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SYNTHESIS

Integrating the Bright and Dark Sides of Aquatic Resource Subsidies—A Synthesis

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ABSTRACT

Aquatic and terrestrial ecosystems are linked through the reciprocal exchange of materials and organisms. Aquatic-to-terrestrial subsidies are relatively small in most terrestrial ecosystems, but they can provide high contents of limiting resources that increase consumer fitness and ecosystem production. However, they also may carry significant contaminant loads, particularly in anthropogenically impacted watersheds. Global change processes, including land use change, climate change and biodiversity declines, are altering the quantity and quality of aquatic subsidies, potentially shifting the balance of costs and benefits of aquatic subsidies for terrestrial consumers. Many global change processes interact and impact both the bright and dark sides of aquatic subsidies simultaneously, highlighting the need for future integrative research that bridges ecosystem as well as disciplinary boundaries. We identify key research priorities, including increased quantification of the spatiotemporal variability in aquatic subsidies across a range of ecosystems, greater understanding of the landscape-scale extent of aquatic subsidy impacts and deeper exploration of the relative costs and benefits of aquatic subsidies for consumers.

1 | Introduction

Aquatic and terrestrial ecosystems are intimately linked through reciprocal fluxes of dietary energy and materials (Nakano and Murakami 2001; Baxter et al. 2005; Marleau et al. 2020; Little et al. 2022). Terrestrial ecosystems have long been considered important sources of nutrients, organic matter and contaminants to aquatic ecosystems (Fisher and Likens 1973; Junk et al. 1989; Likens and Bormann 1974). Because of the concave shape and lower position of aquatic ecosystems in the landscape (Leroux and Loreau 2008), terrestrial subsidies concentrate in aquatic ecosystems and they

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are often on the same order of magnitude as aquatic primary production (Gounand et al. 2018). Subsidies from aquatic to terrestrial ecosystems move against this gravitational gradient via seasonal flooding, animal emergence and direct transport by terrestrial consumers (Junk et al. 1989; Quinn et al. 2009). Aquatic-to-terrestrial subsidies are sparser, around 2–3 orders of magnitude smaller than rates of terrestrial production (Gounand et al. 2018). However, both aquatic and terrestrial consumers use allochthonous resources at similar rates (Allen et al. 2024). This difference in the relative magnitude versus assimilation of aquatic vs. terrestrial subsidies may be because aquatic subsidies are generally of relatively higher quality (Harvey et al. 2023; Pichon et al. 2023; Závorka et al. 2023), which can offset asymmetries in resource quantity and lead to spatial complementarity at the meta-ecosystem scale (Pichon et al. 2023).

Aquatic subsidies are often rich in elemental nutrients that can be limiting for terrestrial consumers (Twining et al. 2019; Figure 1). Moreover, physiologically important omega-3 long-chain polyunsaturated fatty acids (n-3 LC-PUFA), which are virtually absent in terrestrial primary producers, are often abundant in aquatic food webs (Twining, Brenna, Hairston Jr, and Flecker 2016; Twining, Brenna, Lawrence, et al. 2016). However, aquatic ecosystems can also be a significant source of contaminants transferred to land, often referred to as the ‘dark side’ of resource subsidies (Walters et al. 2008; Figure 1). Aquatic ecosystems aggregate a range of contaminants from across watersheds, including both organic and inorganic contaminants (Schmidt et al. 2012; Drenner et al. 2013; Bishop et al. 2020; Smalling et al. 2021; Waite et al. 2021; Nowell et al. 2024). In some cases, contaminants reduce aquatic biomass and thus aquatic-to-terrestrial fluxes (Kraus, Schmidt, and Walters 2014; Kraus et al. 2020). In other cases, aquatic consumers, from insects to fish to amphibians, can end up transporting contaminants back to land in often more concentrated, organic forms linked with potentially limiting nutrients that can be readily assimilated by terrestrial consumers (Vander Zanden and Sanzone 2004; Walters et al. 2008; Drenner et al. 2022). Riparian and coastal zones are often hotspots of consumer foraging, facilitating the consumption and transfer of aquatic subsidies and associated contaminants farther inland than they would reach through abiotic vectors alone (e.g., Raikow et al. 2011; Gerber et al. 2023). Consequently, aquatic subsidies can play outsized positive as well as negative roles in ecosystem function, even when relatively small in magnitude (Marcarelli et al. 2011; Bartels et al. 2012).

Global change processes are increasingly shifting the balance of aquatic resource quantity and quality in a myriad of ways. Land use changes can increase inputs of sediment, nutrients and contaminants from terrestrial to aquatic ecosystems, which can decrease the quantity of aquatic-to-terrestrial subsidies while also changing their quality (Larsen et al. 2016; Kraus, Walters, et al. 2014). Climate change can increase temperatures and alter hydrological regimes (Häder and Barnes 2019), which may foster conditions that increase contaminant loads (Hall, Cobb, et al. 2020; Hall, Woo, et al. 2020), while also altering the phenology of both aquatic and terrestrial consumers (Shipley et al. 2022). Biodiversity loss can lead to declines in native species and changes in community composition (Rumschlag et al. 2023) that can lead to loss of biomass and functional trait diversity of aquatic subsidies and alter the ratio of nutrients to contaminants (Brandt et al. 2024). Together, these processes can shift the relative cost: benefit ratio of aquatic subsidies for consumers, which may lead to riparian and coastal habitats becoming ecological traps for consumers who rely upon aquatic subsidies only to find them increasingly laden with contaminants.

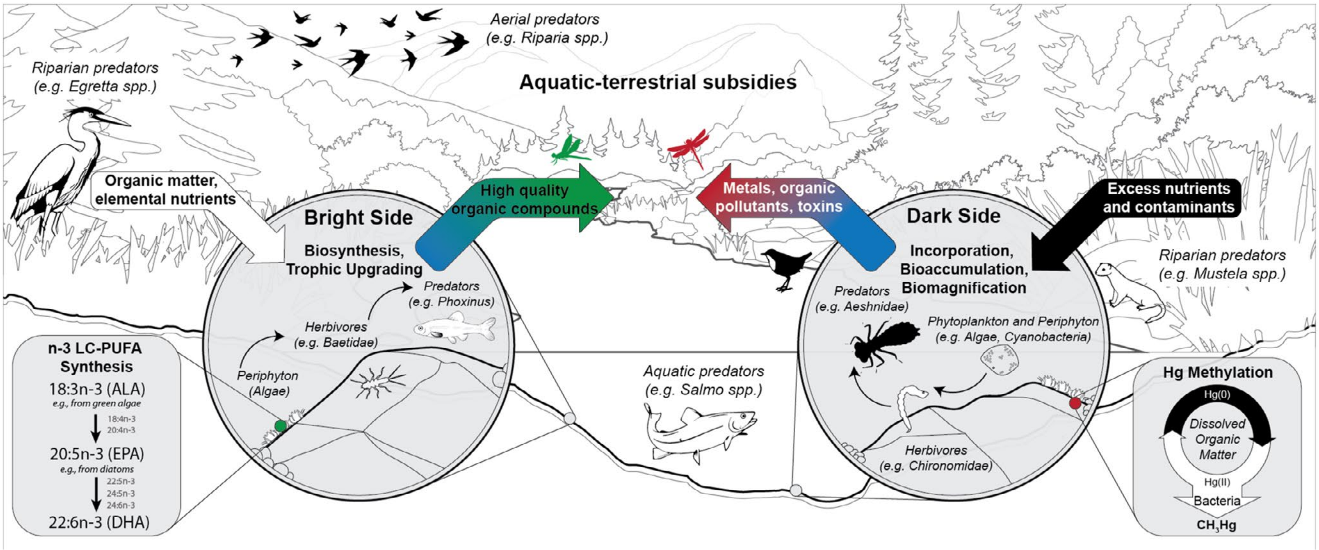

FIGURE 1 | Terrestrial inputs of organic matter and nutrients to aquatic ecosystems can fuel aquatic primary production, including the production of limiting resources such as omega-3 long-chain polyunsaturated fatty acids (n-3 LC-PUFA). Aquatic ecosystems also can accumulate contaminants from the watershed, which may be further transformed by aquatic ecosystem processes (e.g., mercury methylation). Primary and secondary consumers may assimilate both resources and contaminants in aquatic ecosystems and transport them back to the terrestrial ecosystem through biotic and abiotic pathways. These aquatic-terrestrial subsidies can provide both critical resources (‘bright side’) and contaminants (‘dark side’) for terrestrial consumers such as birds, mammals, or arthropods like spiders and eventually humans.

Here, we review the state of research on aquatic-to-terrestrial subsidies with a focus on several key processes that transform the quality of resources within freshwater ecosystems (Figure 1). First, we highlight multiple aspects of aquatic resources, from algae to animals, that make them particularly high quality for a diversity of consumers—the 'bright side' of resource subsidies. We then synthesise research on the 'dark side' of aquatic-to-terrestrial subsidies, explaining how freshwater ecosystems can simultaneously serve as sources of harmful compounds. Finally, we discuss how global change is altering key transformative processes that occur within water and influence the quantity and quality of subsidies. We end by highlighting the benefits of greater integration between basic food web ecology research on the bright side of subsidies with more applied ecotoxicology research on the dark side of subsidies.

2 | The Bright Side of Subsidies

2.1 | Dietary Energy

Aquatic ecosystems, from lakes and ponds to rivers and streams, can be important sources of dietary energy that subsidise primary producers as well as consumers in adjacent terrestrial food webs (Naiman et al. 2002; Schindler et al. 2003; Baxter et al. 2005; Figure 1). Differences in the phenological timing of subsidies, and their quantity (e.g., biomass) and quality (e.g., nutrient or contaminant content), can significantly impact how subsidies influence production in recipient ecosystems (Subalusky and Post 2019). In temperate forested streams, aquatic-to-terrestrial subsidies are typically greatest during early spring insect and amphibian emergence prior to leaf-out (e.g., Nakano and Murakami 2001; Baxter et al. 2005), while in temperate lakes large fluxes of insect biomass often continue throughout the summer (e.g., Martin-Creuzburg et al. 2017). Though aquatic subsidies may be greatest during the spring and/or summer, small fluxes of emergent insects that continue during the winter, thanks to the greater thermal inertia of water compared to air, can be extremely important resources for riparian consumers in temperate areas where terrestrial insect biomass is near zero (e.g., Nakano and Murakami 2001; Iwata et al. 2003). Spatially, the importance of subsidies is typically greatest along ecotones, such as coastal, littoral and riparian areas. However, landscape characteristics of both the donor (i.e., subsidy source) and recipient (i.e., subsidy destination) ecosystems can enhance or constrain such subsidies. For example, aquatic subsidy availability in terrestrial ecosystems typically decreases with distance from shore (Gratton and Vander Zanden 2009; Muehlbauer et al. 2014; Chari et al. 2020). Steep banks or confined valleys can further limit the transfer of nutrients via emerging insects (Power and Rainey 2000; Hagen and Sabo 2011). Meandering or braided streams and rivers with complex stream edges promote high riparian connectivity and subsidise a diversity of terrestrial predators, such as birds during periods of low abundance of terrestrial prey in the winter (Iwata et al. 2003). Depth and shape influence subsidy magnitude in lakes, whereby deeper lakes with larger pelagic zones export smaller per area subsidies to riparian consumers compared with ponds or shallower lakes with larger littoral zones (Fehlinger et al. 2022; Martin-Creuzburg et al. 2017; Mathieu-Resuge et al. 2021).

2.2 | Nutrients

Resource quality across both aquatic and terrestrial ecosystems is often defined in terms of the stoichiometric ratio of carbon to essential elemental nutrients, such as nitrogen or phosphorus (Elser, Fagan, et al. 2000; Elser, Sterner, et al. 2000). Terrestrial vegetation typically has the highest C:N and C:P ratios, while algae, animals and heterotrophic microbes like fungi and bacteria typically have C:N and C:P ratios that are several orders of magnitude lower (Elser, Fagan, et al. 2000). Vegetation, especially leaves, tends to dominate terrestrial-to-aquatic subsidies, with smaller inputs of higher protein and lower C:N terrestrial insects, large animal carcasses, or faeces (Baxter et al. 2005; Edwards and Huryn 1995; Mason and MacDonald 1982). In contrast, most aquatic-to-terrestrial subsidies tend to be in the form of animal bodies, such as the emerging adult phases of aquatic insects or fish that are transported to riparian ecosystems by other consumers. For example, migratory fish like salmon or suckers that are rich in both P and N are important resources for P-limited stream food webs (e.g., Gende et al. 2002, 2004; Childress and McIntyre 2015; Kurasawa et al. 2024) and also a substantial source of aquatic-derived N to riparian trees and shrubs (Helfield and Naiman 2001). Aquatic primary producers can also subsidise consumers from terrestrial systems either when consumed from the water (Bakker et al. 2016; Lopez et al. 2020) or when receding water exposes algal mats (Bastow et al. 2002). Aquatic subsidies rich in essential elemental nutrients can also increase soil nutrients (Dreyer et al. 2015), terrestrial plant production (Bultman et al. 2014) and terrestrial predator biomass (Eriksson et al. 2021), which may alter top-down effects on terrestrial prey (Henschel et al. 2001; Sabo and Power 2002).

Fatty acid composition also varies fundamentally between aquatic and terrestrial ecosystems starting at the base of food webs (Hixson et al. 2015; Twining, Brenna, Hairston Jr, and Flecker 2016), creating further differences in the quality of aquatic versus terrestrial subsidies for consumers. Aquatic primary producers including phytoplankton, benthic algae and some aquatic plants produce n-6 as well as n-3 LC-PUFA, which are essential for somatic growth, reproduction and survival of consumers (Twining, Brenna, Hairston Jr, and Flecker 2016). In contrast, terrestrial plants have relatively poor capabilities for producing LC-PUFA and tend to have higher ratios of n-6 to n-3 PUFA (Hixson et al. 2015; Twining, Brenna, Hairston Jr, and Flecker 2016). LC-PUFA are critical structural components of cell membranes, are required as parts of many metabolic pathways and can be used to store energy (Arts et al. 2001). Crucially, unlike stoichiometric differences which are most pronounced at lower trophic levels (Elser, Fagan, et al. 2000), differences in PUFA composition also persist at higher trophic levels (Hixson et al. 2015; Twining, Brenna, Hairston Jr, and Flecker 2016). For instance, aquatic insects have substantially higher n-3 LC-PUFA content than terrestrial insects (Parmar et al. 2022). These differences arise when aquatic animals consuming aquatic primary producers retain LC-PUFA (Strandberg et al. 2015), which can then accumulate at higher trophic levels (Guo et al. 2017).

Aquatic LC-PUFA can be transferred to land via a variety of pathways, including emerging insects or amphibians (e.g., Martin-Creuzburg et al. 2017; Moyo et al. 2017; Fritz et al. 2019), terrestrial consumers feeding directly on freshwater prey (e.g., Koussoroplis et al. 2008) and terrestrial carcass-scattering during major fish migrations (e.g., Gende et al. 2004; Gladyshev et al. 2009). The quality and quantity of LC-PUFA exported from aquatic to terrestrial ecosystems depend on a variety of factors, including the composition of both aquatic primary producers (Guo et al. 2017; Moyo and Richoux 2022) and consumers (e.g., Martin-Creuzburg et al. 2017; Mathieu-Resuge et al. 2022). Aquatic subsidies of LC-PUFA can represent substantial benefits for growth, condition, immune function and reproduction of terrestrial consumers, such as birds (Twining, Brenna, Lawrence, et al. 2016; Twining et al. 2018, 2019) or spiders (Fritz et al. 2017; Kowarik et al. 2021; Kirschman et al. 2024) in riparian zones. Thus, even when small relative to terrestrial subsidies, aquatic resources can be exceptionally important for consumers and ecosystems in adjacent habitats due to their quality (Twining et al. 2019).

3 | The Dark Side of Subsidies

Freshwaters collect and concentrate contaminants throughout their watersheds, which can lead to widespread contamination in many aquatic systems and subsequent impacts on ecosystem function (Fleeger et al. 2003). These contaminants can impact the quantity, quality, timing and composition of aquatic-to-terrestrial subsidies (Figure 1) by: (1) reducing aquatic production and subsequently aquatic-to-terrestrial subsidies, (2) accumulating in tissues of aquatic consumers that subsidise terrestrial ecosystems and (3) becoming more concentrated at higher trophic levels in aquatic consumers that serve as subsidies. Contaminant classes, such as trace metals, organo-metals, pharmaceuticals, pesticides and persistent organic pollutants (POPs) differ in the types of effects they have on subsidies (Kraus 2019; Kraus et al. 2020). For example, organo-metals like methylmercury (MeHg) and non-insecticide POPs tend to accumulate in aquatic insect larvae and be retained in the bodies of the adult aquatic insects, thus altering the quality of aquatic-to-terrestrial subsidies (Walters et al. 2008, 2016). On the other hand, trace inorganic metals, insecticides and other compounds that are highly toxic to aquatic insect larvae generally exhibit limited accumulation, and instead decrease aquatic secondary production (e.g., Carlisle and Clements 2003) and emergence (Paetzold et al. 2011; Kraus, Walters, et al. 2014), thus reducing aquatic subsidy quantity (Schmidt et al. 2013, 2022; Wesner et al. 2014; Miller et al. 2020).

3.1 | Metal(Loid)s

Metals enter aquatic ecosystems from the atmosphere through both natural processes like volcanoes and volatilization from soils or water as well as through industrial processes (Nriagu and Pacyna 1988). Trace metals (e.g., Cu, Cd and Zn) from hardrock mining and natural mineralization can also leach into surface and groundwater from tailing piles, open mining tunnels, soil and exposed rock (Schmidt et al. 2012). Sulfur oxidation in minerals can generate acidity that lowers pH and further elevates dissolved metal concentrations and bioavailability in aquatic ecosystems (Balistrieri et al. 2020). Unlike trace metals, the metal(oid)s mercury, selenium and arsenic can enter aquatic ecosystems in both inorganic (e.g., Hg^{2+}) and organic forms (e.g., MeHg) and can be converted from inorganic to organic forms by bacteria, primary producers, or other biotransformative processes (Stadtman 1974; Gilmour et al. 2011, 2013). Environmental conditions can influence the bioavailability of all metals and metalloids, which in turn impacts their bioaccumulation and toxicity. For example, the bioaccumulation of trace metals and inorganic metalloids within biota is largely determined by the bioavailable fraction of the metal in the environment (e.g., sediment, water and diet). Trace metals can be very toxic to organisms at lower trophic levels, but they tend to be excreted through processes like metamorphosis and trophic transfer and thus do not bioaccumulate within food webs (Pickhardt and Fisher 2007; Mathews and Fisher 2008; Revenga et al. 2012; Kraus, Walters, et al. 2014; Herman et al. 2021). Similarly, the availability of organic metalloids (e.g., Chapman et al. 2010; Rahman et al. 2012; Erickson et al. 2019) like MeHg for aquatic consumers, such as insect larvae, zooplankton and fish, depends on environmental conditions that favour the production of MeHg, especially redox conditions at the sediment/water interface (Ullrich et al. 2001; Tang et al. 2020). MeHg availability also depends on the biomass of primary producers: higher primary producer biomass generally results in lower MeHg content per unit biomass (i.e., MeHg biodilution; Pickhardt et al. 2002), which in turn results in lower MeHg content in aquatic consumers (Walters et al. 2015). However, in contrast to trace metals, organic metalloids accumulate more readily within biota, are well-retained across life stages like metamorphosis and in the case of MeHg biomagnify along food chains (e.g., Lavoie et al. 2013). Much of the toxic effects of organic metalloids, therefore, occur at higher trophic levels (Basu and Head 2010; Hallinger et al. 2011; Chételat et al. 2020), although metalloids differ in their toxicity at the base of the food web depending on chemical species (Chapman et al. 2010; Rahman et al. 2012; Erickson et al. 2019).

As a result of these differences in bioaccumulation and toxicity, trace metals and organic metals like MeHg have very different impacts on aquatic-to-terrestrial subsidies (Kraus 2019; Kraus et al. 2020). For example, animal-mediated fluxes of MeHg from aquatic to terrestrial food webs can be driven by food web structure and nutrient concentrations as well as the MeHg contents of consumers themselves (Chumchal and Drenner 2015, 2020). Specifically, predators like fish can decrease emergent insect fluxes of MeHg, while nutrients and MeHg accumulation in predatory insects can increase emergent insect fluxes of MeHg. MeHg contents in riparian insectivores are also correlated with insect-mediated fluxes of MeHg (e.g., Twining, Bernhardt, et al. 2021; Twining, Razavi, et al. 2021). Unlike MeHg, insect-mediated fluxes of trace metals tend to be negatively correlated with bioavailable concentrations of trace metals, which are highly toxic to insect larvae (Schmidt et al. 2010; Mebane et al. 2020) and metamorphosing insects (Schmidt et al. 2013; Wesner et al. 2017). Consequently, high concentrations of trace metals in aquatic ecosystems typically reduce emergent insect biomass and prevent contaminants from moving into terrestrial ecosystems (Paetzold et al. 2011; Kraus, Schmidt, and Walters, 2014). As a result, trace metals impact riparian insectivores indirectly through their effects on emergent insect biomass (Kraus, Schmidt, and Walters, 2014). Comparing the physico-chemical properties of individual compounds to their retention across metamorphosis can help predict their potential for bioaccumulation. The propensity for inorganic trace metals to be retained across metamorphosis appears related to their protein-binding affinity (Kraus, Walters, et al. 2014; Bogstie et al. 2024), and detoxification processes that mineralise the metal (Wanty et al. 2017). For instance, trace metals are more toxic to insect larvae and less likely to be retained across metamorphosis than organic metals such as MeHg or selenium. These patterns explain why contaminant content in riparian insectivores, such as spiders and swallows, is much more effective as a sentinel of MeHg and selenium pollution than for trace metal pollution (Alberts et al. 2013; Otter et al. 2013; Chumchal et al. 2022).

3.2 | Organic Pollutants

Organic pollutants as a group are extremely diverse in terms of their source, accumulation in biota and behaviour within aquatic ecosystems. Similarly to metals, organic pollutant contents vary based on landscape context, their physico-chemical properties and other aspects of water quality like temperature and dissolved oxygen content. Unlike most metals, organic pollutants contain carbon-nitrogen or carbon–carbon bonds. Numerous organic pollutants have been studied with respect to their effects on aquatic-to-terrestrial subsidies, including polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons (PAHs), pharmaceuticals and endocrine-disrupting chemicals, flame retardants, pesticides (i.e., herbicides, insecticides and fungicides) and surfactants and antifouling adjuvants (added to chemical mixtures). Some of these classes, such as PCBs, historically used insecticides (e.g., dichlorodiphenyltrichloroethane [DDT]) and dioxins, are considered persistent organic pollutants (POPs), which are mostly highly lipophilic halogenated organic compounds that do not readily break down in the environment and are extremely toxic to humans and other organisms. Unfortunately, because they are fat soluble, these highly toxic lipophilic compounds often bioaccumulate and biomagnify within both terrestrial and aquatic food webs (e.g., Vander Zanden and Rasmussen 1996; Kelly et al. 2008; Kelly and Gobas 2003). Other compounds, such as PAHs and some current pesticides, are more likely to be metabolised within organisms, and as such show a pattern of biodilution with trophic transfer higher up the food web (e.g., Erasmus et al. 2020; Fu et al. 2022; Jin et al. 2023).

As a result of these differences in patterns of accumulation and toxicity, organic contaminants vary greatly in their impacts on aquatic-to-terrestrial subsidies (Kraus 2019; Bundschuh et al. 2022). Persistent organic contaminants like PCBs that are not highly toxic to aquatic animals can accumulate and then enter terrestrial food webs as subsidies, e.g., via aquatic insect emergence or consumption of contaminated fish. For example, contents of such compounds in riparian spiders eating aquatic insects can be closely related to the contents of these compounds in river sediment (Walters et al. 2010). Migratory fishes, such as salmonids, that move across multiple aquatic ecosystems as part of their life cycle can also be important vectors of persistent organic contaminants into both aquatic (Merna 1986; Gerig et al. 2018) as well as riparian food webs (Morrissey et al. 2012). Other organic compounds like PAHs appear to be metabolised during metamorphosis and biodilute within food chains, making them less of a threat to subsidised terrestrial food webs. For instance, the concentration of PAHs in adult *Chironomus* (Meigen 1803; non-biting midges) was 2.9 times higher in larvae than in adults, making them (or at least their parent compounds) less of a threat to subsidised terrestrial food webs. However, compounds belonging to many classes of compounds like pharmaceuticals and personal care products, endocrine-disrupting chemicals, pesticides and flame retardants appear to vary greatly in their bioaccumulation properties within those classes and thus in their effects on aquatic-terrestrial linkages (Richmond et al. 2018; Previšić et al. 2021; Rosi et al. 2023).

Understanding the relative toxicity and bioaccumulation of contaminants in insects may help us estimate insect-mediated contaminant fluxes from aquatic to terrestrial food webs. For example, the octanol–water partitioning coefficient (log K_{ow}), which is a metric of how soluble the compound is in lipids compared with water (i.e., lipophilicity) and the size of the compound, appears to be related to the retention of some contaminants across metamorphosis. In a meta-analysis, Kraus, Walters, et al. (2014) found that log K_{ow} was negatively correlated with the metamorphic retention of less lipophilic (log $K_{ow} < 5$; mainly PAHs) and larger compounds, and positively correlated for more lipophilic (log K_{ow} 5–7) and smaller compounds (Liu et al. 2018). Liu et al. (2021) also found a negative relationship between log K_{ow} and metamorphic retention for organophosphorus flame retardants and plasticizers with log K_{ow} ranging from ~0 to 10. Consequently, Kraus (2019) predicted that current-use insecticides, which are not expected to accumulate in insect tissues but are expected to reduce metamorphosis, should lead to reduced emergence and decreased insecticide flux from contaminated waters.

However, the most recent studies in this area have failed to show a consistent relationship between physico-chemical properties and metamorphic retention of organic compounds. In fact, empirical work suggested that while current-use insecticides accumulated in wetland insects and led to a 43% decline in emergence biomass, there was also a 50% increase in overall pesticide flux via emergent insects across an insecticide gradient (Kraus et al. 2022). Additional recent studies also suggest that emergent aquatic insects can indeed be important sources of current-use pesticides, including those with log $K_{ow} < 5$ as well as neonicotinoids, for riparian ecosystems (Roodt et al. 2022; Roodt, Huszarik, et al. 2023; Roodt, Schaufelberger, and Schulz 2023), and that such pesticides can bioaccumulate in both emerging aquatic insects as well as in riparian spiders (Roodt, Huszarik, et al. 2023). However, at very high doses, such pesticides are lethal to most taxa, resulting in major declines in emergent insect biomass and thus minimal organic contaminant transport (Barmentlo et al. 2021). Given the strong negative effects that current-use pesticides like neonicotinoids can also have on terrestrial vertebrates (Eng et al. 2017, 2019), more research on the transfer of such compounds across aquatic-terrestrial meta-ecosystems will help fill this current knowledge gap.

3.3 | Cyanobacterial Toxins

Another group of harmful organic compounds that largely originate in aquatic systems and have the potential to alter the quality of aquatic-terrestrial subsidies are cyanobacterial toxins. Cyanobacteria comprise a diverse group of prokaryotic organisms of which many can produce secondary metabolites that are potentially harmful to consumers (Sivonen 1996). As the frequency of toxic cyanobacterial blooms increases, their effects on aquatic and nearby terrestrial communities are of increasing interest and concern. Cyanobacteria can expose zooplankton and other consumers to cyanobacterial toxins. These toxins may affect aquatic-to-terrestrial subsidies by altering aquatic subsidy production as well as through bioaccumulation. The sensitivity of emergent aquatic insect larvae to cyanobacterial toxins has not yet been studied systematically (Fadel et al. 2023). The available studies have focused mostly on microcystins, a well-studied group of harmful secondary metabolites produced by many cyanobacteria, especially those of the genera *Microcystis*, *Anabaena*/*Dolichospermum* and *Planktothrix*. In mosquito larvae, microcystin exposure has been reported to damage the epithelial cells of the midgut, increase mortality (Saario et al. 1994) and delay development (Rey et al. 2009). In larvae of the *Ecdyonurus angelieri* (Thomas 1968; mayfly), microcystin accumulation has been shown to cause severe histological damage in the fat body and alterations in the tracheal system, thus increasing mortality (Liarte et al. 2014). In general, however, it seems that invertebrates, including aquatic insect larvae, may be less sensitive to these toxins compared to mammals (Stewart et al. 2008), which experience neurotoxicity from cyanobacterial poisoning that often leads to death.

Researchers are just beginning to study fluxes of cyanobacterial toxins across the aquatic-terrestrial interface. For instance, larvae of non-biting midges have been shown to feed on cyanobacteria and to accumulate microcystins as well as the potent neurotoxin anatoxin-a in high amounts without experiencing increased mortality (Toporowska et al. 2014). Microcystins have also been shown to accumulate in larvae of the genus *Hexagenia* (Walsh 1863; mayfly) and to be present in the terrestrial adult life stage, suggesting that emergent aquatic insects could be important vectors for the transport of cyanotoxins across the aquatic-terrestrial interface (Moy et al. 2016; Woller-Skar et al. 2020). Moy et al. (2016) reported the transfer of microcystins from *Hexagenia* mayflies to their consumers, that is, spiders and *Protonotaria citrea* (Boddaert 1783; Prothonotary Warblers). In Prothonotary Warblers, the highest microcystin concentrations were found in nestlings, especially at sites where the nestlings received higher proportions of aquatic insects in their diet. A recent study found that microcystins derived from *Planktothrix* accumulate in zooplankton, but not in emergent aquatic insects, including *Chaoborus* (Lichtenstein 1800), whose larvae feed on zooplankton (Riehle et al. 2024). In general, the microcystin content seems to be lower in secondary consumers, suggesting biodilution (Ferrão-Filho and Kozlowsky-Suzuki 2011). However, the bioaccumulation of microcystins in emerging insects might be species-specific (Poste et al. 2011; Cianci-Gaskill et al. 2022; Glidewell et al. 2024). Whether this is also true for other cyanobacterial toxins across the aquatic-terrestrial boundary is unclear. In light of the predicted increase in the frequency and severity of harmful cyanobacterial blooms (see below), understanding the trophic transfer of cyanobacterial toxins within aquatic food webs and across ecosystem boundaries will become increasingly relevant.

4 | Global Change Impacts on Aquatic-to-Terrestrial Subsidies

Global change processes are increasingly shifting the balance between the 'dark' and 'bright' sides of cross-ecosystem subsidies. Interacting processes like land use and climate change are already altering factors including the timing, magnitude and, especially, the quality of aquatic subsidies (Manning and Sullivan 2021; Schulz et al. 2023). For example, the net effect of aquatic to terrestrial subsidies can shift from beneficial to harmful with increased inputs of contaminants in areas with intensive anthropogenic land use. This shift has the potential to turn riparian zones and their associated resource subsidies into ecological traps for consumers, who may continue to use them as important resources despite their new contaminant load (e.g., Hale and Swearer 2016). Human-induced climate and land-use change are also expected to influence species composition, production and phenology in riparian and aquatic ecosystems (Larsen et al. 2016), in turn altering subsidy quantity, quality and temporal dynamics at the aquatic-terrestrial boundary (Jentsch and White 2019). In particular, climate change has a high potential to shift the phenology and variability of subsidies, making them either more or less pulsed (Nash et al. 2023; Leathers et al. 2024), as well as changing their nutritional quality (Strandberg et al. 2020; Twining et al. 2022; Shipley et al. 2022). Biodiversity change within aquatic ecosystems, often driven by land use intensification and/or climate warming (Haase et al. 2023; Wilkes et al. 2023), also has the potential to further alter the dynamics and quality of aquatic to terrestrial fluxes. Such changes in subsidy characteristics will interact with characteristics of the recipient ecosystem, such as the phenology of producers and consumers (Subalusky and Post 2019).

4.1 | Land Use Change

Land use changes, such as agricultural intensification and urbanisation, often result in changing inputs of contaminants, sediment and elemental nutrients from terrestrial ecosystems. In turn, this can alter both the quality and quantity of aquatic-to-terrestrial subsidies (e.g., Krell et al. 2015; Larsen et al. 2016; Figure 2a). For example, aquatic ecosystems polluted by trace metals are likely to have reduced emergent insect biomass (Paetzold et al. 2011; Kraus, Schmidt, and Walters 2014). Direct inputs of elemental nutrients from terrestrial ecosystems, such as those from intensive agriculture or sewage discharges in human-impacted landscapes, can also likely have strong effects on aquatic ecosystems (Watzin and McIntosh 1999), and their subsidies. For instance, some studies suggest that increased N and P inputs may boost aquatic primary productivity, translating into larger aquatic subsidies in agricultural areas compared to forested areas (Carlson et al. 2016; Raitif et al. 2022). However, high levels of elemental nutrients can shift aquatic primary producer composition towards cyanobacteria that are less palatable, nutritionally inadequate (e.g., lacking sterols and n-3 LCPUFA) and potentially toxic (Martin-Creuzburg and von Elert 2008).

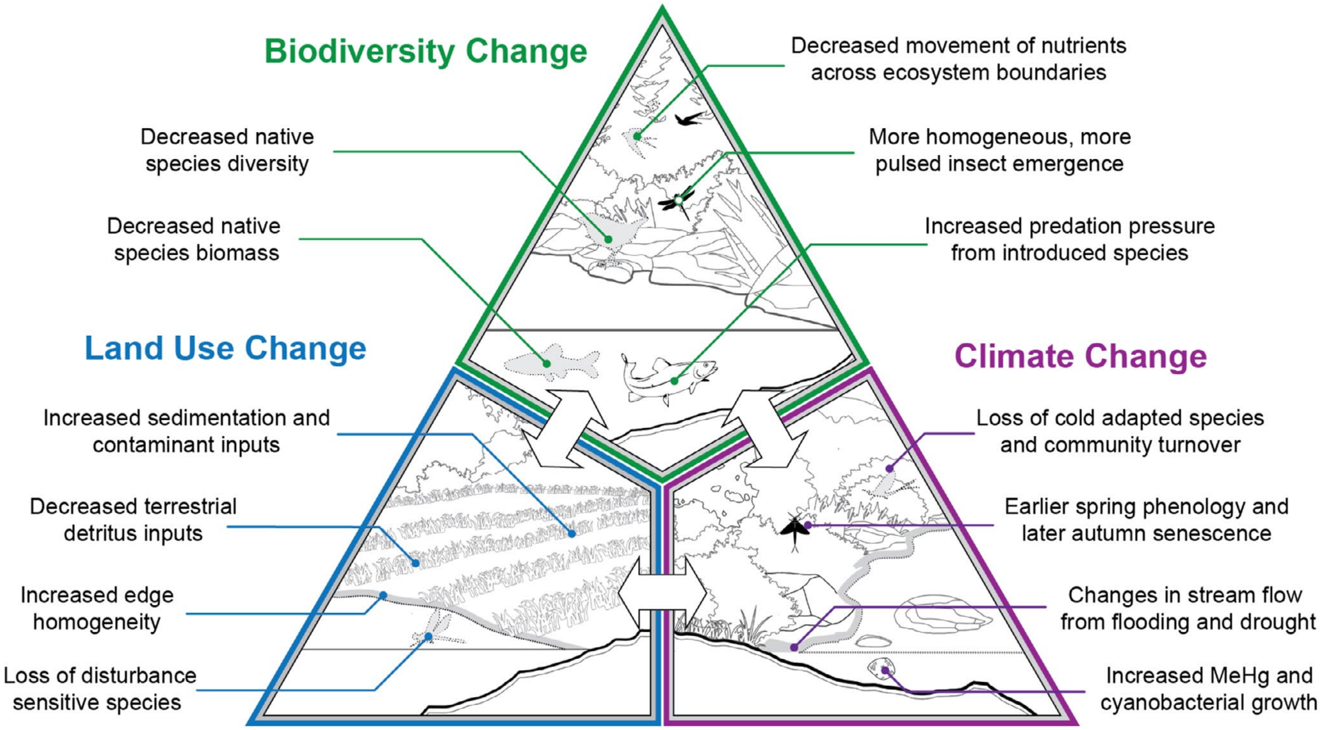

FIGURE 2 | Both the bright and dark sides of resource subsidies can be shaped by several inter-linked (arrows between sections) drivers of global change. (a) Land use change can alter inputs from terrestrial to aquatic ecosystems, often increasing sediment, nutrients and contaminants and lead to changes in aquatic community structure. Together, these changes may lead to more homogenous pulsed resources of aquatic subsidies with higher concentrations of contaminants. (b) Climate change can increase temperatures and alter hydrological regimes, which may increase the occurrence of conditions that favour mercury methylation and growth of harmful algal blooms, while also altering the phenology of both aquatic and terrestrial consumers. These changes may lead to phenological mismatches with riparian consumers and increased ratios of contaminants to resources. (c) Biodiversity change, including widespread declines of native species and the spread of invasive species, can alter the biomass and functional trait diversity of both aquatic and terrestrial consumers. These changes may lead to more homogenous pulses of aquatic resources that may be uncoupled from terrestrial consumers.

Cyanobacterial blooms, including those containing microcystin toxins, are strongly associated with intensive human land use, especially agricultural and urban areas, as well as climate warming (e.g., Beaver et al. 2014; Kakouei et al. 2021). Increased cyanobacterial blooms due to ongoing climate and land use change could potentially reduce aquatic-to-terrestrial subsidies or substantially alter their quality (Moy et al. 2016).

Land use can also have a drastic impact on emergent insect community composition in terms of the functional traits of emerging insects, including their dispersal ability (Frainer and McKie 2015; Stenroth et al. 2015; Carlson et al. 2016; McKie et al. 2018) and nutritional quality (see below). For instance, agricultural areas typically support fewer large-bodied taxa like Ephemeroptera, Plecoptera (Burmeister 1839) and Trichoptera and more small-bodied taxa, especially Diptera, which are relatively weak flyers and disperse over short distances (Stenroth et al. 2015; Carlson et al. 2016; Raitif et al. 2019). Urbanisation, including the transition from agricultural to urban areas, can also further shift communities to dipteran dominance (Kautza and Sullivan 2015, 2016). These changes in communities leading to differences in dispersal and emergence traits could alter riparian connectivity, such that subsidies in areas with intensive human land use could have more localised effects compared to those from less disturbed areas (Alberts and Sullivan 2016; Sullivan et al. 2021; Kowarik et al. 2023). However, riparian cover can also influence the degree to which aquatic subsidies are incorporated into terrestrial food webs (Raitif et al. 2022): for instance, streams with a riparian forested buffer zone had higher n-3 LC-PUFA (i.e., nutrients primarily of aquatic origin) in certain spider groups such as wolf spiders (Lycosidae; Sundevall 1833) compared to streams without a buffer zone (Ramberg et al. 2020).

Land use change can also lead to shifts in the quality of subsidies by increasing their contaminant content. For instance, aquatic subsidies from areas with intensive human land use can include pesticides, pharmaceuticals and a range of other contaminants (see Table 1). Of particular concern are MeHg and other organic compounds, which biomagnify within aquatic food webs and are well retained across life stages like metamorphosis and emergence. Exposure to such compounds often varies with local land use: multiple studies have documented increased MeHg exposure in insectivorous riparian birds in areas heavily altered by industrial and agricultural activities (e.g., Hallinger et al. 2011; Twining, Razavi, et al. 2021). Recent work also highlights how emergent aquatic insects can serve as major sources of neonicotinoid pesticides for riparian ecosystems (Roodt et al. 2022; Roodt, Huszarik, et al. 2023; Roodt, Schaufelberger, and Schulz 2023). Of particular concern, researchers found that even in instances where heavy use of insecticides for row crop agriculture resulted in declines in emergent insect biomass, the insects that

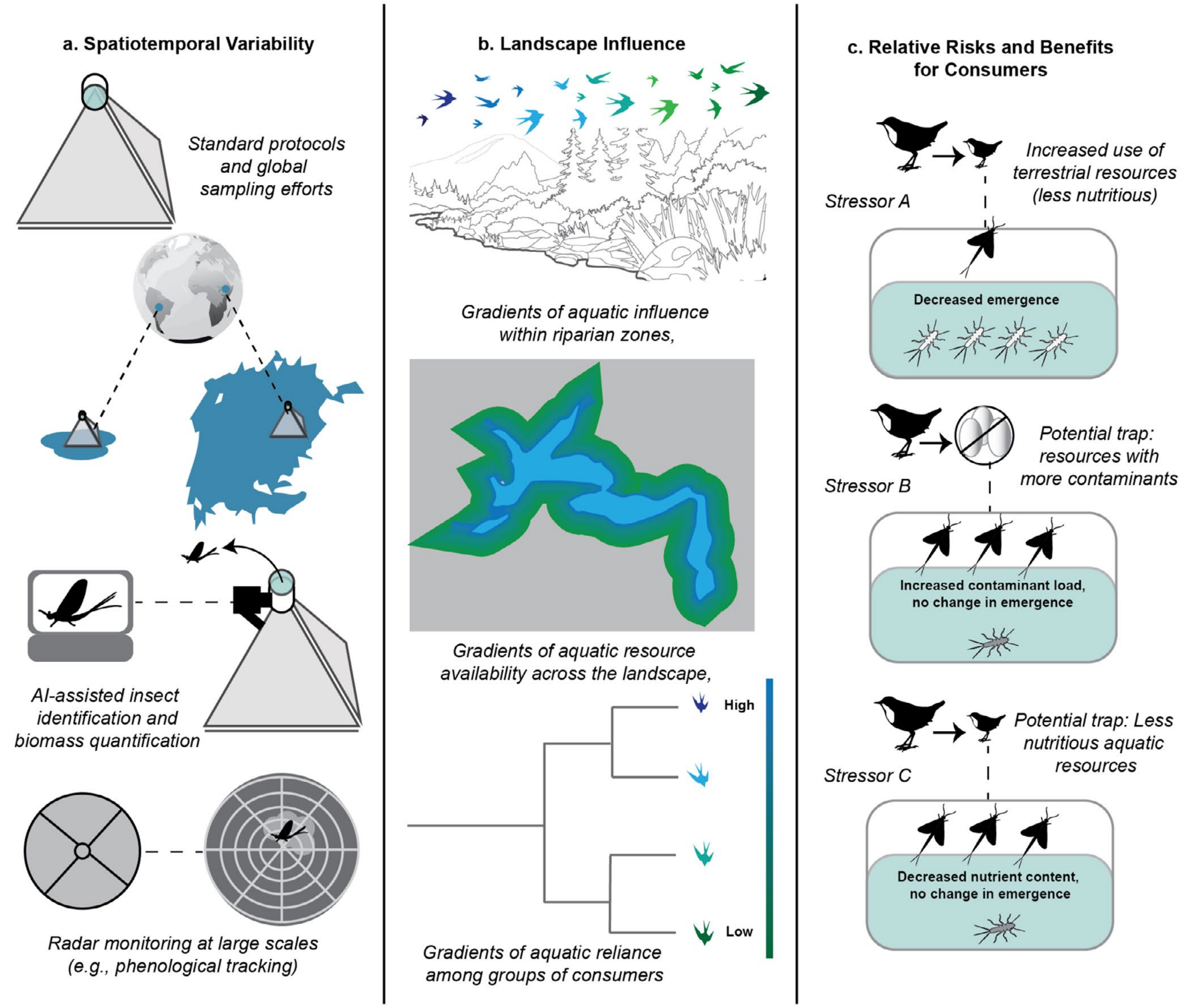

FIGURE 3 | Future priorities for research encompassing both the bright and dark sides of aquatic-to-terrestrial subsidies include: (a) incorporating more spatiotemporal variability into sampling efforts, (b) working at the landscape scale across a diversity of consumers that vary in their reliance upon aquatic resources as well as their evolutionary history and (c) understanding the mechanisms through which subsidies shift from being beneficial resources to functioning as ecological traps for consumers.

did emerge resulted in increased fluxes of contaminants relative to areas with lower insecticide use (Kraus et al. 2022).

Subsidy quality may also shift with continued land use change due to changes in the species composition of aquatic invertebrates (Dwyer et al. 2018; Parmar et al. 2022) or their basal resources like algae (Whorley et al. 2019). For example, some studies of periphyton along urbanisation and agricultural gradients have found decreased n-3 LC-PUFA content in heavily modified systems that receive large N and P inputs (Cashman et al. 2013; Guo et al. 2015), while others have found higher proportions of these fatty acids in such systems (Guo et al. 2021; Whorley et al. 2019). Within taxa, in a mesocosm study, Scharnweber et al. (2020) found that higher P levels were associated with lower eicosapentaenoic acid (20:5n-3, EPA) content in emergent insects. Guo et al. (2017) found that grazer LC-PUFA content became more similar to that of periphyton when periphyton LC-PUFA content increased under low light, high nutrient conditions. Other studies of consumer fatty acid composition along land use gradients have found little consistent effect of land use on either periphyton or emergent aquatic insect fatty acid composition (e.g., Larson et al. 2013; Twining et al. 2021). However, even without land use-induced changes in their own nutrient content, the relative nutritional value of aquatic insects may be greater in urbanised areas where the n-3 LC-PUFA content of terrestrial arthropods is lower (Shipley et al. 2024).

Land use change can also lead to changes in the composition and timing of subsidies due to light pollution as well as urban heat island effects (see climate change section below). Many aquatic ecosystems in urban and suburban areas also are receiving increased inputs of light due to artificial light at night (ALAN). ALAN can have complex species-specific and context-dependent effects that can influence aquatic-terrestrial linkages (Hirt et al. 2023). In aquatic systems, shredder insects exposed to artificial light increased rates of consumption, although without subsequent increases in growth rates, suggesting resulting increases in litter breakdown rates and

TABLE 1 | Contaminants that comprise the dark side of resource subsidies, their ecological effects on aquatic taxa and their effects on aquatic-terrestrial subsidies (see also Kraus 2019; Kraus et al. 2023).

Contaminant Type	Contaminant	Ecological effect	Effect on subsidy
Metals and Metaloids	Inorganic mercury and metals	Toxic to lower-trophic level organisms; do not bioaccumulate	Decrease subsidy quantity of lower trophic level organisms
Metals and Metaloids	Methylmercury (MeHg)	Bioaccumulate and biomagnify; toxic effects of exposure are content dependent and mostly occur at higher trophic levels	Decrease subsidy quality through increased contaminant concentration
Organic pollutant	Polychlorinated biphenyls (PCBs)	Bioaccumulate in aquatic animals	Decrease subsidy quality through increased contaminant concentration
Organic pollutant	Polycyclic aromatic hydrocarbons (PAHs)	Metabolised during metamorphosis and biodilute in food webs	Moderately decrease subsidy quantity or quality
Organic pollutant	Pharmaceuticals and personal care products (PPCPs)	Can accumulate in aquatic animals, but impacts can be highly variable by compound	Can decrease subsidy quantity and quality, but impacts can be highly variable by class
Organic pollutant	Current-use insecticides (e.g., neonicotinoids)	Accumulate in aquatic animals and reduce metamorphosis	Decrease subsidy quantity through decreased emergence; decrease subsidy quality through bioaccumulation in those that do emerge
Cyanobacterial toxins (i.e., naturally produced within aquatic systems)	Cyanobacterial toxins	Accumulate in aquatic insects and increase mortality	Decrease subsidy quantity through decreased emergence; decrease subsidy quality through bioaccumulation in those that do emerge

potential declines in invertebrate fitness (Czarnecka et al. 2021). Flying insects, and emerging aquatic invertebrates in particular, are impacted by ALAN through modification in behaviour and emergence patterns (Szaz et al. 2015). ALAN can decrease richness and mean body size of emerging insects, while increasing mean body size of riparian consumers (Meyer and Sullivan 2013). In another study, experimental increases in ALAN increased the emergence rates of aquatic insects, total amount of flying insects and the proportion of flying insects that were aquatic, which cascaded through the riparian food web to alter the composition of riparian consumer and scavenger species (Manfrin et al. 2017). These effects point to the complex changes in the magnitude and effect of aquatic-terrestrial fluxes that can result from changes in natural light regimes, which are becoming increasingly common (Sullivan and Manning 2019; Parkinson and Tiegs 2023).

4.2 | Climate Change and Warming

Climate warming is already influencing key processes that shape the quantity and quality of aquatic subsidies (Figure 2b; Häder and Barnes 2019). Aquatic food webs are typically dominated by ectotherms ranging from zooplankton to fish (Borer et al. 2005; Ward and McCann 2017). Consequently, metabolic processes like growth and development are directly related to temperature in most aquatic consumers, making them especially likely to respond to climate warming as well as urban heat island effects generated through land use change (Angilletta Jr et al. 2004; Zuo et al. 2012; Vanni and McIntyre 2016). The phenology of emergent insects is highly dependent upon water temperature, through its influence on development, resulting in strong seasonal pulses of subsidies to land in many temperate environments (e.g., Walters et al. 2018; Shipley et al. 2022). The spawning phenology of migratory fishes is also typically linked to water temperature (Asch et al. 2019; Nack et al. 2019; Opdal et al. 2024). Urban aquatic ecosystems can also exhibit altered temporal patterns of insect emergence, with emergent insect biomass export peaking earlier in urban systems than in forested systems (Carlson et al. 2016). This is likely due to the profound differences in temperature and growing degree day accumulation between urban and rural areas (Brans et al. 2018). For instance, stream water temperatures are typically higher in areas without the shading effect of riparian canopy cover (e.g., Moore et al. 2005). Small dams that release surface water can also increase stream temperatures (Lessard and Hayes 2003; Zaidel et al. 2021), while large dams that release deeper water can have a cooling effect on rivers and streams (Heggenes et al. 2021). In addition to temperature, lower water levels, which are also occurring as a consequence of climate change in many aquatic systems, can cue emergence in aquatic insects, leading to smaller emerging adults and thus a smaller and earlier aquatic-to-terrestrial flux (Harper and Peckarsky 2006; Leathers et al. 2024). As aquatic phenology shifts, this may translate into changes in the availability of high quality aquatic-derived nutrients for riparian consumers (Shipley et al. 2022) and/or result in shifts to lower quality terrestrial resources (Deacy et al. 2017). Such shifts as a result of changes in phenological synchrony could entail ecosystem-wide effects such as lower fitness in certain riparian consumers (Twining et al. 2018). They may also lead to reduced transport of aquatic nutrients that fertilise terrestrial primary producers (e.g., Helfield and Naiman 2001; Deacy et al. 2017).

The overall effects of warming on processes that influence aquatic-to-terrestrial subsidies will likely vary across ecosystems. For instance, freshwater systems in the tropics are predicted to have reduced emergent insect biomass and species richness with warming (Nash et al. 2021), while warming in temperate and arctic regions may increase aquatic insect emergence biomass (Hannesdóttir et al. 2012). Climate change is also predicted to reduce the strength of seasonal insect emergence patterns (Nash et al. 2023), potentially disrupting terrestrial consumers that time their life history events with highly pulsed aquatic insect emergence (e.g., Adams et al. 2023). In addition, warmer water temperatures can lead to accelerated larval insect development, resulting in reduced emergent adult body size and female fecundity (e.g., Dallas and Ross-Gillespie 2015; Sweeney et al. 2018; Anderson et al. 2019; Bonacina et al. 2023). However, the effects that this will have on subsidies may vary with life history strategy: multivoltine species that have multiple generations per year may end up exporting more total aquatic-derived biomass over the entire year if warmer temperatures allow them to complete more life cycles, whereas univoltine species may export less biomass by producing one brood of smaller adults (e.g., Zeuss et al. 2017). Recent work suggests that having a diverse community of emergent species that differ in their responses to temperature may help stabilise overall subsidy biomass, but that warmer temperatures may still lead to a change in phenology and species composition (Leathers et al. 2024). Moreover, as climate change is predicted to lead to species loss in many ecosystems, biodiversity's buffering potential may be decreasing.

In addition to its effect on aquatic-to-terrestrial subsidy phenology and quantity, temperature may alter subsidy quality (e.g., LC-PUFA). Higher water temperatures tend to increase the dominance of cyanobacteria (e.g., Kosten et al. 2012), which contain little to no LC-PUFA (Galloway and Winder 2015) and sterols (Martin-Creuzburg and von Elert 2008) and are thus considered poor food quality compared to other phytoplankton. Temperatures are also predicted to lower LC-PUFA production within individual phytoplankton taxa (Hixson and Arts 2016) via homeoviscous adaptation, a process in which the proportion of unsaturated fatty acids in cellular membranes is increased at lower temperatures in order to maintain vital membrane properties. Combined, both mechanisms could have reverberating consequences for the dietary LC-PUFA availability for aquatic consumers. As is the case for primary producers, climate change is already causing shifts in aquatic invertebrate community composition as communities shift towards those more tolerant of warmer temperatures and/or lower dissolved oxygen content (Baranov et al. 2020; Birrell et al. 2020; Khaliq et al. 2024), which could lead to changes in the nutritional composition of subsidies. Furthermore, within species, ectothermic aquatic consumers themselves, including *Daphnia* (O.F. Müller 1776) (e.g., Zeis et al. 2019) and non-biting midge larvae (Strandberg et al. 2020, 2021), appear to contain lower LC-PUFA content when grown at higher temperatures, suggesting that they may also regulate their fatty acid composition based on temperature. Decreased n-3 LC-PUFA content because of climate change could make aquatic subsidies less valuable for terrestrial consumers.

Climate warming also has the potential to exacerbate the dark side of aquatic subsidies through temperature-based effects on Hg methylation as well as cyanobacterial growth (see above). Specifically, conditions that promote greater bioavailability of methylmercury are likely to increase with climate warming. Higher temperatures and low oxygen conditions both stimulate the microbial activity of methylating anaerobic bacteria, such as sulfate reducing bacteria (Parks et al. 2013; Ullrich et al. 2001). Aquatic ecosystems ranging from streams (e.g., Carter et al. 2021) to lakes (e.g., Jane et al. 2021; Jenny et al. 2016; Tellier et al. 2022) are experiencing increasing deoxygenation with climate warming. Climate change is also already leading to longer periods of lake stratification, promoting earlier and longer onsets of hypolimnetic oxygen depletion (Jane et al. 2021), making low oxygen Hg methylating conditions more prevalent across lakes and reservoirs, increasing Hg exposure and accumulation in freshwater food webs. For example, consumers that forage in hypoxic environments represent an elevated source of MeHg to both fish and birds (Hall, Cobb, et al. 2020; Hall, Woo, et al. 2020; Baldwin et al. 2022). However, because primary productivity changes with hypoxia (e.g., Preece et al. 2019), and controls Hg bioaccumulation (e.g., Beutel et al. 2014; Razavi et al. 2015), there remain many unknowns regarding how changing climate will affect Hg exposure from aquatic subsidies across organisms and habitats.

4.3 | Changing Biodiversity

Changes in the abundance and diversity of organisms are occurring across ecosystems, with endemic species declining and introduced nuisance species increasing in many areas (Sánchez-Bayo and Wyckhuys 2019; van Klink et al. 2020; Dahlin et al. 2021; Jähnig et al. 2021). Land use change, especially habitat destruction and the release of contaminants into the environment, climate change and their interactive effects on ecosystems underlie many of these shifts in biodiversity (above, Figure 2). Aquatic ecosystems are no exception to this pattern and recent work suggests that, globally, freshwater biodiversity is declining at a higher rate than terrestrial biodiversity (Williams-Subiza and Epele 2021). Such declines are concerning because many studies have demonstrated the strong links between biodiversity and many beneficial ecosystem functions (e.g., van der Plas 2019), including the outsized importance of freshwater biodiversity for key nutritional functions across ecosystems (Shipley et al. 2024). Within the context of subsidies specifically, having multiple species or multiple populations of migratory fishes can result in greater stability of subsidies via portfolio effects when species or populations vary in their life history (e.g., Schindler et al. 2010) and/or functional traits (e.g., nutritional composition; Twining and Palkovacs 2017; Kurasawa et al. 2024). Such biodiversity-portfolio effects also appear likely to generate increased temporal stability for other aquatic taxa that subsidise terrestrial ecosystems, including emergent aquatic insects (Uno and Pneh 2020; Nash et al. 2023).

In addition to richness, the loss or gain of species with distinct functional traits may have strong impacts on ecosystem function across aquatic-terrestrial meta-ecosystems. For example, declines of individual species with unique dispersal, migration and life history traits (Childress and McIntyre 2015; Uno and Power 2015) or mass pulsed emergence (e.g., Walters et al. 2018; Stepanian et al. 2020) can have major impacts on ecosystem function. Introduced species also demonstrate the strong impacts that individual species with novel functional roles can have on meta-ecosystems (e.g., Peller and Altermatt 2024). For example, fish introductions to formerly fishless lakes result in dramatic reductions in emerging aquatic insects as well as avian insectivores in riparian zones (e.g., Epanchin et al. 2010). Such effects can also be indirect: introduced fish species that consume most of the subsidised terrestrial prey base in streams can force other fish to predate more heavily on aquatic insects, thus reducing fluxes of emergent aquatic insects and riparian spider biomass (e.g., Baxter et al. 2004; Benjamin et al. 2011).

In addition to altering the benefits of subsidies, changes in aquatic biodiversity may also have consequences for their associated risks (Figure 2c). Research on biodiversity-ecosystem function has typically focused on quantifying relationships between biodiversity and beneficial functions or ecosystem services rather than on understanding how biodiversity might influence risks. Aquatic biodiversity could potentially buffer terrestrial communities from contaminant transfer because

BOX 1 | Research topics for future studies of reciprocal aquatic–terrestrial subsidies under global change.

Spatial and Temporal Variability in Reciprocal Subsidies

Better understanding of spatiotemporal variability in the quantity, quality and phenology of aquatic-to-terrestrial subsidies can help close this key knowledge gap (Figure 3a). Our understanding of subsidy dynamics is best in Northern Hemisphere temperate systems and in small streams. Increased spatiotemporal sampling of such subsidies across a greater array of aquatic ecosystems across geographical regions (e.g., Dézerald et al. 2018) will help us fill key gaps in our current understanding. Working across a greater diversity of systems will also improve our understanding of global change impacts, as freshwater systems in different geographic regions are facing distinct threats– for instance, while some areas stand to get wetter with more high-flow events, other areas are rapidly drying (Trenberth 2011; Arnell and Gosling 2016; McCabe et al. 2023), and while some regions have already experienced major impacts from industrialisation and urbanisation and are recovering, many regions are only at the onset of industrial and urban development (Haase et al. 2023; Li et al. 2024). Large-scale coordinated aquatic subsidy monitoring efforts with common sampling schemes, equipment and units, as is used for monitoring many other ecological variables in long-term ecological research, can help with this. Emerging tools, such as AI-based identification to rapidly identify taxa and quantify biomass based on photos (e.g., phenopype, Lürig 2022), as well as radar-based monitoring (e.g., Stepanian et al. 2020) throughout the hydrological year and during high and low flow events, may enable future researchers to better understand the future roles of aquatic subsidies across a diversity of contexts.

Landscape-Scale Influence of Reciprocal Subsidies

Second, we currently lack a full understanding of the importance of aquatic-to-terrestrial subsidies across the landscape and how this importance may vary by ecosystem and consumer (Figure 3b). For example, while aquatic-derived energy is most important within riparian zones (e.g., Muehlbauer et al. 2014), even small quantities of aquatic-derived nutrients or contaminants may have major consequences on food webs further inland. A better understanding of aquatic subsidy dependence and use across a wider array of terrestrial animals will help inform management decisions. Taking a macroevolutionary perspective may be particularly helpful in making these assessments across taxa. Studies of aquatic subsidy dependence across entire clades of consumers that exhibit a wide range of specialisation on aquatic resources will help us understand which taxa are most likely to experience both the risks and benefits that aquatic subsidies present at the landscape scale.

Reciprocal Subsidies as an Ecological Resource or Trap in Changing Environments

A final topic for future research is understanding the conditions in which subsidies shift from beneficial resources into ecological traps for consumers (Figure 3c). The dual roles of aquatic subsidies have the potential to lead to surface waters becoming ecological traps for riparian consumers seeking important nutrients and instead finding them bound with contaminants (e.g., Hale and Swearer 2016).

Characterisation and comparison of bioaccumulation across a range of beneficial compounds, which are often internally regulated via rates of synthesis, as well as a diversity of contaminants, which are largely regulated through removal processes like excretion or shedding, will also improve our general understanding of such processes (e.g., Kainz et al. 2008; Kraus, Walters, et al. 2014). Mechanistic experimental work will also help us understand how contaminants themselves might alter the production of beneficial compounds from subsidies (Kolbenschlag et al. 2023; Pietz et al. 2023). Importantly, understanding the context in which global change processes are likely to lead to increased production of nutrient-rich subsidies and dilution of contaminants, versus when they will lead to increases in harmful metals and organic compounds, can help guide management decisions (Schmidt et al. 2013; Kraus 2019; Schulz et al. 2023).

species and functional groups often vary in their contaminant content. For example, Brandt et al. (2024) found that migratory salmon species varied in their contaminant loads based on their life history and trophic level, and the risks and benefits they posed to consumers shifted over time with changes in species composition. Overall, the effects of aquatic biodiversity on the 'dark' side of subsidies likely vary based on contaminant class. Trace metals and other contaminants that cause high mortality in aquatic taxa will also likely select for a less diverse, more pollution-tolerant community of species with the potential to increase contaminants at the per biomass level or even overall contaminant fluxes (e.g., Kraus et al. 2022). In the case of contaminants that biomagnify with trophic levels, such as MeHg, having a more diverse community with more trophic levels could result in increased biomagnification and thus increased risk as subsidies. In contrast, for those that do not appear to magnify, such as microcystins, increased diversity of taxa and trophic levels could act to dilute or buffer such risks, especially if contaminants enter food webs through specific food resources (i.e., phytoplankton and periphyton in the case of microcystins). As biodiversity loss often occurs alongside or as a consequence of pollution, further research addressing how biodiversity shapes not only the 'bright' but also the 'dark' sides of aquatic subsidies would be useful.

5 | Conclusions

A growing body of recent research reveals that freshwater ecosystems play an outsized role as sources of both nutritionally vital resources and harmful contaminants to a diversity of consumers across aquatic to terrestrial food webs. Aquatic-based biochemical transformations are responsible for shaping subsidies into those that are beneficial as well as harmful. Typically, these 'bright' and 'dark' sides of aquatic-to-terrestrial subsidies have been studied in isolation, but in today's ever-more human-modified landscapes, these risks and benefits are likely to be coupled within the same ecosystems (Brandt et al. 2024; Subalusky et al. 2020), complicating management decisions (Box 1). Integrative studies that examine how the bright and dark sides of subsidies vary relative to one another and in response to multiple interlinked global change stressors (Figure 2)include: (1) quantifying spatiotemporal variation in reciprocal subsidies, (2) illuminating the full landscape-scale effects of such subsidies and (3) assessing global change effects on the relative risks and benefits of subsidies.

Throughout this review, we have illustrated the important and complex role that aquatic subsidies can play in terrestrial food webs, demonstrating that aquatic ecosystems must be factored into landscape-scale studies. We have also highlighted how the role of surface waters on the landscape in the future will become increasingly important and dynamic with global change processes, like climate change, land use change and biodiversity loss. Artificial boundaries between aquatic and terrestrial research have historically limited our understanding of both systems and are an impediment to transformative research that accurately reflects the complexity of real interconnected ecosystems. Furthermore, divisions between ecological research on resource subsidies and ecotoxicological research on contaminants, which have historically been funded by different agencies and published in different journals, have precluded until recently a holistic examination of the coupled transport of nutrients and contaminants in many cases. Collaborative and integrative research approaches at the landscape scale will improve understanding of the nuances of linked ecosystems and the consequences of global change (Box 1).

Author Contributions

All authors contributed substantially to writing manuscript drafts, C.W.T. and A.L.S. synthesised and edited drafts, and J.R.S. and C.W.T. created figures.

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Data Availability Statement

Data sharing not applicable to this article as no new datasets were generated or analysed during the current study.

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