** (0.786)	0.122	AD
% Caenidae abundance					0.095 (0.078)	**0.005** (0.208)	**<0.001** (0.826)	0.368	AD
Ephemerellidae abundance	**0.021** (0.29)	0.192	0.075 (0.185)	AD	0.845	0.509	**0.042** (0.113)	0.32	O
% Ephemerellidae abundance	0.057 (0.208)	0.296	**0.001** (0.511)	+S	0.213	**0.036** (0.12)	**<0.001** (0.317)	0.101	AD
Leptophlebiidae abundance					0.364	0.243	**0.04** (0.115)	0.395	O
% Leptophlebiidae abundance					0.464	0.851	**0.008** (0.187)	0.509	O
Hydropsychidae abundance					0.817	0.128	**<0.001** (0.362)	**0.011** (0.169)	-S

% Hydropsychidae abundance					0.432	0.129	**<0.001** (0.364)	**0.015** (0.159)	-S				
Lepidostomatidae abundance	0.309	0.218	0.909	O									
% Lepidostomatidae abundance	0.627	0.228	**0.047** (0.224)	-S									
Leptoceridae abundance	0.309	0.218	0.909	O									
% Leptoceridae abundance	0.426	0.212	0.543	O									
Perlidae abundance	0.751	0.176	0.238	O									
% Perlidae abundance	0.749	0.453	0.261	O									
Erpobdellidae abundance										0.077 (0.183)	0.631	0.836	O
% Erpobdellidae abundance										0.138	**0.01** (0.347)	**<0.001** (0.609)	+A

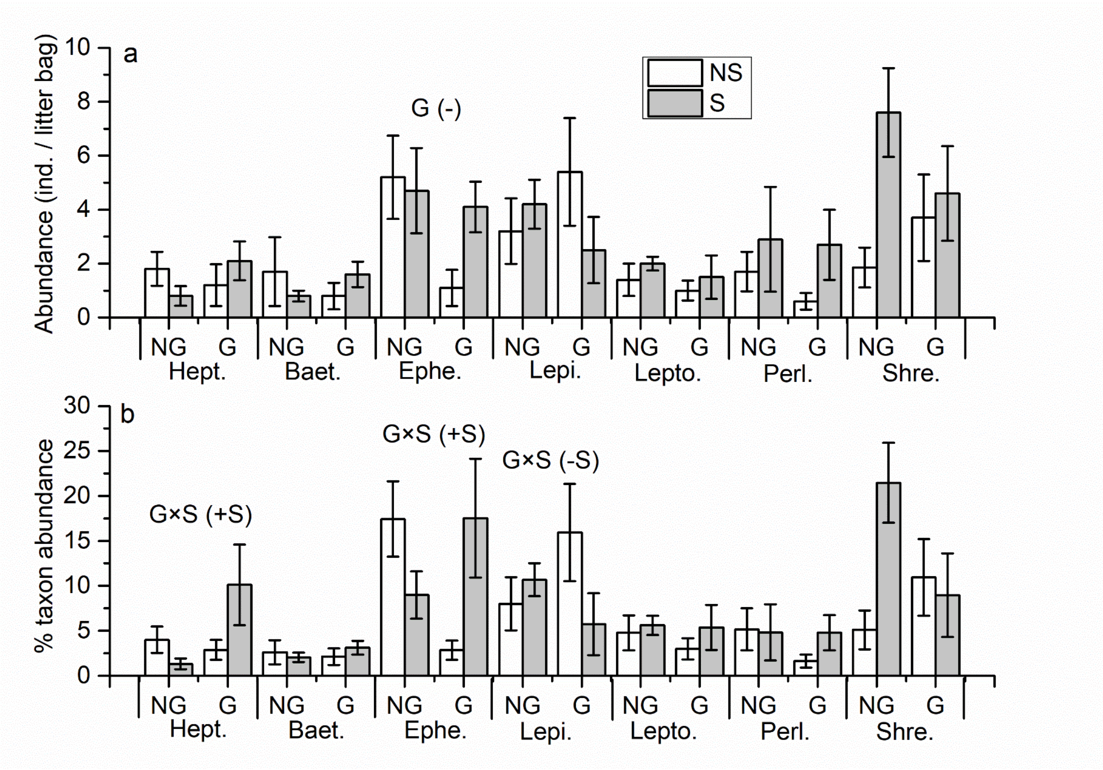

Figure S4.1 Averages of macroinvertebrate abundance and % abundance of dominant taxa (% abundance > 2 %, except for Chironomidae) across the experimental treatments (No glyphosate: NG, with Glyphosate: G, no subsidy: NS, with subsidy: S) sampled in forest stream. Values are mean ± SE. Text above the column indicates significant main effects or interactive effects (Glyphosate: G, Subsidy: S), with effect classifications (for abbreviations see Table S4.1) in parentheses. Full name of each taxon name please see Table S4.1.

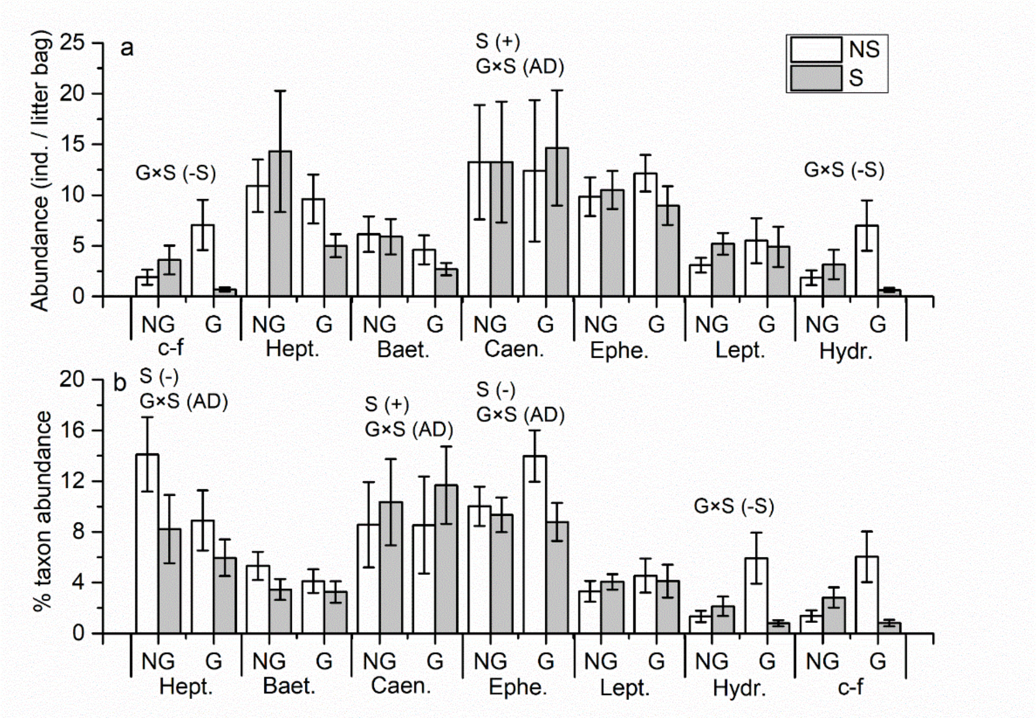

Figure S4.2 Averages of macroinvertebrate abundance and % abundance of dominant taxa (% abundance > 2 %, except for Chironomidae) across the experimental treatments (No glyphosate: NG, with Glyphosate: G, no subsidy: NS, with subsidy: S) sampled in village streams. Values are mean ± SE. Text above the column indicates significant main effects or interactive effects (Glyphosate: G, Subsidy: S), with effect classifications (for abbreviations see Table S4.1) in parentheses. Full name of each taxon name please see Table S4.1.

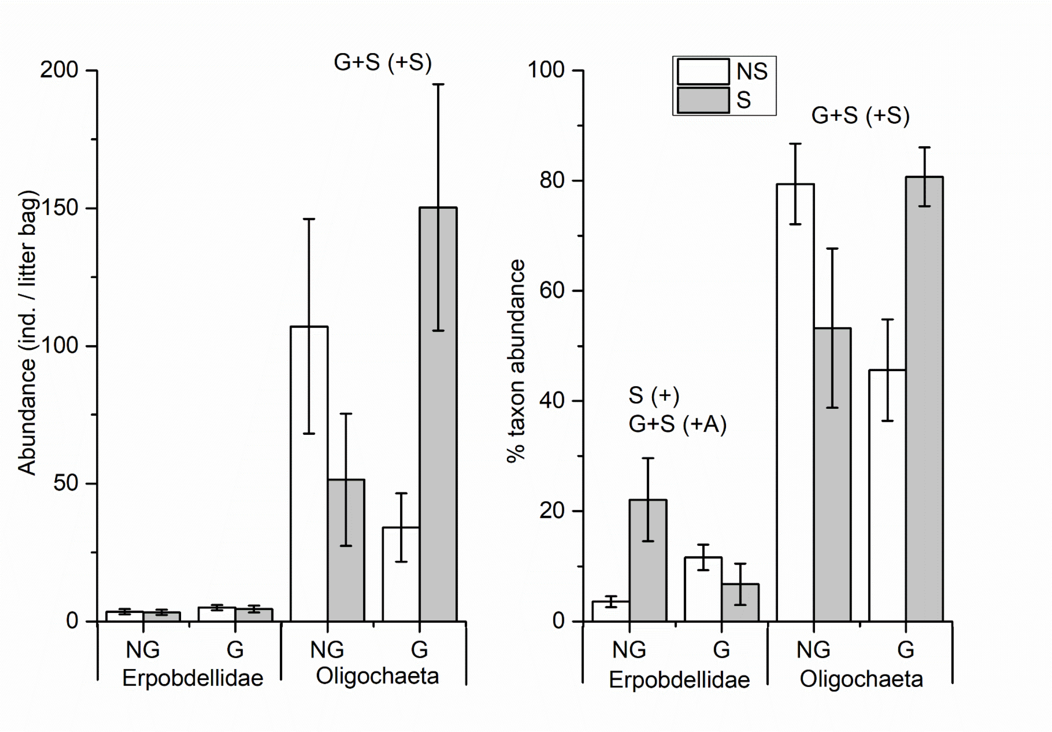

Figure S4.3 Averages of macroinvertebrate abundance and % abundance of dominant taxa (% abundance > 2 %, except for Chironomidae) across the experimental treatments (No glyphosate: NG, with Glyphosate: G, no subsidy: NS, with subsidy: S) sampled in suburban stream. Values are mean ± SE. Text above the column indicates significant main effects or interactive effects (Glyphosate: G, Subsidy: S), with effect classifications (for abbreviations see Table S4.1) in parentheses. Full name of each taxon name please see Table S4.1.

Chapter 5

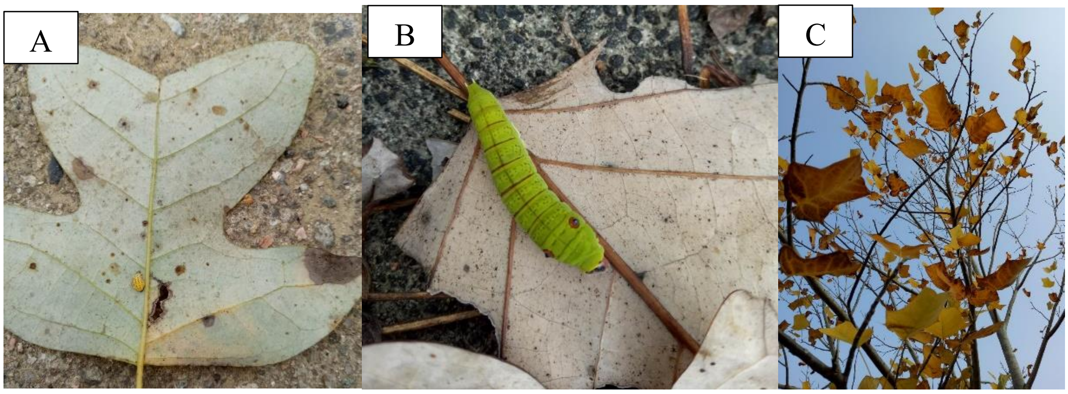

Figure S5.1 Terrestrial insects found on the leaves (A and B) and intact leaf litter (C).

Figure S5.2 Experimental Mesocosms installed on the riparian zone of an urban stream.

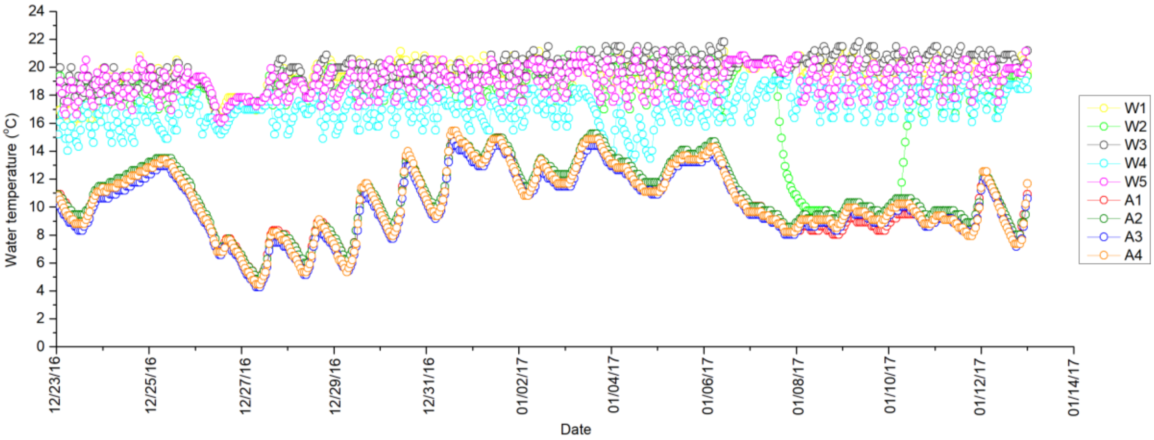

Figure S5.3 Hourly changes of water temperature in five warming (W1-W5) and four ambient (A1-A4) treatments during the experimental period.

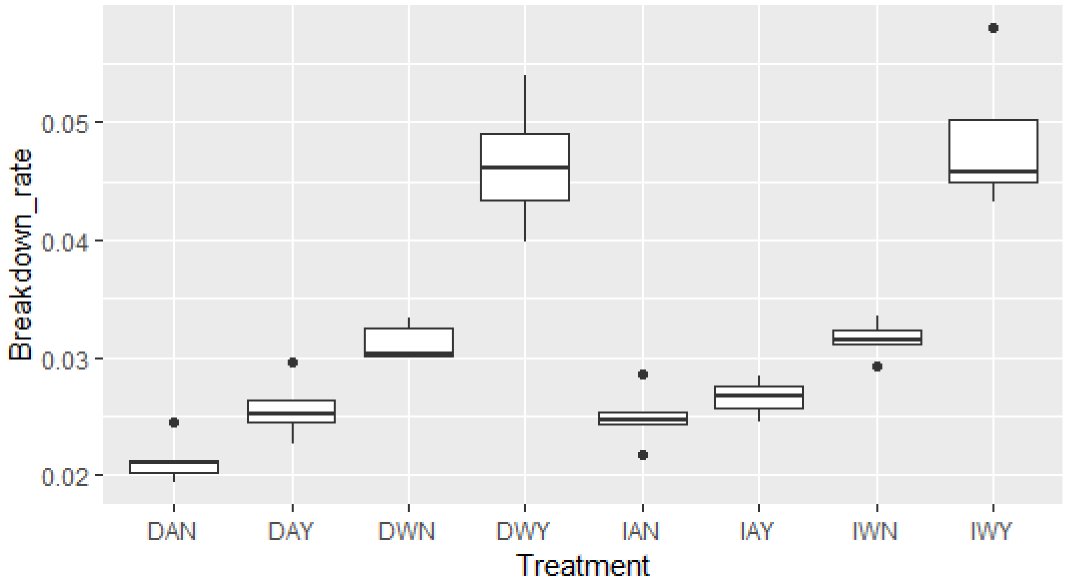

Figure S5.4 Boxplot of leaf litter breakdown rates for each treatment. Letters in the x axis mean: D (insect damaged); I (intact leaves); A (ambient temperature); W (warming); N (without snails); Y (with snails).

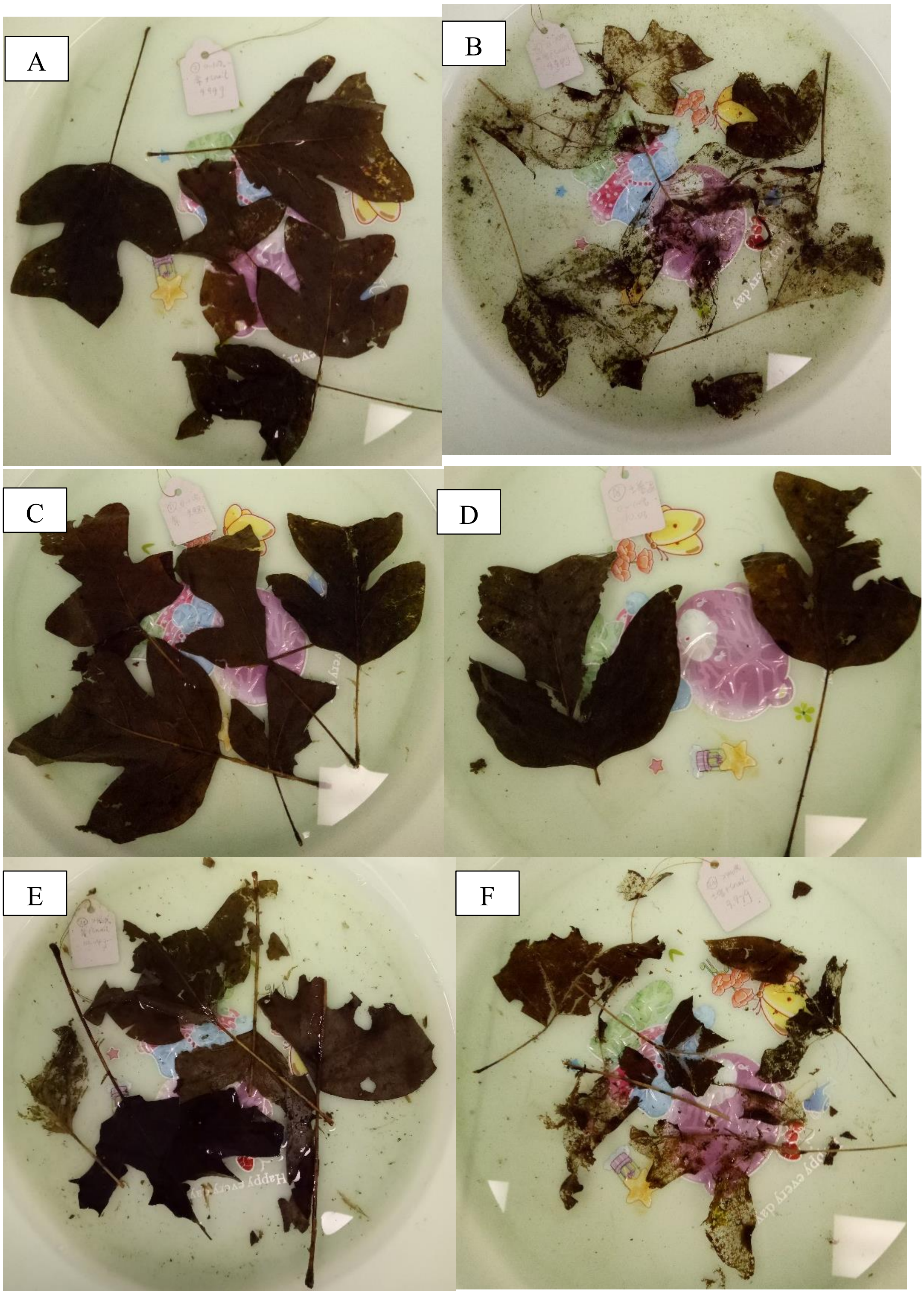
A
B
C
D
E
F

Figure S5.5 Leaf appearance after the experiment (Day 25) in treatments of (A) intact leaves + ambient temperature + snails; (B) intact leaves + warming temperature + snails; (C) intact leaves + ambient temperature + no snails; (D) intact leaves + warming temperature + no snails; (E) terrestrial insect damaged leaves + ambient temperature + snails; (F) terrestrial insect damaged leaves + warming temperature + snails; (G) terrestrial insect damaged leaves + ambient temperature + no snails; and (H) terrestrial insect damaged leaves + warming temperature + no snails.

Table S5.1 Summary results of three-way ANOVA with repeated measures for the effects of water temperature (T), snail (S), and litter quality (Q) on water quality in experimental mesocosms. *P*-values < 0.05 are in bold print.

Source of variation		pH		Turbidity (NTU)		DO (%)		DO (mg/L)		Ammonia (mg/L)			Conductivity (μs/cm)	
Between-Subjects effects	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	df	*F*	*P*
Q	1	10.559	**0.003**	1.051	0.313	2.039	0.163	0.169	0.684	1.000	0.325	1	0.662	0.422
T	1	69.820	**<0.001**	424.048	**<0.001**	260.390	**<0.001**	513.690	**<0.001**	251.504	**<0.001**	1	300.323	**<0.001**
S	1	16.757	**<0.001**	51.027	**<0.001**	5.357	**0.027**	0.598	0.445	30.959	**<0.001**	1	0.878	0.356
Q × T	1	2.182	0.149	0.747	0.394	0.008	0.928	0.574	0.454	1.361	0.252	1	1.042	0.315
Q × S	1	21.549	**<0.001**	0.782	0.383	1.517	0.227	0.784	0.383	5.189	**0.030**	1	0.523	0.475
T × S	1	1.711	0.200	14.898	**0.001**	0.718	0.403	0.049	0.827	8.302	**0.007**	1	0.520	0.476
Q × T × S	1	1.603	0.215	10.346	**0.003**	3.021	0.092	1.512	0.228	0.151	0.700	1	<0.001	0.996
Error	32											32		
Within-Subjects effects														
Time	2	44.196	**<0.001**	230.871	**<0.001**	59.741	**<0.001**	153.381	**<0.001**	195.765	**<0.001**	1.434	15.607	**<0.001**
Time × Q	2	1.842	0.167	3.653	**0.031**	1.173	0.316	0.359	0.700	6.153	**0.004**	1.434	4.101	**0.035**
Time × T	2	29.390	**<0.001**	14.033	**<0.001**	6.438	**0.003**	76.869	**<0.001**	3.181	**0.048**	1.434	93.201	**<0.001**
Time × S	2	0.635	0.533	10.012	**<0.001**	2.683	0.076	1.400	0.254	0.317	0.729	1.434	0.833	0.406
Time × Q × T	2	6.254	**0.003**	4.861	**0.011**	0.465	0.630	0.707	0.497	2.164	0.123	1.434	0.587	0.506

Time × Q × S	2	4.903	**0.010**	4.596	**0.014**	0.147	0.864	0.002	0.998	4.263	**0.018**	1.434	0.806	0.416
Time × T × S	2	0.204	0.816	0.136	0.873	0.310	0.735	0.573	0.567	0.900	0.411	1.434	0.399	0.605
Time × Q × T × S	2	1.601	0.210	5.110	**0.009**	2.554	0.086	2.549	0.086	1.270	0.288	1.434	0.570	0.514
Error	64											45.895		

Chapter 6

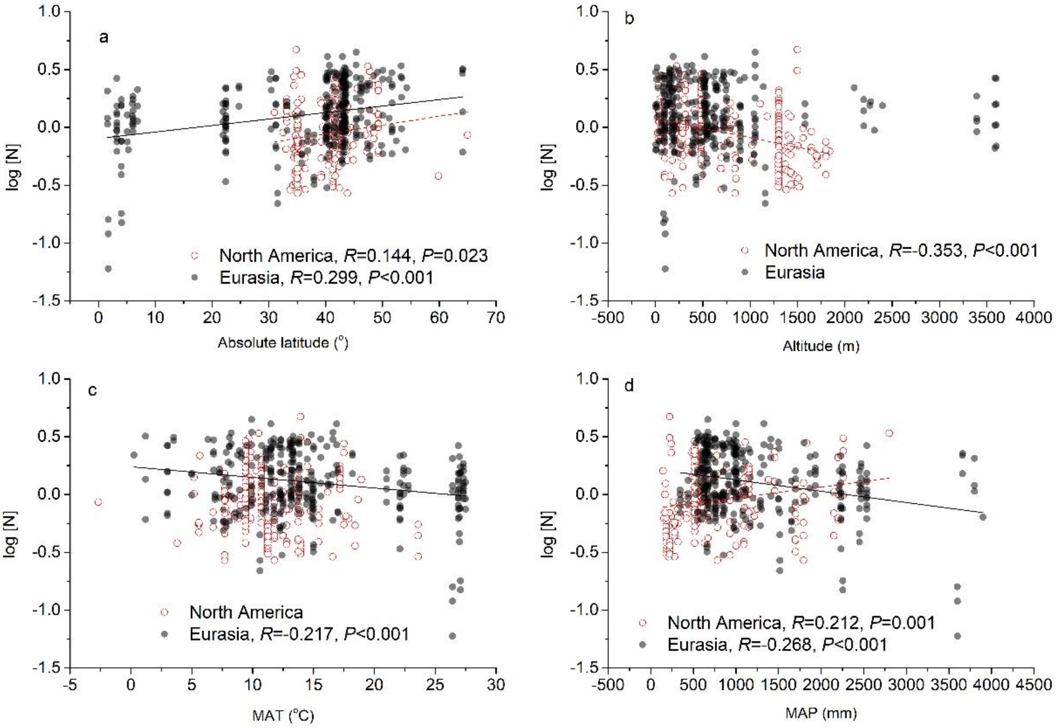

Figure S6.1 Senesced riparian leaf litter N in relation to (a) absolute latitude (^{o}), (b) altitude (m), (c) mean annual temperature (MAT, ^{o}C), and (d) mean annual precipitation (MAP, mm) in Eurasia (black solid circles and black solid lines) and North America (red hollow circles and red dashed lines). Regression lines were plotted for relationships with $P<0.05$. The coefficients of determination (*R*) and *P* are shown in each panel if $P<0.05$.

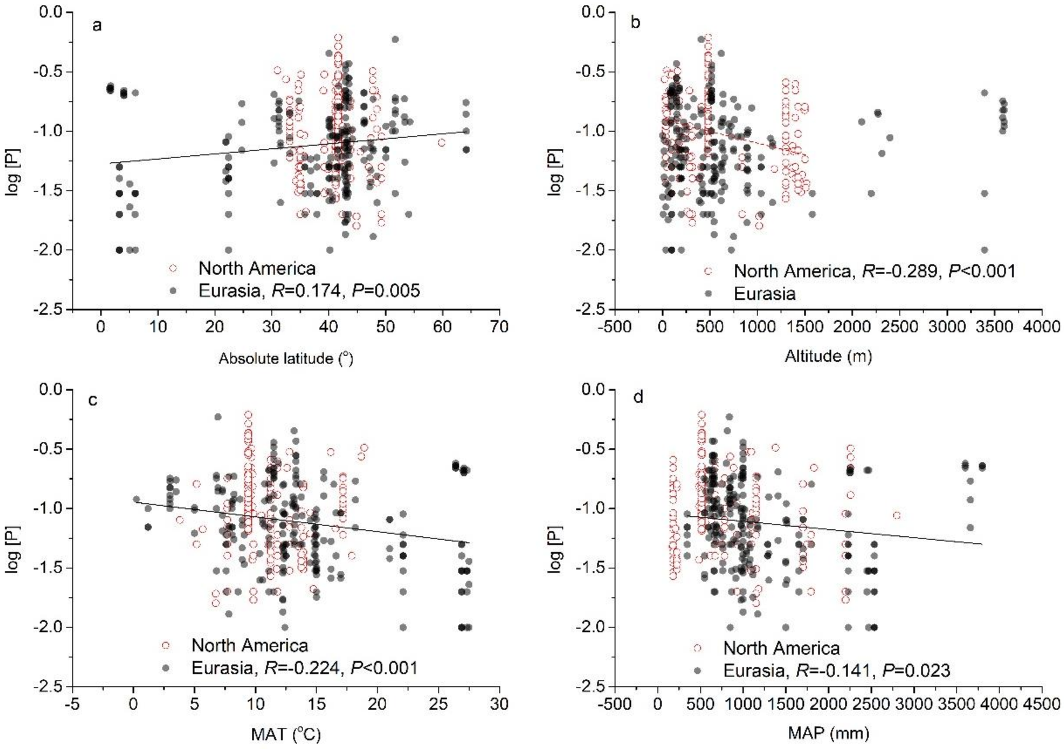

Figure S6.2 Senesced riparian leaf litter P in relation to (a) absolute latitude (°), (b) altitude (m), (c) mean annual temperature (MAT, °C), and (d) mean annual precipitation (MAP, mm) in Eurasia (black solid circles and black solid lines) and North America (red hollow circles and red dashed lines). Regression lines were plotted for relationships with *P*<0.05. The coefficients of determination (*R*) and *P* are shown in each panel if *P*<0.05.

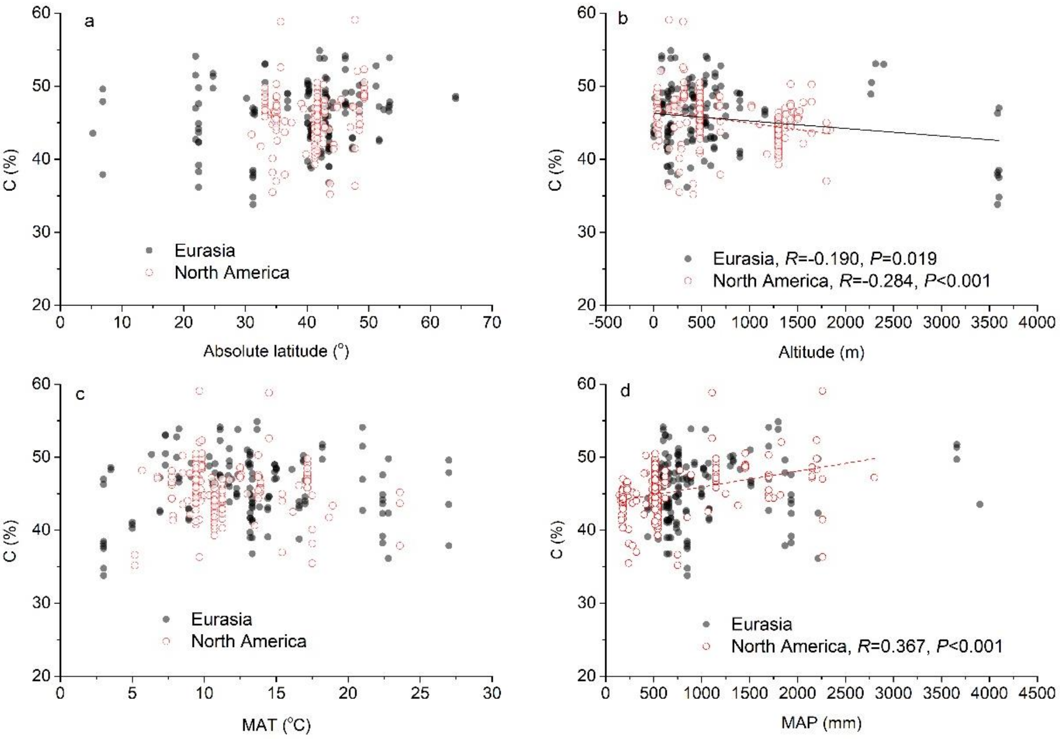

Figure S6.3 Senesced riparian leaf litter C in relation to (a) absolute latitude (°), (b) altitude (m), (c) mean annual temperature (MAT, °C), and (d) mean annual precipitation (MAP, mm) in Eurasia (black solid circles and black solid lines) and North America (red hollow circles and red dashed lines). Regression lines were plotted for relationships with $P<0.05$. The coefficients of determination (R) and P are shown in each panel if $P<0.05$.

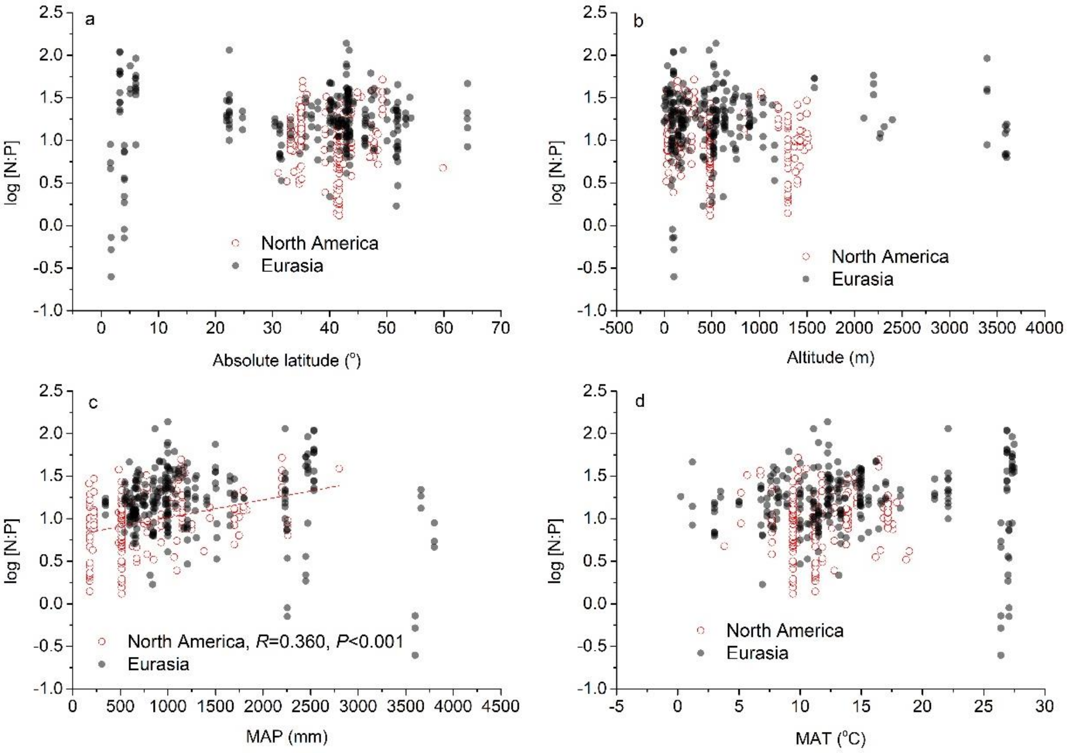

Figure S6.4 Senesced riparian leaf litter N:P in relation to (a) absolute latitude (°), (b) altitude (m), (c) mean annual precipitation (MAP, mm), and (d) mean annual temperature (MAT, °C) in Eurasia (black solid circles and black solid lines) and North America (red hollow circles and red dashed lines). Regression lines were plotted for relationships with $P<0.05$. The coefficients of determination (R) and P are shown in each panel if $P<0.05$.

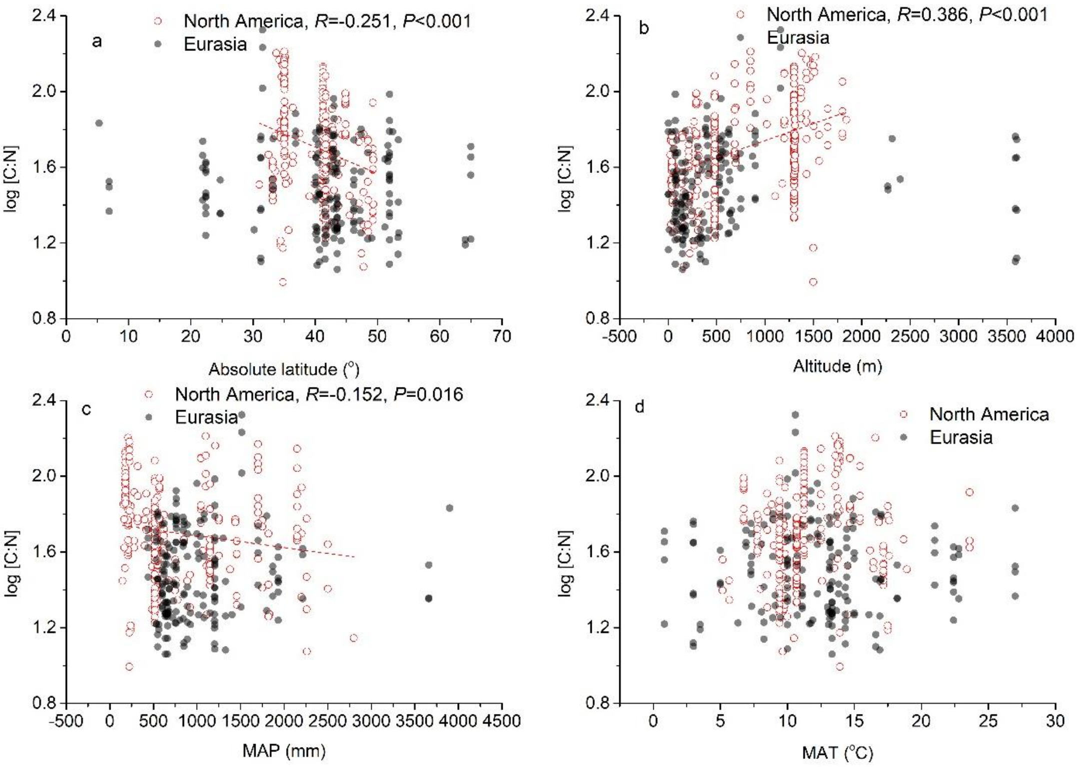

Figure S6.5 Senesced riparian leaf litter C:N in relation to (a) absolute latitude (°), (b) altitude (m), (c) mean annual precipitation (MAP, mm), and (d) mean annual temperature (MAT, °C) in Eurasia (black solid circles and black solid lines) and North America (red hollow circles and red dashed lines). Regression lines were plotted for relationships with *P*<0.05. The coefficients of determination (*R*) and *P* are shown in each panel if *P*<0.05.

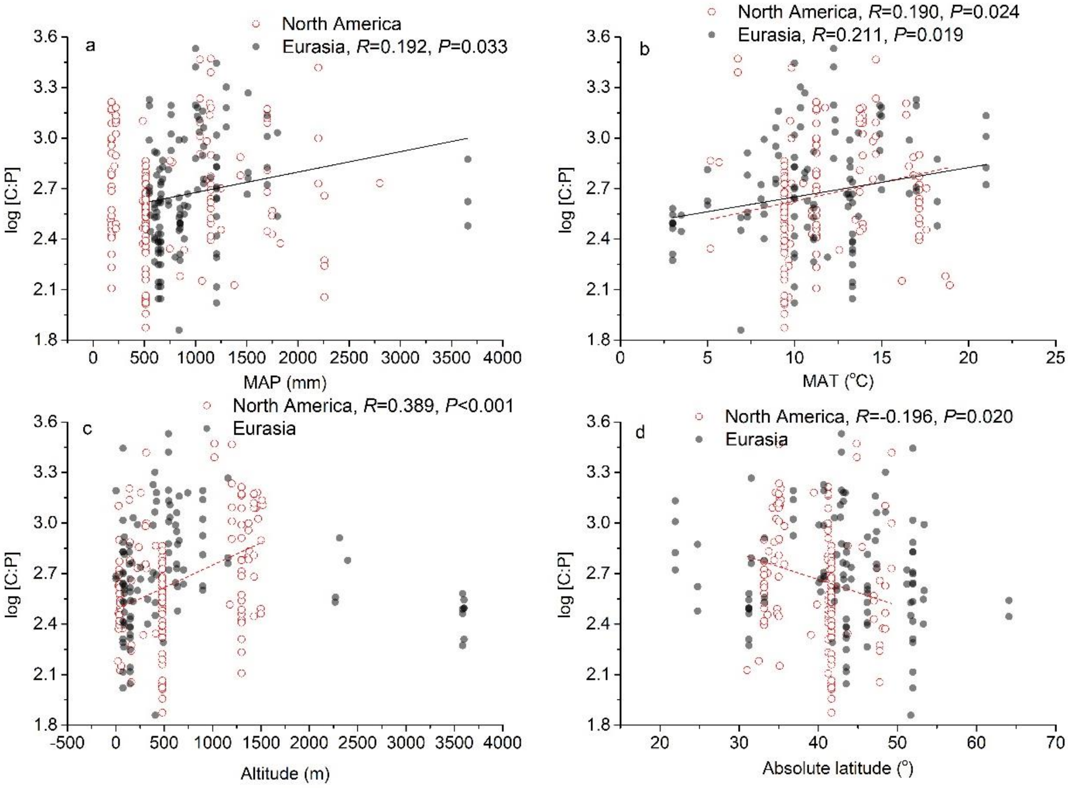

Figure S6.6 Senesced riparian leaf litter C:P in relation to (a) mean annual precipitation (MAP, mm), (b) mean annual temperature (MAT, °C), (c) altitude (m), and (d) absolute latitude (°) in Eurasia (black solid circles and black solid lines) and North America (red hollow circles and red dashed lines). Regression lines were plotted for relationships with $P<0.05$. The coefficients of determination (R) and P are shown in each panel if $P<0.05$.

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