Research Article

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Importance of Riparian Zone: Effects of Resource Availability at Land-water Interface

Abstract: Riparian zone provides a variety of resources to organisms, 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 change water availability and affect the flux dynamics of cross-system subsidies. Yet, we still lack sufficient empirical studies assessing impacts of disturbances of land use, climate change and invasive species individually and interactively on aquatic and riparian ecosystems through influencing subsidy resource availability. In filling this knowledge gap, we can make more effective efforts to protect and conserve riparian habitats and biodiversity, and maintain riparian ecosystem functioning and services.

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

1 Introduction

Cross-ecosystem resource flux linking terrestrial and aquatic systems is an important ecological concept for scientists and managers [1-10]. Understanding it is crucial while restoring and managing aquatic and terrestrial ecosystems [3, 11-14], because aquatic ecosystems (including streams, rivers, lakes, and ponds) and their riparian zones are closely linked as a whole system and resources can be transferred between one another. As one of resources across ecosystem boundaries, subsidies are donor controlled allochthonous resource flux [3, 15] and can benefit recipient ecosystems in multiple ways and ultimately influence consumer populations and communities through greater reproduction, immigration, and higher rates of consumer survival [1, 16, 17]. 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 [2]. Riparian zones benefit from their proximity to river ecosystems, deriving food resources from the river in the form of subsidies of algae, emerging arthropods [3, 18, 19] and anadromous fish [20, 21].

Allochthonous resource inputs across riparian and aquatic ecosystems are often shown to go in both directions [6, 22], with each ecosystem receiving a resource pulse during its least productive season [23]. The numerous resources transferred across the riparian zone are not only beneficial for terrestrial species [2, 19], but also provide multiple necessary services for aquatic species [24, 25]. These services can 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, all of which can benefit aquatic consumers such as microbes, algae, invertebrates and fish [1, 3, 5, 23, 24, 26]. The effect of subsidies can be altered based on top consumers in the trophic system [27-29]. As typical, asymmetrical or one-sided dynamics can occur in habitats with higher order consumers including lizards and birds, they merely consume the aquatic subsidy, yet provide little benefit back to the freshwater ecosystem [27].

When assessing the relationship between freshwater and terrestrial ecosystems, it is important to take hydrology into account for studying water resource by assessing the

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relationship between ecological factors and hydrological variables at the catchment scale for successful ecosystem management [30-32]. 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 [33]. Stream and river ecosystems through hydrological dynamics 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, recent 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 [34].

Theoretical studies postulate the potential impacts of subsidies on food web, the consequences to differing quantity [35] and quality [36] of inputs, and at which level of the trophic system the resource enters [37]. Low levels of resource input have the ability to stabilize food webs, but can potentially cause detrimental effects if allochthonous inputs are too large [38]. The strength of the effects of a subsidy depends not only on its quantity, but also on its quality relative to *in situ* food resources [39]. For example, for experimental treatment with grass litter addition, mesocosms had highest treefrog biomass export, while for that with white oak litter addition, the treefrog biomass export was lowest. This was induced by the differences in litter quality (e.g. leaf N, P, and tannin content) [22]. While resources move from areas with productivity gradient, as the amount of input increases, the system (e.g. caves, headwater streams, and some small marine islands) can become unstable due to the increase in predator numbers [38, 40]. 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 [41-43].

Trophic cascades, a potential consequence of subsidies, vary in strength and are commonly thought to be influenced by consumer body size [44], quantity of subsidy input [45], general system productivity, diversity of primary producers [46], and predator traits [47, 48], as well as habitat heterogeneity [8]. In addition, physical and ecological attributes of each ecosystem (aquatic or terrestrial) can give insight into potential trophic cascades following a particular amount of allochthonous resources they receive [45]. Generally, aquatic ecosystems experience stronger trophic cascades than in terrestrial systems [49-51] with several reasons, including their low level and concave structure naturally attracting a greater

rate of input, in comparison with mountain areas or even flat terrestrial areas [47].

Allochthonous resource pulses can be viewed in two ways: as singular events and as recurrent environmental events [41]. 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 subsidy pulses, and then disperse to adjacent habitats when those subsidies are disappeared. However, at community level, resource subsidy pulses not only influence species diversity, but also alter community structure through complex interactions by influencing coexistence mechanisms, such as hampering predator coexistence, resource partitioning, and keystone predation [41, 43, 48].

The distribution of necessary resources in a riparian zone has been shown to affect the resource acquisition of consumers, particularly in predatory terrestrial taxa. We present a review of literature about the acquisition of food and water by riparian populations and communities. We 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. The aims of this article are to review: i) the importance of resources, including water and subsidies, in supporting and maintaining consumer populations along the riparian zone, ii) land use, climate change and invasive species can influence water and subsidies to riparian consumers, iii) riparian consumers are influenced by the altered water availability and subsidies, iv) the dynamic interactions of consumers, hydrology, and subsidies within their ecosystems. Figure 1 presents a framework of relationships among landscape disturbance, hydrological changes, resource subsidies and consumer communities that are discussed in this review.

2 Impacts 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 [9, 18]. The majority deposition of emerging adult aquatic insects occurs in riparian area and the deposition rate into the terrestrial habitats is related to the distance to the water edge [52]. These inputs can be particularly important to consumers during certain periods
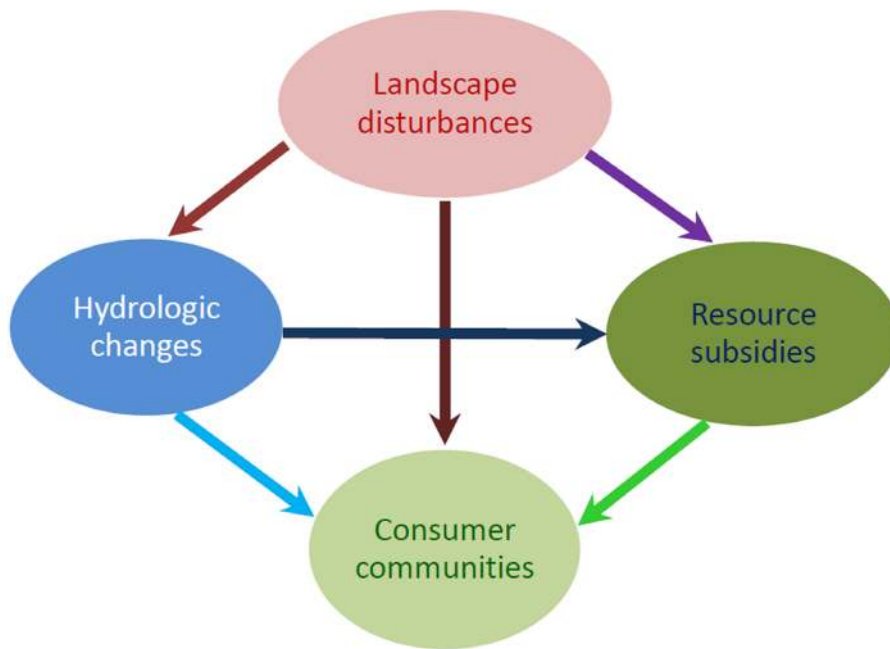
Figure 1: A diagram of relationships among landscape disturbances, hydrological process, subsidies, and consumers.

of low resource availability in recipient ecosystems [53]. The flow of food resources from freshwater to terrestrial ecosystems has the potential to create the high abundance of consumers along the edge of aquatic habitats [17, 54-56]. Since the flux of adult aquatic insects is an important subsidy for many terrestrial consumers / predators [2, 10, 19, 23, 27], managing aquatic and riparian habitats must consider trophic linkage of aquatic resource and terrestrial organisms [1, 4, 17]. This section will focus on studies in the field of subsidies and their impact on specific riparian taxa, including: spiders, birds, mammals, plants, as well as aquatic predators and their particular influence on riparian zone trophic dynamics.

Spiders – Spiders living in riparian zones receive a large proportion of food resources from freshwaters in the form of emerging aquatic insect subsidies [58-60]. Briers et al. (2005) found that over 40% of the diet of riparian spiders comprised of adult aquatic insects, but this decreased to less than 1% at 20 m from the stream [61]. Higher aquatic insect abundance caused higher overall density of spiders [19], but this distribution model was species dependent, and was strongest for horizontal orb weavers (Tetragnathidae), which mainly feed on emerging aquatic insects [19, 29, 58, 60]. Therefore, factors that reduce the flux of emerging aquatic insects, such as the presence of predatory fish, may limit the abundance of terrestrial spiders [29]. However, while the distributional models of web-building spiders are closely linked to the temporal dynamics of aquatic insect subsidies [60], the availability of web-building substrates can also influence

the distribution of spiders [58]. 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. PCBs, heavy metals, methylmercury - MeHg) [62]. And whether spiders 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 [62, 63].

Birds – Riparian habitats often have higher abundance and more species of birds than in adjacent areas [77]. Insectivorous birds rely on emerging insects in riparian zones for their food resource [78], which can maintain their population size, especially when these subsidies were crucial for feeding their young [79]. A study of insectivorous bird density found that bird density fluctuated based on seasonal events [80]. During a resource pulse of insects (in spring) from the aquatic ecosystem, bird density significantly increased in the riparian zone [80]. Insectivorous birds aggregated in riparian habitats because adult aquatic insects were more abundant, especially in spring when the biomass of terrestrial prey is low [81]. Habitat heterogeneous structure relating to stream geomorphology, such as meanders, and stream channel density and frequency associating with drainage-basin geomorphology support the functional relationship of the adult aquatic insect flux and insectivorous bird abundance in riparian areas [81, 82] (Fig. 2, A). Within a watershed, longer and denser stream channels sustained
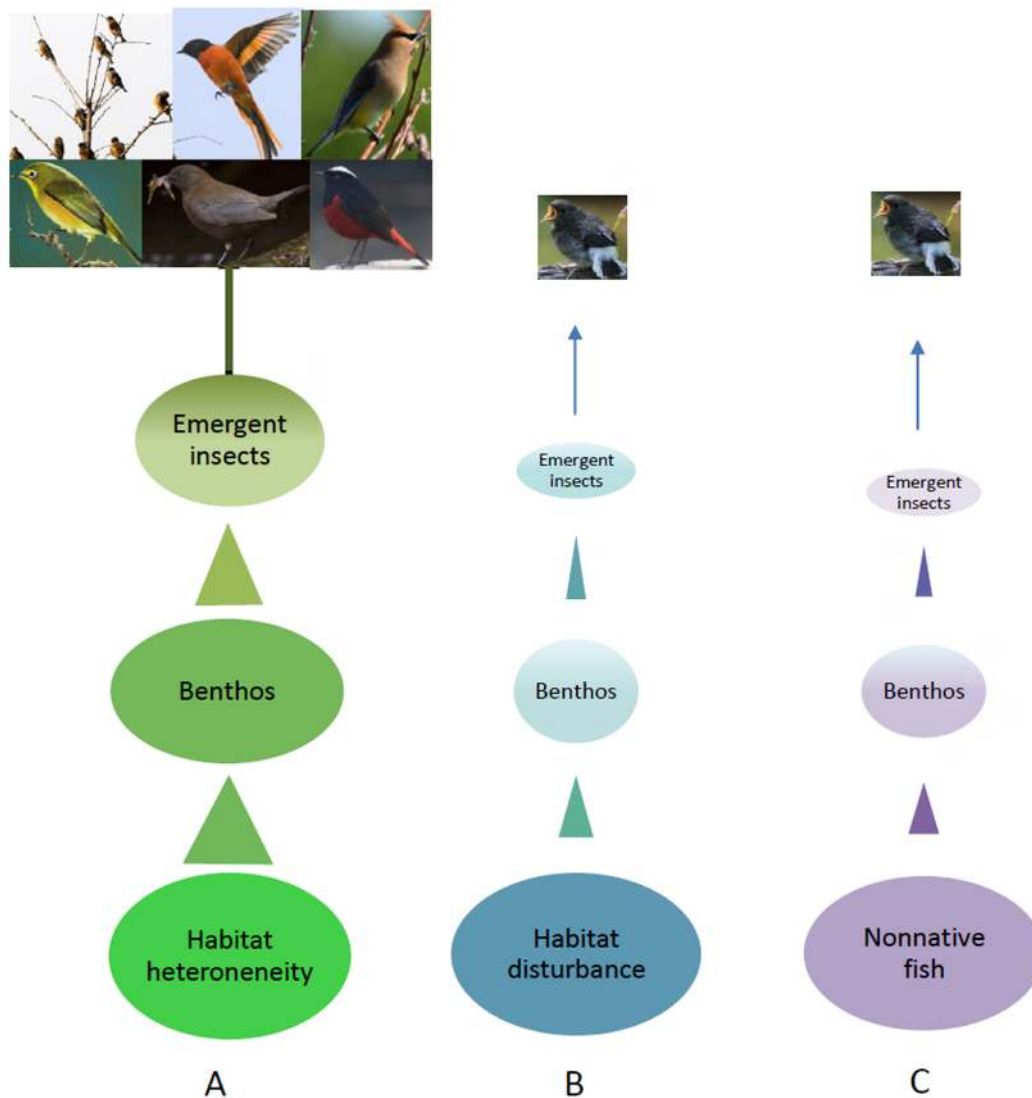
Figure 2: Conceptual model of the influences of (A) habitat heterogeneity (stream meander density), (B) anthropogenic habitat disturbances, such as pollution and flow regulation, and (C) non-native species in streams and rivers on benthic invertebrate diversity and community abundance, and on subsidy flux for birds in riparian ecosystems. A: Habitat heterogeneity enhances benthic communities and supports aquatic insects emerging from aquatic ecosystems, and thus, benefiting birds both on species richness and abundance by supplementing their foods. B and C: Habitat disturbances and non-native species in streams and rivers have negative impacts on benthic communities and cause the reduction of aquatic insect emergence that is related to the food supplies of birds, so that those disturbances limit the strength of cross-ecosystem trophic interactions. The size of ellipse for emergent insects represents the hypothetic community biomass of emerging aquatic insect adults.

higher abundance of adult insects in riparian zone, as well as greater density of insectivorous birds [81], which was a consequence of increases in the length of stream edge and the amount of stream water surface, and increased suitable foraging sites for birds [82]. On the other hand, anthropogenic habitat disturbances, such as river-flow regulation by dams to produce hydropower, can influence bird assemblages through altered aquatic insect emergence [83] (Fig. 2, B). Jonsson et al. (2012) found that cumulative

densities of two feeding groups of birds (seed/large insect feeding and small insect-feeding) in the breeding season were higher along free-flowing rivers than regulated rivers in northern Sweden, which were consistent with the emergence pattern of aquatic insect adults in these river sites [83] (Fig. 2, B). Furthermore, aquatic invasive species can also influence bird foraging activity in riparian areas through indirect effect. Nonnative trout (*Oncorhynchus mykiss aguabonita, O. mykiss, Salvelinus fontinalis*) in five

headwater lakes in the southern Sierra Nevada caused 98% lower mayflies than that in lakes without fish [79]. This difference led to an aggregative response of a local bird Gray-crowned Rosy-Finches (*Leucosticte tephrocotis dawsoni*) to emerging aquatic insects, and there were nearly 6 times more bird at fishless lakes than lakes with fish. Such reduction in the aquatic subsidy due to effects of nonnative trout introduced in the donor system on the resource-limited recipient habitats may have reduced the local bird abundances from historic levels [79] (Fig. 2, C).

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 resource [53, 57, 64-69]. Yoshikura et al. (2011) found that species richness and total abundance of two tree-roosting specialists (*Myotis ikonnikovi, Murina ussuriensis*) and the Japanese large-footed bat (*M. macrodactylus*) were significantly higher in riparian habitats than those in non-riparian habitats [70]. This pattern was related to abundant emerging aquatic insects that are a major food resource for bats. For instance, the majority diet of the long-fingered bat (*Myotis capaccinii*) represented by aquatic insects, up to 62% [71]. Seasonal emergence of aquatic insects was a dominant factor to influence riparian-foraging bat distribution in Japan [53]. The foraging activity level of bats often was correlated with aquatic insect emergence and the strongest peak in bat activity occurred with the peak in aquatic insect emergence in riparian forest [64]. During aquatic insects' peak emergence season, bat foraging activity in areas with natural aquatic insect emergence was nearly 34 times greater than in the treatment areas with limited insect emergence, but after this time period, bat foraging in both areas was shown to be at a similar level, due to the decreased insect resource subsidy [53]. Therefore, factors to alter the magnitude of emerging aquatic insects can influence the foraging activity of bats. This resource-consumer relationship is also indicated by a case of bats benefiting from beavers [72]. Beaver flowages can enhance the production of aquatic invertebrates, with 5 times higher abundance of emerging aquatic insects in the ponds with beavers than without beavers, consequently, *Eptesicus nilssoni* and *Myotis daubentoni* showed 8 times in average more usage of beaver ponds than non-beaver ponds [72]. Yet, prey abundance may not fully explain the activity of insectivorous bats, physical structure may also constrain the accessibility of aquatic insects to bats [73]. Foraging long-fingered bats (*M. capaccinii*) showed a disproportionate use of river stretches with increased accessibility and detectability, i.e. open smooth water surfaces [74]. In addition, bats community structure was related to riparian vegetation characteristics [75]. 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 [76].

Other terrestrial mammals – Mammals are highly mobile consumers. Their presence in riparian zones can have a large impact on the dynamics of riparian trophic systems and modify riparian ecosystem structure and functioning [84-86]. The migrating animals usually evolve to track seasonal variation of available prey such as migration salmons [87]. Many terrestrial mammal consumers (e.g. bears, pine marten, cougar, and wolverine) travel among patched habitats following environmental cues to time the seasonal arrival of peak food "rain" [88, 89]. A suitable example of large mammal predators influencing nutrient dynamics along riparian zones is bears with their salmon prey (marine-derived nutrients, MDN) [84, 90]. Quinn et al. (2009) reported that 49% of chum (*Oncorhynchus keta*) and pink (*Oncorhynchus gorbuscha*) salmon captured by bears (genus *Ursus* L., 1758) were carried into the riparian forests in southeastern Alaska [91]. The consumption of salmon by species varied widely among bears, age class, sex, and location [92, 93]. Studies have shown that bears transferred MDN to terrestrial systems through excrement and urine [94] and to riparian forests by physically moving salmon carcasses [91] via foraging activities to enhance soil nitrogen pools, and thus beneficial to many other terrestrial organisms including plants, beetles, flies, and birds [95-103].

Further, there are other mammals that are not subsidy consumers but play an important role in terrestrial-aquatic subsidies. For instance, hippopotamus can act as ecosystem engineers that transport carbon and nutrients from savanna grasslands to aquatic ecosystems. Daily contribution of *Hippopotamus amphibius* population to Mara River were estimated up to 8,563 kg dry matter, 3,499 kg C, 48 kg P and 492 kg N [26]. And these nutrient subsidies were beneficial to aquatic invertebrate and fish [104]. In addition, some small mammals themselves can be terrestrial subsidies for aquatic consumers. In the Wood River basin in Alaska, rainbow trout (*Oncorhynchus mykiss*) and Arctic grayling (*Thymallus arcticus*) consumed an average 24% (11–38%) mammal prey of Sorex shrews, although these predatory fish were gape-limited [44]. 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 [105], or created suitable habitats for many other species such as bats through the habitat management [72]. Thus, mammals can

enhance trophic and energetic aquatic-terrestrial linkage and affect ecosystem functioning in aquatic systems [86, 106, 107].

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 [5, 10, 39, 56, 108, 109], or as recipient ecosystems for terrestrial consumers to enjoy the aquatic subsidy feast [7, 9, 23, 27, 54], ecologists investigated effects of aquatic subsidies (e.g. organic matter, emerging aquatic insects, salmon carcasses) on riparian plants [97, 100, 110, 111]. As most adults of aquatic insects deposited within 100 m into the land [18], and this nutrient subsidy can significantly affect primary production in nutrient-limited ecosystems adjacent to waterbodies [9]. In one study, midge deposition peaked at 12 kg N·ha^{-1}·yr^{-1} near shore during a high midge-emergence year [9], and this N contribution from midges can be three to five times the level of background atmospheric deposition in the subarctic [112]. Consequently, % N dry weight of willow leaves in high midge sites was 8-11% higher than low-midge sites, and this was further beneficial to the herbivorous insects (*Hydriomena furcata* Thunberg) with 4-6 times higher density and 72% heavier individual biomass [111]. By comparing 50 rainforest watersheds of British Columbia's central coast in Canada, Hocking and Reynolds (2011) found that carcasses of Pacific salmon (*Oncorhynchus* spp.) influenced nutrient loading to plants, and caused shifting plant community structure toward nutrient-rich species that in turn reduced plant diversity in riparian zones [100].

2.1 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 [23-25]. Stream fishes, primarily in the low productivity of the headwaters, often heavily depend on terrestrial insects for prey items [25]. However, their linkage to the riparian food web can be tighter [113], as predators in streams have the potential to produce ecosystem effects on the riparian trophic system throughout aquatic-terrestrial food web linkages [114]. 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 [114]. Such cross-ecosystem connectivity is crucial to assess anthropogenic effects of landscape disturbance on metaecosystem dynamics [115-117].

3 Impacts of landscape disturbance on cross-ecosystem subsidies and riparian consumers

Human-induced disturbances including 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 [106].

Land use – Almost all ecosystems suffer from some degradation due to impacts of land use, such as by agriculture, urbanization and deforestation or forest harvesting [108, 118, 119], which were the dominant changes in the past 100 years and seriously impacted biodiversity and ecosystem functioning at local, regional and global scales [120]. 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 [121]. Aquatic ecosystems are especially 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 [122]. In addition, the consequences of land use are various, including effects on water quality, habitat change, altered canopy cover and sediment inputs [123, 124]. The effects of land use can propagate to adjacent habitats through subsidies and influence adjacent ecosystems (Fig. 1).

- Land use can change 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 (e.g. Trichoptera and Plecoptera) were more related to 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 [119].
- Land use can change 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 were terrestrial

insects in undeveloped lakes, whereas it was only 2% in developed lakes [108].

- Land use can change the 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 [125].
- The impact of land use on ecosystems can last for a long time, i.e. legacy effect. Historical logged streams transport more material subsidies to downstream compare to unlogged streams [126].

Climate change - Global climate change has significant impacts on freshwaters all over the world. Climate warming can alter the size structure of adult aquatic insects, e.g. an increase of 3°C above ambient temperature caused an average of 57-58% fewer emerging Chironomidae. However, total aquatic insect emergence biomass was not influenced by warming, and thus caused an average larger individuals emerging from warm waterbodies [127]. Conversely, another study showed that only the emerging Chironomidae adults were larger with raised temperature, while the emergence of both medium and large-sized insects were decreased, moreover, rising temperature decreased time to emergence [128]. 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 [129]. 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 [130]. 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 [131].

Drought is another aspect of climate change and results in drying of streams and rivers, which has occurred in a higher frequency and a longer period in many parts of the world. The earlier emerging aquatic insects can be induced by drought. Leberfinger *et al.* (2010) found an earlier pupation for 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 [132]. Furthermore, drought can reduce the fluxes of terrestrial organic matter subsidies transfer to streams, thus weaken the linkage between terrestrial and aquatic ecosystems [133]. However, extreme drought may cause unexpected subsidies due to large scale mortality of invasive bivalves, and this unexpected resource subsidy may contribute remarkable amounts of nutrients and energy to the adjacent terrestrial ecosystem [134].

Invasive species - As predators, invasive fish have the ability to reduce the efficiency of the food web as well as overall aquatic insects export [79] and terrestrial insects available to native species [28], which can reduce the magnitude of a resource subsidy and weaken the strength of ecosystem connections [28, 79]. The addition of invasive fish species to a linked stream-forest web in one study showed 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 [28]. 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 [79]. 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, and therefore, altered ecosystem function in stream-riparian food webs [59].

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. The invasive plant species *Rhododendron* has poor leaf quality and densely shaded canopy that reduced leaf litter breakdown and algal production, and transported poorer quality detrital subsidies to stream consumer assemblages [135], which indicates that invasive species may reduce functional diversity [136]. 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, Russian olive (*Elaeagnus angustifolia*) transported 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 predicted stream ecosystem efficiency (i.e. ecosystem respiration/ organic matter input) reduced 14%, and it was a stress for the stream ecosystem [137, 138]. The effects of nonnative species on

recipient ecosystems may be quantity dependent. For example, an invasive alga *Caulerpa taxifolia* reduced the total abundance and species richness of subsidized macroinvertebrates relative to controls, and the adverse effects increased with higher detrital loading [139]. 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 [140]. 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 [141].

However, invasive species may have some positive effects on native species, which have been proved in a wide range of habitats [142]. For example, the engineering activities of invasive beavers caused greater terrestrial derived organic matter subsidies flow into stream food webs in the South American mainland [105]. 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 *Pacifastacus leniusculus* can contribute up to 30% of population diet of a native omnivorous cyprinid fish, European barbel *Barbus barbus* [143].

4 The role of water availability in shaping riparian trophic systems

Trophic effects of water limitation - The influence of hydrology on trophic system within a particular habitat is an essential ecological question for individual organisms and populations in that area [144]. Water may act as a trophic currency determining species interactions in terrestrial food webs [145]. Sabo et al. (2008) found that in riparian areas of reduced freshwater discharge, populations of tree species had leaves laden with groundwater and were consumed by primary consumers such as crickets [34]. Cricket body water content had been shown to be 25% higher near river habitats, so the further an organism's home territory was 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" [34]. 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 [146].

In addition, environmental water conditions, usually categorized as wet or dry, have the potential to impact the consumption habits of riparian consumers [147,

148]. 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 [144]. 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 [147]. These preferences indicate that food consumption can vary across multiple levels of the trophic system depending upon water availability [34, 147]. Seasonal variation of water availability in a desert riparian habitat caused a shift in predator diet, with predators selecting to forage closer to the river during dry conditions and moving further out during wet conditions [148]. 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 [149].

Impact of water availability on riparian community - Looking at the issue of water availability from a larger scale helps scientists understanding the impacts of water availability on an entire community. River drying in the United States has been shown to significantly decreased terrestrial arthropods in riparian zones [150]. A decrease in terrestrial arthropod abundance has the potential to impact all riparian zone consumers, including lizards [2]. In this same vein, a general study of 36 American rivers showed that food chain length increased with drainage area and decreased with discharge variation [151]. While the importance of available water is established, the quality of the water 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 [152].

Riparian zone inhabitants benefit from easily accessing stream water, but also receiving high amount of water from uplands due to the low topographic position [153]. 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 by better soil conditions (e.g. high values in soil pH and nitrogen availability, low in C/N ratio) [153]. 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 [154]. Furthermore, riparian trees in arid zone may developed many strategies to adapt to high groundwater and soil water salinities [155].

Effects of hydrology on cross-system subsidies - Flow regime is a key factor to drive the exchanges of subsidies between linked ecosystems [156] (Fig. 1). Floodplain is one of the most dynamic habitats and is prone to be affected by watershed hydrology. The percentage of floodplain inundated was strongly related to river discharge [157]. Short, stochastic floods stand for a strong environmental stressor which induces pronounced impact on the floodplain community, as well as on dramatic change of plant assemblages (e.g. lower plant diversity, reduced proportion of introduced, weedy, and upland plant taxa) compared to the static wetlands [158]. In addition, anthropogenic disturbances, such as dredging, causing changes in the hydrology of lakes, may reduce algae and detritus inputs to midge habitats, and thus, leading to higher-amplitude fluctuations of midge populations. Consequently, the fish and bird populations that feed on midges were negatively influenced [159]. However, not only do subsidy flux is influenced by hydrology, riparian consumers are also driven by hydrological pressures of the stream because they are required to possess some specific traits. These traits may benefit terrestrial consumers through enhanced aquatic subsidy processing ability, and easier access to the floodplain. Riparian coleopteran species with rapid dispersal ability linked to highest abundance of aquatic prey. While less able consumers were least depend on aquatic subsidy and shifted to a more terrestrial diet under medium inundation stress. However, all trait groups shifted their diet to terrestrial prey in the early spring when inundation pressures were highest [160].

Longitudinally subsidy fluxes within streams and rivers can also be influenced by hydrological change. Wheeler et al. (2015) studied how stream hydrology affected consumer excretion subsidies, and found that the ratio of fish migrant biomass to system size which was measured by discharge, was related to spatiotemporal hydrologic variation [21]. The excretion subsidies that were produced by potamodromous fishes were changed with the maximum influence of consumer feces occurred during low flow periods [21]. The downstream subsidy fluxes were another case that was driven by hydrology. For example, drier conditions induced by climate events such as in-phase El Niño could decrease downstream organic matter flow, which reduced the growth and survival of stream invertebrates, as well as vertebrates that relied on these resource subsidies in recipient systems [133].

Furthermore, the effects of hydrological change on resource subsidies usually combined with human disturbance impacts. Dams and weirs that impound streams and rivers could reduce flow velocities, and enhance nutrient retention because water retention time was longer, and this may further reduce downstream subsidy flux [161]. High flow events, which may rapidly transport both storm inputs and organic matter retained at base flow, 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 [162]. 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 a significant energy subsidy for the estuarine invertebrates, particularly in winter when river discharge was high. However, marine POM may be replaced by river POM to act as an important food resource for the estuarine benthos during the rest time of the year [163].

Seasonal hydrological change is a key driver of aquatic food web structure and ecosystem processes [156]. 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 matter within or between elements of the hydrologic cycle [164], 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 hydrology, but may also be influenced by other factors such as temperature [133, 165]. More aquatic subsidies were consumed in riparian zones of wet-dry tropical rivers in dry seasons in Australia [156, 166]. While riparian predators consume more aquatic insects in wet seasons (50%) than in dry seasons (21%) in Hong Kong [17]. Therefore, while considering the importance of cross-system subsidies for freshwater conservation and restoration, we should take all possible factors into consideration including hydrological change.

5 Implications of resource subsidies for ecosystem conservation

Preserving freshwater ecosystems presents a challenge for maintain a representative sample of freshwater diversity due to overall connectivity and variability of aquatic systems [167]. Décamps (2011) described the term "hotline" specifically for river networks in an attempt to link their diversity as a more linear example of a biological hotspot and imply the necessity for their conservation [168]. Freshwater ecosystems, diverse in species and benefits, are highly threatened and yet in high demand for their numerous ecosystem services [169]. Threats to freshwater biodiversity are numerous, but can be categorized under the following general terms: anthropogenic disturbance, climate change, and invasive species [169]. These changes can influence lotic and lentic systems alike. Anthropogenic activities have cumulative effects on watersheds, and the modification of riparian forests may have impacts on lake communities and food webs [108].

Landscape disturbance pressure on ecosystems is increasing at an alarming rate for preserving biodiversity and protecting ecosystem functioning. Understanding ecological linkage with land and water interaction is crucial to manage terrestrial and aquatic ecosystems [15]. 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 [11]. Fortunately, researchers have started to value the importance of cross-system subsidies while restoring or managing aquatic and terrestrial ecosystems [12, 170]. Saunders and Fausch (2012) compared the impacts of three general grazing systems on terrestrial invertebrate subsidies to adjacent streams and their consumption by trout in northern Colorado [171]. They found that rotational grazing management (either intensive or simple) led to more riparian vegetation, higher input of terrestrial invertebrates, greater terrestrial invertebrate consumption by trout. Rotational grazing systems can effectively maintain terrestrial invertebrate subsidies, which were needed to sustain robust trout populations [171].

Marine subsidies from salmon spawning can be also important for stream restoration as they can increase lipid concentrations, production, and condition of resident and anadromous salmonids in the streams, which may further enhance survival and reproduction of freshwater and marine salmonids [172]. However, this will need to balance between socio-economic barriers and salmon protection, because most salmon are highly commercially valuable fish [173, 174]. 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 trophic subsidy flux such as the abundance, biomass, and species richness of emerging insects. This change in subsidy caused a higher total bird abundance, which reflected a positive numerical response to large-bodied emerging aquatic insects through enhanced biological connectivity between the river and forest [175]. 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 among recovering marsh sites with various ages, or between reference sites and restoration sites [176].

Results from a long-term experiment showed that physical structure alone failed to produce any noticeable changes in production, abundance, or biomass of invertebrates [12], which indicated that the addition of structures without concomitant changes on energy base, i.e., addition of leaf subsidies from riparian trees, did not influence stream benthic assemblages [12]. The community structure of riparian trees is one main factor to influence terrestrial subsidies dynamics. Kominoski et al. (2012) found that peak insect emergence was 1 month earlier and at two to three times greater density in coniferous forest streams than in deciduous and mixed forest streams, but there was no significant difference of total biomass of emerging insects between forest types throughout the study period. In addition, the community structure of aquatic insect emergence varied between deciduous and coniferous forest streams, and deciduous streams held nearly 2 times greater taxon richness and diversity than coniferous forest streams [177]. Moreover, riparian forest community structure is associated with different magnitude of terrestrial prey inputs, for which streams adjacent to conifer forests receive less terrestrial prey subsidies, which may reduce salmon abundance [170].

The research presented in this review highlights the need for preserving resource subsidies as they have the ability to influence ecosystems across all scales, from an individual consumer species, to a riparian community, all the way up to an entire drainage basin. Ecohydrology tonuts the importance of increased riparian habitat complexity due to its ability to amplify the self-purification process [30]. By ensuring that the resource requirements

of riparian consumers are met, even in degraded areas, ecosystem complexity can be maintained.

5.1 Dark sides of cross-system subsidies

Not all cross-system subsidies are beneficial to recipient ecosystems, as subsidies can also propagate pollutants [116, 117, 152] and pathogen [178] to consumers, and lower ecosystem stability [179]. Contaminants in aquatic ecosystems such as heavy metals 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* (4.1 ng/g) and *Tetragnatha* (130 ng/g) compared with contaminated sites [117]. Walters *et al.* (2008) estimated the aquatic insect export of PCBs to the 25 km of Twelvemile Creek riparian zone they sampled was 6.13 g/yr, which is equivalent to the PCBs mass delivered by 50,000 returning Chinook salmon [180]. This high levels of PCBs in terrestrial predators highlight the importance of emerging aquatic insects as "biotransporters" of contaminants to terrestrial ecosystems [181]. 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 was least at the streams with heaviest contamination, 96% reduction among sites. Therefore, spiders were affected the prey biomass reduction [152], but not by the metal exposure or metal flux to land by aquatic insect adults [116]. Interestingly, adult insect emergence may be more sensitive to reflect the impact of low metals concentrations on the communities of aquatic insect when compared to larvae, mainly because adult insect emergence is co-restricted by larval survival and other factors that limit successful emergence [182].

Although many emerging aquatic insects are food resources for various terrestrial consumers, some of adult insects (e.g. blackflies) are pathogen vectors that can attack birds and mammals including human [178]. The biting-rate of a blackfly species (*Simuliidae woodi ethiopiense*) was 9.5/man-hour at 10-1100 hours and was 12/man-hour at 14-1600 hours in August [183]. The blackfly (*Sitnulium innocens*) has been considered to be the prime vector

in the transmission of a blood parasite (*Leucocytozoon simondi*) to Canada geese (Branta Canadensis) goslings, which caused the decrease of population size [184].

Even though we have been aware of some adverse impacts of cross-system subsidies, empirical studies are 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 invertebrates 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, rivers, 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 stenothermal invertebrate species in high altitude and latitude areas may affect the community dynamic of terrestrial consumers due to the decreased insect subsidy fluxes. For others that expand their distribution ranges caused by climate warming, they may also expand the distribution area of pathogens. And this new introduced pathogens carried by emerging aquatic insects can threaten the health of many other organisms including human. Therefore, more empirical and theoretic research works are needed to examine adverse effects of cross-system subsidies.

6 Summary

Riparian ecology and stream restoration must integrate into a broader scale to consider the importance of cross-system linkages such as subsidies and water currency [11]. Riparian zones and their adjacent aquatic ecosystems exchange various types of subsidies (e.g. terrestrial insects, leaf litters, 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 human landscape disturbances, such as land use, climate change and invasive species, so that cross-ecosystem subsidies should be impacted by these changes [119, 127]. Understanding how ecological and physical processes of resource subsidies respond to these changes needs interdisciplinary research approaches, including ecohydrology and ecogeomorphlogy [185], as well as ecological stoichiometry [186] and community and

ecosystem genetics [187, 188]. In addition, land use, climate change and invasive species always interact with each other, and weaken or strengthen the effects on ecosystem functioning and subsidy dynamics, thus complicate the ecological interaction of food webs. Moreover, we should conduct more research about newly emerged cross-system subsidies under changed environmental conditions (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 [143, 189-191], and think more about their effects on subsidy quality, quantity, and fluctuation intensity/frequency [10, 36]. Also, we should not ignore the dark side of cross-ecosystem subsidies [117, 152], which may also influence riparian biodiversity and ecosystem functioning through interactions of resource subsidy fluxes, consumer communities and their ecological feedbacks [192]. Future research should also consider metacommunity framework [193] to understand cross-ecosystem dynamics of subsidy flux in materials and energy influenced by food-web species traits through top-down and bottom-up control in riparian and aquatic ecosystems.

Conflict of interest: Authors declare that they have nothing to disclose.

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