Johanna M. Kraus
David M. Walters
Marc A. Mills *Editors*

Contaminants and Ecological Subsidies

The Land-Water Interface

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Editors
Johanna M. Kraus
Columbia Environmental Research Center
U.S. Geological Survey
Columbia, MO, USA

David M. Walters
Columbia Environmental Research Center
U.S. Geological Survey
Columbia, MO, USA

Marc A. Mills
National Risk Management Research Laboratory
U.S. Environmental Protection Agency
Cincinnati, OH, USA

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Foreword

Defying Gravity: Aquatic-Terrestrial Subsidies in the Anthropocene

Humanity has eagerly embraced the idea of “better living through chemistry” and indeed chemical innovations have changed the lives of many for the better. Chemical fertilizers enabled the green revolution, pharmaceuticals have improved human health outcomes, and green chemistry is reducing waste. This expansion of the chemical industry has been accompanied by an exponential increase in both the mass and the variety of chemical compounds that are entering the natural environment.[1] The Anthropocene is best characterized by the novel and persistent chemical compounds that have imparted a unique stratigraphic signature in the modern era.[2]

This explosion in chemical innovation is not without costs. In 1962, Rachel Carson published her influential book *Silent Spring* which warned that increasing the application of pesticides was leading to widespread losses of biodiversity. Modern concerns about urban air pollution, algal blooms, contaminated aquifers, feminized and deformed fish and amphibians, and overly fragile bird eggs all arise from the inadvertent addition of industrial chemicals into our environment. Indeed, although scientists agree that we have entered a new era on Earth marked partly by the global distribution of human contaminants, to date, the envelope for safe operating space for humanity in the dimension of contaminants is not currently well understood[3]. We don’t know how much contamination the Earth can withstand and still be safe for human habitation in large part because research on this topic at the interface of toxicology and ecology has neither been encouraged nor adequately funded[1].

Aquatic ecosystems, which collect water and materials by virtue of their low-lying position within landscapes, are the recipients of the widest possible variety of

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[1] Bernhardt et al. 2017 *Frontiers in Ecology and the Environment* 15:84–90.

[2] Waters et al. 2018 *Earth Science Reviews* 178:379–429.

[3] Rockström et al. 2009 *Ecology and Society* 14:32.

anthropogenic chemicals. A great deal of our management and regulatory attention to contaminants is focused on reducing the concentration and loads of pollutants within aquatic ecosystems. Yet, as the chapters in this book make abundantly clear, pollution does not always follow the rule of gravity.

One of the highlights of aquatic ecology over the last two decades has been the recognition that aquatic organisms provide substantial energy and element subsidies to terrestrial ecosystems as insects emerge and fish are removed by terrestrial predators. Through this exchange, researchers have documented the importance of salmon migration to forest growth along the Pacific coast, the fertilizing effects of dead midges on boreal plant communities, and the role of aquatic insects in supporting the diets of bats, birds, and lizards.

This book explores how aquatic pollution can alter the rate, timing, and form of these aquatic-terrestrial subsidies AND how pollutants can be transported in the tissues of aquatic biota into terrestrial ecosystems. Dubbed "the dark side of subsidies," these contaminant fluxes change the way we understand modern aquatic pollution issues and should affect the way we regulate and mitigate their impacts.

Collectively the chapters provide abundant evidence for two critical points that merge perspectives from toxicology and ecology. First, ***contamination of aquatic ecosystems can, by killing aquatic organisms, reduce the flow of energy and nutrients out of aquatic ecosystems into terrestrial food webs.*** Second, ***contaminants that do not kill aquatic organisms are transported by them,*** fundamentally changing the fate, transport, and impact of pollutants.

The chapters in this volume fundamentally advance our understanding of the ecological consequences of shifts in either the energy or contaminant exchange between aquatic and terrestrial food webs and expand our understanding of the fate and transport of aquatic contaminants through ecosystems. Chapters in the book span from theoretical discussions of how contaminants move through complex ecological systems, to synthesis of the mechanisms through which contaminants can alter energy, and to interactions between contaminants and other factors of global change. In its final chapters, experts provide recommendations for how managers can incorporate this new understanding into ecological risk assessments and contaminant remediation and management.

Readers of this book will come away with a sophisticated understanding of contaminant fate and transport within ecological systems, and although this volume is focused on aquatic terrestrial interactions, the principles set for will resonate for those studying any ecological system subject to contamination. This book would be a useful companion for courses in ecotoxicology and ecology and is an essential reference text for any environmental scientist seeking a more comprehensive view of the Anthropocene.

Millbrook, NY, USA
November 6, 2019

Emily S. Bernhardt
Emma J. Rosi

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About the Editors and Contributors

Editors

Johanna M. Kraus, Ph.D., is a Research Ecologist with the U.S. Geological Survey Columbia Environmental Research Center where she applies principles of community ecology to study the effects of chemical contaminants on food webs, biodiversity, and environmental health in aquatic and terrestrial ecosystems. She began her career with the USGS in 2011 researching how trace metals from acid rock drainage impact adult aquatic insect emergence and contaminant flux to terrestrial insectivores near mountain streams. Since then her work has continued to improve understanding of how chemical contaminants impact food webs at the landscape scale. Dr. Kraus received her B.A. in Biology from Brown University and Ph.D. in Biology from the University of Virginia.

David M. Walters, Ph.D., is a Research Ecologist with the U.S. Geological Survey (USGS) Columbia Environmental Research Center. His research focuses on the effects of human stressors on the form, function, and structure of aquatic and riparian ecosystems with an emphasis on food web dynamics and contaminants. He began his career at the U.S. Environmental Protection Agency National Exposure Research Laboratory in 2002 before joining the USGS in 2008. His publications have addressed the impacts of contaminants, land use and climate change, invasive species, and hydrologic alteration on aquatic and riparian organisms and are geared toward furthering the conservation and restoration of these valued ecosystems. He received an M.S. and Ph.D. from the Odum School of Ecology at the University of Georgia.

Marc A. Mills, Ph.D., is an Environmental Engineer at the U.S. EPA's Office of Research and Development and is a principal investigator for projects characterizing the occurrence, transport, and fate of contaminants of emerging concern (CECs) and legacy contaminants in the environment and the management of contaminated sediments. Dr. Mills leads research to identify sources of contaminants to aquatic systems and tracing their movement through the environment and food webs. He also leads the development of analytical methods for CECs (e.g., PFAS, EDCs, PPCPs) and stable isotope chemistry for environmental samples in water, wastewater, solids, and tissues at the Center for Environmental Solutions and Emergency Response (CESER) for U.S. EPA. These methods are used to characterize potential sources of CECs and legacy contaminants, their management in water, wastewater treatment, water bodies, and new technology development. Dr. Mills has a B.S. in Civil/Environmental Engineering from Texas A&M University and a M.S. and Ph.D. from the Texas A&M University.

Contributors

Candice Bauer Region 5, United States Environmental Protection Agency, Chicago, IL, United States

Colden V. Baxter Stream Ecology Center, Department of Biological Sciences, Idaho State University, Pocatello, ID, USA

Gale B. Beaubien Molecular BioSciences, Middle Tennessee State University, Murfreesboro, TN, USA

U.S. Environmental Protection Agency, Office of Research and Development, Cincinnati, OH, USA

Mirco Bundschuh iES Landau, Institute for Environmental Sciences, University of Koblenz-Landau, Mainz, Germany

Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Sweden

Francis J. Burdon School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

Matthew M. Chumchal Department of Biology, Texas Christian University, Fort Worth, TX, USA

Scott F. Collins Department of Natural Resources Management, Texas Tech University, Lubbock, TX, USA

Daniel A. Cristol Department of Biology, William and Mary, Williamsburg, VA, USA

Ray W. Drenner Department of Biology, Texas Christian University, Fort Worth, TX, USA

Erik J. S. Emilson Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, ON, Canada

Sally A. Entrekin Department of Entomology, Virginia Tech, Blacksburg, VA, USA

Michelle Evans-White Department of Biological Sciences, University of Arkansas, Fayetteville, AR, USA

Brianna Henry Department of Biology, University of South Dakota, Vermillion, SD, USA

Natural Resources Conservation Service, Washington, DC, USA

Micael Jonsson Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

Jacob Kerby Department of Biology, University of South Dakota, Vermillion, SD, USA

Christopher J. Kotalik Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO, USA

Johanna M. Kraus U.S. Geological Survey, Columbia Environmental Research Center, Columbia, MO, USA

Stefano Larsen Department of Civil, Environmental and Mechanical Engineering, University of Trento, Trento, Italy

Computational Biology Unit, Fondazione Edmund Mach, San Michele all'Adige, Italy

Christopher A. Mebane U.S. Geological Survey, Idaho Water Science Center, Boise, ID, USA

Marc A. Mills U.S. Environmental Protection Agency, Office of Research and Development, Cincinnati, OH, USA

Jeffrey D. Muehlbauer U.S. Geological Survey, Southwest Biological Science Center, Grand Canyon Monitoring and Research Center, Flagstaff, AZ, USA

Connor I. Olson Department of Biology, Middle Tennessee State University, Murfreesboro, TN, USA

Department of Civil and Environmental Engineering, Syracuse University, Syracuse, NY, USA

Ryan R. Otter Department of Biology, Middle Tennessee State University, Murfreesboro, TN, USA

Molecular BioSciences, Middle Tennessee State University, Murfreesboro, TN, USA

Justin P. F. Pomeranz Department of Biology, University of South Dakota, Vermillion, SD, USA

Department of Environmental Sciences and Technology, Colorado Mesa University, Grand Junction, CO, USA

Travis S. Schmidt U.S. Geological Survey, Colorado Water Science Center, Denver, CO, USA

Ralf Schulz iES Landau, Institute for Environmental Sciences, University of Koblenz-Landau, Landau, Germany

Eusserthal Ecosystem Research Station, University of Koblenz-Landau, Landau, Germany

S. Mažeika P. Sullivan Schiermeier Olentangy River Wetland Research Park, School of Environment and Natural Resources, The Ohio State University, Columbus, OH, USA

David M. Walters U.S. Geological Survey, Columbia Environmental Research Center, Columbia, MO, USA

Jeff Wesner Department of Biology, University of South Dakota, Vermillion, SD, USA

Matthias Wieczorek iES Landau, Institute for Environmental Sciences, University of Koblenz-Landau, Mainz, Germany

Jochen P. Zubrod iES Landau, Institute for Environmental Sciences and Eusserthal Ecosystem Research Station, University of Koblenz-Landau, Mainz, Germany

Introduction: Ecological Subsidies as a Framework for Understanding Contaminant Fate, Exposure, and Effects at the Land-Water Interface

David M. Walters, Johanna M. Kraus, and Marc A. Mills

> *Food webs are a central organizing theme in ecology.*
>
> (Polis et al. 1997)

1 Introduction

Food webs are a principle framework used by ecologists to organize our understanding of organism interactions in the environment. This sentiment, directly quoted above, forms the opening sentence of Polis et al.'s (1997) seminal paper aimed at integrating food web and landscape ecology via the lens of spatial subsidies. Polis et al. (1997) inspired a generation of research that greatly advanced our understanding of food web dynamics and ecological processes that were found to operate at much larger spatial scales than were previously considered. A goal of this book is to expand on these advances by using spatially subsidized food webs as a paradigm for further integrating the fields of ecology and ecotoxicology. In doing so, we expect to gain greater insight into the ecological effects of contaminants on linked ecosystems as well as the ways in which food web dynamics and ecosystem process can themselves govern the fate, transport, and exposure mechanisms of contaminants in the environment.

Over the last 15 years, researchers have stressed the need to integrate ecological conceptual frameworks with ecotoxicology to better understand contaminant fate, exposure, and effects (Schiesari et al. 2018; Relyea and Hoverman 2006; Rohr et al. 2006; Clements and Newman 2003). Yet progress toward this goal, particularly with regard to food webs, has been slowed due to differences in the historical

D. M. Walters (✉) · J. M. Kraus
U.S. Geological Survey, Columbia Environmental Research Center, Columbia, MO, USA
e-mail: waltersd@usgs.gov

M. A. Mills
U.S. Environmental Protection Agency, Office of Research and Development,
Cincinnati, OH, USA

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underpinnings, research foci, and methods utilized by the fields of ecology and ecotoxicology. For example, ecotoxicological researchers have emphasized changes in chemical concentrations within food webs and have asked questions such as how do chemical properties, food web structure, and animal movements affect wildlife exposure (Walters et al. 2016; Lavoie et al. 2013, 2015; Gobas 1993). In contrast, ecologists have emphasized nutrient fluxes, particularly carbon and nitrogen, in food webs and have addressed questions such as how do fluxes of organic matter and organisms affect community and ecosystem properties such as diversity and productivity (e.g., Benke and Wallace 1997). Quantifying contaminant fluxes within and between food webs is a growing line of inquiry (e.g., Richmond et al. 2018; Kraus et al. 2014a; Tweedy et al. 2013; Runck 2007), yet more work needs to be done to improve our understanding of food web dynamics and animal community responses to contaminants and to improve our ability to predict contaminant fate and subsequent wildlife exposure to toxins in the environment (Kraus 2019; Schiesari et al. 2018; Gessner and Tlili 2016). Furthermore, the role of contaminants as a global driver of the structure and function of ecosystems, communities, and food webs has not been integrated into mainstream ecological theory despite increased calls to do so (Bernhardt et al. 2017; Clements and Rohr 2009; Rohr et al. 2006). Papers exploring contaminants as stressors to ecological communities are often published in ecotoxicological or applied ecology journals rather than ecology journals (e.g., Graf et al. 2019; Kraus et al. 2014a; Clements and Rohr 2009), further emphasizing the segregated thinking on this topic compared with other global stressors such as nutrient enrichment and climate change.

2 Subsidies as an Integrating Framework

Ecological subsidies are generally defined as flows of nutrients, energy, organic matter, or organisms between ecosystems that augment consumer populations (Power and Huxel 2004; Polis et al. 1997). A well-characterized example of this is reciprocal flows in freshwater ecosystems such as streams where terrestrial detritus and algae are converted to aquatic insect biomass that ultimately emerges to land to feed a host of terrestrial invertivores (Baxter et al. 2005). Polis et al. (1997) explicitly defined a spatial subsidy as:

> "… a donor-controlled resource (prey, detritus, nutrients) from one habitat to a recipient (plant or consumer) from a second habitat which increases population productivity of the recipient, potentially altering consumer-resource dynamics in the recipient system."

The focus on positive ecological benefits of subsidies, such as increased productivity in the recipient system, emphasizes the "bright side of subsidies." However, there is growing recognition that harmful contaminants can "hitch a ride" on fluxes of organic matter and organisms (i.e., "the dark side of subsidies"; Bundschuh et al. 2019; Moy et al. 2016; Speir et al. 2014; Walters et al. 2008) or that contaminants in one system can reduce the abundance of animal subsidies or change their phenology with negative consequences for consumers in recipient systems (Raby et al. 2018; Lee et al. 2016; Richmond et al. 2016; Rogers et al. 2016; Kraus et al. 2014a; Paetzold et al. 2011).

Because the concept of spatial subsidies bridges multiple ecosystems and incorporates movements of resources and responses of consumers, a study of resource subsidies provides a framework for integrating disciplines (Muehlbauer et al. 2019). In this book, we explore how the study of spatial subsidies can serve as a construct for bridging the fields of ecology and ecotoxicology with the goal of increasing understanding and improving decision-making regarding the ecological effects of contaminants in linked aquatic-terrestrial ecosystems (Fig. 1). If contaminants are accumulated in the bodies of animals in a donor ecosystem and those animals move to another ecosystem, then this subsidy and associated contaminants contribute to unexpected contaminant exposure in the recipient system ("subsidies drive exposure," blue arrow in Fig. 1). On the other hand, if contaminants in the donor system reach toxic levels that limit animal survival and movement, then exposure controls subsidies and associated energy flow to the recipient system ("exposure drives subsidies," yellow arrow in Fig. 1). Characterizing these two types of responses requires an integration of approaches from ecotoxicology (e.g., quantifying mechanisms of contaminant uptake, accumulation, and toxicity) with approaches from the field of ecology (e.g., quantifying animal biomass, production, trophic dynamics, and material fluxes) (Fig. 1). This integration can reveal new insights into the ecotoxicological consequences of contaminant exposure in linked ecosystems.

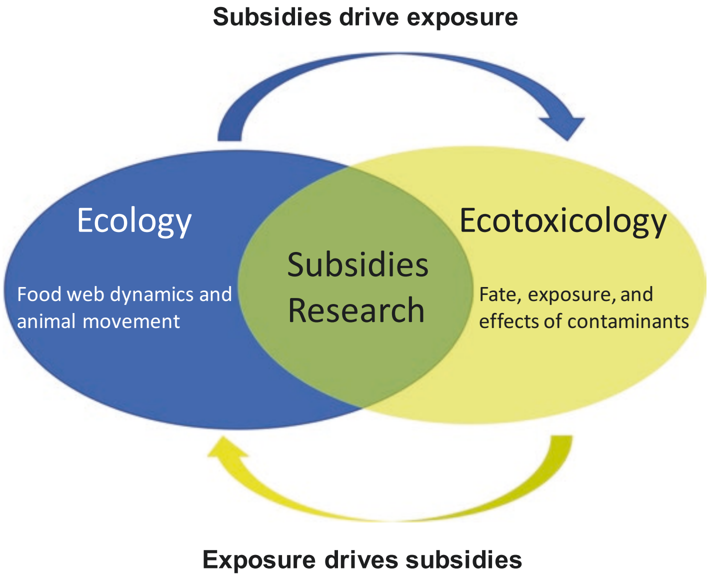

Fig. 1 A model for using research on ecological subsidies to bridge the disciplines of ecology and ecotoxicology

In constructing this volume, we made two editorial decisions which helped to structure and to limit the scope of this book, but which also simplify the complex interactions between subsidies and contaminant exposure at the land-water interface. First, we recognize that our dichotomous construct ("subsidies drive exposure" vs "exposure drives subsidies") is ecologically simplistic and that the responses are likely to be more nuanced (e.g., gradient or threshold responses to contaminant concentrations or subsidy magnitude), but this construct serves as a useful thematic scaffold for this volume. Second, we frequently emphasize emergent aquatic insects as a model for interdisciplinary studies framed in the context of spatial subsidies because of their importance to riparian consumers (Allen and Wesner 2016; Marcarelli et al. 2011; Baxter et al. 2005) and because their responses to a broad suite of contaminants are well characterized (e.g., Griffith 2017; Bundschuh et al. 2016; Kraus et al. 2014b; Wesner et al. 2014; Schmidt et al. 2011; Clements et al. 2000). Many other examples of animal subsidies and contaminant exposure exist including amphibians (Heyes et al. 2014; Relyea et al. 2005), anadromous fishes (Gerig et al. 2015; Sarica et al. 2004; Krummel et al. 2003), seabirds (Michelutti et al. 2009; Blais et al. 2005), and bats (Clark et al. 1995), and these linked systems could also be used to illustrate the principle themes of this book.

3 Contaminants and Subsidies: Organizing Themes

3.1 When Subsidies Drive Exposure

Kraus (2019) developed a heuristic model predicting the effects of various contaminants on aquatic insect emergence and contaminant concentrations (Fig. 2 in Kraus 2019). From a subsidies' perspective, contaminants that bioaccumulate in larval insect tissues and are retained through insect metamorphosis pose "an exposure problem" for recipient food webs (Kraus 2019). A classic example are legacy contaminants such as polychlorinated biphenyls (PCBs) which are relatively non-toxic to larval insects, accumulate and biomagnify in insects, have limited effects on insect metamorphosis and emergence, and are conserved through metamorphosis (Fig. 2, right panel). This pathway leads to risk of contaminant exposures for insect-eating wildlife. For example, tetragnathid spiders are specialized predators of aquatic insects and accumulate aquatically derived PCBs at levels comparable to stream-dwelling insectivorous fishes (Walters et al. 2008). Similar transfers occur for other bioaccumulative toxins such as methyl mercury (Jackson et al. 2019; Ortega-Rodriguez et al. 2019; Becker et al. 2018; Williams et al. 2017), and this risk of exposure is pervasive in freshwater systems embedded in human-impacted landscapes (Chumchal and Drenner 2015; Sullivan and Rodewald 2012).

In this volume, Chumchal and Drenner (this volume) expand on the ecologically simplified model presented in our Fig. 2. They explicitly address the ecological complexity inherent in linked aquatic-terrestrial food webs and demonstrate the

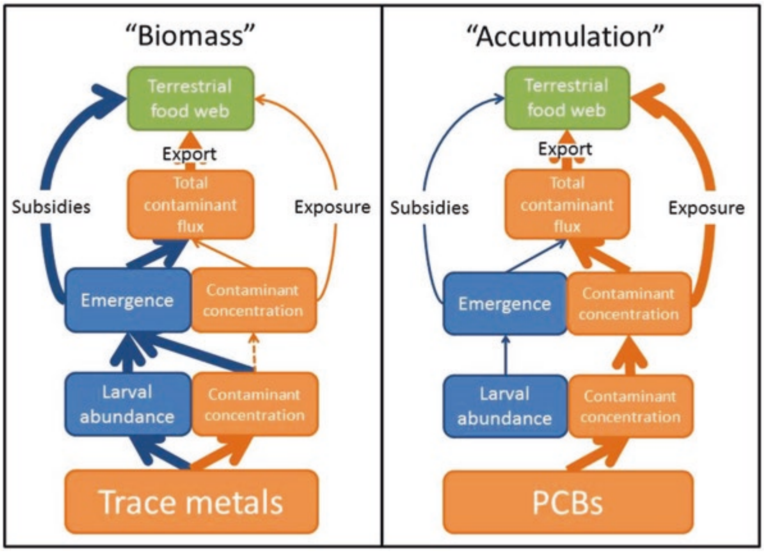

Fig. 2 An example illustrating when subsidies drive exposure and when exposure drives subsidies derived from studies on freshwater insects. The "Accumulation" panel illustrates an exposure problem for the recipient food web, and the "Biomass" panel illustrates a loss of subsidy (i.e., adult insect prey biomass) for the recipient system. Solid lines indicate significant relationships between factors. Thick arrows represent the pathway by which the pollutant alters cross-ecosystem linkages (blue = biomass transfer; orange = contaminant transfer). Trace metals and PCBs are presented as two ends of the contaminant spectrum (i.e., biomass effects dominate vs accumulation effects dominate). This figure is from Kraus et al. (2014a) and is used by permission

important role that other factors such as predation and community structure, nutrient limitation and productivity, and the seasonal aspects of hydrology and insect emergence can have on subsidy-driven exposures to mercury. Similarly, Schultz and Bundschuh (this volume) move beyond the typical focus on biotic pathways of contaminant flux to highlight abiotic pathways such as contaminant flows to terrestrial systems via groundwater and overland flows. Importantly, they move beyond the historical emphasis on documenting exposures in recipient ecosystems to address the potential effects of these contaminant transfers on terrestrial food webs.

3.2 *When Exposure Drives Subsidies*

The heuristic model in Kraus (2019) also described a scenario where contaminants can limit the flows of animal subsidies via toxicity creating a "resource problem" for consumers. Contaminants such as trace metals, current use pesticides, and polyaromatic hydrocarbons (PAHs) are relatively toxic to aquatic insects, either during larval stages or during metamorphosis (Kraus 2019; Wesner et al. 2014; Schmidt et al. 2013). These more toxic compounds are less likely to be retained in insects through metamorphosis (Kraus 2019; Kraus et al. 2014b). From an ecological subsidy perspective, these types of contaminants can regulate or limit flux of prey to the recipient food webs (Fig. 2, left panel) which can reduce foraging opportunities for riparian insectivores (Kraus and Pomeranz this volume) and reduce predator biomass in riparian habitats (Kraus et al. 2014a; Paetzold et al. 2011).

Chapters in this book identify multiple mechanisms driving contaminant effects on aquatic insect subsidies. Burdon (this volume) illustrates the context dependency of different land uses and how their associated contaminants alter productivity gradients in insect subsidies to riparian predators. Higher nutrient loading in agriculture-impacted streams led to increasing stream periphyton and aquatic insect biomass resulting in higher arachnid biomass than in reference streams (i.e., a bottom-up process). In contrast, streams in catchments with hard-rock mining were impacted by acid mine drainage (e.g., low pH and high metal concentrations) leading to reduced larval insect and arachnid biomass. Kraus and Pomeranz (this volume) further illustrate that trace metals alter stream benthic communities via loss of sensitive taxa and reduced insect emergence. This loss of subsidy reduces riparian predator biomass (by lowering their prey base) while simultaneously increasing the reliance of aquatic insect predators such as fish on terrestrial arthropods. This illustrates a case of contamination in one system altering the dynamics of reciprocal subsidies and predator-prey interactions between ecosystems. Wesner et al. (this volume) investigate the interaction between contaminants and the critical life stage of metamorphosis for aquatic organisms such as amphibians and insects. They illustrate that metamorphosis plays a key role in the movement of aquatic contaminants to land, that metamorphosis itself is a physiologically stressful event, that mortality during metamorphosis is enhanced via chemical exposure, and that ecotoxicological studies must include this critical life stage to fully understand the risks of contaminant exposure in these linked systems.

3.3 Other Global Stressors

The interactive effects of contaminants and subsidies at the land-water interface do not occur in isolation of other ecosystem drivers. Rather, they are themselves strongly influenced by the myriad of other human stressors affecting aquatic and riparian ecosystems (Schulz et al. 2015). Rockström and colleagues developed a “planetary boundaries” framework illustrating how such stressors operating at the global scale could affect earth systems and humanity (Rockström et al. 2009). Their framework identifies nine interlocking stressors, many of which could directly influence or interact to influence contaminant flux, fate, and effects at the land-water interface. These stressors are ubiquitous and deleterious to freshwater-riparian ecosystems and include chemical pollution, biodiversity loss, eutrophication through excessive nitrogen and phosphorus loading, climate and land use change, and overuse of global freshwater resources. Yet we remain in the early stages of conducting the empirical studies and developing the conceptual frameworks necessary for incorporating these anthropogenic stressors to aquatic systems into a broader understanding of the interplay of material and organismal fluxes across ecosystem boundaries (Debecker et al. 2017; Alberts and Sullivan 2016; Schulz et al. 2015; Rowse et al. 2014).

Two chapters in this volume synthesize our understanding of the effects of external stressors on aquatic subsidies to terrestrial ecosystems. Muehlbauer and colleagues (this volume) apply a generalized match-mismatch framework to illustrate how stressors such as climate and land use change, species invasions and extinctions, and human water use could create asynchronies between subsidy resources over gradients of time, space, and magnitude. Through this analysis, they illustrate interactions of multiple variables that affect lotic to land subsidies in unpredictable and nonlinear ways compared to the independent effects of stressors operating in isolation. In identifying future research needs, the authors note that while the above stressors have been studied extensively within the disciplines of ecology and conservation, there is a paucity of research on how such stressors might affect subsidy-contaminant interactions, either singularly or in unison. Collins and Baxter (this volume) investigate impacts from the global biodiversity crisis to investigate how species loss, invasion, and replacement (which themselves result from multiple interactive stressors) alter the exchanges of energy, material, and organisms between ecosystems. Using a series of case studies, the authors illustrate how changes in species composition on land or in water can lead to “reverberating effects” back and forth across ecosystem boundaries via a series of direct and indirect effects and feedback loops. These cases demonstrate the pressing need for a more complex treatment of the interconnectedness of aquatic-terrestrial food webs in order to better characterize and predict the interaction of spatial subsidies with ubiquitous stressors such as contaminants.

3.4 Management Applications and Tools

Our expanding knowledge of the connections between ecological subsidies and contaminants provides opportunities to apply our understanding to protect, manage, and remediate aquatic ecosystems. Managing risks associated with contaminants typically starts with the development of a site-specific conceptual model synthesizing the existing information on physical, chemical, and biological processes driving contaminant exposure and adverse impacts. These models are then used to characterize sources of contaminants, to assess ecological impacts from contaminants and co-occurring stressors, and to design remediation and restoration projects aimed at reducing risks (U.S. Environmental Protection Agency 1998). Understanding how linkages between aquatic and riparian food webs affect the movement of contaminants and animals between these systems can facilitate this process through identification of ecological metrics, receptors, or endpoints that could be affected through management actions. In turn, these ecological indicators reflecting aquatic-riparian linkages can be used to inform the design of management actions and to assess the efficacy of these actions following their implementation.

Four chapters in this book provide guidance on how to implement our knowledge of contaminants at the land-water interface into the risk management paradigm. Otter et al. (this volume) develop a heuristic model illustrating how the ecological processes of contaminant accumulation, toxicity, and retention through metamorphosis collectively modulate insect-mediated contaminant flux. Building on this model, they propose a "riparian impact test" as a decision-making tool to inform risk assessment of contaminant exposure to terrestrial consumers. Evans-White et al. (this volume) investigate how changes in detrital pathways in freshwater ecosystems can be integrated into regulatory frameworks. Using wadeable streams in the United States as a case model, they examine the ways that co-occurring contaminants such as nutrients and salts (i.e., major ions) can alter stream microbial and macroinvertebrate communities and detrital processing pathways and identify a suite of ecological endpoints indicative of these altered detrital pathways. These endpoints can serve as ecological indicators that themselves can be used to inform management of detrital-based systems within the context of aquatic-terrestrial linkages.

The final two chapters in the section highlight the underutilized role of experiments in assessing and managing contaminant risks at the land-water interface. Kotalik et al. (this volume) illustrate how mesocosm experiments complement traditional toxicity testing by allowing researchers to include community-level responses and responses across multiple life stages, including aquatic insect emergence. Their experimental framework could help identify aquatic life criteria that account for contaminant sensitivities across all insect life stages, thereby providing a more holistic assessment of contaminant effects that extends beyond the single-species, single life-stage model of traditional toxicity testing. Bundschuh et al. (this volume) overview the use of mesocosm and microcosm experiments to identify causal linkages between aquatic contaminants and effects on terrestrial ecosystems, a major gap in the current state of our knowledge. They highlight experimental designs that combine aquatic and terrestrial habitats into a single experimental unit. Such designs extend traditional mesocosm studies that typically replicate a single ecosystem (aquatic or terrestrial) and that do not consider linkages across ecosystem boundaries. Such experiments document how aquatic contaminants can alter the quantity (e.g., biomass) and quality (measured using isotopic signatures and fatty acid content among other chemical traits) of prey subsidies and how these changes can in turn affect a host of bottom-up and top-down processes operating in riparian ecosystems. Collectively, the chapters in this section emphasize how recent advances in the field of contaminants at the land-water interface have real-world applications that are in turn advancing the assessment and management of contaminant risk.

3.5 Syntheses

The effects of contaminants on ecological subsidies at the land-water interface are modulated by various factors including landscape, ecotoxicological, and ecological processes. Syntheses that knit together these processes provide useful models to visualize, study, predict, and manage the effects of contaminants. Furthermore, synthetic approaches are useful for illustrating data gaps and outlining next steps needed to predict effects of contaminants in these systems. In this book, we present two synthesis approaches to understanding and predicting effects of aquatic contaminants on food web resource and contaminant linkages between the aquatic and terrestrial realms.

Sullivan and Cristol (this volume) use network models to map the multitude of interactions between these habitats. Using a real-world example, the authors showed that dam removal led to changes in fish species composition and in trophic dynamics that could reduce contaminant biomagnification within a riverine food web. Further, they demonstrate that including human social-ecological interactions within these networks can improve predictions of human exposure risk to aquatic contaminants as mediated by connections within the aquatic food web. Kraus et al. (this volume) use conceptual models to highlight landscape, ecotoxicological, and ecological pathways that control the effects of contaminants on subsidy production and contaminant flux from water to land. These models emphasize that the critical pathways driving these effects vary considerably for different classes of contaminants. The authors demonstrate the potential utility of this framework to identify fruitful areas for future research and as a tool to guide risk assessment and data collection in the face of high uncertainty.

4 Conclusions

Studies of the environment have a common attribute: a spatial limit of inquiry imposed by the researchers themselves. Establishing this limit is a critical step driven by consideration of the time scale, logistics, and level of ecological complexity (among many others) that can feasibly be studied. Recognition of the important interconnectedness of ecosystems has made this task no easier – in fact the studies highlighted here include two very different ecosystems (land and water) as well as the porous boundaries between them. Even though we began this chapter highlighting the need for greater integration between the fields of ecology and ecotoxicology (as many others have done before us), the mere existence of this volume shows that large strides have already been made. Evoking the statement from Polis et al. (1997) opening this chapter, these advances may be attributed to the fact that food webs are a central organizing theme in ecology *and* ecotoxicology, providing a common ground for synergy between the fields (Rohr et al. 2006). Research on spatial subsidies represent just one possible avenue to further connect these disciplines and to better address the complex interplay between contaminants and the fluxes of material and organisms at the land-water interface.

While we have accumulated a substantial body of information on processes governing the dynamics of resource subsidies and contaminants, more work remains to be done in this growing field of inquiry. Common research needs that emerged across the sections and chapters of this book include a pressing need for more nuanced models accounting for the complexity of contaminant-subsidy dynamics across spatial and temporal scales; better conceptual frameworks and more empirical studies that account for interactive effects of multiple stressors common to aquatic and riparian habitats; spatial modeling approaches that improve our ability to predict or forecast areas where contaminants have large impacts on resource subsidies and, conversely, where resource subsidies can play a large role in contaminant fate and exposure; and expanding the application of this knowledge base to provide the tools and processes needed to better manage the risks of contaminants in highly valued ecosystems.

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Part I

Ecological Subsidies Drive Exposure

Ecological Factors Controlling Insect-Mediated Methyl Mercury Flux from Aquatic to Terrestrial Ecosystems: Lessons Learned from Mesocosm and Pond Experiments

Matthew M. Chumchal and Ray W. Drenner

> *Ecological understanding must be integrated into toxicology for a better, more coherent whole.*
>
> (Chapman 2002)

1 Introduction

The diets of terrestrial consumers can be subsidized by emerging adult aquatic insects that transport energy and nutrients from aquatic to terrestrial ecosystems (Polis et al. 1997; Baxter et al. 2005). However, this cross-ecosystem movement of materials by aquatic insects can have a "dark side" because emerging aquatic insects also transport bioaccumulative contaminants such as methyl mercury (MeHg) and polychlorinated biphenyls (PCBs) to terrestrial ecosystems (Walters et al. 2008; Tweedy et al. 2013). The concentration of MeHg and PCBs in emerging aquatic insects is correlated with the level of contamination of aquatic ecosystems (Cristol et al. 2008; Walters et al. 2010; Tweedy et al. 2013; Gann et al. 2015) and can be high enough to pose a health hazard to terrestrial consumers (Brasso and Cristol 2008; Walters et al. 2010; Jackson et al. 2011; Gann et al. 2015; Williams et al. 2017). Although ecological factors (such as aquatic community structure) are known to influence adult aquatic insect emergence and the cross-ecosystem transport of energy and nutrients (e.g., McCarty 1997; Davis et al. 2011; Greig et al. 2012; Wesner 2016), less is known about the ecological factors that regulate the cross-ecosystem transport of contaminants by emerging insects (Chumchal and Drenner 2015; Schiesari et al. 2018).

This chapter provides an overview of our mesocosm and pond experiments that investigated how ecological factors affect the transport of MeHg out of aquatic ecosystems by emerging insects (hereafter insect-mediated MeHg flux). In our studies, we calculated insect-mediated MeHg flux as the product of the MeHg concentrations and biomass of emerging insects (typically measured on a per area

M. M. Chumchal (✉) · R. W. Drenner
Department of Biology, Texas Christian University, Fort Worth, TX, USA
e-mail: m.m.chumchal@tcu.edu

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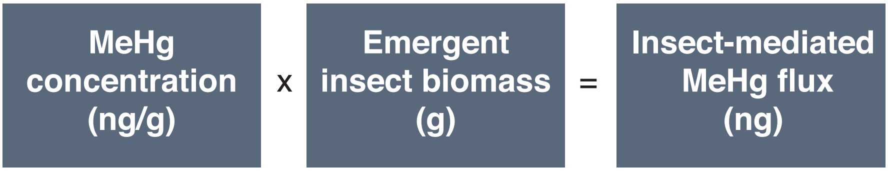


Fig. 1 Insect-mediated MeHg flux is calculated as the product of MeHg concentrations and biomass of emerging adult aquatic insects (typically measured on a per area basis over a fixed period of time). The resulting product represents an estimate of the absolute amount of contaminant leaving an ecosystem within the tissues of emerging insects

basis over a defined period of time; Fig. 1). Therefore, any factor that affects either the MeHg concentration or the biomass of emerging insects could influence insect-mediated MeHg flux. Multiplying MeHg concentration (ng/g) by the biomass (g) of emerging insects results in an estimate of the absolute amount of MeHg (ng) leaving the aquatic ecosystem within the tissues of emerging insects. Our experimental studies examined how four ecological factors affect aquatic insect-mediated MeHg flux: (1) fish predation and community structure, (2) nutrient levels and trophic state, (3) drying disturbance and pond permanence, and (4) seasonality of insect emergence.

2 Mercury Cycle

Methyl mercury is a toxic, biomagnifying contaminant of global significance (Chen and Driscoll 2018). Elemental and inorganic forms of mercury (Hg) are emitted to the atmosphere from industrial activities and can circulate around the globe before being deposited on the earth's surface, resulting in elevated concentrations of Hg in remote environments (Chen and Driscoll 2018). In aquatic ecosystems, the inorganic forms of Hg that are typically deposited from the atmosphere are converted by anaerobic bacteria to toxic MeHg (Chen and Driscoll 2018), which bioaccumulates in organisms at the base of the food web (i.e., algae) (Miles et al. 2001; Pickhardt and Fisher 2007). Consumers are exposed to MeHg through their diet (Hall et al. 1997; Tsui and Wang 2004; Pickhardt et al. 2006), and MeHg biomagnifies as it is transferred through the food web, reaching elevated concentrations in organisms with high trophic positions (Lavoie et al. 2013) such as predatory insects and fish. Terrestrial consumers can be exposed to MeHg by consuming emerging aquatic insects or by consuming spiders that feed on aquatic insects (Gann et al. 2015; Chumchal et al. 2017). Methyl mercury concentrations in terrestrial spiders that consume adult aquatic insects are correlated with insect-mediated MeHg flux (Tweedy et al. 2013).

3 Effects of Ecological Factors on Aquatic Insect-Mediated MeHg Flux

3.1 *Fish Predation and Community Structure*

Freshwater fish are top predators and important consumers of aquatic insects (Wesner 2016). Most large-bodied insectivorous fish in lentic freshwater ecosystems, such as bass and sunfish (Centrarchidae), locate their prey visually and are size-selective predators, preferentially feeding on large and vulnerable prey items, such as dragonflies and damselflies (Odonata) (Mittelbach 1988). Because fish predation reduces the population density of larval insects that are capable of emerging from ponds as adults, we hypothesized that fish presence could reduce insect-mediated MeHg flux from aquatic ecosystems (Henderson et al. 2012).

We tested the hypothesis that fish predation reduces insect-mediated MeHg flux in experimental ponds located near Fort Worth, Texas, USA (Fig. 2a, b), with and without centrarchids: largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) (Tweedy et al. 2013). We used floating emergence traps to collect five taxa of emerging adult aquatic insects over a 6-week period during May and June 2011: dragonflies (Odonata:Anisoptera), damselflies (Odonata:Zygoptera), predatory chironomids (Chironomidae:Tanypodinae), microcaddisflies (Trichoptera:Hydroptilidae), and herbivorous chironomids (Chironomidae:Chironominae and Orthocladiinae) (Fig. 2c). We calculated MeHg flux for each of the five insect taxa separately as well as the sum (aggregate) of the MeHg flux from all five insect taxa. Because our experimental ponds varied in baseline levels of MeHg contamination, we used MeHg concentrations in herbivorous chironomids as a proxy for baseline MeHg contamination of the food web.

Both the level of MeHg contamination and the presence of fish had effects on insect-mediated MeHg flux. Methyl mercury flux from each insect taxon (Figs. 3a–d) except microcaddisflies (Fig. 3e) was positively and significantly related to MeHg concentrations in herbivorous chironomids (baseline contamination of the food web). Methyl mercury flux from large taxa (dragonflies and damselflies) was reduced in ponds with fish (Fig. 3a, b). The MeHg flux from small taxa (herbivorous and predatory chironomids and microcaddisflies) was not significantly affected by fish presence (Fig. 3c–e). Aggregate MeHg flux was positively and significantly related to MeHg concentrations in herbivorous chironomids (a proxy for baseline MeHg contamination of the food web) and was significantly lower in ponds with fish (Fig. 3f).

The reduction of aggregate insect-mediated MeHg flux in the presence of fish was caused by the suppression of biomass of large taxa (dragonflies and damselflies) emerging from ponds and not alteration of MeHg concentrations within taxa (Tweedy et al. 2013). The suppression of emerging dragonflies and damselflies led to a relatively large reduction of aggregate MeHg flux because these predatory taxa have high MeHg concentrations and occur at high biomasses, thus they account for a large proportion of aggregate MeHg flux. The difference in aggregate

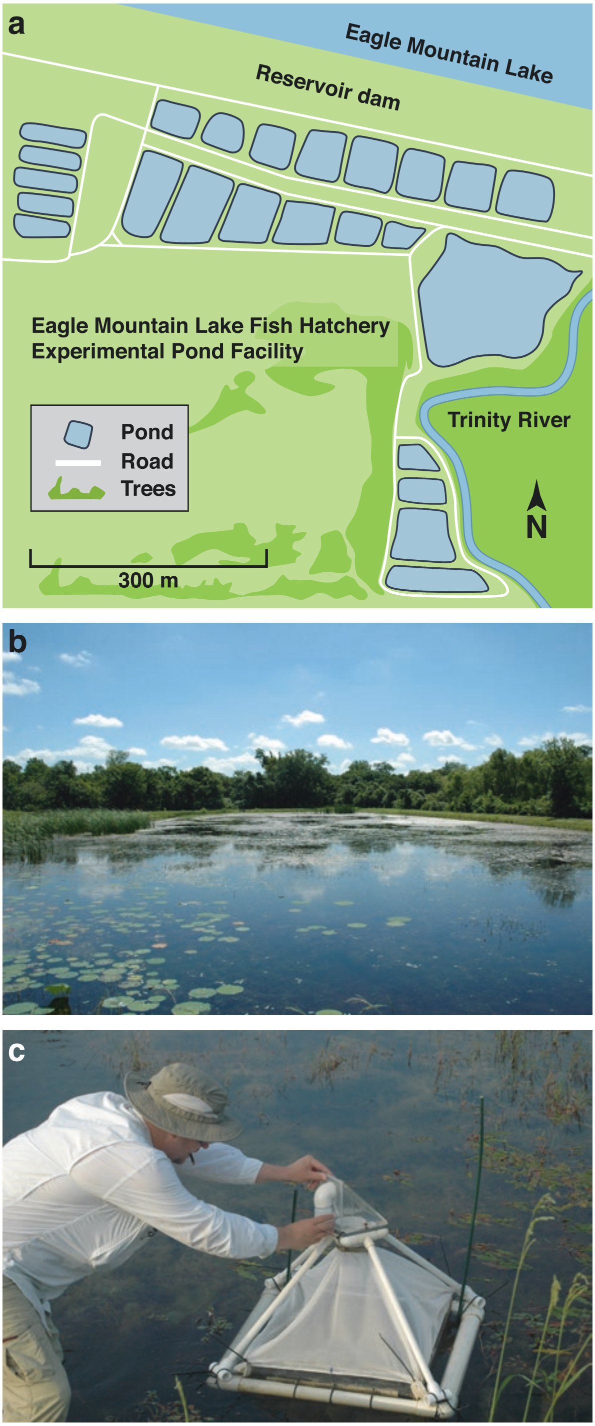


Fig. 2 (continued)

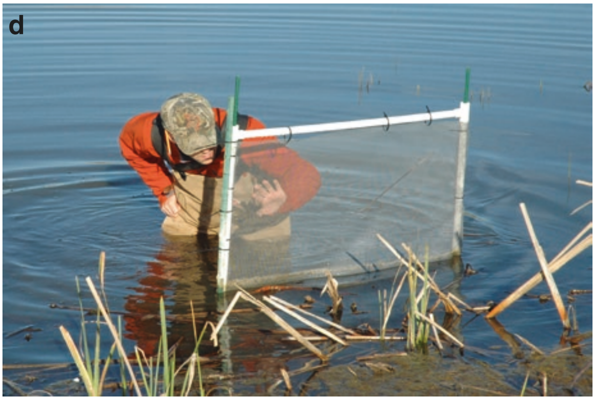


Fig. 2 (**a**) The Eagle Mountain Fish Hatchery Experimental Pond Facility consists of ponds supplied with water from Eagle Mountain Lake, a large eutrophic reservoir near Fort Worth, Texas, USA (32°52’32.95”N, 97°28’29.00”W). Atmospheric deposition to the pond surfaces and the watershed of Eagle Mountain Lake contaminates ponds with Hg, allowing us to conduct studies without having to add Hg to the ponds. (**b**) Ponds are shallow with maximum and average depths of 1.2 and 0.6 m, respectively, and range in size from 0.23 to 0.54 ha. Ponds have earthen bottoms and contain complex communities of macrophytes, benthic invertebrates, reptiles, and amphibians that colonize the ponds (Williams et al. 2017). Ponds can be stocked with any combination of fish species, and fish will reproduce in ponds. Image reprinted with permission from Tweedy et al. (2013). Copyright 2013 American Chemical Society. (**c**) In Tweedy et al. (2013) and Chumchal et al. (2017), we captured emerging insects using 0.53 m × 0.53 m area (0.28 m^2) floating emerging insect traps. (**d**) In Williams et al. (2017), dragonfly emergence was monitored with 1 m × 1.5 m (width × height) emergence platforms

insect-mediated MeHg flux between ponds with and without fish was greatest in ponds with high MeHg contamination (Fig. 3f), suggesting that the effects of fish on insect-mediated MeHg flux would be expected to be greatest in highly Hg-contaminated ecosystems. In summary, we found that the potential for insect-mediated MeHg flux increased with MeHg contamination levels of the ponds but that the realized MeHg flux from individual insect taxa was determined by fish presence.

3.2 Nutrient Levels and Trophic State

In addition to fish predation, the population biomass of emerging aquatic insects is also determined by the level of primary production (Blumenshine et al. 1997). In aquatic systems, primary production can be limited by the nutrients nitrogen (N) and phosphorus (P) (Elser et al. 1990, 2007). In combination, high concentrations of N and P enhance primary production (Elser et al. 1990, 2007) and increase the biomass of primary and secondary consumers, including emerging insects (McCarty

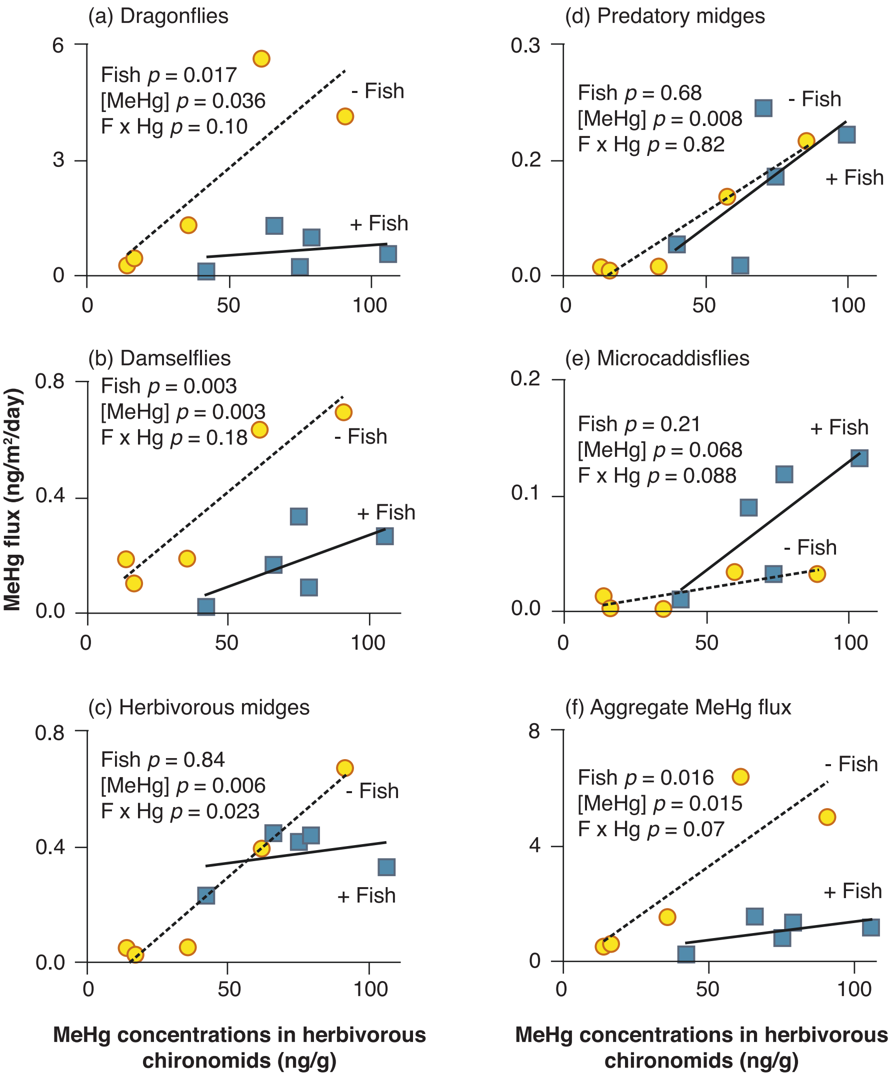


Fig. 3 Relationship between herbivorous chironomid MeHg concentration (a proxy for baseline MeHg contamination) and MeHg flux from (**a**) dragonflies, (**b**) damselflies, (**c**) herbivorous chironomids, (**d**) predatory chironomids, (**e**) microcaddisflies, and (**f**) an aggregate of all taxa in ponds with and without fish. Solid lines with blue squares represent ponds with fish (+ fish), and dashed lines with yellow circles represent ponds without fish (− fish). P-values from an ANCOVA testing for the main effects of chironomid MeHg concentration ([MeHg]) and fish presence (fish) and their interaction (F × Hg) on MeHg flux are included in each panel. The assumption of heterogeneous slopes was violated in the case of herbivorous chironomids; therefore, we report the treatment effect of fish at the average of the covariate. Note the scale of the y-axis differs for each taxon. Used with permission from Tweedy et al. (2013). Copyright 2013 American Chemical Society

Fig. 4 Our experimental mesocosms are 550 l conical fiberglass tanks (0.6 m^2 surface area) located at the Texas Christian University mesocosm facility in Fort Worth, Texas, USA. Water is supplied from a nearby pond. The mesocosms were aerially colonized by aquatic insects and stocked with fish. Sediments collected from nearby ponds (LBJ National Grasslands, Decatur, TX, USA) contaminated with Hg from the atmosphere were added to the tanks to serve as a source of Hg. In Jones et al. (2013), mesocosms were covered with mesh netting to capture all emerging insects

1997; Davis et al. 2011; Greig et al. 2012). We hypothesized that nutrient addition would increase insect-mediated MeHg flux by increasing the biomass of emerging insects more in systems without fish than in systems with insectivorous fish.

To examine how nutrient addition and the presence of predatory fish may interact to affect insect-mediated MeHg flux, we conducted a mesocosm experiment at the Texas Christian University mesocosm facility in Fort Worth, Texas, USA (Fig. 4). We used a 2 × 2 factorial design in which two levels of nutrient addition (presence and absence of simultaneous N and P addition) were cross-classified with two levels of fish (presence and absence of juvenile green sunfish [*Lepomis cyanellus*]) (Jones et al. 2013). This experimental design allowed us to examine the main effects of nutrients and fish and their potential interaction effects on insect-mediated MeHg flux. Mesocosms were filled with water (day 1), and 51 and 52 days later, fish were stocked and nutrient additions began, respectively. Adult aquatic insects were allowed to aerially colonize the mesocosms from days 1 to 101 of the experiment. One hundred and two days after filling the mesocosms with water, we began capturing adult aquatic insects emerging from the mesocosms. We used tent-shaped emergence traps that covered the entire surface of the mesocosm (Fig. 4) to capture all emerging insects including small midges (defined as Chironomidae <4.0 mm total length), large midges (Chironomidae ≥4.0 mm total length), and dragonflies for 20 days.

Nutrient addition led to an increase in nutrient concentrations (Fig. 5a, b) and chlorophyll a concentration (a proxy for primary producer biomass, Fig. 5c) in the water column. Nutrient additions increased insect-mediated MeHg flux from small and large midges and dragonflies (Fig. 5d–f) primarily by enhancing biomass of emerging adults (Fig. 5g–i). This experiment suggests that an increase in nutrients can lead to an increase in emerging insect biomass and enhanced flux of MeHg from aquatic to terrestrial ecosystems.

The effects of nutrient additions on MeHg concentrations in emerging adult aquatic insects were inconsistent among taxa. Methyl mercury concentrations in small midges were enhanced by nutrient additions (Fig. 5j), whereas the MeHg concentrations in large midges and dragonflies were not affected by nutrient additions (Fig. 5k, l). An increase in nutrients has been hypothesized to lead to reduced contaminant concentrations in aquatic organisms because an increase in primary production or consumer growth rates without a concomitant increase in contaminant levels could reduce the amount of MeHg available per algal cell or per gram of consumer tissue (i.e., the bloom dilution and somatic growth dilution hypotheses, respectively) (Pickhardt et al. 2002; Karimi et al. 2007, 2010). The predictions of the bloom and growth dilution hypotheses were not supported here nor in some other studies (reviewed in Jones et al. 2013) suggesting that more work is needed to determine the conditions under which bloom and growth dilutions occur.

The presence of fish led to a decrease in insect-mediated MeHg flux from small and large midges and dragonflies (d–f), primarily by reducing biomass of emerging adults (Fig. 5g–i). In this study, all insects were suppressed, not just the largest taxa like in Tweedy et al. (2013). Fish suppression of small midges in this study and not Tweedy et al. (2013) may have occurred because the fish species differed between studies. Alternatively, the fiberglass mesocosms used in this study were less environmentally complex than the experimental ponds used in Tweedy et al. (2013) which contained abundant macrophytes that provided a refuge from predation. The effects of nutrient additions and fish presence were interdependent such that the effects of nutrients on insect-mediated MeHg flux were more pronounced when fish were absent, and the effects of fish on insect-mediated MeHg flux were more pronounced when nutrient concentrations were high (Fig. 5d–f).

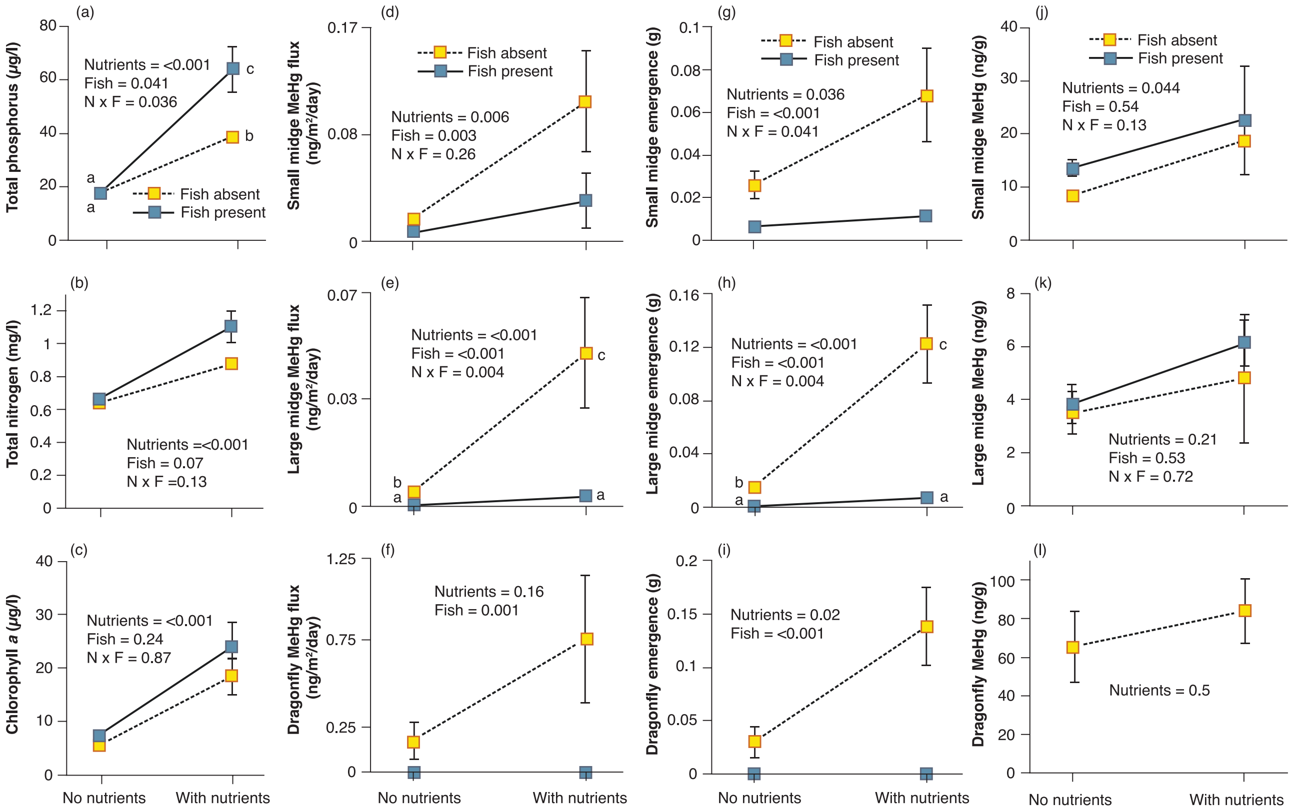


Fig. 5 Two-way interaction plots illustrating the main effects of nutrient additions (nutrients) and fish presence (fish) and their interaction effect (N × F) on (**a–c**) water quality, (**d–f**) emerging insect MeHg flux, (**g–i**) emerging insect biomass, and (**j–l**) emerging insect MeHg concentration in experimental mesocosms. Water samples were collected twice a month throughout the experiment after nutrient additions began. Values for water quality represent the treatment combination average (± S.E.) of four sampling dates (**a–c**). Values for MeHg flux and MeHg concentration represent the treatment combination average (± S.E.) (**d–f**, **j–l**). Values for emerging insect biomass represent the treatment combination average (± S.E.) collected during 20 days (**g–i**). MeHg concentrations were not determined in dragonflies from tanks with fish because fish completely eliminated dragonfly emergence (**l**). Copyright 2013 Wiley. Used with permission from Jones et al. (2013)

3.3 Drying Disturbance, Pond Permanence, and Seasonality of Insect Emergence

Drying disturbance is a key ecological factor affecting the community structure of small ponds (Batzer and Wissinger 1996; Wellborn et al. 1996). Small ponds (0.005–1 ha) exist across a permanence gradient from permanent (that do not dry and often contain fish) to semi-permanent (that dry periodically and therefore usually do not contain fish) (Chumchal and Drenner 2015; Chumchal et al. 2016). Because pond permanence determines if fish are present or absent, and fish presence suppresses emergence of large-bodied adult aquatic insects, permanence may control insect-mediated MeHg flux.

Although insect emergence and associated insect-mediated MeHg flux from permanent ponds is not interrupted by drying disturbances, insect-mediated MeHg flux in semi-permanent ponds ceases during drying disturbances. Insect-mediated MeHg flux in semi-permanent ponds restarts after ponds refill with water and are recolonized by aquatic insects (Batzer and Wissinger 1996). We hypothesized that as insect populations reestablished in recently refilled semi-permanent fishless ponds, insect-mediated MeHg flux would recover and eventually reach higher levels in semi-permanent fishless ponds than permanent fish ponds. We also hypothesized that the effects of pond permanence on insect-mediated MeHg flux were dependent on season because insect development is regulated by temperature, photoperiod, and food availability, all of which vary seasonally (Corbet 1980). Specifically, we expected that insect-mediated MeHg flux would be lower in winter than in summer.

To test the two hypotheses above, we conducted a two-phase experiment in ten experimental ponds near Fort Worth, Texas, USA (Fig. 2a, b) (Chumchal et al. 2017; Williams et al. 2017). In spring 2013, we filled ten dry ponds with water and stocked them with bluegill. On April 1, 2014, five of the ten ponds were drained and fish removed to simulate drying disturbance. The five dried ponds were refilled with water on May 13, 2014, to simulate semi-permanent ponds without fish. After drying disturbance and refilling of semi-permanent ponds, aquatic insect communities were reestablished by recruitment of insect populations from eggs deposited by aerially colonizing adults that migrated from nearby waterbodies (Chumchal et al. 2017). Phase I of the experiment focused on recovery of insect-mediated MeHg flux immediately after the drying disturbance and refilling of semi-permanent ponds (Chumchal et al. 2017). In phase II of the experiment, we examined the seasonality of insect-mediated MeHg flux from permanent fish ponds and semi-permanent fishless ponds from winter through summer 2015 (Williams et al. 2017). Phase II began 8 months after the semi-permanent ponds were refilled.

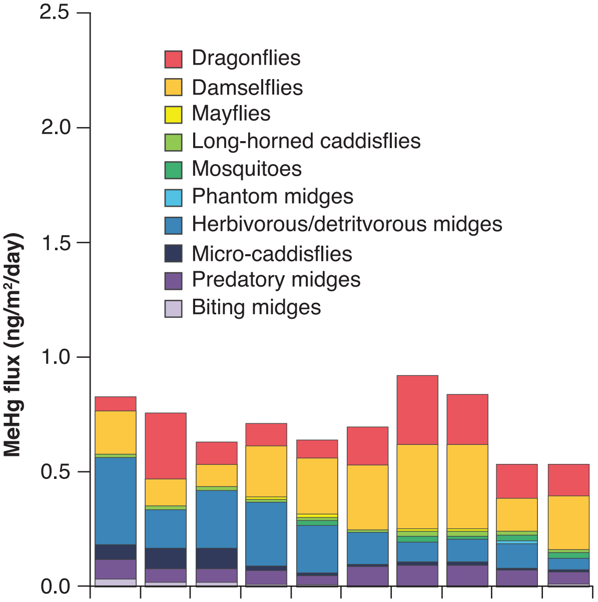
Phase I: Recovery of insect-mediated MeHg flux in semi-permanent ponds after a drying disturbance. In phase I, we used floating emergence traps (Fig. 2c) to collect emerging insects. We collected emerging insects over a 73-day period that began immediately after ponds were refilled. During the 73-day period after semi-permanent ponds were refilled, aggregate MeHg flux from semi-permanent ponds was greater than aggregate MeHg flux from permanent ponds (although the difference was not statistically significant), indicating that insect-mediated MeHg flux had rapidly recovered in semi-permanent ponds following drying disturbance (Fig. 6a, b). The taxonomic composition of insect-mediated MeHg flux was relatively consistent in permanent ponds throughout the experiment (Fig. 6a) but changed in semi-permanent ponds as the insect communities underwent succession after refilling (Fig. 6b). In the permanent ponds, both small and large taxa (e.g., midges and dragonflies, respectively) contributed to the MeHg flux during the 10-week experiment (Fig. 6a). In semi-permanent ponds, we detected MeHg flux from the eight smallest insect taxa 11 days after refilling (Fig. 6b). The three largest taxa (mayflies, damselflies, and dragonflies) did not emerge and contribute to the MeHg flux from semi-permanent ponds until days 18, 25, and 32, respectively (Fig. 6b). This phase of the study demonstrated the potential for rapid recovery of insect-mediated MeHg flux following drying disturbance. The rapid rate of recovery of insect-mediated MeHg flux following drying disturbance in our study was likely due to the proximity of our experimental ponds to nearby permanent waterbodies that served as sources of adult aerially colonizing insects (Niemi et al. 1990) and warm water temperatures (mean = 27.8 °C in this experiment) that facilitated insect growth and development (Corbet 1980; Gillooly and Dodson 2000).

Phase II: Seasonality of insect-mediated MeHg flux from permanent fish ponds and semi-permanent fishless ponds. In phase II of the experiment, we examined the seasonality of insect-mediated MeHg flux from permanent fish ponds and semi-permanent fishless ponds from winter through summer 2015, beginning 8 months after the semi-permanent ponds were refilled. Because odonates (dragonflies and damselflies) dominated the flux during phase I, we focused on odonate-mediated MeHg flux during phase II. Odonate emergence was monitored with emergence platforms (Fig. 2d), and water temperature data were collected using temperature loggers.

During the experiment, temperature and odonate-mediated MeHg flux varied with month (Fig. 7). Temperature increased from winter to summer in permanent and semi-permanent ponds (Fig. 7a). Odonate-mediated MeHg flux was first detected for damselflies (Fig. 7b) in March and for aeshnid and libellulid dragonflies in April (Fig. 7c–d). Peak MeHg flux from damselflies, aeshnid dragonflies, and libellulid dragonflies occurred in April, May, and June, respectively. Methyl mercury flux from aeshnid dragonflies was suppressed in permanent ponds with fish.

These seasonal patterns in MeHg flux were caused by changes in emerging odonate biomass over time and not MeHg concentrations (Williams et al. 2017). This phase of the study demonstrated that at the warm temperate latitude where the study occurred (32°N), odonate-mediated MeHg flux is regulated by the interaction of season and pond permanence. Season is an important factor regulating MeHg flux because odonate-mediated MeHg flux does not occur during cold seasons. For all three taxa, most odonate-mediated MeHg flux occurred primarily in the spring and early summer. During periods of insect emergence, MeHg flux was affected by pond permanence and fish such that semi-permanent ponds without fish had higher MeHg flux than permanent ponds with fish.

(a) Permanent



(b) Semi-permanent

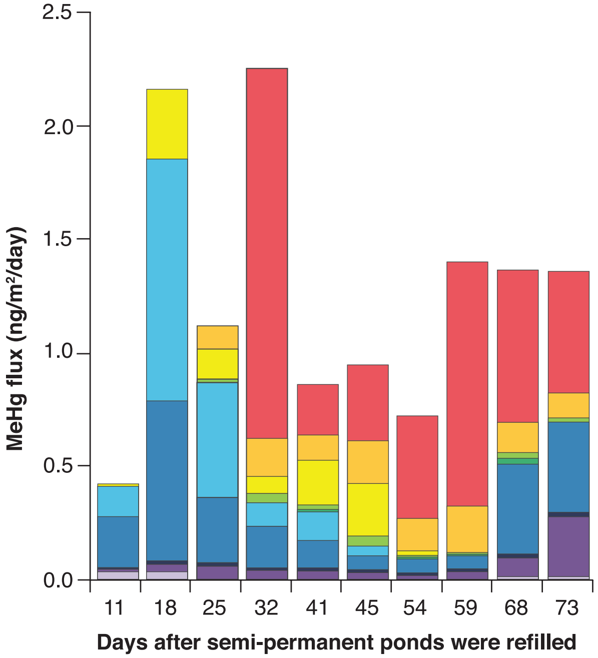


Fig. 6 Average MeHg flux (ng/m^2/d) for ten emerging insect taxa collected on ten sampling dates from (**a**) permanent and (**b**) semi-permanent ponds following drying disturbance. In the legend, taxa are listed in order of body length, from largest to smallest. Copyright (2017) Wiley. Used with permission from Chumchal et al. (2017)

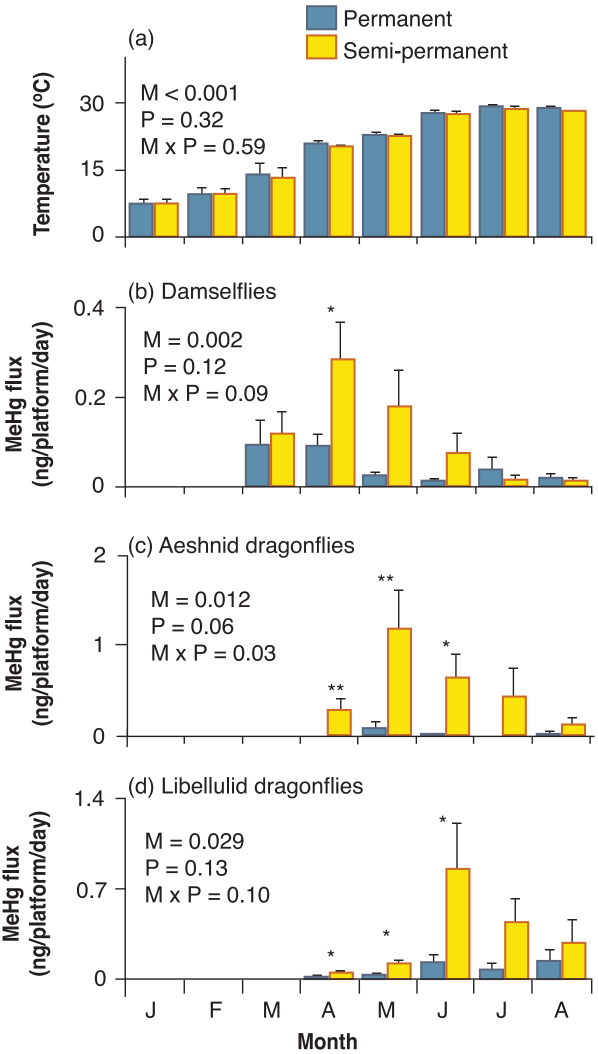


Fig. 7 (**a**) Average (± S.E.) monthly water temperature and (**b**) damselfly-, (**c**) aeshnid dragonfly-, and (**d**) libellulid dragonfly-mediated MeHg flux in permanent and semi-permanent ponds. *P*-values from repeated measure ANOVAs examining the main effects of month (M), pond permanence (P), and the month × pond permanence interaction (M × P) are shown on each panel. When a significant month × pond permanence interaction was detected, we tested for simple effects of pond permanence in a given month. The symbols ** and * represent a significant simple effect between semi-permanent and permanent ponds equivalent to $p \leq 0.05$ and $p \leq 0.10$, respectively. Copyright 2017 Wiley. Used with permission from Williams et al. (2017)

4 Conceptual Model

Based on the results of our experiments, we developed a conceptual model of the influence of MeHg contamination and ecological factors on insect-mediated MeHg flux. In the model (overviewed below), we propose that the potential for insect-mediated MeHg flux increases with the level of MeHg contamination of the ecosystem but that the realized MeHg flux is determined by ecological factors such as pond permanence, fish presence, nutrient levels, and trophic state (Fig. 8).

Methyl Mercury Contamination of Ecosystems The potential for insect-mediated MeHg flux is set by Hg contamination of the ecosystem (Tweedy et al. 2013; Fig. 8). Our model predicts that insects from more contaminated sites will have higher concentrations of MeHg and therefore have the potential to transport more MeHg per unit of insect biomass to terrestrial ecosystems. The model would not apply to ecosystems with MeHg contamination levels high enough to be toxic to insects.

Pond Permanence and Fish Presence Pond permanence regulates insect-mediated MeHg flux by determining the presence and absence of insectivorous fish (Chumchal and Drenner 2015). Our model predicts that systems without fish will have higher insect-mediated MeHg flux relative to those with fish and that the suppression of MeHg flux by fish will be greater in high-nutrient than low-nutrient systems (Fig. 8).

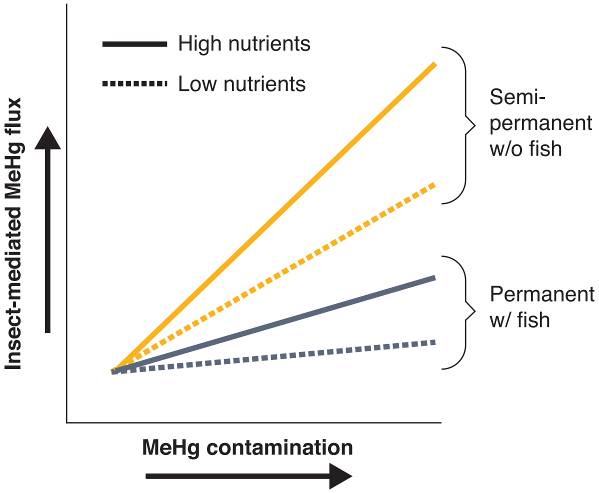


Fig. 8 Conceptual model of the influence of MeHg contamination of ecosystems and ecological factors regulating emerging insect biomass on insect-mediated MeHg flux. The potential for insect-mediated MeHg flux increases with MeHg contamination of the ecosystem but the realized MeHg flux is determined by ecological factors. Semi-permanent ponds without fish have higher insect-mediated MeHg flux than permanent ponds with fish. High-nutrient ponds have higher insect-mediated MeHg flux than low-nutrient ponds. This model applies during seasons when insects are emerging

This model is based on the results of our experiments conducted with large-bodied centrarchids that are ubiquitous and abundant in the Southern United States. These fish have large mouth gapes that allow them to consume large insects such as dragonflies. Small-bodied fish with smaller gapes (e.g., three-spined stickleback [*Gasterosteus aculeatus*]) might not have the same effect on large-bodied insects and instead could suppress insect-mediated MeHg flux from smaller taxa (Greig et al. 2012). Although, in our region (the southern Great Plains of the United States), drying is the primary disturbance that creates fishless lentic systems, other disturbances (e.g., winterkill) that eliminate fish may impact insect-mediated MeHg flux in other regions (Wellborn et al. 1996).

Nutrient Levels and Trophic State Nutrients regulate insect-mediated MeHg flux by enhancing emerging insect biomass (Fig. 8). Our model predicts that systems with high concentrations of nutrients will have elevated insect-mediated MeHg flux. The enhancement of insect-mediated MeHg flux by nutrients will be greater in semi-permanent ponds without fish than in permanent ponds with fish. This model was developed based on the results from our experiments conducted in oligo-mesotrophic and eutrophic systems (Jones et al. 2013) and may not apply to hyper-eutrophic systems that experience anoxia and fish kills.

5 Conclusions

Almost 20 years ago, Chapman (2002) suggested that “ecological understanding must be integrated into toxicology for a better, more coherent whole.” Our community-level experiments demonstrate how concepts such as the “dark side” of aquatic insect subsidies can be more fully understood by integrating the fields of toxicology and ecology. Although the integration of the fields of ecology and toxicology is just beginning (e.g., Chumchal and Drenner 2015; Schiesari et al. 2018), it has great potential to further our understanding of environmental contamination.

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Pathways of Contaminant Transport Across the Aquatic-Terrestrial Interface: Implications for Terrestrial Consumers, Ecosystems, and Management

Ralf Schulz and Mirco Bundschuh

1 Introduction

Due to their geomorphology and position in the landscape, freshwater ecosystems are recipients of allochthonous inputs such as nutrients, detritus, and contaminants (Blais 2005; Blais et al. 2007; Kaushal et al. 2013, 2014; Leroux and Loreau 2008; Schwarzenbach et al. 2006; Stehle and Schulz 2015). The flow of matter from terrestrial to aquatic systems is formalized in the River Continuum Concept, which describes the functional attributes from upstream to downstream along rivers as a function of the progressive shift in energy sources supporting river food webs (Vannote et al. 1980) – a pattern which is relatively well studied (Richardson and Sato 2015) though it does not apply in all cases. Furthermore, Burcher et al. (2007) developed the land-cover cascade as a conceptual framework to link land use via hydrologic, geomorphic, erosional, and depositional elements with changes in freshwater fish and macroinvertebrate community structure. The concept of the riparian environment having an impact on freshwater ecosystems, e.g., via matter input, is thus well established.

R. Schulz (✉)
iES Landau, Institute for Environmental Sciences, University of Koblenz-Landau, Landau, Germany

Eusserthal Ecosystem Research Station, University of Koblenz-Landau, Landau, Germany
e-mail: schulz@uni-landau.de

M. Bundschuh
iES Landau, Institute for Environmental Sciences, University of Koblenz-Landau, Landau, Germany

Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden
e-mail: bundschuh@uni-landau.de

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At the same time, freshwater ecosystems can export resources to terrestrial ecosystems (Bartels et al. 2012; Marcarelli et al. 2011; Nakano and Murakami 2001; Schiesari et al. 2017; Sullivan and Rodewald 2012). Flux of carbon and energy from the aquatic to terrestrial environment has, for example, been conceptualized in the flood pulse concept (Junk et al. 1989). The flood pulse concept describes flood pulses as the principal driving force responsible for the existence, productivity, and interaction of the major biota in river floodplain systems. Furthermore, Menzie (1980) suggested that the adult aquatic insect-mediated contaminant transport from aquatic to terrestrial ecosystems may be important. Although insect-mediated transport of aquatic contaminants into terrestrial ecosystems does occur (Walters et al. 2008), Menzie's (1980) hypothesis has not yet been proven.

In this chapter, we review the pathways of contaminant transport across the aquatic-terrestrial interface. We identify two categories of pathways, namely, biologically mediated (e.g., adult aquatic insect emergence or terrestrial consumption of aquatic organisms) and abiotic (e.g., flooding), that can lead to *exposure* in the terrestrial ecosystem. We briefly discuss *effects* of aquatic contamination on terrestrial consumers and food webs. Finally, we provide insights into the *risk assessment and management* based on the combined consideration of exposure and effects.

2 Pathways of Contaminant Transport

Scientific interest on the topic of aquatic-terrestrial linkages has increased over the past 30 years (Schulz et al. 2015; Fig. 1) at a rate above the annual average increase of 5% in scientific publications (Larsen and von Ins 2010). Research dealing with biologically mediated or abiotic aspects of this linkage have acted largely separately from each other: the respective publications retrieved from scientific search engines overlap only by approximately 3% (Schulz et al. 2015).

Recently, researchers have made efforts to simultaneously consider both biologically mediated and abiotic pathways of energy, nutrient, and contaminant transport from aquatic to terrestrial ecosystems. For example, Loreau et al. (2013) provided a framework (i.e., the meta-ecosystem concept) to unify ecosystems that export and those that receive living and non-living entities. By including both biologically mediated and abiotic inputs within one framework, they also provided a mechanism for testing the relative importance of these two pathways, which may also be applied to contaminant transport. They further differentiated between ecosystems which are always exporting or receiving and those that change roles depending on condition. These two different ecosystem representations are both relevant for biologically mediated and abiotic transport of contaminants across aquatic-terrestrial interfaces. Schiesari et al. (2017) recently linked the meta-ecosystem concept to fluxes of contaminants. They found that contaminant transport by dispersing (or emerging) organisms can link contaminant stocks, i.e., contaminant reserves, in spatially

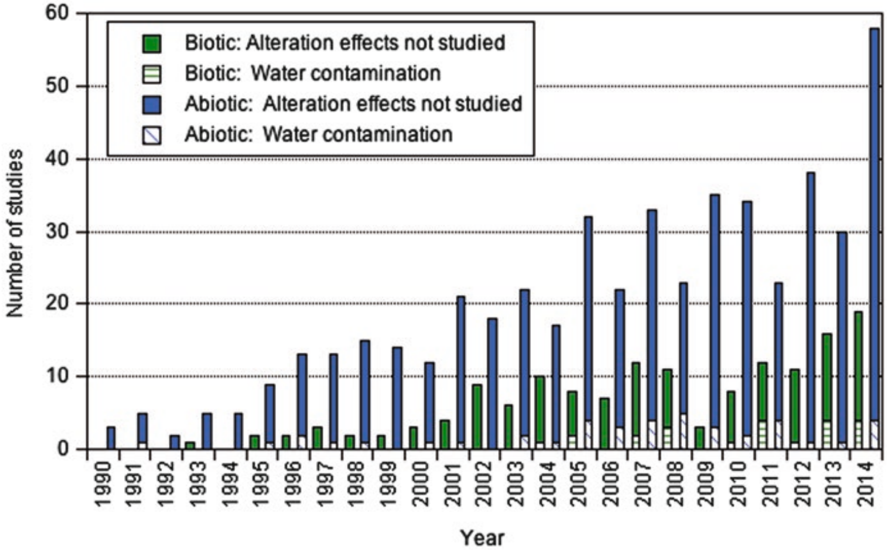

Fig. 1 Number of peer-reviewed publications per year targeting aquatic-terrestrial linkages between 1990 and 2014 with regard to abiotic (blue, right bars) and biologically mediated (green, left bars) coupling. Striped bar sections highlight those publications dealing with aquatic contamination as the alteration in the aquatic ecosystem potentially translating into an effect in the adjacent terrestrial ecosystems (replotted from Schulz et al. 2015)

separate ecosystems. The consideration of biologically mediated and abiotic pathways in a contaminated aquatic-terrestrial environment may thus combine separate contaminant stocks into a "meta-contaminant stock."

Finally, in a review on the state of knowledge, Schulz et al. (2015) discussed two main pathways for the aquatic energy or matter transport to terrestrial ecosystems (see also Fig. 2). First, flooding processes including groundwater flux transfer contaminants along with water and inorganic or organic matter to terrestrial riparian ecosystems (abiotic pathway). Second, either animals with complex life cycles like aquatic insects and amphibians that enter terrestrial systems as part of their ontogeny or terrestrial consumers of aquatic prey transfer contaminants from aquatic to terrestrial food webs (biologically mediated pathway). Schulz et al. (2015) found that these pathways have most often been investigated in relatively pristine systems exhibiting no or negligible anthropogenic disturbances (i.e., in approx. 70% of the 661 publications identified in the review by Schulz et al. 2015). Due to the dominance of human activities, however, such near-natural conditions of freshwater systems may rather be an exception than the general condition. Of the 30% (i.e., 224) of the publications which addressed the consequences of anthropogenic alterations in the aquatic ecosystems, the vast majority focused on the consequences of hydromorphological and hydraulic modifications in aquatic systems (e.g., channelization, water abstraction, hydropower dams and dikes, Nilsson et al. 2005; Vitousek et al. 1997). The consequences of biologically mediated and abiotic transfer of

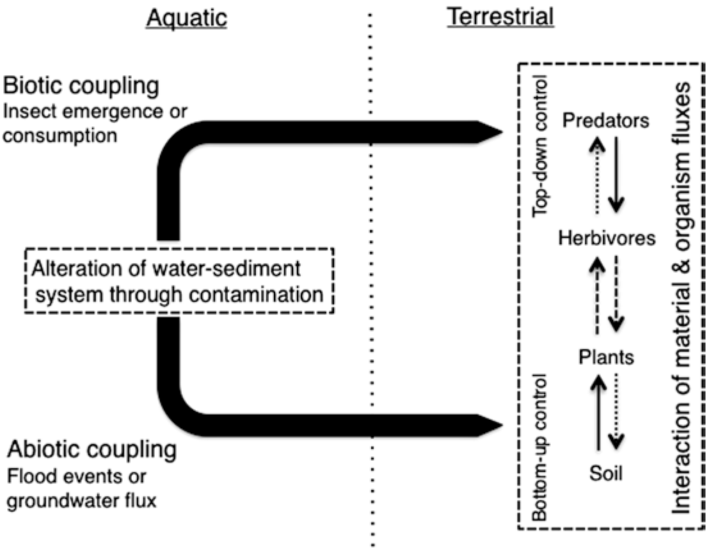

Fig. 2 Conceptual scheme indicating two pathways for aquatic contaminants to be transported into adjacent terrestrial ecosystems and how they may influence terrestrial biogeochemical processes and species interactions via biotic or abiotic coupling. Please note that for reasons of simplification, sediments were not specifically highlighted in this scheme, although they play a crucial role in both biotic (sediment-dwelling insects) and abiotic (particle-associated contaminant export) coupling. The implications on the terrestrial system can be – largely depending on the stressor and pathway – either bottom-up or top-down regulated. The term "soil" refers here to the soil compartment including its biotic component such as fungi and bacteria. The intensity of the arrows in the "terrestrial" box indicates the anticipated strength of the interactions among trophic levels (modified after Schulz et al. 2015)

contaminants from freshwater to terrestrial ecosystems are far less frequently studied (62 studies; see Fig. 1).

3 Exposure in Terrestrial Systems by Contamination from Aquatic Sources

3.1 Biologically Mediated Pathway: Emergence or Consumption

Biologically mediated contaminant transport to terrestrial systems is likely, since emergence of aquatic insects is an important source of energy for terrestrial food webs (Bartels et al. 2012; Bartrons et al. 2018; Popova and Kharitonov 2012; Sullivan and Rodewald 2012) and of particular importance for terrestrial insectivores, such as spiders (Gergs et al. 2014; Wieczorek et al. 2015), birds (Custer et al.

2010, 2014; Williams et al. 2017), and bats (Becker et al. 2018; Kalcounis-Rueppell et al. 2007; Stahlschmidt et al. 2012). For example, small rainwater detention ponds in vineyards of southwest Germany make up <0.1% of the vineyard landscape area, yet about 90% of the feeding activity of two endangered bat species takes place in close proximity to these rare aquatic landscape features (Stahlschmidt et al. 2012). These detention ponds are regularly contaminated by agrochemicals (Bundschuh et al. 2016; Stehle et al. 2011) that may be taken up by bats as they prey on adult aquatic insects emerging from the ponds. Moreover, aquatic contaminants can affect the quantity (Burdon this volume; Hatakeyama et al. 1997; Kraus and Pomeranz this volume; Wesner et al. this volume), community composition (e.g., Schäfer et al. 2011), and timing (Fig. 3; Schulz and Liess 2001b) of adult aquatic insect emergence, also with potential impacts for terrestrial insectivores (Graf et al. 2019).

A variety of contaminants have been shown to cross the aquatic-terrestrial interface and thus may affect the quality of emergence (Fig. 3). Persistent organic contaminants or organometals accumulate in aquatic organisms (Plénet 1995). These contaminants enter terrestrial food webs through emerging aquatic insects, increasing the daily intake of the first recipient in the terrestrial food chain, such as riparian spiders, by up to 40% (Daley et al. 2011; Kraus et al. 2014a; Walters et al. 2008).

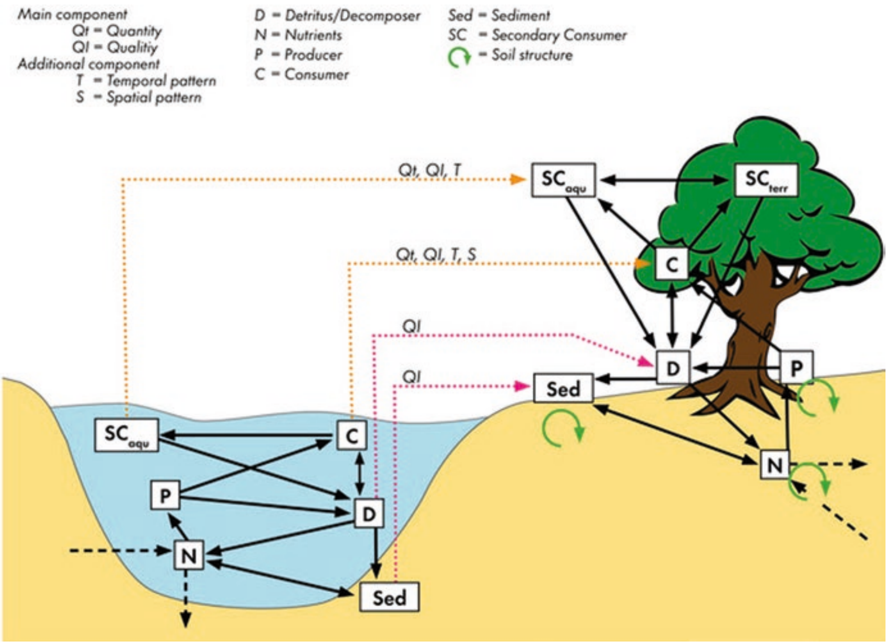

Fig. 3 Schematic figure (developed from Soininen et al. 2015) illustrating how aquatic ecosystems act as source of contaminants for recipient terrestrial ecosystems functioning as sinks. Dotted lines indicate the fluxes from water to land (orange = biotic coupling via emergence; pink = abiotic coupling via floods, i.e., surface and subsurface flow-related pathways) and solid lines within ecosystem fluxes. The dashed arrows indicate exchanges with groundwater

The aquatic-terrestrial contaminant link has also been illustrated by an opposite pattern that occurred along lakes in northeastern Iceland: in their riparian zones, terrestrial arthropods shifted toward aquatic midges, which reduced their MeHg levels. Aquatic midges represent a lower trophic level in the food web relative to the MeHg-contaminated prey of terrestrial origin, which was also reflected in the terrestrial arthropod isotopic signal (Bartrons et al. 2015). Taking an energetic pathway perspective, Sullivan and Rodewald (2012) focused on insect emergence as a transport vector for contaminants from aquatic to terrestrial ecosystems. They expected community structure to be one of the strongest mediators of aquatic-terrestrial contaminant fluxes and discussed how these fluxes may change as a result of landscape alterations and climate change. Metals (Kraus et al. 2014b; Pennuto and Smith 2015; Reinhold et al. 1999; Runck 2007), polychlorinated biphenyls (PCBs; Daley et al. 2011; Raikow et al. 2011; Reinhold et al. 1999; Walters et al. 2008, 2010), polycyclic aromatic hydrocarbons (PAHs; Reinhold et al. 1999), organochlorine insecticides (Reinhold et al. 1999), and algal bloom-related microcystin (Moy et al. 2016) are all transferred from aquatic to terrestrial systems via emerging insects. Recently, Richmond et al. (2018) have detected more than 60 pharmaceuticals to occur in emerging aquatic invertebrates and riparian spiders along 6 streams in South Australia. Since concentrations of various compounds found in aquatic invertebrates and terrestrial spiders were correlated, trophic transfer across the aquatic-terrestrial boundary appears likely. Accumulation and transfer of current-use pesticides and nanomaterials by emerging insects is much less documented (Al-Jaibachi et al. 2018; Kraus et al. 2014b). This may be due to constraints in analysis: detecting and quantifying these contaminants at low levels in small samples of biomass such as individual adult insects is challenging. However, both gold- and titanium-based nanoparticles have been found in adult caddisflies emerging from larvae exposed in laboratory stream microcosms (Bundschuh et al. 2019).

Metals and PAHs are predominantly lost during metamorphosis of insects. The relative loss in body burden varied, however, to a large extent among metals from about 126 times higher levels in larvae compared to adult insects for manganese to about 1.5 times higher levels in larvae for mercury (Kraus et al. 2014b). In contrast, synthetic organic contaminants such as PCBs were retained and concentrated in adults. PCB156 and Clophen A50, for example, reached relative concentrations about 3 times higher in adults relative to larval life stages (Kraus et al. 2014b). Despite the loss of metals during metamorphosis, terrestrial predators may contain considerably higher metal concentrations than their emerging prey as a result of biomagnification in the case of organometals. Biomagnification has been demonstrated for mercury in spiders and midges in the Buffalo River Area of Concern, USA (Pennuto and Smith 2015). Moreover, in cases of high insect production rates, even industrially highly contaminated, nutrient-enriched stream sites may contribute to a substantial mercury export via midges (*Cricotopus* spp.) into the terrestrial environment. The ratio of Hg(II) export in emergence production to surface area from a stream had been shown to be 10 to 10^3 times higher than for lake data taken from the literature (Runck 2007). A suite of studies looked at the export of MeHg from experimental ponds in north Texas (Chumchal and Drenner 2015; Henderson et al. 2012; Jones et al. 2013; Tweedy et al. 2013; Williams et al. 2017). They found that insects emerging from fishless ponds were larger (dragonflies and damselflies) and collectively provided more biomass to terrestrial food webs than those stocked with fish. Because of these differences, fishless ponds exported about five times more MeHg per m^2 per day than ponds containing fish. Interestingly, the presence of fish increased MeHg levels in small insects, such as micro-caddisflies, and thus also their contribution to MeHg export, which, however, is in absolute amounts much smaller than for the larger insects (see also Chumchal and Drenner this volume).

The extent of biologically mediated contaminant transport may also depend on the sex of specimens considered. A study using mayflies (*Hexagenia* spp.) from the Great Lakes looked at sex-specific bioamplification, i.e., biomagnification as a result of body weight loss, of sediment-associated PCBs during emergence (Daley et al. 2011). Male mayflies lose 36–64% of their lipids during emergence, while female imagos do not lose lipids. Since the total amount of PCBs remained constant per individual at about 150–3000 ng total PCB/g lipid equivalent (depending on the lake), lipid loss increased the relative body burden of PCBs in males. Depending on the sex composition of their prey, terrestrial consumers may thus increase considerably their total daily PCB intake.

Contaminants may also affect the quantity of emergence (Fig. 3), which then may feed back on contaminant transfer. Besides the transfer of contaminants, aqueous-phase pollutants reduce the emergence of aquatic insects and subsequently the abundance of terrestrial web-building spiders (Paetzold et al. 2011). However, in situations where the aquatic subsidy of terrestrial systems via the emergence of aquatic insects is substantially suppressed, the transfer of these contaminants across ecosystem boundaries may be limited (Kraus et al. 2014a; Paetzold et al. 2011). A study along a metal gradient in central Colorado identified emergence as a more sensitive bioindicator than aquatic invertebrate data (Schmidt et al. 2013). The authors suggested this high sensitivity of emergence to be triggered by a combination of larval survival and other factors acting jointly. One of the factors affecting emergence success is predation, which was among others documented for amphipod predators (Schulz and Liess 2001a). Nonetheless, the field study by Schmidt et al. (2013) shows interesting similarities with earlier work documenting high sensitivity of adult emergence following chronic or pulsed insecticide (lindane or fenvalerate) exposure (Liess and Schulz 1996; Schulz and Liess 1995).

Consequences of larval exposure for the fitness of the adult life stages are hardly assessed. However, multigenerational effects have been studied in chironomid larvae exposed, e.g., to various endocrine-disrupting chemicals (Tassou and Schulz 2009, 2011, 2012), and such an experimental design has even led to the release of the OECD (Organisation for Economic Co-operation and Development) study guideline no. 233. A recent study by Tuzun and Stoks (2017) provided first evidences that insecticide (fenvalerate) exposure in the aquatic ecosystem indeed changes lifetime mating success of the terrestrial adult damselflies. The extent to which these emergence-related effects depend on concentration levels of a given contaminant depends, however, on the contaminant itself, namely, some classes are excreted during metamorphosis (as discussed above).

Similarly, knowledge on the distance contaminants can be transported (lateral movement) as part of emerged organisms (Fig. 3), which may also be driven by its physiological condition, is rather limited: Raikow et al. (2011) have shown most of the PCB exported from a lake into spiders can be found within 5 m from the shore. This study, however, also indicated that more mobile social wasps, another terrestrial predator of emerging aquatic prey, show elevated levels of these contaminants about 30 m inland. Muehlbauer et al. (2014) reviewed the literature to define the spatial extent of a stream signature, i.e., the distance typically travelled by stream insects into the terrestrial surrounding. Although the half-maximum subsidy level was found at about 1.5 m, about 10% of the maximum subsidy level was still found at >500 m away from the stream. This suggests that the emergence signal can reach considerable distances inland. This assumption is supported by the reports that larger dragonflies can transfer biomass over several kilometers (Popova and Kharitonov 2012). Schindler and Smits (2017) proposed that the river morphology also affects the spatial extent of aquatic subsidies. More complex channel characteristics with a water level close to the land surface likely will have subsidies reaching further into land compared to constricted rivers with deeply incised channels. Lateral movement of emerging insects also changes along the longitudinal gradient of running waters (Schindler and Smits 2017) with adult insects in wider downstream sections being more prone to wind-related transport (Power and Rainey 2000). Yet, this aspect still requires quantitative analysis (Walters et al. 2008).

Another aspect of importance for the aquatic-terrestrial contaminant transport is the temporal pattern of emergence (Fig. 3). Early studies on short-term or chronic pesticide exposure of larval caddisflies have shown that the temporal emergence pattern changes. Exposed larvae usually showed a delayed emergence and a shorter total time of emergence of a cohort of larvae compared to control animals (Liess and Schulz 1996; Schulz and Liess 1995). A recent study exposing larval caddisflies to metal-based nanoparticles also reported a delay of emergence by up to 30 days compared to control organisms (Bundschuh et al. 2019). Altered temporal emergence pattern may thus decouple the nutritious requirements by terrestrial predators from the provision of high-quality prey of aquatic origin, which may translate to a shift in the magnitude of contaminant transfer into the terrestrial food web.

The biologically mediated aquatic-terrestrial transport ultimately leads to contaminant exposure in terrestrial recipient organisms. It is well known that various terrestrial predators such as mammals (Hilderbrand et al. 1999), birds (Kolb et al. 2010), some spiders (Greenwood and McIntosh 2011), and beetles (Turin et al. 2003) heavily rely on aquatic organisms in their diet. Apart from feeding on emerging aquatic insects, terrestrial predators may take up aquatic-derived contaminants via the consumption of aquatic organisms. It has, for instance, been shown that endangered California condors take up mercury, chlorinated pesticides, PCBs, and polybrominated diphenyl ethers (PBDEs) by consuming marine mammals (Kurle et al. 2016). Another study reported elevated mercury levels in various bird species and provided evidence that the birds likely had taken up MeHg from spiders, which themselves likely fed on MeHg-contaminated aquatic emerging insects (Cristol et al. 2008). Necrophagous blowfly larvae feeding on beached fish carcasses can take up and accumulate mercury, yet the heavy metal burden is eliminated by the adults following emergence (Sarica et al. 2005). As an example highlighting the transfer of contaminants from aquatic to terrestrial systems, Noël et al. (2014) documented the uptake of mercury by grizzly bears from salmon in British Columbia, Canada, using hair samples. In a broader context, Blais et al. (2007) reviewed the role of biologically mediated contaminant transport across long distances. They highlighted migrating fish such as salmon and Arctic as well as Antarctic seabirds as biovectors for contaminant, e.g., for PCBs, DDT, toxaphene, or MeHg. Although usually showing lower importance on a mass balance basis than long-range physical contaminant transport, this biovector transport should not be neglected as it refers to large-scale food web with consequences in the fate and effects that are not yet addressed.

Stable isotope analysis, as discussed in detail in another chapter of this book (Bundschuh et al. this volume), can be a powerful tool to assess for the fate of contaminants transported via aquatic emergence (Schulz et al. 2015). Consumption of emerging aquatic insects contaminated with PCBs by spiders had, for example, been studied using $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios at the Lake Hartwell Superfund site, SC, USA (Raikow et al. 2011), to indicate aquatic-terrestrial transfer. Similarly, Walters et al. (2008) used $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios to indicate that a South Carolina stream acts as a meaningful source of PCB contamination into web-building and ground-dwelling spiders but also amphibians. Using $\delta^{15}N$ stable isotope ratios in combination with MeHg analysis, Speir et al. (2014) provided evidence that long-jawed orb weaver spiders (*Tetragnatha* sp.) feed on aquatic prey and take MeHg up through this pathway. Interestingly, stable isotope studies have also shown that $\delta^{15}N$, an indicator of trophic position, became enriched on average by 1‰ (absolute) during metamorphosis (Kraus et al. 2014a, b; Tibbets et al. 2008). This nontrophic enrichment could influence the interpretation of stable isotope signals (30% over- or underestimation) and thus the trophic position of a predator if the wrong (larval vs. adult) signature is informing calculation. Consequently, the biomagnification potential of contaminants in food webs may be biased (Kraus et al. 2014a, b).

3.2 *Abiotic Pathway: Flooding or Groundwater Flux*

Aquatic-derived contaminants are transported to terrestrial ecosystems in water as particulates or dissolved solids or as solids associated with particles during flooding (Pease et al. 2007; Wölz et al. 2011). Numerous environmental contaminants, such as PAHs (Hilscherova et al. 2007; Pulkrabova et al. 2008), PBDE (Lake et al. 2011), metals (Cebula and Ciba 2005), and pesticides (Katayama and Kuwatsuka 1991), are transported via this pathway from aquatic to terrestrial systems, specifically in floodplain soils. A study of 14 sites in the Morava and Drevnice catchment in the

Czech Republic (Hilscherova et al. 2007) clearly showed decreasing PAH levels in sediments and increasing levels in floodplain soils after a major flooding event in 1997. While floods regularly increase the contaminant levels in floodplain soils, the opposite has been observed following the 2002 flood event at the River Elbe, Germany (Oetken et al. 2005). Using toxicity tests with mud snails and midges, the authors showed that biological effects were lower after the Elbe flood, which is likely a result of dilution as well as reduced bioavailability due to increased organic carbon levels binding contaminants. Xiao et al. (2011) compared heavy metal concentrations in sediments and floodplain topsoils in the Lean River catchment, China. They found an overall strong linkage between sediment and soil concentrations for Cd, Cu, Pb, and Zn. Data from some sites suggested dilution effect of the flood-derived sediments since the present soils showed already high metal levels prior to flooding as a result of mining activities. At other sites, however, mining-related sediment contamination originating from upstream sources, contaminated the floodplain soils which were relative pristine. Overall, the catchment history-dependent actual contaminant levels in the main river relative to the pre-flooding levels in the floodplain at the time of an event are important when interpreting the contaminant transfer across ecosystem boundaries particularly in light of the source-sink concept (Loreau et al. 2013).

Another example for the abiotic contaminant pathway is two studies focusing on the export of polychlorinated dibenzodioxins and dibenzofurans (PCDD/Fs), PCBs, and PBDE via flooding into adjacent pasture land on the River Trent, an industrial catchment in central UK (Lake et al. 2005, 2011). PBDE levels were increased in soil, yet not in grass or cows' milk on flood-prone farms compared to control farms. Both PCDD/F and PCBs, in contrast, occurred at elevated levels in soil, grass, and cows' milk from flood-prone farms. These insights provide strong evidence that flooding is the cause of the observed contaminant transfer in the terrestrial plant-herbivore food chain (Lake et al. 2005). In contrast, low flow conditions may of course also have effects on the adjacent terrestrial habitats, which, however, have not yet been studied regarding their importance for aquatic-terrestrial contaminant transfer.

Spatiotemporal dynamics are important drivers on how floods lead to contaminant exposure in the terrestrial recipient ecosystem via surface flow or groundwater fluxes (Fig. 3). The relative importance of surface and groundwater flux in determining aquatic contamination of terrestrial ecosystems depends on the strength of the flooding event, distance of the terrestrial area under study from the source (i.e., the flooded waterbody), soil properties, and contaminant characteristics. Sites with lower flooding duration, which were further away from the main channel of the River Rhine, received depositions of smaller sediment particles which contained higher metal (As, Cd, Cr, Cu, Hg, Ni, Pb, Zn) concentrations compared to sand depositional areas in more extensively flooded areas closer to main channel (Schipper et al. 2011). These higher contaminant concentrations affected plant biodiversity negatively. Contaminants transported laterally during flood events thus seem capable of modifying the interplay of flooding and biological responses typically occurring under more pristine conditions. As flood frequency is projected to increase globally and past flooding regimes can affect plant community composition over up to 19 growing seasons (Sarneel et al. 2014), drivers of global change (contaminants, temperature- and rainfall-related runoff; Bernhardt et al. 2017) may yield unpredictable joint effects on aquatic-terrestrial linkages. The consequences of these effects are, however, not well understood.

A set of studies on MeHg export, already introduced above, also considered the aspect of (ground)water level for the contaminant export into the terrestrial ecosystem. While permanent ponds, if stocked with fish, only exported comparably few MeHg, semi-permanent ponds make a much larger contribution (Chumchal and Drenner this volume; Chumchal and Drenner 2015). This is due to an indirect effect, in that drying out of the ponds eliminates fish, which in turn is not controlling any further the emergence of larger aquatic insects, such as dragonflies and damselflies. These large insects do however make a much higher contribution to MeHg export than smaller dipteran or micro-caddisfly species. Insect emergence recovered quickly, and MeHg export was not different within the first 73 days after drying of the ponds. Overall, water level is a strong controlling variable for contaminant export with semi-permanent (fishless) ponds being the habitats showing considerably larger MeHg flux than permanent ponds (with fish) or temporary (fishless) ponds (Chumchal and Drenner 2015).

The river morphology also has an effect on nutrient export into the root zones of floodplain plants (Schindler and Smits 2017), which likely is similar also for contaminant export (see also Fig. 3). Processes leading to a strong aquatic-terrestrial linkage likely take place to a much larger spatial extent in semi-natural free-flowing river ecosystems allowing water to move along hyporheic flow paths compared to constricted ecosystems with deep water tables. This phenomenon is well known and benefits multiple agricultural activities in fertile floodplain soils of large rivers (Noe and Hupp 2005). Fluvial dynamics as one driver of a high level of spatiotemporal heterogeneity also contribute to the tremendous biodiversity observed in undisturbed river floodplains (Ward et al. 1999). On the other hand, human-mediated alterations of river ecosystem morphology, leading to channelization, floodplain destruction, and disconnection between rivers and their floodplain negatively affect both the subsidy dynamics and the biodiversity, which makes it difficult to study the natural mechanisms that control sediment and nutrient cycling (Schindler and Smits 2017). Yet, this situation provides ample opportunity to study hydrodynamically driven contaminant activation, deposition, and cycling processes.

In conclusion, it appears up to now difficult to make quantitative comparisons of the biologically mediated and the abiotic pathway in terms of the extent of contaminant transport. Yet, our knowledge on these cross-ecosystem exposures warrants looking into potential biological effects in the terrestrial environment.

4 Potential Cascading Effects of Aquatic Contaminants on Terrestrial Food Webs

Here, we first provide some examples on how aquatic contaminants transported via biotic or abiotic pathways (Fig. 2) may affect individual trophic levels of terrestrial organisms, particularly predators. Subsequently, we discuss whether aquatic-derived chemical stress translates into cascading effects within terrestrial food webs.

An impressive example of the impact of chronic metal mining on riparian predatory spiders comparing 15 affected versus 15 control stream sites in England has been provided by Paetzold et al. (2011). Similarly, the community composition of riparian spiders studied along a gradient of agricultural activity in Romania was best explained by in-stream pesticide toxicity and habitat quality using shading of the stream bank as a proxy (Graf et al. 2019). This study, however, did not separate direct toxicity of pesticides via food or overspray from indirect effects induced by reduced aquatic and terrestrial prey availability. Organic contaminants transported to terrestrial recipient systems during floods may be degraded at varying rates depending on the soil microbial and metabolic activities in floodplain soils but also environmental conditions (Accinelli et al. 2005; Rath et al. 1998). These degradation processes may in turn influence the (genetic) structure and function of the soil microbial community (Gelsomino et al. 2006), which may among others be a result of the development of a pollution-induced community tolerance (e.g., Kamitani et al. 2006). In the floodplain soils, numerous aspects such as nutrient availability or groundwater level drive mobility (Soininen et al. 2015) and phytoavailability (Camps et al. 2003; Vandecasteele et al. 2010) of contaminants. Apart from microorganisms, flooding may substantially affect terrestrial vegetation by increasing the phytoavailability of toxicants, such as metals, but also nutrients from soils during flooding (Schipper et al. 2011).

Largely unknown appears whether the aquatic-derived chemical stress translates into cascading effects within terrestrial food webs. Bartels et al. (2012) suggested in their review that aquatic subsidies to terrestrial systems showed the highest energetic contribution in primary consumers and predators in contrast to other parts of the food web. This highlights the importance of these allochthonous inputs for bottom-up and top-down mediated interactions (see also Fig. 3). Applying a meta-ecosystem model, Leroux and Loreau (2012) supported this view and concluded that spatial and temporal variability in resources and consumers, although often not understood well, can have strong impact on the strength of cascading trophic interactions in the recipient ecosystem (sensu Richardson and Sato 2015). Surprisingly, observations on the role of the aquatic subsidy for the terrestrial food web beyond the level of the first terrestrial recipient (i.e., the soil or a predator species) are rare. This strongly limits our understanding of bottom-up or top-down directed effect cascades (Fig. 2) in both natural and anthropogenically modified systems (as reviewed in Schulz et al. 2015). Subsidies resulting from the abiotic, flood-related coupling, for instance, will directly affect terrestrial producers or detritivores, potentially regulating terrestrial food webs in a bottom-up directed manner. In contrast, as a result of the biologically mediated coupling via emerging aquatic insects, predators may be introduced in the receiving terrestrial food web (e.g., dragonflies), or prey will be provided for terrestrial predators (Wieczorek et al. 2015), thus potentially altering predation pressure in the terrestrial food web in a top-down yet potentially also bottom-up direction (Fig. 2).

It appears thus remarkable that virtually no studies have addressed how anthropogenic stressors in aquatic ecosystems lead to cascading effects in riparian food webs (Schulz et al. 2015). Whether such effects could result from aquatic contaminants is largely unknown. One of the very few examples of aquatic-derived cascading terrestrial effects deals with the invasion of lake trout in the Yellowstone National Park (Middleton et al. 2013), which caused a dramatic decline of native cutthroat trout. Since cutthroat trout represented no longer a sufficient resource for a generalist consumer, the grizzly bear, these bears compensated the reduction of cutthroat trout by predation on the calves of migratory elk that summer inside the park. Taken together, this example, though not involving contaminants, nicely illustrates how an alteration of an aquatic resource can have cascading top-down mediated effects in an adjacent terrestrial ecosystem. Along these lines, a study by Brasso and Cristol (2008) reported elevated levels of Hg in an experimentally established tree swallow population nesting in the headwaters of the Shenandoah River, Virginia. Female birds had significantly elevated blood and feather levels of Hg compared to control sites, as had insects fed by these insectivorous birds to their nestlings. Most importantly, young females in the contaminated area that were breeding for the first time produced fewer fledglings than those in reference areas. Studies by Poulin (2012) and Poulin et al. (2010) implied that mosquito control spraying of *Bacillus thuringiensis* var. *israelensis* (Bti) in the Camargue in South France led to a shift in the prey consumed by birds. This effect likely reduced clutch sizes and fledgling survival of these birds. This kind of processes may have – although not yet reliably quantified – far-reaching consequences for bottom-up or top-down mediated effects in coupled aquatic and terrestrial food webs (Leroux and Loreau 2008). This aspect is of importance also for the understanding of the energy, nutrient, and contaminant spiraling at the water-to-land interface (Bartels et al. 2012).

Considering our current knowledge on contaminant effects in recipient terrestrial ecosystems, the question arises: what is required to indeed unravel potential cascading effects in the terrestrial system? By determining the qualitative, quantitative, spatial, or temporal availability of biologically mediated and abiotic (biogeochemical) aquatic subsidies along with contaminants, bottom-up or top-down directed interactions in the receiving terrestrial ecosystem can be quantified (Fig. 3). Such an approach follows the source-sink concept as proposed by Loreau et al. (2013), which includes both abiotic (e.g., floods) and biotic (e.g., emergence) linkages of aquatic to terrestrial ecosystems. This concept further allows assessing the altered resource flow within the terrestrial system as a consequence of a shift in the aquatic subsidy in response to contamination. Consequently, conditional as well as unconditional sinks/sources are characterized. A consumer represents, for example, a conditional sink for nutrients and energy from detritus and changes after its death into a source of resources for primary producers or represents detritus. At the same time, a consumer may represent an unconditional source for secondary consumers. Thereby, the source-sink concept can be applied as recently suggested by the meta-ecosystem theory (Gounand et al. 2014) mainly to the flow of energy from the aquatic to the terrestrial system, yet with a special focus on the bottom-up and top-down regulation within the terrestrial system (Schulz et al. 2015). By doing so – as illustrated in Fig. 3 – the quantitative and qualitative and also the spatial and temporal variability (Bartels et al. 2012; Grimm et al. 2003; Soininen et al. 2015) of the aquatic subsidy and its associated contaminant load and the consequences for the terrestrial ecosystem can be considered.

Despite the fact that the available literature does not yet allow for a conclusive evaluation, evidence suggests that the aquatic-terrestrial cross-ecosystem effects should also be considered during the risk evaluations for chemicals.

5 Implications for Risk Assessment and Management

Available data suggest consideration of a number of aspects related to aquatic-terrestrial contaminant transfer in future risk assessment:

- Direct effects of aquatic contaminant levels transported to land via biotic or abiotic pathways in addition to contaminants already present from terrestrial sources

Terrestrial consumers may, for example, be affected by aquatic emergence carrying contaminants, particularly since aquatic prey is an important food source for riparian predators (e.g., spiders, birds, and bats; Custer et al. 2014; Stahlschmidt et al. 2012; Wieczorek et al. 2015; Williams et al. 2017). This may lead to additional exposure and cumulative effects in concert with the chemical exposures arising from the terrestrial environment which should be considered in risk assessment and management. Long-term cadmium exposure, for example, resulted in a genetically based reduced growth rate and increased egg size of a wolf spider (Hendrickx et al. 2008) with potential implications for their population development.

- Indirect effects of aquatic-derived contaminants via species interactions and cascading effects in the terrestrial environment

Despite these direct implications, indirect effects may occur, when predatory spiders are forced to shift from aquatic emergence as the preferred food source to terrestrial prey (Gergs et al. 2014). This may increase the predation pressure on terrestrial species leading to cascading top-down effects (Schulz et al. 2015). Another example of an indirect interaction affecting aquatic-terrestrial contaminant transfer had been illustrated above: fish presence reduced the emergence of large aquatic insects, which in turn substantially reduced the export of MeHg (Tweedy et al. 2013). Besides the carriage of contaminants with emerging aquatic organisms, as a direct dispersal effect (sensu Schiesari et al. 2017), the quality in the sense of the provisioning of essential amino and fatty acids of the prey may change (Gladyshev et al. 2009), with yet unknown consequences for the terrestrial predator

(Schindler and Smits 2017). Although it requires a substantial effort in sciences to understand such consequences, they could be far reaching and require attention in risk assessment. Based on these results, joint risk assessments considering contaminants and their transfer in linked aquatic-terrestrial ecosystems are required.

- Biomagnification (and nontrophic $\delta^{15}N$ isotope enrichment) in the terrestrial recipient food web

Riparian spiders are one example of animal groups currently discussed within US EPA for consideration in chemical risk assessment. Walters et al. (2010) concluded that terrestrial predators, such as the riparian tetragnathid spiders, have a great potential as biological monitors of stream conditions supporting risk management of contaminated aquatic sediments. Indeed, PCB concentrations in spiders reflect the sediment contamination (Kraus et al. 2017). Spiders' body burdens were used by Walters et al. (2010) to derive potential risks to birds leading to levels about 14 times higher than those relevant for the most sensitive bird species, chickadee nestlings (*Poecile* spp.). Studying organic contamination in various bird species at the Upper Hudson River, New York, Custer et al. (2010) found total PCB concentrations to be by a factor of 2 lower in insectivorous tree swallows compared with piscivorous kingfisher or omnivorous sandpiper. This observation followed in general the typical food chain biomagnification paradigm. Contrary to this, PCB toxic equivalents as well as PCDD-F concentrations were higher in tree swallows, as has been also shown in another study in Green Bay, Wisconsin (Custer et al. 2014), possibly due to metabolic pathway differences. Care must be taken to not underestimate the exposure risks to higher-order terrestrial predators such as amphibians, birds, or bats. Nontrophic enrichment of nitrogen isotopes during aquatic insect metamorphosis may lead to misinterpretations of the trophic position of organisms within the food web (Kraus et al. 2014b; Wesner et al. 2017). Considering the importance of $\delta^{15}N$ to estimate trophic position in biomagnification studies, nontrophic enrichment requires attention in chemical risk assessment.

- Impact of environmental conditions on aquatic-terrestrial contaminant transport

As outlined above, environmental conditions, either natural or through their human-mediated alterations, affect the aquatic-terrestrial contaminant transport. Maes et al. (2009) suggested a model that can be used to predict the impact of land use changes on water-related ecosystem services (e.g., evapotranspiration). The approach assumes, for instance, that the natural river discharge that would have occurred in the absence of human impacts has a central role in sustaining biodiversity and ecosystem services. The existing model certainly requires a number of adaptations in order to be used for the assessment of contaminants across the water-land barrier. Since the aquatic and terrestrial systems are considered in an integrated way, this kind of approaches holds nonetheless a great potential to cover the aquatic-terrestrial interface with regard to contaminant transfer and associated ecological effects.

- Carry-on contamination for humans via consumption

Some studies also aimed at considering the potential hazards of aquatic contaminants for terrestrial vertebrates or humans. Richmond et al. (2018) estimated for some drug classes, they found regularly in emerging insects, that vertebrate predators, such as platypus, could consume, e.g., antidepressants at as much as one-half of a recommended therapeutic dose for humans. As mentioned above, Walters et al. (2010) estimated, based on PCB and stable isotope data from riparian spiders, wildlife values as the minimum spider PCB concentrations causing physiologically significant doses in consumers such as vertebrates. They found values in wildlife to be exceeded for most considered bird species based on data from the most heavily contaminated site. In another study, it had been shown that midges although they were emerging from the metal- and PAH-contaminated Biesbosch river in the Netherlands did not exceed diet contaminant levels that are considered to be safe for mammals (Reinhold et al. 1999), and bats inhabiting less contaminated areas had elevated PCB body burdens suggesting a meaningful transfer of contaminants from aquatic into terrestrial food webs over time.

Different studies have considered Hg contamination in the context of levels in fish as a human food source. Through a forest fire-mediated restructuring of the food web in a lake, rainbow trout showed a fivefold increase in whole-body Hg accumulation (Kelly et al. 2006). Permanent ponds containing fish were shown to harbor a food web leading to MeHg accumulation in fish (Chumchal and Drenner 2015; Schiesari et al. 2017). This in turn means that these fish may act as carriers of Hg into humans through consumption, a likely pathway as indicated by the fact that in North America, Hg contamination is already the most frequent reason for advice regarding fish consumption (USEPA 1999).

Provided that currently predicted global change processes besides yielding ever-increasing chemical exposure will alter river flooding frequencies, but also species composition and their interactions, the consideration of cross-ecosystem effects of chemicals requires thorough attention in an aquatic-terrestrial chemical risk assessment and management scheme. These may include modeling approaches along with targeted field and aquatic-terrestrial mesocosm studies.

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Ralf Schulz is a Professor in Environmental Sciences heading the group Ecotoxicology and Environment at the University of Koblenz-Landau in Landau, Germany, since 2004. His research areas include exposure and effect assessment of chemicals, risk management, and ecology and genetics of crayfish and fish. He received a PhD from Braunschweig University in 1997 and has conducted field research in South Africa, Argentina, Australia, and the USA. Since 2019, he has acted as the coordinator of SystemLink, a large research program dealing with aquatic-terrestrial coupling.

Part II
Exposure Drives Ecological Subsidies

Agriculture and Mining Contamination Contribute to a Productivity Gradient Driving Cross-Ecosystem Associations Between Stream Insects and Riparian Arachnids

Francis J. Burdon

> *One strong insight for applied ecology is that the dynamics of seemingly distinct systems are intimately linked by spatial flow of matter and organisms. [P]rocesses and policies in aquatic systems…affect both aquatic and terrestrial systems*
>
> Polis et al. (1997)

1 Introduction

The reciprocal flow of resource subsidies from one habitat to another can strongly influence the structure and dynamics of food webs in a wide range of ecosystems (Polis et al. 1997). This pattern challenges ecologists to redefine interaction webs to include strong links both within and across traditional habitat and ecosystem boundaries (Sabo and Power 2002). For example, stream and terrestrial ecosystems can be highly connected via reciprocal subsidies that include exchanges of organic matter and prey (Power and Rainey 2000; Nakano and Murakami 2001). In particular, the emergence of adult aquatic insects forms an important prey subsidy for a wide range of riparian consumers that include spiders, birds, lizards, and bats (Baxter et al. 2005). However, human pressures from activities such as mining and agriculture frequently degrade stream ecosystems (Allan 2004), with potential consequences

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F. J. Burdon (✉)
School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden
e-mail: francis.burdon@slu.se

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for cross-habitat linkages through impacts on stream assemblages (Baxter et al. 2005).

Food web theory suggests that productivity gradients in both recipient and donor habitats can drive the magnitude of subsidy influences across habitats (Polis et al. 1997). The strength of this influence may also depend on the trophic level at which the subsidy is received, with effects generally greater on detritivores than higher trophic levels (Marczak et al. 2007). Moreover, the magnitude of indirect effects resulting from subsidies may decrease as the trophic level of resource and consumer fluxes increases (Allen and Wesner 2016). However, resource quality should also be considered in combination with the magnitude of subsidy fluxes between ecosystems, because many consumers preferentially favor low-flux, high-quality resources (Marcarelli et al. 2011). For example, stream insects can be an important source of essential, highly unsaturated fatty acids (HUFAs), which may disproportionately mediate their effects on receiving food webs (Twining et al. 2016a). Thus, the quality and quantity of aquatic-derived prey subsidies should influence communities of terrestrial consumers, and their importance may be greatest where in situ prey production and quality is low in the receiving habitat, such as resource-scarce riparian gravel bars (Naiman et al. 2005).

Stream productivity gradients have the potential to influence cross-habitat resource flows (Burdon and Harding 2008). However, these gradients may be ultimately driven by abiotic and biotic factors affecting the flux of subsidies, such as the thermal regimes in the donor habitat (Uno and Power 2015; Uno 2016) and the dispersal traits of organisms forming resource flows (Greenwood and Booker 2016, McKie et al. 2018). Consequently, human perturbations that reduce stream productivity and prey export could disrupt the flow of energy to recipient food webs (Baxter et al. 2005; Paetzold et al. 2011). For example, pollution in streams greatly reduced the flux of adult aquatic insects to the adjacent terrestrial habitat, which was associated with declines in riparian web-building spiders (Paetzold et al. 2011; Kraus et al. 2014a; Kraus and Pomeranz this volume). What is less clear, are what impacts other human activities have, such as agricultural land uses, which can increase aquatic productivity (e.g., due to the reduction of riparian shading and the leaching of fertilizers), yet greatly alter biotic communities (Quinn 2000; Niyogi et al. 2007; Beketov et al. 2013; Burdon et al. 2013).

Disturbances are a dominant force shaping stream communities and can be natural or anthropogenic in origin (Resh et al. 1988). Hydrodynamic disturbance is a notable feature of streams in mountainous regions, and the frequent bed-moving floods can act as a strong environmental filter on stream communities while constraining standing biomass of primary producers, organic matter, and higher consumers (Winterbourn and Ryan 1994; Townsend et al. 1998). However, these events are generally regarded as “pulse” disturbances (Lake 2000), and stream organisms can be adapted to this type of perturbation, thereby enhancing the ecological resilience of these systems (Winterbourn 1997; Lytle and Poff 2004). In contrast, anthropogenic pollution that is toxic to stream organisms, such as acid mine drainage (AMD), can have wide-ranging impacts on stream food webs, with invertebrate assemblages characterized by a loss of pollution-sensitive insect taxa (Hogsden and

Harding 2012b). The impacts of mining disturbances can have "pulse" aspects but are typically construed as a "press" disturbance adversely impacting stream insects with negative consequences for riparian consumers (Paetzold et al. 2011; Kraus et al. 2014a).

Another common human perturbation to stream ecosystems involves agricultural activities, which can cause a myriad of changes including landscape disturbance leading to deforestation and habitat fragmentation, increased inputs of fine inorganic sediment and nutrients, and altered hydrology (Allan 2004). Depending on the level of agricultural activities in catchment, stream ecosystems may exhibit positive or negative responses to this land-use type (i.e., a "subsidy-stress" relationship, Evans-White et al. this volume), demonstrating how human impacts can induce non-linear ecosystem responses (Niyogi et al. 2007). The subsidy-stress relationship describes how, at low levels, anthropogenic perturbations may enhance ecosystem functioning and species abundances, whereas higher levels depress these responses (Odum et al. 1979). By altering stream communities, agricultural land uses can modify the quality and quantity of the emerging adult insect prey subsidy, which may have profound consequences for terrestrial consumers (Stenroth et al. 2015; Carlson et al. 2016; Raitif et al. 2018). However, despite such studies quantifying the effects of land use on stream insect emergence, relatively little is known about how agricultural land uses indirectly affect recipient communities in coupled aquatic-terrestrial food webs. This data gap partly reflects the challenges of quantifying cross-habitat trophic connectivity (Terui et al. 2018; Bundschuh et al. this volume) but is also due to the environmental contingencies, multiple stressors, and complex ecological responses often associated with human pressures (Burdon et al. 2016). This is highly relevant in a rapidly changing world, because although the importance of resource subsidies for riverine ecosystems is well recognized, how natural and anthropogenic perturbations alter the trophic connectivity between coupled ecosystems remains poorly understood (Larsen et al. 2016).

2 Human Pressures in Heterogeneous Landscapes

Human populations and their associated demands on natural resources impact freshwater ecosystems globally (Vorosmarty et al. 2010). As described in the previous section, these changes are often linked to anthropogenic pressures associated with human activities including landscape disturbance and habitat degradation, water extraction, and pollution (Allan 2004; Friberg 2010). In turn, these pressures can increase the presence and magnitude of multiple environmental stressors, such as inputs of nutrients, pesticides, and fine inorganic sediment that are commonly associated with eutrophication and reductions in pollution-sensitive organisms (Burdon et al. 2013, 2016, 2020b; Munz et al. 2016). Anthropogenic pressures generally do not occur randomly in landscapes, but typically spatially co-occur with human populations (Burdon et al. 2019). As a consequence, the overall impacts of these impacts can scale with human population density (Vorosmarty et al. 2010). This general pattern also means that environmental conditions favoring the location of human activities can influence the types of habitat affected by anthropogenic pressures, with lowland and freshwater ecosystems particularly threatened (Sala et al. 2000; Dudgeon et al. 2006). The co-occurrence of specific habitats with human pressures may confound our ability to detect and predict the impacts of environmental stressors, especially if no analogous reference state remains as a benchmark of a non-impacted ecosystem (Poikane et al. 2014).

Lowland ecosystems throughout the world are impacted by multiple co-occurring pressures (Sala et al. 2000; Ruffell and Didham 2017). These systems have typically experienced dramatic reductions in natural vegetation cover to make way for production land uses, so habitat loss is usually seen as the principal threat (Sala et al. 2000). However, lowland ecosystems are frequently beset by additional pressures, such as pollution and invasive species (Burdon et al. 2013; Ruffell and Didham 2017). In particular, human activities in New Zealand exemplify these patterns, where native forest cover has been drastically reduced in most lowland landscapes for conversion to agricultural land uses (Quinn 2000), and the pressure for further reduction is likely to increase as the human population grows (Ewers et al. 2006).

Keeping this general problem in mind and how it may impede our ability to detect human-induced changes across coupled aquatic-terrestrial ecosystems, I present a case study reanalyzing previously published data on ecosystem resource gradients, aquatic insects, and riparian arachnids from 37 forested streams located in New Zealand's South Island (Fig. 1, Table 1; Burdon and Harding 2008). In that study, I expected that standing benthic insect biomass was an effective surrogate measurement for the flux of adult prey to recipient riparian predator communities. In turn, stream insect biomass had an apparent positive influence on riparian arachnids after accounting for confounding environmental variables (Burdon and Harding 2008). Here I explore this relationship further by applying advanced statistical methods to explain variation in terrestrial predator biomass among land-use types and various biotic and abiotic variables. These new approaches allow me to elucidate the potential impact of different human pressures on productivity gradients driving trophic connectivity between stream and riparian ecosystems.

3 Case Study: Agriculture and Mining Impacts on Coupled Stream-Riparian Ecosystems

Using the dataset from Burdon and Harding (2008) as a case study, I wanted to test explicitly how human pressures (i.e., streams impacted by agricultural or mining activities versus non-impacted streams in reference condition) influenced aquatic insect and riparian predatory invertebrate standing biomass. Specifically, I predicted that human pressures (land use hereafter) would be a strong contributor to the stream "productivity" gradient observed in Burdon and Harding (2008). Mining (i.e., acid mine drainage – the acidic and metalliferous leachate from mining operations and other construction activities) was expected to have a strong negative influence on

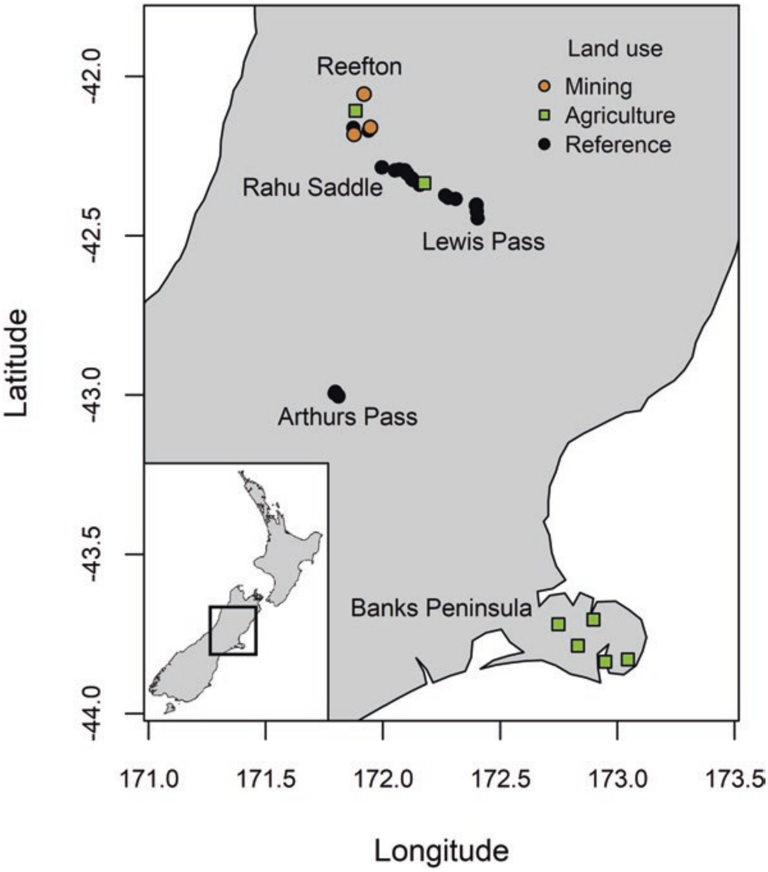

Fig. 1 The 37 forested streams sampled across the central South Island of New Zealand in Burdon and Harding (2008). Land use indicates forest streams affected by mining (i.e., acid mine drainage; *n* = 4), agriculture (i.e., streams located in forest fragments surrounded by agricultural land uses; *n* = 7), and unimpacted reference sites in pristine forest (*n* = 26). Refer to Table 1 for characteristics of the corresponding site groups by region

stream insect and riparian predatory invertebrate standing biomass. In contrast, agriculture (i.e., streams flowing through forest fragments embedded in agricultural landscapes) was hypothesized to increase production (i.e., standing biomass) of aquatic and terrestrial invertebrates via nutrient "subsidies" to primary producers and decomposers (i.e., via bottom-up processes). As a more general test of ecological theory, I also contrasted the influence of these anthropogenic impacts with natural hydrodynamic disturbance to place my findings in context with the broader literature on physical disturbance and stream-riparian food webs. A better understanding of how different perturbations impact aquatic production and terrestrial responses would enhance our ability to predict how humanactivities influence cross-habitat food web interactions (Burdon et al. 2020a).

Table 1 Characteristics of the 37 forested streams sampled across the central South Island of New Zealand

Region	Land use	pH	Nitrate (mg/l)	Phosphate (µg/l)	Elevation (m a.s.l)	Stream widths (m)	Vegetation types	References
Banks Peninsula	Agriculture (n = 5)	7.6–7.8	0.2–1.0	10–50	34–230	2.3–3.7	Podocarp forest (mainly *Podocarpus totara*, *P. dacrydioides*, and *P. spicatus*), gorse (*Ulex europaeus*), tussock (*Festuca actae*), and pasture (e.g., cocksfoot and ryegrasses)	Harding (2003), Burdon and Harding (2008), Burrell et al. (2013), Stewart et al. (2018)
Arthur's Pass	Reference (n = 4)	6.7–7.0	<0.1	<15	510–585	1.9–6.6	Beech forest (mainly mountain beech *Nothofagus solandri* var. *cliffortioides* and red beech *N. fusca*)	Burdon and Harding (2008), Burrell et al. (2013)
Lewis Pass	Reference (n = 9)	7.6–7.8	<0.1	<15	513–811	4.6–12.6	Beech forest (mainly silver beech *N. menziesii* and red beech *N. fusca*)	Burdon and Harding (2008), Burrell et al. (2013)
Rahu Saddle	Reference (n = 10) Agriculture (n = 1)	6.6–7.7	<0.1–1.4	1–24	416–689	2.0–8.1	Mixed beech-podocarp forest and pasture	Burdon and Harding (2008), LAWA (2018)
Reefton	Mining (n = 4) Reference (n = 3) Agriculture (n = 1)	3.3–7.4	<0.1–1.8	2–25	213–472	0.5–5.0	Mixed beech-podocarp forest, gorse, tussock, and pasture	Burdon and Harding (2008), Niyogi et al. (2013)

"Land use" indicates forested streams affected by mining (acid mine drainage; $n = 4$), agriculture (streams located in forest fragments surrounded by agricultural land uses; $n = 7$), and unimpacted reference sites in pristine forest ($n = 26$)

3.1 Methods

3.1.1 Study Sites

I sampled 37 forested streams across 3 different land-use types. These included streams located in pristine forest (i.e., reference sites, $n = 26$), streams affected by mining (i.e., acid mine drainage, $n = 4$), and streams located in forest fragments surrounded by agriculture (e.g., native and improved pasture, $n = 7$). Sites were distributed across the central South Island of New Zealand in five geographical regions: Banks Peninsula, Arthur's Pass, Lewis Pass, Rahu Saddle, and Reefton (Fig. 1; Burdon and Harding 2008). Five study sites were located on the Banks Peninsula, a doublet of extinct shield volcanos on the east coast of the South Island, with the remaining sites located in mountainous areas of the Southern Alps and Westland (Table 1).

Banks Peninsula rises to ≈1000 m a.s.l. and is dissected by >100 isolated, short (<10 km), and steep stream catchments (Harding 2003; Harding et al. 2006). Streams on the Peninsula are generally less than third order with lowland reaches of only a few kilometers (Harding et al. 2006). Similar to most lowland areas of New Zealand, the uplands of the Peninsula have been heavily modified by anthropogenic activities in the last 150 years. The native forest cover (i.e., podocarp-dominated) has been largely removed and replaced by native and introduced plant species, including non-indigenous grass species (e.g., cocksfoot and ryegrasses) for pasture (Harding 2003). Due to agricultural activities that include aerial top-dressing of soil with fertilizers and the presence of livestock, these streams typically have higher nitrate concentrations (0.2–1.0 mg/L) than pristine forested streams (> 0.1 mg/L) found inland in the main range of the Southern Alps (Burrell et al. 2013). In addition, streams in the Banks Peninsula region often have naturally higher phosphorus concentrations than other waterbodies in the South Island because of the underlying volcanic geology, largely comprising of phosphorus-rich basalts (Burrell et al. 2013; Stewart et al. 2018).

The other study regions comprised streams with varying human pressures. The Rahu Saddle region contained ten reference streams, while one stream was located in a large forest fragment with intensive pastoral agriculture in its surrounding catchment (Table 1). The eight streams in the Reefton region included one forest fragment site surrounded by pasture and gorse (*Ulex europaeus*) and four affected by mining (Table 1). These mining-affected streams are impacted by acid mine drainage (AMD) and typically have low pH (3.4–4.9), high levels of deposited metal hydroxide, and elevated concentrations of potentially toxic metals such as aluminum, manganese, nickel, and iron (Hogsden and Harding 2012a; Niyogi et al. 2013). For further details about study locations, see Table 1 and Burdon and Harding (2008).

3.1.2 Stream and Gravel Bar Survey

The full-field methods are reported in Burdon and Harding (2008). Briefly, in each stream, I sampled one gravel bar and an instream riffle within 10 m of each other for riparian and aquatic invertebrates. Sampling was undertaken in late summer/early autumn 2003 (8 April to 15 May) during stable base flows. I selected exposed "gravel" bars according to minimum size (> 4 m^2), a maximum slope (<10°), and maximum vegetative cover (≤ 20% vegetation covering). I recorded the length and width of the bar and assessed habitat complexity using a subjective index

(Burdon and Harding 2008). Briefly here, habitat complexity was estimated using a 1–5 index describing the three-dimensional structure of the exposed gravel bar, with 1 being the least structured and 5 being the most, i.e., 1 = bedrock or large, flat boulders embedded; 2 = rocks packed tightly with few interstitial spaces; 3 = some spaces or cracks present, layering evident; 4 = range of rock sizes with layering, numerous refugia; and 5 = largest variety of gravel/cobble/boulders with extensive layering. I also recorded the longest axis (e.g., mean length) of 30 randomly selected substrate particles for an estimate of substrate size distributions. I measured stream and channel widths across three transects at each site and described the stability of the streambed and bank using the Stream Reach Inventory and Channel Stability Evaluation (Pfankuch 1975), hereafter referred to as the Pfankuch Stability Index (PSI). This index is used extensively for catchment assessment and studies investigating relationships between channel stability and biota in North America and internationally (Death and Winterbourn 1995; Rosgen 2006). The index is calculated by summing the scores assigned to 15 attributes (weighted in relation to their perceived importance) in 3 regions of the stream channel (i.e., upper banks, lower banks, and stream bottom), according to the observer's evaluation of predetermined criteria (Pfankuch 1975). I estimated the proportion of canopy cover at each site using ocular estimation with a systematic approach and measured specific conductivity and pH of stream water using an Oakton PC10 pH/conductivity meter.

I measured the standing biomass of basal resources (i.e., periphyton and coarse particulate organic matter), aquatic insects, and terrestrial riparian invertebrates within or near each stream riffle. To estimate periphyton biomass (g m^{-2}), I randomly collected five cobbles from a transect across each riffle and scrubbed them to collect attached periphyton. Periphyton was scrubbed off using 100 ml of water, with the resulting solution filtered through a GF/C glass fiber filter. Filters were dried at 70 °C for 48 h, weighed, then ashed at 450 °C for 2 h, and weighed again to obtain an ash-free dry mass. To standardize periphyton biomass for a given surface area of rock, cobble area was estimated using Eq. (1) (Biggs and Kilroy 2000).

$$\text{Stone surface area}\left(\mathrm{m}^2\right) = 1.59 + 0.811\left(xy + yz + xz\right) \tag{1}$$

where x, y, and z are the lengths of the three main axes of the stones. This formula has been adjusted to only include the area of cobble normally protruding into the water column on which the periphyton can colonize (≈ 65% of the total surface area).

To measure invertebrate density and standing biomass, I collected three randomly selected Surber samples (0.065 m^2, 250 μm mesh) from a riffle thalweg within each focal stream to estimate standing biomass of aquatic insect larvae in the benthic community. On each exposed gravel bar within or adjacent to the stream channel, I sampled four randomly selected 0.25 m^2 quadrats for terrestrial invertebrates. Invertebrates were collected with a modified leaf vacuum similar to that described in Stewart and Wright (1995) and by hand using forceps. Samples were placed on ice and transported to the laboratory where they were frozen until processing.

I used standing benthic insect biomass as a surrogate measurement of adult emergence (Burdon and Harding 2008). Prior to the estimation of biomass, I separated stream invertebrates into insect and non-insect taxa and terrestrial invertebrates into the Arachnida (Araneae and Opiliones only, excluding the Acarina and Pseudoscorpiones) and other taxa groups (Burdon and Harding 2008). Aquatic invertebrates were identified to phylum and insects further identified to genus or species following Winterbourn et al. (2000), except for some Diptera and Coleoptera, which I only identified to family level. Terrestrial invertebrates were identified to phylum, and insects were further identified to family following CSIRO (1991) and references contained within. I identified arachnids to family-level for spiders (Araneae) and order for Opiliones following identification keys described in Burdon and Harding (2008).

After enumeration and identification, samples were dried for 48 h at 70 °C before weighing. After removing invertebrates, the gravel bar and stream coarse particulate organic matter (CPOM) from invertebrate samples were each separated from inorganic material and oven-dried for 48 hours at 70 ° C before weighing to estimate CPOM (g m^{-2}).

3.1.3 Data Analysis

Rivers and streams are often highly productive ecosystems that produce fluxes of adult aquatic insects that can match or exceed terrestrial production per unit area (Gray 1989; Gratton and Zanden 2009). Consequently, the productivity and emergence rates of adult aquatic insects can influence the biomass, spatial distributions, and growth rates of riparian consumers including arachnids (Baxter et al. 2005; Burdon and Harding 2008; Marczak et al. 2007). The production of benthic lotic insects is strongly correlated with adult aquatic insect emergence (Jackson and Fisher 1986; Statzner and Resh 1993; cf. Schmidt et al. 2013), so I used standing benthic insect biomass as a surrogate measurement of the potential adult prey flux to recipient riparian predators (Burdon and Harding 2008). Stream insect biomass was used as a key predictor variable because adult aquatic insects were more likely to be incorporated into terrestrial food webs than other non-insect aquatic invertebrates (e.g., snails and worms), and non-insect invertebrate biomass was a relatively minor component of total invertebrate biomass at all sites in the Burdon and Harding (2008) dataset. The total flux of adult aquatic emergence is strongly driven by habitat size (Gratton and Zanden 2009), so I scaled stream insect biomass according to wetted channel width (Eq. 2).

$$\text{Stream insect biomass}\left(\text{g m}^{-1}\right) = \text{Biomass}\left(\text{g m}^{-2}\right) \times \text{Width}\left(\text{m}\right) \tag{2}$$

I determined that Eq. 2 was an appropriate way to account for donor habitat size in the context of my case study, where stream widths were relatively small (i.e., < 10 m). Thus, following Gratton and Zanden (2009), standing stream insect biomass at the reach scale is expressed as g m^{-1}.

Likewise, predatory arachnid biomass was used as a key response variable, as it was expected that arachnids would be a major group utilizing aquatic insect subsidies. Insects dominate prey biomass of arachnids globally (Nyffeler and Birkhofer 2017), and experimental studies have shown how reductions in emerging adult aquatic insects negatively affect riparian spiders (Kato et al. 2003; Marczak and Richardson 2007). I did not scale riparian invertebrate biomass according to recipient habitat size (i.e., using gravel bar width), because predator densities and biomass in these recipient habitats were not expected to be influenced by in situ habitat size.

Variation Partitioning I used variation partitioning to test the independent and shared contribution of different predictors to variation in arachnid biomass as a response variable. Although typically used with multivariate response data, variation partitioning can also be applied to a single response variable *y* since the algebra of partial linear regression is the same as that of partial canonical analysis (Legendre 2008). Here I tested an a priori hypothesis regarding the influence of three predictors: stream insect biomass (g m^{-1}), land-use type (mining, agriculture, and reference), and elevation (m a.s.l.). The significance of each fraction was tested by permutation tests using 999 randomizations (Peres-Neto et al. 2006). Variation partitioning was performed in R using the "varpart" function in the "vegan" package; results in Fig. 2 were visualized using the "venneuler" package.

Quantile Regression I used quantile regression to describe the influence of stream insect biomass (g m^{-1}) on riparian arachnid biomass (g m^{-2}). Regression quantiles (10–90%) were tested using the "rq" function in the "quantreg" R package. Riparian and stream invertebrate data was log-transformed ($\log_{10}$ [x + 1]) to minimize heteroscedasticity prior to analyses.

Linear Mixed-Effect Models To test the influence of stream land-use types on key response variables, I used linear mixed-effect models (LMMs). LMMs were specified using the "lme" function in the "nlme" R package. Each model included the fixed effects of land use (mining and agriculture contrasted with reference sites) and site elevation as a fixed-effect covariate. The LMMs also included a "varIdent" function to enable different variances per stratum for land-use type (Zuur et al. 2009) and a random effect term for stream region. Post hoc tests were conducted with the Bonferroni-Holm correction for multiple comparisons using the "glht" function in the "multcomp" R package. Riparian and stream invertebrate data were transformed using $\log_{10}$ [x + 1]; all other data was $\log_{10}$-transformed.

Structural Equation Modelling I used structural equation modelling (SEM) to test causal hypotheses about the influence of anthropogenic and natural perturbations on coupled stream-riparian ecosystems. A SEM approach recognizes that ecological systems are often driven by numerous interconnected processes that operate simultaneously in "causal networks" (Grace et al. 2014). Thus, SEMs are probabilistic models that unite multiple predictor and response variables and are often repre-

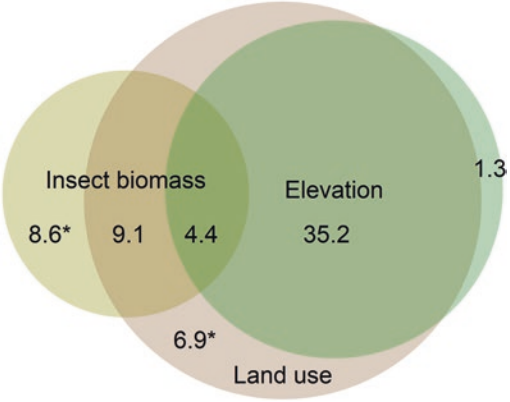

Fig. 2 Results from variation partitioning analysis of riparian arachnid biomass (g m^{-2}) recorded from exposed gravel bars in 37 forested streams across the South Island of New Zealand. Shown is variation (%) in arachnid biomass explained by mean stream insect biomass (g m^{-1}), land use, and site elevation (m a.s.l.). Arachnid biomass includes spiders and opiliones. Insect biomass accounts for the size of the donor habitat by scaling according to stream size (wetted channel width). Land use describes forest streams affected by mining (i.e., acid mine drainage), agriculture (i.e., streams located in forest fragments surrounded by agricultural land uses), and unimpacted reference streams located in pristine forest. The independent influence of stream insect biomass significantly explains 8.6% of variation in arachnid biomass ($F_{1,32} = 9.12$, $P < 0.01$), with a further 13.5% shared with land use. Independently, land use explained 6.9% of variation in arachnid biomass ($F_{2,32} = 4.37$, $P < 0.05$). Although site elevation alone (1.3%) did not significantly explain variation in arachnid biomass ($F_{1,32} = 2.23$, $P = 0.157$), there was a strong shared influence with land use (35.2%). The residual (unexplained) variation was 35%. * $P < 0.05$

sented in path models, where arrows drawn between observed variables indicate possible directional relationships.

The SEM used data from all 37 study sites to test how land use influenced the direct and indirect relationships between riparian arachnid biomass and predictor variables. Stream land use (mining, agriculture) was used as a categorical predictor variable contrasted with the reference streams. Natural hydrodynamic disturbance (i.e., the PSI) as a continuous predictor variable was also included. Specific conductivity (mS cm^{-1}) was used as a surrogate measurement for dissolved nutrient concentrations (Greenwood et al. 2012; Burdon et al. 2013). Stream basal resources were characterized by periphyton and CPOM standing biomass (g m^{-2}). Stream insect biomass was considered at the patch scale (g m^{-2}), in addition to at the reach scale (g m^{-1}; Eq. 2). The former was considered more relevant as a response to stream conditions, whereas the latter was hypothesized to be a better predictor of the prey subsidy flux influencing riparian arachnids (i.e., biomass). Other variables considered included site elevation (m a.s.l.), stream width (m), canopy cover (%), gravel bar area (m^2), habitat complexity (1–5), mean substrate size (m), gravel bar CPOM (g m^{-2}), and non-arachnid terrestrial invertebrate biomass (g m^{-2}).

Table 2 Model variables for the structural equation model (SEM) shown in Fig. 5

Model variable	Indicator	Units	Transformation
Arachnid biomass	Standing biomass of predatory arachnids collected from exposed riparian gravel bars	g m^{-2}	log+1
Stream insect biomass	Standing biomass of benthic insects scaled by the wetted channel width (Eq. 2)	g m^{-1}	log+1
Stream insect biomass	Standing biomass of benthic insects	g m^{-2}	log
Periphyton biomass	Standing biomass of periphyton on cobbles	g m^{-2}	log
Habitat complexity	A subject index (1–5) characterizing the properties of the exposed riparian gravel bar	Numerical	log
Specific conductivity	Specific conductivity (mS cm^{-1}) of stream water at 25 °C	µS cm^{-1}	log
Mining	Streams impacted by acid mine drainage (AMD)	Categorical	
Agriculture	Streams located in forest fragments surrounded by agricultural land uses	Categorical	

Data were first transformed to improve normality and homoscedasticity (see Table 2 for information about variables used in the final model) and then standardized using the "decostand" function in the "vegan" R package (i.e., centered on the column means and scaled by unit variance). Some constraints were applied *a priori* to model selection. An upper limit was placed on the number of potential paths included in the global SEM, meaning some relationships were not explicitly considered in the final model (i.e., the influence of land use on conductivity). Co-linear variables ($r > 0.75$) were also removed where their inclusion would affect the interpretation of the results. Following these initial steps, I used a forward selection procedure to select a subset of explanatory variables for each model component following Blanchet et al. (2008). For this procedure, land-use types (mining, agriculture) were defined using a binary descriptor (i.e., 0, absent; 1, present). Site elevation was considered for all model components but was never selected in the forward selection procedure. Similarly, stream CPOM and the PSI were not included in the final SEM because they had no significant influence on stream insect or arachnid biomass in the forward selection procedure and the SEM, despite the PSI having a negative influence on the standing biomass of stream CPOM.

The selected variables for each model component were then included in a global SEM. Each model component included a "varIdent" function to enable different variances per stratum for land use and a random effect term for stream region. To achieve model parsimony, non-significant paths were removed where possible. Shipley's test of directed separation was used to identify significant paths that were emergent properties of the SEM, and thus not identified in the forward selection procedure previously described. Akaike Information Criterion (AIC) and AICc values were compared for all model iterations to check that the final model was the most appropriate. AIC is a measure of the relative goodness of fit for a statistical model; the preferred model is the one with the lowest AIC value (Burnham and Anderson 2002). AICc is AIC with a correction for the sample size and number of parameters used. I used the R package "piecewiseSEM" to fit the mixed-effect SEMs (Lefcheck 2016). All analyses were conducted in R (R 2015).

3.2 Results and Discussion

3.2.1 Disentangling Effects of Multiple Stressors on Aquatic-Terrestrial Linkages

In this case study, I attempt to disentangle the confounding influences of human land uses and their location in the landscape (i.e., elevation) on the potential linkage between stream and riparian communities using the Burdon and Harding (2008) dataset. However, these efforts highlight the challenges with inferring causality solely attributable to human land uses such as agriculture when multiple stressors vary with environmental context (Burdon et al. 2016). Using variation partitioning analysis, I found that overall, three predictors explained 65% of the variation in arachnid biomass, with land use accounting for 56%, elevation 40%, and stream insect biomass 21% (Fig. 2). However, stream insect biomass independently explained 9% of variation in arachnid biomass, with a further 9% shared with land use (Fig. 2). The independent influence of land use accounted for 7% of variation in arachnid biomass, but there was a strong shared influence with elevation (35%; Fig. 2). This result indicates that human land uses (e.g., agriculture) are not randomly located in the landscape but are typically confined to lower elevations in montane regions (although not exclusively for activities such as mining).

Most pristine (i.e., protected) forest in the New Zealand landscape is found at higher elevations (i.e., mountainous regions). The reasons for this upland-lowland imbalance result from the high economic value of lowland environments for human activities such as agriculture (Norton 1999). Thus, one potentially confounding factor illustrated by the variation partitioning analysis (Fig. 2) is that the agricultural sites (i.e., streams in forest fragments) generally tend to be at lower elevations where warmer temperatures may have positive effects on invertebrate metabolism including rates of adult aquatic insect emergence (Uno 2016; Raitif et al. 2018). Burdon and Harding (2008) recorded a negative independent influence of elevation on both stream and riparian invertebrate biomass, meaning elevation-mediated temperature differences could plausibly be an important causal pathway driving the trophic connectivity between aquatic and terrestrial ecosystems. However, in Burdon and Harding (2008), the influence of land use was never assessed explicitly, so while an effect of elevation-mediated temperature differences co-occurring with changes in land use cannot be excluded, there may be other aspects of human activities (e.g., the leaching and runoff of fertilizers from agriculture) influencing cross-ecosystem linkages.

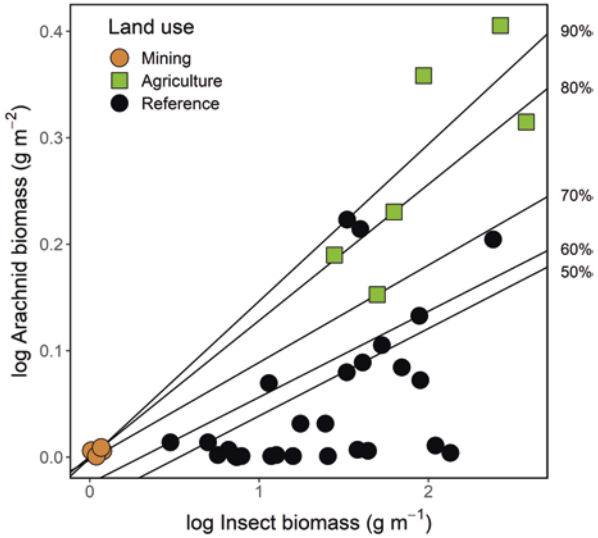

Fig. 3 Standing biomass of benthic insects and riparian arachnids from adjacent exposed gravel bars in 37 forested streams of the South Island, New Zealand, plotted with the 90, 80, 70, 60, and 50% regression quantile estimates. Regression quantile estimates 10–40% were not significant and thus are not shown. Arachnid biomass includes spiders and opiliones. Insect biomass accounts for the size of the donor habitat by scaling according to stream size (wetted channel width). Land use indicates sites affected by human activities, including forest streams receiving acid mine drainage (Mining; $n = 4$) and streams flowing through forest fragments embedded in agricultural landscapes (Agriculture, $n = 7$), in addition to the unimpacted reference streams in pristine forest (Reference, $n = 26$). Both predictor and response are log+1 transformed

3.2.2 Human Impacts Contribute to a Stream Resource Continuum

In Burdon and Harding (2008), I argued that standing benthic insect biomass was an effective surrogate measurement for the potential flux of adult prey to the receiving riparian habitat. There was an apparent positive influence of stream insect biomass (g m^{-1}) on terrestrial predators after accounting for potentially confounding factors. Using the same dataset, here I show how human activities might contribute to the "productivity gradient" linking stream donor ecosystems with their receiving riparian habitats (Figs. 2, 3, and 4). These human influences seemingly conformed with the perturbation framework introduced by Odum et al. (1979), with mining streams (impacted via acid mine drainage) having strong negative impacts on aquatic insect standing biomass (i.e., a "toxic input"), whereas agricultural streams in the context of my study had greater benthic insect biomass (i.e., a "subsidy effect"; Fig. 3). The standing biomass of riparian arachnids (Araneae, Opiliones) from adjacent exposed gravel bars was significantly associated with the biomass of benthic insects (Fig. 3), but only for the upper quantiles (i.e., 50–90%). This result suggests a wedge-shaped response, where the standing biomass of stream insects imposes an upper bound on the biomass of riparian arachnids. Polis and Hurd (1995) similarly found contingencies in the relationship between kelp fly densities and spiders on desert islands, a

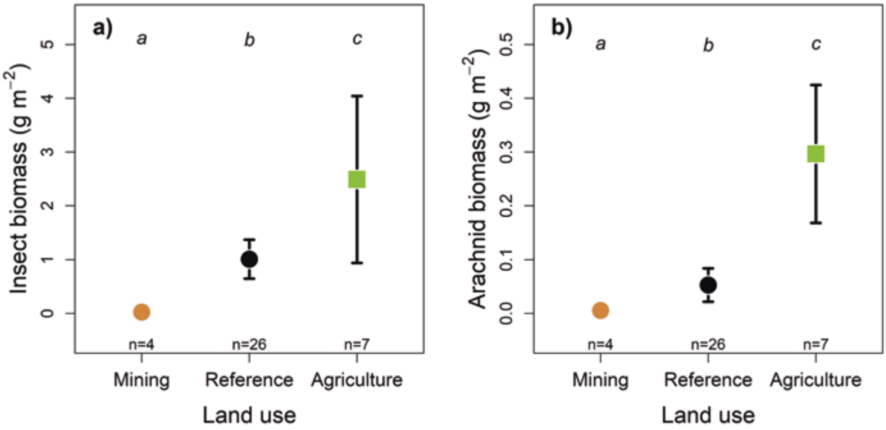

Fig. 4 Mean standing biomass (g m^{-2}) of (**a**) benthic insects and (**b**) riparian arachnids from adjacent exposed gravel bars in 37 forested streams of the South Island, New Zealand. Arachnid biomass includes spiders and opiliones. Land use indicates sites impacted by human activities, including forest streams receiving acid mine drainage (mining) and forest fragments embedded in agricultural landscapes (agriculture), in addition to the streams located in pristine forest (reference). Error bars indicate the 95% confidence interval. Results from linear mixed-effect models (LMMs) showed that benthic insect biomass (**a**) varied by land-use type ($F_{2,29} = 37.5$, $P < 0.001$) and was significantly lower in mining-impacted streams compared with the reference (Bonferroni-Holm comparison, $P < 0.001$) and agricultural streams ($P < 0.001$). In turn, streams impacted by agriculture had significantly greater benthic insect biomass than reference streams ($P < 0.05$). Likewise, arachnid biomass (**b**) varied among land-use types ($F_{2,29} = 24.9$, $P < 0.001$), and it was significantly lower in mining streams compared with the reference ($P > 0.001$) and agricultural streams ($P < 0.001$). Agricultural streams had significantly greater benthic insect biomass than reference streams ($P < 0.001$). Both LMMs accounted for site elevation as a fixed covariate and included a "varIdent" function to enable different variances per stratum for land use and a random effect term for stream region (Table 1)

result they attributed to the varying influence of top-down predation by scorpions and arthropodivorous land birds. While similar contingencies likely exist in my wedge-shaped relationship (Fig. 3), the influence of land use was apparent. Agricultural streams appeared to have a stronger linkage between aquatic prey and terrestrial consumers, whereas, consistent with published research (Paetzold et al. 2011; Kraus et al. 2014a, b), mining impacts (i.e., AMD) seemed to disrupt the connection between stream insects and riparian arachnids (Fig. 3; also see Fig. 4).

3.2.3 Understanding Causal Pathways Through Structural Equation Modelling

Clearly, there are multiple influences affecting the relationship between stream insect and arachnid biomass (e.g., Fig. 3). Thus, I used structural equation modelling (SEM) to better understand the different causal pathways potentially contributing to the trophic connectivity between stream and riparian habitats. Starting from the base of the food web with stream periphyton, we can see that mining (i.e., AMD) had a *positive* influence on this basal resource in comparison with the reference sites (Fig. 5). Similar relationships were reported by Bray et al. (2008) in a larger survey of streams in the same study region. Those authors found a negative relationship between algal biovolume and pH, meaning the low pH AMD-impacted streams had greater algal biomass than the circumneutral reference streams. This result may be specific to the study region, as other field studies have indicated that physical stress from metal hydroxides can negatively affect periphyton biomass (McKnight and Feder 1984; Niyogi et al. 1999). However, even in highly acidic waters ($pH < 3$) where metals remain dissolved, tolerant filamentous green algae can proliferate (Hogsden and Harding 2012b).

Periphyton had a significant positive influence on stream insect biomass after accounting for the direct toxicity effects of mining, indicating a positive "bottom-up" effect contributing to the stream productivity gradient (Fig. 5). A similar result was shown by Terui et al. (2018), where algal biomass was significantly correlated with the flux of emergent adult stream insects, which in turn had a positive influence on the densities of ground-dwelling beetles in the adjacent riparian zone. In my SEM, I included stream insect biomass at the patch scale ($g\ m^{-2}$) and then at the reach scale by accounting for stream width ($g\ m^{-1}$). This measure ($g\ m^{-1}$) was significantly positively associated with riparian arachnid biomass (Fig. 5) and could be considered more analogous to the flux of emergent adult stream insects as measured by Terui et al. (2018). Interestingly, there was a significant positive influence of periphyton biomass on arachnid biomass (Fig. 5), which may be also related to the flux of emergent stream insects mediated by periphyton (see Terui et al. 2018). Increased algal biomass could also indicate an increase in the quality of prey subsidies. Stream insects may have acquired greater concentrations of polyunsaturated fatty acids (PUFAs) via algal resources, thereby contributing an additional indirect benefit to riparian predators mediated through an increase in resource quality (Twining et al. 2016b). It should be mentioned here that excessive proliferations of periphyton, such as that seen with 'blooms' of the stalked diatom *Didymosphenia geminata* may adversely impact cross-habitat linkages via negative effects on sensitive stream insects (Bray et al. 2020).

Despite positive relationships between mining and periphyton and periphyton and aquatic insect biomass, the SEM showed a strong *negative* influence of mining on stream insect biomass ($g\ m^{-2}$) at the patch scale (Fig. 5). This highlights the negative *direct* effect of metal toxicity on stream insects that overrides any potential for positive *indirect* effects mediated through increased periphyton biomass in the presence of mining impacts (i.e., AMD). The effects of AMD on stream ecosystems are well documented and normally result in depauperate stream assemblages characterized by a loss of pollution-sensitive insects (Hogsden and Harding 2012b). AMD streams in New Zealand and elsewhere are generally characterized by thick coatings of metal hydroxides, which can reduce habitat and exert toxic effects on benthic organisms (McKnight and Feder 1984; Hogsden and Harding 2012b). Furthermore, these streams often have elevated levels of dissolved metals, including iron, and more toxic heavy metals such as aluminum, manganese, and zinc (Paetzold

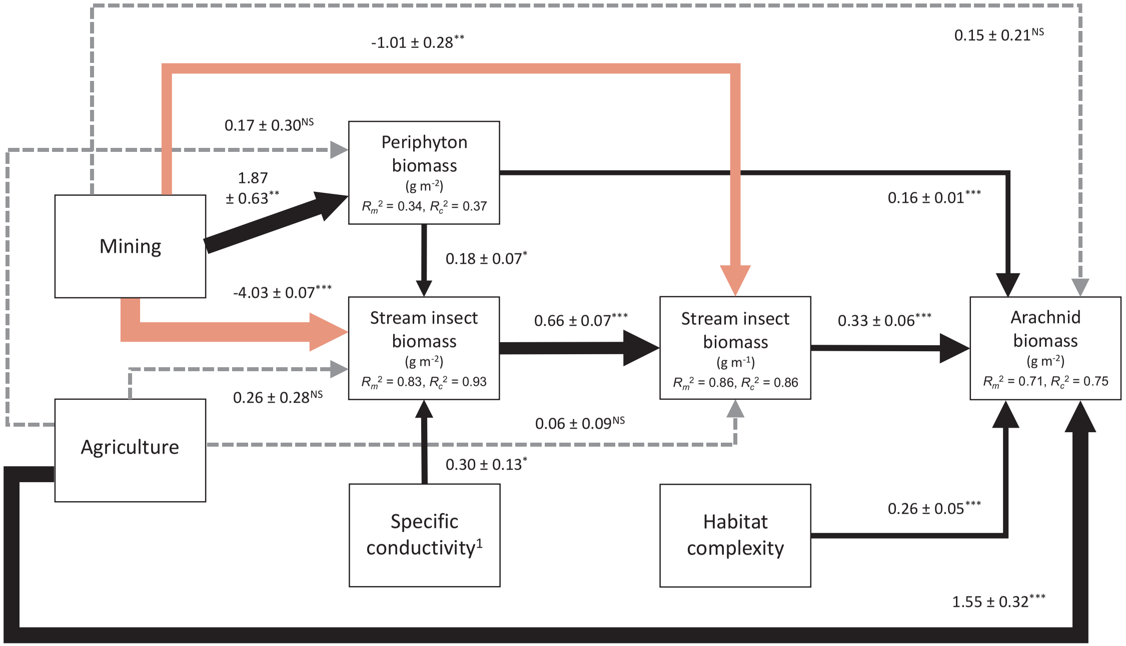

Fig. 5 Piecewise structural equation model (SEM) describing a causal network between 37 forested stream ecosystems and riparian arachnids from adjacent exposed gravel bars in the South Island, New Zealand. See Table 2 for further description of model parameters. Solid black arrows indicate significant positive associations; solid red[2] arrows significant negative associations. Non-significant paths are indicated by dashed gray arrows. Arrow width is scaled according to the standardized path coefficient, which is also indicated (± 1 S.E). Coefficients of determination for component models are shown as the marginal R^2_m, based on the variance of the fixed effects, and as the conditional R^2_c, based on the variance of both the fixed and random effects. Model components included a “varIdent” function to enable different variances per stratum for stream land use and a random effect term for stream region (Table 1). [1]Paths between land-use types (mining, agriculture) and specific conductivity could not be fitted without over-specifying the model, but both impacts led to significantly higher values relative to reference sites (LMM, $F_{2,29} = 12.1$, $P < 0.01$). [2]Solid arrows describing significant negative associations may appear as gray in figure versions. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$

et al. 2011; Niyogi et al. 2013). Such toxicity may exert stronger effects on emerging insects undergoing metamorphosis than larval forms, thus further reducing the subsidy potential for riparian consumers (Schmidt et al. 2013; Wesner et al. this volume).

Although emerging aquatic insect biomass was not measured directly in the Burdon and Harding (2008) dataset, the SEM (Fig. 5) indicated a negative influence of mining on stream insect biomass at the reach scale (g m^{-1}). There were no significant differences in wetted stream widths among the different stream types (LMM, $F_{2,29} = 2.00$, $P = 0.154$). This result indicated that within the causal network of the SEM, the influence of mining on reach-scale stream insect biomass (g m^{-1}) may have derived from a factor unrelated to stream width or insect biomass at the patch scale. Thus, one interpretation of this result is that the negative influence of AMD on reach-scale stream insect biomass (g m^{-1}) was *possibly* an emergent property of the SEM related to a disproportionate decline in emergence flux potential relative to instream biomass, as previously demonstrated by Schmidt et al. (2013).

There was no significant direct influence of mining on arachnid biomass (Fig. 5). Paetzold et al. (2011) surveyed AMD streams in England and observed reduced biomass of benthic and emergent aquatic insects in impacted stream reaches, matched by lower abundances and biomass of web-building spiders in the adjacent riparian zone. Similar results were reported by Kraus et al. (2014a) in mining-affected streams of Colorado, USA. In addition, subsidy manipulation studies have shown that removing the export of emergent aquatic insects from streams to riparian habitats can lead to reduced densities of web-building spiders (Kato et al. 2003; Marczak and Richardson 2007). Therefore, this case study and those studies described above (Paetzold et al. 2011; Kraus et al. 2014a) further corroborate the premise that mining (i.e., AMD) streams are located at one extreme of a “productivity” gradient where linkages between stream donor ecosystems and recipient riparian habitats are disrupted. The reduction in trophic connectivity emerges because the negative impacts of mining contamination on terrestrial food webs are mediated via effects on aquatic production.

In contrast with the strong effects of mining (i.e., AMD), the streams in forest fragments surrounded by agriculture did not have significantly greater periphyton biomass, and there was no detectable direct influence on benthic insects relative to the reference sites (Fig. 5). However, specific conductivity was associated with greater insect biomass, and although not explicitly tested in the SEM, the agricultural streams had significantly higher conductivity relative to the reference sites when tested separately (LMM, $F_{2,29} = 12.1$, $P < 0.01$, Bonferroni-Holm comparison, $P < 0.05$). In streams of New Zealand’s South Island, nitrate concentrations are strongly correlated with conductivity (Greenwood et al. 2012; Burdon et al. 2013). The elevated nitrate levels observed by Burrell et al. (2013) in the same streams sampled in Burdon and Harding (2008) were the result of anthropogenic sources in the surrounding catchment, which includes fertilization from aerial top-dressing (Harding 2003), and detrital inputs of non-native nitrogen-fixing leguminous shrubs (e.g., *Ulex europaeus*) (Stewart et al. 2018). Moreover, higher concentrations of nitrogen and phosphorus are a general feature of agricultural streams in New Zealand and globally (Allan 2004; McDowell et al. 2009). Thus, these studies suggest the positive influence of conductivity on stream insect biomass (Fig. 5) may have been strongly related to nutrient enrichment from agricultural land uses. Although mining (i.e., AMD) streams can have elevated nutrient concentrations, the typically high conductivities observed at these sites most likely result from the extremely high concentrations of metal cations deriving from dissolved iron and aluminum, among others (Niyogi et al. 2013). In Burdon and Harding (2008), conductivity had a positive influence on stream insect biomass excluding the mining-impacted streams, thus highlighting the strength of the SEM approach used here to account for contingencies like land use in the dataset. However, the conundrums highlighted above ultimately suggest that experiments disentangling the effects of productivity and environmental stressor gradients (e.g., nutrient enrichment and toxic pollution) are required to help better predict human impacts on aquatic-terrestrial linkages (Bundschuh et al. this volume; Kotalik et al. this volume; Kraus and Walters this volume; Muehlbauer et al. this volume).

Interestingly, there was a strong, direct influence of agriculture on riparian arachnid biomass (Fig. 5). There are various non-exclusive explanations for this result. It may have been the product of warmer temperatures in the forest fragments surrounded by agriculture, which could be due to a combination of lower elevations (Fig. 2) and forest fragment "edge effects." Microclimate conditions within remnant forest patches are frequently warmer, drier, and more variable (Murcia 1995). In addition, agricultural intensification in the surrounding matrix can lead to soil nutrient enrichment within forest fragments (Didham et al. 2015), potentially also explaining why, in certain contexts, fragmentation can increase terrestrial insect densities (Grez et al. 2004). Likewise, forest fragment streams in agricultural landscapes often experience altered thermal regimes, with generally greater mean temperatures, in addition to nutrient enrichment associated with surrounding land uses (Harding 2003; Goss et al. 2014).

It is highly likely that these multiple stressors interact, and the strong direct effect of agriculture may have been the result of synergistic interactions between warming and nutrients. For example, a pond experiment showed that warming and nutrient enrichment stimulated insect emergence both individually and when in combination (Greig et al. 2012). Similarly, in a field study, the emerging biomass of stream insects (Trichoptera and Ephemeroptera) increased significantly as water conductivity and temperature increased (Raitif et al. 2018). However, it should be noted that Terui et al. (2018) observed virtually no direct effect of temperature on riparian beetle densities, although their consumption rates did increase with warmer air temperatures. Nonetheless, my results combined with the studies described above suggest that terrestrial and aquatic habitats in forest fragments surrounded by agriculture are warmer with greater nutrient availability, thus potentially contributing to positive influences on cross-ecosystem productivity. This hypothesis potentially helps to explain the direct positive influence of agriculture on arachnid biomass in the context of my study. It also adds credence to the premise that the forest fragment streams in agricultural catchments are located at the upper extreme of a "productivity" gradient linking stream donor ecosystems with receiving riparian habitats.

A surprising feature of the SEM analysis was that hydrodynamic disturbance as measured by the Pfankuch Stability Index (PSI) had no significant direct or indirect effect on the biomass of riparian arachnids, leading to its exclusion from the final model (Fig. 5). Invertebrate assemblages in New Zealand mountain streams are highly persistent despite many streams having physically unstable beds, highly variable and unpredictable discharge patterns, and different riparian vegetation (Winterbourn 1997). This is because stream assemblages are dominated by the same widely distributed species characterized by life history flexibility, lack of habitat specificity, and strong colonizing abilities. The inherent ecological resilience to hydrodynamic disturbance in New Zealand streams potentially helps to explain why the PSI was not a significant predictor of variation in stream insect biomass in the Burdon and Harding (2008) dataset. Regardless, hydrodynamic disturbance may still influence habitat availability with consequences for riparian invertebrates. In another New Zealand study, intermediate levels of flooding provided the most suitable habitat for a large riparian arachnid, the pisaurid spider *Dolomedes* spp. (Greenwood and McIntosh 2008). Likewise, I found a positive influence of riparian habitat complexity on arachnid biomass (Fig. 5), confirming the result reported in Burdon and Harding (2008), but unlike Greenwood and McIntosh (2008), I was unable to detect a relationship between the PSI and habitat complexity. Despite this discrepancy, my results and that of Greenwood and McIntosh (2008) suggest that physical processes controlling habitat suitability (i.e., boundary properties) can be an important factor mediating the ability of terrestrial consumers to use aquatic-derived subsidies.

4 Synthesis: Anthropogenic Pressures and Productivity Gradients

Aquatic insects have been shown to increase the exposure of terrestrial consumers to aquatic contaminants, but some toxicants can reduce contaminant flux to riparian consumers by strongly disrupting the resource linkage (Walters et al. 2008; Kraus et al. 2014a). In the case study I have presented, the significant negative indirect effect of mining on riparian arachnids was mediated by greatly reduced standing crops of stream insects (Fig. 5). However, there are instances where low-impact mining pollution is insufficient to denude stream ecosystems of their insect faunas, meaning the prey subsidy may be diminished but still present. In those situations, bioaccumulation of metals and other toxicants in stream insects may be transported to terrestrial food webs via emerging adults, depending on the contaminant types (Schmidt et al. 2013; Kraus et al. 2014b; Kraus 2019). These studies suggest there may be a triumvirate of key factors determining the risk of effects propagating to adjacent habitats, with the threat contingent on the bioaccumulative potential of contaminants present, their realized toxicity, and the inherent propensity of the system to export prey subsidies. Thus, aquatic ecosystems experiencing low to intermediate levels of pollution stress could conceivably pose a greater ecotoxicological threat to recipient food webs than the most heavily impacted systems (i.e., due to acute toxicity effects). Such trade-offs can be further modulated by the presence of co-occurring stressors, including habitat loss and nutrient enrichment (Jones et al. 2012; Chumchal and Drenner 2015).

Nutrient enrichment of aquatic habitats from agricultural land uses may be relevant in the context of contaminant transport via emerging insects. For example, Jones et al. (2012) showed that insect-mediated mercury flux from aquatic mesocosms was positively impacted by nutrient additions. Contaminant transport via emerging aquatic insects in agroecosystems potentially threatens ecosystem integrity, with particular relevance to bioaccumulative toxicants including mercury and cadmium (Currie et al. 1997; Kraus et al. 2014a; Chumchal and Drenner 2015). One pathway for cadmium is the extended use of phosphate fertilizers, which can lead to its gradual accumulation in agricultural soils, thus making this metal a priority contaminant in New Zealand (MfE 2011) and global agroecosystems (Jacob et al. 2013; Khan et al. 2017). Likewise, these types of stressor combinations (nutrients, toxicants) are also common in urban systems, where inputs of municipal wastewater commonly lead to elevated levels of nutrients and micropollutants (e.g., metals and organic toxicants) downstream of the discharge (Burdon et al. 2016). A recent study by Richmond et al. (2018) showed that in streams influenced by wastewater inputs, a wide range of pharmaceutical compounds were present in benthic aquatic invertebrates and riparian spiders, thus raising important questions about mixture toxicity, contaminant transport, and bioaccumulation in higher consumers. However, there is still relatively little known about the fate of such contaminants in coupled stream-riparian ecosystems or how multiple stressors might exacerbate or dampen pollutant transfers across the ecotone (Chumchal and Drenner this volume). Understanding how gradients of productivity interact with toxicity gradients would help to better predict the transport of contaminants to receiving environments (e.g., Fig. 5). It is plausible that where human pressures cause the donor ecosystem to be beset by multiple stressors, certain combinations of stressors (e.g., nutrient enrichment and toxic pollution) may heighten the ecotoxicological risks to recipient habitats (Kraus and Walters this volume).

The case study presented in this chapter also showed evidence for a positive influence of agriculture on productivity of streams in forest fragments (Fig. 5). Here, I hypothesized that the observed positive influences reflected the "subsidy" portion along a "subsidy-stress" gradient of agricultural development. In other New Zealand streams, Niyogi et al. (2007) found that densities of stream insects (i.e., Ephemeroptera, Plecoptera, Trichoptera (EPT)) peaked at intermediate levels of pastoral land cover and nutrient enrichment, indicating the potential for positive "subsidy" effects of agriculture on the productivity of stream ecosystems. While streams in forest fragments surrounded by agriculture often have elevated temperatures, nutrient concentrations, and levels of fine sediment compared with reference streams, these effects of agriculture can attenuate over relatively short instream distances. This “buffering” effect of surrounding forest may additionally help protect forest fragment streams from the most extreme “stress” effects of intensive agriculture, meaning that the invertebrate community composition is more similar to that seen in contiguous forest (Goss et al. 2014). However, any positive influence of upstream agriculture on aquatic-terrestrial linkages may also be dependent on stream reaches retaining intact assemblages of larger-bodied EPT stream insects (McKie et al. 2018), thus invoking metacommunity dynamics mediated by the regional species pool (Heino et al. 2015).

Human land uses change the composition of emergent aquatic insect assemblages (e.g., Cavallaro et al. 2019), thus potentially driving trait-mediated influences on recipient predators. The recent study by Raitif et al. (2018) indicated that in French agricultural streams, most of the emergent biomass belonged to Trichoptera (56%), Chironomidae (25%), and Ephemeroptera (19%). In contrast, other studies have suggested that agricultural streams in Northern Europe typically have emergent insect faunas dominated by small aquatic insects (Chironomidae), whereas larger-bodied aquatic insects (Plecoptera and Trichoptera) are more associated with forested land uses (Stenroth et al. 2015; Carlson et al. 2016). Such shifts may influence the quality of the prey subsidy and the type of terrestrial consumers found in the riparian zone (Stenroth et al. 2015). While it remains to be seen what benefits the larger total biomass of emergent aquatic insects provides to riparian consumers in agricultural reaches (Stenroth et al. 2015; Carlson et al. 2016), Akamatsu et al. (2007) suggested that abundant smaller prey might enable females of the web-building spider *Nephila clavata* to grow to a size sufficient to handle larger prey. However, irrespective of prey body size, in agricultural catchments where pesticide-intensive arable cropping is the dominant land-use pressure (e.g., much of the Midwestern United States), stressors such as the metal selenium, the herbicide atrazine, and the neonicotinoid insecticides can reduce the total biomass of emerging aquatic insects (Henry and Wesner 2018; Cavallaro et al. 2019). As observed with mining impacts in Fig. 5, there may be negative indirect effects of agricultural pesticides on riparian spiders mediated through reduced abundances and biomass of stream insects (Graf et al. 2019).

In addition to affecting the quantity of adult aquatic insect subsidies to terrestrial food webs, human land uses may also affect the nutritional value of aquatic-derived prey. There is evidence that the increased light and nutrient availability typical of agricultural and urban streams can alter the nutritional quality of periphyton (Cashman et al. 2013). By decreasing the availability of essential, long-chain (20–22C) highly unsaturated fatty acids (HUFAs) relative to forested streams, these land-use types may have unseen consequences for stream and riparian consumers (Cashman et al. 2013; Twining et al. 2016a). Riparian spiders and birds that rely on small but essential HUFA fluxes via emergent aquatic insects are more likely to be limited by food quality (Gladyshev et al. 2013; Twining et al. 2016b, Chari et al. 2020), meaning there could be a mismatch between resource quality and quantity in streams impacted by human activities. Thus, overall resource quality may decline dramatically in impacted streams if there are shifts in key organismal traits such as body size, declines in fatty acid availability (HUFAs), and increased contaminant loads of toxic stressors.

In the case study presented here, the positive influence of agriculture on riparian arachnid biomass (Fig. 5) may also reflect other processes occurring in the landscape matrix. Connectivity can enhance trophic subsidies in fragmented landscapes by enabling resource flows between habitat patches (Hawn et al. 2018). For example, the stream-riparian corridor could be used as a "highway" by volant (i.e., flying) terrestrial and aquatic insects to move through forested patches bidirectionally from the more productive agricultural reaches. Many volant insects are known to fly toward light in open spaces (Goldsmith 1990), and in addition to the large numbers of aquatic insects, slightly higher densities of terrestrial insects have been observed over streams (Lynch et al. 2002). Therefore, effects of agricultural subsidies (aquatic and terrestrial) to forested habitat patches should include measuring the flux of volant insects along the river network. This could help establish how important longitudinal connectivity is for aquatic-terrestrial linkages relative to the lateral connections based on in situ production.

5 Conclusions

Multiple stressors and the complex ecological responses often associated with human pressures challenge researchers to understand how anthropogenic perturbations impact stream and riparian ecosystems. My previous research indicated that standing benthic insect biomass (after scaling for stream size) was an effective proxy measurement for the potential flux of adult prey to recipient terrestrial food webs, with an apparent positive influence on riparian arachnids (Burdon and Harding 2008). In this chapter, I demonstrated how the "productivity" of aquatic insects linking stream donor ecosystems with recipient riparian habitats could be influenced by anthropogenic perturbations. Streams impacted by mining supported less benthic insect and riparian arachnid biomass than reference sites, whereas agricultural streams in forest fragments were seemingly more productive, with greater standing crops of stream and riparian invertebrates. These findings highlight how multiple anthropogenic pressures affecting stream habitats may contribute to productivity gradients determining the trophic connectivity between aquatic and terrestrial ecosystems.

Future research should further consider how multiple stressors and biotic interactions affect cross-ecosystem subsidies. There is a need for more experiments disentangling the effects of productivity and environmental stressor gradients (e.g., nutrient enrichment, warming, and toxic pollution) on cross-habitat linkages. In particular, synergistic interactions between toxicity and productivity gradients may facilitate the transport of contaminants into receiving environments via prey subsidies and bioaccumulation. Some studies have begun the work of disentangling these effects. For example, experimental evidence has shown that bottom-up (nutrient enrichment) and top-down (fish predation) processes differentially affect insect emergence and insect-mediated mercury transport (Jones et al. 2012). Greig et al. (2012) provided a non-ecotoxicological example where they experimentally tested the influence of warming, nutrients, and fish impacts on aquatic insect emergence. However, there are very few studies that have actually quantified how such changes affect recipient consumers. The approaches employed in this chapter and by Terui et al. (2018) provide one direction towards addressing this knowledge gap. Clearly, food web theory has a role to help guide hypothesis testing and establish a solid mechanistic basis for how multiple stressors alter networks of interacting species across ecosystem boundaries (Gray et al. 2014; Burdon 2018; Sullivan and Manning 2019; Wesner 2019). Combined with a better empirical understanding of when, where and how aquatic predation affects the emergence of aquatic insects (e.g., Wesner 2010), such approaches will help us to better predict human impacts on aquatic-terrestrial linkages (Kraus and Walters this volume; Muehlbauer et al. this volume).

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Francis J. Burdon is a research associate currently working in the Department of Aquatic Sciences and Assessment at the Swedish University of Agricultural Sciences in Uppsala, Sweden. Originally from New Zealand, F.J.B. conducted his doctoral studies at the University of Canterbury advised by Profs. Jon Harding and Angus McIntosh. He has since completed postdoctoral research at Eawag, Switzerland, before moving to Sweden. He has published in peer-reviewed journals on a variety of topics including stable isotopes, food webs, and anthropogenic impacts in stream ecosystems. F.J.B. is presently working on a European project “Crosslink” that investigates aquatic-terrestrial linkages in human-impacted landscapes.

Cross-Ecosystem Linkages and Trace Metals at the Land-Water Interface

Johanna M. Kraus and Justin P. F. Pomeranz

> *The loss of food has also struck hard at the swallows that cruise the sky, straining out the aerial insects as herring strain the plankton of the sea.*
>
> Carson (1962)

1 Introduction

Bioaccumulation and biomagnification of toxic chemicals in food webs have been a major concern driving the development of the field of ecotoxicology (Carson 1962; Truhaut 1977; Chapman 2002). Concerns about accumulation of contaminants in tissues are warranted given their cascading, sometimes unexpected, effects on ecosystems and human health (Otter et al. this volume). However, contaminants that do not biomagnify or even bioaccumulate at high concentrations in tissues can also have major cascading and unanticipated effects on consumer abundance and distribution, community composition, and ecosystem production by altering abundance and biomass of resources (Carlisle and Clements 2005; Nebel et al. 2010; Schmidt et al. 2011; Kraus et al. 2014a; Rioux Paquette et al. 2014; Hallman et al. 2017; Kraus 2019). These indirect effects of contaminants on communities and food webs have been increasingly appreciated and elucidated over the last two decades (Clements and Newman 2002; Rohr et al. 2006; Clements and Rohr 2009; Gessner and Tlili 2016). In particular, the deleterious effects of trace metals on emergence of adult aquatic insects, known to provide important resource subsidies to terrestrial

J. M. Kraus (✉)
U.S. Geological Survey, Columbia Environmental Research Center, Columbia, MO, USA
e-mail: jkraus@usgs.gov

J. P. F. Pomeranz
Department of Biology, University of South Dakota, Vermillion, SD, USA

Department of Environmental Sciences and Technology, Colorado Mesa University,
Grand Junction, CO, USA

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insectivores, have garnered increased interest and incorporation into environmental monitoring by management agencies (e.g., Walters et al. 2008; Muehlbauer et al. 2019). Here we review the mechanisms and patterns driving these effects of trace metals on aquatic insects at the land-water interface.

The effects of contaminants on adult aquatic insects result from both direct and indirect effects of contaminants on aquatic insect communities and food web structure that can propagate within and across ecosystem boundaries. Similar to nutrients and salts (Evans-White et al. this volume), trace metals are critical micronutrients for sustaining life at low concentrations but at high concentrations are a global stressor that alter aquatic and terrestrial food webs. These metals alter emergence of adult aquatic insects via toxicological responses that reduce survival of larval aquatic insects through metamorphosis and by changing aquatic community composition and structure (Clements et al. 2000; Carlisle and Clements 2003; Kraus et al. 2014a, 2016; Wesner et al. this volume). These reductions in aquatic insect production and changes in community structure can alter insect prey availability and the distribution of both aquatic and terrestrial insectivores such as fish, birds, bats, lizards, spiders, and other arthropods. For example, riparian spiders that rely on resource subsidies of adult aquatic insects are less abundant and comprise less standing biomass near mine-impacted stream reaches (Paetzold et al. 2011; Kraus et al. 2014a).

In this chapter, we highlight mechanisms driving effects of trace metals on terrestrial insectivores mediated by effects of metals on resource subsidies of adult aquatic insect prey. First, we give an overview of the mechanisms driving how trace metals impact aquatic organisms, mainly insects and fish, and why toxic effects are often uncorrelated with bioaccumulation for individual trace metals both in larvae and adult aquatic insects. Second, we review how trace metals impact community structure and community dynamics (e.g., competition and predation) and influence aquatic insect assemblages in freshwater ecosystems. Finally, we describe how these effects of trace metals on individuals and communities within the aquatic ecosystem play out for emergence of adult aquatic insects and terrestrial insectivores of these prey, as well as for use of terrestrial insect prey subsidies by insectivorous fish. Specifically, we focus on three examples where (1) trace metals reduce aquatic insect prey availability for stream trout, but fish populations are maintained by terrestrial insect prey subsidies, (2) trace metals eliminate aquatic insect subsidies to terrestrial consumers and lead to declines in terrestrial consumer populations, and (3) insect metamorphosis decouples metal accumulation in adult aquatic insects from aqueous exposure experienced by aquatic insect larvae. We discuss the implications of these findings for management, specifically for assessing resource damage, remedy effectiveness, and restoration in linked aquatic-terrestrial ecosystems. Understanding the mechanisms, patterns, and causes of these effects are particularly important for aquatic ecosystem management within the context of widespread impacts of contaminants and global declines in populations of both insects and insectivores (Bernhardt et al. 2017; Rohr et al. 2017; Otter et al. this volume).

2 Trace Metal Accumulation and Impacts on Aquatic Organisms

Elevated concentrations of trace metals can be global biological stressors that enter the surface environment from myriad pathways including weathering of mineralized rocks, mining operations, extensive use and application in urban environments, and combustion activities. In freshwater ecosystems, metals can negatively affect organisms by interfering with normal metabolic functioning and directly inhibiting gas exchange (e.g., gill smothering; Adams et al. 2011; Maret and MacCoy 2002; Greig et al. 2010). Because many trace metals are essential minerals for maintaining cellular function (i.e., incorporated into enzymes to satisfy essential needs of the cell; Bury et al. 2003), their uptake and effects on the body follow pathways much different from many manufactured contaminants. These pathways ultimately determine not only how trace metals impact aquatic-terrestrial linkages but also how toxicity and bioaccumulation in invertebrates are related in these systems.

Uptake of trace metals into the bodies of aquatic insects and other invertebrates can occur directly from the environment during exchange of respiratory gases and maintenance of ionic and water concentrations or through ingestion of contaminated food. Many freshwater organisms, including the insect orders Ephemeroptera (mayflies) and Plecoptera (stoneflies) (Komnick 1977), and fish (Perry 1997), also have specialized chloride cells located on their gill or body epithelium that allow them to perform osmoregulatory processes directly on the body surface (Buchwalter and Luoma 2005). These cells contain high concentrations of ion transport proteins and provide a pathway for dissolved trace metals (both essential and non-essential) to enter the body (Buchwalter and Luoma 2005). Ingestion of metal-contaminated food particles can also be a significant source of bioaccumulation and toxicity to aquatic organisms (Hare et al. 2003; Besser et al. 2001; Farag et al. 1999; Miller et al. 1993; Cain et al. 2011). Contaminated food is digested, releasing the metal ions, which are then available to be actively transported into the body through the gut epithelium, Malpighian tubules, and rectum.

Once trace metal ions enter an aquatic invertebrate or fish, they can have three fates: excretion in waste products, accumulation in the body in a metabolically available form, and accumulation in the body in an inert or “detoxified” form (Fig. 1). Accumulated metals that are metabolically available are taken up into cytosol of cells and are available to bind to any molecule with an affinity for that ion. Metal ions generally have high affinity for sulfur and nitrogen, and because proteins are made of amino acids which can contain both of these elements, there are many potential binding sites for metabolically available metals (Rainbow 2002). Any essential metals present in excess of metabolic needs and non-essential metals that are metabolically available become potentially toxic to the organism because they can interfere with cellular functions and lead to increased metabolic costs. This primarily occurs by competing for protein binding sites or by denaturing the protein and inhibiting osmoregulatory function in the cell (Rainbow 2002; Bury et al. 2003; Adams et al. 2011). For example, in freshwater fish, both silver (Ag) and copper

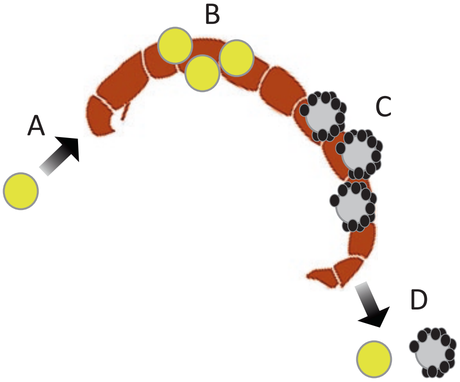

Fig. 1 Fate of trace metal ions within the insect body. Metals are taken up into the body through diet or absorption (*A*) and are stored in the body as metabolically available forms (*B*) or are stored in metabolically inert granules (*C*). Both forms can be egested (*D*) through normal waste functions or during metamorphosis into the adult form

(Cu) can enter the cell via sodium transport channels and can ultimately inhibit both sodium-potassium adenosine triphosphatase (Na^+/K+−ATPase, aka the sodium-potassium pump) and cellular carbonic anhydrase. Likewise, the similarity of cadmium (Cd) to calcium (Ca) means that it competes for Ca binding sites, disrupting the efficiency of metabolic pathways (Adams et al. 2011).

To reduce toxic effects of excess metals, many aquatic organisms bind accumulated metals in detoxified forms. Detoxified metals are removed from the cytosol of the cell and stored in insoluble granules, or they are bound at the active sites of metal binding proteins, such as metallothionein, within the cytosol (Rainbow 2002; Adams et al. 2011; Ruttkay-Nedecky et al. 2013). Detoxified metals do not illicit adverse response within the organism. As a result, they can accumulate in some organisms in disproportionately large quantities compared to their effects (see examples below; Adams et al. 2011). Detoxified metals can also be excreted after a period of storage (e.g., during life history transitions like metamorphosis in aquatic insects; Wanty et al. 2017).

Aquatic organisms display variability in their responses to trace metals, both in their toxic effects, and in the bioaccumulation of trace metals in their bodies. The variation in toxicity and accumulation patterns of trace metals among taxonomic groups is due in part to how metals are stored (Luoma and Rainbow 2005; Buchwalter et al. 2008; Adams et al. 2011). For example, barnacles (Cirripedia arthropods) are considered Zn "accumulators" because they are able to store large amounts of detoxified trace metals within their bodies without direct toxic effects (Luoma and Rainbow 2005). On the other hand, some species like the decapod crustacean *Palaemon elegans* store most metals in metabolically available form. These taxa cannot store high concentrations of metals and must excrete these metals quickly or suffer an adverse toxic response (e.g., death or metabolic decline; Rainbow 2002; Luoma and Rainbow 2005; Adams et al. 2011). As a result of this taxonomic variation in metal accumulation and storage patterns, toxicity of a given trace metal is often uncorrelated with its bioaccumulation across taxa (Luoma and Rainbow 2005; Adams et al. 2011). Similarly within a taxonomic group, accumulated metal can sometimes parallel patterns of toxic effect on the individual or population (e.g., Zn in *Drunella* spp. and *Rhithrogena* spp., Schmidt et al. 2011; Cd in adult mayflies, Kraus et al. 2014a) or be completely unrelated (e.g., Zn in *Arctopsyche grandis*, Schmidt et al. 2011; Zn in *Palaemon elegans*, Rainbow 2002). These patterns contrast those seen for organometals and bioaccumulative organic contaminants that generally show proportional bioaccumulation and effects with increases in exposure concentration of bioavailable compounds.

In addition to having a variable relationship with toxicity, bioaccumulation of trace metals by aquatic organisms can also vary disproportionately with concentration of that metal in the environment (i.e., environmental exposure). For example, the ratio of predator to prey Hg concentrations is higher when concentrations of Hg in the water and sediment are lower (DeForest et al. 2007; Lavoie et al. 2013; Kraus et al. In Review). This pattern occurs for many trace metals including Zn, Cu, and Cd, such that bioaccumulation is proportionately highest at lowest exposure concentrations (McGeer et al. 2003; DeForest et al. 2007; Kraus et al. In Review). For example, Cu concentrations in chironomid midge (Chironomidae: Diptera) tissues may be 100,000× dissolved water concentration when Cu concentrations in the water are low, but by contrast, they are <10,000× higher when contamination is high (Deforest et al. 2007). These patterns can result from metabolic mechanisms, including increased cellular regulation of metal concentrations in more contaminated environments and saturation uptake kinetics (DeForest et al. 2007), and from survivor bias, where observed tissue concentrations in high-metal environments are reduced because organisms with high tissue concentrations have died. Regardless of mechanism, observed patterns of metal accumulation in the field suggest that no one bioaccumulation or transfer value can represent metal bioaccumulation and/or trophic transfer across an exposure concentration gradient (DeForest et al. 2007).

Aquatic organisms vary in the type of toxic responses they have to elevated metal concentrations. Lethal effects imply that death results directly from exposure. Sub-lethal effects include all effects not resulting directly in death (although life span might be shortened). Lethal and sub-lethal effects occur when metal concentrations are elevated, or the exposure time is sufficient, for metabolically available metals to accumulate and reach a critical level in a given taxon, although concentrations linked to lethal effects are usually higher. Lethal effects occur when metabolic or cellular effects of metal exposure are great enough to cause the organism's systems to completely shut down. For example, interference with cellular functions and increased metabolic costs of detoxifying metal ions can lead to mortality in aquatic insects. Mortality is most likely to occur when the organism is coping with other stressors such as during sensitive life stages when surface area to volume ratios are large (i.e., size is small) or when transitioning through life history switch points like metamorphosis (Wilbur 1980; Kiffney and Clements 1996; Wesner et al. 2014).

Sub-lethal effects of trace metal contamination occur when physical, metabolic, or cellular effects of metals are not large enough to completely overwhelm the organism, usually at concentrations significantly lower than lethal concentrations (Boyd 2009). Sub-lethal responses include slowed growth, reduced reproductive rates, weakened immune system, and altered behavioral responses (e.g., habitat selection, food gathering, and predator avoidance). For example, larval chironomid midges avoid metal-contaminated sediments (Wentsel et al. 1978). Rainbow trout (*Oncorhynchus mykiss*) chronically exposed to sub-lethal concentrations of nickel (Ni) show no effects to their resting physiology but have reduced exercise capacity due to a thickened oxygen barrier present on the gill surface (Pane et al. 2004). When caddisfly larvae were exposed to sub-lethal Cd concentrations, their interspecific competition behaviors were modified, with the exposed individuals generally being less aggressive (Vuori 1994). Variation in the lethal and sub-lethal responses of aquatic organisms to metal exposure influences community structure such as taxonomic composition and community dynamics such as predation and competition in metal-impacted ecosystems.

3 Impacts of Trace Metals on Community Structure and Dynamics

Elevated trace metal concentrations impact aquatic community structure and community dynamics, such as competition, predation, and food web stability, in aquatic ecosystems by altering the abundance and distribution of species attracted to and able to live in contaminated waters. Reductions in individual survival and fitness can lead to significant changes in population densities and may lead to changes in community composition (Fig. 2). Broadly speaking, taxa can be classified into two

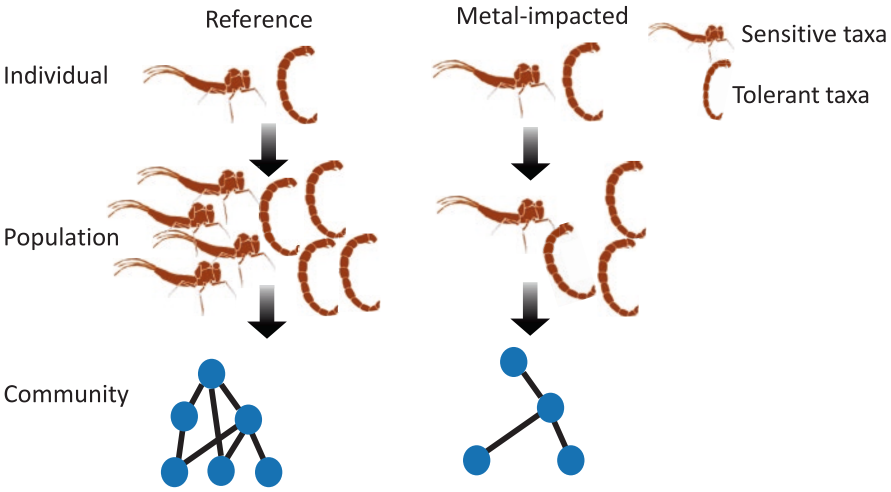

Fig. 2 Changes in aquatic communities due to elevated trace metal concentrations. Metal-sensitive taxa show stronger reductions in individual survival and fitness than tolerant taxa (top panel). This can lead to the extirpation of sensitive taxa, as well as the reduction in population densities of tolerant taxa (middle panel). Both of these can lead to significant changes in community composition and food web structure (lower panel)

categories, tolerant and sensitive, or taxa which can persist despite elevated metal concentrations and those which cannot persist in the presence of elevated metal concentrations, respectively. Individuals of both sensitive and tolerant taxa are susceptible to lethal and sub-lethal effects of elevated trace metal concentrations (Clements et al. 2000; Carlisle and Clements 2003). However, because sensitive species are more susceptible to lethal effects, elevated trace metal concentrations can lead to their local extirpation even while more tolerant species persist.

When the local species pool contains metal-tolerant taxa, the loss of sensitive species can coincide with replacement by more tolerant species (Hogsden and Harding 2012a). For example, invertebrate communities become dominated by a few tolerant taxa, including true flies (Diptera) and beetles (Coleoptera), and non-insect taxa such as oligochaete worms (Oligochaeta: Annelida). Mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) are generally the most sensitive, but these responses are species-specific and can vary significantly based on geography (Clements et al. 2000; Gray and Harding 2012). Although species richness was similar between reference and metal-contaminated sites in Andean streams, community composition shifted from reference communities dominated by Crustacea, Ephemeroptera, Plecoptera, and Trichoptera to communities dominated by Diptera, Coleoptera, and Collembola (Loayza-Muro et al. 2010).

As trace metal concentrations increase, nearly all biotic measures in freshwater communities can be significantly affected (Clements et al. 2000; Hogsden and Harding 2012a). In general, species richness, diversity, and abundance of periphyton (diatoms and algae), bacteria, fungi, invertebrates, and fish are all reduced in response to increases of trace metals (reviewed in Hogsden and Harding 2012a). The distribution of macroinvertebrate biomass and body size can also be significantly altered in acid mine drainage (AMD) impacted streams (e.g., high metals and low pH; Hogsden and Harding 2012b; Pomeranz et al. 2019). Small body sizes are generally thought to be more sensitive because of larger surface area to volume ratios (i.e., more area over which to be exposed). But individuals of species which have larger mature stages (particularly invertebrate predators) are also thought to be more sensitive than smaller species. Such predators are likely limited by small body sizes during early instars and by lack of prey resources later in life. Finally, the quantity and quality of primary producers and detrital resources can respond to increasing metal impacts (Evans-White et al. this volume).

In addition to species composition being strongly affected based on sensitivity to metals, the relative proportions of functional feeding groups can be altered (Clements et al. 2000; Pomeranz et al. 2019). For example, the abundance of predators significantly declined in medium and high metal concentration streams in Colorado, USA (Clements et al. 2000). Changes in relative proportions of functional feeding groups within a community can lead to a reduction in the number of energy pathways available, resulting in smaller (e.g., fewer number of species and/or number of feeding links between species) more well-connected food webs (Hogsden and Harding 2012b). Because the food webs are smaller and have fewer energy pathways available, they may become dominated by a few interactions. This pattern has important implications for food web stability. Here, we discuss stability as it relates to local asymptotic stability, or the likelihood of a community returning to its original state after some small disturbance (Emmerson and Raffaelli 2004).

Both empirical and theoretical studies have demonstrated that the stability of food webs is dependent on the structure (number and arrangement of links) as well as the distribution of interaction magnitudes (i.e., strength of effect of species *i* on species *j*; Emmerson and Raffaelli 2004; de Ruiter et al. 1995; Neutel et al. 2002; Wootton and Stouffer 2016). The structure and strength of interactions can have confounding effects. For example, food webs with many weak interactions are generally more stable than those dominated by a few strong interactions (de Ruiter et al. 1995; Neutel et al. 2002; Wootton and Stouffer 2016). However, interaction strength is largely determined by consumer-resource body size ratios, where large predators have stronger interactions with small prey (Emmerson and Raffaelli 2004). Indeed, Wootton and Stouffer (2016) found that both the strength and proper arrangement of interactions are necessary for food webs to be stable. In general, stable food webs include (1) diverse webs with lots of weak interactions and (2) simple food webs where interaction strengths are weak.

These interacting effects can be difficult to parse in metal-impacted communities. On one hand, metal-impacted communities are likely to be small and less diverse due to the extirpation of sensitive species, increasing the likelihood that these communities are dominated by a few strong interactions, and thus have lower stability. On the other hand, however, because trace metals can remove the largest body sizes from a community (Greig et al. 2010; Hogsden and Harding 2012b; Pomeranz et al. 2019), the resulting strength of interactions may be weak, leading to more stable communities. Indeed, empirical evidence from acid-impacted stream communities in the UK became small and simple but had relatively weak interaction strengths and thus had higher stability than unimpacted streams (Layer et al. 2010). Likewise, simulations in streams across a gradient of AMD inputs in New Zealand indicated that stability increased in more heavily impacted streams (Pomeranz et al. In Review). Thus, in metal-impacted streams, small communities (few interactions, potentially destabilizing) in which animals with large body sizes have been lost (e.g., marge magnitude interaction strengths) is the norm. The resulting increase in community stability suggests that the strengths of the interactions are more important to maintaining stability than the complexity/number of interactions.

While the effects of elevated trace metal concentrations on food web stability remain difficult to predict, direct effects of metals on predators can have cascading effects on aquatic food webs. For example, apex predators, such as fish, can be highly sensitive to metal exposure and can be completely absent in waters with elevated metal concentrations (Maret and MacCoy 2002; Greig et al. 2010; Kraus et al. 2016). In moderately impacted streams, tolerant invertebrate predators can replace fish as the top trophic level (Liess et al. 2017). Invertebrate predators released from fish predation pressure are able to increase their predation intensity (Kiffney 1996) of invertebrate primary consumers, lowering their densities. These changes in community composition and trophic interaction set up a classic trophic cascade; lower densities of invertebrate primary consumers reduce grazing pressure, resulting in increased biomass of primary producers such as diatoms and algae (Rogers et al. 2016). Alternatively, invertebrate predators may also be extirpated from highly impacted streams (Pomeranz et al. 2019), which may result in increased abundances of primary consumers and reduced biomass of basal resources. Trace metals can also influence community dynamics by altering the strength of predator-prey interactions. Trace metals in combination with predator presence can significantly lower community abundance and taxa richness. These results were observed where metal concentrations were lower than those expected to directly affect community structure, and this was attributed to stronger predation intensity in the presence of metal contamination (Kiffney 1996).

Loss of sensitive species, species replacement, and change in relative dominance of tolerant taxa all result in significant changes to community structure and community dynamics in metal-impacted streams. Many of these impacts of elevated trace metal concentrations on aquatic communities indirectly impact insectivorous consumers in the water, like fish, and can increase reliance of such consumers on terrestrial prey. These impacts of trace metals can also cascade to alter terrestrial insectivores and terrestrial food webs. These cascades are mediated by aquatic insects that spend their larval periods in the water and adult stages as winged adults in the air and on land.

4 Cascading Consequences for Food Webs at the Land-Water Interface

Animals with complex life cycles form an important link between freshwater and terrestrial ecosystems (Nakano and Murakami 2001; Baxter et al. 2005; Regester et al. 2006). In particular, aquatic insects with aquatic larvae and terrestrial adult forms are important prey resources for consumers in the water and on land. These insects link food web dynamics and ecosystem fates across the aquatic-terrestrial boundary. Trace metal impacts on aquatic insect prey alter food webs at the land-water interface in several ways (Fig. 3; Paetzold et al. 2011; Kraus et al. 2014a, b). First, trace metals can alter aquatic insect prey composition and availability for insectivorous predators, altering reliance on terrestrial insect prey (Kraus et al. 2016). Second, trace metals can alter aquatic insect subsidies to terrestrial consumers and lead to declines in terrestrial consumer populations (Paetzold et al. 2011; Kraus et al. 2014a). Finally, insect metamorphosis can decouple metal exposure in terrestrial consumers of adult aquatic insects from aqueous contaminant levels due to the high excretion rates of metals during the transition from aquatic larvae to terrestrial adult (Kraus et al. 2014b; Wesner et al. 2017).

Although most information about the effects of trace metals on aquatic insects are for larvae, adult insect emergence production seems to be more sensitive to metal exposure, especially at low metal concentrations (Schmidt et al. 2013; Kraus et al. 2014a; Wesner 2019; Wesner et al. this volume; Kotalik this volume).

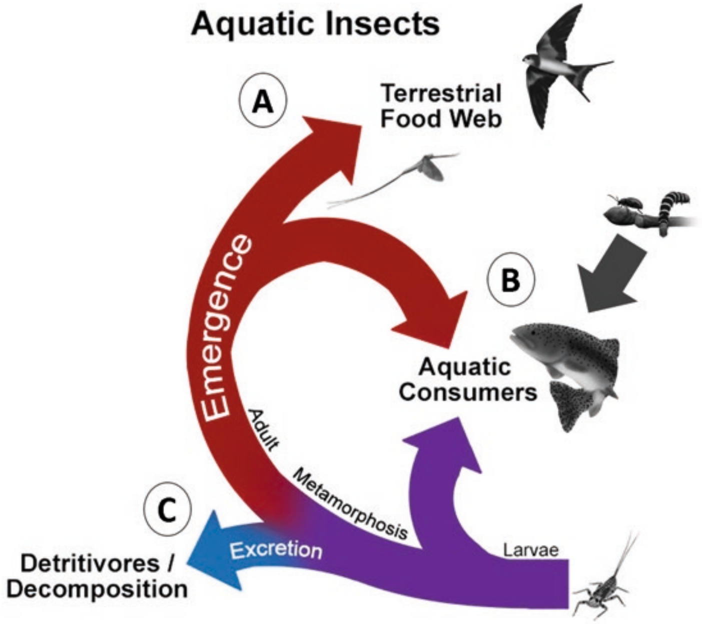

Fig. 3 Pathways of aquatic insect-mediated impacts of trace metals on aquatic and terrestrial insectivores in freshwater and riparian ecosystems. Trace metals can reduce aquatic insect subsidies to terrestrial birds, bats, and spiders (*A*) and aquatic insect prey availability for fish, causing them to increase their reliance on terrestrial prey (*B*). Because trace metals are excreted during insect metamorphosis (*C*), exposure to diet-borne metals is more likely to affect consumers of larval insects than consumers of adult aquatic insects. (Figure is adapted from Kraus et al. 2014b. Original drawings by Jeremy Monroe at Freshwaters Illustrated)

Metal concentrations in adult aquatic insects, on the other hand, remain low in streams with moderate to high-metal contamination (Kraus et al. 2014a). Metamorphosis from larval to adult stages is a key life history switch point regulating the impacts of aquatic metals on terrestrial consumers by increasing sensitivity to lethal effects of metals (Wesner et al. this volume) and by providing a mechanism for excreting stored metals from tissues (Kraus et al. 2014b; Wanty et al. 2017). Because adult aquatic insects fall prey to terrestrial consumers, the main effects of metals on cross-ecosystem linkages are through reduction in prey availability and shifts in prey taxonomic composition toward smaller-bodied, more metal-tolerant taxa (like dipterans), rather than contamination of adult prey (Paetzold et al. 2011; Kraus et al. 2014a). This loss of aquatic prey tends to cause loss of predator biomass and/or shift of consumer diets toward terrestrial prey sources (Kraus et al. 2016). Thus, managing for increased terrestrial production near moderately impacted systems could elevate consumer abundance and biomass (Kraus et al. 2016). In the remainder of this section, we present several case studies illustrating these patterns as well as the ecological context likely to determine how they impact community structure and community dynamics in the environment.

4.1 Effects of Metals on Terrestrial Prey Use by Aquatic Insectivores

By altering the taxonomic and size distribution of insect prey toward smaller-bodied taxa and reducing aquatic prey availability, aqueous metals can elevate the importance of terrestrial prey in subsidizing aquatic insectivore populations (Kraus et al. 2016). In a study of trout diets in the central Colorado Rocky Mountains, we found that salmonids in metal-contaminated streams consume proportionally more terrestrial insect biomass than fish in streams with lower metal concentrations (Kraus et al. 2016). We attributed this to an increased reliance on terrestrial prey as the availability of aquatic insect prey, especially large-bodied mayflies, decreases with increasing metal concentrations. As a result of the increased use of terrestrial prey, fish populations are maintained at similar densities in clean and moderately contaminated streams. All fish are extirpated from heavily contaminated streams, however, due to direct effects of metals on fish physiology and cellular functioning (i.e., aqueous Zn concentrations 132–7770 μg/L and Cu 78–497 μg/L; Kraus et al. 2016).

Environmental context often determines responses to pollution (Clements et al. 2016). The most common salmonids we studied (brown trout and brook trout) are less sensitive to the direct effects of metal contamination than the aquatic insect community as a whole. Aquatic insect production drops steadily over this metal gradient, and community composition generally shifts from a more diverse assemblage consisting of mayflies, stoneflies, caddisflies, and true flies to a less diverse community dominated by dipterans (true flies) and caddisflies (Clements et al. 2000; Kraus et al. 2014a). However, the trout studied show a threshold response to metals; fish are present at similar densities from low to moderate contamination but at high levels are totally absent. Furthermore, the year 1–3 fish we studied are not large enough to be piscivorous and were generalist insectivores. As a result, they are able to respond to decreased availability of aquatic insect prey by shifting to a diet higher in terrestrial insects. In other words, they are more likely to suffer from a lack of prey than a direct exposure stress (Clements and Rees 1997; Kraus 2019; Kraus 2019). Finally, focal streams are mostly low order, which often receive proportionally more terrestrial inputs than larger streams and rivers (Collins et al. 2016). Salmonids tend to be more supported by local terrestrial production in these streams than further downriver as stream order increases (Wipfli and Baxter 2010; Collins et al. 2016).

4.2 Effect of Metals on Aquatic Prey Subsidies to Terrestrial Consumers

Riparian insectivores are not as directly impacted by aqueous metal exposure in the same way as aquatic insectivores living in contaminated water area, but terrestrial consumers can be affected indirectly through aquatic-terrestrial food web linkages. For example, aqueous metals alter the biomass and taxonomic composition of aquatic insect resource subsidies to terrestrial consumers, which can change consumer population densities and their feeding behavior (Paetzold et al. 2011; Kraus et al. 2014a). In another study of streams in the Colorado Rocky Mountains, we found that biomass of emerging adult aquatic insects declines 97% over a gradient in stream metal concentrations, even at concentrations too low to affect larval densities (Schmidt et al. 2013; Kraus et al. 2014a). This decline in resource availability impacts riparian consumer communities. Riparian spider standing biomass declines with reduced biomass of adult aquatic dipterans but is unrelated to metal concentrations or to the flux of metals in aquatic prey (Kraus et al. 2014a). Similarly, bats feed less frequently above streams impacted by metals, presumably because of lower aquatic prey availability (Fig. 4; Heiker 2017).

4.3 Metal Bioaccumulation and Transfer Across the Aquatic-Terrestrial Boundary

Aquatic insects excrete trace metals from their bodies before and during metamorphosis from aquatic larvae to terrestrially flying adults and are thus less likely to be a contaminant vector to terrestrial insectivores (i.e., “the dark side of subsidies”; sensu Walters et al. 2008) when trace metals are the primary aquatic pollutant

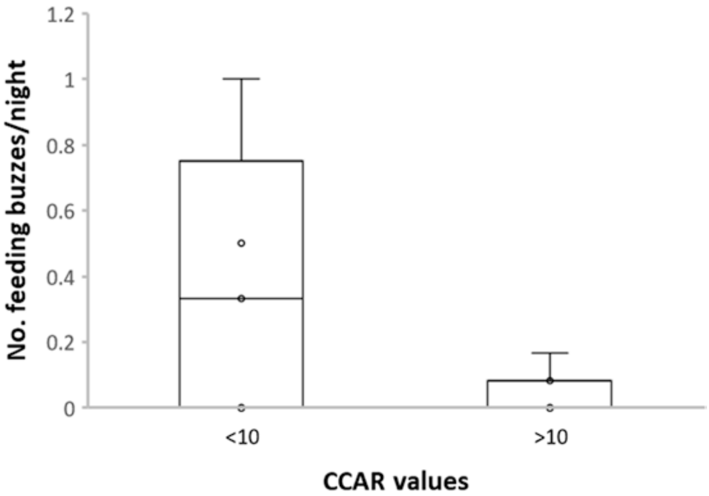

Fig. 4 Changes in *Microtis* bat feeding attempts above streams in the Colorado Mineral Belt (USA). Feeding “buzzes” represent bat sonar pulses that occur as bats approach flying insect prey above a stream reach. CCAR is the chronic criterion accumulation ratio (Schmidt et al. 2011). A CCAR of 1 represents the summed dissolved metal concentration threshold for aquatic life. CCAR values <10 are considered reference to moderately contaminated (N = 5). CCAR >10 are highly contaminated (*N* = 7; Kraus et al. 2014a). Box plots represent the median, 75th quantile, and maximum mean nightly feeding buzzes per stream reach. Circles are values from each stream reach. No feeding buzzes were detected at multiple reaches. (Data are extracted from Heiker 2017)

compared with polychlorinated biphenyls (PCBs) or mercury (Walters et al. 2008; Chumchal and Drenner 2015; Chumchal and Drenner this volume). Insects excrete detoxified metal granules from their gut lumen shortly before or after adult emergence (Kraus et al. 2014a; Wanty et al. 2017; Wesner et al. 2017). Using meta-analysis comparing contaminant concentrations and burdens in larval and adult insects before and after metamorphosis, we estimated that, depending on the metal, between 39 and 94% of trace metal burdens are lost during metamorphosis (Kraus et al. 2014b). This loss leads to a 68% decline in average metal concentrations between larval and adult life stages of insects (Kraus et al. 2014b). On the other hand, some contaminants like PCBs actually increase in concentration across metamorphosis because insects lose 20–80% of their biomass during that time (i.e., bioamplification; Walters et al. 2008; Kraus et al. 2014b).

In addition to losing a large proportion of their metal burdens during metamorphosis, aquatic insects emerging from high-metal streams appear to excrete proportionally more metals than insects from low-metal conditions (i.e., "exposure-dependent transfer"; Lavoie et al. 2013; Kraus et al. 2014b, In Review). As a result, adult aquatic insects from high-metal streams have proportionally lower metal concentrations than from low-metal environments, and metal concentrations in terrestrial insectivore tissues are more similar than expected across environments varying in metal concentrations (McGeer et al. 2003; DeForest et al. 2007; Lavoie et al. 2013; Kraus et al. In Review).

Thus, metamorphosis is not only a life history switch point where insects are able to shed excess trace metal burdens but also an equalizer that causes metal concentrations to be more similar among adult insects than would be predicted from larval concentrations. In streams of the central Colorado Rocky Mountains, we find that concentrations of trace metals (e.g., Cu, Cd, and Zn) in adult insects are similar between high- and low-metal streams even though metal concentrations in larval insects from these or neighboring streams vary from 1 to 3 orders of magnitude (Schmidt et al. 2011; Kraus et al. 2014a, In Review). These patterns explain why riparian consumers of adult aquatic insects (e.g., spiders and birds) had similar tissue metal concentrations across a gradient of stream metal contamination (Custer et al. 2009; Kraus et al. 2014a). They also further support our conclusion that the impacts of aqueous trace metals on linked aquatic-terrestrial food webs mediated by aquatic insects occur mainly through loss of prey biomass.

5 Conclusions and Implications for Restoration, Resource Damage, and Remediation

The patterns and processes described in this chapter have strong implications for management of metal-impacted freshwater ecosystems, specifically for targeting restoration efforts and assessing resource damage and remedy effectiveness in linked aquatic-terrestrial food webs. Trace metal uptake into organisms has taxa-specific effects on survival, reproduction, and bioaccumulation. As a result, aquatic communities and food web dynamics are altered through changes in community composition, animal production, trophic interactions, and food web stability. These impacts have cascading effects on aquatic-terrestrial linkages.

First, loss of mayflies and other sensitive taxa can reduce the aquatic prey base for insectivorous fish. Riparian restoration that leads to increase terrestrial prey input to aquatic ecosystems can subsidize impacted fish populations, especially in moderately impacted streams. For example, terrestrial insect inputs from vegetated riparian areas support fish populations in the metal-impacted Arkansas River and other streams in Colorado (USA; Pomeranz 2015; Kraus et al. 2016). Thus, riparian restoration activities aimed at erosion control may be responsible for the recent designation of Gold Medal Trout Waters status to the Upper Arkansas River. This section of the Arkansas River was previously impacted by AMD and, despite years of restoration efforts, is still subjected to moderate seasonal pulses of elevated dissolved metal concentrations (Clements et al. 2016; Colorado Parks and Wildlife 2014). Ultimately, damage to fish populations may be mitigated in some cases by managing riparian vegetation to maximize terrestrial insect inputs, particularly in areas of low aquatic insect production and relatively high importance of terrestrial inputs to food webs in comparable reference streams (i.e., lower-order streams; Wipfli and Baxter 2010; Kraus et al. 2016).

Second, trace metals are likely to cause declines in aquatic insect resource availability for insectivores and in so doing also reduce a source of aquatic contaminant exposure for those same consumers in scenarios involving contaminant mixtures (Kraus 2019). For example, aquatic mercury contamination of freshwater ponds leads to elevated methylmercury concentrations in riparian spiders mediated by adult aquatic insect mercury transfer (Chumchal and Drenner this volume). If such ponds were also contaminated with trace metals, adult aquatic insect emergence would be reduced, and mercury flux to terrestrial consumers would likely also be lowered. This example also implies that ecological endpoints may be more relevant than exposure endpoints for predicting resource damage associated with trace metal contamination when trace metals are the sole or major pollutant. For example, in a study of adult insect emergence and metal flux from mountain streams, metal flux was highest from the low-metal streams because the biomass of emergent insects was also highest in those streams (Kraus et al. 2014a). Furthermore, Custer et al. (2009) found trace metal concentrations in insectivorous birds around metal- and mining-impacted stream sites in Summit Co., Colorado, USA, were predominantly "at background levels" and lower than those predicted to toxicological effects. However, they did not measure adult aquatic insect production which in a subsequent study showed to be the most likely pathway by which dissolved metals impacted riparian insectivores living near those streams (Kraus et al. 2014a). In contrast to organic contaminants, such food web metrics are more likely to reveal the actual impacts of metal contamination on terrestrial consumers than internal concentrations.

Finally, riparian consumers are increasingly being used to monitor aquatic ecosystem health. Trace metals are lost during metamorphosis and show lower transfer to riparian habitats from high-metal streams. Thus, the ability to use tissue concentrations of riparian consumers as an indicator of remedy or restoration effectiveness is compromised for many trace metals. Patterns of accumulation of some persistent organic pollutants have been used to determine the effectiveness of aquatic remedies (i.e., dredge and cap practices) in slowing or eliminating the uptake of these pollutants into wildlife (Kraus et al. 2017; Walters et al. 2018). However, such a strategy would be inappropriate for metals that are lost during insect metamorphosis and lost during trophic transfer, especially when they are lost in an exposure-dependent manner. Larval stages of aquatic insects could be a more appropriate endpoint for such monitoring, but even in that case, there are many caveats (see Adams et al. 2011).

Trace metals have been long known to have strong ecological impacts on communities and ecosystems because of their toxicological effects. Because of the metabolic regulation of these metals by many organisms, however, the accumulation patterns are often not straightforward. Effects of contaminants on ecosystems can be underestimated if focus is placed on contaminant bioaccumulation or even direct toxicological effects but excludes cascading ecological impacts propagated by direct and indirect effects of metal exposure (McGeer et al. 2003; Rohr et al. 2006; Adams et al. 2011; Ankley et al. 2010; Kraus 2019). Because attempts to restore ecosystem function after contamination often involve a strong focus on restoring physical habitat (Palmer et al. 2010; Montoya et al. 2012), the role of food availability or prey sensitivity to exposure in driving responses of focal consumers such as fish and birds can be overlooked (Fleeger et al. 2003; Rohr et al. 2006; Clements and Rohr 2009). We suggest that future research on trace metal pollution at the land-water interface should focus on ecological endpoints and, in particular, food web processes and cross-ecosystem linkages that are indirectly impacted by direct effects of metal contamination on resources.

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Metamorphosis and the Impact of Contaminants on Ecological Subsidies

Jeff Wesner, Johanna M. Kraus, Brianna Henry, and Jacob Kerby

> *When the germ cells change, that is evolution; when the bodies change, that is metamorphosis.*
>
> Wald (1981)

1 Introduction

Metamorphosis is a significant reorganization of an organism's body plan during development (Truman and Riddiford 1999; Hodin 2006). This reorganization results in substantial differences in morphology between life stages and has evolved in at least 13 phyla or subphyla, including insects, amphibians, plants, fish, fungi, algae, and marine invertebrates (Wald 1981; Werner 1988; Truman and Riddiford 1999; Hodin 2006). In freshwater ecosystems, insects and amphibians are the most conspicuous organisms that undergo metamorphosis. The immature larval or juvenile stages of insects and amphibians are typically fully aquatic, while the reproductive adult stages are terrestrial or semi-aquatic. This shift in body plan and habitat allows insects and amphibians to exploit diverse food sources and habitats, such as temporary ponds and intermittent rivers, and supports dispersal (Müller 1974; Wilbur 1980; Wald 1981; Lancaster and Downes 2013).

J. Wesner (✉)
Department of Biology, University of South Dakota, Vermillion, SD, USA
e-mail: Jeff.Wesner@usd.edu

J. M. Kraus
U.S. Geological Survey, Columbia Environmental Research Center, Columbia, MO, USA
e-mail: jkraus@usgs.gov

B. Henry
Department of Biology, University of South Dakota, Vermillion, SD, USA

Natural Resources Conservation Service, Washington, DC, USA

J. Kerby
Department of Biology, University of South Dakota, Vermillion, SD, USA

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These benefits come at a cost, however. Metamorphosis is a physiologically stressful event (Heyland and Moroz 2006; Campero et al. 2008), and organisms undergoing metamorphosis often succumb to the pressures of additional ecological stressors such as contamination (Hodin 2006; Wesner et al. 2014; Debecker et al. 2017) and predation (Oliver 1971; Arnold and Wasserug 1978; Crump 1984; Planes and Lecaillon 2001; Campero et al. 2008; Merritt et al. 2008). For example, insects stressed by contaminants and fish chemical cues as larvae die during metamorphosis (Hatakeyama and Yasuno 1981; McCauley et al. 2011; Wesner et al. 2014; Debecker et al. 2017), and garter snakes prey on metamorphosing frogs to take advantage of the frogs' limited movement during metamorphosis (Arnold and Wasserug 1978). Even in the absence of other stressors, metamorphosis can have sublethal (Campero et al. 2008) effects. Morphological asymmetry increased in damselflies following metamorphosis, even when the larvae were not exposed to other environmental stressors (Campero et al. 2008).

Metamorphosing organisms such as insects and amphibians are central to the recent emphasis in ecology on cross-ecosystem linkages (Polis et al. 1997; Baxter et al. 2005; Marczak et al. 2007; McCoy et al. 2009; Gounand et al. 2018). Specifically, aquatic insects and amphibians bring nutrients and energy obtained in the aquatic ecosystem to the terrestrial ecosystem (Jackson and Fisher 1986; Werner 1988; Nakano and Murakami 2001; Baxter et al. 2005) when they transition from water to land during metamorphosis. This counteracts the unidirectional flux of passive inputs from the surrounding terrestrial landscape via leaf fall, terrestrial invertebrates, and nutrients (Hynes 1975; Vannote et al. 1980; Kraus et al. 2011). For example, Gounand et al. (2018) estimated that insects, amphibians, and fish export roughly 6% of annual freshwater gross primary production to terrestrial ecosystems each year, resulting in a flux of ~3.6 gC/m^2/year. As a result, mortality of larval organisms can have impacts that extend across ecosystem boundaries by impacting both the donor aquatic food web and the recipient terrestrial food web (Baxter et al. 2005).

Mortality during metamorphosis ((e.g., death as pupa or subimago versus death as pre-metamorphic larva) may disrupt relationships between aquatic juvenile and terrestrial adult insect densities (Wesner 2019). For example, increased pupal mortality may not substantially alter estimates of aquatic juvenile densities or production, particularly in populations of mixed cohorts, because pupae often comprise a small percentage of total juvenile insect standing stock. As an example, if 50% of pupae die, but they represent only 4% of the total aquatic population at any given time, then the high mortality rate of pupae would have only a minimal effect on juvenile insect standing stock (2% reduction). However, it would have a large effect on subsequent adult populations, reducing them by the same 50%. Adult but not juvenile populations of mayflies, damselflies, and amphibians declined when aquatic life stages were exposed to elevated levels of zinc (Wesner et al. 2014), pesticides (Rohr et al. 2006; Debecker et al. 2017), predators (Warmbold and Wesner 2018), or temperature (Debecker et al. 2017).

As with insects, metamorphosis also represents a likely bottleneck between the densities of aquatic and terrestrial life stages of amphibians, in which the success of metamorphosis is strongly tied to tadpole condition. For example, larval amphibians (aka tadpoles) are known to modify timing of metamorphosis in response to surrounding conditions (Wilbur and Collins 1973). A long-term population study on wood frogs found that tadpoles that began metamorphosis at a later date and larger size were better equipped to survive as terrestrial juveniles (Berven 1990). Even in the absence of lethal effects on tadpoles with contaminant exposure, a shift to earlier metamorphosis could lead to sublethal effects that can carry over to the terrestrial juvenile and adult stages.

The above examples demonstrate the importance of stage-dependent mortality in insects and amphibians for understanding cross-ecosystem interactions. In this chapter, we summarize evidence from laboratory and field studies that document the sensitivity of metamorphosing organisms to aquatic contaminants. We then discuss the implications of enhanced mortality during metamorphosis for the ecology and conservation of linked freshwater-terrestrial ecosystems.

2 Sensitivity of Animals to Contaminants During Metamorphosis

To examine how metamorphosis affects survival of animals with complex life histories exposed to contaminants, we surveyed the literature for ecotoxicological studies that exposed larval insects and amphibians to a gradient of contaminant concentrations and measured survival at different life stages before and after metamorphosis. We only included studies that measured both the proportion of larvae that survived *to* metamorphosis (e.g., survival to the pupal stage in holometabolous insects or the wingpad stage in hemimetabolous insects) and the proportion of larvae that survived *through* metamorphosis (e.g., successfully completed metamorphosis to the reproductive adult stage). We then plotted the proportion of larvae surviving to each stage across the contaminant gradient reported in each paper and visualized the shape of the dose-response curve using generalized additive modeling via the *gam* function in *ggplot2* (Wickham 2009) in R version 3.4.2 (R Core Team 2017). Generalized additive models use smoothing functions to fit curves to bivariate relationships and are ideal for visualizing trends in nonlinear data (Hastie 2017). Our analysis provides a visual comparison of how responses may differ when measured during or after metamorphosis within a given study.

In total, we surveyed ~50 papers on insects and 65 papers on amphibians, but only six papers (all on insects) fit our criteria of reporting survival both *to* and *through* metamorphosis (Table 1). The remaining papers reported the percentage of insects or amphibians exposed to contaminants that completed metamorphosis or time to metamorphosis but did not report survival through larval stages. For amphibians, one study reported growth during the larval period and through metamorphosis but did not measure survival through these stages (Chelgren et al. 2006). Without information on survival through specific metamorphic stages (e.g., proportion of

Table 1 Summary of study designs depicted in Fig. 1, including the species and families used (Taxon), contaminants (Cont.), range of dose concentrations (Dose range), age of larvae when first exposed (Age), maximum length of exposure in days (Days), and our interpretation of the shape of the dose-response curves between insects that survived up to metamorphosis and those that successfully completed metamorphosis

							Effect of concentration on survival to or completion of metamorphosis:	
Study	Fig.	Taxon	Cont.	Dose range	Age	Days	Survival to	Completed
Nebecker et al. (1984)	Fig. 1a	*Clistoronia magnifica* (Limnephilidae)	Cu	0–98 µg/l	5th instar	>7[a]	Linear decline	Concave upward
Nebecker et al. (1984)	Fig. 1b	*Clistoronia magnifica* (Limnephilidae)	Ni	0–3669 µg/l	3rd or 4th instar	>7[a]	Concave downward	Concave upward
Wesner et al. (2014)	Fig. 1c	*Centroptilum triangulifer* (Baetidae)	Zn	0–600 µg/l	20-d	17	No effect	Concave upward
Mebane et al. (2008)	Fig. 1d	*Chironomus dilutus* (Chironomidae)	Pb	0–546 µg/l	1st instar	55	No effect	Concave upward
Soucek and Dickinson (2015)	Fig. 1e	*Neocloeon triangulifer* (Baetidae)	Cl^-	37–700 mg/L	0-d	36	Concave downward	Concave downward
Soucek and Dickinson (2015)	Fig. 1f	*Neocloeon triangulifer* (Baetidae)	NO_4	12.5–200 mg/L	0-d	36	Linear decline	Concave upward
Soucek and Dickinson (2015)	Fig. 1g	*Neocloeon triangulifer* (Baetidae)	SO_4^{2-}	59–1300 mg/L	0-d	56	Linear decline	Linear decline
Sibley et al. (1996)	Fig. 1h	*Chironomus tentans* (Chironomidae)	Zn	0.7–47.9 μmol/g	4	56	Linear decline	Linear decline
Grosell et al. (2006)	Fig. 1i	*Chironomus tentans* (Chironomidae)	Pb	0–724 mg/L	8	27	Linear decline	Linear decline

[a]Could not determine length of exposure from paper. This is a minimum estimate based on an ~8 month development period for this taxon

larvae that survived to adult versus the proportion that survived to pupation), it is impossible to isolate the effects of mortality during metamorphosis from mortality during the larval stage. For example, if adult densities decline with increasing contaminant concentrations, but no information on pupal or wingpad densities is

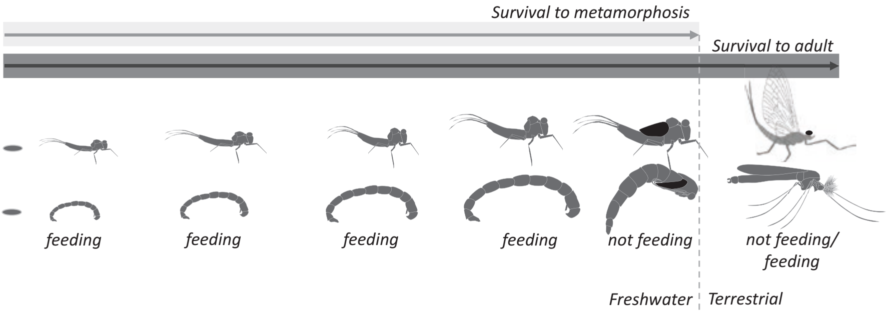

Fig. 1 Metamorphic stages of a hemimetabolous insect (mayfly, top panel) and a holometabolous insect (midge, bottom panel). In hemimetabolous insects, the pre-emergent stage of metamorphosis does not feed and is often identified by the presence of dark wingpads. In holometabolous insects, this stage is marked by a non-feeding pupal stage

presented (Fig. 1), then it is impossible to know whether the decline in emergence is due to death during metamorphosis per se or death during earlier life stages.

The papers we retained were laboratory experiments that reported a total of nine experiments in which aquatic insects were exposed to Pb, Ni, Zn, Cu, NO_4, SO_4, and NaCl (Table 1). All papers tested chronic exposures of larval insects, with experiments lasting until most insects had emerged or died (~7–56 days; Table 1). Several trends are apparent. First, the percentage of insects that successfully completed metamorphosis was lower than the percentage that survived up to metamorphosis across all treatments in all but one study (Grosell et al. 2006). This indicates that even under presumably ideal control conditions, not all insects successfully complete metamorphosis. Metamorphosis appears to be a bottleneck in which conclusions about survival depend on whether an organism completed metamorphosis or not.

Failure to complete metamorphosis is common in nature. In an estimate from one amphibian species, as little as 1–2% of *Hemisus marmoratus* frog eggs survived to metamorphosis (Grafe et al. 2004). Statzner and Resh (1993) estimated that >76% of benthic insect production in streams never emerged as reproductive adults from relatively unimpacted small streams. However, they also urged caution in using emergence as a proxy for estimating larval insect production, due to the variation among sites. Their 95% confidence intervals indicated that the proportion of benthic production that was lost before adult emergence was between 70 and 82%. Our results suggest that this range may be highly conservative and varies widely across contamination gradients (Schmidt et al. 2013). In aqueous exposures to dissolved copper, Nebecker et al. (1984) found that 100% of larvae pupated when exposed to 36 μg/L Cu, but 0% successfully emerged to adulthood (Fig. 2a). In contrast, at control concentrations of copper (0 μg/L), 80% of insects pupated and nearly all successfully emerged as adults (Fig. 2a). While these estimates (and others in our dataset) are not estimates of production per se, it is clear that the proportion of benthic insect production that is lost before emergence is likely to vary far wider than the estimates provided by Statzner and Resh (1993) when contaminated ecosystems

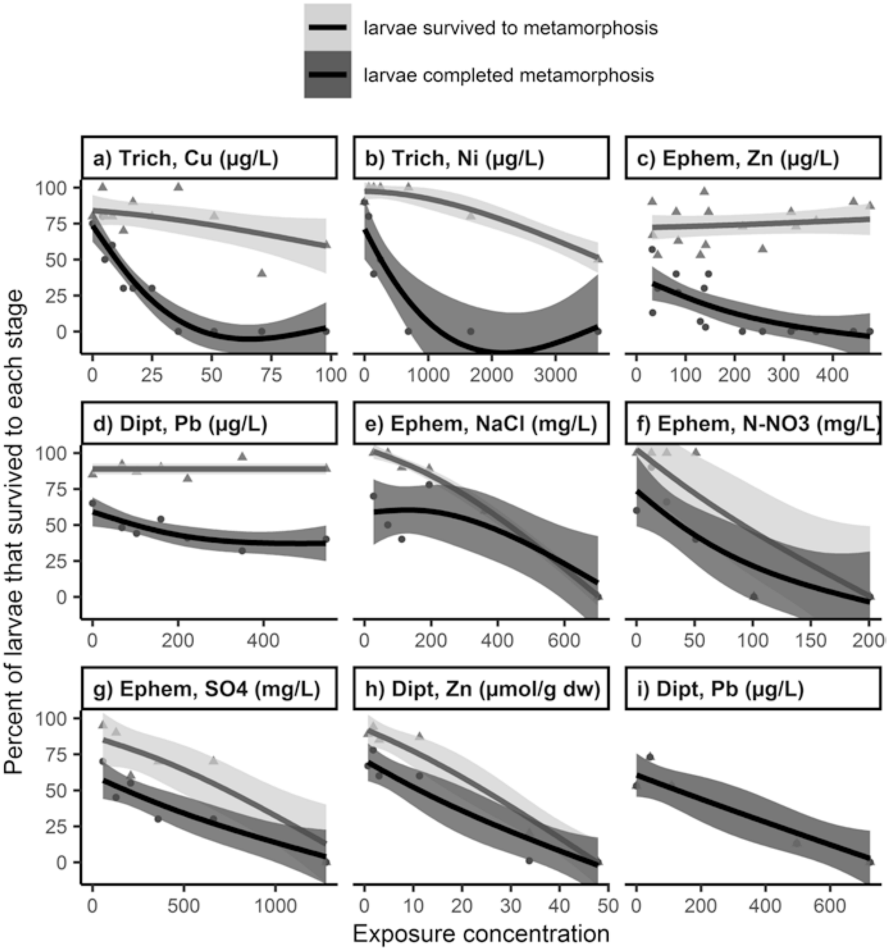

Fig. 2 Response curves of insect survival to two stages across a contamination gradient in laboratory exposures. The y-axis shows the proportion of initial larvae that survived up to at least metamorphosis (light gray, triangles) or the proportion of initial larvae that survived through metamorphosis (dark gray, circles). Lines represent fitted values from generalized additive models. Shading represents 95% confidence intervals. Diverging curves indicate higher mortality (death) during metamorphosis. *Trich* Trichoptera, *Ephem* Ephemeroptera, *Dipt* Diptera

are considered further supporting their caution against using production of either life stage as a proxy for the other, particularly under stressful conditions (e.g., Schmidt et al. 2013).

While survival *to* and *through* metamorphosis generally declined with increasing contaminant concentrations, the shape of these declines differed. The percentage of larvae that survived to metamorphosis was not related to contaminant concentrations in two cases (Fig. 2c, d). In the remaining seven cases, it showed either a concave downward relationship indicating an initial slow decline in percent survival to metamorphosis as contaminant concentrations increased followed by high mortality at high contaminant concentrations (Fig. 2b, e), or a negative linear relationship indicating a constant decline in survival with increasing contaminant concentrations (Fig. 2a, f, g, h, i). In contrast, the percentage of insects that survived through metamorphosis declined with increasing contaminant concentrations in all cases. Five of those cases showed concave *upward* relationships between survival and concentration (Fig. 2a–d, f) indicating rapid mortality at low contaminant concentrations. In four of those cases (Fig. 2a–c, f), the rapid decline stopped only when survival reached zero percent. These patterns indicate greater sensitivity of metamorphosing organisms to contaminants, due either to direct toxicity during metamorphosis or to failed metamorphosis after exposure to contaminants in the larval stages.

While our graphical comparison is clearly limited by number of studies (n = 6), contaminants (n = 7), and taxa (n = 3 families from 3 orders), it is notable that the most strikingly divergent patterns in survival between life stages (Fig. 2a–e) came from four different studies representing the effects of five contaminants (Cu, Ni, Zn, Pb, and NaCl) on three insect orders: caddisflies (Nebecker et al. 1984), mayflies (Wesner et al. 2014; Soucek and Dickinson 2015), and chironomids (Mebane et al. 2008). This suggests that the sensitivity of metamorphosis to contaminants is potentially widespread among insect taxa.

3 Consequences of Sensitive Metamorphosis for Ecology and Conservation

The potential decoupling of larval and adult survival across gradients of aquatic contaminant concentrations has important implications for the interpretation of ecological patterns in aquatic and terrestrial ecosystems (Wesner 2019). An implicit assumption in many studies of cross-ecosystem linkages via insect or amphibian emergence is that abundance of one life stage can serve as a proxy for estimating abundance of the second life stage. That is, a reduction in the benthic production of larvae indicates a proportional reduction in the emergence production of adults, or vice versa (Statzner and Resh 1993; Vonesh and De la Cruz 2002; Grafe et al. 2004; Greenwood and McIntosh 2008; Gratton and Vander Zanden 2009). This assumption appears valid in pristine habitats and across broad differences in larval production (i.e., there are likely more emerging adults from a benthic population of 10,000 individuals/m^2 than from a population of 100 individuals/m^2). However, under stressful environmental conditions, high and variable mortality of insects and amphibians *during* metamorphosis may disrupt the relationship between larval and adult stages (Smith 1987; Schmidt et al. 2013; Wesner et al. 2014). Understanding at which developmental stage mortality occurs prior and during metamorphosis can be key to understanding dynamics of linked aquatic-terrestrial ecosystems.

In addition, stage-dependent mortality, in which mortality rates differ among ontogenetic stages, can have important implications for understanding how contaminants affect ecological interactions within and across ecosystem boundaries (Schreiber and Rudolf 2008; Miller and Rudolf 2011; Wesner 2019). For example, larval, pupal, and adult stages of aquatic insects are ecologically distinct; larvae are aquatic and feed on detritus, algae, or prey in benthic habitats; pupal (or wingpad) stages are aquatic but do not feed; and adults are terrestrial and, in many common taxa, do not feed (Oliver 1971; Lancaster and Downes 2013). As a result, a contaminant that kills non-feeding pupal or adult stages would have limited indirect effects on lower trophic levels because those stages have no feeding links in the aquatic food web.

Failure to include metamorphosis may also introduce unintended bias in laboratory ecotoxicology tests. Laboratory toxicity tests used to define water quality criteria are typically short term and focused only on larval survival. Of those that measure survival to adulthood as an end point, most only record survival as a binary in which organisms either did or did not survive to adulthood. However, because death during any larval stage will reduce survival to adulthood, end points of adult emergence do not provide information on survival through metamorphosis. Brix et al. (2011) reviewed 32 studies of insect responses to chronic exposure to metals (dietary and/or dissolved exposures). Of those, nine measured emergence as an end point, but only one specifically measured death during metamorphosis by noting death of chironomid pupae in response to copper exposure (Hatakeyama and Yasuno 1981). Notably, while only a small number of insects died at low copper concentrations, those that did all died in the pupal stages rather than earlier larval stages. At higher copper concentrations, both larvae and pupae died.

Despite the dearth of knowledge of metamorphic effects of contaminants in general, for endocrine-disrupting chemicals (EDCs), there is a significant focus on the impacts of these contaminants on amphibian metamorphosis. In fact, a key regulatory test often recommended by the EPA is the Amphibian Metamorphosis Assay (AMA) which screens for particular chemical effects related to endocrine-disrupting chemicals (US EPA 2011; Miyata and Ose 2012). This test is recommended because many EDCs are known to impact the thyroid systems of amphibians, which are critical to their metamorphosis (Marlatt et al. 2013). Known EDCs such as bisphenol A are associated with a host of negative effects on frog metamorphosis (Goto et al. 2006). Other chemicals such as triclosan have mixed results; in the model EPA species, *Xenopus laevis*, there were no significant effects (Fort et al. 2009), while in an ecologically relevant North American species, *Pseudacris regilla*, there are strong negative impacts to their morphology (Marlatt et al. 2013).

Understanding how contaminants affect the success of metamorphosis in organisms is important for interpreting field-based biomonitoring. The use of field-collected freshwater invertebrates in biomonitoring is common globally, including in the United States, where most states have developed monitoring programs based on freshwater invertebrates (Carter et al. 2006). A broad array of metrics has been developed to describe invertebrate communities (Bonada et al. 2006), but the most common are often insect-only metrics focused largely on mayflies (Ephemeroptera, E), stoneflies (Plecoptera, P), and caddisflies (Trichoptera, T) such as EPT richness, percent EPT, percent ephemeropterans, and ephemeropteran richness (Carter and Resh 2013). Such metrics provide valuable information on the structure and composition of benthic invertebrate communities. However, these metrics focus on only the larval stages of organisms, meaning they do not include metamorphosis. If metamorphosis is a substantial source of mortality in insects and amphibians, then it may be difficult or impossible to use benthic samples of larvae to predict adult emergence, and vice versa, particularly when organisms are under stress (Schmidt et al. 2013; Wesner 2019).

4 Limitations and Recommendations for Future Research

A clear deficit in the study of metamorphosis and contaminants is the relative lack of field or mesocosm studies (but see Kotalik et al. this volume). All the studies included in our literature review were controlled laboratory manipulations. Very few studies in the field or in mesocosms directly quantify stage-dependent mortality. Such a study would be most tractable in mesocosm experiments in which organisms are exposed to environmentally relevant contaminant concentrations for at least a full life cycle, and in the presence of more complex communities, including predators, resources, and multiple taxa.

Mesocosm studies may be more common with amphibians, where one early estimate stated that 10/60 amphibian ecotoxicology studies were mesocosm based (Boone and James 2005), with many studies focused on the timing of metamorphosis as a response variable. This approach was pioneered by students of the late Ray Semlitsch who examined a wide range of chemicals on Missouri amphibians in mesocosm and field settings. Most typically, amphibians would metamorphose earlier and at a smaller size when exposed to relatively high concentrations of contaminants to escape the stress of the contaminant. This pattern was found for metal exposures such as cadmium (James et al. 2005; James and Semlitsch 2011) and for insecticides such as atrazine and chlorpyrifos (Britson and Threlkeld 1998; Langlois et al. 2010). Yet in other insecticides, such as carbaryl and malathion, amphibians grew larger than controls and metamorphosed later (Boone and Bridges 2003; Boone and Bridges-Britton 2006; Boone et al. 2007; Boone 2008). These counterintuitive effects are posited to be due to an insecticide-caused reduction in invertebrate competitors (Mills 2002). Intriguingly, while nearly all these studies provide cumulative measures of effects, they do not examine effects at multiple stages. Therefore, it is difficult to discern when mortality occurs and whether it is happening solely at the early tadpole phase, or just prior to metamorphosis. Regardless of the direction, these shifts in metamorphic timing are likely to have important impacts to the aquatic and terrestrial ecosystems these organisms inhabit. The availability of larger tadpoles for a longer period of time or smaller emerging metamorph froglets has clear implications for the predators in each system and the transport of nutrients and contaminants across ecosystems.

Although the patterns of survival across contaminant gradients shown in Fig. 2 come from laboratory exposures under highly controlled conditions, they are also reflected in field surveys. For example, adult aquatic insects emerging from subalpine streams in the central Colorado Rocky Mountains showed a strong negative response to increased stream metals at levels that only slightly reduced abundance of larval insects in the same region (Schmidt et al. 2013; Kraus et al. 2014). As a result, the proportion of insects predicted to survive through metamorphosis relative to larval density was not constant but shifted over the metal gradient. For example mayfly, caddisfly, and stonefly (EPT) proportion emerging decreased rapidly and then increased slightly after the aquatic life criteria threshold was reached (Schmidt et al. 2013).

However, caution is needed when comparing field and laboratory results (Clements et al. 2013; Iwasaki et al. 2018; Kotalik et al. this volume; Bundschuh and Schulz this volume). Laboratory studies test one species at a time or in natural assemblages representing a subset of the full community (Clements et al. 2013; Wesner et al. 2014; Soucek and Dickinson 2015; Rogers et al. 2016; Wesner et al. 2017). End points include proportion surviving through metamorphosis, timing of metamorphosis, and adult size and fecundity. In the field, populations represent multiple cohorts and sizes of individuals that were oviposited into or colonized later the habitat from which they emerged. These populations could be adapted to local conditions, having been exposed to whatever contaminants are present throughout their life cycle and are impacted by other stressors and resource conditions at the site. Also, their population densities are driven by immigration and emigration, not just birth and death. In the field, end points include number and biomass of adults emerging over a certain time period (e.g., 48 h or 4 days), rather than over an entire experiment as in the laboratory. Traps in the field are often set to maximize production (i.e., are set over pools, Iwata 2007) and can be biased toward taxa emerging over the surface of the water (midges and mayflies, instead of stoneflies and dragonflies, Cadmus et al. 2016). Finally, timing of metamorphosis is less frequently monitored in the field and can be strongly impacted by other variables such as temperature (Uno and Power 2015) and species identities.

For plastic life history switch points like metamorphosis, differences among laboratory and field studies in test populations, timing of exposure, and presence of other stressors (including density) can have large impacts on timing, size, and possibly survival through metamorphosis (Wilbur 1980; Vonesh and Osenberg 2003; Tüzün and Stoks 2017). Perhaps most importantly, disparate exposure regimes and population histories can lead to divergent emergence strategies for coping with or responding to contaminants. For example, early emergence can be a phenotypic response to a novel stressor (i.e., escape in space) and a sign that animals have favorable enough conditions to grow to the minimum size required for metamorphosis (Wilbur and Collins 1973; Wilbur 1980). In the laboratory, animals that are exposed to contaminants at later life stages may show earlier emergence times because they are already past the minimum size and the abrupt change in environmental conditions prompts them to “escape” into adulthood. On the other hand, field populations in contaminated conditions may be exposed to suboptimal conditions for all of their larval period. This difference may lead to stronger numerical responses in emergence in the field and possibly more shifts in timing of emergence under standard laboratory conditions.

Although field collections might lend themselves to more realism, there are drawbacks to correlative studies that can be balanced out by comparing them with controlled laboratory experiments (Bundschuh and Schulz this volume). For example, in addition to allowing conclusions about causes of mortality, laboratory studies can guarantee that individuals from the same populations and species are being compared as adults and larvae. In the field, adults and larvae may not even be collected in the same year (e.g., Schmidt et al. 2013). These benefits from utilizing both field and laboratory data to derive conclusions about the potential differential effects of stressors on survival to and through metamorphosis can best be realized when emergence and larval results are reported in a comparable manner. For example, calculating the proportion of individuals surviving to and through metamorphosis, as we present here, provides an intuitive metric that facilitates direct comparisons among studies and between laboratory and field outcomes. Furthermore, presenting response curves on similar scales (i.e., scale of analysis vs. scale of the data) is crucial when making these comparisons because scale alters the perceived shape of responses and can obfuscate similarities. For example, in Schmidt et al. (Schmidt et al. 2013), field data are shown on the log-log scale, which linearizes nonlinear relationships like those presented in this chapter (e.g., *concave up*, in Fig. 2). Ultimately, more laboratory and field results are needed to fully test our hypotheses about larval and adult responses. Given the relative paucity of research that directly compares responses of larval and emerging insects to stressors in either the field or the lab, there is a clear need to conduct more studies in such a way as to make these comparisons possible.

5 Conclusions

Despite recognition of the importance of metamorphosis in organism life histories (Wilbur 1980; Werner 1988; Polis et al. 1997), its explicit inclusion in empirical ecotoxicology studies has often been overlooked as ecologists tend to focus on species or on single stages of organisms within specialized habitats such as freshwater, riparian, pelagic, and benthic (Polis et al. 1997; Doherty et al. 2004; Hodin 2006). As we have discussed in this chapter, explicit consideration of metamorphosis, and the stage-specific metrics that it entails, has the potential to strongly alter conclusions about contaminant effects that are derived from only a single life stage. Incorporating metamorphosis in field and laboratory studies is needed to derive common patterns and identify areas where conclusions based on single life stages fail or succeed. To date, only a handful of laboratory studies (and a single field study, Schmidt et al. 2013) have explicitly measured organism responses to contaminants in different stages of metamorphosis. There is a clear opportunity for ecologists to explicitly consider metamorphosis in studies of contaminants. Doing so will benefit future bioassessment protocols (Kotalik et al. this volume) and will help to resolve the complexity inherent in predicting how contaminants affect aquatic-terrestrial food webs.

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Part III
Other Global Stressors

Variables Affecting Resource Subsidies from Streams and Rivers to Land and their Susceptibility to Global Change Stressors

Jeffrey D. Muehlbauer, Stefano Larsen, Micael Jonsson, and Erik J. S. Emilson

> *The importance of reciprocal resource subsidies between habitats indicates that the loss or degradation of one habitat may have more detrimental effects on neighbouring communities than we have previously recognized.*
>
> (Nakano and Murakami 2001)

1 Introduction

The observation that organisms can cross ecosystem boundaries and that biological energy can therefore be transferred between adjacent ecosystem food webs is not new. In fact, recognition of such exchanges pre-dates the emergence of ecology as a discipline (see, e.g., Darwin 1839 for discussion of beetles at sea). Quantification of the magnitude of these exchanges is also well-established, and it has been nearly a

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J. D. Muehlbauer (✉)
U.S. Geological Survey, Southwest Biological Science Center, Grand Canyon Monitoring and Research Center, Flagstaff, AZ, USA
e-mail: jmuehlbauer@usgs.gov

S. Larsen
Department of Civil, Environmental and Mechanical Engineering, University of Trento, Trento, Italy

Computational Biology Unit, Fondazione Edmund Mach, San Michele all'Adige, Italy
e-mail: stefano.larsen@fmach.it

M. Jonsson
Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden
e-mail: micael.jonsson@umu.se

E. J. S. Emilson
Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, ON, Canada
e-mail: erik.emilson@canada.ca

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century since the first study to make such measurements was published (Summerhayes and Elton 1923). Over the past few decades, however, research in this area has gained an increased level of scientific interest, rigor, and nuance (Polis and Hurd 1995; Nakano and Murakami 2001; Sabo and Power 2002). Now united under the term "subsidies," defined as the transfer of a donor-controlled, biologically fixed energy source from one ecosystem to another that augments consumer populations (Polis et al. 1997; Richardson et al. 2010), such research has burgeoned to the point where it has become a mainstay of ecology (Polis et al. 2004).

Aquatic resources can travel from streams and rivers (hereafter lotic ecosystems) to land, particularly as biologically fixed energy in the form of emergent aquatic insects (Richardson et al. 2010). The magnitude of this subsidy can be large and also of higher nutritional quality relative to energy available from within the terrestrial ecosystem (Schindler and Smits 2017), as exemplified even by the earliest investigations of emergent insect energy flux from lotic ecosystems (e.g., 20 $g \cdot m^{-2} \cdot year^{-1}$ in one desert stream; Jackson and Fisher 1986). Nonetheless, lotic subsidies have historically been depicted as unidirectional in the opposite direction (land–lotic), with leaves, sediment, and nutrients being transferred from the upland and riparian ecosystems into the lotic environment (e.g., Leopold et al. 1964; Hynes 1975; Vannote et al. 1980; Caraco and Cole 2004). In this paradigm, lotic–land subsidies were largely ignored.

More recently, the paradigm of subsidy research in lotic ecosystems has shifted, and substantially more research is now directed at what are referred to as bi-directional resource exchanges between lotic and terrestrial ecosystems (Nakano and Murakami 2001), with lotic–land subsidies gaining increasing prominence (Power et al. 2004). In fact, several review papers have recently synthesized research related to aquatic resource transfer into terrestrial ecosystems, particularly by emergent insects (Baxter et al. 2005; Ballinger and Lake 2006; Marczak et al. 2007b; Paetzold et al. 2007; Gratton and Vander Zanden 2009; Richardson et al. 2010; Marcarelli et al. 2011; Parkyn and Smith 2011; Bartels et al. 2012; Richardson and Sato 2015; Schindler and Smits 2017). These reviews all demonstrate the potential for subsidies from lotic ecosystems to significantly affect terrestrial food webs.

In spite of these recent reviews, the rationale for when, where, and why lotic–land subsidies are important to terrestrial food webs lacks broad theoretical synthesis (but see, e.g., Leroux and Loreau 2008 for how subsidies in certain locations may influence trophic cascades). With this in mind, our first objective is to formulate and present a comprehensive list of biotic and abiotic variables and their interactions that may logically affect lotic–land subsidy magnitude, transmission distance into terrestrial ecosystems, and utilization by consumers. We focus predominantly on resource subsidies in the form of emergent aquatic insects to terrestrial arthropod predators because most studies in the literature have focused on these taxa.

After developing this list, our second objective is to explore how these variables and linkages may be affected by stressors, specifically by broad-scale drivers of global change. Recent research has highlighted the potential importance of stressors, and in particular multiple stressors, in altering the dynamics of lotic and adjacent terrestrial ecosystems (Tockner et al. 2010). Some research does exist on how stressors such as nonnative species introductions, nutrient enrichment, and land use affect lotic–land subsidies (e.g., Baxter et al. 2004; Davis et al. 2011; Carlson et al. 2016); however, such stressors tend to be treated in isolation and we lack a general framework for addressing how multiple stressors may impact these subsidies. We therefore apply the match-mismatch framework proposed by Larsen et al. (2016) to our list of variables, and describe how the influence of multiple stressors may lead to asynchronies between subsidy resources and consumers across gradients of time, space, or magnitude. Throughout the remainder of this chapter we use the term stressors to mean novel drivers that are exogenous to our list of variables and that alter subsidy dynamics by affecting these variables in some way. We focus specifically on global change-related stressors that can interact with contaminants to influence subsidies: climate change, land-use conversion, damming and water abstraction, and species invasions and extinctions, which inherently represent the cumulative interaction of multiple stressors acting in concert.

2 Variables Affecting Lotic–Land Subsidies

The following variables are thought to be the major factors affecting subsidies from lotic to terrestrial ecosystems (Table 1). In cases where their scaling and dimensionality is inconsistent throughout the literature (e.g., "aquatic productivity," which can mean primary or secondary production, and can be calculated on different spatiotemporal scales), variables are included qualitatively; in others where quantification is more straightforward (e.g., bank height), variables are more rigidly defined. Variables are generally approached as predictors in a model, and regression-related terminology such as "factor" and "interaction" is used throughout.

2.1 Production

Some assessment of aquatic productivity is common in many studies of lotic–land subsidies (Marczak et al. 2007b), and it is reasonable to assume that more productive ecosystems should have more energy and nutrient resources available for export as subsidies (but see, e.g., Kraus and Vonesh 2012; Scharnweber et al. 2014 for discussion of aquatic subsidies recycling terrestrial carbon). In a general sense, high lotic productivity does seem to exert a strong, positive control on the distance that aquatic subsidies travel through the landscape (Muehlbauer et al. 2014). Floating algal mats, which are patches of locally high primary productivity, may also indirectly promote lotic–land subsidies by acting as "hotspots" of insect emergence (Power et al. 2004) or serving as "launch pads" for newly emerged insects. In the latter case, insects emerging on these mats may be relatively less exposed to terrestrial predators than insects that emerge on the channel banks (Paetzold et al. 2007), potentially affecting the distance that such subsidies travel into the terrestrial landscape before being incorporated into food webs.

Table 1 List of variables potentially affecting the magnitude, transmission distance, or consumer utilization components of lotic–land subsidies, along with the general predicted nature of this effect (i.e., to increase or decrease a given subsidy component, as further described in the available, listed references)

Variable	Effect on subsidy	Key references
Aquatic production	Increase	Jackson and Fisher (1986), Marczak et al. (2007b), Davis et al. (2011), Muehlbauer et al. (2014)
Terrestrial production	Decrease	Hering and Plachter (1997), Henschel et al. (2001), Paetzold et al. (2005), Marczak et al. (2007b)
Dominant aquatic taxa	Varies	Griffith et al. (1998), Paetzold et al. (2006), Finn and Poff (2008), Muehlbauer et al. (2014)
Dominant terrestrial taxa	Varies	Sanzone et al. (2003), Power et al. (2004), Paetzold et al. (2005), Marczak et al. (2007a)
Vegetation density	Varies	Collier et al. (1997), Briers et al. (2002), Petersen et al. (2004), Macneale et al. (2005)
Bank height	Decrease	Paetzold et al. (2008)
Geomorphic complexity	Increase	Iwata et al. (2003), Sabo and Hagen (2012), Muehlbauer et al. (2014), Venarsky et al. (2018)
Lotic ecosystem size	Increase	Henschel (2004), Ballinger and Lake (2006), Gratton and Vander Zanden (2009), Muehlbauer et al. (2014)
Weather/climate	Varies	Briers et al. (2003), Finn and Poff (2008), McCluney and Sabo (2009)
Season	Varies	Nakano and Murakami (2001), Paetzold and Tockner (2005), Marczak and Richardson (2008)

Increased aquatic secondary production—of aquatic macroinvertebrates in particular—provides a more direct mechanism for increasing the magnitude of emergent insect subsidies than increased primary production and should result in terrestrial ecosystems receiving a higher biomass of potential subsidies. In theory, higher lotic secondary production should ultimately lead to larger-bodied and more abundant insects emerging from the lotic ecosystem and traveling onto the terrestrial landscape, resulting in greater subsidy magnitude (Jackson and Fisher 1986) and potentially longer transmission distances as well. However, this relationship turns out to be multifaceted (Davis et al. 2011; Wesner et al. this volume), as discussed later in the "multivariate interactions" section.

While lotic ecosystem production is thought to generally enhance the magnitude and consumer utilization of lotic–land subsidies, the relative importance of this subsidy to recipient food webs also depends on productivity within the terrestrial ecosystem. This is perhaps best illustrated in cases where terrestrial production of both vegetation and consumers is relatively low (Paetzold et al. 2007). In one such case, riparian beetles derive more than 80% of their energy from subsidies obtained via direct feeding on benthic and emergent aquatic insects (Paetzold et al. 2005). In contrast, riparian beetles in another study of smaller streams that had more dense vegetation (and, consequently, more terrestrial consumers as potential prey) fed primarily on terrestrial prey resources (Hering and Plachter 1997). As such, much as terrestrial leaf inputs are more important to stream food webs when in-stream production is limited (Minshall 1967), aquatic subsidies can be particularly important when productivity in the recipient terrestrial ecosystem is low (Polis and Hurd 1995; Marcarelli et al. 2011).

2.2 Dominant Taxa

The species composition of both lotic and terrestrial communities can influence the magnitude, transmission distance, and consumer utilization of subsidies from lotic to terrestrial ecosystems (Muehlbauer et al. 2014). Aquatic macroinvertebrate taxa emerge at different times of day and times of year, in different densities, and adult body size also varies widely (Jackson 1988). For example, some stonefly species are large-bodied and long-lived, but they emerge fairly asynchronously and in low numbers in winter (Müller 1973). As such, they may represent a large subsidy in individual cases where a single predator eats a single stonefly, but this effect is highly patchy and localized, and the overall food web of a riparian zone may be relatively unaffected by the subsidy. Chironomid midges, in contrast, are small-bodied and short-lived but often emerge in great swarms in summer and can represent a large subsidy to the entire riparian zone (Gratton and Vander Zanden 2009). Some insects also tend to disperse more widely than others to search for food or mates (Macneale et al. 2005; Finn and Poff 2008), and they have the potential to provide a subsidy to terrestrial food webs even at great distances from the lotic ecosystem. Combined, these dynamics affect whether aquatic organisms expend energy to fly far into the terrestrial landscape (Griffith et al. 1998; Finn and Poff 2008) and the spatio-temporal dynamics of where and when the aquatic subsidy resource is available to predators.

The structure of terrestrial communities receiving subsidies is also important (Sanzone et al. 2003), as they are ultimately responsible for how much aquatic biomass gets incorporated into the terrestrial food web. For instance, if terrestrial predators are predominantly water surface or ground-dwelling (Paetzold et al. 2005; Marczak et al. 2007a), then many insects may be consumed at emergence, making the subsidy effect highly concentrated at the bank. Similarly, arboreal predators living in the overhanging vegetation surrounding streams (e.g., spiders in the family Tetragnathidae) will be more effective at capturing flying insects (Power et al. 2004), so emergent aquatic insects that escape predation by these consumers likely stay lower to the ground and possibly do not travel as far as a result (Didham et al. 2012). Finally, the feeding strategies of some terrestrial taxa make them more reliant on aquatic taxa than other terrestrial organisms: whereas arboreal, web-building spiders can capture and eat any organisms (terrestrial or aquatic) that are caught in their webs, taxa that forage by moving onto exposed cobbles on the water surface are necessarily more limited in their feeding options within that habitat and are more dependent upon lotic–land subsidies (Paetzold et al. 2005; Paetzold et al.

2007). Thus, the relative utilization of the potential subsidy can depend on the adaptations of predators to consume the resource.

2.3 Terrestrial Vegetation Structure

The movement of aquatic subsidies from lotic to terrestrial ecosystems can also be affected by the structure of terrestrial vegetation. Boundaries between vegetation types, such as between poorly vegetated, active floodplain corridors and densely forested uplands, can act as barriers to organism dispersal (Cadenasso and Pickett 2001) and, therefore, the transmission distance and consumer utilization of subsidies (Cadenasso et al. 2004). Such boundaries may also concentrate aquatic subsidies: in one study, a small break in forest cover in the middle of a forested transect between two streams received an anomalously high density of stoneflies relative to their abundance elsewhere along the transect (Macneale et al. 2005). Similarly, the abundance of emergent caddisflies and stoneflies declined across a gradient from open pasture to forest in other studies (Collier et al. 1997; Briers et al. 2002). Additionally, humidity, vertical habitat structure, and potentially other microclimate or habitat gradients provided by vegetation cover may allow certain prey and predator species to persist, facilitating the transfer of subsidy resources at least at the vegetated boundary (Power et al. 2004; Chan et al. 2009; Collins and Baxter 2014). The effect of vegetation on subsidies is therefore complex; nonetheless, dense terrestrial vegetation seems to have a general negative effect on subsidy transmission distance throughout the landscape (Greenwood 2014).

2.4 Geomorphology

In much the same way that vegetation structure seems to affect the ability of aquatic subsidies to move through the terrestrial environment, physical channel-bank conditions may also act as impermeable barriers to dispersal (Anderson and Polis 2004). Certain aquatic taxa, such as stoneflies, crawl out onto banks immediately prior to emergence as winged adults, and in some cases possess life-history strategies that require them to travel on the ground for long distances away from the lotic ecosystem after metamorphosis (Thomas 1966, 1969; Müller 1973). The presence of a steep bank may result in high mortality for these taxa. Such individuals provide the majority of energy for riparian ground-dwelling terrestrial predator communities dominated by taxa such as by beetles and wandering spiders (Hering and Plachter 1997; Paetzold et al. 2005; Paetzold et al. 2007). It is possible that the fluid dynamics of steep banks carry subsidy resources from the water and aggregate them at the top of the bank (Witman et al. 2004). However, assuming most taxa disperse actively rather than via wind currents, steep banks most likely serve to vertically disconnect terrestrial predators at the ground surface from prey resources at the water surface some distance below, effectively eliminating this subsidy pathway (Muehlbauer et al. 2014). In one study, increased channelization due to flow regulation reduced riparian arthropod densities significantly (Paetzold et al. 2008), although this may be in part a response to increased inundation and may also be due to declines in aquatic species abundance (and, by extension, subsidy magnitude) associated with anthropogenic change in general (Gerken et al. 1991; Greenwood et al. 1995; Violin et al. 2011). Similarly, levees and other geographic features located away from the bank may also prevent lateral subsidy transmission away from the lotic ecosystem. Many taxa do seem to preferentially disperse at the level of the forest canopy, but many others still rely on near-ground dispersal and should therefore be affected by such barriers (Jackson and Resh 1989; Didham et al. 2012). It thus seems likely that this physical connectivity impairment between aquatic and terrestrial ecosystems should adversely affect lotic–land subsidy dynamics, at least in terms of subsidy resources being transmitted beyond a very short distance from the shoreline.

Aside from bank morphology, the physical structure (geomorphology) of the lotic ecosystem itself should also influence subsidy magnitude, utilization by consumers, and possibly transmission distance as well (Muehlbauer et al. 2014). The hydrogeomorphic setting of a stream or river establishes a habitat mosaic that is colonized differently by various taxa (Greenwood et al. 1995; Greenwood and McIntosh 2008). Further, increasingly complex and more sinuous channel morphologies serve to increase stream or river length. At scales on the order of square meters, such complex geomorphology may reduce subsidy magnitude by virtue of diluting emergent aquatic insect densities overall a greater shoreline length (Venarsky et al. 2018). However, on the reach scale, the presence of multiple channels in a stream or river may lead to increased overall levels of subsidy utilization by consumers due to increased physical interaction between aquatic and terrestrial ecosystems (Paetzold et al. 2007). This prediction has been supported by studies of birds feeding on emergent aquatic insects (Iwata et al. 2003; Iwata et al. 2010), by meta-analysis (Muehlbauer et al. 2014), and by mathematical modeling efforts (Sabo and Hagen 2012), although all of these have been based only on varying sinuosity within single-channel streams and rivers and the dilution of aquatic resources across multiple channels may decrease the magnitude of subsidy available to a given individual consumer (Venarsky et al. 2018). Aquatic subsidies have also been shown to be very important to consumer diets in a braided river, which is more geomorphically complex than single-channel streams (Paetzold et al. 2005).

Similarly, channel length-to-width ratios are higher in smaller streams relative to larger rivers, meaning the amount of aquatic-terrestrial interaction along banks is proportionally larger between small streams and adjacent terrestrial zones, aquatic subsidies may be expected to be more important in terms of consumer utilization in these reaches as a result (Polis et al. 1997; Power and Dietrich 2002; Ballinger and Lake 2006). However, larger lotic ecosystems (i.e., higher order streams) should theoretically support greater exports of aquatic subsidies to terrestrial ecosystems (Henschel 2004) based purely on their increased ecosystem size (Post et al. 2007), representing a potentially larger magnitude of subsidy due to the larger area and potential source pool of aquatic resources (Gratton and Vander Zanden 2009). In reality, both assumptions likely hold true to a point (length:width ratio in smaller streams, stream order or ecosystem size in larger rivers), and the interaction of subsidy magnitude and consumer utilization may be such that the overall importance of a subsidy to the recipient ecosystem may be greatest in mid-order lotic ecosystems where the combination of the two is maximized (Muehlbauer et al. 2014).

2.5 Weather and Climate

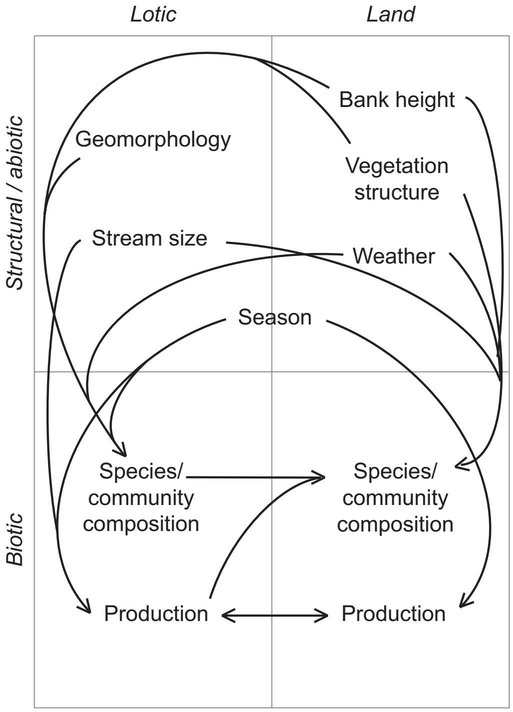
Weather and climate may play a role in affecting lotic–land subsidies, especially with respect to the dispersal of emergent aquatic insects. Strong wind conditions, for instance, can potentially serve to disperse the subsidy resource farther from the lotic ecosystem (den Boer 1990; Witman et al. 2004), potentially making the distribution of the subsidy on land more random (Muehlbauer et al. 2014). In reality, however, the effect of wind on lotic–land subsidies can be variable and is not predictable based on wind speed alone (Briers et al. 2003; Finn and Poff 2008).

Other conditions related to weather and climate, notably temperature, may affect lotic–land subsidies as aquatic resources respond to warmer or cooler conditions. In one study, for example, daytime temperature was correlated with emergent stonefly abundance in terrestrial zones across multiple streams (Briers et al. 2003). However, in a lab setting high air temperatures shortened the lifespan of mayfly adults from a desert stream (Jackson 1988), potentially constraining the temporal availability of this subsidy to terrestrial predators. Likely, increased temperature is beneficial to organism metabolism (and, by extension, emergence, and lotic–land subsidy magnitude) to a certain point (sensu Brown et al. 2004), above which it becomes an impediment to long-term survival.

3 Multivariate Interactions

Many of the variables described above seem to have important effects on lotic–land subsidy dynamics in their own right. However, in many cases the interaction of multiple variables can affect the subsidy in ways that are not predictable based on the independent effect of each variable in isolation. The purpose of this section is to discuss situations in which such interactions are likely to be highly important in affecting lotic–land subsidies (Fig. 1), and to note some of the most commonly described interactions.

Fig. 1 Potential interactions among lotic–land subsidy-related variables. The direction of the arrow indicates the probable direction of the interaction, as discussed in the text



3.1 Productivity Gradients

The difference in productivity between donor and recipient ecosystems is thought to be key in determining the magnitude of a subsidy to recipient ecosystems (Polis et al. 1997). In the case of aquatic subsidies to terrestrial ecosystems, it is common for a substantial portion of emergent aquatic biomass to be comprised of energy that was originally terrestrially derived and is thus "recycled" back to terrestrial ecosystems via these subsidies (Kraus and Vonesh 2012). For example, many aquatic insect larvae consume leaf litter and other terrestrial detritus, then return that energy back to land upon their emergence as winged adults (Kraus and Vonesh 2012; Scharnweber et al. 2014). In this respect, strongly heterotrophic freshwater ecosystems may be incapable of exporting high magnitudes of subsidies if their adjacent terrestrial ecosystems also support low levels of productivity. However, in cases such as larger streams and rivers where the aquatic ecosystem is more autotrophic, or where allochthonous inputs may be coming from farther up in the watershed rather than from the riparian zone immediately adjacent to the water's edge, the interaction of a high-productivity lotic environment with a less productive adjacent terrestrial ecosystem should result in a higher magnitude lotic–land subsidy (Henschel 2004). Although there are exceptions (e.g., Marczak and Richardson

2007), the results of several studies have generally supported this theory (synthesized in Marczak et al. 2007b), and large productivity gradients between lotic and terrestrial ecosystems do seem to set the stage for aquatic subsidies to be important in terrestrial food webs. Further, high lotic ecosystem productivity can lead to high densities (and, in some cases, higher quality, Bartels et al. 2012) of aquatic insect emergence. This large magnitude of subsidy prey resources to terrestrial predators can have cascading effects on terrestrial prey species by relieving some of their predation stress (Henschel et al. 2001; Murakami and Nakano 2002).

In some cases, however, high aquatic productivity can be detrimental to the ability of a lotic resource to subsidize terrestrial food webs, adding nuance to the aquatic-terrestrial productivity interaction. In a study of lotic–land subsidies in a nitrogen-enriched stream, Davis et al. (2011) found that increased stream secondary production resulting from the nutrient enrichment led to an increase in the biomass (subsidy) of emergent aquatic insects. Surprisingly, this increase in prey biomass led to a decline in spider feeding on this subsidy, because the taxa that came to dominate under higher nutrient conditions were too large bodied to be captured by spiders (although it could potentially have led to an unmeasured increase in larger-bodied consumers, such as birds; e.g., Stenroth et al. 2015). Thus, in the case of extremely high ratios of aquatic:terrestrial production, this interaction may actually serve to decrease a subsidy's incorporation into the terrestrial food web. Similarly, from the perspective of subsidies from high aquatic productivity freshwaters having unexpected outcomes for terrestrial food webs, research in mercury-contaminated ponds has shown that nutrient enrichment did increase the biomass of aquatic insect emergence, but this increase in subsidy magnitude came with a concomitant export of methyl mercury (Jones et al. 2013; Chumchal and Drenner this volume).

3.2 Community Composition

The interaction between aquatic and terrestrial organisms in determining the transmission of a lotic–land subsidy is also influenced by taxon or species-level factors. For example, many mayfly taxa emerge from the water as winged adults and fly (albeit weakly) to land directly from the water surface. As discussed earlier, however, many stoneflies crawl out of the water onto land prior to their imaginal molt (Thomas 1966, 1969). Thus, stoneflies, by virtue of this aspect of their life history, are likely to provide more of a subsidy than mayflies to ground-dwelling riparian fauna such as carabid beetles (a common ground predator along banks, Hering and Plachter 1997; Hering 1998). Emergent mayflies and true flies, in contrast, may be more likely to become prey to arboreal, web-building spiders at the water's edge (sensu Sanzone et al. 2003; Raikow et al. 2011). Terrestrial, subsidy-reliant predators are also presumably adapted to effectively capitalize on the aquatic resource (e.g., fewer web-building spiders along a lotic ecosystem dominated by stoneflies). This was supported by one study in which removing ground beetles had the most positive effect on stoneflies, while caddisflies benefitted most from the exclusion of spiders (Paetzold and Tockner 2005), and in a similar study where the removal or addition of aquatic subsidies affected riparian predators differently (Paetzold et al. 2006).

The temporal nature of emergence likely also dictates the magnitude and extent of lotic–land subsidies. Because different aquatic insects emerge or are most active at different times of day and night (Jackson and Fisher 1986; Ward et al. 1996), their utility as a subsidy to terrestrial taxa should be dependent on the specific predator food web. For instance, the food webs of nocturnally foraging groups (e.g., bats; Kalcounis et al. 1996) likely do not include many daytime-emergent taxa.

3.3 Habitat Structure

Vegetation structure has been mentioned earlier in the sense that the presence of trees and other vertical landscape features near lotic ecosystems allows the establishment of arboreal predators, affecting the transfer of ground vs. aerial-based subsidies. Vegetation also serves as a focal point for the swarming behavior of certain taxa, such as adult aquatic midges, which can therefore concentrate around vegetation (Armitage et al. 1995). In an interaction sense, specific aquatic and terrestrial taxa may be more or less effective as subsidy sources and recipients depending on their ability to avoid or capitalize on this vegetation or other habitat structure. For example, in one study along a gradient of flood disturbance, the physical habitat structure of moderately flood-disturbed sites allowed greater fishing spider colonization and aquatic prey utilization, even though the magnitude of aquatic insect emergence was higher at undisturbed sites (Greenwood and McIntosh 2008). In another study of moorland vs. forest habitats, almost all mayflies were caught in the open moor, while proportionally more stoneflies and caddisflies were found in the forest (Petersen et al. 2004). Therefore, the importance of vegetation and other habitat structure to subsidies may vary depending on the type or taxonomic group of subsidy resource or consumer being considered. Aside from forcing emergent aquatic insects to navigate through dense vegetation and acting as a purely physical barrier to dispersal (Cadenasso and Pickett 2001; Cadenasso et al. 2004), the presence of vegetation allows certain groups of terrestrial predators to exist where they would otherwise be absent (e.g., web-building spiders in trees; Chan et al. 2009). Thus, vegetation apparently provides habitat that favors or disfavors certain groups in a taxon-specific fashion.

Lotic ecosystem size may further influence this habitat structure-aquatic/terrestrial taxa interaction, as small streams are often densely forested, with a closed canopy (Minshall 1978). In very small streams in the Coweeta Hydrologic Lab (North Carolina, USA; Swank and Crossley 1988), for example, vegetation can effectively close off the entire stream in all three dimensions (including <1 m above the stream). The density of web-building spiders in the family Tetragnathidae that rely on subsidies can be very high within this wall of vegetation (J.D. Muehlbauer, unpublished), and spider guilds in general can be closely tied to specific vegetation structure (Uetz 1991). It seems likely that the interaction of vegetation and lotic ecosystem size has a strong effect on subsidies to arboreal predator food webs in such sites, and that utilization of subsidies can be high at distances very near the stream. Nonetheless, such dense vegetation also likely serves to limit the transmission distance of the subsidy and may also depress aquatic productivity via intense shading (and therefore subsidy magnitude as well, although localized carbon recycling may be high; Minshall 1978; Marcarelli et al. 2011; Kraus and Vonesh 2012).

Similarly, the possible effect of bank steepness and levee height noted earlier may have differential impacts on lotic vs. terrestrial fauna. The presence of these geographic features may block the emergence of certain taxa that contribute to subsidies (e.g., stoneflies that crawl, rather than fly, onto land), but may be less of an impediment to other taxa so long as the bank or levee height is below some limit (perhaps ~2 m, based on Jackson and Resh 1989; Didham et al. 2012). Foraging at or on the water's edge by subsidy-reliant, ground-dwelling taxa (Bastow et al. 2002; Paetzold et al. 2005; Paetzold et al. 2007) may also be prohibitive at sites with steep banks, although it may have little effect on more arboreal predators (Sanzone et al. 2003). This pattern results in a potential interaction effect between banks and terrestrial taxa as well, in that bank characteristics may preclude certain groups of taxa and predator-prey interactions and yet may be innocuous to others. This potential subsidy-affecting phenomenon has been posited in general terms (Witman et al. 2004) and quantified to some extent in marine shoreline areas (Anderson and Polis 2004), but has not been thoroughly described for the freshwater-land interface (Muehlbauer et al. 2014). However, in one study, bats (i.e., an arboreal predator) preferred stream habitat with valley confinement (perhaps akin to steep banks), even though aquatic resources were more abundant in unconfined reaches (Hagen and Sabo 2011).

More broadly, the geomorphology of the stream or river channel and its floodplain may have some interaction with both aquatic and terrestrial taxa and their role in subsidy dynamics. Braided morphologies, for example, support multiple channels with small terrestrial zones between them, effectively reducing a large river to a series of smaller stream channels. In addition to increasing the length of the aquatic-terrestrial interface locally, such morphologies shorten the distance that aquatic taxa must fly before first encountering some form of land. Middle channel braids may serve a similar role to the algal mat "emergence hotspots" noted by Power et al. (2004). Thus, for weak-flying taxa that would normally suffer high mortality via drowning, their potential to act instead as a terrestrial subsidy may be improved by increasingly complex fluvial geomorphology. Some research has been conducted that shows subsidy magnitude and utilization can be high at stream or river meanders (Iwata et al. 2003; Sabo and Hagen 2012) and along braided rivers (Paetzold et al. 2005). As discussed earlier, another study found that streams with multiple channels within a valley supported more emergence at the reach scale, but also diluted the magnitude of the subsidy reaching a given unit of stream bank because there was more shoreline area in multi-channel reaches (Venarsky et al. 2018). This research suggests that the interaction of ecological subsidies with fluvial geomorphology may be complex and that the ecosystem responses may be scale-dependent.

3.4 Weather, Climate, and Season

Weather and climate can also interact with the behavior and physiology of aquatic and terrestrial taxa at the level of individual organisms. Strong winds, for example, do seem to entrain and disperse small, weak flying insects such as midges over long distances (Finn and Poff 2008; Muehlbauer et al. 2014). However, they may also force larger-bodied taxa such as stoneflies to remain nearer the water (Briers et al. 2003), keeping the potential subsidy from these organisms highly localized and concentrated. Similarly, terrestrial taxa such as spiders may lose some ability to capitalize on subsidies if winds are strong enough to destroy webs. Terrestrial taxa may also respond to water stress, and subsidies may become more pronounced in certain terrestrial food webs as water becomes more limiting. In a stream in the arid US southwest, for instance, riparian wandering spiders in the family Lycosidae seem to rely on prey resources more for their stored water capacity than for their energy and nutrients (McCluney and Sabo 2009, 2010). Riparian-associated spiders such as Tetragnathidae and some Lycosidae may also remain near the water not necessarily for the subsidy of energy, but rather to avoid desiccation (DeVito et al. 2004; Power et al. 2004). Thus, water-laden aquatic prey subsidies may become more important to such predators under drought conditions when water becomes more limiting (sensu McCluney and Sabo 2009).

Finally, seasonality (time of year) can have a potentially large interaction effect on lotic subsidies to terrestrial food webs when considered in concert with other variables. This effect seems largely due to the temporally heterogeneous emergence of aquatic taxa, which varies from site-to-site on a species and community-wide scale (Müller 1973; Paetzold and Tockner 2005; Davis et al. 2011). As an extreme example, resource pulses of aquatic insects emerging *en masse* represent a subsidy that may be massive in magnitude, yet that is available for only a few days (Nowlin et al. 2008; Walters et al. 2018). Particularly where such seasonally high aquatic productivity coincides with seasonally low terrestrial productivity, lotic–land subsidies can be very important to the terrestrial ecosystem (e.g., early spring in temperate climates; Nakano and Murakami 2001), and asynchronous, seasonal emergence timing of different taxa can affect the growth of terrestrial subsidy-dependent predators (Marczak and Richardson 2008). However, the interaction of taxon-specific emergence with season can also affect the susceptibility of certain groups to be preyed upon as subsidies. One notable example is species in the family Capniidae, the “winter stoneflies” in northern Sweden. Individuals emerge onto snow-covered land in early spring (Müller 1973), during a season of hibernation or low activity for many terrestrial predators and prior to the arrival of migratory insectivorous birds that would capitalize on subsidies during warmer months. Thus, although the effect of seasonality seems to be based primarily on its interaction with other variables rather than as a variable acting in isolation, these seasonal effects on productivity and species-specific behaviors can be quite important in lotic–land subsidy dynamics.

4 Stressors to Subsidies under Global Change

In this section, we consider how environmental stressors may influence the magnitude, transmission distance, and utilization of lotic–land subsidies. Keeping in mind the purpose of this book, we focus on large, anthropogenic stressors that can interact with the effects of aquatic contaminants, including climate change, land-use conversion, damming and water abstraction, and species invasion and extinctions. We chose to emphasize these four classes of stressors because of their nearly ubiquitous, global significance, because they encapsulate multiple stressors operating in tandem, and because they provide useful, comparative examples of the different ways in which subsidies may respond to stressors. Additionally, within the context of this volume, all of these stressors can interact with contaminants to have potentially synergistic effects on subsidies (Debecker et al. 2017). For example, climate change can induce stream drying and concomitant ultraviolet light exposure, and aquatic insects are more sensitive to the effects of ultraviolet light when they are also exposed to physiological stress from heavy metal contamination (Clements et al. 2008). Such an interaction likely leads to decreases in aquatic insect abundance and subsequently reduced insect emergence and lotic–land subsidy magnitude as well. In exploring the effects of these global stressors on subsidies we utilize the match-mismatch framework described by Larsen et al. (2016), which attempts to identify disconnects between subsidy resource delivery and the ability of consumers to capitalize on this resource (Fig. 2). Although the four classes of stressors considered here represent only a subset of stressors affecting aquatic and terrestrial ecosystems, this framework should be useful in considering other stressors as well.

4.1 Climate Change

In the broadest sense, anthropogenic climate change should affect subsidies by manipulating weather and season-related variables (Fig. 1). Specifically, warmer temperatures that occur earlier in the near future should lead to earlier phenologies of emergence for aquatic insects, and potentially smaller-bodied emergent individuals as well (Larsen et al. 2016; Jonsson and Canhoto 2017; but see Jonsson et al. 2015). Such temperatures may also cause extirpations of thermally sensitive (e.g., warm or cold-adapted) species and populations (Hering et al. 2009), thus affecting overall emergence availability. This can potentially lead to multiple mismatches between the emergent aquatic insect subsidy source and terrestrial recipient consumers. For instance, earlier emergence creates a temporal mismatch that may weaken the “reciprocal subsidy” between lotic and terrestrial ecosystems, whereby terrestrial consumers are adapted to take advantage of aquatic subsidies when the availability of terrestrial resources is seasonally low (Nakano and Murakami 2001; Jonsson and Canhoto 2017). By emerging at a slightly different time of year, the phenology of aquatic insect emergence may shift to overlap more closely with the

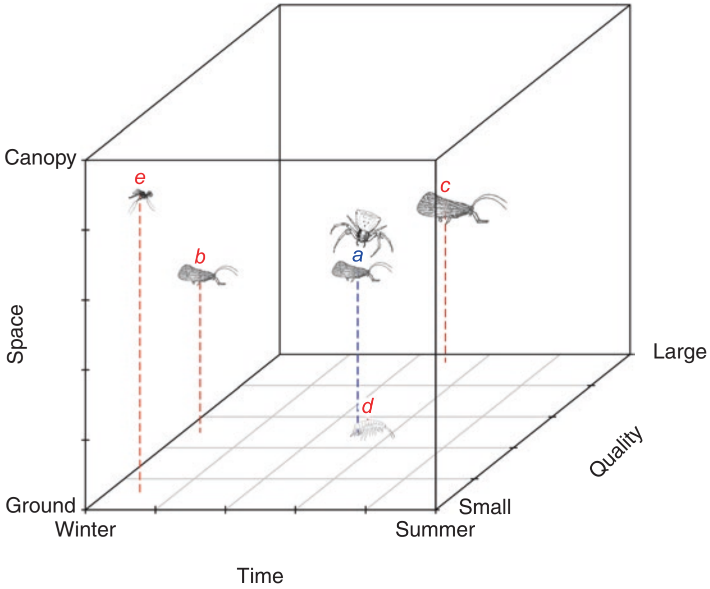


Fig. 2 Depiction of the match-mismatch framework for how subsidy resources and consumers may be decoupled by global-change stressors along axes of time, quality, and space. *a*) A matched subsidy resource–consumer interaction between a caddisfly and a riparian spider. *b*) A temporal mismatch, such as via climate warming, where caddisflies emerge earlier in the year when spiders do not need the subsidy resource. *c*) A quality mismatch where caddisflies grow bigger, such as under nutrient enrichment, and become invulnerable to spider predation. *d*) A spatial mismatch where an invasive amphipod without a terrestrial, winged adult stage replaces the caddisfly and is invulnerable to predation by web-building spiders. *e*) Multiple mismatches where multiple stressors such as climate change and species extinctions interact to support smaller-bodied Chironomidae that emerge earlier in the year and fly higher in the canopy over larger-bodied caddisflies that emerge later and fly at lower altitudes

abundance of terrestrial prey, decreasing their importance to terrestrial consumers. In the case of migratory consumers such as many insectivorous birds, emerging earlier may mean that these insects become wholly unavailable to some subsidy-dependent species that arrive in summer (Iwata et al. 2003), and such a pattern has been shown in the case of terrestrial caterpillars (Burgess et al. 2018). Due to seasonal migrations of consumers that are tied to daylight or other phenological cues (Dingle 1996), migratory species may not be expected to simply begin their migrations earlier to mirror the earlier emergence of aquatic prey. These reciprocal subsidy patterns appear most pronounced in temperate climates; if climate change causes regions to shift from temperate to more Mediterranean or tropical-like climates, lotic–land subsidies may become less important or may lose their seasonal, pulsed nature altogether (Rundio and Lindley 2008; Siqueira et al. 2008; Larsen et al. 2016).

Even if terrestrial consumers are present during the earlier emergence periods of aquatic insects, changes in emergent aquatic insect body size associated with consistently warmer temperatures may create a quality mismatch (Fig. 2). For instance, warmer temperatures can allow aquatic insect and amphibian individuals to develop more rapidly and thus emerge and be reproductively successful at smaller body sizes (Larsen et al. 2016). In this scenario, terrestrial consumers at a minimum will need to consume more individuals to meet their energetic demands, or the consumer community will shift to individuals that favor smaller prey (Stenroth et al. 2015). In contrast, on the community level, climate change can favor larger-bodied taxa, such as Trichoptera over Chironomidae (Jonsson et al. 2015). In this scenario, predators may be less successful in capitalizing on subsidy resources, due to specific morphological adaptations in the consumers such as mouth size or web mesh openings that may affect their ability to prey upon appreciably smaller or larger individuals (sensu Davis et al. 2011).

Other than these direct weather and seasonal controls on subsidy dynamics, rapid climate change can also indirectly affect subsidies through many other pathways. For example, changes to precipitation regimes can influence lotic ecosystem size, bank height, geomorphology, and vegetation structure (Wolman and Gerson 1978). As changing climate makes certain areas more arid, lotic ecosystems are likely to become more intermittent (Datry et al. 2014), with flashier hydrographs and associated changes to bank height (due to incision), channel form (due to stream power alterations), and riparian species composition (due to aridity). Such physical habitat changes can lead to spatial mismatches between aquatic resources and terrestrial consumers. Additionally, associated changes in aquatic and terrestrial communities as lotic ecosystems dry may decouple subsidy pathways as well (McCluney and Sabo 2012). Nonetheless, subsidy dynamics in intermittent streams in general (irrespective of climate change) remain an open area of research exploration (Datry et al. 2016).

4.2 Land-Use Conversion

The conversion of forests and other unmanaged landscapes to agricultural fields, urban developments, and other uses is one of the most significant ways in which humans have effected global change (Lambin and Meyfroidt 2011). Because these conversions affect both freshwater and adjacent terrestrial ecosystems (Allan 2004), their potential to influence lotic–land subsidies is substantial. Specifically, in terms of the variables considered here (Fig. 1), land-use conversion directly affects vegetation structure by removing or replacing it with crops and also affects aquatic and terrestrial production and contaminant load via fertilizer and pesticide usage (Burdon this volume), with implications for insect emergence and subsidy magnitude (Cavallaro et al. 2018).

With respect to vegetation structure, one study on a large river in the United States found that the abundance and biomass of emergent aquatic insects tended to increase with increased grassland cover along a gradient from urban, heavily modified riparian zones to less-affected rural zones (Kautza and Sullivan 2015).

Additionally, the dispersal of emergent aquatic insects can be used as a surrogate for subsidy transmission (Muehlbauer et al. 2014), and the question of how vegetation and land use affect dispersal has been addressed in multiple studies. In one study of mayfly, stonefly, and caddisfly dispersal across plantation forest, recently cleared forest, and moorland streams in the UK, the more open moorland contained the most even and diverse community of aquatic dispersers. The overwhelming majority of mayflies and most caddisflies were also captured in moorland (stonefly abundance was co-equal in moorland and cleared forest, but was lowest in plantation forest; Petersen et al. 2004). In a similar UK study focusing on stoneflies, riparian forest reduced the dispersal of most species, although several were unaffected by whether the riparian zone contained planted conifers, recently cleared forest, or sheep-grazed moorland (Briers et al. 2002). Another similar study focused on Trichoptera in New Zealand streams found that the taxonomic composition of emergent aquatic insect dispersers varied from pine-forested to natural or pasture sites, and that abundance and richness was lowest at the pine-forest sites (Collier et al. 1997). Collectively, these studies emphasize the role of land-use-related changes in vegetation structure on dispersal, and therefore presumably the transmission distance of subsidies from lotic to terrestrial ecosystems, with more dense vegetation generally decreasing the lateral extent to which emergent aquatic insects fly. Within a match–mismatch framework, land-use conversion to more open or densely vegetated riparian zones may therefore create spatial disconnect where, for example, organisms adapted to feed on subsidy resources very near the water in heavily forested zones may be disadvantaged if the forest is converted to more open pasture or cropland.

In addition to altering vegetation structure, land-use conversion adjacent to freshwaters is often also associated with the installation of artificial light sources (Manfrin et al. 2017). The addition of artificial light at night serves as an attractant to some emergent aquatic insect taxa and terrestrial arthropod predators (e.g., many Trichoptera and Tetragnathidae), while discouraging habitat use by others (e.g., Carabidae; Manfrin et al. 2017). In a match-mismatch framework, artificial light can therefore serve as a stressor leading to a potential mismatch between aquatic subsidy magnitude and the terrestrial consumer density present to take advantage of the subsidy. Indeed, in one study of an agricultural ditch in Germany, artificial light led to overall increase in the availability of the aquatic insect subsidy, and while this led to an increase in consumption of aquatic resources by some terrestrial arthropods it nevertheless decreased aquatic subsidy consumption by others (Manfrin et al. 2018). This suggests that artificial lighting in and around the riparian zone concomitant with land-use conversion can yield subsidy quantity mismatches that are species-specific.

Beyond affecting the riparian zone, land-use change also alters other aspects of lotic ecosystems via inputs of contaminants—including fertilizers, pesticides, heavy metals from mining, industrial chemicals, and pharmaceuticals—which affect lotic ecosystem productivity. In a study of one stream affected by experimental nutrient enrichment, Davis et al. (2010) found that increased aquatic primary production allowed aquatic insects to emerge at a larger body size, making them invulnerable to terrestrial arthropod predators. In another study, the body size of emergent individuals decreased with agricultural intensity, with relatively more smaller-bodied Diptera and fewer larger-bodied Plecoptera and Trichoptera along a gradient from forest to agriculture (Stenroth et al. 2015). Due to these changes, the terrestrial consumer community changed as well, and was dominated by beetles and sheet web-building spiders capable of feeding on smaller-bodied taxa in agricultural streams, compared to larger-bodied spiders and birds at forested sites. These examples represent a quality mismatch (Fig. 2), and also emphasize the way in which multiple stressors may interact to affect subsidy dynamics: land-use conversion from forest to agriculture may affect not only where subsidies are consumed due to changes in vegetation structure and contaminant inputs, but also which consumers are even able to capitalize on subsidies due to changes in the size of donor individuals.

As a consequence of land-use conversion, secondary effects on these subsidies are also likely. These include increased flashiness caused by additional impervious cover that leads to bank incision and height adjustment, stream burial and wastewater and irrigation inputs changing lotic ecosystem size, and habitat change altering the taxonomic composition of ecological communities (Groffman et al. 2003; Elmore and Kaushal 2008). These alterations may lead to additional resource–consumer mismatches in space and quality (Fig. 2) but, as with the other aspects of land-use conversion on lotic–land subsidies, their effects remain largely unexplored.

4.3 Water Abstraction and Damming

Another class of global changes affecting freshwaters and adjacent environments is damming, abstraction of water for agricultural, municipal, and industrial use, and other modifications to flow (Carpenter et al. 2011). Aside from reducing the amount of water in affected lotic ecosystems (Richter et al. 1997), these anthropogenic actions also tend to stabilize and homogenize flows and temperatures globally while simultaneously increasing daily flow variation (Poff et al. 2007), to reduce sediment flux (Syvitski et al. 2005), and to fundamentally alter the natural flow regime of these ecosystems to which organisms are adapted (Poff et al. 1997). However, while many of the impacts of damming and related stressors have been well studied in general, their impact on subsidies remains poorly understood (Larsen et al. 2016). Those studies that do exist have found that dam flow regulation tends to create a quality mismatch (Fig. 2), with lower emergent insect biomass relative to unregulated reaches effecting a decrease in the abundance or breeding success of riparian arthropod predators and insectivorous birds (Jonsson et al. 2013; Strasevicius et al. 2013). More broadly, we expect flow-related changes to influence aquatic species composition, leading to potential mismatches between the aquatic community and terrestrial consumers that may be adapted to capitalize on now-extirpated species across all three match-mismatch axes. Additionally, flow and temperature tend to be cues for emergence in many aquatic insect species (Harper and Peckarsky 2006), so alterations to hydrologic and thermal regimes associated with damming and water abstraction may subsequently affect emergence timing, leading to potential temporal subsidy mismatches. This class of stressors should also have many of the same impacts as described in the preceding climate and land-use change sections, due to their general influence on making lotic ecosystems smaller, at times warmer (or, in some cases markedly colder, with hypolimnetic dam releases; Zolezzi et al. 2011), and modifying their riparian vegetation structure. Additional research will be necessary, however, to better quantify the effect of these and other impacts of damming, water, abstraction, and related hydrologic alterations on lotic–land subsidy dynamics.

4.4 Species Invasions and Extinctions

The final class of stressors we consider is species invasions and extinctions, which collectively represent central elements in the global biodiversity crisis (McKinney and Lockwood 1999; Collins and Baxter this volume). Unlike the other global classes of stressors discussed in this section that have emphasized changes to structural or abiotic variables affecting lotic–land subsidies, species invasions and extinctions represent alterations to biological controls on these dynamics (Fig. 1). By directly altering the species pool of subsidy prey resources and of consumers, they also can create potential mismatches across all three axes of time, quality, and space (Fig. 2). If an introduced insect has a different phenology than the native species it replaces, for example, resulting changes in the availability of resources in a given month or season may create a temporal mismatch, affecting whether those species are consumed, or needed as subsidy resources, by terrestrial consumers (Kato et al. 2003).

In terms of mismatches in quality, changes to the species pool have been demonstrated to affect the abundance of subsidy resources being exported from lotic ecosystems. In studies of introduced trout, for example, the species introduction led other fish species to shift their feeding habits in one case, leading to a decrease in emergent insect biomass that dramatically reduced the abundance of orb-weaving spiders in the family Tetragnathidae (Baxter et al. 2004). Similar responses have also been shown for invasive trout effects on riparian bird abundance, albeit in a lake setting (Epanchin et al. 2010). In another study involving an aquatic invasive species and Tetragnathidae, the invasion of an aquatic amphipod similarly reduced spider densities (Gergs et al. 2014). However, rather than being driven by an overall decrease in benthic aquatic invertebrate densities, this effect was more likely due to a spatial mismatch: the fully aquatic, flightless amphipods may be consumed to some extent by terrestrial consumers willing to forage along shorelines at ground level, but they are invulnerable to web-building spiders adapted to capture aerial insects. As with most of the global change stressors described here, additional research would shed light on the extent to which lotic species invasions or extinctions lead to local invasions or species replacement of terrestrial consumers.

5 Conclusions and Future Research

This chapter has highlighted what we believe to be primary controls on lotic–land subsidies that may be affected or modified by global stressors. Specifically, we have explored some of the major ways in which these variables may interact to affect subsidy dynamics, and then have considered how some broad classes of global change and multiple stressors may alter the magnitude, transmission distance, or utilization of the subsidy. Where possible, the theoretical underpinnings behind these have been backed up by support from existing data; however, many variables and stressors remain understudied in conjunction with lotic–land subsidies. In particular, variables related to the physical environment have received less attention in the literature, yet conditions related to lotic ecosystem size, geomorphology, vegetation structure, etc., seem almost certain to have an effect on the magnitude of aquatic subsidies as well as the distance that this subsidy propagates through the terrestrial landscape (Gratton and Vander Zanden 2009; Muehlbauer et al. 2014; Venarsky et al. 2018). Taxon-specific interactions between aquatic prey and terrestrial consumers deriving from differences in species' life-history and behavioral traits also have been shown to be important in affecting the quantity and quality of the subsidy (e.g., Paetzold et al. 2006), and research into such traits may help explain the substantial variation in subsidy magnitude and utilization that can be found between sites (Marczak et al. 2007b). Similarly, climate change, land-use conversion, damming, and species invasions and extinctions all represent major areas of ecological and conservation research, but the effects of these stressors on subsidies—and their interactions with the effects of contaminants on subsidies—have generally received scant attention. As discussed in greater detail elsewhere in this volume, contaminants are likely to independently affect subsidy magnitude, transmission, and utilization. However, their effects are likely to be exacerbated or altered by the global change stressors identified here. We suggest that more explicit consideration of these variables, interactions, and stressors can be beneficial in working toward a more mechanistic understanding of subsidy dynamics between aquatic and terrestrial ecosystems.

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Beyond “Donors and Recipients”: Impacts of Species Gains and Losses Reverberate Among Ecosystems Due to Changes in Resource Subsidies

Scott F. Collins and Colden V. Baxter

1 Introduction

Biodiversity losses are evident worldwide, while species additions have also occurred both locally and regionally due to the introduction and spread of invasive species (Sax and Gaines 2003, Simberloff et al. 2013). Indeed, species gains and losses represent both a cause and consequence of human-mediated global change (Wardle et al. 2011). The combined influence of species losses, invasions, and replacements has reconfigured food webs by altering interactions among animals, as well as interactions between animals and their environment (e.g., Williams and Jackson 2007). Because ecosystems are open to exchanges of energy, nutrients, or organisms with other ecosystems, species losses or additions in one ecosystem may directly and indirectly influence linkages with other ecosystems (e.g., Wardle et al. 2011; Hooper et al. 2012). Although the impacts of species gains and losses within single ecosystems are well documented (Zavaleta and Hulvey 2004; Wardle et al. 2011), how such impacts may propagate via resource subsidies to influence connected ecosystems is less understood, and the potential for effects that reverberate among multiple ecosystems has only just begun to be considered.

Much of this book focuses on applications of spatial food web ecology in the context of the impacts of contaminants. Yet such pollution is but one in an array of multiple interacting stressors influencing ecological systems worldwide, including other forms of habitat degradation, biological invasions, and climate change, which together are driving declines in biodiversity worldwide (Vitousek et al. 1997;

S. F. Collins (✉)
Department of Natural Resources Management, Texas Tech University, Lubbock, TX, USA
e-mail: scott.collins@ttu.edu

C. V. Baxter
Stream Ecology Center, Department of Biological Sciences, Idaho State University,
Pocatello, ID, USA
e-mail: baxtcold@isu.edu

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Sala et al. 2000; Barnosky et al. 2011; Chapin et al. 2013; Muehlbauer et al. this volume). In this chapter, we examine how the species losses and gains caused by a variety of environmental stressors change the exchange of resources (including materials and organisms) within and among ecosystems. We give specific consideration to how changes in species gains and losses that occur within an ecosystem may reverberate (e.g., directly, indirectly, and via feedbacks) back and forth across ecological boundaries and propagate to multiple ecosystems. Our synthesis thus explores the generality of such "reverberating effects," which we define as a series of mutually dependent responses that often result from an initial environmental stimulus but that are transmitted via linkages within (e.g., food web interactions) and reciprocal or propagating connections among ecosystems (e.g., resource subsidies, animal movements). In the following sections, we first provide cursory overviews of ecosystem "openness" as it has been addressed by community ecologists and the conceptual development of ecological frameworks used to examine resource exchanges among ecosystems. We then describe four cases where species losses and gains affect food web structure via resource exchanges between ecosystems, with particular emphasis on effects spanning land-water boundaries. Finally, we discuss the need for more complex conceptual treatment of the interconnectedness of food webs among ecosystems and changes in the gains and losses of species in the context of multiple stressors.

2 The Openness of Ecological Systems: Evolving Spatial Frameworks for Community Ecology

Openness, i.e., a condition allowing for exchanges of matter and energy, is a defining characteristic of living systems (von Bertalanffy 1950), including ecosystems (Odum and Barrett 2005). The boundaries that separate ecosystems are permeable to the exchange of many types of materials including organic matter, energy, animals, and genetic material originating from many different locations. From the deepest oceanic crevices to the highest mountain peaks, even the most extreme environments receive inputs from above (e.g., settling particles; Turner 2002) and below (e.g., elements from geothermal vents and deceased mountain climbers; Jannasch and Mottl 1985, Firth et al. 2008). Indeed, no known ecosystem on Earth is closed to the input of energy or matter from external locations (Lovett et al. 2005).

The history of subdisciplines in ecology is marked by divergent treatment of spatial connectedness. Early community ecologists once considered the physical and biotic environment that defined a given organism's habitat (i.e., place where an organism can find food, shelter, protection, and mates) to be predominantly closed off from other habitats, and the structure of local communities was governed almost entirely by internal dynamics (Forbes 1925). Forbes (1925) noted that "The animals of such a body of water [referring to a lake] are, as a whole, remarkably isolated,…so far independent of the land about them that if every terrestrial animal were suddenly annihilated, it would doubtless be long before the general multitude of the inhabitants of the lake would feel the effects of this event in any important way." Obviously, this sentiment does not reflect contemporary ecological thinking. The development of the subdiscipline of ecosystem ecology marked a transition, in that ecosystems were specifically defined as open systems where exchanges of materials are integral in shaping the biotic community and the abiotic environment (see Golley 1996 for review). Among ecosystem ecologists, openness has long been treated as a focus of investigation (e.g., Odum and Odum 1955; Likens and Bormann 1974). In contrast, for decades, most community ecologists tended to treat such connectivity as a source of noise that was to be avoided in attempts to study and understand community dynamics, and notwithstanding efforts like island biogeography theory (e.g., MacArthur and Wilson 1967; Haila 2002), it was not really until the advent of the subdiscipline of landscape ecology (e.g., Forman and Godron 1981; Turner et al. 2001) that attempts to integrate community and landscape ecology principles and approaches steered scientists toward developing a "spatial ecology" of food webs and communities (e.g., Polis et al. 1997, 2004; Leibold et al. 2004; Gounand et al. 2018).

The first steps made by community and food web ecologists toward a spatial ecology of resource fluxes among ecosystems are evidenced by the development and popularity of the "donor-recipient" conceptual framework (Polis et al. 1997). The "donor-recipient" framework proposes that surplus productivity from a donor habitat (or ecosystem) is transported through biotic or abiotic processes to a recipient habitat where it can have consequences for food web structure and dynamics (Polis et al. 1997). There has been widespread application of this framework by ecologists (Polis et al. 2004; Marczak et al. 2007; Allen and Wesner 2016; Burdon this volume), perhaps owing to the abstract simplicity of the model and the ubiquity of resource subsidies in nature. The donor-recipient model describes the transport of materials (e.g., nutrients, organic matter, or organisms) from a donor habitat across an ecological boundary to a recipient habitat. The receiving habitat is considered "subsidized" when the transported resource increases productivity above what ambient resources could otherwise support (Polis et al. 1997; Marczak et al. 2007; Allen and Wesner 2016).

In its simplest formulation, the donor-recipient framework represents a singular and unidirectional exchange of material across an ecological boundary (Fig. 1a). Although simple, this framework provides a straightforward and generalized means of describing how resource fluxes alter the behaviors, activities, and demographics of organisms and the structure and function of recipient food webs (reviewed in Polis et al. 1997; Marczak et al. 2007). Eventually, ecologists examined the potential for, and importance of, multiple subsidies that could be exchanged in either direction between two habitats or ecosystems (Fig. 1b). This empirical step forward is perhaps best characterized by the publication of Nakano and Murakami's (2001) classic examination of the interdependence of stream and forest food webs. By tracking reciprocal fluxes of prey between stream and forest habitats, Nakano and Murakami observed that seasonal fluxes of prey subsidized consumers at times when in situ resources were scarce, thus sustaining higher densities of aquatic and

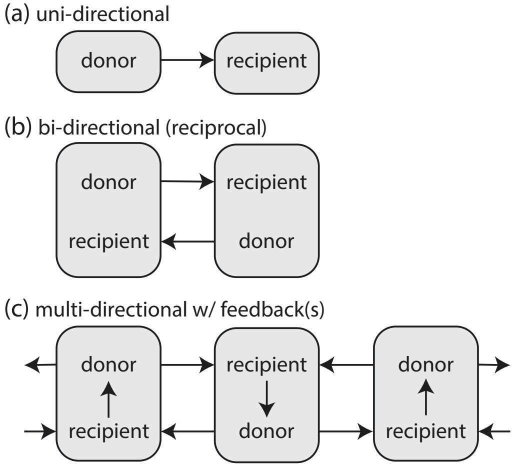

Fig. 1 (**a**) The donor-recipient model consists of a donor and recipient habitat (denoted by boxes) and a material that crosses an ecological boundary (black arrows), in its simplest formulation. This unidirectional configuration represents most ecological studies that examine the effects of resource subsidies. (**b**) Materials can be exchanged in a bidirectional manner. In such cases, a habitat is both a donor and recipient, and reciprocal subsidies are exchanged across an ecological boundary. (**c**) Among a mosaic of many habitats, the exchanges of resource subsidies are likely multidirectional, as effects propagate across ecological boundaries, which in turn produce effects that further reverberate back and forth among habitats. Feedbacks between ecosystems can arise when outputs from an ecosystem affect a recipient ecosystem and those effects are routed back to the original ecosystem

terrestrial consumers in both habitats. During times when availability of aquatic prey biomass was low, stream fishes switched to terrestrial invertebrates, and when terrestrial invertebrates were low, insectivorous forest birds fed on emerging adult aquatic insects. Since this study, many others have pointed to the generality and importance of reciprocal fluxes between land and water (e.g., Baxter et al. 2005; Marcarelli et al. 2011; Bartels et al. 2012; Sabo and Hoekman 2015; Schindler and Smits 2017).

Although the spatial ecology of resource subsidies is rooted in the properties of openness, community and food web ecologists have been slow to empirically investigate other aspects of open systems, particularly the potential for reciprocal feedbacks (e.g., when outputs of a system are directly or indirectly routed back as inputs) or effects that propagate among multiple, heterogeneous habitats (but see Baxter et al. 2004; Collins and Wahl 2017, and descriptions below). Moreover, theoretical models examining resource subsidies treat space implicitly as a single habitat with inputs or as two interacting habitats (e.g., Leroux and Loreau 2008). This approach can be problematic: while organisms may be born and develop within an ecosystem, the sources of carbon and nutrients that are assimilated into animal tissue within that ecosystem have flowed, cycled, or been recycled from potentially many ecosystems (Iwata 2007; Kraus and Vonesh 2012; Scharnweber et al. 2014). Inclusion of many habitats or ecosystems adds complexity to studies of food webs and communities, and both experiments and models often seek to reduce such heterogeneity, treating it as noise in an effort to isolate and test specific mechanisms. To date, most field and manipulative experiments assess the effects of resource subsidies in a single "recipient" ecosystem.

When resource exchanges are strong and produce potentially many subsidy effects, the responses of consumers (e.g., increased numbers) themselves may become subsidies when organisms disperse, or organic matter is transported into other ecosystems (Fig. 1c). Indeed, subsidy effects can propagate through space into potentially many other contiguous or noncontiguous ecosystems. Although many studies examine exchanges between contiguous ecosystems (e.g., uni- or bidirectional exchanges between land and water), the flows and fluxes of materials among ecosystems are more realistically characterized by multidirectional exchanges among ecosystems (e.g., Fig. 1c). Theoretical consideration of such multidirectional exchanges of materials, which considers the movements of organisms and the transport of inanimate materials (e.g., pools of detritus, dissolved nutrients), is arguably best represented by the "meta-ecosystem" concept (Loreau et al. 2003), which is defined as a set of ecosystems connected by flows of energy, materials, and organisms across ecosystem boundaries. The explicit consideration of mutual and reciprocal constraints that contiguous and noncontiguous ecosystems exert on the functioning of each other is particularly relevant (Loreau et al. 2003), as exchanges of carbon and nutrients among ecosystems can occur as a subsidy or the dispersal of any ecological effects. These propagating exchanges can form feedbacks when the output of an ecosystem is routed back as an input. Given the ubiquity and importance of resource subsidies in nature, and that effects can propagate into other habitats, feedbacks involving multiple habitats are not only possible but perhaps common. However, such phenomena have received less attention by ecologists.

3 Reverberating Effects of Species Gains and Losses: Four Case Study Illustrations

Here, we discuss four cases that illustrate the consequences of species gains and losses in the context of multidirectional resource exchanges between ecosystems. The first two are (1) impacts of lost spawning runs of Pacific salmon (*Oncorhynchus* spp.) and consequences for stream-riparian food webs (Fig. 2a) and (2) aquaculture-mediated invasion by bighead carp (*Hypophthalmichthys* spp.) and impacts on river-floodplain food webs (Fig. 2b). These two cases have been explicitly investigated in the context of spatial food web ecology and resource subsidies, and we focus on examples from our own studies. In these two cases, we describe how the loss of salmon and the introduction of carp influence food web linkages via their complex effects that span multiple ecosystems. Rather than describe a single unidirectional flux of material, we describe the multidirectional exchanges of materials as part of the ecology and natural history of these fishes.

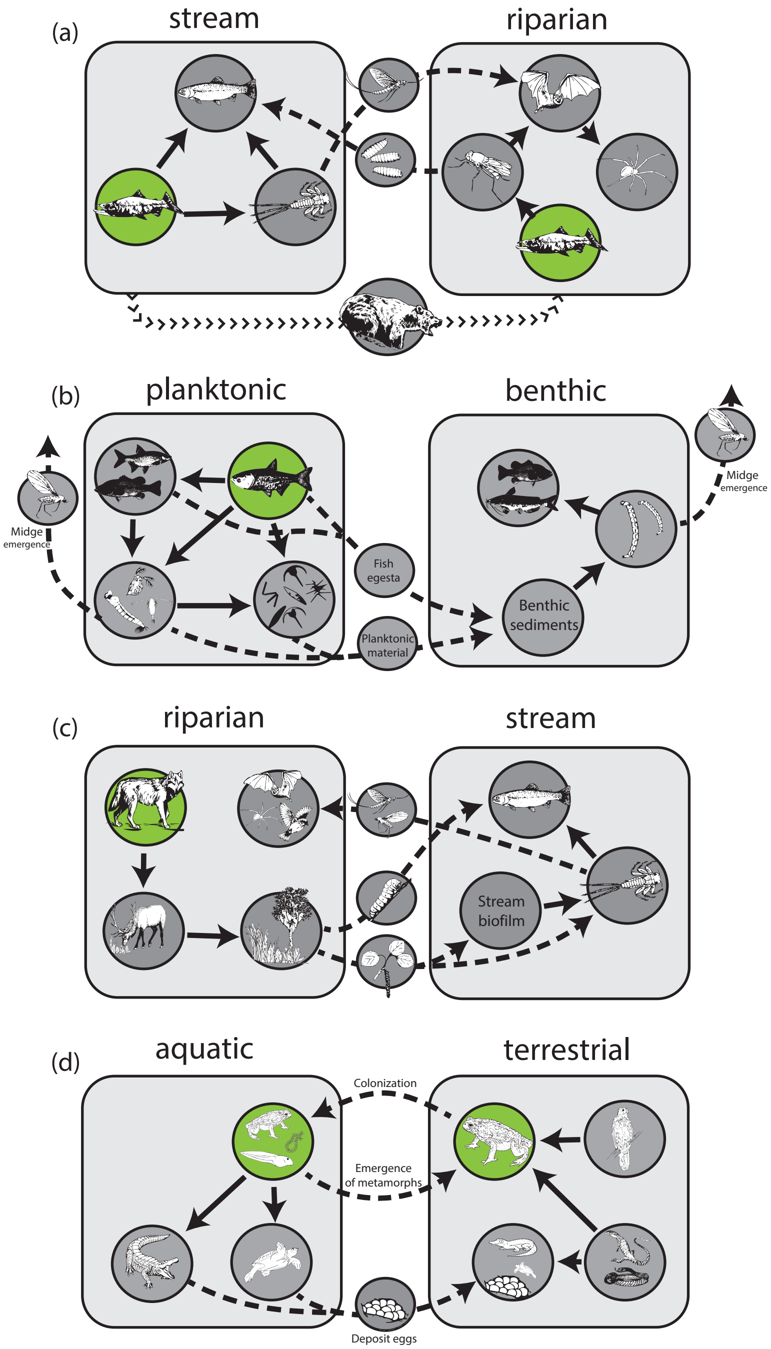

Fig. 2 A generalized diagram describing propagating and reverberating effects within and among ecosystems. Contexts include the (**a**) reverberating effects of salmon-derived resource subsidies, the (**b**) aquaculture-mediated fish introductions and impacts that propagate among multiple river-floodplain habitats, and the potential (**c**) for reverberating responses to the loss and return of an

The second two cases involve species gains or losses that have not been explicitly studied in the context of resource subsidies but perhaps should be because their ecological effects likely propagate among habitats. These are (3) potential responses to the loss and return of a native apex predator, the gray wolf (*Canis lupus*), that may reverberate between land and water (Fig. 2c) and the (4) likely propagating impacts via lost resource exchanges driven by another invasive species, the toxic cane toad (*Rhinella* [*Bufo*] *marinus*) (Fig. 2d). In the latter two cases, we consider how two well-documented ecological contexts, the extirpation of wolves across North America and the invasion of a toxic toad across Australia, may disrupt multidirectional resource exchanges between ecosystems. In all cases, considering species losses or gains in terms of multidirectional resource exchanges highlights the need for a framework that embraces the potential for effects that propagate and/or reverberate among multiple habitats and ecosystems.

3.1 Case Study 1: Reverberating Effects of Salmon-Derived Resource Subsidies in Stream-Riparian Ecosystems

Adult Pacific salmon (*Oncorhynchus* spp.) migrate to their natal streams to spawn and then die. While alive, salmon scour stream beds to build their nests, they release eggs that are consumed by other organisms, and they are directly consumed by many predators (Gende et al. 2002). In death, decomposing salmon carcasses leach nutrients to their surroundings and are also directly consumed by many aquatic and terrestrial consumers (Ben-David et al. 1998; Gende et al. 2002; Janetski et al. 2009; Flecker et al. 2010; Hocking and Reynolds 2011; Collins et al. 2015a). Unfortunately, dams, habitat destruction, and overharvest by humans have all contributed to the widespread decline of Pacific salmon in the Pacific Northwest (Lichatowich 2001, Montgomery 2004), eliminating salmon from approximately 40% of their historic range and dramatically reducing their numbers where connectivity persists (NRC 1996; Gresh et al. 2000). Consequently, many streams, rivers, lakes, and riparian forests no longer experience salmon migrations nor receive the inputs of marine-derived organic matter and nutrients contained in their tissues (Collins et al. 2015a, b; Schindler and Smits 2017). Coincident with the loss of nutrients and energy delivered by salmon are the scores of lost animal, plant, and microbial interactions that shape the structure and productivity of aquatic and terrestrial food webs.

How animals interact with live salmon and salmon carcasses has important consequences for organismal responses, trophic interactions, and the structuring of stream-riparian food webs in salmon-bearing watersheds. Because salmon carcasses are energy dense and of higher quality than many other food resources, many

Fig. 2 (continued) apex predator, the gray wolf (*Canis lupus*), and (**d**) for propagating impacts of the invasive, toxic cane toad (*Rhinella* [*Bufo*] *marinus*) between land and water. The hatched line indicates the transport of salmon carcasses by wildlife. Dashed lines represent ecological effects that bridge land and water. Solid lines represent generalized food web linkages terrestrial scavengers like bears exploit them (Quinn et al. 2009). In doing so, terrestrial scavengers often move carcasses into riparian forest environments (e.g., Reimchen 2000). This simple process exposes more organisms to the carcass subsidy material (i.e., aquatic and terrestrial organisms). Decomposing salmon carrion in terrestrial habitats quickly attract a multitude of opportunistic organisms such as carrion flies (larvae and adults) and other arthropods from riparian and forest ecosystems, which consume and colonize carcasses, and many proliferate in number as a result (e.g., Gende et al. 2002; Hocking and Reimchen 2006; Collins and Baxter 2014).

In a large-scale, multiyear experiment, we documented complex direct and indirect effects of salmon subsidies within and among stream and riparian ecosystems. The addition and breakdown of carcasses directly stimulated stream biofilms, enhanced benthic insect standing-crop biomass, and increased the growth and production of fishes (Marcarelli et al. 2014; Collins et al. 2016). In riparian ecosystems, scavengers removed salmon carcasses from streams, and in turn, carcasses were rapidly colonized by flies and other arthropods (Collins and Baxter 2014).

Because ecosystem boundaries are permeable, both salmon carcasses and their effects propagated across ecological boundaries and influenced consumers in adjacent habitats (Fig. 2a). For instance, our experiment demonstrated that subsidized terrestrial carrion flies (adults and larvae) fell into streams in large quantities where they were consumed by stream fishes, generating a subsidy-mediated reciprocal feedback from stream to riparian and back to stream ecosystems (e.g., Collins et al. 2016; Fig. 2a). Along another pathway, we observed that subsidized fishes mediated insect emergence from water to land. By intensifying predation (i.e., an effect of the carcass subsidy) on benthic insect larvae, stream fishes also reduced the emergence of adult life stages, which resulted in fewer Tetragnathidae spiders and reduced bat activity in riparian environments (Collins et al. 2020). As direct and indirect subsidy effects reverberated between adjacent habitats, the sign and magnitude varied with the outcome of trophic interactions. The complex suite of direct, indirect, and feedbacks we observed in response to salmon subsidies is decidedly more complicated than what is generally represented by a unidirectional donor-recipient model. Indeed, the multidirectional exchanges of the salmon subsidy and its many subsidy effects through ecosystems are more representative of a meta-ecosystem.

3.2 Case Study 2: Aquaculture-Mediated Fish Introductions and Impacts That Propagate Among Multiple River-Floodplain Habitats

In the confines of aquaculture facilities, bighead carp (*Hypophthalmichthys* spp.; also commonly referred to as Asian carp) can improve water quality by consuming nuisance plankton. In captivity, such traits provide a useful benefit to society, but in freshwaters outside their native range, these fishes pose a major ecological threat to freshwater food webs and biodiversity. Presently, the Mississippi River and many of its larger tributaries harbor extremely high densities of bighead carps. These mobile fishes utilize both mainstem river and floodplain lake ecosystems (e.g., Sass et al. 2010; MacNamara et al. 2016) and are often the dominant fish encountered by fisheries scientists (Irons et al. 2007; Sass et al. 2010; Collins et al. 2015b, 2017a). As planktivores, bighead carps do not occupy a high trophic position within riverine ecosystems. Nevertheless, their consumptive effects on phyto- and zooplankton can be substantial. By efficiently exploiting multiple planktonic resources (Collins and Wahl 2017), and by outcompeting native fishes (e.g., Schrank et al. 2003; Nelson et al. 2017), bighead carps have accumulated tremendous population biomass and constitute a large pool of organic matter within invaded riverine ecosystems. Like all biological invasions, exotic species introduce new and sometimes strong interactions with native organisms (Paine 1980). Experiments have shown that the presence of carp can alter prey behaviors, and in turn, the encounters of native predators and prey (Collins et al. 2017b). As a result, these invasive fishes may substantially alter their surroundings by altering the exchanges of materials and organisms between pelagic and benthic habitats and with surrounding terrestrial ecosystems.

Although most studies have focused on the effects of bighead carp in planktonic habitats, impacts are not limited to the upper strata of the water column. Research on recycling and translocation of materials between benthic and planktonic habitats by fishes has largely concentrated on excretion (e.g., Vanni 2002), yet habitat coupling via sedimentation of egested particulates (i.e., fish feces) is also widely recognized as ecologically important (Wotton and Malmqvist 2001; Schindler and Scheuerell 2002). For instance, evidence from our own work found that bighead carp caused strong reductions in pools of organic matter within planktonic habitats. In turn, bighead carp shunted large quantities of organic matter from pelagic to benthic habitats in the form of egested fish waste (Collins and Wahl 2017) (Fig. 2b), which increased densities of larval midges in benthic sediments (Chironomidae; Collins and Wahl 2017; Nelson et al. 2017). Interestingly, these increases were not constrained to the aquatic environment. Rather, the reverberating effects of bighead carp, mediated through egested waste particles and subsidized midge larvae, increased the emergence of adult midges from aquatic to terrestrial ecosystems by 228% (Collins and Wahl 2017). By amplifying fluxes from planktonic to benthic habitats and across land-water boundaries, bighead carp may indirectly subsidize terrestrial insectivores as effects propagate (e.g., Muehlbauer et al. 2014), potentially altering terrestrial community dynamics along other food web pathways (e.g., Henschel et al. 2001; Murakami and Nakano 2002).

The gain of a species, here the invasion of bighead carp, resulted in a new pool of fish biomass that processed planktonic food resources and altered fluxes of organic matter within and among ecosystems. As in the previous example, the propagating effects of this invasive species are not easily conceptualized within a simple donor-recipient model, further demonstrating the need for a more realistic framework that draws attention to complex responses that link ecosystems.

3.3 Case Study 3: Potential Reverberating Responses to the Loss and Return of an Apex Predator, the Gray Wolf

Globally, the expansion of human populations, degradation of habitats, and direct exploitation have resulted in the loss of many apex predators (Berger 1999; Estes et al. 2011). A prime example has been the extirpation of many large-bodied terrestrial carnivores. In North America, gray wolves (*Canis lupus*) and other large predators have been eradicated from >95% of their historic ranges (Berger 1999; Ripple et al. 2014), often minimizing their ecological roles to near functional extinction. In the absence of wolves, herbivory by elk (*Cervus canadensis*) and other ungulates can be excessive, directly altering the composition and character of riparian vegetation (e.g., Peinetti et al. 2002; Beschta 2005; Ripple and Beschta 2012) with apparent indirect consequences for stream channel form (Beschta and Ripple 2006). Subsequently, in some locations like Yellowstone National Park, USA, reintroduction of wolves has been successful, and in this context, evidence suggests that their return has triggered large reductions in herbivory through apparent changes in browsing by elk and deer (Ripple and Beschta 2004) and driven attendant positive responses by riparian woody plants such as willow, cottonwood, and alder via this trophic cascade (Ripple and Beschta 2012; Beschta and Ripple 2016). The apparent cascading effects of wolves on riparian vegetation are remarkable, and similar investigations elsewhere suggest analogous responses to the roles of other top predators such as cougars (e.g., Ripple and Beschta 2006). However, the effects of such changes may propagate further if such changes impact resource subsidies that link land and water—a possibility that remains largely uninvestigated.

Owing to the well-documented linkages between streams and their riparian habitats (e.g., Vannote et al. 1980; Naiman et al. 1993; Naiman and Decamps 1997; Baxter et al. 2005), stark changes to riparian vegetation like those observed in Yellowstone National Park, as mediated by loss and subsequent restoration of large predators, may have predictable effects that reverberate between land and water. Reverberating effects would be particularly likely if these changes to riparian vegetation alter fluxes of resources such as inputs of leaf litter and terrestrial invertebrates or exports of emergent adult aquatic insects (Fig. 2c). Regeneration of woody riparian vegetation could decrease light input, which may or may not reduce in-stream primary production (e.g., Warren et al. 2017), but would likely increase allochthonous litter and terrestrial invertebrate inputs to streams—both of which fuel stream animals like insects and fishes (e.g., Wallace et al. 1997; Rosemond et al. 2001; Baxter et al. 2005). In turn, the net consequences of such changes in land to water subsidies for aquatic insect larvae could be expected to influence the magnitude, composition, and timing of adult insect emergence, with potential feedbacks to terrestrial consumers. Emergent adults of aquatic insects are important to terrestrial insectivores like birds, bats, lizards, and spiders in terms of energy (e.g., Baxter et al. 2005; Marczak et al. 2007; Bartrons et al. 2013; Schindler and Smits 2017) and also nutrients and key fatty acids (e.g., Sanzone et al. 2003; Martin-Creuzburg et al. 2017). Therefore, any process that might alter emergence, including changes in riparian vegetation induced by a terrestrial trophic cascade, has the potential to not only affect in-stream food webs but also reverberate to influence consumers and food webs back in the adjacent terrestrial environment. While the extended consequences of the trophic cascade driven by wolf reintroduction to Yellowstone National Park have been widely discussed in popular science and in the media, empirical studies have not yet quantified the influence of recovering riparian vegetation on aquatic food webs. Moreover, no studies have considered the potential for reverberating effects of terrestrial trophic cascades into aquatic systems, and back again to affect the abundance of terrestrial predators. Thus, this case represents an example where the application of spatial food web ecology is needed and another in which consideration of multidirectional exchanges of materials more realistically reflects the linkages among aquatic and terrestrial ecosystems.

3.4 Case Study 4: Potential for Propagating Impacts of the Invasive Toxic Cane Toad

Cane toads (*Rhinella* [*Bufo*] *marinus*) were imported to Australia in the 1930s as a biological control for agricultural pests of sugar cane (Sabath et al. 1981; Phillips et al. 2003). Shortly thereafter, cane toads began migrating from the agricultural fields to the wilds of Australia where they compete with native species for prey resources. Like many amphibians, cane toads lay their eggs in temporary or permanent waterbodies where early life stages reside but eventually move to terrestrial environments as adults. Like some amphibians, cane toads are highly toxic (bufotoxin secreted from glands) at all life stages (Phillips et al. 2003). Because of a lack of co-evolution with predators in Australia, most consumers are naive to the chemical defense and die shortly after ingesting the toad. The complex life history of the cane toad exposes them, and their toxins, to a wide range of aquatic and terrestrial organisms. Moreover, their emergence from water to land constitutes a potentially large flux of energy and nutrients between ecosystems (e.g., Earl and Semlitsch 2012). These factors hold potential for complex multidirectional exchanges of energy and nutrients in the broader meta-ecosystem. The semiaquatic life history of cane toads and the many species they affect may drive strong feedbacks between land and invaded waterbodies and to new waterbodies as these toads disperse across the landscape.

Although cane toads can achieve high densities, they constitute a pool of biomass that may go largely unexploited, at least by higher trophic levels in water and on land. These toxic invaders are an organic contaminant to the food web (e.g., Walters et al. 2008) and appear to function as something of an "anti-subsidy," in that they can enhance mortality (rather than productivity) of some consumers, particularly the adults which are more toxic. The expansion of cane toads across Australia has corresponded with the decline of some native predators and competitors (e.g., amphibians, snakes, monitors, lizards, marsupials, crocodiles; Phillips et al. 2003;

Letnic et al. 2008; Shine 2010), although declines are not ubiquitous (e.g., Somaweera and Shine 2012). The reduction or loss of such semiaquatic animals compromises their important functional roles, including the transfer of organic matter and nutrients as part of diel movements and egg deposition (e.g., Bouchard and Bjorndal 2000). Yet, the ecological effects of cane toads are not directly negative for all species, as their invasion has often had strong positive and indirect effects on perceived competitors by enhancing mortality of shared predators (Doody et al. 2006, 2013; Shine 2010, 2014; Brown et al. 2013). By changing predator functional responses, cane toads appear to facilitate several native species in some cases (e.g., apparent mutualism and commensalism; Holt and Lawton 1994; Bruno et al. 2003). Some raptors only consume the cane toads' tongue, allowing the scavenger to utilize an abundant resource free of the toxin (Beckmann and Shine 2011).

Beyond the well-described effects of cane toads within land and water, the suite of positive and negative changes to species and trophic interactions likely propagate among many ecosystems, as highlighted in previous cases (Fig. 2d). Although toad eggs and tadpoles are constrained to the aquatic environment, they may disrupt fluxes of other organisms from water to land like that of other invasive species (e.g., Baxter et al. 2004; Epanchin et al. 2010; Collins and Wahl 2017), either by feeding on aquatic prey or by being preyed upon by other aquatic predators that are unaffected by their toxins (Shine 2010). The toads themselves propagate via the emergence of adults from water to land and via the dispersal of adults as they invade new waterbodies. Cane toad metamorphs (i.e., earliest terrestrial life stage) are small upon leaving water and most susceptible to predation by arthropods including ants (Ward-Fear et al. 2009). When consumption of juvenile or adult cane toads by native nest predators (i.e., predators that eat eggs in a nest) increases the mortality of such predators, cane toads can indirectly enhance hatching success of other native semiaquatic and terrestrial species including tree snakes (*Dendrelaphis punctulatus*), herbivorous pig-nosed turtles (*Carettochelys insculpta*), predatory freshwater crocodiles (*Crocodylus johnstoni*), and predatory Gilbert's dragons (*Amphibolurus gilberti*) (Doody et al. 2009; 2013; Webb and Manolis 2010). Consequently, these bolstered populations may themselves propagate to influence other aquatic or terrestrial environments, depending on life history attributes of the species involved. To our knowledge, cane toads and their extended food web effects have not been explicitly investigated in the context of resource subsidies (but called for by Doody et al. 2013). The combined direct responses of aquatic and terrestrial prey, competitors, and predators, as well as the many positive and negative indirect effects described here are only a small and incomplete representation of how food webs have been restructured by these invasive toads. Consistent with previous cases, the cane toad invasion is another context in which the application of spatial food web ecology, coupled with the robust literature describing the natural history of cane toads, and quantification of their effects on multidirectional resource exchanges among ecosystems, could be used to advance ecological theory by describing the complexities of linkages within meta-ecosystems where these toads have invaded, as well as between newly colonized waterbodies to track the gradual change in material exchanges that accompany biological invasions.

4 From Donors and Recipients to Meta-ecosystems: Conceptual Advances to Encompass Reverberating Effects

A clearer understanding of the broader consequences of species losses and gains requires improved understanding regarding how resource linkages between ecosystems have been affected and the type of linkages (e.g., animal movements, nutrients) involved. Our examples demonstrate that this involves investigating complex spatial dynamics involving fluxes of nutrients, movements of organisms, trophic dynamics, and feedbacks—not simple donor-recipient relationships. There has been a concerted effort to distinguish the types (e.g., active vs. passive dispersal; organic vs. inorganic composition; inanimate vs. mobile forms) of subsidies exchanged between ecosystems (Kraus et al. 2011; Earl and Zollner 2017; Gounand et al. 2018). In our opinion, such distinctions are sorely needed, as the implications of organismal movements among communities and ecosystems are likely to be inherently different from those associated with fluxes of inanimate materials (e.g., pools of detritus, dissolved nutrients) that rely on transport processes (e.g., gravity, flowing water, wind, animal vectors) for their dispersal (e.g., Reiners and Driese 2004; Leroux and Loreau 2008; Bartels et al. 2012). Yet, simple donor-recipient frameworks of resource exchanges among ecosystems include no explicit consideration of such subsidy characteristics. Because ecosystems are open to the input and export of materials, strong subsidy effects may well be exported to other ecosystems as organisms increase in number and then disperse, as evidenced by our work with salmon and carp. How far into the coupled ecosystem these reverberating effects of resource subsidies propagate may depend on the mode of transport. Thus, the export and degree of spatial coupling with other ecosystems may depend on the material itself (e.g., animal, organic matter, or nutrient) and the processes that facilitate its transport. Each means of transport has implications for how effects of subsidies may propagate to or reverberate among ecosystems and, in turn, how species losses and gains impact many ecosystems.

An evolving spatial ecology of food webs may require more explicit consideration of the potential for the subsidy and its effects to propagate through and feedback among multiple recipient ecosystems (Fig. 1c), including changes to other resource subsidies (Loreau et al. 2003; Gounand et al. 2018). Across a diverse assortment of cases, the documented or potential cross-boundary effects suggest that a multidirectional framework is more appropriate for characterizing how species losses and gains influence meta-ecosystems. Based on prevailing understanding, the donor-recipient framework seems poorly suited to describe the complex interactions and exchanges of animals and materials between many habitats or ecosystems. Too often, the loss or addition of a species is considered only within the confines of the ecosystem it once inhabited or currently occupies. Our assessment and the examples we have reviewed raise the possibility that changes to biodiversity, particularly those that involve strong interactions with surrounding environments, may have impacts that reverberate among many ecosystems.

Based on the examples we have presented here regarding extended consequences of species losses and gains, we argue that expanding basic understanding of reverberating responses and acting on the applied consequences of such connectivity may require the development and use of a conceptual framework that goes beyond the simple donor-recipient model.

Framing studies in terms of a simple donor and recipient, in our opinion, fails to capture the complexity of food web responses to the loss or addition of a species. Clearly, the unidirectional flux is too simplistic when the objective is to describe how resource exchanges influence the structure of spatially coupled food webs. However, what kind of a framework can serve as a replacement?

In recent years, there have been a suite of theoretical models and concepts presented that are beating a path toward replacement of the donor-recipient framework. Theoretical food web models have, step by step, been extended to encompass more and more facets of realism, including models that link multiple habitats via exchanges of materials and organisms (e.g., McCann et al. 2005; Rooney et al. 2008; Leroux and Loreau 2012). Similarly, there have been several conceptual advances aimed at embracing more complexity in the spatial ecology of food webs and communities. The extension of the metapopulation concept (e.g., Hanski 1998) to that of a "metacommunity" (e.g., Leibold et al. 2004) was an important step, but this concept limited exchanges among subcommunities to dispersal of individuals important to the demographics of the populations comprising communities. Subsequently, the need to incorporate flows of various resources that included not only movements of organisms but also transport of inanimate organic and inorganic materials led to the proposal of the "meta-ecosystem" concept (Loreau et al. 2003), which also attempted to address the potential for feedback interactions among subsystems. Critical to this step was the recognition that a spatial ecology of communities and food webs that encompassed such resource exchanges, and which had been inspired by the desire to integrate with landscape ecology (Polis et al. 1997, 2004), would also require integration of principles and approaches between the largely disparate subdisciplines of community and ecosystem ecology (Loreau et al. 2003; Marcarelli et al. 2011; Massol et al. 2011). Perhaps inspired by these efforts, ecosystem ecologists have been working largely in parallel with community ecologists in the past few decades toward their own integration with landscape ecology (for review, see Lovett et al. 2005).

These arcs of activity in different subdisciplines may finally be converging, perhaps setting the stage for a unification in ecology that has long been envisioned but has remained elusive. Indeed, recent efforts to extend, refine, and apply meta-ecosystem concepts and models to food webs (e.g., Earl and Zollner 2017; Gounand et al. 2018; Leroux et al. 2017), while marked by the struggles of reconciling dialects and definitions from previously insular bodies of literature, appear to us to be exhibiting the signs of just such a unification. Consequently, theoretical and conceptual advances in spatial ecology seem to be outstripping empirical efforts to evaluate and apply these ideas, though there are of course exceptions (e.g., see Spiller et al. 2010; Bellmore et al. 2015). The meta-ecosystem framework is poised to replace the donor-recipient framework, but we expect that its refinement and improved utility (e.g., Gounand et al. 2018) lie not only in revisiting definitions but also in stronger interactions between empirical and theoretical efforts. For example, food web and meta-ecosystem models (e.g., McCann et al. 2005; Leroux and Loreau 2012) have recently attempted to represent some of the kinds of complexity we have highlighted here, and these have included the potential for feedback between ecosystems. However, they typically do not incorporate the suite of direct and indirect interactions we have observed that typically mediate such feedbacks (e.g., in the case of reverberating effects of salmon carcasses on stream-riparian food webs). We anticipate that field studies investigating responses that reverberate among habitats via changes in flows of materials and organisms will become more common. If so, it is to be hoped that understanding of the true, extended impacts of species losses and gains, as well as those of the various major agents of global change, will also grow and take root—not only in the scientific community but also among the collective perspectives and attitudes of society.

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Part IV

Management Applications and Tools

Practical Considerations for the Incorporation of Insect-Mediated Contaminant Flux into Ecological Risk Assessments

Ryan R. Otter, Gale B. Beaubien, Connor I. Olson, David M. Walters, and Marc A. Mills

> *By broadening the arena of food web ecology to consider trophic interactions across ecotones and at the landscape level, our efforts will become increasingly relevant to conservation and resource management decisions.*
>
> Vander Zanden and Sanzone (2004)

R. R. Otter (✉)
Department of Biology, Middle Tennessee State University, Murfreesboro, TN, USA

Molecular BioSciences, Middle Tennessee State University, Murfreesboro, TN, USA
e-mail: ryan.otter@mtsu.edu

G. B. Beaubien
Molecular BioSciences, Middle Tennessee State University, Murfreesboro, TN, USA

U.S. Environmental Protection Agency, Office of Research and Development, Cincinnati, OH, USA
e-mail: beaubien.gale@epa.gov

C. I. Olson
Department of Biology, Middle Tennessee State University, Murfreesboro, TN, USA

Department of Civil and Environmental Engineering, Syracuse University, Syracuse, NY, USA

D. M. Walters
U.S. Geological Survey, Columbia Environmental Research Center, Columbia, MO, USA
e-mail: waltersd@usgs.gov

M. A. Mills
U.S. Environmental Protection Agency, Office of Research and Development, Cincinnati, OH, USA
e-mail: mills.marc@epa.gov

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1 Introduction

The management of chemicals of concern (COCs; e.g., chemicals listed under the US Environmental Protection Agency's (US EPA) Toxic Substances Control Act that may present an unreasonable risk of injury to health and the environment) to protect human health and the environment has progressed as our understanding of the factors that influence the fate and effects of COCs has evolved. Presently, most contaminated sites in the USA are managed under the widely applied ecological risk assessment framework (USEPA 1998). This framework, as used today, is a workflow designed to evaluate the likelihood of adverse human health and ecological effects from exposure to one or more contaminants (Fig. 1).

Risk assessment in the USA began in the 1970s in response to a series of environmental laws, specifically the Clean Air Act of 1970, the Federal Insecticide, Fungicide, and Rodenticide Act of 1972, the Safe Drinking Water Act of 1974, the Toxic Substances Control Act of 1976, and the Clean Water Act of 1977 (Suter 2008). In 1981, the US National Academy of Sciences was commissioned to review the "institutional means of assessment of risks to public health" (Suter 2008). The review produced *Risk Assessment in the Federal Government: Managing the Process*, commonly referred to as "the Red Book" because of its red cover. The Red Book provides a framework for human health risk assessment that included hazard identification, dose-response assessment, exposure assessment, and risk

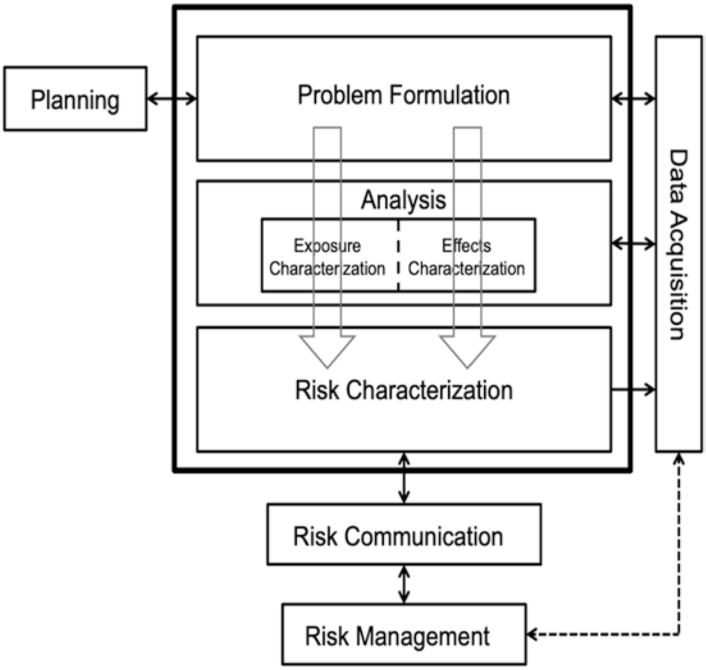

Fig. 1 The ecological risk assessment framework. Modified from USEPA (1998)

characterization. Risk assessment is informed by research and guides the risk management process that would identify options for addressing environmental risks. The criteria for selecting among risk management options were weighted toward human health risks but also included economic, social, and political considerations (Suter 2008).

Early risk assessments focused on COCs that could cause cancer and other health problems in humans; ecological effects were not a part of this initial formulation. This emphasis began to shift in the late 1980s when a growing interest in ecological processes and effects of contaminants on nonhuman end points prompted the US EPA to develop guidelines for risk assessment that focused on the ecological effects of stressors. By the early 1990s, the US EPA generated a framework and a guidance document for the conduct of ecological risk assessment (USEPA 1992, 1997, 1998), while similar guidance documents were developed in Europe, Canada, and Australia (NAS 2016).

The ecological risk assessment framework is informed by research and uses previously collected data to estimate future outcomes, similar to the human risk assessment that preceded it (Fig. 1). The framework was designed not as a rigid structure but rather as a flexible process to be modified over time and used in both human and ecological risk contexts. Since the original ecological risk assessment framework was proposed, it has been updated as the state of the science has advanced. These modifications include recognizing risks from nonchemical stressors (e.g., heat, silt, and habitat loss), expanding the framework to include watershed level assessments and encompass multiple stressors (Suter 2008; Van den Brink et al. 2016), and most recently recognizing ecosystem services as a general ecological assessment end point (Munns et al. 2016). As described by Greenberg et al. (2015), risk assessment has evolved as a result of policy needs, scientific advancements, and resource availability.

The understanding that ecological interactions at the land-water interface influence the fate and transport of COCs has advanced the state of the science (Schiesari et al. 2018). Sufficient knowledge now exists that site managers and risk assessors can incorporate these concepts and apply them within the framework of ecological risk assessment. The goals of this chapter are to (1) provide an overview of contaminant interactions at the land-water interface, (2) present a conceptual model of the major processes that govern insect-mediated contaminant flux, and (3) provide site managers with practical considerations for implementing these ideas within the ecological risk assessment framework.

2 Contaminants and Ecological Subsidies at the Land-Water Interface

The exchange of basic food web components (nutrients, detritus, and prey) between two habitats is referred to as a subsidy (Polis et al. 1997). In this chapter, we focus on a specific and ecologically important type of subsidy: the exchange of components that occur when organisms move from the aquatic ecosystem and enter the terrestrial ecosystem (e.g., salmon are a prey subsidy for bears; Naiman et al. 2002).

In addition to the transfer of food web components between these two habitats, aquatic subsidies can also serve as a vehicle for COCs to move into the terrestrial ecosystem. A tragic example of contaminant-linked subsidies affecting humans occurred in the 1950s in Minamata Bay, Japan. A release of mercury-laden effluent into the bay resulted in toxic levels of Hg moving from sources on land to fish and shellfish inhabiting the aquatic ecosystem. The subsequent consumption of fish and shellfish by humans, cats, and other terrestrial animals resulted in acute mercury poisoning. Another historical example of contaminant-linked subsidies can be found in studies from the 1960s and 1970s focused on egg shell thinning in birds. Here, reproductive failure in piscivorous birds (e.g., eagles and pelicans) was linked to dichlorodiphenyltrichloroethane (DDT) exposure via fish from contaminated aquatic food webs (Hellou et al. 2013).

Similar to fish, certain aquatic insects are a source of high-quality nutrition (Marcarelli et al. 2011; Muehlbauer et al. 2014) as well as contaminants (Menzie 1980; Larsson 1984) for terrestrial predators. These aquatic insects live their early lives underwater as larval aquatic insects before transforming their bodies through metamorphosis and emerging to the terrestrial landscape (Fig. 2). Contaminants can accumulate in these insects during their larval aquatic life stage (Menzie 1980; Larsson 1984; Odin et al. 1995), and certain contaminants can be retained, or even concentrated, in these organism as they go through metamorphosis and emerge as adult aquatic insects (Kraus et al. 2014a). When insects transport contaminants from the aquatic to terrestrial habitat, we refer to this phenomenon as insect-mediated contaminant flux. Insect-mediated contaminant flux deserves significant attention from risk assessors due to the sheer biomass of insects that emerge from the aquatic compartment every year (Gratton and Zanden 2009), which in turn can lead to large contaminant fluxes to the terrestrial landscape (Walters et al. 2008; Raikow et al. 2011). For example, Walters et al. (2008) estimated that for a 25-km

Fig. 2 Most larval aquatic insects live much of their lives underwater and then undergo metamorphosis (arrow) to become flying adult aquatic insects (e.g., dragonflies)

riparian zone, aquatic insects exported ~6.1 g of polychlorinated biphenyls (PCBs) each year, which they calculated to be equivalent to the PCB mass delivered by 50,000 Chinook salmon returning to their breeding grounds in the Pacific Northwest of the United States.

Insect-mediated contaminant flux has been well documented with insectivorous birds. The Tree Swallow (*Tachycineta bicolor*) is a model organism to study this phenomenon since their diets typically contain a large proportion of adult aquatic insects captured at relatively local scales (Bishop et al. 1995; McCarty 2001; Custer et al. 2010). Tree Swallows were foundational in documenting the environmental risks of insect-mediated contaminant flux by mapping direct linkages between aquatic contamination and exposure in terrestrial animals. Diet studies confirmed that Tree Swallows eat aquatic insects and that COCs in insects were high enough to induce sublethal or reproductive effects (McCarty 2001; Custer et al. 2003, 2005).

Walters et al. (2008) broadened this approach by investigating insect-mediated contaminant exposure in a diverse predator assemblage (including reptiles, amphibians, and spiders) living next to a stream contaminated with PCBs and showed that PCB concentrations in predators were linked directly to their relative consumption of adult aquatic insects. Walters et al. (2008) termed insect-mediated contaminant flux the “dark side of subsidies” where “subsidy” referred to the adult aquatic insects consumed by riparian predators and the “dark side” referred to the contaminant burden to which predators are exposed by consuming those insects.

3 Conceptual Model of Insect-Mediated Contaminant Flux

Understanding, predicting, and assessing insect-mediated contaminant flux is challenging. In this section, we present a conceptual model that describes four major processes that govern insect-mediated contaminant flux and alters the extent to which adult aquatic insects expose terrestrial food webs to aquatic contamination. We recognize that many site-specific environmental factors are vital to understanding COC fate and transport (see Table 1 for examples). For the sake of simplicity, all factors other than environmental contaminant concentrations are held constant in the following model. The processes underpinning insect-mediated contaminant flux are presented as a sequence of graphs that introduce a single layer of complexity at a time. Please note that the model presented here is theoretical in nature and the relationships observed between processes may vary depending on site-specific environmental factors.

The following are the four major processes that govern aquatic insect-mediated contaminant flux:

1. Contaminant bioaccumulation in larval aquatic insect tissue
2. Contaminant toxicity to larval aquatic insects
3. Contaminant-induced stress during metamorphosis
4. Preferential contaminant excretion or retention during metamorphosis

Table 1 Core concepts: ABCs of environmental factors. Numerous environmental factors can affect the magnitude and composition of insect-mediated contaminant flux, broadly categorized here into the ABCs of environmental factors: *Abiotic* factors shape biological communities and dictate organism-contaminant interactions, making them the largest group of environmental effects. Included in this category are geographical, chemical, and meteorological mechanisms. *Biotic* factors include an organism's life history and its interactions within a community, including predator-prey interactions, competition, and trophic cascades. *Contaminant* factors consist of exogenous, chemical stressors that interact with the biota in a community. Collectively, these factors can interact with one another, causing complex interactions and effects on insect-mediated contaminant flux. The amount that any particular factor affects contaminant flux varies between sites, species, and contaminants. Below is a list of some common environmental factors and examples of their effects

	Modulator	Effect
Abiotic	Organic carbon	Organic carbon can bind with contaminants, reducing bioavailabiliy.[1]
	Temperature	Temperature will determine rates of biological and chemical processes.[2]
	Nutrients	Nutrient additions can increase the biomass of aquatic emergent insects, leading to greater contaminant export.[3]
	pH	Elevated levels of methylmercury have been observed in acidfied lakes.[4]
	Sulfate/Sulfide	Sulfate is required for mercury methylation via sulfate-reducing bacteria. Sulfide can reduce metal bioavailability and inhibit methylation.[5]
Biotic	Introduced predators	Introduced predators can alter community structures resulting in variations in insect emergence.[6,7]
	Community structure	The presence of predators or prey availability can affect the emergent biomass.[8]
	Seasonality	Insect development and emergence is tied to temperature, light and food availability.[9]
	Allochthonous prey	The removal of terrestrial subsidies can lead to higher rates of predation on aquatic invertebrates.[10]
Contaminant	Predator toxicity	Alterations to predator survival or reproduction can alter community structure.[11]
	Elimination of competition	The removal of competition can cause overall losses in emergence; however, removal of less sensitive species can cause increase in abundance and emergence of hardier taxa.[12]

[1]Di Toro et al. (2001), [2] Ullrich et al. (2001), [3] Jones et al. (2013), [4] Ullrich et al. (2001), [5] Gilmour et al. (1992), [6] Benjamin et al. (2011), [7] Gergs et al. (2014), [8] Tweedy et al. (2013), [9] Williams et al. (2017), [10] Nakano et al. (1999), [11] Gibbons et al. (2015), [12] Rogers et al. (2016)

3.1 Process 1: Contaminant Bioaccumulation in Larval Aquatic Insect Tissue

Many well-studied COCs (PCBs, methylmercury, etc.) bioaccumulate in larval aquatic insects (Menzie 1980; Larsson 1984; Odin et al. 1995; Froese et al. 1998). The relationship between the environmental contaminant concentration and the concentration within the larval aquatic insects is a function of contaminant

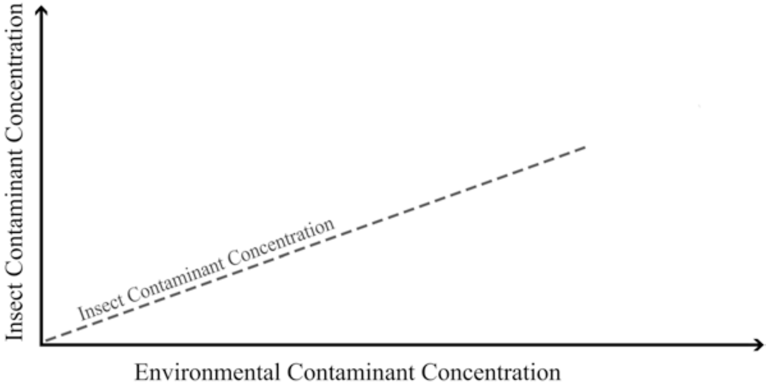

Fig. 3 Contaminant bioaccumulation in larval aquatic insects

bioavailability, uptake, and elimination (Froese et al. 1998). Although these factors vary among COCs, here we assume a positive linear relationship between environmental contaminant concentration and contaminant bioaccumulation in larval aquatic insect tissue (Fig. 3).

3.2 Process 2: Contaminant Toxicity to Larval Aquatic Insects

The concentration at which the contaminant begins to affect larval aquatic insect survival needs to be considered when modeling insect-mediated contaminant flux. As larval aquatic insect survivorship decreases, fewer insects survive to the adult stage. By expanding the bioaccumulation model (Fig. 3) to incorporate contaminant toxicity to larval aquatic insects at higher concentrations, the percentage of larval aquatic insects surviving will eventually approach zero, greatly reducing or eliminating the number of adult aquatic insects emerging (Fig. 4).

3.3 Process 3: Contaminant-Induced Stress During Metamorphosis

Due to sublethal contaminant effects, adult aquatic insect emergence may decline sharply prior to larval aquatic insect mortality (Schmidt et al. 2013; Kraus et al. 2014b). This observation has been framed as the "stressful metamorphosis hypothesis" – larval insects may survive in contaminated environments, but the metabolic costs associated with detoxification leave them too depleted to complete the physiologically costly step of metamorphosis to adulthood (Wesner et al. 2014). The percentage of adult aquatic insect emergence approaches zero before larval aquatic insect survival approaches zero because of contaminant-induced stress during metamorphosis (Fig. 5).

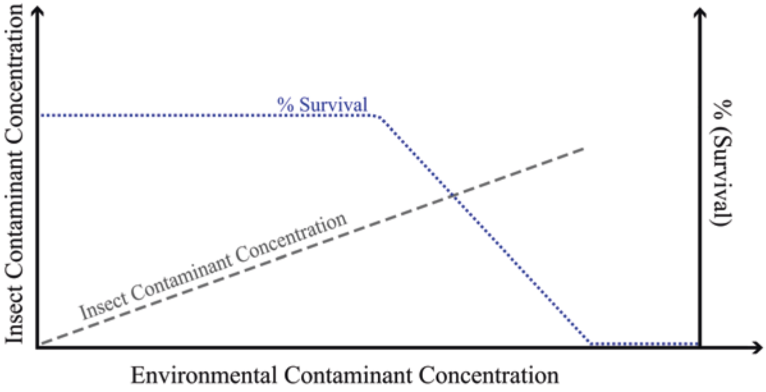

Fig. 4 Larval aquatic insect bioaccumulation and % survival

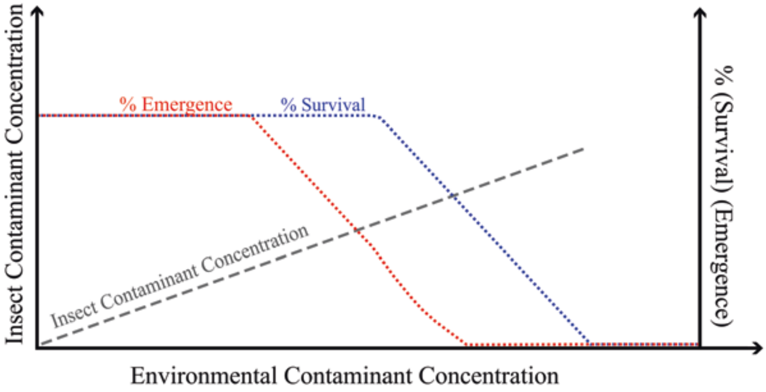

Fig. 5 Larval aquatic insect bioaccumulation, % larval survival, and % adult emergence

3.4 Process 4: Contaminant Concentration Changes During Metamorphosis

Whereas some contaminants are retained or even concentrated in adult aquatic insects through metamorphosis, other contaminants may be lost via shedding of the larval exoskeleton (exuvium) or excretion (Kraus et al. 2014a). Depending on the contaminant, metamorphosis can greatly increase or decrease exposure risk to insectivorous terrestrial predators (Kraus et al. 2014a). For simplicity, this model does not take into account possible contaminant concentration changes during metamorphosis.

3.5 Summary

In this final step of the conceptual model, % survival, % emergence, and % insect-mediated contaminant flux each represent the percent of their respective theoretical maximum values (Fig. 6). Even when environmental and contaminant specific

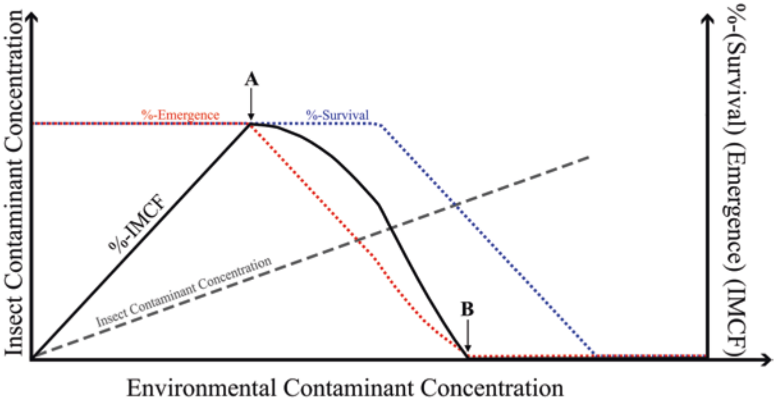

Fig. 6 Larval aquatic insect bioaccumulation, % survival, % emergence, and % insect-mediated contaminant flux (% IMCF). Key inflection points A = % IMCF reaches its apex (100%) with no inhibitory effects and B = % IMCF approaches zero, due to restricted emergence

factors are held constant, contaminant flux remains a dynamic target. Two noteworthy points on the insect-mediated contaminant flux line are highlighted in Fig. 6 and described below.

Point A: Contaminant flux reaches its theoretical maximum, at the point where flux reaches its apex with no inhibitory effects. Even though the environmental contaminant concentration and the concentration in insects continue to increase linearly, insect-mediated contaminant flux begins to decline due to the deleterious effect the contaminant has on insect emergence.

Point B: Even after adult aquatic insect emergence has declined to zero, larval aquatic insects can survive in the aquatic ecosystem. This point describes where larval aquatic insects are present, but emergence is severely or totally restricted.

The conceptual model of insect-mediated contaminant flux considers four major processes. Points A and B highlight the necessity of viewing insect-mediated contaminant flux as a concentration-specific phenomenon.

Core Concept: Calculating Insect-Mediated Contaminant Flux

Insect-mediated contaminant flux is the product of the adult aquatic insect contaminant concentration and adult aquatic insect biomass leaving a specified area using the following equation:

$$\mathrm{IMCF} = [\mathrm{A}] \times \left(\mathrm{E}_{\mathrm{biomass}} / \mathrm{Area} / \mathrm{T}\right)$$

where:

IMCF is the insect-mediated contaminant flux (ng m^{-2} d^{-1})
[A] is the adult insect contaminant concentration (ng/g)
E_{biomass} is the emergent insect biomass leaving the area (g)
Area is the aquatic habitat in square meters (m^2)
T is the time in days (d)

4 The Riparian Impact Test

To assess the likelihood of adverse impacts to terrestrial ecosystems via insect-mediated contaminant flux, we have translated the technical science into actionable conditions for site managers. The major processes described previously have been integrated into a decision-making tool, the Riparian Impact Test (Fig. 7). This tool provides a stepwise series of four conditions that inform terrestrial exposure via aquatic insect-mediated contaminant flux to the riparian ecosystem.

The first condition focuses on the bioaccumulation potential of the contaminant. If the contaminant bioaccumulates in larval aquatic insects (condition 1), then the focus turns to whether contaminant concentrations are lethal to larval insects (condition 2) or if concentrations are sufficient to inhibit insect emergence (condition 3). If the contaminant bioaccumulates and does not cause mortality or inhibit emergence, then the focus moves to whether it is retained during metamorphosis (condition 4). If the four conditions of the Riparian Impact Test are met, then COC exposure to terrestrial predators from adult aquatic insects should be considered for the impact to the riparian ecosystem. If any of the four conditions are not met, insect-mediated contaminant flux should not be considered an exposure pathway for the terrestrial environment. If data are not available to assess if these four conditions are met or not, insect-mediated contaminant flux cannot be ruled out as a potential COC exposure pathway from the aquatic system to the terrestrial environment.

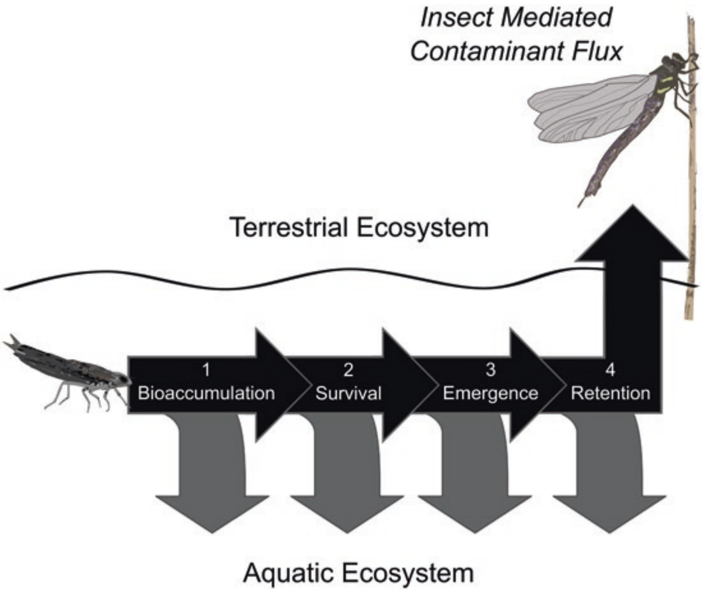

Fig. 7 The Riparian Impact Test: A stepwise decision tool to assess if insect-mediated contaminant flux should be considered in an ecological risk assessment. Each numbered arrow represents a condition of the test. If the condition is not met, then the contaminant is retained in the aquatic ecosystem (gray arrows)

5 Practical Considerations for Site Managers and Decision Makers

The Riparian Impact Test was developed for site managers to determine if adult aquatic insects are distributing aquatic contaminants to the terrestrial ecosystem. For sites where insect-mediated contaminant flux is a potential concern, there are a few practical considerations to keep in mind.

5.1 Practical Consideration 1: Do Not Assume the Biomass and Contaminant Concentrations of Larval Aquatic Insects Are Equivalent to Those of Adult Aquatic Insects

Currently, the state of the science lands on two common points. First, traditionally used Ecological Condition Assessment metrics, like total number of distinct EPT (Ephemeroptera, Plecoptera, and Trichoptera) taxa and the SPEcies At Risk (SPEAR) bioassessment index, may be inappropriate for measuring insect-mediated contaminant flux because larval insect biomass may not be representative of emergent insect biomass (Campero et al. 2008; Arambourou et al. 2012; Janssens and Stoks 2013; Schmidt et al. 2013; Kraus et al. 2014a, b; Wesner et al. 2014; Stoks et al. 2015; Dinh et al. 2016; Debecker et al. 2017; Wesner et al. 2017; Henry and Wesner 2018). Even when emergence is almost completely inhibited by contaminant effects that manifest during metamorphosis, larval aquatic insects can still survive (Point B, Fig. 6; Schmidt et al. 2013; Wesner et al. 2014). Second, if larval aquatic insects complete metamorphosis and emerge, contaminants are not necessarily transported with them. A meta-analysis investigating the effects of insect metamorphosis on contaminant body burdens of adult aquatic insects showed that depending on the contaminant, concentrations can vary between a 125-fold decrease and a 3-fold increase (Kraus et al. 2014a). In this study, metals and polycyclic aromatic hydrocarbons (PAHs) were mainly lost during metamorphosis, and bioaccumulative chlorinated compounds, such as PCBs, became more concentrated after insects emerged.

The consequence of sublethal contaminant stress and metamorphosis on insect-mediated contaminated flux is vital for risk assessors to acknowledge and understand, especially when determining which end points to use when assessing a site. Based on this, we encourage site managers to view *larval aquatic insects and adult aquatic insects as separate end points, even if they are the same species at the same site*.

5.2 *Practical Consideration 2: Make Sure You Are Looking in All the Right Places*

Choosing proper sampling locations is vital to site managers. This consideration raises the following question: where is insect-mediated contaminant flux the highest? Without taking into account the impact of contaminant concentrations on insect-mediated contaminant flux (Fig. 6), it is possible that site managers may be overlooking a potential route of exposure. The immediate area surrounding a contaminant "hot spot" may not be the area of highest risk for insect-mediated contaminant flux. Instead, areas downstream may present higher flux potential once the contaminant concentration has diluted to the point where insect mortality or emergence is less impacted (Fig. 6 – Point A). Based on these concerns, we encourage site managers to *consider not only hot spots but also nearby, less contaminated areas when investigating insect-mediated contaminant flux*.

5.3 *Practical Consideration 3: Choose Your Bioindicator of Insect-Mediated Contaminant Flux Wisely*

Determining the potential for insect-mediated contaminant flux can be challenging. The most direct measure of insect-mediated contaminant flux is adult aquatic insects; however, this approach can be both logistically difficult and time-consuming. Describing a water body's contaminant output requires lengthy sampling regimes, as emergence events are often sporadic and species-dependent. As an alternative to sampling adult aquatic insects directly, bioindicators can be used as an indirect measure of insect-mediated contaminant flux. Ideally, bioindicators of insect-mediated contaminant flux would have a diet composed entirely of adult aquatic insects, would have a small home range, and would be easy to collect.

Two organisms commonly utilized as bioindicators of insect-mediated contaminant flux are Tree Swallows (Custer et al. 1998; Froese et al. 1998; Secord et al. 1999; Echols et al. 2004; Neigh et al. 2006; Spears et al. 2008; Walls et al. 2014) and web-building riparian spiders (e.g., Araneidae and Tetragnathidae) (Otter et al. 2013; Gann et al. 2015; Kraus et al. 2017; Walters et al. 2018). These organisms have diets with significant contributions of adult aquatic insects, which can fluctuate based on food availability and their distance from water (Blancher and McNicol 1991; Akamatsu et al. 2004). Tree Swallows actively feed in an approximately 300–400 m radius around their nests giving a larger spatial resolution than web-building spiders, which are passive predators (Quinney and Ankney 1985) that typically feed on aquatic insects within a few meters of the shoreline (Raikow et al. 2011; Schindler and Smits 2017). Collection of both Tree Swallows and spiders can be relatively easy. Tree Swallow collection involves the construction of nest boxes, which, once built, can be re-sampled or re-deployed for years (Custer et al. 2003, 2005). Riparian spiders are collected by hand directly from their webs. When choosing between Tree Swallows and spiders, considerations should include the biomass needed for chemical analysis, the natural differences that occur between vertebrate and invertebrate organisms, the life cycle of the bioindicator, and the available habitat for sampling.

Based on the state of the science concerning bioindicators of insect-mediated contaminant flux, we suggest that *if adult aquatic insects cannot be measured directly, Tree Swallows or riparian spiders should be considered as bioindicators of contaminant flux from aquatic to riparian habitats*.

5.4 Practical Consideration 4: Be Aware of the Potential Risk Associated with Riparian Bridges

Terrestrial insectivores are not always apex predators and may serve as an intermediate step in a food chain (Cristol et al. 2008). These terrestrial organisms, which we describe as Riparian Bridges, share three common characteristics: (1) at some point in their life cycle, they consume a high proportion of aquatic prey; (2) the COC biomagnifies in their tissues; and (3) at some point in their life cycle, they serve as a prey item for another terrestrial organism.

To date, most work on Riparian Bridges has focused on spiders, which do not simply act as a bioaccumulative repository or a benign mechanism that links aquatic contamination to terrestrial predators but also serve as an additional opportunity for the COC to biomagnify as it moves through the terrestrial food chain (Walters et al. 2010; Gann et al. 2015). Cristol et al. (2008) found spiders had higher concentrations of methylmercury than fish in the same area, and these same spiders composed close to 30% of the diet of two local bird species. At Lake Hartwell (a Superfund site in South Carolina, USA), it was estimated by Walters et al. (2010) that nestlings of small passerine birds were “exposed to physiologically significant doses of PCBs by ingesting a single, typically sized araneid spider.”

Based on current research, we encourage site managers to *investigate the diet of terrestrial organisms to assess the potential for biomagnification in the terrestrial food web, keeping in mind that certain prey items may be Riparian Bridges of aquatic-insect-mediated contaminant flux*.

6 Conclusions

Understanding the interconnectedness of ecosystem compartments and the movement of COCs between them is a complex undertaking (Schiesari et al. 2018). In this chapter, we have focused on some of the specific interactions that occur at the land-water interface between contaminants, aquatic insects, and terrestrial predators with the goal of distilling the complexity of this issue into actionable steps that can be taken by site managers. Specifically, three main conclusions can be drawn:

1. Aquatic COC exposure can become a terrestrial risk via insect-mediated contaminant flux.
2. Larval aquatic insect biomass and contamination may not equal adult aquatic insect biomass and contamination.
3. The Riparian Impact Test can be used to determine the potential for insect-mediated contaminant flux to the terrestrial ecosystem.

Ecological risk assessment and the framework that supports it were founded, and continue to operate, on the principle of adaptability so that the best available science can be used to inform an assessment to drive decision-making. The state of the science concerning insect-mediated contaminant flux is now at a point where the incorporation of these contaminant-subsidy linkages into a risk assessment framework is possible. This chapter can aid site managers and risk assessors to include this phenomenon into their assessment protocols when presented with contaminated sediment sites and at-risk terrestrial species.

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When Nutrients Become Contaminants in Aquatic Systems: Identifying Responses to Guide Terrestrial-Derived Detrital Endpoint Development for Managers

Michelle A. Evans-White, Candice Bauer, and Sally A. Entrekin

> *"The presence and success of an organism or a group of organisms depends upon a complex of conditions. Any condition which approaches or exceeds the limits of tolerance is said to be a limiting condition or a limiting factor."*
>
> E.P. Odum, Fundamentals of Ecology

1 Introduction: Effects of Nitrogen (N), Phosphorus (P), and Salts on Aquatic Life Mediated Through Detrital Pathways

Detritus from terrestrial vegetation is an important terrestrial energy subsidy to aquatic ecosystems. These subsidies not only support but also stabilize ecosystem production, meaning the sum of production across all populations shows a predictable fluctuation around a mean year to year (Holling 1973; Polis and Strong 1996). In contrast to primary production, terrestrial detritus stabilizes aquatic ecosystem processes (i.e., reduced temporal and spatial variation) via independence from variations within the aquatic system because donor-controlled processes from terrestrial inputs and retention are functions of the donor system (Cebrian 1999). Human landscape modifications can change the magnitude and form of terrestrial detritus and alter in-stream retention via habitat modifications that interact with elevated nutrient and salt inputs to modify microbial- and detritivore-driven decomposition rates (Figs. 1 and 2). As detrital inputs (quality and quantity) change, ecosystem

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M. A. Evans-White (✉)
Department of Biological Sciences, University of Arkansas, Fayetteville, AR, USA

C. Bauer
Region 5, United States Environmental Protection Agency, Chicago, IL, United States

S. A. Entrekin
Department of Entomology, Virginia Tech, Blacksburg, VA, USA
e-mail: sallye@vt.edu

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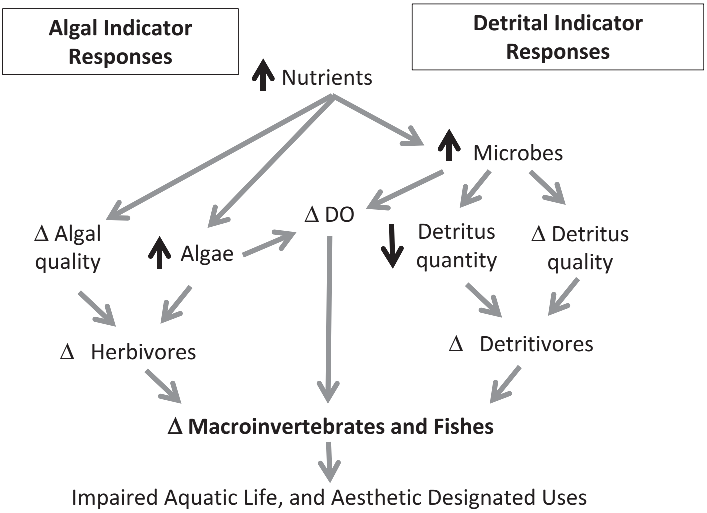


Fig. 1 A conceptual model showing the effects of nutrient enrichment on aquatic life designated uses

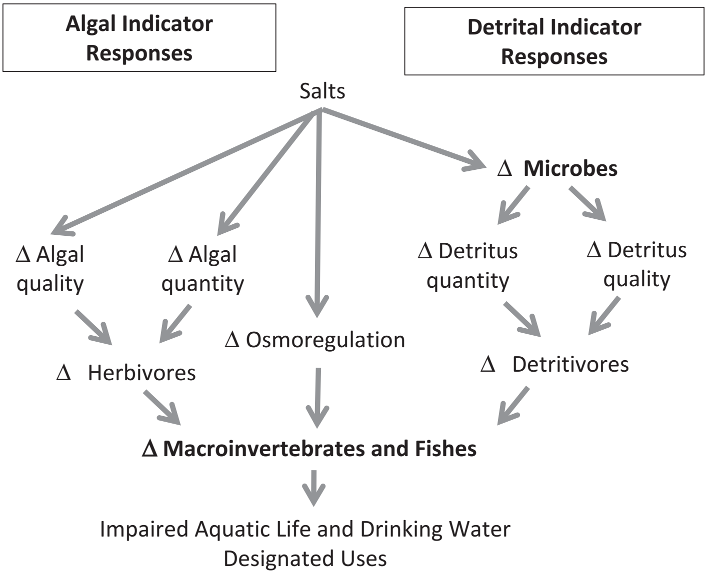


Fig. 2 A conceptual model showing the effects of salt enrichment on aquatic life designated uses

instability increases from deterioration of the biological condition that is intimately linked to the decomposition functional process (e.g., detritivore species loss; Cardinale et al. 2006; McKie et al. 2008).

Nitrogen (N) and phosphorus (P) nutrient additions to streams alter how detrital subsidies are processed. Dissolved N and P additions to wadeable streams tend to stimulate microbial decomposers (Kaushik and Hynes 1971; Gulis et al. 2008; Suberkropp et al. 2010; Tant et al. 2015a, b; Ferreira et al. 2016) leading to an increase in decomposition rates (Kominoski et al. 2015; Rosemond et al. 2015; Ferreira et al. 2016), a decrease in the quantity of coarse detrital standing stocks (Benstead et al. 2009; Rosemond et al. 2015), and altered detrital quality (i.e., nutritional quality) for macrodetritivores (Cross et al. 2003; Davis et al. 2010a, b; Danger et al. 2013; Fuller et al. 2015; Halvorson et al. 2015, 2016b). Macrodetritivores include shredding and collector-gathering functional groups. Shredders, macroinvertebrates that consume food by shredding mouthparts, mostly eat leaves and the affiliated microbes, and so they often contribute more than 50% to leaf decomposition rates (Hieber and Gessner 2002). Collector-gathering taxa tend to eat fine organic particulates that are often a byproduct of shredder feeding. Detrital quality for shredding macroinvertebrates can be defined by the effect of the chemical composition and the microbial community structure on consumption, growth, and production. Increased microbial biomass associated with elevated nutrient concentrations can lead to more nutritious detritus (Chung and Suberkropp 2009a, b; Tank et al. 2010a; Halvorson et al. 2016a) but does not always accompany increases in growth (Boersma and Elser 2006; Fuller et al. 2015; Halvorson et al. 2015a). Detritivorous macroinvertebrate production may be negatively affected by reductions in coarse detrital quantity (Wallace et al. 1999; Entrekin et al. 2007). However, moderate levels of nutrient enrichment can increase biomass and production of macroinvertebrates per unit of detrital standing stocks (Cross et al. 2006), particularly in larger-bodied detritivore taxa (Davis et al. 2010a, b). Field studies across broader nutrient gradients have also found that richness of detritivorous stream insects can have a negative threshold relationship with increasing nutrients (Evans-White et al. 2009); taxa with higher nutrient demands tend to numerically dominate the community at nutrient concentrations above richness threshold concentrations and sensitive taxa are lost (subsidy-stress relationship, Fig. 3).

While salts and salt mixtures can reduce detrital subsidy processing by causing taxon-specific physiological stress and altered trophic interactions, low-level salt concentrations can increase processes by alleviating taxon-specific stress and changing trophic interactions. Historically, salts have been studied as a contaminant, whereas N and P have been studied as agents of enrichment leading to bias in research and terminology. Heterotrophic microbes/fungi and macroinvertebrate leaf-eating detritivores often regulate the rate of leaf decomposition (Wallace and Webster 1996; Graca et al. 2001; Hieber and Gessner 2002). Salt inputs raise freshwater total dissolved ion concentration and electrical conductivity to impair freshwater communities as measured by changes in macroinvertebrate community structure. Stoneflies, mayflies, and caddisflies tend to be most sensitive because their external gills, size, and other morphological features increase contact with the

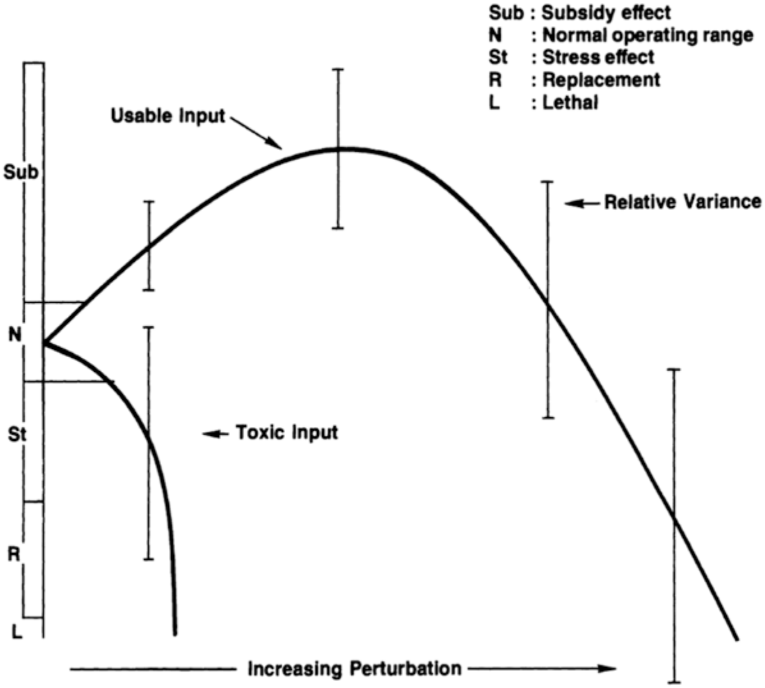


Fig. 3 Subsidy-stress model from Odum, Eugene P., John T. Finn, and Eldon H. Franz. "Perturbation theory and the subsidy-stress gradient." *Bioscience* 29.6 (1979): 349–352. The two responses represent contrasts in biological response to a system perturbation. The first line shows a perturbation has only a stress response to organisms that results in that response below the normal operative range with concurrent increase in variation. In contrast, a perturbation (like nutrients and salts) can results in an increase in a measured biological response (like growth, respiration) to a threshold where subsidy is measurable until increases in that perturbation eventually leads to a response decline below the normal range and can be interpreted as a stress effect, replacement, or lethal depending on the extent of the response relative to the normal operating range

environment (Buchwalter et al. 2002; Piscart et al. 2011; Pond et al. 2014; Szocs et al. 2014; Olson and Hawkins 2017). Salt concentrations toxic to macroinvertebrates also tend to be toxic to prokaryotes and fungi. Excess ions, often two to four orders of magnitude above ambient concentrations or 2000 μS/cm electrical conductivity, result in osmotic imbalances between organisms and their environment (Kefford et al. 2007; Canhoto et al. 2017; Castillo et al. 2018). Ion imbalance can cause mortality from the increased energy expenditure and investment in morphological structures that are required to maintain homeostasis (Buchwalter et al. 2002; Kefford et al. 2004; Scheibener et al. 2015).

Salts can alter microbial-macroinvertebrate detritivore interactions to suppress trophic transfer and reduce detrital quality through changes to heterotrophic exoenzyme production and nutrient immobilization (Sinsabaugh et al. 2009; Swan and DePalma 2012), which lead to altered detrital nutrient ratios (i.e., stoichiometry;

stress-response sensu Evans-White et al. 2009; Sinsabaugh and Follstad Shah 2012; Rosemond et al. 2015). However, macroinvertebrate detritivores and microbes can also show subsidy responses to salts that are ion and concentration specific making ecosystem consequences difficult to predict (Clark et al. 2004; Hassell et al. 2006; Kefford et al. 2007, 2016). Subsidy-stress responses of detritivores and detrital processing to rising salts suggest low salt levels can reduce energy expenditures associated with osmoregulation (Hart et al. 1991; Scheibener et al. 2015; Kefford et al. 2016) and indicate complex dynamics not currently considered in a regulatory framework.

In this chapter, we make the case for including detrital endpoints that serve as indicators of changes in water quality into the US regulatory framework for wadeable freshwaters. Detrital subsidies support and stabilize aquatic life and ecosystem function. Macroinvertebrate and microbe communities in freshwater ecosystems respond both positively and negatively to inputs of nutrients and salts, depending on their concentration. Detrital-based streams experience excessive inputs of nutrient and salt which can destabilize and degrade freshwater ecosystems. To accomplish our goal, we review existing US water quality endpoint response characteristics and present a suite of endpoints derived from a literature review that can be used to detect changes in detrital-based wadeable streams caused by elevated nutrient and salt contaminants.

2 N, P, and Salts: Too Much of a Good Thing?

Excessive nutrient (N and P) and salt inputs in their soluble forms can sorb to soils and elevate nutrient and salt content in terrestrial plant material changing intrinsic detrital quality inputs to streams (Cross et al. 2003; Scott et al. 2013) or be carried into streams via surface flow (Entrekin et al. 2019). At acutely toxic concentrations, nutrients and salts have direct negative impacts on freshwater aquatic ecosystems that result in the mortality of some or all of community members (direct pathway). However, more commonly, increased nutrients and salts could have a subsidy effect that stimulates biological production above via autotrophic and heterotrophic pathways [Fig. 1; (Odum et al. 1979)]. Increasing concentrations that are "perturbed" past the subsidy level can also lead to stress manifested in changes in community structure and performance variability that is illustrated by perturbation theory and the subsidy-stress gradient (Fig. 3). For example, P can stimulate growth but may cause declines in growth once nutritional demands are met due to C-limitation driven by increased metabolic costs of P excretion or reduced consumption caused by an artificial sense of satiation tied to the elevated P content of the detritus (Boersma and Elser 2006). In addition, low-level increases in ions in freshwaters result in a less hypotonic environment for ion-sensitive freshwater organisms, thus reducing energy expenditures associated with osmoregulation (Hart et al. 1991; Scheibener et al. 2015; Kefford et al. 2016). However, once homeostasis is achieved via rising external salt inputs, energy toward osmoregulation will increase causing a concurrent decline in biological performance down the falling limb of the perturbation gradient. Performance below "normal operating range" is a measure of stress that is characterized by increasing relative variance. Regulatory approaches to nutritional elements try to reduce concentrations below the level where stress occurs.

3 Terrestrial Detritus-Based Streams Experience Excess Inputs of N, P, and Salt

Nutrient (Fig. 4a, b) and salt concentrations and composition in freshwater ecosystems vary not only from differences in geology and precipitation (Fig. 5a) but also from human activities that result in increases in freshwaters around the world (Fig. 5b; Smith et al. 2003; Anning and Flynn 2014). Agriculture, road deicers, water softeners, sewage, resource extraction effluent, fossil fuel combustion, and weathering of rock formations exposed by mining and drilling contribute significant nutrients and salts (typically as anions and cations) to freshwaters. In fact, the most recent available assessment of US wadeable streams estimated poor biological condition of aquatic life in 46% of the nation's waters caused by excessive nutrients, pathogens, sediment, habitat degradation, and organic contaminants like pesticides [Fig. 6, (USEPA 2006, 2016)]. The percentage scoring poor for biological condition increases from about 27 to 50% from the west to the east coast (Fig. 6). Many of the streams with poor condition were located in deciduous forested ecoregions (USEPA 2006, 2016) where detritus in the form of autumn-shed leaf litter can be a large energy subsidy resulting in significant aquatic life production (Fisher and Likens 1973; Wallace et al. 1997). Up to 90% of all fixed carbon ends up as terrestrial detritus that enters aquatic systems and is an abundant and stable food to aquatic ecosystems (Polis and Strong 1996; Moore et al. 2004).

Land cover modifications also alter terrestrial detrital inputs to detrital-based streams. Globally, land cover modifications by humans are the single largest threat to species and ecosystems. For example, 35% of Earth's ice-free land is devoted to agriculture (Ellis and Ramankutty 2008). Furthermore, approximately 80% of terrestrial net primary production is commandeered for anthropogenic uses (Ellis 2015) reducing and altering organic matter inputs to receiving streams (Tank et al. 2010a, b). Finally, detrital input amount, form, and quality interact with altered aquatic habitats (e.g., lower retention) and water quality (e.g., novel chemical combinations) to disrupt ecosystem function (Craig et al. 2017; Arthington et al. 2018; Kaushal et al. 2018) and drive reductions in specialized indigenous species and increases in generalist species (Devictor et al. 2008). As a result, freshwater aquatic organisms are among the most at risk of extinction due to human watershed alterations (Dudgeon et al. 2006; Strayer and Dudgeon 2010; Carpenter et al. 2011), particularly those organisms adapted to feeding on leaf litter, a low-nutrient food resource (Fig. 6).

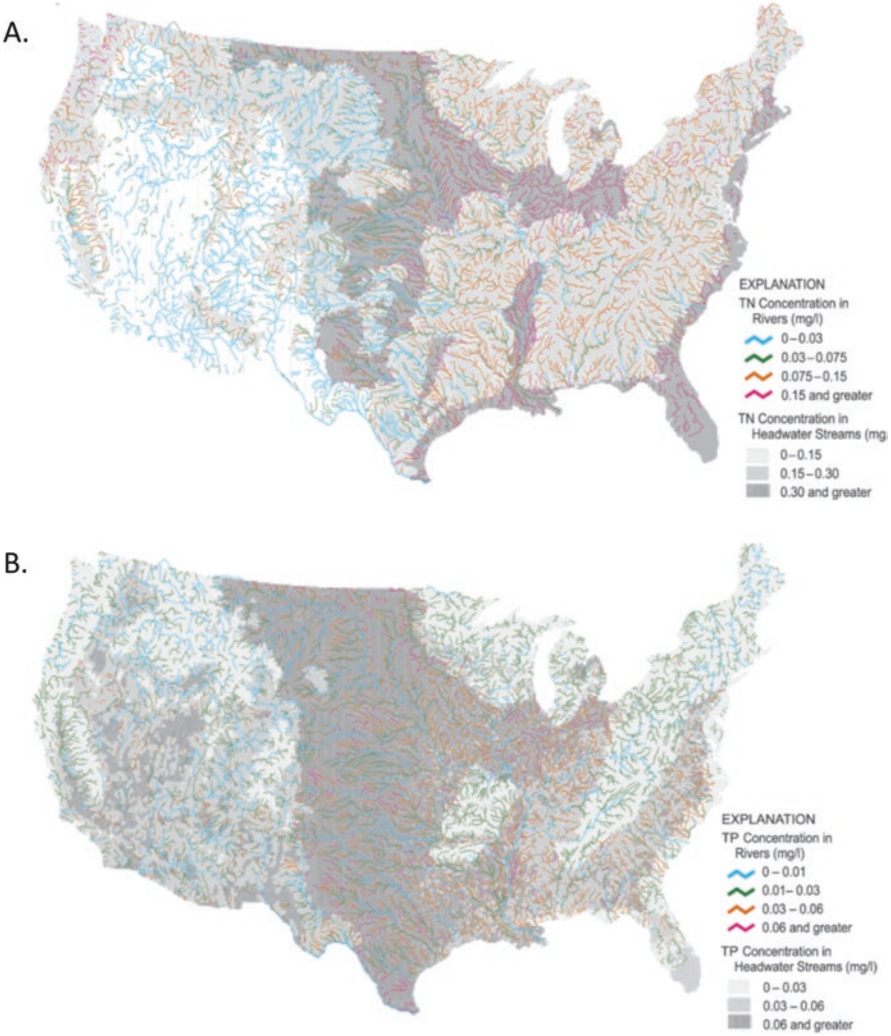
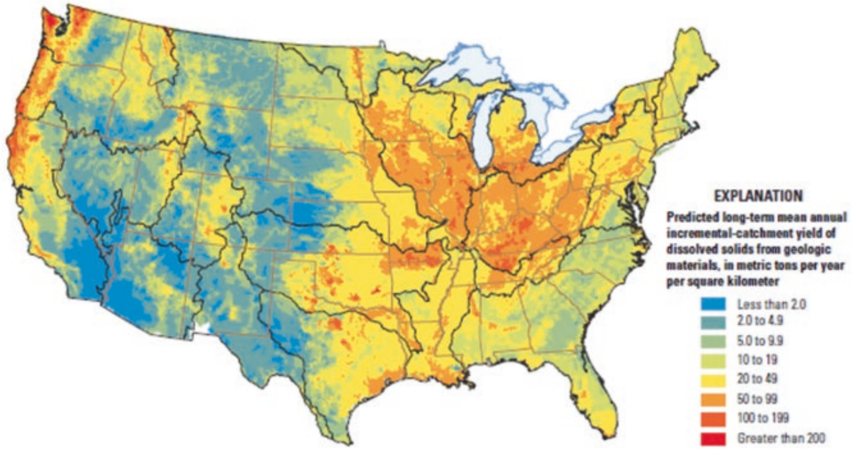


Fig. 4 Model prediction of background concentrations of nutrients in headwater streams (shaded areas) and streams and rivers with drainage area greater than 500 km^2: (**a**) total nitrogen corrected for atmospheric deposition; (**b**) total phosphorus. Taken directly and written as in Smith, Richard A., Richard B. Alexander, and Gregory E. Schwarz. "Natural background concentrations of nutrients in streams and rivers of the conterminous United States." (2003) Environmental Science & Technology, 14: 3039–3047

A. Incremental-catchment yield.



B. Source-share contributions.

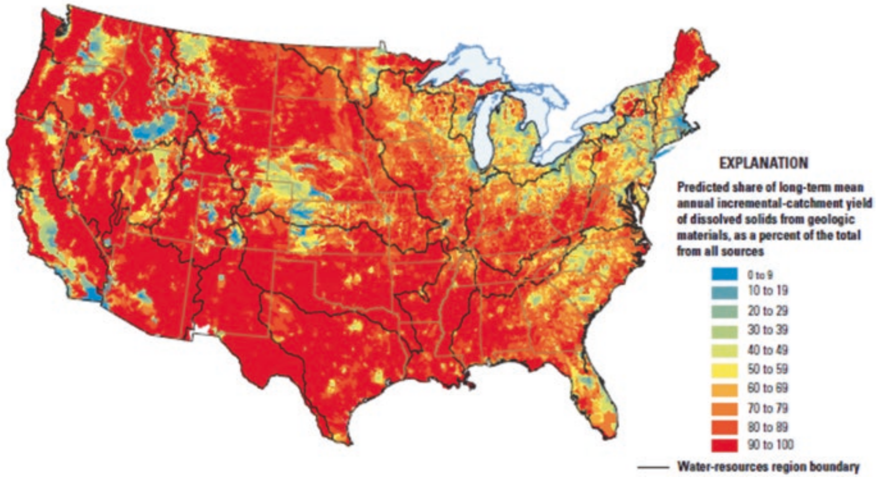


Fig. 5 US maps showing long-term annual incremental-catchment yield from Anning, David W., and Marilyn E. Flynn. *Dissolved-solids sources, loads, yields, and concentrations in streams of the conterminous United States*. No. 2014-5012. US Geological Survey, 2014. Predicted total dissolved solids from geologic materials where hotter colors show where geology contributes the most to dissolved solids (**a**) and predicted dissolved solids from SPARROW model where more red means greater proportion geology contributed to dissolved solids (**b**)

4 Regulatory Approach to Aquatic N, P, and Salt Impairment

Inclusion of detrital-based metrics that inform water managers about nutrient and salt contaminants and are protective of aquatic life intimately linked to detrital pathways could utilize existing US water quality regulatory infrastructure. All states

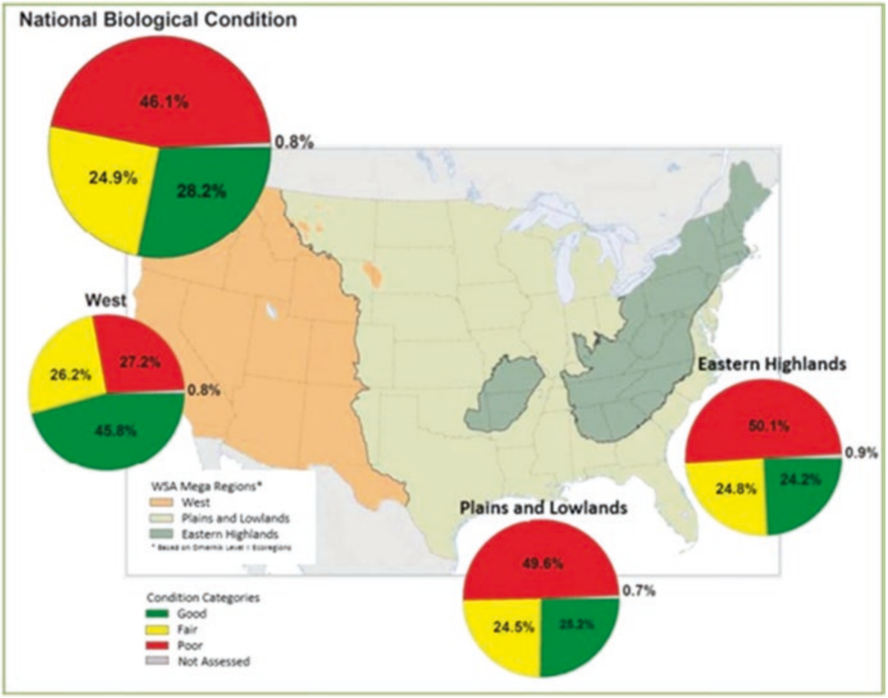


Fig. 6 Biological condition of United States rivers and streams based on a macroinvertebrate multi-metric index (USEPA 2016). Data comes from EPAs National River and Stream Assessment data collected in 2008

must adopt total nitrogen (TN) and total phosphorus (TP) numeric criteria as described in the 1998 US Clean Water Action Plan (USEPA 2000). These TN and TP criteria are currently informed primarily by algal-based endpoints; development of detrital-based endpoints can be modeled after the development of algal-based endpoints. Development of ion-specific salt numeric criteria could be modeled after TN and TP criteria development because both nutrients and salts are nutritional elements that can have subsidy-stress effects on aquatic life. As described in the US Clean Water Act (CWA) and accompanying regulations (see 40CFR131), water quality standards adopted by state environmental agencies must include a description of the goals for all waters called “designated uses,” which include uses such as “support of aquatic life,” “recreation in and on the water,” and “drinking water.” These water quality standards should therefore work to ensure the protection of human health and the aquatic environment. Standards in the form of narrative and numeric water quality criteria are derived in part from *endpoints*, which are measurable biotic or abiotic indicators of changes in water quality that can derive or be included as criteria, narrative or numeric. Standards define the conditions necessary to ensure designated uses are protected and, along with strategies to protect exceptional water quality (called anti-degradation policies), form the backbone of Clean Water Act strategies to control water pollution.

Endpoints are metrics that indicate change in an ecosystem due to a stressor such as nutrients and salts. They can be in the form of the stressor (e.g., nutrient concentration) or be functionally related to the stressor or the effect of the stressor on aquatic communities, ecosystems, or designated uses. Effective endpoints should be responsive to additions of the stressor, and the response should be consistent and predictable. Endpoint responsiveness or sensitivity can be demonstrated by scientific, peer-reviewed statistical (i.e., empirical) relationships to water quality (USEPA 2010). An ideal indicator has a high rate of change relative to the change in the water quality component of interest (e.g., large effect size, slope, or threshold) and low natural variability and should return to unimpacted levels quickly after the water quality stressor of interest returns to background levels (USEPA 2014).

With the development of guidance to derive nutrient criteria, US EPA and individual states of the United States have worked to identify a variety of biological endpoints based on field-measured parameters that represent important components of the food web and can be used to derive or refine numeric nutrient water quality criteria for regulatory purposes. Two main approaches have been used to develop numeric nutrient criteria (USEPA 2000) and should be considered for the development of criteria for other stressors, such as salts, where a body of scientific knowledge exists to show that the pollutant impairs aquatic life: reference-condition and stressor-response methods (also called dose-response relationships (USEPA 2010)).

The reference-condition approach estimates conditions based off of a percentile analysis of data collected on the endpoint of interest (e.g., TN, TP, turbidity) from a population of minimally impacted water bodies (USEPA 2000; Smith et al. 2003; Palmstrom 2005; Robertson et al. 2006; Herlihy and Sifneos 2008; Griffith 2014), although other approaches to identifying reference conditions can use regression techniques (Dodds and Oakes 2004). For example, the US EPA proposed regional TN and TP criteria using percentile analysis that states could adopt if they chose (USEPA 2000). In contrast, the stressor-response approach focuses on developing a statistical relationship between a biological endpoint and the contaminant in the laboratory (e.g., toxicological studies) or from field measurements using a variety of statistical approaches (Dodds et al. 2010; USEPA 2010; Evans-White et al. 2013). For example, Florida, Minnesota, and Wisconsin numeric TP criteria were developed based upon field measurements analyzed to determine the relationships between TP concentrations and biological endpoints including, but not limited to, measurements of algal chlorophyll *a*, diatom indexes of biological integrity, sensitive macroinvertebrates, and fish taxa or indices. Further, the Minnesota and Florida numeric criteria approaches incorporate biological endpoints such as sestonic algal chlorophyll *a* and macroinvertebrate index scores directly into the expression of their numeric criteria. In both cases, TP criteria were chosen based on the value of TP concentration where the functional relationship between these biological metrics changed (e.g., threshold reduction in richness) or the biological response was deemed problematic (e.g., sestonic chlorophyll *a* concentration).

Similarly, where salt numeric criteria have been adopted by individual states, the measures incorporated into water quality standards and in the basis for their derivation vary. For example, some states have adopted the EPA's 1988 criteria recommendation for chloride concentration (one of the ions of several common salts) or its predecessor, which was an aquatic life criteria recommendation for total dissolved solids (e.g., Ohio); both criteria recommendations were derived using laboratory toxicity data in a way similar to many other EPA-derived criteria for the protection of aquatic life, while others have derived criteria for measures of various salts using reference-based approaches (e.g., Arkansas).

Currently, regulatory assessments conducted by states and localities focus on water-quality measurements of stressors including nutrients and salts, although some states also use biological endpoints to document impacts to aquatic life. More recent efforts have also developed criteria based on the negative effects of contaminants on plants and algae (e.g., for the common herbicide atrazine) and criteria for primary productivity endpoints such as algal chlorophyll *a* necessary to prevent eutrophication. These criteria more often include measurements of endpoints that represent the quantity (e.g., sestonic and benthic chlorophyll *a*) and quality (e.g., algal or macrophyte taxonomy) of primary producers in the aquatic ecosystems (Figs. 1 and 2) rather than endpoints based on macroinvertebrates and fish measures. No solely detrital endpoints or measures that indicate change in aquatic detrital-based systems have been adopted.

5 A Suite of Possible Detrital Endpoints

This section evaluates common, standardized measures of microbial decomposer and detritivore structure and function (i.e., detrital endpoints) where peer-reviewed literature exists to assess consistency and sensitivity of responsiveness to elevated nutrients and salt concentrations. We do this to help assess ease of implementation into regulatory frameworks. We defined consistency as the number of studies that similarly reported positive, negative, or no response of a given endpoint to increases in nutrient or salt concentrations (Tables 1 and 3). If responses across a concentration gradient yielded a functional relationship, we reported the relationship type (Tables 2 and 3). Functional relationship constants like slope from linear regression or response maximums and half-maximum response concentrations from Michaelis-Menten saturating relationships can inform our estimate of endpoint sensitivity. We examined sensitivity by comparing effect sizes among endpoints if readily available (larger effect sizes were more sensitive) and by looking at the concentration range and time duration of the response. The data available to inform detrital endpoints for nutrients was much greater than the data available to inform endpoints for salts. Therefore, we provided a more definitive analysis of endpoint consistency and sensitivity for nutrient than for salt endpoints. The objective of the salt endpoint section was to generate the data needed to inform possible future salt endpoints.

Terrestrial detrital microbial and macroinvertebrate responses to nutrient and salt concentrations in freshwater ecosystems have been measured using many different experimental units, experimental designs, gradients, techniques, and terrestrial detrital types (Tables 1, 2, and 3) that could cause variation in response consistency

Table 1 Detrital response types, method, response directions, dissolved nitrogen concentration [N] and phosphorus [P] experimental ranges, and detrital litter types used in nutrient enrichment studies with detrital-dependent variables

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (µg/L[d])	Nutrient effect size	Detrital type
Baldy et al. (2007)	Bacterial biomass	Cell counts +biovolumes	+	5000–6700 [DIN]	3.4–89 [SRP]		Alder
Stelzer et al. (2003)	Bacterial biomass	Cell counts +biovolumes	0	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Sugar maple
Stelzer et al. (2003)	Bacterial biomass	Cell counts +biovolumes	0	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		American
Stelzer et al. (2003)	Bacterial biomass	Cell counts +biovolumes	0	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Red oak wood veneers
Stelzer et al. (2003)	Bacterial biomass	Cell counts +biovolumes	0	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Black cherry wood veneers
Stelzer et al. (2003)	Bacterial biomass	Cell counts +biovolumes	0	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Sugar maple wood veneers
Stelzer et al. (2003)	Bacterial biomass	Cell counts +biovolumes	0	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Yellow birch wood veneers
Stelzer et al. (2003)	Bacterial biomass	Cell counts +biovolumes	0	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		American beech wood
Suberkropp and Chauvet (1995)	Bacterial biomass	Maximum ATP	+	20–313[DIN]	8–92 [SRP]		Yellow poplar
Suberkropp et al. (2010)	Bacterial biomass	Cell counts +biovolumes	0	26.2–506 [DIN]	8.1–80 [SRP]		Mixed
Tant et al. (2013)	Bacterial biomass	Cell counts +biovolumes	+	22–506 [DIN]	6.8–80 [SRP]	1.39	Red maple
Tant et al. (2013)	Bacterial biomass	Cell counts +biovolumes	+	22–506 [DIN]	6.8–80 [SRP]	4.53	Rhododendron
Tant et al. (2013)	Bacterial biomass	Cell counts +biovolumes	+	22–506 [DIN]	6.8–80 [SRP]	0.31	FPOM

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (μg/L[d])	Nutrient effect size	Detrital type
Suberkropp et al. (2010)	Bacterial biomass (area-specific)	Cell counts +biovolumes	0	26.2–506 [DIN]	8.1–80 [SRP]		Mixed
Gulis and Suberkropp (2003, 2004)	Bacterial carbon	Cell counts	+	11–199 [DIN]	4–34 [SRP]		Red maple
Gulis and Suberkropp (2003, 2004)	Bacterial carbon	Cell counts	+	11–199 [DIN]	4–34 [SRP]		Rhododendron
Gulis and Suberkropp (2003, 2004)	Bacterial cell number	Cell counts	+	11–199 [DIN]	4–34 [SRP]		Red maple
Gulis and Suberkropp (2003, 2004)	Bacterial cell number	Cell counts	+	11–199 [DIN]	4–34 [SRP]		Rhododendron
Ferreira et al. (2006)	Decomposition (k)	Field litter bags (10-mm) 35-d incubation	+	65,82 [DIN]	91,71 [SRP]		Alder
Ferreira et al. (2006)	Decomposition (k)	Field litter bags (10-mm) 35-d incubation	+	65,82 [DIN]	91,71 [SRP]		Oak
Ferreira et al. (2006)	Decomposition (k)	Field litter bags (10-mm) 84-105-d incubation	+	65,82 [DIN]	91,71 [SRP]		Balsa wood veneers
Gulis et al. (2006)	Decomposition (k)	Field litter bags (500-μm), 57-d incubation	+	72–2995 [DIN]	3–56 [SRP]		Oak
Gulis et al. (2006)	Decomposition (k)	Field litter bags (500-μm), 26-d incubation	+	72–2995 [DIN]	3–56 [SRP]		Alder
Gulis et al. (2006)	Decomposition (k)	Field litter bags (10-mm), 57-d incubation	+	72–2995 [DIN]	3–56 [SRP]		Oak

(continued)

Table 1 (continued)

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (µg/L[d])	Nutrient effect size	Detrital type
Gulis et al. (2006)	Decomposition (k)	Field litter bags (10-mm), 26-d incubation	+	72–2995 [DIN]	3–56 [SRP]		Alder
Kominoski et al. (2015)	Decomposition (k)	Field litter bags (500-µm), 59-d incubation	+	54–545 [DIN]	4–78 [SRP]	4.75	*Acer rubrum*
Kominoski et al. (2015)	Decomposition (k)	Field litter bags (500-µm), 59-d incubation	+	54–545 [DIN]	4–78 [SRP]	7.00	*Rhododendron maximum*
Rosemond et al. (2002)	Decomposition (k)	Field litter bags (2-cm) 28-d incubation	+	59–223 [DIN]	5–230 [SRP]		*Ficus insipida*
Woodward et al. (2012)	Decomposition (k): detritivore-mediated	Field litter bags (10-mm and 500-µm) incubation time of ≥ 50% mass loss	+,–	14–21641 [DIN]	<1 to 926 [SRP]		*Quercus robur*
Woodward et al. (2012)	Decomposition (k): detritivore-mediated	Field litter bags (10-mm and 500-µm) incubation time of ≥ 50% mass loss	+,–	14–21641 [DIN]	<1 to 926 [SRP]		*Alnus glutinosa*
Rosemond et al. (2002)	Fungal biomass	Ergosterol	+	59–223 [DIN]	5–230 [SRP]		*Ficus insipida*
Baldy et al. (2007)	Fungal biomass	Ergosterol	+/–	5000–6700 [DIN]	3.4–89 [SRP]	3.36	Alder
Cheever et al. (2012)	Fungal biomass	Ergosterol	+	5–896 [NO3]	2.7–7.4 [SRP]		Red maple
Cheever et al. (2013)	Fungal biomass	Ergosterol	0	bd-1396 (NO3)	bd-10.5 [SRP]		Sugar maple
Gulis and Suberkropp (2003, 2004)	Fungal biomass	Ergosterol	+	11–199 [DIN]	4–34 [SRP]		Red maple

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (μg/L[d])	Nutrient effect size	Detrital type
Gulis and Suberkropp (2003, 2004)	Fungal biomass	Ergosterol	+	11–199 [DIN]	4–34 [SRP]		Rhododendron
Gulis et al. (2006)	Fungal biomass	Ergosterol	+	72–2995 [DIN]	3–56 [SRP]		Oak
Gulis et al. (2006)	Fungal biomass	Ergosterol	0	72–2995 [DIN]	3–56 [SRP]		Alder
Gulis et al. (2008)	Fungal biomass	Ergosterol	+	11–199 [DIN]	12–82 [SRP]		Wood
Gulis et al. (2008)	Fungal biomass	Ergosterol	+	11–199 [DIN]	12–82 [SRP]		Rhododendron
Kominoski et al. (2015)	Fungal biomass	Ergosterol	+	54–545 [DIN]	4–78 [SRP]		*Acer rubrum*
Kominoski et al. (2015)	Fungal biomass	Ergosterol	+	54–545 [DIN]	4–78 [SRP]		*Rhododendron maximum*
Stelzer et al. (2003)	Fungal biomass	Ergosterol	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Sugar maple
Stelzer et al. (2003)	Fungal biomass	Ergosterol	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		American beech
Stelzer et al. (2003)	Fungal biomass	Ergosterol	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Red oak wood veneers
Stelzer et al. (2003)	Fungal biomass	Ergosterol	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Black cherry wood veneers
Stelzer et al. (2003)	Fungal biomass	Ergosterol	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Sugar maple wood veneers

(continued)

Table 1 (continued)

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (μg/L[d])	Nutrient effect size	Detrital type
Stelzer et al. (2003)	Fungal biomass	Ergosterol	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Yellow birch wood veneers
Stelzer et al. (2003)	Fungal biomass	Ergosterol	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		American beech wood veneers
Suberkropp et al. (2010)	Fungal biomass	Ergosterol	+	26.2–506 [DIN]	8.1–80 [SRP]		Mixed
Tant et al. (2013)	Fungal biomass	Ergosterol	+	22–506 [DIN]	6.8–80 [SRP]	0.64	Red maple
Tant et al. (2013)	Fungal biomass	Ergosterol	+	22–506 [DIN]	6.8–80 [SRP]	5.52	Rhododendron
Tant et al. (2013)	Fungal biomass	Ergosterol	0	22–506 [DIN]	6.8–80 [SRP]	0.21	FPOM
Suberkropp et al. (2010)	Fungal biomass (area-specific)	Ergosterol	–	26.2–506 [DIN]	8.1–80 [SRP]		Mixed
Baldy et al. (2007)	Fungal biomass (conidial)	Incubation + microscopy	0	5000–6700 [DIN]	3.4–89 [SRP]		Alder
Gulis et al. (2008)	Fungal growth rate	Radiolabeled acetate	+	11–199 [DIN]	12–82 [SRP]		Wood
Gulis et al. (2008)	Fungal growth rate	Radiolabeled acetate	+	11–199 [DIN]	12–82 [SRP]		Rhododendron
Gulis et al. (2008)	Fungal production	Biomass*growth	+	11–199 [DIN]	12–82 [SRP]		Wood
Gulis et al. (2008)	Fungal production	Biomass*growth	+	11–199 [DIN]	12–82 [SRP]		Rhododendron
Suberkropp et al. (2010)	Fungal production	Radiolabeled acetate	+	26.2–506 [DIN]	8.1–80 [SRP]		Mixed

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (μg/L[d])	Nutrient effect size	Detrital type
Suberkropp et al. (2010)	Fungal production (area-specific)	Radiolabeled acetate	+	26.2–506 [DIN]	8.1–80 [SRP]		Mixed
Gulis and Suberkropp (2003, 2004)	Fungal richness	Microscopy	+	11–199 [DIN]	4–34 [SRP]		Red maple
Gulis and Suberkropp (2003, 2004)	Fungal richness	Microscopy	+	11–199 [DIN]	4–34 [SRP]		Rhododendron
Gulis and Suberkropp (2003, 2004)	Fungal sporulation	Incubation + microscopy	+	11–199 [DIN]	4–34 [SRP]	20.50	Red maple
Gulis and Suberkropp (2003, 2004)	Fungal sporulation	Incubation + microscopy	+	11–199 [DIN]	4–34 [SRP]	34.00	Rhododendron
Gulis et al. (2006)	Fungal sporulation	Incubation + microscopy	+	42–2995 [NO3]	3–56 [SRP]		Oak
Gulis et al. (2006)	Fungal sporulation	Incubation + microscopy	+	42–2995 [NO3]	3–56 [SRP]		Alder
Suberkropp and Chauvet (1995)	Fungal sporulation (maximum)	Incubation + microscopy	+	20–313 [DIN]	8–92 [SRP]		Yellow poplar
Suberkropp et al. (2010)	Microbial production	Radiolabeled leucine	+	26.2–506 [DIN]	8.1–80 [SRP]		Mixed
Suberkropp et al. (2010)	Microbial production (area-specific)	Radiolabeled leucine	0	26.2–506 [DIN]	8.1–80 [SRP]		Mixed
Baldy et al. (2007)	Respiration	0.25 h incubation	+	5000–6700 [DIN]	3.4–89 [SRP]	6.12	Alder

(continued)

Table 1 (continued)

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (μg/L[d])	Nutrient effect size	Detrital type
Gulis and Suberkropp (2003, 2004)	Respiration	0.5 h incubation	+	11–199 [DIN]	4–34 [SRP]		Red maple
Gulis and Suberkropp (2003, 2004)	Respiration	0.5 h incubation	+	11–199 [DIN]	4–34 [SRP]		Rhododendron
Gulis et al. (2008)	Respiration	0.5 h incubation	+	11–199 [DIN]	12–82 [SRP]		Rhododendron
Gulis et al. (2008)	Respiration	0.5 h incubation	+	11–199 [DIN]	12–82 [SRP]		Wood
Howarth and Fisher	Respiration	2 h incubation	+	10000 [NO3]	10000 [SRP]	2.00–3.00	Red maple
Kominoski et al. (2015)	Respiration	0.5 h incubation	+	54–545 [DIN]	4–78 [SRP]		*Acer rubrum*
Kominoski et al. (2015)	Respiration	0.5 h incubation	+	54–545 [DIN]	4–78 [SRP]		*Rhododendron maximum*
Niyogi et al. (2013)	Respiration	8–18 h incubation	+	11–1872 [DIN]	2–340 [SRP]		Red beech
Stelzer et al. (2003)	Respiration	4 h incubation	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		American beech
Stelzer et al. (2003)	Respiration	4 h incubation	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Red oak wood veneers
Stelzer et al. (2003)	Respiration	4 h incubation	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Black cherry wood veneers
Stelzer et al. (2003)	Respiration	4 h incubation	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Sugar maple wood veneers

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (μg/L[d])	Nutrient effect size	Detrital type
Stelzer et al. (2003)	Respiration	4 h incubation	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Yellow birch wood veneers
Stelzer et al. (2003)	Respiration	4 h incubation	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		American beech wood veneers
Stelzer et al. (2003)	Respiration	4 h incubation	+	9.9,196.1,174.1 [NO3]	0.8,1.1,29.9 [SRP]		Sugar maple
Suberkropp et al. (2010)	Respiration	0.5 h incubation	+	26.2–506 [DIN]	8.1–80 [SRP]		Mixed
Tant et al. (2013)	Respiration	0.5 h incubation	+	22–506 [DIN]	6.8–80 [SRP]	3.00	Rhododendron
Tant et al. (2013)	Respiration	0.5 h incubation	+	22–506 [DIN]	6.8–80 [SRP]	0.50	FPOM
Tant et al. (2013)	Respiration	0.5 h incubation	+	22–506 [DIN]	6.8–80 [SRP]	1.22	Red maple
Suberkropp et al. (2010)	Respiration (area-specific)	0.5 h incubation	+	26.2–506 [DIN]	8.1–80 [SRP]		Mixed
Bergfur and Friberg (2012)	Respiration (bacterial)	24–25 h incubation	+	0, 337,674,1011 [NO3]	0, 5,10,15 [SRP]		Alder
Bergfur and Friberg (2012)	Respiration (bacterial)	24–25 h incubation	+	0, 337,674,1011 [NO3]	0, 5,10,15 [SRP]		Oak
Bergfur and Friberg (2012)	Respiration (fungal)	24–25 h incubation	+	0, 337,674,1011 [NO3]	0, 5,10,15 [SRP]		Alder
Bergfur and Friberg (2012)	Respiration (fungal)	24–25 h incubation	+	0, 337,674,1011 [NO3]	0, 5,10,15 [SRP]		Oak
Cross et al. (2003)	Litter C:P	Field litter grab samples; 2 year enrichment	0	29,383[D1N]	7,46[SRP]		Mixed

(continued)

Table 1 (continued)

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (µg/L[d])	Nutrient effect size	Detrital type
Cross et al. (2003)	Litter C:P	Field litter grab samples; 2 year enrichment	–	29,383[DIN]	7,46[SRP]		Mixed
Cross et al. (2003)	Litter N:P	Field litter grab samples; 2 year enrichment	–	29,383[D1N]	7,46[SRP]		Mixed
Kominoski et al. (2015)	Litter C:N	Field litter bags (500-µm), 59-d incubation	–	54–545 [DIN]	4–78 [SRP]	−0.64	*Acer rubrum*
Kominoski et al. (2015)	Litter C:N	Field litter bags (500-µm), 59-d incubation	–	54–545 [DIN]	4–78 [SRP]	−1.85	*Rhododendron maximum*
Kominoski et al. (2015)	Litter C:N	Field litter grab samples	–	NR	8–62.3 [TP]	−1.80	Mixed
Kominoski et al. (2015)	Litter C:P	Field litter bags (500-µm), 59-d incubation	–	54–545 [DIN]	4–78 [SRP]	−3.40	*Acer rubrum*
Kominoski et al. (2015)	Litter C:P	Field litter bags (500-µm), 59-d incubation	–	54–545 [DIN]	4–78 [SRP]	−5.79	*Rhododendron maximum*
Scott et al. (2012)	Litter C:P	Lab mesocosms, 139-d incubation	–	1300 [DIN]	0,550,500 [SRP]	−4.00	*Acer saccharum*
Scott et al. (2012)	Litter C:P	Lab mesocosms, 139-d incubation	–	1300 [DIN]	0,550,500 [SRP]	−2.50	*Quercus Stellata*
Scott et al. (2012)	Litter C:P	Field litter grab samples	–	NR	8–62.3 [TP]	−3.20	Mixed
Scott et al. (2012)	Litter N:P	Lab mesocosms, 139-d incubation	–	1300 [DIN]	0,550,500 [SRP]	−2.63	*Acer saccharum*
Scott et al. (2012)	Liner N:P	Lab mesocosms, 139-d incubation	–	1300 [DIN]	0,550,500 [SRP]	−1.89	*Quercus Stellata*
Scott et al. (2012)	Litter N:P	Field liner grab samples	–	NR	8–62.3 [TP]	−2.18	Mixed

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (μg/L[d])	Nutrient effect size	Detrital type
Small and Pringle (2010)	Litter C:P	Field liner grab samples	–	117–228 [DIN]	2.3–135 [SRP]		
Small and Pringle (2010)	Litter N:P	Litter grab samples	–	117–228 [DIN]	2.3–135 [SRP]		
Tant et al. (2013)	Litter C:N	Field litter bags (5-mm) 28-d incubation	–	22–506 [DIN]	6.8–80 [SRP]		Red maple
Tant et al. 2013	Litter C:N	Field litter bags (5-mm) 49-d incubation	–	22–506 [DIN]	6.8–80 [SRP]		Rhododendron
Tant et al. (2013)	Litter C:P	Field litter bags (5-mm) 28-d incubation	–	22–506 [DIN]	6.8–80 [SRP]		Red maple
Tant et al. (2013)	Litter C:P	Field litter bags (5-mm) 49-d incubation	–	22–506 [DIN]	6.8–80 [SRP]		Rhododendron
Rosemond et al. (2002)	Macroinvertebrate biomass	Field litter bags (2-cm) 28-d incubation	+	59–223 [DIN]	5–230 [SRP]		*Ficus insipida*
Cross et al. (2006)	Litter standing crop	Quantitative sampling	–	29,3 83 [DIN]	7,46[SRP]	−0.57	Mixed
Cross et al. (2006)	Macroinvertebrate secondary production (mixed substrate)	Quantitative sampling	+	29,383[D1N]	7,46[SRP]	1.61	
Cross et al. (2006)	Macroinvertebrate secondary production (mixed substrate)	Quantitative sampling	+	29,3 83 [DIN]	7,46[SRP]	1.35	
Cross et al. (2006)	Macroinvertebrate secondary production (bedrock substrate)	Quantitative sampling	+	29,383[D1N]	7,46[SRP]		
Cross et al. (2006)	Macroinvertebrate abundance (mixed substrate)	Quantitative sampling	+	29,383[DIN]	7,46[SRP]	1.34	

(continued)

Table 1 (continued)

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (μg/L[d])	Nutrient effect size	Detrital type
Cross et al. (2006)	Macroinvertebrate biomass (mixed substrate)	Quantitative sampling	+	29,383[D1N]	7,46[SRP]	1.17	
Cross et al. (2006)	Macroinvertebrate abundance (bedrock)	Quantitative sampling	0	29,383[DIN]	7,46[SRP]	NA	
Cross et al. (2006)	Macroinvertebrate abundance (bedrock)	Quantitative sampling	0	29,383[D1N]	7,46[SRP]	NA	
Cross et al. (2006)	<1 year life span macroinvertebrate secondary production (whole stream)	Quantitative sampling	+	29,383[DIN]	7,46[SRP]		
Cross et al. (2006)	>1 year life span macroinvertebrate secondary production (whole stream)	Quantitative sampling	+	29,383[D1N]	7,46[SRP]		
Evans-White et al. (2009)	Shredder richness (US Central Plains, all seasons)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		
Evans-White et al. (2009)	Collector-gatherer richness (US Central Plains, all seasons)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		
Evans-White et al. (2009)	Shredder richness (US Central Plains, all seasons)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		
Evans-White et al. (2009)	Collector-gatherer richness (US Central Plains, all seasons)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		
Evans-White et al. (2009)	Shredder C:P (US Central Plains, all seasons)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		
Evans-White et al. (2009)	Collector-gatherer C:P (US Central Plains, all seasons)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		

Citation	Response type[a]	Method	Response direction[b]	[N] range (mg/L[c])	[P] range (μg/L[d])	Nutrient effect size	Detrital type
Evans-White et al. (2009)	Shredder richness (US Central Plains, spring+autumn)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		
Evans-White et al. (2009)	Collector-Gatherer Richness (US Central Plains, spring+autumn)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		
Evans-White et al. (2009)	Shredder richness (US Central Plains, spring+autumn)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		
Evans-White et al. (2009)	Collector-gatherer richness (US Central Plains, spring+autumn)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		
Evans-White et al. (2009)	Shredder C:P (US Central Plains, all seasons)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		
Evans-White et al. (2009)	Collector-gatherer C:P (US Central Plains all seasons)	Qualitative 2-h bioassessment sampling	–	40–32,080 [TN]	5–8,700 [TP]		

[a] All variables are expressed per unit of detrital mass (dry or ash-free dry)

[b] + = an increase, – = a decrease, +/– = an increase to a maximum, then a decrease

[c] [DIN] Dissolved inorganic nitrogen concentration, [NO_3] Nitrate concentration, [TN] Total nitrogen concentration

[d] [SRP] Soluble reactive phosphorus concentration, [TP] Total phosphorus concentration

[*] If effect is positive, then *it* is calculated as the mean of the most enriched treatment divided by the mean in the control
If the effect is negative, then it is calculated as the negative of the mean in the control divided by the mean in the most enriched treatment

Table 2 Functional relationships between nutrient concentrations (independent variables) and detrital measures (dependent variables) and their associated model coefficients if reported

Citation	Functional type	Independent	Dependent	Litter type
Kominoski et al. (2015)	Linear fixed effects models (AIC)	log[DIN],log[SRP],DINxSRP	Decomposition (k)	*Acer rubrum*
Kominoski et al. (2015)	Linear fixed effects models (AIC)	log[DIN],log[SRP],DINxSRP	Decomposition (k)	*Rhododendron maximum*
Cheever et al. (2012)	Linear regression	[NO_3]	Decomposition (k)	Red maple
Cheever et al. (2012)	Linear regression	[NH_4]	Decomposition (k)	Red maple
Cheever et al. (2012)	Linear regression	[SRP]	Decomposition (k)	Red maple
Gulis et al. (2006)	Linear regression	[SRP]	Decomposition (k)	Alder
Gulis et al. (2006)	Linear regression	[SRP]	Decomposition (k)	Oak
Ferreira et al. (2006)	Michaelis-Menten model	[NO_3]	Decomposition (k)	Alder
Ferreira et al. (2006)	Michaelis-Menten model	[NO_3]	Decomposition (k)	Oak
Ferreira et al. (2006)	Michaelis-Menten model	[NO_3]	Decomposition (k)	Balsa wood veneers
Gulis et al. (2006)	Michaelis-Menten model	[SRP]	Decomposition (k)	Alder
Gulis et al. (2006)	Michaelis-Menten model	[SRP]	Decomposition (k)	Oak
Kominoski et al. (2015)	Michaelis-Menten model	[DIN]	Decomposition (k)	*Acer rubrum*
Kominoski et al. (2015)	Michaelis-Menten model	[DIN]	Decomposition (k)	*Rhododendron maximum*
Kominoski et al. (2015)	Michaelis-Menten model	[SRP]	Decomposition (k)	*Acer rubrum*
Kominoski et al. (2015)	Michaelis-Menten model	[SRP]	Decomposition (k)	*Rhododendron maximum*

(continued)

Table 2 (continued)

Citation	Functional type	Independent	Dependent	Litter type
Rosemond et al. (2002)	Michaelis-Menten model	[SRP]	Decomposition (k)	*Ficus insipida*
Suberkropp and Chauvet (1995)	Pearson correlation	[NO_3]	Decomposition (k)	Yellow poplar
Suberkropp and Chauvet (1995)	Pearson correlation	[SRP]	Decomposition (k)	Yellow poplar
Rosemond et al. (2002)	Michaelis-Menten model	[SRP]	Ergosterol	*Ficus insipida*
Kominoski et al. (2015)	Linear fixed effects models (AIC)	[DIN],[SRP],time	Fungal biomass ergosterol	*Acer rubrum*
Kominoski et al. (2015)	Linear fixed effects models (AIC)	[DIN],[SRP],time	Fungal biomass ergosterol	*Rhododendron maximum*
Cheever et al. (2012)	Linear regression coefficients	[NO_3]	Fungal biomass ergosterol	Red maple
Cheever et al. (2012)	Linear regression coefficients	[NH_4]	Fungal biomass ergosterol	Red maple
Cheever et al. (2012)	Linear regression coefficients	[SRP]	Fungal biomass ergosterol	Red maple
Ferreira et al. (2006)	Michaelis-Menten model	[NO_3]	Into condia (%)	Alder
Ferreira et al. (2006)	Michaelis-Menten model	[NO_3]	Into condia (%)	Oak
Ferreira et al. (2006)	Michaelis-Menten model	[NO_3]	Into condia (%)	Balsa
Rosemond et al. (2002)	Michaelis-Menten model	[SRP]	Invertebrate biomass	*Ficus insipida*
Kominoski et al. (2015)	Linear fixed effects models (AIC)	log[DIN],log[SRP],DINxSRP, time	Litter C:N	*Acer rubrum*

(continued)

Table 2 (continued)

Citation	Functional type	Independent	Dependent	Litter type
Kominoski et al. (2015)	Linear fixed effects models (AIC)	log[DIN],log[SRP],DINxSRP, time	Litter C:N	*Rhododendron maximum*
Kominoski et al. (2015)	Linear fixed effects models (AIC)	log[DIN],log[SRP],DINxSRP, time	Litter C:P	*Acer rubrum*
Kominoski et al. (2015)	Linear fixed effects models (AIC)	log[DIN],log[SRP],DINxSRP, time	Litter C:P	*Rhododendron maximum*
Scott et al. (2012)	Linear regression	[TP]	Litter C:P	Mixed
Small and Pringle	Linear regression coefficient	[SRP]	Litter C:P	Mixed
Small and Pringle	Linear regression coefficient	[SRP]	Litter N:P	Mixed
Suberkropp and Chauvet (1995)	Pearson correlation	[NO_3]	Maximum ATP	Yellow poplar
Suberkropp and Chauvet (1995)	Pearson correlation	[SRP]	Maximum ATP	Yellow poplar
Suberkropp and Chauvet (1995)	Pearson correlation	[NO_3]	Maximum sporulation rate	Yellow poplar
Suberkropp and Chauvet (1995)	Pearson correlation	[SRP]	Maximum sporulation rate	Yellow poplar
Kominoski et al. (2015)	Linear fixed effects models (AIC)	log[DIN],log[SRP],DINxSRP	Respiration	*Acer rubrum*
Kominoski et al. (2015)	Linear fixed effects models (AIC)	log[DIN],log[SRP],DINxSRP	Respiration	*Rhododendron maximum*
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TN]	Shredder richness (US Central	
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TN]	Collector-gatherer richness (US	

(continued)

Table 2 (continued)

Citation	Functional type	Independent	Dependent	Litter type
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TP]	Shredder richness (US Central	
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TP]	Collector-gatherer richness (US	
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TP]	Shredder C:P (US Central Plains,	
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TP]	Collector-gatherer C:P (US	
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TN]	Shredder richness (US Central	
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TN]	Collector-gatherer richness (US	
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TP]	Shredder richness (US Central	
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TP]	Collector-gatherer richness (US	
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TP]	Shredder C:P (US Central Plains,	
Evans-White et al. (2009, 2013)	Spearman + NCPA	[TP]	Collector-Gatherer C:P (US	
Woodward et al. (2012)	Hump-shape	[DIN]	Decomposition (k): detritivore-	
Woodward et al. (2012)	Hump-shape	[SRP]	Decomposition (k): detritivore-	

AIC Akaike's Information Criterion, *NCPA* Nonparametric Changepoint Analysis, *[DIN]* Dissolved inorganic nitrogen concentration, *[SRP]* Soluble reactive phosphorus concentration, *[NO_3]* Nitrate concentration, *[TN]* Total nitrogen concentration, *[TP]* Total phosphorus concentration

Table 3 Freshwater animal responses to changes in total dissolved solids as an indicator of salt concentration

Citation	Taxa response	Total dissolved solids (g/L) dominant major ion	Response direction[a]	Study type
Clark et al. (2004)	*O. taeniorhynchus* growth rates	3.5–175 g/L NaCl	0	Lab gradient
Drover (2018)	Shredder density less Leuctridae	0.014–9.4 *g/L* SO_4	–	Coal mining
Hassell et al. (2006)	*Chironomous dilutus* larvae % emerged	0.44–17.4 g/L NaCl	+/–	Lab gradient
Hassell et al. (2006)	*Chironomous dilutus* larvae time to emerge	0.44–17.4 *g/L* NaCl	+	Lab gradient
Entrekin et al. (2019)	*Amphinemura* daily growth rate	0.016–0.064 g/L NaCl; $NaHCO_3$	+	Lab gradient
Mogilevski (2019)	*Lepidostoma* sp. instantaneous growth rates	0.016–0.064 g/L NaCl; $NaHCO_3$	+	Lab gradient
Drover (2018)	Leuctridae density	0.014–9.4 g/L SO_4	+	Field gradient
Castillo et al. (2018)	Macroinvertebrate shredder LC50	8.7–285 g/L NaCl	–	LC50
Castillo et al. (2018)	Macroinvertebrate collector-gatherer	0.68–14.3 g/L NaCl	–	LC50
Castillo et al. (2018)	Macroinvertebrate collector-filterer LC50	0.8–19.6 g/L NaCl	–	LC50
Castillo et al. (2018)	Macroinvertebrate scraper LC50	3.1–28.6 g/L NaCl	–	LC50
Clark et al. (2004)	*A. aegypti* larval growth rate	3.5–17.5 g/L NaCl	–	Lab gradient
Hassell et al. (2006)	*Centroptilum* sp. and *Cleon* sp. mortality	6.8 g/L NaCl	+/–	Lab gradient
Hassell et al. (2006)	*Centroptilum* sp. and *Cleon* sp. LC 50	0.612–1.8 g/L NaCl	+/–	Lab gradient
Hassell et al. (2006)	*Chironomous dilutus* larvae growth	0.44–17.4 g/L NaCl	+/–	Lab gradient
Tyree et al. (2016)	*Lirceus* sp. change in length	0.003–0.214 g/L NaCl	–	Lab gradient
Tyree et al. (2016)	*Tipula* sp. instantaneous growth	0.003–0.214 g/L NaCl	0	Lab gradient
Clark et al. (2004)	*O. taeniorhynchus* pupal mass	3.5–17.5 g/L NaCl	+	Lab gradient
Clark et al. (2004)	*O. taeniorhynchus* larval state development time	3.5–17.5 g/L NaCl	+	Lab gradient
Clark et al. (2004)	*A. aegypti* larval state development time	3.5–17.5 g/L NaCl	+/–	Lab gradient
Venancio et al. (2017)	Basidiomycete and zygomycete fungi EC50	10.1–14.9 g/L NaCl	–	Lab gradient

(continued)

Table 3 (continued)

Citation	Taxa response	Total dissolved solids (g/L) dominant major ion	Response direction[a]	Study type
Venancio et al. (2017)	Basidiomycete and zygomycete fungi EC50	13.7–23.1 g/L sea water	–	Lab gradient
Van Meter et al. (2011)	Copepod density	0.645 g/L Cl	–	Lab
Van Meter et al. (2011)	Tadpole growth	0.645 g/L Cl	+	Lab
Van Meter et al. (2011)	Tadpole time to adult	0.645 g/L Cl	–	Lab
Schuler et al. (2017)	Amphipod abundance	0.025–0.200 g/L NaCl	0	Mesocosm gradient
Schuler et al. (2017)	Amphipod abundance	0.025–0.200 g/L $MgCl_2$	+	Mesocosm gradient

[a] + = an increase, – = a decrease, +/– = an increase to a maximum, then a decrease

and sensitivity. Experimental designs span from replicated artificial aquatic systems to surveys of streams with differing nutrient or salt concentrations. Many studies reported categorical manipulations of nutrients or salt and compare a “high” concentration with a control (ambient) concentration. Fewer studies take a gradient approach and examine responses across three or more concentrations.

The time-integrated endpoint response to exposure varied. For example, many endpoints that estimate microbial decomposer responses to nutrients and salts represent a snapshot (< 1 day) of the community structure or function such as respiration, biomass, growth, and production. These endpoints are often measured at multiple points throughout the study. In contrast, decomposition rates are a possible endpoint that integrates ecosystem responses to contaminant exposure over a longer period of time and provides an estimate of the life span (i.e., weeks to years) of the detrital matter in the stream. Similarly, detritivorous macroinvertebrate metrics integrate responses to nutrients and salts over time frames of their life spans (i.e., weeks to years).

5.1 Responses to Nutrients

5.1.1 Microbial Detrital N and P Endpoints

Measurement Method Fungal and bacterial biomass, growth, and production are good endpoints for managers to consider given the prevalence of studies measuring their responses to nutrient concentrations in freshwater ecosystems (N = 15 studies; Table 1). Microbial responses to nutrients have been measured using multiple techniques. Often passive samplers such as senescent, dried leaf litter, unstained wood veneers, and standardized cellulose material (e.g., cotton fabric strips) are deployed in situ for weeks to months, colonized by fungi and bacteria, and then collected over time and analyzed in the laboratory. Most studies report general increases in microbial measures with deployment duration. Therefore, it is not clear if there is a "best" time to sample deployed detrital material to assess a microbial nutrient response, which will make standardization of methodology more difficult. Managers may need to visit sites more than twice to assess responses adding difficulty to bioassessment designs.

Most studies that estimate fungal biomass first measure ergosterol content, a biomolecule unique to fungi, using a liquid-phase extraction of a known mass of the deployed detrital material followed by high-performance liquid chromatography (e.g., Gulis and Suberkropp 2003; Cheever et al. 2013; Tant et al. 2013). Conversions to fungal biomass are completed using a known relationship between ergosterol and fungal biomass (Gessner and Chauvet 1994; Gulis and Suberkropp 2004). Bacterial biomass, on the other hand, has primarily been estimated by microscopy. Bacterial cells are stained with 4′,6-diamidino-2-phenylindole (DAPI), counted, and measured so that biovolume can be estimated. Fungal sporulation rates (Gulis and Suberkropp 2003) and conidial production (Baldy et al. 2007) have also been quantified as an indicator of fungal growth, which also involves short-term incubations, filtration of incubation water onto filters, and microscopy to identify spores and conidia (Baldy et al. 1995, 2007). Biovolumes can be estimated from conidia dimensions (Barlocher and Schweizer 1983). Microbial growth rates have occasionally been measured using isotopically-labeled biomolecules (Gulis et al. 2008; Suberkropp et al. 2010); microbial biomass coupled to growth allows for estimation of microbial production. Respiration rates have been estimated from measuring dissolved oxygen changes over time in short-term detrital incubations (0.5–25 h). Few have measured fungal and bacterial respiration rates separately because of the complex experimental manipulations with fungicide and antibiotic that are needed (Bergfur and Friberg 2012).

None of these common microbial respiration and biomass measures require more effort than measurements for other commonly used water quality endpoints. In general, microscopic examination needed to estimate sporulation rates takes several hours per sample but should not differ appreciably from time spent on other common bioassessment measures, such as benthic macroinvertebrate community or algal community endpoints. Laboratory chemical measures of ergosterol require less time than microscopic counts examining bacterial biomass or fungal community structure and sporulation as multiple samples can be analyzed during one event, but they require chemical consumables and laboratory expertise similar to those needed for water chemistry analysis. Respiration incubations are short, usually less than 1 day (Table 1), and only require a dissolved oxygen/temperature probe.

Response Direction, Functional Relationship, and Consistency Heterotrophic microbial responses to an elevation in water nutrient concentrations should be consistently positive given that bacteria and fungi tend to have a more stable and lower tissue C:nutrient ratio than terrestrial plant detritus (Elser et al. 2000; McGroddy et al. 2004) and their growth can be nutrient limited. Elevated water nutrient concentrations should relieve nutrient imbalances between microbes and their detrital food substrate causing an increase in microbial respiration, biomass, growth, and production. Indeed, nutrient enrichment studies consistently found that fungal and bacterial biomass, growth, and production on terrestrial plant detritus expressed as a rate per unit mass increased in a statistically significant way when dissolved nutrient concentrations were elevated compared to ambient conditions regardless of the substrate type (n = 68 of 84 responses; Table 1); area-specific (system-level) rates were rarely reported (n = 2 of 84), but one study showed a decline with increased dissolved nutrients likely due to a decline in detrital resource standing stocks and availability for decomposers (Cross et al. 2006; Suberkropp et al. 2010).

Functional relationships between microbial measures and nutrient concentrations were not often reported (Table 2). Some studies did report positive linear relationships between nutrient concentrations and detrital ATP concentrations (Suberkropp and Chauvet 1995), fungal sporulation rates (Suberkropp and Chauvet 1995), fungal biomass (Cheever et al. 2012), and the percent of initial ash-free dry mass converted to conidia (Ferreira et al. 2006; Michaelis-Menten model). Future studies should include concentration gradients in their design.

Sensitivity of Metric The quantitative results needed to compile and calculate the magnitude of the nutrient response relative to a control, which can be used to gauge endpoint sensitivity, were less readily reported. Further, in most studies, dissolved N and P were manipulated in tandem, and results did not allow for separation of effects by nutrient type. However, combined nutrient responses relative to controls could sometimes be estimated (Table 1). The magnitude of fungal and bacterial biomass responses ranged from 0.21 to 5.5 times above the control. Respiration response range (0.5–6) was similar to microbial biomass response range. Quantitative fungal growth or sporulation responses to nutrient manipulations relative to controls were high (20–35) relative to reported biomass and respiration responses, suggesting that this rarely measured variable may be more sensitive to nutrient enrichment than other common microbial measures.

Sensitivity may also be estimated by examining the range of stressor concentrations where a response is observed. The concentration range of studies reporting statistically significant nutrient effects was large (Table 1). However, responses were commonly reported in studies where the maximum manipulated dissolved inorganic nitrogen (DIN) or nitrate concentrations were less than 2000 μg/L and soluble reactive phosphorus (SRP) was less than 85 μg/L. Nutrient criteria in wadeable streams are often in the form of total nitrogen (TN) and total phosphorus (TP) (Evans-White et al. 2013), which may or may not be highly correlated with DIN and SRP (Dodds 2003). Many algal metrics show responses between 270 and 1790 μg TN/L and 6 and 280 μg TP/L (Evans-White et al. 2013). Therefore, microbial responses may be just as sensitive as autotrophic metrics to changes in water quality.

One important trait of a good endpoint involves its sensitivity to the decline in the stressor as well as to the presence of the stressor (USEPA 2014). These types of studies are rarely done. One study did report declines in detrital microbial production rates after detritus was transplanted to a lower nutrient concentration site [5 days or less (Suberkropp and Chauvet 1995)]. Examining the microbial response and rate of return after cessation of the stressor would be helpful in future research.

5.1.2 Detrital C, N, and P Stoichiometry Endpoints

Measurement Method Detrital C, N, and P stoichiometry is the molar ratio of the dry mass of these elements in detritus and the associated microbial community and should be considered as an endpoint because it is an important indicator of decomposition and of nutritional quality for benthic detritivorous macroinvertebrates (Manning et al. 2015; Halvorson et al. 2015a; Manning et al. 2016). Resources that have more similar stoichiometric ratios to their consumers (i.e., usually more enriched in N and P relative to C) are usually more nutritious. Stoichiometric ratios are often, but not always, measured along with the measures of fungal and bacterial biomass, growth, or production (Table 1). Laboratory techniques are relatively standard; it is measured on dried (24–48 h, ≤ 60 °C to avoid N-volatilization), finely ground detrital material collected from the field or from an experimental system (Benstead et al. 2017). Percent C and N can be obtained on dried material (usually <10 mg) using a CHN Analyzer, which are often readily available in laboratories that specialize in stable isotopic analysis. Percent P is usually quantified by chemically digesting a known dried quantity of the sample followed by an ascorbic acid colorimetric analysis for soluble reactive phosphorus. The laboratory time required for C, N, and P analyses is no more time intensive or expensive than standard water nutrient or algal measures.

Most studies examining nutrient effects on detrital stoichiometry placed passive samples of litter originating from the dominant tree species or a mix of common tree taxa in study streams or experimental mesocosms (Table 1). Several studies utilized field litter bags filled with a known litter type or grab samples of mixed litter. Some studies examined detrital stoichiometry on known litter types in laboratory mesocosms.

Response Direction, Functional Relationship, and Consistency Response direction and the functional relationship over time can inform passive sample incubation duration standardization. Litter C:nutrient ratios generally decreased over time due to colonization by microbes with lower C:nutrient ratios than the detritus (i.e., became more nutritious). One study found a saturating Michaelis-Menten (M-M) relationship between litter P:C and time (Scott et al. 2013), which would suggest that passive sample duration time could be standardized to occur after the maximum P:C is reached and was stable. Post oak tended to reach its minimum C:P (maximum P:C) earlier than sugar maple detritus. In addition, oak (48-d) and maple (142-d) incubated at 500 mg DIP/L tended to take longer to reach their minimum C:P than oak (16-d) and maple (129-d) incubated at 50 mg DIP/L. Additional studies examining detrital stoichiometry over time across a variety of litter types would confirm the use of M-M models of this dynamic and would inform incubation time necessary for field assessments.

Nutrient enrichment of stream water consistently reduced detrital C:nutrient and N:P ratios (n = 19 of 20; Table 1). Linear models reporting the relationships between nutrient concentrations and detrital nutrient stoichiometry (i.e., ratios) could serve to develop nutrient criteria (Table 3). Linear relationship slopes and intercepts depend upon litter type (Kominoski et al. 2015), but laboratory mesocosm studies that incorporate a recalcitrant and labile species can estimate the bounds of field detrital stoichiometry from field mixed litter grab samples (Scott et al. 2013). Linear models of detrital elemental composition including dissolved inorganic N and soluble reactive P concentrations were better than those including only one of those variables, suggesting both nutrients interact to affect detrital stoichiometry (Kominoski et al. 2015; Manning et al. 2016).

Sensitivity of Metric The effect size of the decline ranged from −0.64 to −1.80, −2.5 to −5.79, and − 1.89 to −2.63 for C:N, C:P, and N:P, respectively (Table 1). Variation in the magnitude of change with a given nutrient increase was likely related to variation in initial litter stoichiometry (Manzoni et al. 2008, 2010) and biochemical composition that can vary widely across plant species (McGroddy et al. 2004). Specifically, nutrients tended to have a greater negative effect on the C:nutrient ratio of litter when microbial decomposition rates were low and amounts of recalcitrant lignin and cellulose compounds were high, for tree species such as oak and rhododendron. Nutrients had less of a stoichiometric effect on litter with a faster microbial decomposition rate and more labile carbohydrate compounds, for species such as maple (Table 1; Scott et al. 2013; Kominoski et al. 2015). The production of microbial decomposers on recalcitrant detritus may be more nutrient limited than those growing labile detritus. Laboratory mesocosm studies that expose litter from the most recalcitrant and labile species contributing litter to streams in that region to nutrient enrichment (e.g., Scott et al. 2013) may be an effective way for freshwater managers to refine field techniques and predictions and to increase the cost-effectiveness of implementation.

5.1.3 Decomposition N and P Endpoints

Measurement Method Decomposition would be a good endpoint because it consistently responds to increasing dissolved nutrient concentrations (Ferreira et al. 2015) and represents microbial and macroinvertebrate detritivorous aquatic life (Manning et al. 2015). Decomposition decay rates are usually estimated by deploying litter in bags with variable mesh sizes (Table 1) and destructively sampling replicate litter bags over time until ≤50% of the initial detrital mass remains. Larger mesh sizes (> 0.5 mm) allow colonization by macroinvertebrates and thus incorporate macroinvertebrate detritivore-mediated decomposition into estimates of decay rates. Smaller mesh sizes (≤ 0.5 mm) exclude most macrodetritivores and represent mainly microbial decomposer activity. Macroinvertebrate-mediated decomposition can be calculated by the difference in decay rates between large and small mesh sized bags (Table 1, Woodward et al. 2012).

Response Direction, Functional Relationship, and Consistency We did not include an exhaustive literature review for nutrient effects on decay rates in this chapter because a meta-analysis of 99 studies published between 1970 and 2012 has already been completed (Ferreira et al. 2015). The meta-analysis indicated that decomposition was consistently stimulated by nutrient addition in laboratory and field studies (Ferreira et al. 2015) resulting in a high confidence in a predictable effect. To augment these findings, we summarize decay rates from studies that also measured other detrital responses reported in Table 1 or studies that provided functional models between nutrient concentrations and decay rates (Table 2). Microbial decomposition can be linearly related to stream-water dissolved inorganic N and soluble reactive P concentrations at low to intermediate concentrations (Scott et al. 2013; Kominoski et al. 2015). Michaelis-Menten models have also been reported (Rosemond et al. 2002; Ferreira et al. 2006; Gulis et al. 2006; Kominoski et al. 2015).

Sensitivity of Metric Michaelis-Menten model constants include estimates of maximal rates of decomposition with increasing nutrients and an estimate of the nutrient concentration where this maximal rate occurs (half-max concentration) that inform the sensitivity of this metric. The published M-M constants estimate maximum decomposition rate can occur 8–50 μg DIP/L, 15–52 μg NO_3-N/L, and 25 μg DIN/L (Rosemond et al. 2002; Ferreira et al. 2006; Gulis et al. 2006; Kominoski et al. 2015). One continental-scale field study reported a hump-shaped relationship between detritivore-mediated decomposition and N and P concentrations (Woodward et al. 2012) mirroring changes in detritivore community composition with enrichment. Michaelis-Menten relationships may be more representative of microbial decomposition responses as most of the studies reporting M-M models used small mesh ($\leq$ 0.5 mm) or were completed in the laboratory. However, a few studies still report M-M models even when large mesh that allows access by detritivores was used (Rosemond et al. 2002; Gulis et al. 2006). All the M-M models indicate that maximum decomposition rates occur at low levels of dissolved N and P pointing to a very sensitive metric and good biological endpoint.

Ultimately, these increases in decomposition with nutrient enrichment at the whole-stream level can reduce the amount of C stored within the reach (Benstead et al. 2009; Rosemond et al. 2015; Kominoski et al. 2018) and increase the downstream transport of fine particulate detritus (Rosemond et al. 2015); as a result, less of the terrestrial subsidy remains in the stream to support aquatic life and nutrient uptake. This result could be magnified with increasing stream temperatures due to landscape or climate change (Manning et al. 2018).

5.1.4 Macroinvertebrate Detrital N and P Endpoints

Measurement Method Macroinvertebrate shredder and collector-gatherer functional feeding groups are the primary detritivores in US wadeable streams, and their abundance, growth, biomass or secondary production and richness, and other diversity metrics would be excellent candidate endpoints directly representing aquatic life in detrital-based streams. Abundance, biomass, and secondary production require quantitative sampling, and production requires sampling the macroinvertebrates over time (Benke and Huryn 2017; Hauer and Resh 2017). These types of samples are rarely incorporated into bioassessment because they limit the sampling spatially to the depth of the quantitative sampler (e.g., Surber sampler) and they significantly increase the effort required to assess sites relative to semiquantitative or qualitative measures that are often taken once per year. Richness and other diversity-based metrics can be estimated using semiquantitative or qualitative measures that are often taken once per year and standard bioassessment techniques already in place (Barbour et al. 1999; Evans-White et al. 2009).

Response Direction, Functional Relationship, and Consistency Macroinvertebrate responses to nutrient enrichment range from positive to negative and can include both positive and negative (i.e., hump-shaped response; Table 1). While consistency could be questioned, the variety and complexity in response type fit the subsidy-stress model of nutrient enrichment on detritivore species consistently (Fig. 1), and the potential mechanisms of subsidy-stress responses are well described. As detritus becomes enriched, detritivorous taxa tend to have positive per capita consumption and growth responses (Evans-White and Halvorson 2017). However, at a threshold nutrient concentration, species growth decreases due to a shift from N- or P-limitation to C-limitation. Detrital nutrient enrichment can turn from a subsidy to a stress for detritivores when nutritional quality of the resource (C:nutrient ratio) is below a certain point, called the threshold element ratio (TER; Sterner and Elser 2002; Boersma and Elser 2006; Bullejos et al. 2014), even if the quantity of food is not limiting (Fuller et al. 2015; Halvorson et al. 2015a). A TER is defined as the nutrient ratio where growth peaks across a food C:nutrient gradient; it is the location where neither C nor the nutrient component of the TER limits growth (Sterner and Elser 2002; Bullejos et al. 2014). When detrital C:nutrient ratios occur to the right of the TER (greater C:nutrient ratio), organismal growth may be nutrient limited and respond positively to nutrient enrichment explaining the positive or hump-shaped responses observed at the individual, community, and ecosystem level (Table 1). Detrital C:nutrient ratios on the left side of the peak represent where an organism may be C-limited and will respond negatively to any additional nutrient enrichment of food resources.

Growth is limited when energetic costs of living in certain environments are higher than energy obtained from resources. Energetic costs for organisms in nutrient-enriched freshwaters include a metabolic cost to acquiring nutrients beyond those required for growth, and increases in respiration have been observed in aquatic organisms feeding on nutrient-enriched detritus (Boersma and Elser 2006; Halvorson et al. 2015a). Bioenergetic models have yielded TERs for a considerable number of aquatic invertebrates and fishes (Frost et al. 2006; Benstead et al. 2014), and several optimal growth-based TERs have been reported (Bullejos et al. 2014; Fuller et al. 2015; Halvorson et al. 2015a). Further study examining mechanisms for nutrient stress across taxa and linking TERs to detrital stoichiometry could provide even more justification for detrital stoichiometry-based endpoints (see Scott et al. 2013; Fuller et al. 2015; Halvorson et al. 2015a; Manning et al. 2016; Farrell et al. 2018).

Decreases in consumption have also been observed even when growth is less than maximum given that plenty of food is available to eat (Boersma and Elser 2006; Fuller et al. 2015; Halvorson et al. 2015a). This pattern suggests an artifactual feeling of satiation when an organism growth is still C-limited; some insect taxa have the ability to sense biomolecules with N and P with their mouthparts, a trait that may be tied to sensing satiation (Raubenheimer and Simpson 2012). It makes sense that N and P instead of C would be involved with consumption and satiation of detritivores because they have evolved using a low-quality, high C:nutrient (i.e., C replete) detrital food resources (Frost et al. 2006; Farrell et al. 2018) and detritivores tend to have lower C gross growth efficiencies and growth rates and greater threshold elemental C:P ratios than other feeding groups ($TER_{C:P}$, Frost et al. 2006), suggesting that negative effects of detrital nutrient enrichment are more likely for detritivores than other feeding groups.

At the community level, positive (n = 8 of 25), negative (n = 13 of 25), hump-shaped (n = 2 of 25), and M-M relationships (n = 1 of 25) between detritivore abundance, biomass, production, or richness and nutrient concentrations have been observed and could be endpoints (Table 1). Most of the positive and M-M responses to nutrients were in the form of quantitative estimates of community biomass and secondary production (Rosemond et al. 2002; Cross et al. 2005, 2006, 2007) that do not reveal the undesirable community structure shifts that often occur (Evans-White et al. 2009; Woodward et al. 2012). Thus, because of their coarse nature and positive response, they may have limited used for bioassessment.

Most of the negative responses were tied to qualitative bioassessment sampling of detritivore biodiversity. Threshold reductions in shredder and collector-gatherer richness have been associated with increasing nutrient concentrations (Evans-White et al. 2009). Reductions in shredder richness were accompanied by threshold declines in detritivore mean taxa body C:P (Tables 1 and 2) linking detritivore community structure conceptually to detrital stoichiometry as discussed above. Ultimately, this work suggested that detritivore communities undergo a shift toward fewer species with greater nutrient demands, specifically P demand, with increasing TP (i.e., communities with low biodiversity composed of species with a high nutrient demand) (Evans-White et al. 2009). Continental-scale litter-bag experiments across nutrient gradients have reported hump-shaped relationships between nutrient concentrations and associated macroinvertebrate community composition (Woodward et al. 2012). These shifts in community structure had ecosystem consequences leading to a hump-shaped relationship between macroinvertebrate-mediated decomposition and nutrient concentrations (Woodward et al. 2012).

Although other contaminants and stressors may be affecting macroinvertebrate endpoints in the field studies at high nutrient concentrations, laboratory studies provide a mechanistic framework and evidence for subsidy-stress (Boersma and Elser 2006; Bullejos et al. 2014; Fuller et al. 2015; Halvorson et al. 2015a). Statistical relationships between nutrient concentrations and detrital C:nutrient ratios (Scott et al. 2013; Kominoski et al. 2015) can be linked to available detritivore TERs (Frost et al. 2006; Fuller et al. 2015; Halvorson et al. 2015a) to make predictions about the impacts of increasing wadeable-stream nutrient concentrations on macroinvertebrate communities (Evans-White et al. 2009; Manning et al. 2015). This extensive body of work on detrital-based microbial and macroinvertebrate responses to nutrient concentrations provides the conceptual basis and a body of evidence needed to support additional study and to help inform TN and TP numeric concentration criteria.

Sensitivity of Metric The quantitative results needed to compile and calculate the magnitude of the nutrient response relative to a control, which can be used to gauge endpoint sensitivity, were often not reported. In fact, we were only able to estimate effect sizes for the positive community responses, which ranged from 1.17 to 1.61, and were on the lower end of effect sizes estimated from microbial-based detrital responses discussed in earlier sections. Again, as N and P were manipulated in these studies in tandem, it is difficult to attribute these positive effects to N or P alone (Cross et al. 2006). However, the positive shift to greater community biomass can have a saturating M-M relationship with dissolved phosphorus concentrations, and half-maximal biomass can occur at approximately 7 μg SRP/L (Rosemond et al. 2002). No functional regression or M-M relationships between N and macroinvertebrate community biomass or production were reported.

Negative richness responses were more common than positive ones and were often reported as threshold relationships (Evans-White et al. 2009); however, the mean or median of the response before and after the nutrient concentration threshold was not reported and is necessary in the future to allow estimates of effect size and aid in endpoint adoption. The concentration range of negative macroinvertebrate shredder richness thresholds shown in Table 2 occurred between 50 and 80 μg TP/L (Evans-White et al. 2009) and was a little greater than that reported for detrital microbial measures, suggesting less sensitivity of macroinvertebrates than microbes to nutrient enrichment. Collector-gatherer richness thresholds occurred at a much higher TP concentration (800–930 μg TP/L) than the shredder richness thresholds. The greater tolerance of collector-gatherers compared to shredder feeding groups to TP could be due to the more omnivorous nature of collector-gatherer compared to the shredder group (Evans-White et al. 2009, 2013). Further, the concentration range of observed effects on shredder richness and detritivore-mediated decomposition occurred at similar TP concentrations to microbial-based measures suggesting a similar sensitivity. Therefore, shredder-based community metrics were the most consistent and sensitive of all the macroinvertebrate detrital-based endpoints.

5.2 Responses to Salts

5.2.1 Heterotrophic Microbial Salt Endpoints

Measurement Method Microbial and macroinvertebrate detritivores are sensitive to oxygen concentration, ion concentration, and other physicochemical parameters of the water they inhabit. Increases in salt concentrations (i.e., salinization) of freshwaters can affect all of these chemical characteristics of the water. Thus, detrital-based ecosystems exhibit measurable changes from salinization (Swan and DePalma 2012; Van Meter et al. 2012; East et al. 2017). Even relatively low-level salinization changes can change the quantity and quality of detritus by reducing fungal and bacterial enzymatic activity and production or by changing algal, fungal, and bacterial microbial community identity (Castillo et al. 2018; Vander Vorste et al. 2019). Macroinvertebrate-microbial interactions can also have measurable effects on macroinvertebrate detritivore consumption and assimilation (Scheibener et al. 2015; Tyree et al. 2016).

Fungal and bacterial biomass, growth, and production responses to salt concentrations in freshwater ecosystems have been measured using techniques similar to those used to assess nutrient effects (reviewed by Berger et al. 2019). Senescent, dried leaf litter, unstained wood veneers, and standardized cellulose material (e.g., cotton fabric strips) are deployed in stream for weeks to months and then sampled over time. Ergosterol and hydrolysis are used to assess fungal and bacterial biomass and activity through time using the methods described above. Microbial diversity analysis has also been conducted to assess changes in operational taxonomic units as a way to relate diversity to co-measured functions (Berger et al. 2019; Vander Vorste et al. 2019).

Response Direction, Functional Relationship, and Consistency Most studies ($n = 9$ of 12) reported in Berger et al. (2019) show decreases in microbial biomass, growth, production, and diversity measures with detrital incubation time. As with nutrients, the time to sample deployed detrital material to assess a microbial salt response cannot currently be prescribed, potentially suggesting that managers will need to visit sites more than once to assess responses adding difficulty to bioassessment designs. Functional relationships between microbial measures and salt concentrations have been reported (Berger et al. 2019). Most studies reported negative linear relationships between salt concentrations and detrital hydrolysis, microbial functional diversity, fungal sporulation rates, fungal biomass, and fungal respiration.

Sensitivity of Metric The concentration range of studies reporting statistically significant salt effects was large (Berger et al. 2019). However, detrital microbial responses were commonly reported in studies where the maximum manipulated total dissolved salt concentrations were 0.034 g/L up to 67 g/L. Few salts are regulated; however, most US states have chloride and sulfate criteria that vary with

Clean Water Act designated uses in navigable waters of the U. S. The most common maximum allowable concentration for sulfate and chloride is 0.2 g/L. Total dissolved solid (TDS) allowable concentrations vary by state and intrastate navigable waterways in some states, probably due to geology. In the United States, the lowest allowable TDS can be as low as 0.010 g/L in Hawaiian streams and 0.100 g/L in an Arkansas river having low-base ion concentrations according to the Environmental Protection Agency (1988). Many algal metrics show salt responses at as low as 0.260 g/L (Entrekin et al. 2019). Therefore, microbial detritivore responses may also be just as sensitive as autotrophic metrics to changes in freshwater nutrients and salinization. There have currently been no studies that examine the recovery of microbes following the removal of salt stressors.

Carbon, nitrogen, phosphorus, and temperature better predict bacterial production than salinity (Nielsen et al. 2003). The insensitivity of bacteria to changes in salts was attributed to their common physiology with marine ancestors. Still, bacterial composition between freshwater and marine environments is different, and community shifts can be detected along natural saline gradients (Bouvier and del Giorgio 2002). Freshwater cyanobacteria can adapt to changes in salinity to become hazardous to freshwater biota and people (Hart et al. 1991).

5.2.2 Detrital C, N, and P Stoichiometry Salt Endpoints

Measurement Method Detrital stoichiometry was proposed to be a good endpoint to inform nutrient criteria development and assess nutrient stress in fresh waters (see Sect. 5.1.2) and may be useful to inform salt criteria as well. Methods of measurement for quantifying salt effects on detrital C, N, and P stoichiometry would mirror those described in Sect. 5.1.2. Salt contents can increase, and thus, C:salt ratios of terrestrial litter can decline when exposed to salt additions (Entrekin et al. 2019) potentially having consequences for stream detrital input stoichiometry. Therefore, one might expand the suite of elements examined to include salts by coupling an acid digest to ion chromatographic analysis (Huang and Salt 2016). Ion chromatograph systems are now routinely available in water quality laboratories.

Response Direction, Functional Relationship, and Consistency Because salts generally reduce the amount and production of heterotrophic microbes that also tend to have a more stable and lower tissue C:nutrient ratio than terrestrial plant detritus (Elser et al. 2000; McGroddy et al. 2004), salts can probably inhibit changes to litter C:nutrient ratios through time. Elevated salt concentrations should maintain nutrient imbalances between microbes and their detrital food substrate by reducing microbial colonization, activity, and growth causing a decrease in microbial respiration, biomass, growth, and production.

There are currently no salt addition studies that have expressed C:nutrient ratios in response to fungal and bacterial biomass, growth, and production on terrestrial plant detritus as a response to salinization making consistency impossible to gauge.

However, fungal-specific responses to salts have measured mostly declines in fungal biomass and activity across salt gradients (e.g., Berger et al. 2019; Gonçalves et al. 2019).

Sensitivity of Metric Very little data exist to estimate metric sensitivity to changes in salt concentrations. However, some evidence suggests that aquatic hyphomycetes require high salt concentrations to elicit responses (Gonçalves et al. 2019). Therefore, until more research examines the overall change in litter C:nutrient or C:salt concentrations to changing dissolved salt concentrations, we cannot confirm that litter stoichiometry will be biologically significant or useful as an endpoint in determining salt concentrations safe for aquatic life.

5.2.3 Decomposition Salt Endpoints

Measurement Method Leaf litter decomposition has been the most measured proxy for changes in C processing in response to salinized freshwaters (Castillo et al. 2018; Berger et al. 2019; Vander Vorste et al. 2019). It is measured using the same techniques described in Sect. 5.13a.

Response Direction, Functional Relationship, and Consistency Leaf litter and wood veneer decomposition rates, fungal and bacterial community composition, fungal biomass, and the rate of hydrolysis show promise as endpoints to assess changes in microbial performance in response to salinization. A recent review (Berger et al. 2019) found that C processes are mostly negatively affected by increases in salt concentration. Coarse and fine litter bag decomposition was found to be negative in 75% of the studies and had no response in 25% of the studies. Ergosterol on detrital material declined (n = 3 of 5), showed a hump-shaped response (n = 1 of 5), or showed no change (n = 2 of 5), and microbial density also declined (n = 1 of 1). Therefore, reduced microbial diversity, lower fungal biomass, and hydrolysis rates were often the cited mechanism for the decline in decomposition. When the full suite of decomposition measures were included (i.e., all detrital types, field and mesocosm studies), Berger et al. (2019) showed a negative linear relationship between decomposition and salt additions. Certainly, there are currently too few studies to be confident in the currently identified patterns. An additional and pressing need is to understand how salts interact with other stressors to alter detrital processing. More of these time and space integrated metrics that include other common stressors are needed to understand how structural changes in biological communities are changing C processing.

Macroinvertebrate decomposition has shown promise as a nutrient endpoint (see Sect. 5.13) and may also be effective as a salt endpoint. Declines in detrital fungal and bacterial biomass or activity with increasing salts (Berger et al. 2019) might reduce shredder consumption and leaf litter decomposition. Salts may also induce macroinvertebrate osmoregulatory stress (Kefford et al. 2004) leading to increased macroinvertebrate respiration and reduced decomposition rates. These hypothesized changes in the microbial community and activity along with changes in macroinvertebrate community composition in response to salt additions can have measurable effects on detrital processes that support macroinvertebrate secondary production (Stoler et al. 2017) across ecotones. Ultimately, we would predict reductions in secondary production resulting from salt contamination that can lead to less insect-derived nutrients and energy export to downstream and riparian habitats (i.e., reciprocal flows). Cumulatively, riparian-stream salinization could alter energy flow that supports watershed diversity and production (Entrekin et al. 2019).

The few studies examining the effects of salinization on decomposition surprisingly found that macroinvertebrate biomass was not indicative of changes in decomposition rates (Berger et al. 2019), providing no evidence that macroinvertebrate-mediated decomposition was affected. Macroinvertebrate-mediated decomposition has proven responsive to nutrients and has the capacity to be a good endpoint for salt contamination as well. Further investigation is needed before consistency in this endpoint can be assessed.

Sensitivity of Metric While the influence of salinization on decomposition has been studied too little to confidently assess its sensitivity as a metric, it does appear to be sensitive. Negative impacts on decomposition were found in 12 reviewed studies that spanned a range in specific conductivity from 0.5 to 99 ms/cm (or 0.34–67 g/L total dissolved solids). When the full suite of decomposition measures were included (i.e., all detrital types, field and mesocosm studies), the percent magnitude of decline in decomposition rate relative to a low-conductivity control (~1.7 ms/cm) ranged from 200% to <10%. Variation in effect size was caused by differences in leaf litter species, nutrient concentrations, and ion concentrations across studies. Additional studies examining detrital decomposition across a gradient of salts that include fine and coarse mesh bags so that microbial- and macroinvertebrate-mediated decomposition responses can be examined are needed to more confidently assess the sensitivity of this endpoint to salt contamination.

5.2.4 Macroinvertebrate Detrital Salt Endpoints

Measurement Method The methodology examining macroinvertebrate responses to salts differs from that used to study responses to nutrients. Macroinvertebrate nutrient responses have primarily been studied in the field across stream nutrient concentration gradients or after nutrient additions using approaches described in Sect. 5.1.4. However, salts have been studied more as contaminants, rather than nutritional elements, even though they can be both (Jeyasingh et al. 2017) if salts are taken up by plants that supply detritus to streams or stream autotrophic and heterotrophic microbes incorporate salts in their tissues (Entrekin et al. 2019). Therefore, many studies have endeavored to quantify acute and chronic doses of salts. Acute toxicity tests expose several organisms of the same species and lifestage to a gradient of salt concentrations that result in 50% mortality (LC50) in highly controlled laboratory experiments that usually last from 24 to 48 h. Chronic toxicity tests use a similar salt concentration gradient design, but experimental durations exceed 48 h and usually last several days to weeks. They may also focus on responses other than mortality, such as growth and reproduction, which would be expressed as an effect concentration where 50% of organisms responded to the salt (EC50).

Response Direction, Functional Relationship, and Consistency Response direction is often consistently negative when the LC50 and EC50 toxicity test approach is used to examine effects of salts on macroinvertebrates. However, field studies have found that macroinvertebrates belonging to the shredder functional group are consistently tolerant to rising salt concentrations and can even show positive population-growth responses. For example, in temperate streams that have decades-long increases in sulfate (and concurrent declines in pH), one common shredder (*Leuctra* sp.) consistently displayed increases in density and biomass (Jastram et al. 2013). *Leuctra* sp. responded similarly to a mining-induced elevated sulfate gradient (0.014–9.4 g/L SO_4) in the central Appalachians (Timpano et al. 2015; Drover et al. 2019) where their density increased at about 0.2 g/L TDS (Drover et al. 2019). In other laboratory studies, two common shredders, a trichopteran *Lepidostoma* sp. and a plecopteran *Amphinemura* sp., displayed increased growth at a very low (0.016–0.064 g/L NaCl; $NaHCO_3$) but increasing gradient of salt concentration (Table 3; Entrekin et al. 2019; Mogilevski 2019), suggesting salts are a subsidy and may turn into a stressor at greater concentrations. In contrast, an isopod shredder, *Lirceus* sp., displayed a decline in body size at a similarly low (0.003–0.214 g/L NaCl) salt gradient, and a fly larva, *Tipula abdominalis*, showed no response (Tyree et al. 2016).

Sensitivity of Metric Macroinvertebrate species representing detritivores like mayflies, stoneflies, and caddisflies have the greatest proportion of salt-sensitive taxa. These orders also have among the most salt-tolerant taxa, likely from direct osmoregulatory effects, although the exact mechanism for their sensitivity is not well understood (Castillo et al. 2018; Kefford 2019). Stress is generally thought to be from energy used to maintain osmoregulatory homeostasis (Pond et al. 2008; Kunz et al. 2013; Clements and Kotalik 2016); organisms require more energy to regulate internal body salt concentration; less energy is available for growth and respiration and the animals die (Kath et al. 2018). But because different taxa are more sensitive to some ions than others and background ion concentration alters toxicity to freshwater organisms, taxon-specific responses are currently difficult to predict (Olson and Hawkins 2017). Evolutionary history and body morphology (i.e., body parts without cuticle that prevents diffusion and osmosis) alone do not explain patterns of species loss with rising water conductivity and ion concentration (Mount et al. 1997; Dowse et al. 2017).

Sensitive taxa are present in all insect orders. For example, taxa representing all aquatic insect orders can show growth sensitivity at 1 g/L total dissolved solids in Australian streams and wetlands (Hart et al. 1991). In the United States, a conductivity benchmark of roughly 0.2 g/L total dissolved solids has been identified as protective to aquatic life (Cormier et al. 2011). Consistent with the field studies described in Sect. 5.2.4, laboratory toxicity tests indicate that shredders appear to be collectively less sensitive to salts than other functional groups where shredding taxa show the highest range of LC50s (8.7–28.5 g/L; Table 3) across NaCl gradients (review Castillo et al. 2018). Because shredders show little response to increased salt concentrations, negative impacts of salts on fungi and bacteria could be offset by the positive increase in shredder consumption by a few salt-tolerant taxa. However, shredders feed selectively on biofilms making predictions difficult if food palatability and nutrition decline (Anderson and Sedell 1979). Species replacement and compensation require further study to predict how salts affect macroinvertebrate feeding and subsequent effects on C cycling.

Other detritivorous functional groups of macroinvertebrates are more salt sensitive. Specifically, collector-gathering taxa (including sensitive mayflies) that tend to eat fine organic particulates that are often a byproduct of shredder feeding show the lowest LC50s from 0.68 to 14.3 g/L NaCl. Collector-filterers, such as *Chironomus* spp., have LC50s that are nearly as low ranging from 0.8 to 19.6 g/L NaCl (Table 3, Castillo et al. 2018). Caution should be taken in generalizing based on the relatively scant available studies; however, predictions are possible to inform future studies on the macroinvertebrate detritivore extent and magnitude of response that can govern C processing.

A battery of toxicity studies have also been conducted for a suite of model taxa to measure LC50 and EC50 values as indicators and endpoints to support criteria development (Castillo et al. 2018; Mount et al. 2019). For example, lab-reared, common invertebrate and vertebrate test species (*Ceriodaphnia dubia* and *Pimephales promelas*, respectively) were exposed to 2900 ion solutions. Ion toxicity for these taxa was summarized as $K > HCO_3 = Mg^{2+} > Cl^- > SO_4$, where Na^+ and Ca^{2+} showed no detectable effect on mortality (Mount et al. 1997). Since laboratory acute and chronic toxicity tests have been conducted for the most common aquatic organisms using mainly salt combinations (Struewing et al. 2015) or common compounds like NaCl (although see individual ion tests by Mount et al. 1997; Elphick et al. 2011), a further study of direct effects (and the physiological mechanisms responsible for them) across a broader range of aquatic organisms and ion combinations was conducted (Mount et al. 2019). Based on 58 chronic *Ceriodaphnia dubia* geochemical ion responses, individual salts elicit similar toxicity and potency when expressed as osmolarity, *C. dubia* toxicity from Mg, Ca, and K was related to cation activity, *C. dubia* Na and K toxicity can be reduced by adding Ca below toxic concentrations, and salt mixtures that share a common cation have additive toxic effects (Mount et al. 2019). Further examinations will improve our ability to predict the direct effects of various individual and salt mixtures on aquatic communities. Recent toxicity tests have used mesocosms colonized with macroinvertebrates from natural communities and then reported endpoints such as drift and loss of taxa richness (Clements and Kotalik 2016; Olson and Hawkins 2017). As governance bodies consider conductivity and ion-specific regulations, more experimentation is called for to guide progressive policies (Canedo-Arguelles et al. 2016; Olson and Hawkins 2017).

Current toxicity models do not consider the combination of direct osmoregulatory effects and indirect effects from altered detrital resource quality, which could produce subsidy-stress relationships between macroinvertebrate responses and salt concentrations. Detrital resource quality can be defined by the interactions among intrinsic physical and chemical composition and extrinsic microbial composition. Environments where total ions are lower than macroinvertebrate physiological optima can lead to positive growth responses to rising concentrations due to reduced metabolic costs of osmoregulation. As concentrations increase two to four orders of magnitude above ambient, microbial (i.e., algae, bacteria, and fungi) activity slows, likely negatively affecting the detrital quality for detritivorous macroinvertebrates (Sauer et al. 2016; Tyree et al. 2016), and common aquatic invertebrates suffer increased mortality probably from osmoregulatory stress (Kaushal et al. 2005; Kefford et al. 2012; Cook and Francoeur 2013). Subsidy-stress or stimulatory effects on growth and other metrics of performance, up to some critical threshold, may be common before performance declines (Minshall and Minshall 1977; Griffith 2017; Olson and Hawkins 2017).

5.3 Comparing Microbial and Macroinvertebrate Detrital Responses to Nutrients and Salts

The challenge in comparing detrital responses to salts versus nutrients is that salts have been studied as contaminants and N and P as nutrients. The LC50 approaches used to examine salt effects on detrital communities (Table 3) are designed to include concentration gradients that generate high mortality, but these designs can miss significant sublethal effects and can lack real ecological meaning (Cairns 1983). Further, many published studies examining salts do not consider indirect trophic effects of salts on detrital quality (Entrekin et al. 2019; Table 3). The breadth of experiments examining nutrient effects inherently examined sublethal effects on detrital quality and quantity on macrodetritivores (Tables 1 and 2). More studies examining salt effects must take this approach to integrate endpoint development because N and P and many salts are nutritional elements (Jeyasingh et al. 2017), can affect metabolism and energy budgets of aquatic life (Evans-White et al. 2013; Tyree et al. 2016; Entrekin et al. 2019), and can have subsidy-stress effects (Fig. 1, Tables 1, 2, 3; Jeyasingh et al. 2017).

Here, we identify research gaps that exist based on the historically narrow view of each on ecological processes in freshwater. Heterotrophic compositional shifts occur consistently across salinization gradients (see Sect. 5.2) whether they are natural or manipulated gradients with less information on community composition changes with N and P (see Sect. 5.1). Fungal biomass has been measured as an indicator of nutrient and salt availability. Fungal and bacterial biomass consistently increases with N and P and declines with salinization at several orders of magnitude different concentrations (e.g., 50 μg/L P and 2 g/L NaCl). Litter and wood decomposition rates show consistent increase with N and P and decrease with salts, but again orders of magnitude less N and P are required to elicit a response. Leaf and wood detrital C:N:P show predictable declines with nutrients and place constraints on decomposition and aquatic shredder growth, secondary production, and community composition. In fact, these responses can be predicted by TERs, which are essentially subsidy-stress relationships (see Sections 5.2.2–5.2.4). Despite the great promise of this endpoint for nutrient management, there is virtually no information on how detrital stoichiometry might be associated with rising salts or how it may impact macroinvertebrate nutrition (see Sect. 5.2.2). Macroinvertebrate taxonomic shifts that result in 5% taxa lost occur at about 0.2 g/L (200,000 μg/L) TDS and less than 50 μg/L TP (Evans-White et al. 2009, 2013). Taxon-specific shredder responses to C:nutrient are available, but not for salts. One single shredder taxon, *Leuctra* spp., shows increased density at 0.2 g/L total dissolved solids with no identified mechanistic explanation. Because organism identity imparts function, we urge caution in decoupling functions from communities and suggest the development of comprehensive methods that consider functions in the context of diversity (e.g., Evans-White et al. 2009).

6 A Proposed Solution: Including Detrital Endpoints in Water Quality Criteria

Currently, regulatory assessments conducted by states and localities focus on water quality measurements of stressors including nutrients and salts, with a few instances of biological endpoints such as fishes and benthic macroinvertebrates to document impacts to aquatic life. These assessments may include measurements of endpoints that represent the quantity (e.g., sestonic and benthic chlorophyll *a*) and quality (e.g., algal or macrophyte taxonomy) of primary producers in the aquatic ecosystem. However, measures of terrestrial detrital endpoints representing the quantity and quality of this critical food resource subsidy to aquatic ecosystems are not typically included as endpoints for determining aquatic life criteria by regulatory agencies for US fresh waters. As such, negative effects of nutrients and salts mediated through detrital pathways impacting the aquatic community structure and ecosystem function are largely unmeasured by regulatory assessments. Therefore, ecosystems that are spatially or temporally dominated by detrital inputs (e.g., aquatic ecosystems with forest-dominated watersheds) could be experiencing significant, but undetected, alterations to aquatic community structure, as well as ecosystem function in response to nutrient and salt inputs.

While some states or other water quality managers may use data on macroinvertebrate and fish communities or their associated biological indices to detect ecosystem changes, decision-makers may have a difficult time identifying pathways of the change since these communities integrate changes in the algal and detrital pathways (Figs. 1 and 2). Further, identifying the level of the stressor reduction required to reverse the impact is difficult, and linking management activities to restoration is complicated by the time lags in aquatic life response. Perhaps the biggest challenge is the ability to demonstrate "detectable" changes in macroinvertebrate or fish communities using standard indicators such as the index of biotic integrity (IBI) that were not developed to detect trophic shifts from impairment (Kraus et al. 2016). Responses may actually be the result of large-scale changes throughout the food web that would be hard to restore.

A proposed solution to lack of detrital data included in setting water quality criteria is to use sublethal endpoints such as those described above for detrital systems. These endpoints may serve as sentinels of impending species loss and better allow managers to detect and prevent changes to critical ecosystem functions (e.g., community composition) in ecosystems experiencing increased inputs of salts and nutrients. Measurement of and use of these detrital endpoints to guide Clean Water Act decisions would be a more comprehensive and proactive approach to aquatic life use protection, as compared to reactive approaches to management after significant food web and aquatic life changes have already occurred.

Detrital responses that show considerable promise as endpoints are detrital microbial community (Sect. 5.1.1, 5.2.1), stoichiometry (Sect. 5.1.2, 5.2.2), decomposition (Sect. 5.1.3, 5.2.3), and macroinvertebrates (Sect. 5.1.4, 5.2.4). Detrital stoichiometry and decomposition respond consistently to, are sensitive to, and have predictive functional relationships with nutrient concentrations (Sect. 5.1.2 and 5.1.3), and they are linked to aquatic life changes, such as richness thresholds, that allow numeric criteria to be estimated (Sect. 5.1.4). Detrital stoichiometry may be more feasible to incorporate into water nutrient management programs than decomposition because it can require less field and laboratory work (see Sect. 5.1.2 and 5.1.3). The response of detrital stoichiometry to salts has not been studied, but it could be a fruitful area of exploration. Microbial detrital responses that show promise for development as indicators of salinization include decomposition rates, fungal biomass, and microbial community composition. These microbial changes can also change macroinvertebrate detritus feeding rates (e.g., Fuller et al. 2015; Halvorson et al. 2015). Macroinvertebrate community composition changes with salinization; however, fewer detrital endpoints were identified. Shredder density, particularly an increase in Leuctridae, may serve as an indicator, along with declines in collector taxa richness and density (Table 3).

US EPA and state and local management agencies have for many years been working to develop and implement the use of sublethal endpoints for management such as the development of diatom indices to detect changes to algal community structure as an early indicator of changes to aquatic ecosystems, due to a variety of stressors that include nutrients and salts. Here, we identified additional endpoints, integrated with more traditional compositional metrics, whose further characterization within and across ecosystems could serve as early indicators of critical changes to imperiled detrital ecosystems (Tables 1, 2 and 3). Specifically, water quality managers and researchers should collaborate to identify and test appropriate metrics for detrital processes to better understand the effect of stressors. To the extent that these indicators of detrital pathways are indeed confirmed to be early indicators of change that have a consistent response to stressors (i.e., a more consistent signal than algae to changing pollutant loads in light-limited ecosystems) and where these detrital endpoints can be quantified with relative ease and low cost, such scientific advancements could be integrated into water quality standards or more generally used to support Clean Water Act decision-making. Such an advance would ensure that managers are controlling nutrients and salts at concentrations where they become contaminants and altering how terrestrial-derived detritus is being processed in aquatic ecosystems and therefore better consider the effect of cross-ecosystem linkages in the Clean Water Act.

7 Conclusions

This chapter provides an argument and significant supporting evidence for the inclusion of terrestrial-derived detrital endpoints into the regulatory framework for US wadeable streams. Terrestrial detritus is a key subsidy fueling forested-stream ecosystems that are broadly impacted by nutrient and salt contaminants that modify detrital terrestrial form and function in these systems. However, terrestrial detrital endpoints representing the quantity and quality of this critical food resource subsidy to aquatic ecosystems are not typically included as endpoints for determining aquatic life criteria by regulatory agencies for US fresh waters. Detrital microbe, stoichiometry, and decomposition functional measures show consistent and predictable responses to nutrients and have been linked to declines in aquatic life diversity and function, but they have not yet been adopted as endpoints. These same metrics hold promise for indicating salt contamination if future studies examine sublethal, indirect, ion-specific, and interacting effects. The proposed detrital endpoints may serve as sentinels of impending species loss that better allow managers to detect and prevent changes in community composition and critical ecosystem functions. Detrital endpoint responses to N, P, and salt concentrations illustrate how contaminants and ecological subsidies in linked aquatic-terrestrial ecosystems can be used to inform management of these ecosystems.

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Mesocosms to Evaluate Aquatic-Terrestrial Contaminant Linkages Using Aquatic Insect Emergence: Utility for Aquatic Life Criteria Development

Christopher J. Kotalik

> *Ecological realism must come to environmental policy: all systems change, all the time, and our actions are an inevitable part of that change.*
>
> Matthews et al. (1996)

1 Introduction

Aquatic and terrestrial environments interact through movements of resources, nutrients, and prey, and they are not functionally independent of one another (Hynes 1975; Vannote et al. 1980; Nakano and Murakami 2001; Baxter et al. 2005). As a result, aquatic contaminants have the potential to impact terrestrial environments through alterations to aquatic subsidies and contaminant transfer to terrestrial ecosystems (Walters et al. 2008; Paetzold et al. 2011; Kraus et al. 2014a). Developing aquatic life criteria to account for aquatic contaminant effects on linked terrestrial ecosystems requires contaminant evaluation methodologies that have the experimental capacity to assess these relationships. Traditionally utilized single-species assessments fall short of integrating the level of biological complexity needed to evaluate these interactions (Cairns 1986; Clements and Kiffney 1994a, b; Versteeg et al. 1999; Buchwalter et al. 2017). Alternatively, mesocosm toxicity testing offers the spatiotemporal scale, control, and degree of replication required to assess aquatic-terrestrial (A-T) contaminant transfer and subsidy alteration to terrestrial ecosystems and, critically, the potential to contribute A-T data for aquatic life development.

In this chapter, we review aquatic community mesocosm studies that incorporate aquatic insect emergence, with the purpose of synthesizing this literature and providing guidance to researchers and regulators in selecting aquatic insect emergence

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C. J. Kotalik (✉)
Department of Fish, Wildlife and Conservation Biology, Colorado State University,
Fort Collins, CO, USA

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endpoints to make A-T contaminant inferences. We provide key considerations to conducting mesocosm studies using aquatic insect emergence and suggest how these data may be integrated into the aquatic life criteria development process.

1.1 Traditional Single-Species Testing

Single-species toxicity testing is the main source of biological data used for aquatic life criteria development in the USA (Stephan et al. 1985). These tests are acute or chronic exposures on surrogate organisms intended to represent the diversity of aquatic animals in cold and warm waters and with benthic and pelagic life stages. For acute tests, dose-response toxicity tests (generally less than 5 days) estimate lethal concentrations that reduce organism abundance by 50% (LC50). For chronic tests (greater than 24 days), endpoints such as long-term mortality, growth, and reproduction are used to generate no and lowest observed effect concentrations (NOEC, LOEC) or EC20 values (effect concentration that reduced endpoint by 20% from controls). Variation in chronic and acute chemical sensitivity among species is described using an empirical distribution function, the species sensitivity distribution (SSD). The reliance on single-species testing is largely directed by the Environmental Protection Agency's (US EPA) 1985 guidelines for "deriving numerical national water quality criteria for the protection of aquatic organisms and their uses" (Stephan et al. 1985). These guidelines assume that effects which occur in standardized single-species laboratory tests will generally occur for the same species in comparable field situations. If the specified minimum number of organisms is tested, the resultant criteria are expected to be sufficient to protect most aquatic species in most aquatic ecosystems in the USA (Stephan et al. 1985).

Standardized single-species tests are valuable in hypothesis generation, informing relative toxicities of contaminants and testing contaminant mixtures; however, exclusively relying on these tests to develop criteria has been criticized due to the lack of ecological realism and difficulty extrapolating results to higher levels of biological organization (Cairns 1986; Buchwalter et al. 2017). For example, single-species tests of dissolved metal toxicity often find aquatic insects highly tolerant, while effects in the field are observed at significantly lower concentrations (Clements et al. 2013; Iwasaki et al. 2018). Other concerns with the use of SSDs to establish water quality criteria are that they only require aqueous exposures, though diet is a critical route of exposure for contaminants (Xie et al. 2010; Kim et al. 2012; Poteat and Buchwalter 2014). Furthermore, commonly used surrogate test species (e.g., *Daphnia*) do not adequately represent responses of other taxonomic groups such as aquatic insects, which are generally underrepresented in toxicity tests and sensitive species distributions (Cairns 1986; Clements and Kiffney 1994a, b; Pond et al. 2008). Finally, these tests by definition exclude interspecies relationships (e.g., competitive release, resource competition) and trophic interactions (e.g., A-T linkages) that may drive indirect effects of contaminants on natural communities (Clements et al. 2013; Kraus et al. 2016; Rogers et al. 2016).

1.2 Regulatory Perspectives of Mesocosm Testing

One solution to address many of the issues associated with single-species testing for criteria development is to use a methodology that increases realism without sacrificing causality. Aquatic mesocosm studies offer environmentally realistic approaches to aquatic toxicity testing. Here, we define "mesocosms" as experimental systems that integrate the abiotic and biotic components of natural aquatic communities under controlled conditions. We use the term broadly, without attempting to discriminate between typical associations of indoor "microcosms" or outdoor "mesocosms" (see Bundschuh et al. this volume for an alternative size-dependent definition). Mesocosms incorporate higher levels of biological organization compared to single-species tests (e.g., organisms interacting at multiple trophic levels), and they have the potential to more accurately predict changes to actual communities in nature compared to laboratory testing alone (Clements 2004). Traditional endpoints used in single-species toxicity tests such as mortality and growth can also be assessed with mesocosms; however, certain functional endpoints are only possible to assess with mesocosms. For example, rates of aquatic insect emergence and stream metabolism require biological complexity (i.e., natural occurring community assemblages) and realistic testing conditions (i.e., flow through conditions with natural habitat).

Similar to traditional aquatic toxicity testing methodology, mesocosms can generate concentration-response relationships, as well as commonly used metrics for populations (e.g., EC50, concentration reducing maximal response by 50% compared to the controls). These comparisons can integrate results obtained from both single-species testing and field responses. For example, mesocosm-derived EC50 values can be compared to laboratory LC50 results, and metrics characterizing mesocosm community responses can evaluate aquatic communities in the field. Furthermore, these experiments can apply contaminant-gradient relationships to communities and functional endpoints (Clements 2000; Hickey and Golding 2002) and analyze changes in community structure using multivariate approaches (Van den Brink and Ter Braak 1998, 1999) and structural equation models (Grace 2006; Rosseel 2012; Rogers et al. 2016).

In the USA, mesocosm testing has historically received mixed reviews from researchers and regulators on their usefulness for regulatory purposes, but other countries including Canada and the European Union have focused on improving the utility of toxicity data generated by mesocosms. From 1988 through 1992, the US EPA required higher tier risk assessments (e.g., mesocosms) to study secondary effects in nontarget organisms for pesticide registration under the Federal Insecticide, Fungicide, and Rodenticide Act using simulated aquatic field studies (Touart 1988). However, the US EPA rescinded mesocosm testing requirements for pesticides on the basis that "they do not provide substantial information for making risk decisions beyond that already revealed by lower tiered (e.g., single-species laboratory testing) studies," with key criticisms regarding their high variability, lack of repeatability, and impractical experimental scale (US EPA 1993). Instead, the US EPA focused their efforts on improving laboratory-based risk assessments and mitigating and monitoring pesticides in the field, whereas the regulatory focus in Europe was to improve mesocosm practices by standardizing methods for evaluating population *and* community-level effects (Van den Brink 2006).

Presently, development of water quality guidelines in the USA allows for, but does not mandate, the use of mesocosm data in criteria development. Criteria to protect aquatic life can utilize “other data” from mesocosm testing in a secondary role as a validation step that can be used to lower criteria values if mesocosm data indicate that criteria calculations from specified single-species testing are not sufficiently protective (Stephan et al. 1985). In contrast, Canada’s updated aquatic life development process uses available mesocosm data in a primary role to derive criteria, as long as the data meet “quality acceptability” requirements. The Canadian guidelines state, “Controlled microcosm and mesocosm studies are acceptable and are ranked according to the applicable categorization criteria. A clear dose-response relationship should be experimentally established and effects reasonably apportioned to the substance” (CCME 2007).

Mesocosms certainly have their limitations; for example, investigators have encountered enclosure bias (Bloesch et al. 1988; Carpenter 1996; Schmidt et al. 2018), high variability and low signal to noise ratio (Caquet et al. 2001; Van den Brink 2013), significant experimental costs (Perceval et al. 2009), and poor repeatability (Eberhardt and Thomas 1991). Still, comparisons of mesocosm-generated data to single-species and field data have shown valuable mechanistic insights (Clements 2004; Rogers et al. 2016; Mebane et al. 2017), and testing system designs have been developed to reduce variability to the point that concentration-response curves can be fit to larval community metrics (Clements et al. 2013; Schmidt et al. 2018; Mebane et al. 2017).

1.3 Aquatic Insect Emergence: Issues of Conventional Approaches

Adult aquatic insects export detrital material and nutrients from aquatic to terrestrial ecosystems (Nakano and Murakami 2001; Gratton and Vander Zanden 2009), and they provide a significant resource subsidy to linked consumers such as birds, bats, and spiders (Sabo and Power 2002a; Echols et al. 2004; Baxter et al. 2005). Emerged adult aquatic insects are also critical vectors of contaminant transfer from aquatic to terrestrial environments (Walters et al. 2008; Kraus et al. 2014b). Thus, aquatic insect emergence can be used to characterize aquatic contaminant fate and aquatic subsidy alterations to linked terrestrial ecosystems.

Field observations have predominately driven our understanding of these A-T contaminant linkages (Walters et al. 2008; Paetzold et al. 2011; Schmidt et al. 2013; Kraus et al. 2014a, 2016). For example, Schmidt et al. (2013) conducted an analysis of field survey data on macroinvertebrate larval and adult densities along a metal gradient in Colorado (USA) mountain streams. They compared larval and adult responses to metal concentration and observed differences in threshold responses between life stages. Specifically, larvae abundance was reduced at or above the cumulative criterion accumulation ratio (CCAR; a toxic unit model modified from the biotic ligand metal bioavailability model; values at or below 1 are considered protective of aquatic life), but adult emergence declined at CCAR values less than or equal to 1. These results suggest uncertainty whether aquatic life criteria are protective of full aquatic insect life cycles and thus protective of A-T linkages. However, our ability to develop aquatic life criteria using field surveys alone is limited by replication, our general inability to manipulate the variable of interest, extraneous variables that confound results, and naturally high variability.

Furthermore, traditional single-species toxicity tests are too limited in predicting cross-ecosystem effects. For example, aquatic invertebrate species such as *Daphnia* spp. are widely employed because they are relatively sensitive and used in many single-species tests, but zooplankton does not metamorphose into a terrestrial life stage; therefore, no equivalent endpoint exists to estimate these effects. Most natural assemblages of aquatic (e.g., lotic or lentic) communities contain aquatic insect taxa that complete their life cycle as winged-terrestrial adults (Merrit et al. 2004). Some surrogate test organisms employed with single-species testing do metamorphose to an imago (e.g., adult) life stage, such as the hemimetabolous mayfly *Neocloeon triangulifer* (Wesner et al. 2014; Soucek and Dickinson 2015) and the holometabolous midge *Chironomus* spp. (Sibley et al. 1996; Mebane et al. 2008). These metamorphosing invertebrates are important in evaluating contaminant effects through their emerged adult life stages, but using single-species testing alone to predict aquatic-derived terrestrial contaminant effects fails to incorporate the complexity of natural aquatic ecosystems that influence exposure outcomes.

2 Adult Insect Emergence Assessments with Mesocosm Studies

By quantifying adult emergence in aquatic mesocosm experiments, we can estimate potential effects to linked terrestrial ecosystems using experimentally robust methodology. Thus, cause and effect relationships relating aquatic contaminant exposure to terrestrial effects can be quantitatively supported. Importantly, most mesocosm facilities can practically quantify emergence by modifying netting and emergence traps for their respective test systems. Table 1 summarizes aquatic insect adult emergence endpoints conducted with community mesocosm studies described in this chapter. Each mesocosm experiment has accompanying endpoint responses, contaminant and (or) stressor inferences, and potential A-T outcomes. The goal of detailing these mesocosm studies is to provide guidance to researchers and regulators in selecting aquatic insect emergence endpoints that they can apply to research and develop aquatic life criteria.

Table 1 Summary of adult insect emergence assessment endpoints using aquatic mesocosm contaminant exposures to characterize aquatic-terrestrial outcomes

Mesocosm emergence assessment	Endpoint responses	Contaminant (or) stressor inference	Aquatic-Terrestrial (AT) outcomes	Relevant mesocosm studies
Total Emerging Adult Abundance	Reduction in emerging adult populations or communities, but not larvae, respectively	Greater relative contaminant sensitivity during metamorphosis compared to larval life stage development	Population persistence is at risk; Reduced emerging adult subsides to terrestrial predators; Reduced aquatic to terrestrial contaminant flux	O'Halloran et al. (1996), Culp et al. (2003), Brock et al. (2009), Mohr et al. (2012), and Colombo et al. (2013)
	Reductions in larval populations or communities, but not emerging adults, respectively	Greater relative contaminant sensitivity in larval life stages compared to metamorphosis life stages	Population persistence promoted through egg laying by terrestrial adults; Increased aquatic to terrestrial contaminant flux	Arthur et al. (1983), Belanger et al. (2004), Belanger et al. (2005), and Kotalik and Clements (2019)
Timing of Adult Emergence	Increased or delayed rate of emergence	Contaminants can alter neurological function, hormone balance, and altered metabolic rates; Indirect effects of food limitations due to reduced autotrophic production; Delayed developmental effects in longer-lived taxa	Adults may encounter unsuitable terrestrial conditions; Shift timing of subsidies to consumers	Nordlie and Arthur (1981), Dewey (1986), Maund et al. (1992), Gruessner and Watzin (1996), Boyle et al. (1996), Blumenshine et al. (1997), Schulz and Liess (2001), Belanger et al. (2004, 2005), Connolly et al. (2004), Farmer et al. (1995), Pettigrove and Hoffmann (2005), Alexander et al. (2008), Rogers et al. (2016), Richmond et al. (2016), Joachim et al. (2017), Kotalik and Clements (2019)

(continued)

Table 1 (continued)

Mesocosm emergence assessment	Endpoint responses	Contaminant (or) stressor inference	Aquatic-Terrestrial (AT) outcomes	Relevant mesocosm studies
Biomass of Emerging Adults	Increased or reduced biomass of emerging adults	Indirect contaminant effects due to autotrophic stimulation or suppression; Mortality by larvae preventing emergence altogether	Unnatural increases or decreases in subsidies can destabilize AT food-web structure; Increase or decrease in aquatic to terrestrial contaminant flux	Nordlie and Arthur (1981), Mundie et al. (1991), Blumenshine et al. (1997), Perrin and Richardson (1997), Culp et al. (2003), Greig et al. (2012), Piggott et al. (2015), Elbrecht et al. (2016), and Sardiña et al. (2017)
Body Size of Emerging Adults	Increased or reduced body size of emerging adults	Indirect contaminant effects due to autotrophic stimulation or suppression; Metabolic costs associated with stressor; Size-dependent sensitivity to exposure	Unnatural increases or decreases in subsidies through altered body size can destabilize AT food-web structure; Smaller emerging body size can reduce fecundity, fitness, and population persistence; Altered size structure can affect top-down species interactions; Increase or decrease aquatic to terrestrial contaminant flux	Blumenshine et al. (1997), Alexander et al. (2008, 2016), Piggott et al. (2015), Magbanua et al. (2016), Sardiña et al. (2017)
Aerial Recolonization Dynamics by Emerging Adults	Rate of emergence and recovery post-exposure	Duration of contaminant effects and recovery	Recovery of larval communities is facilitated by aerial colonization; Terrestrial environments facilitate movement of adults	Boyle et al. (1996), Schmude et al. (1999), Caquet et al. (2001, 2007), Beketov et al. (2008), Brock et al. (2009, 2010), Mohr et al. (2012)
Contaminant Flux by Emerging Adults Insects	Concentration of contaminants in emerging adults	Contaminant accumulation and fate from larvae through metamorphosis	Export and transfer of contaminants from aquatic environments to terrestrial consumers and biota	Fairchild et al. (1992), Jones et al. (2013), and Tweedy et al. (2013)

2.1 Life-Stage Sensitivity

Mesocosms are particularly useful for assessing contaminant sensitivity through metamorphosis because they can integrate and expose benthic communities through multiple developmental life stages, including the transition to emerged adults (Kotalik and Clements 2019). Larval abundances in aquatic ecosystems are often assumed to be linked to the abundances of emerging insect adults (Statzner and Resh 1993; Gratton and Vander Zanden 2009). However, metamorphosis of aquatic organisms from their larval to adult life stages is a biologically stressful process (Campero et al. 2008), and exposure to contaminants either before or during this transition may cause organisms to be even more sensitive when metamorphosing (Fig. 1, Wesner et al. 2014, this volume). This pattern is seen in both single-species laboratory exposures and field surveys, with adult life stages displaying greater sensitivity compared to larvae (Palmquist et al. 2008; Schmidt et al. 2013; Wesner et al. 2014; Debecker et al. 2017). During the metamorphosis process, substantial reorganization of tissues occurs; and therefore, metamorphosing life stages of invertebrates may be more susceptible compared to earlier molting events (Liber et al. 1996; Wesner et al. 2014). Most acute single-species laboratory toxicity tests lack sufficient exposure duration and variation in size structure to evaluate effects among aquatic insect life stages. Furthermore, field surveys have confounding variables (e.g., seasonality, immigration, emigration) that affect the ability to characterize sensitivity of larvae and emerging adults. If invertebrates are unable to metamorphose and complete their life cycles as emerged adults, population persistence is at risk (Zwick 1990; Rasmussen and Rudolf 2015), and biomass available to terrestrial consumers is reduced (Kraus et al. 2014a).

Differences in sensitivity among aquatic insect life stages, including larvae transitioning to adults, have been confirmed with numerous community mesocosm studies (Kiffney and Clements 1996; Clements and Kotalik 2016; Kotalik et al. 2017, 2019; Kotalik and Clements 2019). Community mesocosm exposures have shown greater relative sensitivity in emerging adults compared to larval populations in Ephemeroptera (Culp et al. 2003; Colombo et al. 2013), Chironomidae (O′Halloran et al. 1996), and other Diptera (Brock et al. 2009; Kotalik et al. 2019). Likewise, Mohr et al. (2012) did not observe a significant difference in larval community structure when exposed to pulses of imidacloprid but did observe significant alterations in emerging adult community structure. In contrast, other mesocosm studies have shown just the opposite relationship, with emerging adult aquatic insects more tolerant to exposure than early larval life stages. Instances of reduced larval abundances, but not emerging adult abundances, have been observed with pesticides (Arthur et al. 1983; Beketov et al. 2008), household and personal care products (Belanger et al. 2004; Belanger et al. 2005), bacterial insecticides (Richardson and Perrin 1994), and metals (Kotalik and Clements 2019).

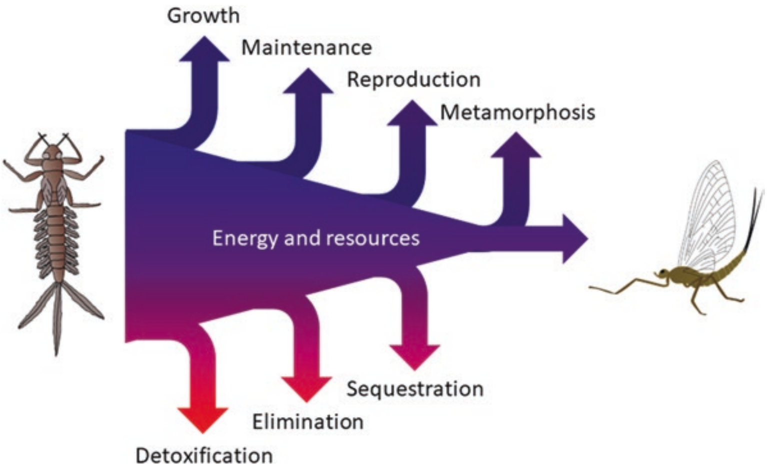

Fig. 1 Bioenergetics of aquatic insects developing from larvae to their adult life stages. Upward arrows represent energy and resources used by individuals for growth, maintenance, reproduction, and metamorphosis. In the presence of contaminants, energy and resource "costs" are associated with detoxification, elimination, and sequestration

2.2 *Timing of Emergence*

Single-species tests are not able to account for consumer-resource interactions, while field surveys lack the experimental control to characterize timing of emergence due to numerous potential confounding effects (e.g., immigration, predation, climatic variability). Mesocosm community exposures are particularly appropriate to evaluate timing of emergence because indigenous taxa at various life stages of development and with complex physiologies respond directly (i.e., toxicant accumulation) and indirectly (i.e., impaired food resources) to contaminants. For example, aquatic insects may speed up or delay their larvae development either to reduce their exposure or as a direct consequence of toxic effects. Irregular timing of emergence may result in individuals encountering terrestrial conditions that are unsuitable for their adult survival (Nebeker 1971) and shift the timing of A-T resource subsidies that terrestrial consumers are temporally cued to encounter (Takimoto et al. 2002; Yang et al. 2010; Hastings 2012; Muehlbauer et al. this volume).

Increased rates of emergence in community mesocosm studies have been observed with trace metals (Joachim et al. 2017; Kotalik and Clements 2019), pesticides (Dewey 1986; Maund et al. 1992; Gruessner and Watzin 1996; Schulz and Liess 2001; Belanger et al. 2004; Farmer et al. 1995; Alexander et al. 2008; Rogers et al. 2016), illicit drugs, and pharmaceuticals (Lee et al. 2016; Richmond et al. 2016). Increases in rates of emergence can be beneficial because emerged adults may reduce larval exposure and complete their life cycle as emerged adults; however, increased rates of development may also reduce size (i.e., fecundity) of emerging adults that have less time for growth. In contrast, delays in emergence have been reported with petroleum exposures (Pettigrove and Hoffmann 2005) and reduced dissolved oxygen treatments (Nebeker 1972; Connolly et al. 2004). Delayed emergence may be the result of contaminant-induced stress that reduces rates of tissue reorganization required for the morphological transition from aquatic to terrestrial life stages. Contaminants can directly affect rates of emergence by altering neurological function (Bloomquist 1996), metabolic rates (Nebeker 1972), and hormone balance (Zhao et al. 2009; Nation 2015). In addition, altered rates of insect emergence have been associated with the effects of contaminants on food palatability (Postma et al. 1994) and reductions in overall food resources (Dewey 1986; Gruessner and Watzin 1996).

2.3 Size and Biomass of Emerging Adults

Mesocosms are unique in identifying the underlying mechanisms influencing changes in emerging biomass because autotrophic functions (e.g., periphyton growth) are included, and changes in food resources can be in direct response to the contaminant. Size and biomass of emerging adult aquatic insects provide a useful endpoint in addressing contaminant effects to A-T linkages. For example, reductions in emerging biomass can be related to direct toxicity to larvae, which obviously eliminates emergence (Belanger et al. 2002), or mortality of individuals during the metamorphosis process (Wesner et al. 2014; Debecker et al. 2017; Wesner et al. this volume). Reductions in biomass and size of adult aquatic insects can be linked to altered food resources, with autotrophic stimulation or suppression resulting in changes to food availability in larvae that then affect emerging adult body size (Blumenshine et al. 1997; Sardiña et al. 2017). Single-species tests commonly feed organisms ad libitum, and the food resource does not directly respond to the stressor. Thus, single-species tests can only characterize direct toxicity on insect larvae leading to reduced emergence biomass or size.

Mesocosm studies are useful to decouple alterations in autotrophic production with emerging size and overall biomass. For example, mesocosm exposures have linked contaminant-induced autochthonous stimulation with increased body size and biomass of emerging insects (Mundie et al. 1991; Blumenshine et al. 1997; Perrin and Richardson 1997; Culp et al. 2003; Piggott et al. 2015; Elbrecht et al. 2016). Similarly, elevated water temperatures that increase primary production have been shown to increase the total biomass of emerging insects (Nordlie and Arthur 1981; Greig et al. 2012; Piggott et al. 2015; Sardiña et al. 2017); however, aquatic insects in some of these thermal exposures actually emerged as smaller adults (Piggott et al. 2015; Sardiña et al. 2017). While autochthonous subsidies contribute to food web stability (Nakano and Murakami 2001), unnatural increases in subsidy biomass may decouple consumer-resource interactions and reduce stability (Huxel and McCann 1998; Hocking and Reynolds 2011). For example, linked terrestrial consumers may shift to more abundant emerging aquatic insects that respond to greater food resources (e.g., strengthening these linkages) but reduce their top-down control of other terrestrial-derived consumer resources (e.g., weakening these linkages).

2.4 *Aerial Recolonization Dynamics*

Long-duration community mesocosm studies have demonstrated the importance of understanding invertebrate responses throughout their life cycles for predicting contaminant effects and recovery dynamics (Boyle et al. 1996; Schmude et al. 1999; Caquet et al. 2007; Beketov et al. 2008; Mohr et al. 2012). Recovery of natural aquatic ecosystems following disturbances by natural and anthropogenic stressors is often facilitated by aerial recolonization by aquatic insect adults (Merrit et al. 2004). Outdoor mesocosms that enable external colonization by winged adults have confirmed the importance of egg laying for benthic recovery following pulse pesticide exposures (Caquet et al. 2007; Beketov et al. 2008). Results from these studies have demonstrated differences in recovery propensity in multigenerational (multivoltine) groups of organisms, compared to longer-lived (uni- or semivoltine) taxa (Caquet et al. 2007; Beketov et al. 2008; Mohr et al. 2012).

Given that multivoltine taxa have greater probability of recolonizing from nearby source populations as adults, mesocosm experiments that compare “open” versus “closed” systems can test recovery duration required to achieve original taxa density and distribution. Single-species exposures, even with longer, chronic exposure durations (e.g., greater than 30 days), lack the environmental complexity and colonization capacity required to examine such endpoints. For example, recolonization by aerial adults to small indoor test systems (i.e., beakers) is simply not possible. Mesocosm studies offer a suitable spatiotemporal scale to characterize and predict trajectories of stream community recovery. Importantly, estimating rates of recovery following contaminant disturbances is important for predicting the responses of linked terrestrial ecosystems that receive aquatic subsidies.

2.5 *Interspecies Interactions and Multiple Stressors*

The effects of interspecies interactions and multiple stressors on contaminant and resource transfer by adult aquatic insects can be effectively separated using mesocosms. For example, mesocosm studies have shown that the presence of fish and nutrients can control methyl mercury (MeHg) flux from aquatic ecosystems via emergent aquatic insects (Jones et al. 2013; Tweedy et al. 2013). Greig et al. (2012) demonstrated enhanced cross-ecosystem subsidy exchanges via emerging insects with warming and increased nutrients, but predatory fish eliminated these effects by reducing emerging insect biomass and delaying insect phenology. Similarly, Alexander et al. (2016) used mayfly emergence and stream mesocosm exposures to decouple density-dependent relationships of imidacloprid, nutrient enrichment, and predation (stonefly *Agnetina capitata*) pressures on subsidy-stress responses. The use of adult insect emergence endpoints in these studies uniquely quantified these complex interactions of subsides and stressors on bottom-up and top-down effects.

Mostly all impaired aquatic systems have more than one stressor contributing to disturbances, and novel experimental methodologies such as mesocosms and aquatic insect emergence provide pragmatic approaches to isolate stressor effects and to characterize the complex interactions of physical and chemical stressors. Multiple stressors can destabilize food webs and decouple trophic linkages that are critical for the recovery of both aquatic and linked terrestrial ecosystems (MacNeale et al. 2010). Mesocosms that measure emergence have separated interactive effects among ubiquitous anthropogenic stressors such as warming temperatures, flow alteration, fine-sediment deposition, pesticides, and nutrients (Greig et al. 2012, Magbanua et al. 2016; Piggott et al. 2015; Alexander et al. 2016; Elbrecht et al. 2016). Magbanua et al. (2016) used mesocosms to demonstrate the additive effects of the insecticide glyphosate and fine sediment on emergence. Similarly, Piggot et al. (2015) observed greater total emergence in response to fine sediment, as well as significant two- and three-way interactions with nutrients and temperature, reflecting life-stage-dependent sensitivity.

3 Mesocosm Testing Considerations for Aquatic Insect Emergence

The scale, duration of exposure, and sources of aquatic communities used in mesocosm exposures will influence data obtained from aquatic insect emergence experiments. Several documents have been developed outlining “appropriate” mesocosm experimental design for research and regulatory applications (Pontasch and Cairns 1989; Graney 1993; Cairns and Niederlehner 1995). The European Union (EU) has produced several guidance documents for micro- and mesocosm studies for pesticides (European Union 1997; Campbell et al. 1999; European Union 2002). Key mesocosm testing considerations for quantifying aquatic contaminant effects to linked terrestrial ecosystems using aquatic insect communities and adult aquatic insect emergence are duration and concentrations of exposure, traits of the sourced communities, size of mesocosms, and appropriate statistical analyses. We address each of these considerations below and provide basic guidance for incorporating these mesocosm data into the criteria development process.

3.1 Exposure Concentration and Duration

One of the first decisions faced by researchers using mesocosms to test effects of a particular contaminant, or contaminants, on aquatic-terrestrial linkages is to choose the concentrations and duration of exposure. Along with concentrations measured in the field, we recommend the concentration-response curves obtained from single-species testing procedures using aquatic species representative of the natural communities in the field bracket exposure concentrations. Exposure duration will influence biological outcomes, and selecting the duration of exposure for mesocosm experiments is a critical decision. Longer duration exposures are more comparable to field conditions, while shorter durations may be more similar to single-species laboratory studies. Researchers must question if their exposure reflects the exposure regime observed in the field, affording adequate time to observe biological effects similar to those in nature. Contaminant exposures in aquatic environments can have both short- (acute) and long-term (chronic) effects, for example, acute aqueous exposure followed by chronic exposure from the release of contaminants bound in sediments (Liess and von der Ohe 2005). Chronic exposure scenarios, such as toxicant inputs from mining activities or point source effluents, may require a longer duration to reflect temporally dependent rates of accumulation and toxic effects (Poteat and Buchwalter 2014). Ultimately, logistical considerations (e.g., monetary costs, technicians, experimental setup) must be weighed with the ecotoxicological relevance from selected exposure regimes.

Longer exposure durations and (or) longer experiment lengths may be required for mesocosm studies aimed at quantifying aqueous contaminant effects on terrestrial ecosystems because most aquatic insects have complex life histories that require much greater time to complete compared to most cultured aquarium species. Therefore, longer-lived taxa such as uni- or semivoltine invertebrates will require longer exposure durations to capture all developmental instars (life stages) through emergence, whereas multivoltine taxa that have numerous life cycles per year may be sufficiently exposed with less time. Life cycle traits should be considered because inadequate duration of larval exposure may underestimate effects to longer-lived species (e.g., uni- or semivoltine; Van den Brink et al. 1996; Caquet et al. 2007; Beketov et al. 2008). For example, Beketov et al. (2008) observed the fastest larval recovery in exposed test systems (open to aerial recolonization) by multivoltine Diptera (e.g., chironomids, simuliids) following pulsed insecticide exposure but much slower recovery in a univoltine stonefly. Most aquatic insects have well-documented life histories (Merrit et al. 2004), and researchers have the opportunity to use this information to determine the appropriate exposure duration.

3.2 Source Community Traits

A second decision by researchers in preparation for mesocosm experiments is to determine which communities to expose and how to collect them from the field. Sourcing communities from reference sites that are devoid of unnatural stressors, and that have not been disturbed by natural stochastic events (e.g., floods, fire, drought), reduces confounding factors that may limit the ability to significantly detect a treatment effect. However, communities sourced from sites with previous exposure, or sites that are exposed to unfamiliar contaminants (i.e., novel stressors), can provide opportunities to examine context-dependent responses.

For researchers interested in measuring emergence endpoints, community assemblages selected for mesocosm experiments need to contain taxa that metamorphose to air-breathing terrestrial adults, which can be determined a priori and referenced using the published literature (Merrit et al. 2004). For example, individuals must be developmentally mature to the point of metamorphosis to capture emergence. One design possibility is to allow larvae to develop during exposure and metamorphose to adults. Another design possibility is to collect developmentally mature larvae from the field and expose them in mesocosms close to their metamorphosis. The season of source community collection will also affect experimental outcomes; for example, communities collected in the winter may have very different A-T exposure outcomes compared to communities in midsummer due to phenological differences in emergence and developmental life stages.

In terms of collecting source communities for mesocosm experiments, various methods exist, such as substrate-filled colonization trays or field collection techniques using quantitative benthic sampling methods (e.g., Surber, core sampling) (Pontasch and Cairns 1989; Clements et al. 1989; Pontasch and Cairns 1991; Cadmus et al. 2018). These methods can be used to target annual differences in developmental life stages (e.g., egg, early-mid-late instar, and pupa) among invertebrates in their selected community assemblage. Including a variety of life stages within an experiment is important because many aquatic insect larvae stop feeding as they near metamorphosis (Merrit et al. 2004), limiting dietary routes of exposure. Moreover, larval size alone can strongly influence sensitivity to contaminants (Kiffney and Clements 1996; Poteat and Buchwalter 2014) and therefore the ability of individuals to survive to metamorphosis.

Developmental and phenological changes within experimental communities can occur very rapidly during an experiment. Duration of emergence varies among insect taxa; for example, some aquatic insects such as *Pteronarcys* spp. or *Hexagenia* spp. emerge for only a few weeks annually (Giberson and Rosenberg 1994; Sheldon 1999), while other taxa have emergence that extends for many months (e.g., midges, mayflies). Even though some insect taxa may only briefly emerge to the terrestrial environment, superabundant “pulsed” subsides can represent disproportionally large carbon and nutrient flux to terrestrial ecosystems compared to relatively constant “press” emergence (Yang et al. 2010; Walters et al. 2018). Therefore, timing of toxicant exposure to source communities should be carefully planned.

3.3 Mesocosm Scale

Mesocosm scale can dictate the community assemblage structure, functional processes, and possible duration of exposure. Small-scale mesocosms (e.g., buckets, small aquaria) typically have greater replication and statistical power and, owing to the need for less infrastructure and fewer resources (less water, less chemical), are relatively more cost-effective. However, smaller-scale mesocosms are generally constrained to shorter exposure periods (weeks to months, not years) due to difficulty maintaining natural functional processes such as delivery of organic matter and colonization of new organisms. Conversely, larger mesocosms (e.g., ponds, large raceways) generally exhibit greater structural and functional realism because functional processes such as immigration maintain natural population and community dynamics. For example, Joachim et al. (2017) allowed aquatic insect adults to seed and maintain larval populations in their mesocosms through aerial deposition of eggs over a 2-year exposure. Larger mesocosms can be implemented for longer exposure assessments; they can be used to evaluate recovery of benthic communities via aerial colonization by adults and incorporate higher trophic-level interactions (e.g., predatory fish). Yet, large mesocosms consume relatively more resources and take up more space, resulting in fewer replicates that reduce statistical power, and because they are often open to the environment are more susceptible to stochastic events (e.g., unwanted predation, weather, vandalism). Researchers do not always have a choice regarding scale of their experiments, which may be limited to available facilities. Although most A-T endpoints are possible to quantify with most mesocosm experimental scales, the relationship between scale and exposure duration is tightly coupled, with extended exposure regimes requiring larger mesocosms to maintain functional processes.

3.4 Statistical Considerations

Finally, researchers must choose statistical analyses that are appropriate to their research questions and experimental design. Statistical analyses of mesocosm treatment effects are often conducted at the population level, and most univariate techniques (e.g., ANOVA, regression, and GLM), as well as post hoc comparisons (e.g., Dunnets, Duncans, and Williams), employed to analyze larval treatment responses can be applied to aquatic insect emergence data. Temporally dependent A-T endpoints can be tested with repeated-measure ANOVA (Magbanua et al. 2016; Kotalik and Clements 2019) or regression-based analyses with normalized timing data (Rogers et al. 2016; Schmidt et al. 2018). For example, the time to 50% of emergence (TE$_{50}$) can be calculated by fitting a logistic equation to time (days) versus the number of individuals emerging each day (Basic OriginPro, Origin Lab, Northampton, MA). The equation to estimate time to reach 50% emergence is as follows:

$$y = a_2 + \left(a_1 + a_2\right) / \left(1 + \left(\frac{x_i}{x_0}\right)^p\right)$$

where y is the number of emerging adults at time x_i, a_1 is the model-predicted minimum number of emergers, a_2 is the model-predicted maximum number of emerging adults, $x_0$is the time at 50% emergence, and p is the power of the equation.

Emergence dynamics (i.e., the cumulative number of emerging insects over time) can be calculated using cumulative deviance of emergence through time. The equation to estimate difference in cumulative adult emergence between treatments is as follows:

$$y_i = \sum T_i - \sum C_i$$

where y_i is the difference in cumulative emergence between treatment (T_i) and control (C_i) and T_i is calculated as the daily sum of emerging adults since the start of the experiment.

Alterations in community structure resulting from differences in population-level sensitivity (e.g., direct mortality) or organism emigration (e.g., emergence) can be the most sensitive indicators of toxicant stress (Cairns and Niederlehner 1995). Thus, a major strength of mesocosm studies is that communities of aquatic organisms are exposed to aquatic contaminants and community-level responses are evaluated. Statistical procedures have been specifically developed for large-scale mesocosm studies to analyze community treatment effects (Van den Brink and Ter Braak 1999). The principal response curve (PRC) method analyzes time-dependent multivariate responses of communities to stress and is frequently applied to emergence data. PRC is based on the redundancy analysis (RDA) technique and is a constrained form of principal component analysis (Van den Brink and Ter Braak 1999). PRC works by separating three sources of variation in community composition: (1) changes in time, (2) differences between replicates, and (3) effects of treatments. Importantly, PRC can include hypothesis testing using Monte Carlo permutation with RDA that is capable of determining community-level "lowest observed effect concentration" and "no observed effect concentration." Functional endpoints such as rates of emergence can exhibit high intra-treatment variability, and analyses at the community level with PRC are particularly valuable and have been shown to be more sensitive in detecting changes over time compared to univariate analyses (Van den Brink and Ter Braak 1998). Permutation testing for "significant" treatment differences should employ low numbers of categorical variables (in contrast to regression-based designs), and experimental duration must be adequate to gather numerous observations. Figure 2 is an example of PRC from Joachim et al. (2017), demonstrating the effects of copper through time on the abundance of emerging aquatic insects.

4 Conceptual Model and Conclusion

Regulatory frameworks such as aquatic life criteria could benefit from the integration of mesocosm studies generally, and aquatic insect emergence is a particularly relevant endpoint for protecting aquatic-dependent life through its A-T linkage. Our hope is that aquatic insect emergence endpoints, along with other endpoints that link A-T contaminant fate and effects, are incorporated into mesocosm testing

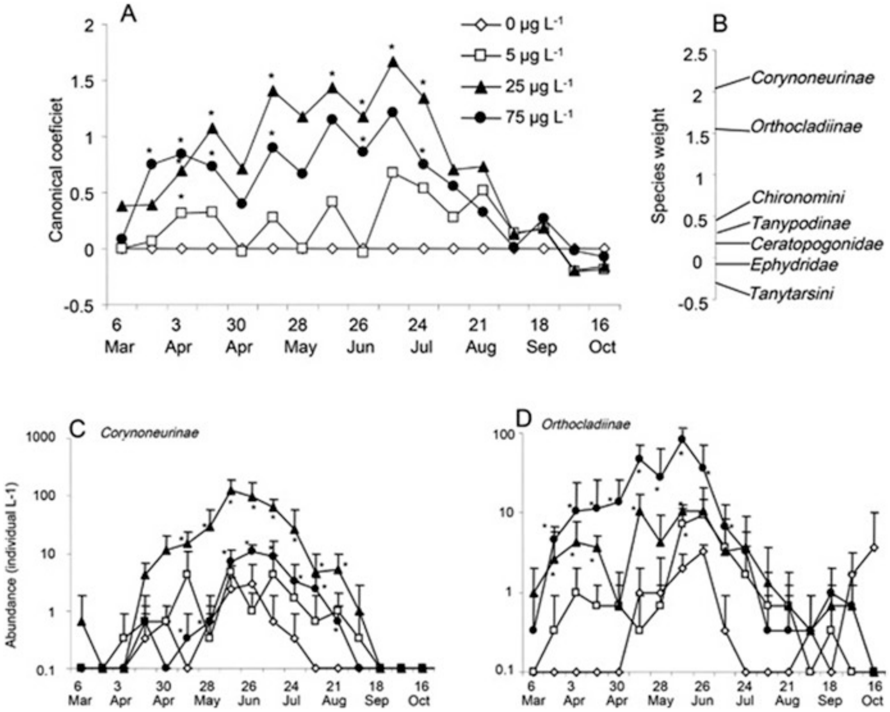

Fig. 2 An example of the use of principal response curves to compare community shifts in treatments against controls over time, including the influence of specific species. (**a**) The effect of copper through time based on the canonical coefficient of the emerging insect community. Curves deviating from the reference value of 0 indicate treatment effects. The species weight can be interpreted as the affinity of the taxon with the curves (**b**). Notice that species weight between 0.5 and −0.5 are not presented, as they were likely to show a weak or unrelated response. Dynamics of the two most important species are presented in a logarithmic scale: Corynoneurinae spp. (**c**) and Orthocladiinae spp. (**d**). Asterisks indicate significant difference relative to controls (Williams test, $P < 0.05$). (From Joachim et al. (2017), reprinted with permission)

procedures and are used in a "primary role" in criteria development. Of course, mesocosm studies represent just one line of evidence in evaluating contaminant effects, and researchers and regulators could benefit by working together to employ a comprehensive approach utilizing laboratory, mesocosm, and field data to develop aquatic life criteria that are inclusive of linked terrestrial effects. As mesocosms become more useful as predictive tools, their utility will no doubt be tested, but we should address rather than shelve these challenges if we wish to make meaningful progress in modernizing aquatic toxicity testing approaches that include the fate and effects of contaminants in linked A-T ecosystems.

4.1 Integrating Aquatic Insect Emergence into Aquatic Criteria Development

Here we provide a very basic conceptual workflow for integrating aquatic insect emergence into the aquatic life criteria development process. First, single-species toxicity tests using a diverse representation of holometabolous and hemimetabolous aquatic insects can be used to evaluate contaminant effects across multiple developmental life stages, including metamorphosis to adults. Second, life-stage sensitivity can be precisely determined using contaminant exposure gradients, and contaminant transfer from larvae and adults can be quantified. Third, species sensitivity distribution (SSD) models (or other normalizing models) can generate, for a specified protection level (e.g., 95%), concentrations for both larvae and adult life stages. Mesocosm testing can then evaluate the laboratory-derived SSD models by comparing single-species SSD results to the responses of natural aquatic communities. Moreover, normalizing models (i.e., SSD) to generate protective concentrations can be applied to mesocosm data, and importantly, they can include the larval and adult life-stage responses of indigenous taxa obtained from mesocosm testing, as well as community-level treatment effect derivations.

Lastly, aquatic (e.g., benthic and emergence) and terrestrial (e.g., riparian consumer density and contaminant concentrations) field sampling methods can be used to calibrate the relationship of altered insect emergence to linked terrestrial effects and (or) contaminant transfer and to verify criteria protectiveness. Reductions in emerging biomass may disproportionally affect riparian consumers (e.g., growth rates, presence or absence) (Sabo and Power 2002a; Murakami and Nakano 2002; Paetzold et al. 2011; Kraus et al. 2014a), or effects may be less than predicted due to the adaptability of terrestrial consumers to subsidy perturbations (Sabo and Power 2002b; Kato et al. 2003; Spiller et al. 2010). The regulatory community can utilize these different approaches together to ultimately decide what rates of aquatic insect adult contaminant transfer and subsidy alterations are acceptable.

Aquatic insect emergence endpoints vary in their ability to be quantified in the laboratory, with mesocosms, or in the field, because of their respective spatiotemporal scales and abilities to control and replicate (Fig. 3; modified from Buchwalter et al. 2017). Nevertheless, these differences should not be seen as a limitation; rather researchers can leverage all applicable ecotoxicological methods, identify their respective strengths and weaknesses, and use these multiple lines of evidence to develop aquatic life criteria that are inclusive of contaminant fate and effects in linked A-T ecosystems. Differences between laboratory and mesocosm results may also be seen as a weakness in applying mesocosm results to aquatic life standards. However, these differences can be used to generate hypotheses of the mechanisms influencing these differences (e.g., indirect effects, seasonality, or other factors), and additional research can refine criteria derivations.

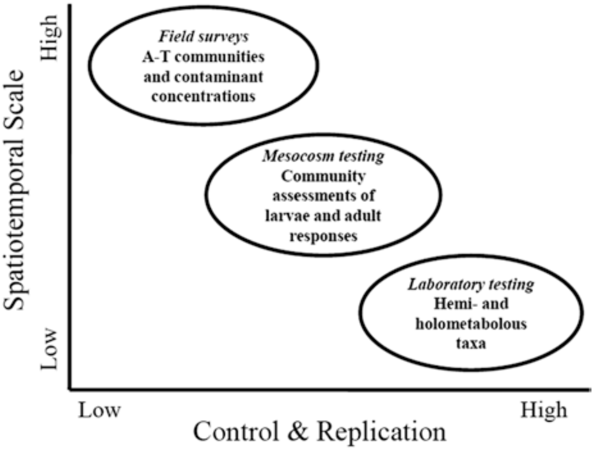

Fig. 3 Relationships of spatiotemporal scale, control, and replication of field surveys, mesocosm testing, and laboratory toxicity tests used to quantify aquatic insect emergence. (Modified from Buchwalter et al. 2017)

4.2 Concluding Remarks

To standardize the effects that A-T linkages have to aquatic ecosystems, we need experimentally robust methods that integrate the appropriate biological complexity. We focused on adult insect emergence because of its linkage to aquatic impairment and terrestrial effects. However, we recognize that subsidy alterations and contaminant delivery to terrestrial ecosystems are affected by other processes such as downstream drift by aquatic insects, aquatic primary productivity, and secondary production. Without field validations, the application of A-T data gathered from mesocosm studies will be limited in deriving aquatic life criteria. More field biomonitoring is needed to link aquatic impairment to terrestrial effects among differing ecosystems if we wish to meaningfully test these relationships in the future. To conclude, mesocosm experiments can successfully quantify A-T linkages, and data obtained from these experiments have great potential to contribute to the aquatic life criteria development process.

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Studying Effects of Contaminants on Aquatic-Terrestrial Subsidies: Experimental Designs Using Outdoor and Indoor Mesocosms and Microcosms

Mirco Bundschuh, Jochen P. Zubrod, Matthias V. Wieczorek, and Ralf Schulz

> *In the spirit of science, there really is no such thing as a 'failed experiment'. Any test that yields valid data is a valid test.*
>
> *Adam Savage*

1 Introduction

The subsidy of terrestrial ecosystems by resources of aquatic origin has gained increased attention by the scientific community over the past 25 years, including recent reviews addressing the ecological (Soininen et al. 2015; Richardson and Sato 2015) and stress-ecological (Schulz et al. 2015; Larsen et al. 2016) perspectives. However, few of these studies have focused on how chemical contamination can impact these subsidies. And even fewer establish a causal link between aquatic contamination and impacts on terrestrial ecosystems. For example, although Schulz et al. (2015) identified nearly 700 papers published on biotic and abiotic linkages from aquatic to terrestrial ecosystems between 1990 and 2014, only around 10% of

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M. Bundschuh (✉)
iES Landau, Institute for Environmental Sciences, University of Koblenz-Landau, Koblenz-Landau, Germany
Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden
e-mail: bundschuh@uni-landau.de

J. P. Zubrod · R. Schulz
iES Landau, Institute for Environmental Sciences and Eusserthal Ecosystem Research Station, University of Koblenz-Landau, Koblenz-Landau, Germany
Eusserthal Ecosystem Research Station, University of Koblenz-Landau, Landau, Germany
e-mail: zubrod@uni-landau.de; schulz@uni-landau.de

M. V. Wieczorek
iES Landau, Institute for Environmental Sciences, University of Koblenz-Landau, Koblenz-Landau, Germany
e-mail: wieczorekm@uni-landau.de

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these studies assessed the impact of chemical stressors. From these roughly 70 studies, 21 dealt with the transfer of contaminants and their effects to terrestrial systems via emerging insects (biotic linkage). Only 2 of these 21 studies used mesocosms (experimental designs), while 19 took place in the field (observational studies). Observational studies are correlative and do not establish a direct cause-effect relationship as do manipulative, experimental studies (i.e. meso- or microcosms).

The relatively low proportion of manipulative experiments involving resource subsidies and contaminants in the published literature might be attributed to the complexity required for experimental designs to adequately assess the impact of chemical stressors on donating aquatic systems' ability to subsidise receiving adjacent terrestrial food webs (Polis and Hurd 1996). Nonetheless, such experimental studies would allow the testing of critical overarching hypotheses regarding bottom-up and top-down direct effects and trophic cascades in the terrestrial ecosystem as a consequence of the chemical stress in aquatic systems (Fig. 1, Schulz et al. 2015). Those manipulative experiments may be informed by observational studies. For example, several studies documented the transfer of mercury (Cristol et al. 2008), polychlorinated biphenyls (PCBs, Walters et al. 2008; Walters et al. 2010) and

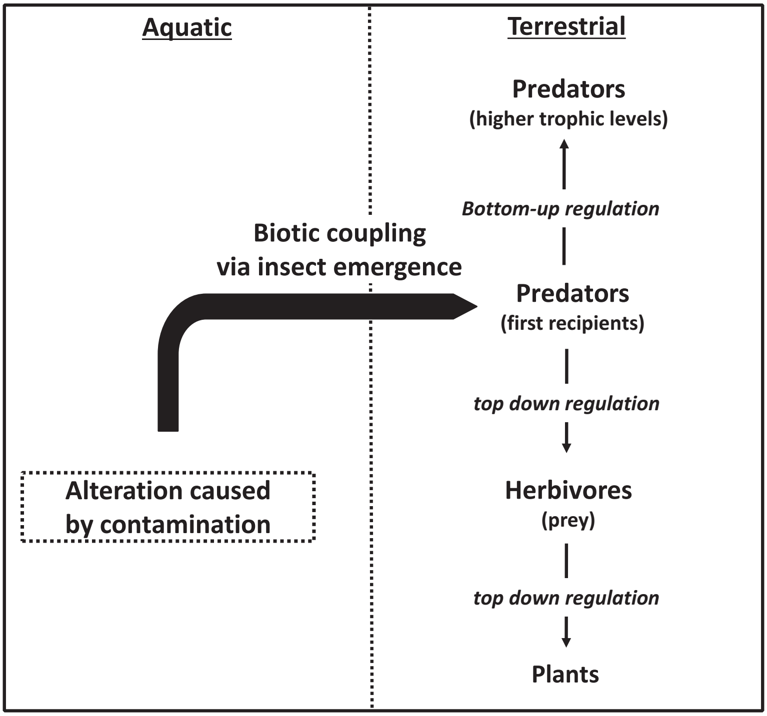

Fig. 1 Conceptual scheme indicating how alterations in aquatic, donor ecosystems induced by chemical stress can influence terrestrial processes by modifications in the biotic coupling (i.e. insect emergence). The implications on the terrestrial, recipient ecosystem can either be bottom-up or top-down regulated (adapted from Schulz et al. 2015).

cyanotoxins (Moy et al. 2016) from aquatic into terrestrial food webs through emerging insects. Moreover, Kalcounis-Rueppell et al. (2007) suggest that toxicants (i.e. micropollutants) from wastewater can alter the community composition of aquatic insects in receiving streams with consequences for bats using riparian ecosystems for hunting. Similarly, Poulin et al. (2010) uncovered that the application of *Bti* (*Bacillus thuringiensis* var. *israelensis*), a microbial agent to control mosquitoes, can modify the prey consumed by birds, which ultimately affects clutch sizes and fledging survival.

Here we focus on lotic systems, which is motivated by their significance for the aquatic-terrestrial interaction driven by their branched watershed networks and consequently long shorelines. We review experimental designs of both lotic out- and indoor meso- and microcosms that were constructed to explicitly address hypotheses related to the implications of chemical stress in aquatic ecosystems and their consequences for the subsidy of adjacent terrestrial (e.g. riparian) ecosystems (Fig. 2). The impact of chemical stress in ecosystem coupling may depend on the

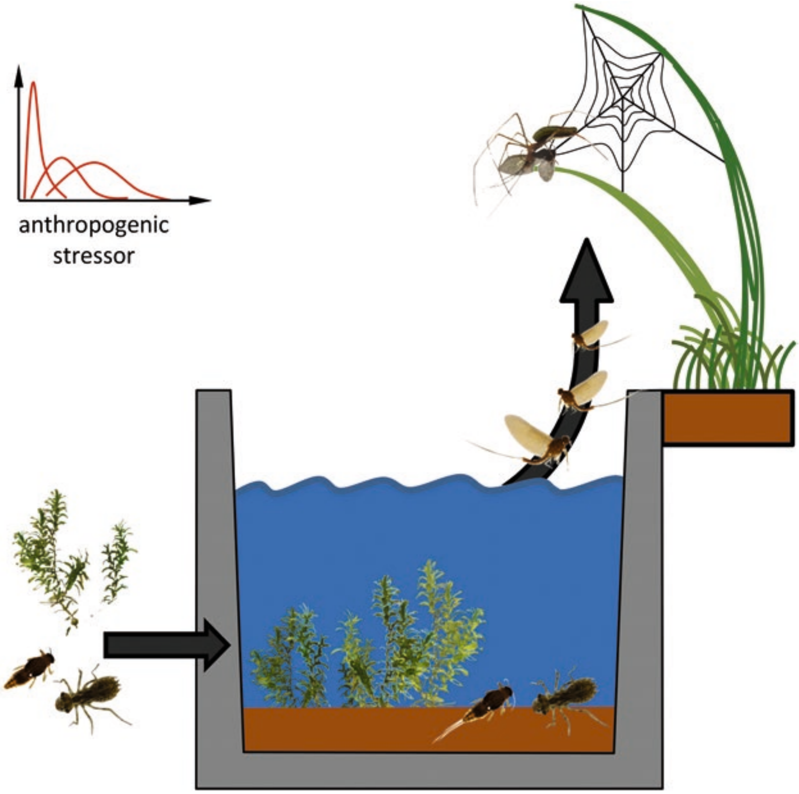

Fig. 2 Exposure to (anthropogenic) chemical stressors can be simulated using field-relevant exposure profiles (e.g. peak vs. press disturbance), while the responses in the aquatic model system (e.g. altered insect emergence) and effects on adjacent terrestrial systems (e.g. to predatory spiders) can be measured

nature of the exposure (e.g. peak vs. press disturbance), the class of chemicals (e.g. insecticides vs. pharmaceuticals) as well as the aquatic community assessed. We further highlight the importance of characterising not only the quantity but also the quality of these subsidies and discuss the potential of stable isotope analysis (SIA) to disentangle trophic interactions within and among aquatic and terrestrial environments.

2 Stream Facilities

2.1 Outdoor Stream Mesocosms

Outdoor stream mesocosms are artificial streams made from various materials defined here as longer than 10 m or more than 1 m^3 in volume (sensu Connell et al. 1999). Such mesocosms often have multiple advantages over laboratory-based microcosms, in part because they are located outside. Outdoor mesocosms receive the full wavelength spectrum of sunlight as well as the natural photoperiod rhythm over the whole calendar year. These factors are important to include in experimental studies because they partially determine emergence patterns of aquatic insects and mating during their adult life stages (Jackson 1988). Moreover, outdoor mesocosms – driven by the full wavelength spectrum – allow for an easy culturing of macrophytes serving as habitat for aquatic microorganisms, as well as macroinvertebrate communities (e.g. Kaenel and Uehlinger 1999). Moreover, outdoor mesocosms facilitate a natural colonisation by macroinvertebrates with a terrestrial life stage from nearby aquatic ecosystems. Sediments ensure a more field-relevant scenario by providing habitat for invertebrates. Some of the features mentioned above can also be realised in laboratory-based microcosms (e.g. Schulz and Liess 2001c); however, they are seldom incorporated. Examples of outdoor mesocosm facilities are the stream and pond systems of the Federal Environmental Agency (Mohr et al. 2005), the artificial streams of Total Petrochemicals (Lacq, France, Bassères and Tramier 2001; Bayona et al. 2015), the artificial stream complex of the Centre for Catchment and In-Stream Research (Queensland, Coominya, Australia, Pusey et al. 1994), the Baylor Experimental Aquatic Research facility (Waco, Texas, King et al. 2016), the experimental ditch systems in Leiden, the mesocosm facilities in Wageningen (Sinderhoeve) or the experimental stream facility at the Helmholtz Centre for Environmental Research. Please see for more examples of aquatic mesocosm systems the respective EU network for freshwater and marine systems (AQUACOSM).

For the purpose of this chapter, the outdoor Landau Stream Mesocosm Facility (LSMF; http://uni-ko-ld.de/hy) at the University of Koblenz-Landau, Campus Landau (Germany), forms the basis of our review. Nonetheless, the underlying principles discussed here are transferrable to comparable facilities. The LSMF comprises 16 independent concrete channels approximately 45 m long, 0.4 m wide and

0.5 m deep. Constant water flow is maintained either in a recirculation mode, meaning that water from the outflow of the channels is pumped back to their inflow for reuse, or a flow-through mode using water from an adjacent 230 m^3 storage reservoir. The overall goal for the LSMF is to allow for replicated assessments of both fate and effects of chemicals in aquatic ecosystems and for testing of hypotheses regarding impacts on connected terrestrial model ecosystems (see for more details Elsaesser et al. 2013; Stang et al. 2014; Wieczorek et al. 2015; Wieczorek et al. 2016).

Each of the channels is equipped with a sediment layer from natural sediments (Liess and Beketov 2011) or artificial sediments such as Organisation for Economic Co-operation and Development (OECD) substrate or sieved top soil from uncontaminated terrestrial ecosystems (Wieczorek et al. 2015). In order to provide habitat for microbial and macroinvertebrate communities over the entire study duration, submerged and emergent macrophytes are added to the experimental system. By introducing decomposing fall leaf litter that accumulated in local uncontaminated streams into the stream channels, leaf-associated aquatic biofilms are added, which play a significant role in the nutrition of macroinvertebrate leaf shredders (Bärlocher 1985). Moreover, the addition of aquatic macrophytes and their root-associated sediment as well as leaf material from pristine streams results in passive introduction of aquatic invertebrates into the experimental units (Wieczorek et al. 2018). This community is possibly supplemented by field catches of a priori defined species or genera ultimately supporting the development of a complex macroinvertebrate community ensuring a wide range of horizontal and vertical food web interactions. Alternatively, or in addition to a priori defined species, natural aerial colonisation of these stream channels by insects from aquatic ecosystems in the vicinity of the experimental system is allowed. We recommend that sediment, macrophyte and insect additions to inoculate each of the channels are made several months before the start of the experiments to ensure a well-developed microbial and macroinvertebrate community (Wieczorek et al. 2018).

A riparian model ecosystem is established in a separate container adjacent to the stream channels to form a linked aquatic-terrestrial model ecosystem (Figs. 3 and 4). Soil and plants collected from a site with limited anthropogenic impact and preferably known composition of the emerging terrestrial insect community are added to the container adjacent to the stream channel to simulate terrestrial or riparian environments (Wieczorek et al. 2015). Such systems are often enclosed in cages built from a mesh-covered frame large enough to allow researchers easy access for sampling. The cages are needed to control for interferences driven by undesired and uncontrolled factors including escape of organisms from the system and intrusion of organisms from the outside (e.g. loss of individuals due to predation by birds, Fig. 4). Adjacent riparian model ecosystems can be installed at various locations along the channel (Fig. 3).

After the physical environment is established within the adjacent terrestrial model ecosystem, small relatively sessile terrestrial predators that use both aquatic and terrestrial emergence as food resources are allocated to each of the cages. Horizontal web-building spiders, *Tetragnatha* spp., are a good choice of model predator for these experimental ecosystems. *Tetragnatha* consumes both adult

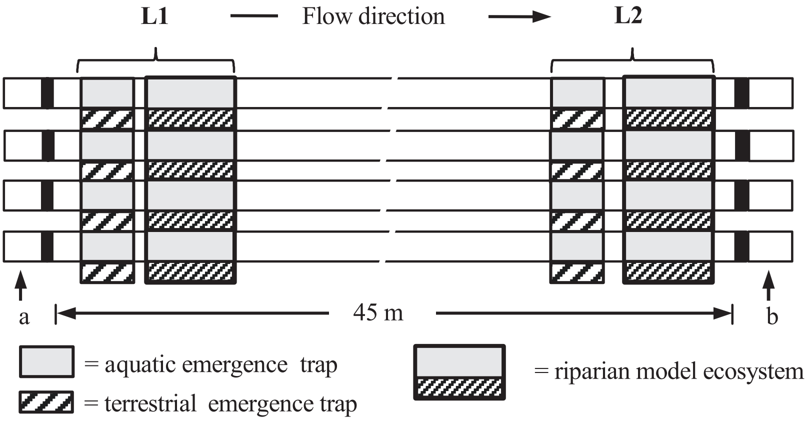

Fig. 3 Example of a mesocosm experiment within the LSMF. Two sampling sites, L1 and L2, were located close to the in- (**a**) and outlet (**b**) of each channel, respectively. Experiments were run in recirculated flow, and thus the water was pumped from the outflow back to the inflow or as flow-through, where water leaves the system at (**b**). Emergence traps, which were used to estimate emergence of both terrestrial and semiaquatic insects over time, were located independently from the aquatic-terrestrial model ecosystem (i.e. 'riparian model ecosystem') to avoid interference of the sampling techniques. Aquatic-terrestrial model ecosystem can be placed at different locations within each channel (=replicate) allowing for the calculation of (weighted) means or the assessment of effect magnitudes depending on the exposure profile (i.e. the peak is higher but shorted at the inlet (**a**) relative to the outlet (**b**)). Alternatively, a larger aquatic-terrestrial model ecosystem over several meters can be established (The figure is republished with permission from Wieczorek et al. 2015)

aquatic and terrestrial insects but prefers to feed on insects of aquatic origin (Gergs et al. 2014). Thus, *Tetragnatha* is expected to respond to alterations in adult aquatic insect emergence, rendering it a potentially sensitive test organism in the terrestrial model ecosystem. In other words, by employing a test species such as *Tetragnatha* spp. as the first recipient (or in some situations top predator) in the terrestrial model systems, a top-down-directed impact on the terrestrial insect community is expected as a consequence of any quantity- or quality-related modification in the aquatic emergence induced by chemical stress with consequences on the predation pressure on terrestrial prey. To also assess bottom-up-directed effects exceeding the level of the first recipient within the terrestrial food web, additional predators (e.g. damselflies, beetles, amphibians) need to be amended to the riparian part of this model system (Fig. 4) to observe potential consequences at higher trophic levels of the terrestrial food web originating from the contamination of aquatic habitats. A major challenge might be the availability of a sufficiently large habitat and food supply supporting the growth and development of these representatives of higher trophic levels.

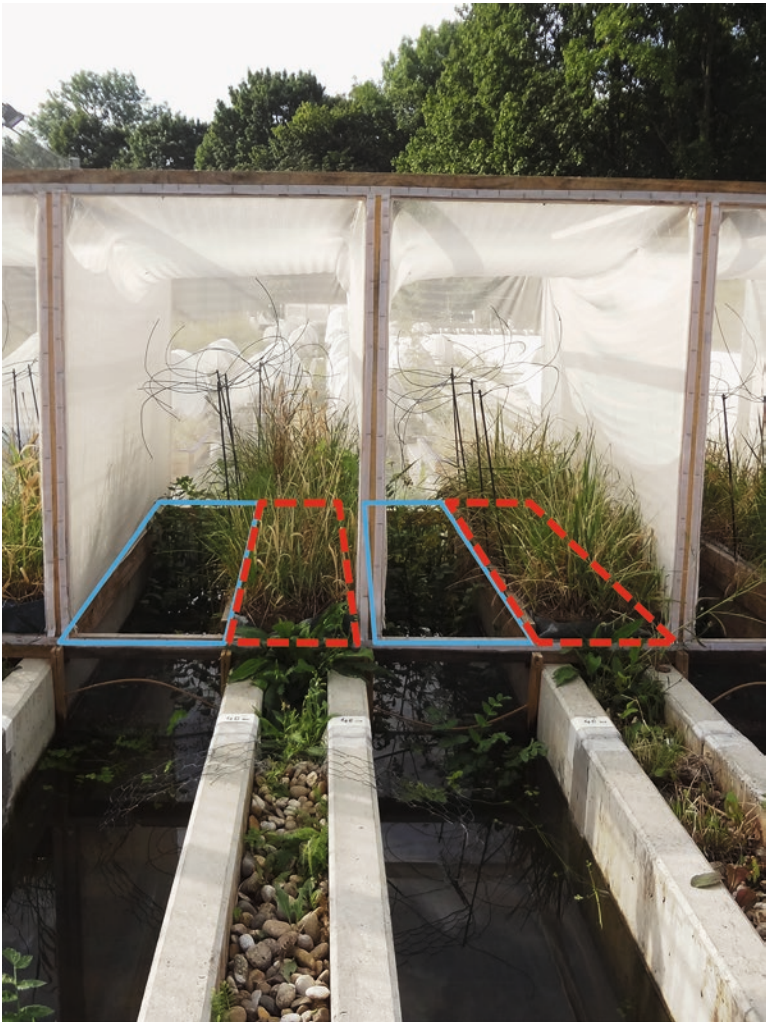

Fig. 4 Picture of the caged model ecosystems containing both an aquatic (solid blue rectangle) and a terrestrial model compartment (dashed red rectangle; Picture is republished with permission from Wieczorek et al. 2015)

2.2 Indoor Stream Microcosms

Indoor stream microcosms, defined here as structures less than 10 m long or less than 1 m^3 in volume that contain flowing water, still allow for a reasonable level of biological complexity accommodating macroinvertebrate populations and well-defined communities (e.g. Zubrod et al. 2017). At the same time, potentially confounding factors that may hamper the establishment of cause-effect relationships in field mesocosm experiments due to introducing non-systematic variation such as temperature, light, wind and velocity are more easily controlled. A limitation of stream microcosms compared with outdoor mesocosm experiments is that optimal or field-relevant conditions may need to be determined and maintained for the assessed communities throughout the study.

Indoor stream microcosm systems have been developed and used by many different research groups testing the effects of chemical stressors on aquatic communities over the last 30 years. For example, facilities were developed at the University of Northern Iowa (Breneman and Pontasch 1994), the Technical University Dresden (Jungmann et al. 2001), the Cary Institute of Ecosystem Studies (Hoppe et al. 2012), US Geological Survey (USGS) Fort Collins Science Center (Rogers et al. 2016) and Colorado State University (Kotalik et al. this book). Artificial streams in these facilities are generally built of fibreglass or stainless steel with 5–30 channels, with a length and width of up to 400 and 25 cm, respectively. Accordingly the Landau Laboratory Stream Microcosm Facility (LLSMF; http://uni-ko-ld.de/f7) consists of 24 independent stainless steel artificial streams (120 × 30 × 20 cm^3; water volume 40–60 L depending on the setting of the passive overflow) serving as experimental units (Fig. 5). The use of stainless steel is preferred as this material allows for an efficient cleaning after the experiment to remove any residual contaminants through either burning or an acid bath.

A schematic design of the experimental units, in which a paddle wheel is ensuring running water conditions, illustrates how the units work (Fig. 6). Six independent technical control units ensure the same treatment in terms of water exchange

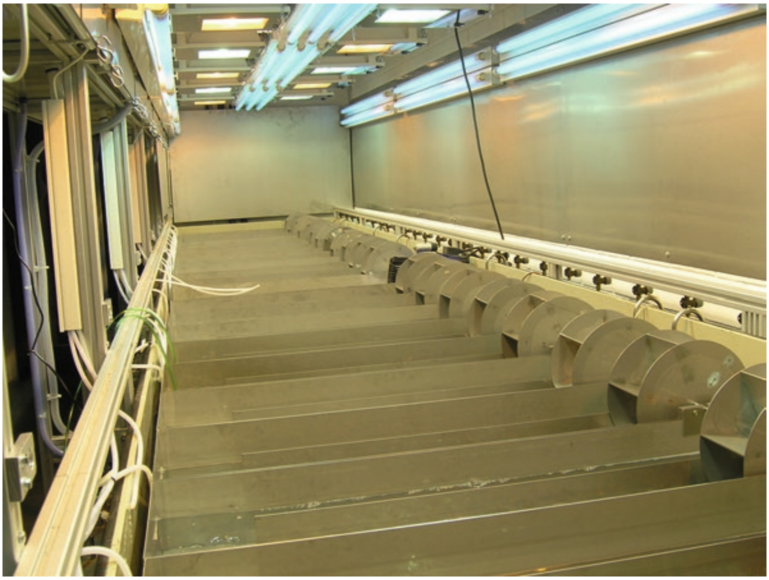

Fig. 5 The Landau Laboratory Stream Microcosm Facility that can be run as flow-through system (including dosing system for reconstituted water, which is not shown) available at the Institute for Environmental Sciences, Landau ($n = 24$, photograph taken by M. Bundschuh)

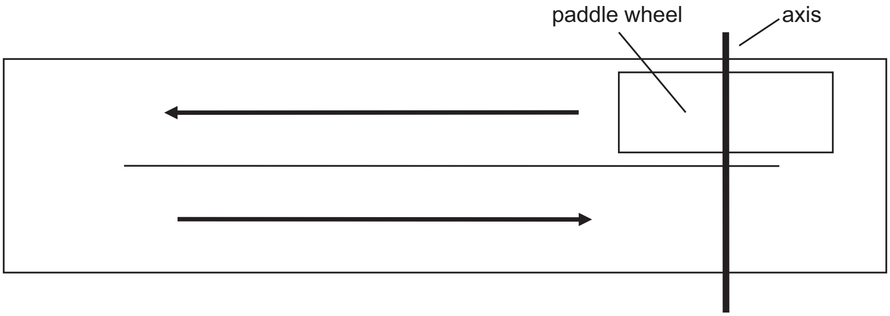

Fig. 6 Top view of one experimental unit (i.e. a stainless steel artificial stream microcosm) equipped with a paddle wheel ensuring running water conditions. Arrows indicate the direction of water flow (The figure is redrawn with permission from Bundschuh and Schulz 2011)

and exposure profile of the selected stressor for four experimental units each. The water input into the system is usually set to allow one complete renewal of the test medium per experimental unit per day and can easily reach up to 2000 L per day. The reconstituted test medium used in this system is continuously provided by an external dosing unit. The dosing unit mixes highly purified deionised and sterilised water with stock solutions of nutrient salts at predefined quantities. After mixing, the medium is cooled down to approximately 16 °C to minimise bacterial growth. As soon as the test medium reaches the target temperature (16 °C), it is transported to the LLSMF, where it is heated up or cooled down to the temperature used in the experiment, which is usually also 16 °C (a common daytime temperature of small streams in the vicinity of the LLSMF during summer) (Fernandez et al. 2015). Just before being released into the stream microcosms, the chemical stressors under investigation will be mixed with the test medium. All experimental units are situated in a water bath set at constant temperature. Above these stream systems, a light system (intensity of approx. 13 klx; lamp types, Philips SON-T AGRO 400 W, Philips MASTER HPI-T Plus 400 W, Osram L36 W/840 Lumilux Cool White, Heraeus Magic Sun 20/160 r Original Hanau SunCare) is designed to support macrophyte growth and can simulate almost the whole natural wavelength spectrum including UV-A (approx. 13 W/m^2) and UV-B (approx. 4 W/m^2; Fig. 5).

Terrestrial model ecosystems can also be coupled with the aquatic microcosm following the description of the aquatic-terrestrial model ecosystem as employed in the outdoor stream mesocosms (see Sect. 2.1). However, in contrast to these, the entire experimental units are completely covered with mesh screen to ensure that replicates are truly independent (Schulz and Liess 2001a, b; Schulz et al. 2002).

3 Experimental Design

3.1 Duration and Timing of Exposure

The experimental stream facilities described above allow the assessment of effects induced by chemical stressors on the subsidy of terrestrial food webs by adult aquatic insects over various timescales (from days to months) reflective of exposure regimes in the environment. Both model systems are suitable to assess the impact of long-term and short-term exposures to chemical stress reflecting the constant and pulsed release of chemicals through, for instance, wastewater treatment plant effluents or edge of field runoff, respectively, into aquatic systems (e.g. Stang et al. 2013). Realistic or worst-case exposure events from nature may, thus, be reproduced in the stream mesocosms using standardised exposure scenarios with durations of ≤1 to ≥24 h (Wieczorek et al. 2016).

Independent of the exposure duration but depending on the physico-chemical properties of the substances, either flow-through or recirculating conditions can be used to simulate environmental exposure typical in the field. Flow-through conditions are appropriate for highly hydrophobic substances (e.g. pyrethroid insecticides) which typically occur in the water phase for only a few hours. This allows for a better control of the intended exposure concentrations in the meso- or microcosms and avoids unintended contamination of pipes transporting the water from the out- to the inlet if recirculating conditions are selected. In contrast to highly hydrophobic substances, exposure events using exclusively hydrophilic substances which occur in the water phase over several days are reproducible on stream mesocosm scale using recirculating conditions. Thereby, constant exposure conditions are obtained with a two-phased, stepwise reduced application technique as described in Wieczorek et al. (2017). Briefly, the chemical is added to the mesocosm over time at rates allowing to approach the nominal concentration to be assessed. As soon as the nominal concentration is reached, application rate is reduced so that the concentration in the mesocosm remains, despite degradation, constant.

If streams are dosed with an ^{15}N tracer (e.g. $^{15}NH_4Cl$) in order to increase ^{15}N levels of adult aquatic insects to facilitate SIA, recirculating conditions are preferred to reduce the amounts of the tracer to be applied. In contrast to the outdoor stream mesocosms, the indoor systems require lower amounts of chemicals to be added to the system and can more easily be connected to advanced water treatment to reduce the amounts released to the sewer system. Consequently, a continuous dosing of a stressor over long periods of time is less costly allowing to employ flow-through experimental test design (Zubrod et al. 2017).

3.2 Response Variables

The ability to measure aquatic and terrestrial community endpoints, as well as collect emerging and metamorphosing insects from both the aquatic and terrestrial model ecosystem over the entire study, is key to understanding how aquatic chemical stressors impact linked aquatic-terrestrial ecosystems. To measure effects on altered food web structures and their implications in the model predator, species composition, quantitative (e.g. biomass) and qualitative (e.g. composition of fatty acids) characteristics of fluxes and the stable isotope composition need to be determined. When taking these measurements, however, the impact in the actual aquatic-terrestrial model system should be minimised. One option for minimising observer impact on linked aquatic-terrestrial model ecosystems is to locate the emergence traps outside of the model ecosystems as proposed by Wieczorek et al. (2015) (see Fig. 3). In this way, the quantity and quality of adult aquatic insects emerging from aquatic ecosystem can be assessed without causing physical damage to the terrestrial ecosystem that could alter observations of terrestrial predators.

Response metrics usually assessed in aquatic meso- and microcosm studies include estimates of primary production, organic matter decomposition, community composition and sporadically the quantity of emerging adult aquatic insects. Here we focus on additional variables that could be relevant: the quality of the emergence (prey) and the consequences of any shift induced by chemical stress are hardly (if at all) assessed. The consideration of amino and fatty acids may be helpful to characterise the nutritious quality of emerging adult aquatic insects for terrestrial predators, such as *Tetragnatha* spp., and can potentially indicate changes in their life history strategy. Although ecological studies connecting the composition of amino or fatty acids with fitness or performance parameters in invertebrates are rare, the importance of essential amino acids in their food has been shown (Guisande et al. 1999). It has, in addition, been demonstrated that amino acids in aquatic species can be reduced as a consequence of chemical stress – in particular, 0.77 mg/L pentachlorophenol reduced the amount of free amino acid by up to 30% in gammarids (Graney and Giesy 1986). Similarly, certain polyunsaturated fatty acids (PUFA) are non-substitutable (Wacker and von Elert 2001), and stressed organisms have the tendency to retain essential PUFAs, while they use at the same time monounsaturated and saturated fatty acids to cover increased energetic needs (Mezek et al. 2010). These studies indicate that aquatic invertebrates respond to chemical or other stressors by an alteration in their amino and fatty acid composition, which indicates implications in their nutritious value for higher trophic levels (Feckler et al. 2016), namely, predators in terrestrial receiving entities. By linking the amino acid and fatty acid profiles of the emergence with those of their predators and quantifying the consequences of these alterations for the life history strategy but also behaviour of the latter, implications in the aquatic and terrestrial food web are uncovered.

Assessing changes in the terrestrial food web through bottom-up or top-down cascades (Fig. 1) is realised by SIA. To this end, stable isotope signatures of the model predator and potential prey items are determined for nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) using isotope ratio mass spectrometry. Predators usually reflect the stable isotope signatures of their prey with a predictable offset (DeNiro and Epstein 1976). However, the stable isotope signature can be confounded by stressors (Karlson et al. 2018) that directly modify stable nitrogen and carbon signatures in organisms (e.g. by around 0.1‰ for chemical contaminants, Ek et al. 2016). This potential confounding impact in stable isotope signatures should be considered when interpreting the data (i.e. identifying isotopic niche occupied by a species in a food web). Nonetheless, SIA allows, in combination with statistical tools, the so-called mixing models (Phillips et al. 2014), to estimate the dietary composition of predators. An obvious prerequisite of this approach is, however, that signatures of prey items are sufficiently distinct to allow differentiation. If this is not the case, isotopic labelling (using, for instance, ^{15}N tracers) is a workaround (but see for practical challenges our thoughts above): if, for instance, aquatic model systems are thought to reflect heterotrophic, leaf litter-dominated habitats, leaf material of trees could be added that were grown under conditions of heavy isotope enrichment well above natural levels (e.g. Compson et al. 2015). Consumers of this basic food resource are expected to differ strongly in their signature to animals consuming unlabelled resources such as plants in the terrestrial model systems. A similar separation in stable isotope signatures is achieved by using plant material from C_4 instead of C_3 plants – which strongly differ in their carbon signals – as resource in the aquatic ecosystems (Kraus and Vonesh 2012; Scharnweber et al. 2014). C_4 plants, however, may differ from C_3 plants in the colonisation by microbes and also the nutritious value for shredders (unpublished data). This modification on the base of the heterotrophic aquatic food web might hence confound responses towards chemical stressors assessed. Another important consideration is that experimental duration as well as the selection of the predators' tissue to be analysed should allow a complete assimilation of the mesocosm community's stable isotope signature (i.e. isotopic equilibrium). For *T. extensa* 1 month of deployment in the aquatic-terrestrial model systems is, for instance, sufficient for their opisthosoma to reflect the signature of their diet in the experiment. For their prosoma, in contrast, the signals were still biased by their source habitat, which may also be linked to the spiders moulting cycle (Fig. 7, Wieczorek et al. 2015). Considering these aspects during the study design allows for the detection of chemical stress-induced shifts in food web structure (e.g. a shift from aquatic to terrestrial food sources). Moreover, in combination with information on chemical stressor concentrations in the prey items (Kraus 2016), pollution fluxes could be traced.

More complex systems or research questions are tackled by compound-specific stable isotope analysis (CSIA) techniques. For instance, shifts in trophic position due to chemical stressors are identified by CSIA of amino acids (Chikaraishi et al. 2009) even without determining an isotopic baseline (Post 2002). CSIA of amino acids and other nutrients, such as sterols, for instance, can identify stressor-induced nutritional constraints (Gergs et al. 2015). However, the feasibility of such methods in chemically stressed systems still needs to be demonstrated. When assessing organic pollutants, such as pesticides or pharmaceuticals, in meso- and microcosms,

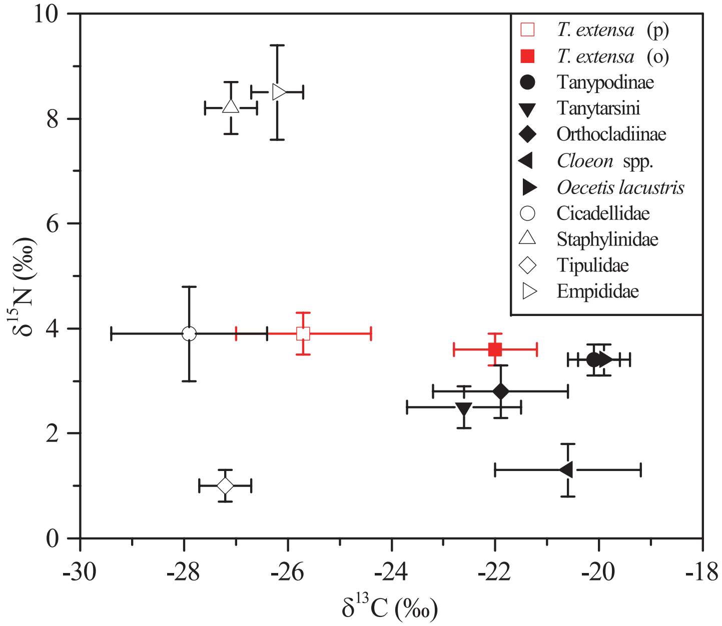

Fig. 7 Average stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$ ± SD) of *T. extensa* (red symbols, prosoma (p; open symbol) and opisthosoma (o; filled symbol)) and insects (filled black symbols) and terrestrial prey (open symbol) species (This figure was taken from Wieczorek et al. 2015)

CSIA of these compounds can be a powerful tool to monitor their fate and/or degradation pathways in the environmental compartments involved (as reviewed by Schmidt et al. 2004). This might, however, require use of labelled test substances (e.g. Wang et al. 2016). Moreover, evaluating potential isotopic fractionation due to sample pretreatment steps (e.g. enrichment and purification) and – if necessary – correcting for it are critical for an accurate and reliable determination of stable isotope signatures (Schmidt et al. 2004).

4 Limitations and Conclusions

Despite their high ecological complexity, the experimental facilities discussed in this chapter can fall short of reflecting the diversity of interactions that play a role in nature. Lack of diversity, even in initial composition of communities, can have large effects on how the effects of chemical stressors play out. Above we highlight an approach in which the community is either actively assembled resulting in a predetermined assemblage of plants and animals or passively introduced together with macrophytes or leaf litter and thus reflects to some degree the macroinvertebrate community composition of the ecosystem from which the substrates have been sampled. Another option to populate the micro- or mesocosms with macroinvertebrates would be a passive colonisation through the direct connection with a natural ecosystem, which is not always possible but is realised, for instance, at the experimental ditch mesocosm facility at Leiden University.

Irrespective of the procedure, the ultimate community tested does not necessarily reflect a system with all relevant interactions as they are observed in the field but appears in some cases to provide a reasonable approximation of complexity in nature (sensu Schmidt et al. 2018). In addition to limitations caused by artificial or only partially natural colonisation of experimental ecosystems, micro- and mesocosm experiments rarely consider the possibility for recolonisation from uncontaminated (upstream) sections, which is a relevant process in freshwater ecosystems mitigating the impact of chemical stressors (e.g. Orlinskiy et al. 2015; Knillmann et al. 2018). On the other hand, the close proximity of non-treated control micro- or mesocosms in experimental setups compared to the situation in the field may lead to an overestimation of the extent of aerial recolonisation by ovipositing adults.

A final important limitation of these experimental approaches is that predators in terrestrial ecosystems may show responses in the experimental units that are an artefact of being caged. For example, if the quantitative or qualitative transfer of energy into the terrestrial food web through aquatic emergence is impacted by contaminants in nature, the recipient predator may not only have the possibility to transmit the effect top-down or bottom-up in the terrestrial food web (see Fig. 1) but could also migrate (e.g. spiders by means of ballooning) to ecosystems that provide better environmental conditions. The latter process is often difficult to capture within experimental ecosystems but might be highly important to patterns observed in nature.

Despite these limitations, mesocosm and microcosm experimental ecosystems are important tools for assessing the impact of contaminants from aquatic to terrestrial ecosystems, as they allow for hypothesis-driven assessments and the establishment of cause-effect relationships. These insights are also relevant for regulators as they provide information about concentrations of contaminants that might be of low risk for the environment (see for more details on the risk assessment and management Schulz and Bundschuh 2019). At the same time, the data generated by experimental tests on complex communities aid in the interpretation of field studies, which are often limited to a correlative approach (see Rogers et al. 2016; Burdon 2019). Furthermore, mesocosms and microcosms allow for the assessment of effects caused by individual contaminants as well as their mixtures. Given work required to run these experiments, however, we do not advise randomly testing toxicological interaction of contaminants (mixture toxicity assessment, see van Gestel 2011). Instead, we recommend selecting mixtures of contaminants based on frequent co-occurrence in the environment (Schreiner et al. 2016; Gustavsson et al. 2017) or commonly observed sequence of ecosystem exposure. Such an approach could be highly relevant from an academic and regulatory perspective.

Acknowledgements Figure 1 was adapted with permission from Schulz, R., Bundschuh, M., Gergs, R., Brühl, C.A., Diehl, D., Entling, M., Fahse, L., Frör, O., Jungkunst, H.F., Lorke, A., Schäfer, R.B., Schaumann, G.E. and Schwenk, K. (2015) (Review on environmental alterations propagating from aquatic to terrestrial ecosystems. Science of the Total Environment 538, 246–261. Copyright 2015 Elsevier). Figures 3, 4 and 7 were reprinted with permission from Wieczorek, M.V., Kötter, D., Gergs, R. and Schulz, R. (2015) (Using stable isotope analysis in stream mesocosms to study potential effects of environmental chemicals on aquatic-terrestrial subsidies. Environmental Science and Pollution Research 22, 12892–12901. Copyright 2015 Springer Nature). Figure 6 was redrawn with permission from Bundschuh, M. and Schulz, R. (2011) (Population response to ozone application in wastewater: an on-site microcosm study with *Gammarus fossarum* (Crustacea: Amphipoda) Ecotoxicology 20(2), 466–473. Copyright 2011 Springer Nature). We acknowledge discussions with colleagues from the iES Landau, Institute for Environmental Sciences, at the University of Koblenz-Landau, Germany, on this topic. This work was supported by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – 326210499/GRK2360 SYSTEMLINK. Moreover, we acknowledge the invitation for a contribution and detailed feedback by the editors of this book.

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Author Biography The author team combines expertise in ecotoxicology, chemical fate and environmental risk assessment and jointly developed a strong interest in assessing the impact of chemical stressors across ecosystem boundaries. In fact, Bundschuh, Zubrod and Wieczorek received their PhD from the University of Koblenz-Landau in 2011, 2016 and 2016, respectively, under the supervision of Schulz. Currently, Mirco Bundschuh holds a Junior Professorship leading a research group on Functional Aquatic Ecotoxicology. Ralf Schulz is Professor in Environmental Sciences heading the group Ecotoxicology and Environment in which Post-docs Jochen Zubrod and Matthias Wieczorek develop their research.

Part V
Syntheses

Ecological Networks as a Framework for Understanding and Predicting Contaminant Movement Across the Land-Water Interface

S. Mažeika Patricio Sullivan and Daniel A. Cristol

1 Introduction

Ecological networks are the interactions that occur among species in a community. Within the context of traditional food webs, these networks commonly include competition and predation (Ings et al. 2009). However, host-parasitoid, mutualistic, parasitic, disease, dispersal or migration, and pollinator interactions have also received increasing recognition as important types of interactions comprising ecological networks (Ings et al. 2009; van Veen et al. 2006; Huxham et al. 1996; Jordano 2016; Sazatornil et al. 2016). The interactions that form ecological networks have important implications for community stability, structure, and persistence (Yen et al. 2016; Krause et al. 2003; Stouffer and Bascompte 2011; Fortuna and Bascompte 2006) and have played an important role in the development of ecological theory (Elton 1927; May 1972). Here, we propose that models of ecological networks functioning at the land-water interface may serve as valuable tools for understanding and predicting the biologically mediated movement of contaminants between aquatic and terrestrial systems (Sullivan and Manning 2019).

Scientists have long recognized that streams and rivers are embedded within, and highly influenced by, their surrounding landscapes (Hynes 1975). Today, we know that aquatic ecosystems and their adjacent riparian zones are inextricably linked through exchanges of water, sediment, organic material, nutrients, contaminants, and organisms (Polis et al. 2004; Junk et al. 1989; Walters et al. 2008). Species

S. M. P. Sullivan (✉)
Schiermeier Olentangy River Wetland Research Park, School of Environment and Natural Resources, Schiermeier Olentangy River Wetland Research Park, The Ohio State University, Columbus, OH, USA
e-mail: sullivan.191@osu.edu

D. A. Cristol
Department of Biology, William and Mary, Williamsburg, VA, USA
e-mail: dacris@wm.edu

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interactions at the interface of aquatic and terrestrial systems form ecological networks (sensu Naiman and Décamps 1997) that can link these ecosystems over space and time and act as a critical mechanism in the cross-boundary transfer of contaminants. Models of these networks (Fig. 1) can help predict how ecosystems respond to change by improving understanding and quantifying the architecture of relationships among species (Bascompte 2010). Thus, elucidating the role of ecological networks in regulating the rate, timing, and magnitude of cross-boundary biological interactions will allow better prediction and risk assessment in cases where contaminants may move across ecotones.

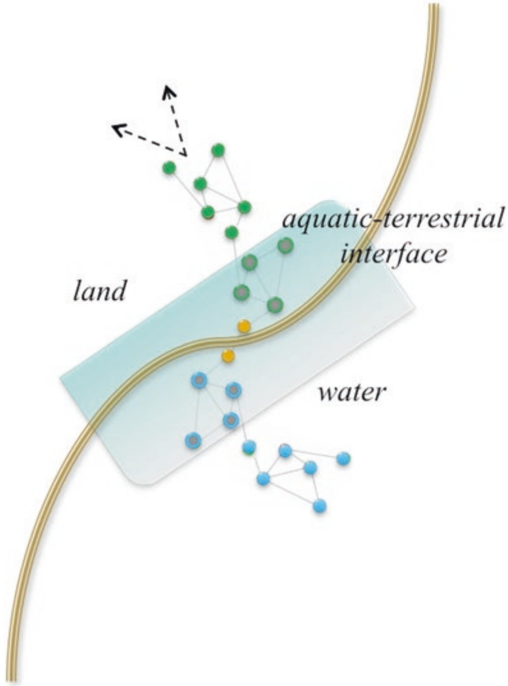

Fig. 1 Stylized image representing the ecological network (connected circles and lines) at an aquatic-terrestrial interface (area in shaded blue rectangle), found at the boundary between land and water. The brown line is the riverbank. Within the network model, circles represent nodes (e.g., species) and lines indicate links (also known as "edges" in network theory) between the nodes (e.g., feeding relationships). Here, the ecological network model depicts a simplified trophic network (food web): blue is the aquatic network and green is the terrestrial network. Grey with blue border is the aquatic component of the network at the aquatic-terrestrial interface, and grey with green border is the terrestrial component of the aquatic-terrestrial network. Orange nodes represent key network linkages between aquatic and terrestrial systems, for example, emergent adult aquatic insects and the shoreline spiders consuming them (see Fig. 2). Black dashed arrows indicate the connectivity of aquatic-terrestrial interface networks with terrestrial networks extending spatially into the broader landscape

Fig. 2 Conceptual diagram of a reciprocal food-web network in a stream-riparian ecosystem. Arrows represent energy-flow pathways. Arrows from emerging aquatic insects and fish also represent potential aquatic to terrestrial transfers of contaminants. (Figure by Robert Keast)

We posit that ecological networks can offer a powerful framework for understanding the transfer of contaminants from aquatic to terrestrial systems, synthesizing complex life histories, organismal mobility, top-down and bottom-up processes, and integrating landscape changes and stressors across spatial and temporal scales (Sullivan and Manning 2019). Here, we focus on three examples of ecological networks that may influence contaminant transfer from aquatic to terrestrial systems: food webs, movement webs, and symbiotic webs. We first discuss properties of ecological networks and network models and their relevance to understanding and predicting biologically mediated contaminant transfer across the aquatic-terrestrial boundary. Then we present a brief overview of each of our three examples of ecological networks (food, movement, and symbiotic webs) and illustrate how they may influence contaminant transfer from aquatic to terrestrial ecosystems. Finally, we review four key characteristics of ecological networks and network models that make them highly relevant to the understanding of ecological subsidies and contaminant transfer, that is:

1. Ecological networks can display variability in links and edges, which capture the unequal movement of contaminants within networks at the aquatic-terrestrial interface.

2. Ecological networks operate across multiple spatial and temporal scales.
3. Ecological networks respond to disturbance or perturbations such as species invasions, land-use change, and climate change, with strong implications for contaminant transport.
4. Ecological networks and contaminant exposure risk can include humans.

2 Interactions, Compartmentalization, and Network Persistence

A suite of properties characterizes ecological networks and thus ecological network models (see Text Box 1). Characteristics of cross-boundary networks include the weight and length of links/edges, as well as the behavioral and physiological traits of each species that act as nodes within these networks. For example, in ecological networks, edges can illustrate the directed movement of energy or nutrients among nodes via feeding, and edge weight can indicate the magnitude, predictability, or frequency of energy or mass in the feeding interaction (Lau et al. 2017 and references therein). Typically, there are numerous paths among nodes in a network, and the length of the path can be defined as its number of edges (Barthélemy 2011). However, edge length can be measured in other ways, including the dispersal of organisms between patches (Costa et al. 2019). Thus, variability in these and other network characteristics shapes the nature of species interactions between the aquatic and terrestrial components of ecological networks (see Fig. 1). For instance, cross-boundary energetic transfers have been tied to variation in species traits and interactions within the aquatic component of the ecological network as a result of environmental perturbations and naturally occurring environmental gradients (e.g., stream size, water chemistry, and temperature; Kautza and Sullivan 2015). Although overall production of emerging aquatic insects was greater in agricultural than forested streams in central Sweden, trait variability related to limited emergent adult aquatic insect dispersal (e.g., body size, flight strength) and emergence timing (e.g., univoltinism, synchronized emergence) implied that this productivity would likely be spatially confined to near the stream channel (McKie et al. 2018), with implications for the diversity and complexity of the terrestrial food web compartment. Feedback loops, such as the input of terrestrial invertebrates into the aquatic environment, may also be affected, for example, if terrestrial consumers such as riparian birds shift to eating more terrestrial invertebrates as emergent aquatic insect prey declines.

Variability in the characteristics of network linkages is strongly related to the degree to which an ecological network is compartmentalized, that is, subsets of species that interact more frequently among themselves than with other species in the trophic network. The degree of compartmentalization (i.e., modularity) can be an important driver of network persistence (Okuyama and Holland 2008; Stouffer and Bascompte 2011). May (1972) illustrated that ecological complexity can constrain the stability of interaction networks. Since then, many studies have shown that structural patterns found in food webs (e.g., interaction strength of omnivory loops) may influence species coexistence and community stability (Montoya et al. 2006; Thebault and Fontaine 2010). Irrespective of network type, Fortuna et al. (2010) found that, at low connectivities, highly nested networks also tend to be highly modular and that the reverse is observed at high connectivities. Modular networks are thought to potentially increase stability and allow complexity to persist by buffering the entire network from the influence of environmental perturbations, but this is a complex notion around which debate continues (Ings et al. 2009; Landi et al. 2018). Thus, the complexity and persistence of cross-boundary energetic and contaminant transfers should be related to modularity and nestedness in ecological networks.

The importance of the strength of interactions between individuals and species – of which all networks are comprised – is increasingly recognized (Ings et al. 2009). Across network types, interaction strength can be quantified in multiple ways (Berlow et al. 2004). For example, Blüthgen et al. (2007) used interaction frequency (i.e., number or rate of visits by pollinators to plants) in mutualistic plant-animal interactions as a measure of link strength. Others have assessed interaction strengths via whole-system responses (e.g., number of species that go extinct following the perturbation of a given species; Solé and Montoya 2001). In contrast, Cross et al. (2013) quantified interaction strengths between fish and their invertebrate prey by estimating the percentage of annual prey production consumed by a given predator. Identifying biologically meaningful metrics that adequately represent species or populations is a challenge for quantifying interaction strengths within networks (Berlow et al. 2004). For example, individual traits (e.g., body size, metabolic rate) and behavioral characteristics (e.g., dispersal distance, foraging strategy) may shed more light on the functions and consequences of changes in network interactions than species-averaged data (Stouffer et al. 2005; Brose et al. 2006). Changes in interaction strengths in aquatic food webs, as well as other types of networks, will likely have quantifiable effects on the transport of contaminants from aquatic to terrestrial systems.

Text Box 1: Key Properties of Ecological Networks, How They Relate to Ecological Subsidies and Contaminant Transfer Across the Land-Water Interface, and Testable Hypotheses

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Complexity: Also known as linkage density, the average number of links per species or node. Complexity reflects both ecological and evolutionary constraints (Ings et al. 2009 and references therein). The complexity of trophic interactions varies with species richness (i.e., diversity) (Banasek-Richter et al. 2009). Debate continues relative to the nature of the relationships between complexity and community stability (Landi et al. 2018). If biomagnification increases with species richness in aquatic systems (due to additional species at top trophic levels or the insertion of species that increase the number of trophic levels), linkage density should be positively related to contaminant transport from aquatic to terrestrial systems. However, linkage density has also been shown to decrease with trophic position (Scotti et al. 2009), indicating that the converse is also possible.

Connectance: The proportion of realized vs. possible ecological interactions (links per species^2). Food webs with greater connectance are usually regarded as more complex and less perturbed by species loss (Dunne et al. 2002b; Cross et al. 2013). Disturbance in aquatic systems, for instance, through flooding or drying, can remove highly connected species from the network and reduce connectance (Cohen and Briand 1984; Dunne et al. 2002b), in turn reducing the maximum contaminant concentrations found in organisms.

Degree distribution: Cumulative distribution for the number of links per species, which can be split into (a) links to a species and (b) links to a species' predators. As the number of links between an aquatic vector species (e.g., emerging aquatic insect) and its predators (e.g., crayfish, fish, or other organisms that commonly provide food to terrestrial predators) increases, so too does the potential for aquatic to terrestrial contaminant transport.

Clustering: Proportion of species that are directly linked to a focal species (found in the middle of a cluster, may be a keystone species), whose loss can have large effects on the network. Contaminant transport may be strongly linked to a focal species that, through trophic and/or movement patterns, will regulate food -web architecture and in turn biomagnification and the magnitude of aquatic to terrestrial contaminant transport.

Compartmentalization: Degree to which a network contains discrete sub-webs; note that this is a topic of considerable debate (see Rezende et al. 2009). Theoretically, compartments increase stability in ecological networks, enabling complexity to persist (Ings et al. 2009; Krause et al. 2003). Highly compartmentalized networks with relatively isolated sub-webs should limit transfers of contaminants beyond the sub-web. For instance, an isolated aquatic food web with a high degree of compartmentalization (e.g., small set of interacting species with few crossing the aquatic-terrestrial boundary) may reduce contaminant transport to terrestrial systems because there are insufficient biovectors to move contaminants out of the water. However, increased persistence of the aquatic-terrestrial interactions typical of a highly compartmentalized network might be expected to lead to consistent levels of contaminant transport.

Interaction: Links between species. Interaction strength (frequency, magnitude, etc.) between species can mediate contaminant transfers (e.g., the frequency with which a given terrestrial consumer feeds on aquatic prey regulates contaminant transfer from aquatic to terrestrial systems).

Macroscopic metrics: Capture overall network size and complexity/structure and provide a single measure for the entire network (Trøjelsgaard and Olesen 2016); examples include species interactions, richness, connectance, nestedness, modularity, and measures of overall network-level specialization (e.g., Bascompte et al. 2003; Olesen et al. 2007).

Microscopic metrics: Reflect network properties at a finer resolution, often assigning a property to each species in a network, and include degree of linkage (i.e., number of interaction partners), individual measures of interaction evenness or specialization, centrality, and trophic position (Trøjelsgaard et al. 2015; Martín González et al. 2010). Changes at the macroscopic level indicate that appreciable reorganization has occurred, but incorporating microscope features and their variability in space and time can help us better understand the entirety of the network (Trøjelsgaard and Olesen 2016). Relevance to aquatic to terrestrial contaminant transfers include relationships between trophic position and bioaccumulation, interaction evenness, or specialization (e.g., riparian spiders with specialized diets on emerging aquatic insects vs. those with generalized diets).

Nestedness: Tendency for species/individuals to interact with a subset of other species/individuals of more highly connected nodes (i.e., interactions of less connected species form subsets of the interactions of more connected species). More nested networks, in which there is greater redundancy of interactions, might be expected to increase biomagnification (versus less nested networks, where interactions are more diffuse and biomagnification potential decreases) and aquatic to terrestrial contaminant transport.

Persistence: How robust a community is, dependent on (a) the strength of environmental variability driving a network away from equilibrium and (b) the interactions between and among species pulling the network toward equilibrium. Network persistence can be measured as the number of species that remain following a perturbation divided by the initial species richness (i.e., proportional persistence; Stouffer and Bascompte 2011). Compartmentalization has been shown to increase the persistence of food webs (Stouffer and Bascompte 2011). Networks characterized by higher persistence should lead to more consistent transport of contaminants across the aquatic-terrestrial boundary.

3 Examples of Ecological Networks Involved in Contaminant Transport

3.1 Food Webs

Food webs are the most widely documented and understood network type (e.g., Collins and Baxter this volume). Reciprocal transfers of energy through these cross-boundary (i.e., aquatic-terrestrial) networks are essential to maintain ecosystem functions such as primary productivity, nutrient cycling, and the maintenance of biodiversity. Transfers of energy between terrestrial and aquatic ecosystems have traditionally been viewed as unidirectional pathways in which terrestrially derived carbon and biota provide energy to aquatic consumers (Covich et al. 1999; Power et al. 2004), but evidence also suggests that reverse flows (aquatic to terrestrial) provide important energy to riparian and terrestrial food webs (Henschel et al. 2001; Baxter et al. 2005; Kautza and Sullivan 2016). Prey items represent critical energetic and informational pathways that bind aquatic and terrestrial ecosystems into an integrated system, particularly at the aquatic-terrestrial interface. In particular, aquatic insects that emerge from streams as adults represent a key nutritional subsidy for terrestrial riparian consumers including arthropods, birds, mammals, and reptiles (Murakami and Nakano 2002; Baxter et al. 2005). For example, certain groups of riparian spiders can be highly reliant on emergent aquatic insects (Sanzone et al. 2003; Burdon and Harding 2008). Riparian birds and other consumers can also be dependent on emergent insects, either directly as a food source (Gray 1993; Iwata et al. 2003; Alberts et al. 2013) or indirectly through other prey that in turn consumes emergent insects.

These feeding (i.e., trophic) relationships serve as pathways for the transfer of contaminants from aquatic to terrestrial systems (Fig. 2). Menzie (1980), for example, suggested that larvae of aquatic insects (e.g., Ephemeroptera, mayflies; Plecoptera, stoneflies; Trichoptera, caddisflies; Odonata, dragonflies and damselflies; Chironomidae, midges; Simuliidae, black flies) that are strongly associated with aquatic sediments would bioconcentrate contaminants and transport them out of the aquatic environment when the insects emerge as adults. A growing body of literature now supports this prediction, showing that emergent insects can transport stream-derived contaminants such as mercury, organochlorines, and polychlorinated biphenyls (PCBs) to the terrestrial environment, where they are incorporated into terrestrial food webs (Cristol et al. 2008; Wada et al. 2010; Morrissey et al. 2004; Alberts et al. 2013; Walters et al. 2008).

Fish, too, are widely recognized as facilitating the transport of contaminants from aquatic to terrestrial systems. Numerous examples have been cited in the literature relative to bioaccumulation of contaminants in piscivorous (i.e., fish-eating) vertebrates (see Hinck et al. 2009; Evers et al. 2005). In cases of “biovector transport,” contaminants that have accumulated in aquatic environments are transported to receptor sites by organisms through direct movement or food webs (Blais et al. 2007). Anadromous fish, for example, are effective biovectors of contaminants from marine or lake to stream ecosystems (Merna 1986; Zhang et al. 2001; Sarica et al. 2004), where contaminants can then be moved into terrestrial food webs. A classic example comes from the Pacific Northwest, where Christensen et al. (2005) estimated that late-summer Pacific salmon (*Oncorhynchus* spp.) runs in British Columbia were responsible for delivering 70% of volatile organochlorine (OC) pesticides, up to 85% of brominated PBDE congeners, and 90% of PCB exposure to salmon-feeding grizzly bears (*Ursus arctos horribilis*).

3.2 Movement Webs

Movement networks, representing the spatial and temporal interactions between individual organisms and their environments, are complex yet represent a critical component of aquatic-terrestrial connectivity. Thus, animal movement (e.g., dispersal along river corridors, regular activity within territories, migration, and long-distance prospecting or mate searching) is another key mechanism that might be expected to regulate the transfer of contaminants from aquatic to terrestrial systems. Animal movement is highly dependent on the physical setting (i.e., habitat, landscape) and the social environment in which the animal exists and can strongly influence disease transmission and the flow of genetic material (Fèvre et al. 2006; Pagacz 2016) and, analogously, contaminant movement. Furthermore, because animal movement can occur at a variety of spatial scales, the extent of animal movement has direct implications for the degree of connectivity between aquatic and terrestrial systems and, in turn, for the distance that contaminants are dispersed. Whereas some terrestrial consumers of aquatic prey are relatively sedentary (e.g., riparian web-building spiders), more mobile consumers such as riparian songbirds and raccoons can move thousands of meters in their daily foraging activities (Kautza and Sullivan 2016). Farther yet, migratory birds can travel tens of thousands of kilometers, linking biogeographic regions and continents.

Mobile, often migratory, top predators that connect discrete local ecological networks are known as spatial couplers (Hagen et al. 2012; Borthagaray et al. 2014). Birds are classic examples of spatial couplers, widely described as movers of nutrients, plants (seeds), and invertebrates between waterbodies and land, across ranges of lateral and spatial connectivity (Sullivan and Vierling 2018). For instance, Faria et al. (2016) showed that Cocoi herons (*Ardea cocoi*) – generalists and top predators in shallow-water ecosystems – connect marine, terrestrial, estuarine, and limnetic habitats during their breeding period through their foraging and provisioning of food to chicks. Waterfowl also play an important role in dispersal of organisms in aquatic environments via internal transport (Figuerola et al. 2003). In this same way, birds can transport contaminants through their daily or seasonal movement patterns. For instance, well-documented biovectors of contaminants include seabirds and penguins, which transport significant amounts of marine-derived contaminants to terrestrial environments through guano that accumulates in large breeding colonies (reviewed in Blais et al. 2007).

Network analysis techniques are increasingly used to understand the spatial movement of individuals. One such study demonstrated the importance of seashore stopover sites in eastern China for maintaining links between Oriental white stork (*Ciconia boyciana*) breeding sites in the Russian Far East and wintering sites in southeastern China (Shimazaki et al. 2004). With technologies emerging rapidly to track increasingly smaller-bodied wildlife, these and other approaches applied to biovector species may have potential advantages for documenting and predicting aquatic-to-terrestrial contaminant transfer. In addition to spatial components, the temporal dimension of animal movement (i.e., arrival and departure times) at network nodes will be an important consideration relative to contaminant movement, as aquatic-ecosystem contamination can be temporally variable. For instance, mercury body burdens in fish and aquatic birds in the United States have varied considerably since the 1960s (increases, decreases, and more complex patterns) (Eagles-Smith et al. 2016 and references therein). Thus, transport of contaminants linked to animal movement will vary based on spatial and temporal bioaccumulation patterns.

3.3 Symbiotic Webs

Symbiotic relationships are ubiquitous features of ecosystems, such as parasites and microbiomes. While less well-understood than food or movement webs and rarely recognized as being influential in contaminant fluxes, symbiotic networks should not be ignored in the context of contaminant fates. Parasites, which can super-concentrate contaminants, may reduce the bioaccumulation of contaminants in edible tissue of their hosts (Sures 2008). This could, in turn, reduce biomagnification factors between sediment and top predators within an aquatic food-web network, if the parasites are not consumed along with the host. In addition, high levels of parasitism can affect behavior and longevity and thereby the likelihood of transporting contaminants into an adjacent terrestrial food web. Contaminants may increase susceptibility to parasitism, further complicating the network with feedback loops. Speculatively, other symbiotic networks could influence contaminant transport. Birds regulate their potentially deleterious feather microbiome, in part, through the application of oily secretions from their uropygial (i.e., “preen”) glands to their plumage. Some contaminants (e.g., PCBs) can become concentrated in these secretions (Yamashita et al. 2007), which are also rich in potentially beneficial microbes (Shawkey et al. 2003). Birds with high levels of contaminants may thus have poorer plumage, which could result in reduced mobility, but perhaps also greater likelihood of attempting dispersal. Clearly, with so many unknowns and contingencies, predictions about effects of symbiotic networks on contaminant transport across aquatic-terrestrial boundaries will be difficult to make without further study.

4 Contaminants Do Not All Move Equally Within Networks

Which contaminants move effectively through ecological networks from aquatic to terrestrial ecosystems? First, the compound must be resistant to rapid environmental breakdown, for example, not easily photodegradable, so that it persists in the environment long enough to encounter organisms. The propensity of a pollutant to enter the biotic component of the ecosystem is typically a function of its lipophilicity, which influences the rate at which it leaves the water and concentrates in tissues of aquatic organisms. However, compounds that are not highly lipophilic, such as many metals, can also bioaccumulate through adsorption or cellular transport. If aquatic organisms cannot eliminate the contaminant from their tissues as fast as it is taken up (through gills, lungs, intestines, or skin), it will accumulate to a higher concentration than in the surrounding environment. As organisms are predated, parasitized, decompose, etc., the contaminant will move through the ecological network. At higher trophic positions, tissue concentrations will be greater if the contaminant is not effectively eliminated by organisms at each trophic step (i.e., the process of increasing tissue concentration through trophic transfers). Bioaccumulation is the engine that drives potentially harmful exports of contaminants from aquatic to terrestrial ecosystems. But not all contaminants move through ecological networks equally.

Ecotoxicologists are most concerned with those xenobiotics that are highly fat soluble, do not hydrolyze easily in aquatic systems or degrade through the action of sunlight or microbes, and have demonstrable toxic effects on organisms. PCBs might be considered the exemplar. Once PCBs are released into an aquatic system, they will concentrate in the fatty tissues of organisms, persist in sediments, and eventually cause harm to aquatic organisms and the terrestrial animals that accumulate high concentrations, usually through their diet of aquatic organisms. The migration of PCBs from aquatic sediments, through food-web networks, into the tissues of riparian spiders is well documented, and levels can be such that birds eating these spiders will likely face health consequences (Walters et al. 2010). But even among different PCB congeners, degradation depends on the number of chlorine atoms and whether the pollutant is circulating in water or sequestered in sediment. Photodegradation of PCBs in shallow water may occur in a matter of weeks or months, whereas PCBs hidden from the sun in buried sediments may resist degradation for decades. Forms of PCBs with more chlorine atoms will photodegrade in shallow water faster than those with fewer, but degree of chlorination has the opposite effect on microbial breakdown in dark sediments (Furukawa et al. 1978; Beyer and Biziuk 2009). Thus, even among congeners of one contaminant, the degree of export from water to land is hard to predict accurately without specific knowledge of environmental characteristics and location within the ecosystem.

At the other end of the spectrum, some contaminants lack one of the characteristics – lipophilicity or persistence – that hasten spread through ecological networks from aquatic to terrestrial systems. For example, pyrethrins are widely used as insecticides because of their dramatic negative effects on invertebrate nervous systems. Pyrethrins and their synthesized chemical cousins are highly lipophilic, but they are in general relatively short-lived in the environment. Thus, they are devastating when applied directly to aquatic systems but likely to be degraded within hours to weeks if exposed to sunlight or microbial communities. The chance of pyrethrins biomagnifying or cycling in the aquatic system is low, and the chance of being exported to terrestrial predators via an ecological network (or even abiotic processes such as flooding) is vanishingly small. Some of the metals that frequently contaminate ecosystems near smelters (e.g., copper, lead, zinc, and cadmium) are toxic to terrestrial and aquatic wildlife at high concentrations but rarely biomagnify through trophic networks, likely due to effective biological excretion mechanisms at each step (Barwick and Maher 2003; Cardwell et al. 2013). Thus, if concentrations are low at the base of the aquatic food web, these metals will not be exported at high concentrations into neighboring terrestrial ecosystems, even if the ecological network effectively exports nutrients and energy. However, the relative degree to which contaminants are conserved in body tissues during insect metamorphosis could alter this pattern (reviewed in Kraus et al. 2014b). Further, if contaminants are toxic, the contaminants can lead to a reduction in food availability at lower levels of food webs (Kraus and Walters this volume), thus impacting characteristics of ecological networks in other ways (e.g., connectance, compartmentalization) that in turn may affect contaminant movement from aquatic to terrestrial ecosystems.

Another consideration in predicting those xenobiotics that will move efficiently through ecological networks from aquatic to terrestrial systems is the component of the physical environment in which they are located. Substances that leach into groundwater are unlikely to be transported back to terrestrial ecosystems, as there are few links to ecological networks that would facilitate transfer. Thus, water-soluble contaminants that move primarily in groundwater, whether or not they are broken down by microbes, are unlikely to pose a risk to terrestrial wildlife. As illustrated above, the fate of aquatic PCBs, and thus their propensity for export to terrestrial ecosystems, is dependent on which compartment of the aquatic ecosystem they reside in, with PCBs in the water column susceptible to rapid photodegradation or volatilization and unlikely to be exported to land.

Even for those substances that are lipophilic and persistent and biomagnify readily in aquatic organisms, some biological processes may short-circuit their movement to terrestrial ecosystems. As mentioned previously, metamorphosis in the life cycle of invertebrates, for example, may alter the concentration of contaminants (Kraus et al. 2014b). Fish carcasses can be a potent vector for water-to-land transfer of mercury, particularly anadromous fish such as salmon that provide disproportionate energy and contaminants to surrounding terrestrial habitats (Gerig et al. 2016). One set of consumers are necrophagous blowflies, larvae of which consume the rotting carcasses at the water's edge and biomagnify mercury when themselves eaten by beetles, spiders, and small fish (Sarica et al. 2005). However, once larval blowflies emerge as adults, they leave behind much of their mercury. Thus, terrestrial organisms such as birds that eat adult blowflies would be exposed to reduced mercury exposure.

Abiotic processes such as deposition in sediment may sequester contaminants so that they cease to be exported to terrestrial ecosystems. Illegal dumping of the highly toxic pesticide Kepone (chlordecone) into the James River, Virginia, USA in the 1970s led to elevated concentrations of the toxin in the aquatic food web; high levels of contamination in all tested aquatic organisms, especially fish (Luellen et al. 2006); and anecdotal reports of elimination of terrestrial wildlife in the riparian zone (personal communication, Richard Terman). However, by the 1980s, most of the Kepone was buried in sediment, tissue concentrations had dropped precipitously throughout estuarine organisms, and most fish advisories were lifted. Because Kepone is lipophilic and persistent like PCBs, the relatively rapid recovery of the watershed in years (rather than many decades) is likely due to the high rate of sedimentation and site-specific characteristics limiting remobilization. The contrast between the fate of Kepone in the James River, and that of industrial mercury in the nearby South River, which has persisted in the riparian food web for over a half century with little abatement, is a striking example of the importance of knowing the specific ways in which a contaminant moves around and through ecological networks.

5 Networks Operate Across Multiple Spatial and Temporal Scales

Nowhere is Polis and colleagues' (Polis and Winemiller 1996; Polis et al. 1997, 2004) conceptual understanding of the integration of landscape and food web ecology more germane than to the discussion of how ecological networks are embedded in complex spatial and temporal habitats. In particular, contaminant transport is based on movement patterns and connectivity of a suite of taxa that integrates aquatic and terrestrial environments across space and time. In turn, movement patterns and connectivity are strongly related to landscape characteristics (Polis et al. 1997; Ward et al. 2002a; Wiens 2002; Trøjelsgaard and Olesen 2016). In fluvial systems, a broader landscape view of river corridors has led to a holistic and fine-grained ecological perspective of streams and rivers, reflecting the diverse internal spatiotemporal and ecological dimensions that constitute linked stream-riparian ecosystems. The complex relationships among these dimensions have contributed to "riverscape" (sensu Wiens 2002) and "riverine landscape" (sensu Ward et al. 2002b; Thorp et al. 2006) perspectives that recognize streams and rivers as both internally heterogeneous and tightly linked with their surrounding landscapes via boundary dynamics. In the context of aquatic-to-terrestrial contaminant transport, taking into account how ecological networks shift spatially and temporally within heterogeneous riverine landscapes is a critical consideration. Here, we focus on two key points with strong implications for contaminant transport from aquatic to terrestrial systems: (1) network interactions extend from local to broader spatial scales, and (2) food-web interactions across the aquatic-terrestrial boundary change seasonally.

Both time and space are important regulators of network variability. The interaction probability between two individuals or species is related to their mutual spatial and temporal overlap; in the extreme, there is no interaction when there is no overlap (Vázquez et al. 2009). Thus, there is no biotic transfer of contaminants without some type of interaction (e.g., trophic, mutualistic, dispersal). One important consequence of space for networks is the cost associated with the length of edges (recall that nodes and edges are embedded in space, nodes represent individuals or species, and edges represent interspecific interactions, e.g., predation), which can have substantive impacts on network structure (e.g., clustering). Nodes with shorter edges have the energetic advantage of clustering, where nodes are highly connected in both interaction space and, typically, physical space. On the other hand, longer edges/links must be compensated by some advantage such as being connected to a highly connected node (e.g., hub) (Barthélemy 2011). For instance, dispersal dynamics (e.g., rate, direction, distance) of aquatic insects between habitat patches can substantially vary based on a variety of factors (Kovats et al. 1996; Griffith et al. 1998; Petersen et al. 2004, Altermatt et al. 2013). Kovats et al. (1996) report that mean dispersal distances of smaller caddisflies (650–670 m) were less than larger caddisflies (1499–1849 m) and the mayfly *Hexagenia* (1213 m). Relative to maintaining network connectivity and, thus, to transporting contaminants, dispersal distances – one potential measure of edge length – must be considered within the context of the nodes that they link. At the Lake Hartwell Superfund Site in South Carolina, USA, PCB transfer via emerging aquatic insects to spiders extended 5 m inland, with measurable but much lower PCB concentrations in other insect predators (e.g., social wasps) up to 30 m inland (Raikow et al. 2011). Dispersal node distance, therefore, may be a critical measure of contaminant transport, with shorter nodes correlated (e.g., emerging insects to shoreline spiders) with higher contaminant transport. On the other hand, the relative connectance of the node is also likely critical. Continuing with the shoreline spider example, if the spider node represents an isolated hub in a highly compartmentalized network, contaminant transport will be contained. Conversely, if the spider node represents a highly connected hub (e.g., at the center of a complex trophic network, with arachnivorous birds and other consumers that prey on spiders; Walters et al. 2010), the terrestrial consequences of this linkage are more substantial.

In large part because of differences in dispersal distance and other movement patterns, network interactions differ between localized and broader spatial scales, with multiple implications for contaminant transport. Movement networks figure prominently in this discussion (Fig. 3). In particular, dispersal and migration are the most spatially exaggerated types of movements for many organisms. In addition to exerting influences on spatial ecology, population growth, metapopulation dynamics, shifts in ranges, and reintroductions (Clobert et al. 2009; Cote et al. 2010), dispersal can regulate the transport of nutrients and other materials (Flecker et al. 2010). Similarly, migrations can impact nutrient and contaminant transport at both landscape and continental scales. For example, high migration activity, ecological

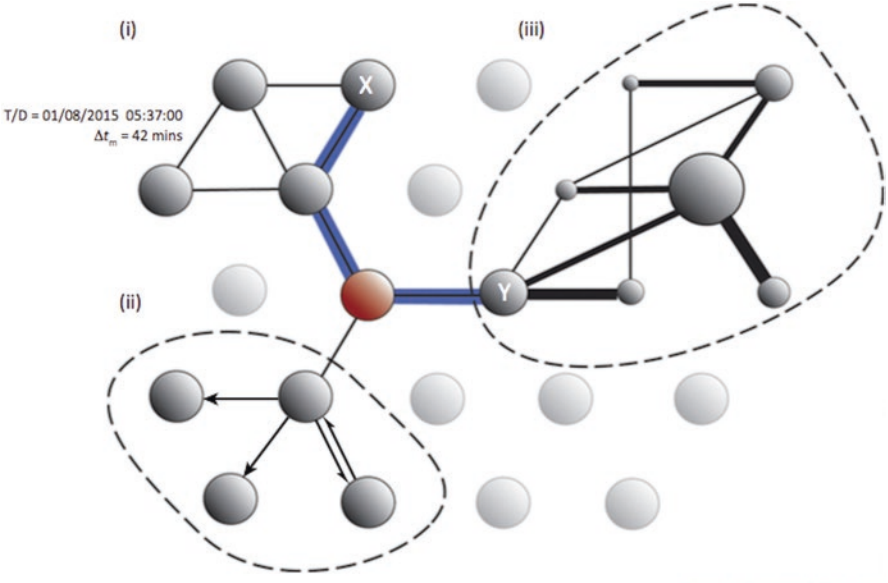

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Fig. 3 Unweighted, binary networks indicate whether an organism has moved between two locations and (ii) can include directionality. Weighing the edges relates to the frequency with which that movement has occurred, and by averaging the sums of the linked weights arriving and departing from a specific location, the relative node strength (iii) (indicated by relative node size) is determined. Note that two temporal components are also incorporated: (1) time the edge occurred and (2) duration – the time taken from leaving one node to arriving at another. The blue lines represent the most efficient paths through complex habitats (particularly relevant for wide-ranging or migratory species). The hashed lines represent the formation of clusters, which form subgroups (high modularity) where activity is greater within vs. between subgroups. Spatially close locations in stochastic environments (e.g., seasonally inundated floodplain waterbodies) favor the formation of clusters. The shortest path length is indicated by the blue line between two node locations (X and Y). Larger "hubs" (i.e., nodes) might be expected to represent more persistent, more frequent, and larger aquatic-to-terrestrial contaminant transfers. Contaminant transfer across the landscape will be constrained in movement networks with a high degree of clustering/modularity and will be mediated by individual personalities such as boldness, exploration tendency, responsiveness to environmental stimuli, and dispersal tendency. Figure from Jacoby and Freeman (2016)

plasticity, and the ability to colonize a wide array of aquatic habitats were implicated as factors facilitating the flux of heavy metals from water bodies to terrestrial zones via emerging dragonflies in the Barabinsk forest steppe region of Western Siberia (Popova et al. 2016). Kitchell et al. (1999) found that geese acted as spatial couplers, transporting large quantities of nutrients assimilated from foraging migrations to alfalfa and corn fields to wetland systems at the Bosque del Apache National Wildlife Refuge (New Mexico, USA). Migrating animals, including birds, fish, and marine mammals, can transport nutrients and contaminants over long distances and across international boundaries; the net transport of contaminants is mediated by spatial patterns of feeding, excretion, spawning, and mortality as well as the direction of pollutant transport (e.g., from water to land or land to water) (Blais et al. 2007; Lavoie et al. 2012).

Many factors can influence movement networks (e.g., physical setting, social setting), as discussed in the introductory material. Habitat geometry and area and distance between interacting habitats interact with organismal mobility and energetic resources to determine animal movement. For example, aerial insectivorous birds that rely on emerging aquatic insects respond to the structure and composition of riverine landscapes as well as the abundance and distribution of flying insects (Sullivan et al. 2007; Alberts et al. 2013). The role of individual animal personalities also has emerged as an important consideration in movement ecology (Spiegel et al. 2017) and could be considered an important microscopic network feature. Individual behavioral traits (e.g., aggressiveness, boldness, sociability, risk taking) have been linked not only to the strength of interactions between individuals (e.g., in food webs; Kalinkat 2014) but also to spatial dynamics (Cote et al. 2010; Réale et al. 2010; Quinn et al. 2012). In fact, the dispersal syndrome is a widely recognized pattern found in various organisms based on individual personalities (Wolf and Cote et al. 2010; Weissing 2012). Social and movement networks have many ecological and evolutionary implications and have already been widely recognized as important in understanding and predicting the spread of disease (e.g., avian influenza; Ren et al. 2016). It is a logical extension that movement networks will be valuable in describing and forecasting biologically mediated aquatic-to-terrestrial contaminant transport across spatial scales.

Ecological networks not only vary spatially but also temporally. Climatic seasonality can strongly influence food -web and mutualistic networks in freshwater systems, with increasing rainfall seasonality associated with smaller and more modular food webs and increasing temperature seasonality associated with more diverse mutualistic networks (Takemoto et al. 2014). Owing to the relationships between precipitation and stream hydrology, the positive relationship between network modularity (and lower diversity/network size) and rainfall seasonality aligns with the notion that environmental variability promotes modularity (which can be related to increased robustness and stability) (Allesina and Tang 2012). However, Thebault and Fontaine (2010) found that network architectures favoring stability were markedly different between trophic and mutualistic networks: highly connected and nested network structure promotes stability in mutualistic networks, whereas high compartmentalization and low connectedness increase stability in trophic networks. Thus, predictions relative to how temporal shifts in environmental conditions will affect broader networks remain elusive.

However, these relationships suggest that phenology is important in regulating ecological networks (Encinas-Viso et al. 2012) (Fig. 4). In temperate systems, seasonality is strongly associated with both primary productivity and changes in community composition of various taxa (e.g., Wise 1980; Francoeur et al. 1999; Gelwick 1990). Emerging insect communities can be highly variable as a function of season (e.g., winter vs. summer, dry vs. wet) (Banks et al. 2007; Yuen and Dudgeon 2016; Kautza and Sullivan 2015; Robinson et al. 2001), and of course spawning runs of anadromous fish are also seasonal, thus altering the magnitude, rate, and

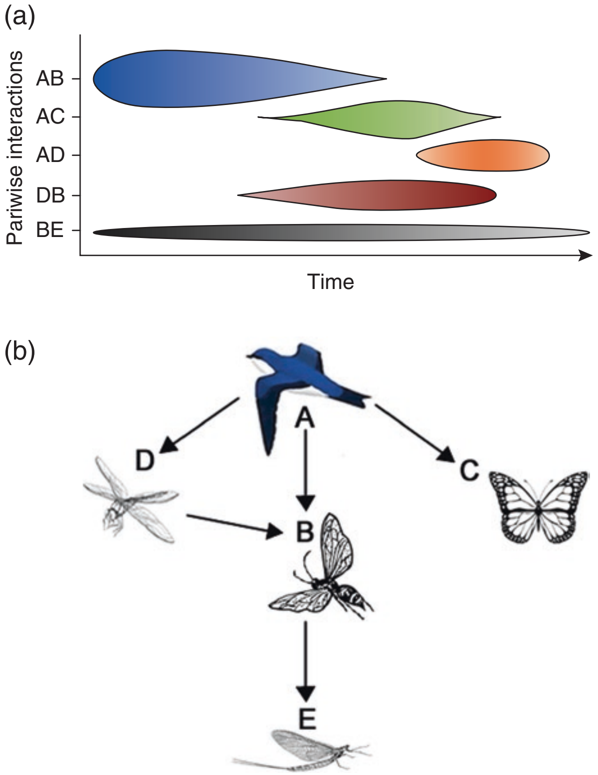

Fig. 4 The phenology of interactions may be an important consideration in understanding network variability over time. In (**a**) the phenology of pairwise interactions (AB, AC, etc.; note AE is also ecologically common, but connections are limited for the purposes of illustration) is represented by the length of the horizontal bars; the intensity of the interactions (e.g., interaction frequency) is represented by the thickness of the bars. Thus, although interactions may overlap phenologically, they may show contrasting patterns of temporal importance if the intensity of the interactions varies. In (**b**), the static and temporally aggregated network is shown. Implications for the magnitude and transport of contaminants from aquatic to terrestrial systems are significant. Here, for instance, migratory riparian birds have limited potential to assimilate aquatically derived contaminants from dragonflies because of their limited temporal overlap; rather, birds would bioconcentrate greater contaminant body burdens from an indirect pathway (*A*-*B*-*E*) with emerging aquatic insects. (**a**) from Trøjelsgaard and Olesen (2016) and (**b**) modified from Trøjelsgaard and Olesen (2016)

predictability of contaminant flux from aquatic systems to terrestrial consumers. Likewise, seasonal shifts in recipient consumer populations and communities (e.g., riparian spiders, aerial insectivorous birds) will change the contaminant-assimilation capacity of terrestrial food webs. These expansions and contractions of food webs, in turn, relate to the degree of modularity, connectance, and other macroscopic network features, with profound implications for aquatic-to-terrestrial contaminant transport: for example, contaminants trapped in highly modular/

compartmentalized networks may not make it out of the water or beyond the riparian zone. The persistence of ecological network complexity across seasons is also an important consideration, as network persistence is likely tied to the predictability, frequency, and magnitude of aquatic-to-terrestrial contaminant fluxes. Lastly, ecological networks not only vary seasonally but also over much broader time scales (years, centuries, and millennia; Trøjelsgaard and Olesen 2016), leading to both short- and long-term shifts in contaminant fluxes from water to land.

6 Disturbances Can Have Strong Effects on Ecological Networks and Contaminant Transport

Understanding and predicting the movement of contaminants across land-water interfaces is most effective when the ecological context is incorporated (Clements et al. 2012). Factors that influence context-dependent ecosystem responses include intrinsic characteristics such as food-chain length and hydrogeographic position (Clements et al. 2016) but also extrinsic disturbances. These can range from inter-annual fluctuations in a watershed's rainfall to the expected massive and novel disruption of anthropogenic climate change. As an example of inter-annual variation, historically high floods on the Mississippi River (USA) in 1973 had no effect on contaminant levels of biota, but the drought of 1976–1977 significantly increased contaminant body burdens in aquatic macroinvertebrates, with potential for increased export to adjacent terrestrial ecosystems (Sparks et al. 1990). Disturbances expected from climate change are discussed below.

Disturbance regimes, whether natural or exacerbated by humans, can alter the structure and weighting of ecological networks and influence aquatic-terrestrial subsidies. For hypothetical ecosystems in a state of natural balance, low-disturbance systems would be dominated by "weedy" species with high reproductive rates. In contrast, ecosystems with intermediate levels of disturbance, according to classic ecological theory applied to aquatic systems (Townsend and Scarsbrook 1997), might be expected to exhibit greater biodiversity (with larger networks) with higher overall productivity and greater stability. High-disturbance systems are inherently less stable with more species at higher risk of extinction. For an aquatic system with the potential to export nutrients and contaminants to adjacent terrestrial habitats, low-disturbance ecosystems might produce higher acute exposures of contaminants as weedy species reproduce and disperse across land, while ecosystems buffeted by intermediate disturbance might export contaminants at a higher chronic rate due to increased productivity overall. The typical contaminant exports from a hypothetical ecosystem with high levels of disturbance are difficult to predict. In reality, though, the aquatic systems with which we are concerned in the discussion of contaminant export are generally not pristine but are heavily impacted by anthropogenic disturbances, three of which are discussed below: invasive species, land conversion, and climate change.

6.1 Invasive Species

Among human-caused disturbances to ecosystems, the introduction of exotic species has obvious potential to affect export of contaminants. Invasive species can have myriad effects on native species, from extirpation to facilitation through habitat modification, provisioning of new hosts, prey sources, or pollinators, or through competitive release of some species through elimination of others (Rodriguez 2006). Thus, the mechanisms for ecosystem disruptions are diverse, and new ones will surely emerge in coming studies. Because food-chain length strongly influences biomagnification of contaminants (Cabana et al. 1994; Rasmussen et al. 1990; Kidd et al. 1995) in aquatic systems, adding an exotic species to the food-web network may strongly influence contaminant export. An invasive species that creates an extra link in the food chain, especially a top predator, would increase biomagnification, whereas one that increases the food available at a lower trophic position should reduce biomagnification. However, such straightforward effects have not been observed, for example, in the case of invasive rainbow smelt (*Osmerus mordax*), which did not elevate mercury in lake trout of boreal lakes they invaded (Johnston et al. 2003), or invasive round goby (*Neogobius melanostomus*), which has not increased contaminant levels in the predatory fish of the Laurentian Great Lakes (Hogan et al. 2007). This result may be due in part to the more efficient foraging and resulting accelerated growth of predators feeding on the abundant new food source (i.e., growth dilution). Consumption of fewer, higher-energy prey items leads to reduction in contaminant intake and dilution of ingested contaminants over more body tissue. This effect was experimentally demonstrated by the introduction of trout to a lake contaminated with mercury, with a resulting decline in mercury concentration in predatory northern pike (*Esox lucius*) credited to growth dilution and increased foraging efficiency (Lepak et al. 2012). If this had been a system in which predatory fish were eaten by terrestrial animals (bears, eagles, humans), the result of the exotic species introduction and increased food web complexity would have been reduced export of contaminants.

Invasive exotic species will have complex effects on food web networks, which is why simplistic predictions of increased biomagnification and resulting aquatic-terrestrial export of contaminants have not often been supported empirically. Invasion of the spiny water flea (*Bythotrephes longimanus*) into Canadian lakes resulted in the predicted elevation of the trophic position of the zooplankton community through increased presence of the predatory water flea as well as reduction of native herbivorous species of zooplankton (Rennie et al. 2011). Modeled results suggested that the increased trophic position of the zooplankton food source for herring should have increased contaminants in the herring. However, increased mercury concentration in herring has not been found (Rennie et al. 2010).

While theory predicts that invasive species that increase trophic position of predators should also increase contaminant biomagnification and potential export to terrestrial predators, other network modifications may mitigate these predicted effects of species invasion. Besides increased foraging efficiency and growth dilution, as described above, invasive species may cause predators to shift their diets to species feeding at a lower trophic position as a result of competition with the invader, and these alternate prey items would then transfer fewer contaminants to predators. One example of how this could happen is the recent illegal introduction of lake trout (*Salvelinus namaycush*) into Yellowstone Lake (Wyoming, USA), with resulting severe depression of native cutthroat trout (*Oncorhynchus clarkii*) populations. The terrestrial grizzly bears that once derived substantial nutrition from the spawning native trout, but cannot catch the deepwater invasive species, have shifted to eating young elk (Middleton et al. 2013). Had this been a system in which trout were delivering aquatic contaminants such as mercury to the terrestrial bears, the lake trout invasion would have strongly reduced export of the contaminant. In some cases, invasive species simply provide a novel, abundant, more contaminated food source to predators, such as with zebra mussels (*Dreissena polymorpha*) and migratory ducks in the Great Lakes (Mazak et al. 1997), and predicting the outcome of greater transport of contaminants out of the contaminated system is straightforward. However, invasive species may also provide more food at lower trophic levels or draw predators into new microhabitats with different contamination regimes. Further research on trophic cascades caused by invasive species will be necessary to allow better predictions of the effects of species invasion on contaminant biomagnification in aquatic systems that impact their terrestrial neighbors.

Clearly, invasive species can alter the biomagnification of contaminants in aquatic ecosystems, sometimes in surprising directions, but how much evidence exists that this affects aquatic-to-terrestrial subsidies of contaminants? The potential mechanisms are clear, but empirical evidence is scarce. Introduced fish species can decimate the populations of emergent aquatic insects that subsidize surrounding terrestrial consumers, such as the case of introduced trout in high-elevation lakes of the Sierra Nevada mountains, where terrestrially nesting gray-crowned rosy finches (*Leucosticte tephrocotis*) rely on emergent mayflies to feed their young (Epanchin et al. 2010). In another example, an invasive amphipod reduced the emergence of chironomids from the Rhine River, thereby causing a shift in the diet of terrestrial spiders away from aquatic-based nutrients (Gergs et al. 2014). Whereas these mechanisms are frequently demonstrated, usually in experimental mesocosms (Greig et al. 2012), studies rarely include a measure of contaminant transfer in the field. Recent studies of mercury export from ponds with and without fish are an important step in the right direction (Henderson et al. 2012; Chumchal and Drenner this volume).

6.2 Land Conversion

Another ecological disturbance that can affect export of contaminants from aquatic to terrestrial habitats is land conversion. When a riparian forest is converted to agricultural or residential/built land, aquatic ecosystems usually receive more sunlight (due to opening of the canopy) and increased nutrient inputs through runoff and erosion. In many cases, this may increase aquatic productivity, with potential to export more contaminants through increased production of emerging aquatic insects. Increased soil erosion from the new land use may add previously sequestered contaminants to the aquatic food web, potentially increasing export, as in rivers in the Amazon basin, where the majority of mercury flux is supplied by anthropogenic soil erosion after deforestation (Roulet et al. 1999). However, many other factors may counter these trends and effectively reduce the cross-boundary transfers. Declining macroinvertebrate density owing to impaired water quality may limit or alter the emergence of contaminated prey, although effects on terrestrial predators such as bats are complex and reflect changes in dominant aquatic species rather than changes in overall productivity (Vaughan et al. 1996; Kalcounis-Rueppell et al. 2007; Abbott et al. 2009). At higher levels, increased contaminants in an aquatic ecosystem may reduce density of emerging aquatic insects to the point that despite their higher contaminant concentrations, overall flux into terrestrial habitats is greatly reduced (Kraus et al. 2014a).

The interplay between human degradation of a stream or river and the rate of contaminant flux also depends on whether flood control is practiced, as contaminants can be directly deposited on terrestrial floodplain habitat by floods. Once there, contaminants in these sediments can enter the terrestrial food web and biomagnify. Whether it is through direct transfer from emerging aquatic insects or indirect transfer from flood-borne sediments to the base of the terrestrial food web, aquatic-originated contaminants are often ingested by spiders and biomagnify further in terrestrial birds (Cristol et al. 2008). Nearshore terrestrial spiders can receive half or more of their carbon from aquatic sources, regardless of whether they are web weavers catching emerging insects or cursorial spiders (Collier et al. 2002). The importance of spiders as vectors of aquatic contaminants has been recognized, but very few studies have examined mechanisms through which spiders obtain their contaminants. Those that have examined mechanisms either lack empirical data on transfer of contaminants from spiders to their predators (Walters et al. 2010; Speir et al. 2014; Gann et al. 2015) or have not demonstrated whether spiders obtain contaminants directly or indirectly from the aquatic ecosystem (Cristol et al. 2008).

Alterations in aquatic ecosystems can have numerous effects on nearby terrestrial systems (Schulz and Bundschuh this volume). Approximately one third of more than 600 studies reviewed concerned anthropogenic disturbance, but of these, few examined network interactions and resulting indirect effects of aquatic disturbance on terrestrial ecosystems (reviewed in Schulz et al. 2015). Only a few examples of top-down effects have been found (reviewed in Schulz et al. 2015), for instance, a disturbance that altered export of emergent aquatic prey to a terrestrial predator, with subsequent cascading effects in the terrestrial food web. An example of this would be fertilizer runoff increasing export of emerging midges, increasing terrestrial spider populations, and thereby reducing populations of leafhoppers, releasing terrestrial plants from herbivory. A few other studies revealed bottom-up effects, for example, increased flooding directly subsidizing terrestrial plant growth, with effects cascading up the terrestrial food web. However, overall the literature lacks examples that examine both abiotic disturbance and biotic networks. With regard to how these complex network interactions affect export of contaminants from water to land, much more can be learned (e.g., see Text Box 2).

6.3 Climate Change

A case study in which global climate change increased cross-boundary contaminant flows has not yet been empirically demonstrated to our knowledge but can be predicted with some confidence based on the nature of the accompanying disturbances – warmer temperatures, greater frequency of droughts, increases in wildfire intensity and occurrence, and melting of polar ice and permafrost contaminant reservoirs. All of these can cause an increase in flux of some aquatic pollutants, none better studied than mercury. With more mercury circulating globally due to wildfires and melting polar reserves, aquatic systems will likely experience increased mercury inputs. Higher temperatures will increase rates of microbial methylation, leading to a higher proportion of the circulating mercury entering the food web as methylmercury and biomagnifying. Predicted drought may increase mercury concentrations in aquatic organisms and the terrestrial species that eat them (Brasso and Cristol 2008), although other responses are conceivable if fewer aquatic organisms disperse from drier systems. Mercury is just one illustrative example of the hypothetical effects of climate change on aquatic-to-terrestrial contaminant transport. In this case, the contaminant transfer not only is larger but also will wreak additional havoc because of an anticipated interaction between contaminants and temperature. For example, among nestling swallows ingesting mercury from emergent aquatic insects in a polluted Virginia, USA, floodplain, mortality was related to higher maximum daily temperatures (Hallinger and Cristol 2011). At uncontaminated sites, warmer temperatures did not correspond with increased mortality, in fact the opposite was observed due to increased food availability. Sadly, the coming decades will be replete with new case studies of how the perturbations of global climate change alter ecological networks, including those responsible for exporting aquatic-originated contaminants to land.

While it is too soon to have much confidence in predictions of how climate change will affect cross-boundary fluxes of contaminants (but see Meuhlbauer et al. this volume; Larsen et al. 2016), there is already a cottage industry of papers summarizing the effects of climate change on ecosystems (e.g., Ficke et al. 2007). The general consensus, with respect to aquatic ecosystems, is that we can expect increased water temperatures, decreased dissolved oxygen, and more deleterious effects of existing contaminants (or effects at lower concentrations). There may also be a blurring of ecosystem boundaries (e.g., changes in ice and fire regimes), intensified agricultural impacts (e.g., water use for irrigation), developmental changes with implications for trophic transfer (e.g., smaller fish cannot eat large prey), and mismatches between consumers and subsidy fluxes (e.g., riparian bird nesting dates and aquatic insect emergences, or see Sato et al. 2016 for an experimental demonstration with fish). If extreme enough and depending on geographic location, these effects would eventually reduce productivity and thus suppress export of contaminants (Chumchal and Drenner this volume), but that effect might be preceded by an era of increased biomagnification and increased productivity that boost nutrient and contaminant flows to surrounding ecosystems. Less certain are predictions that eutrophication will increase, as the predicted increase in variability of hydrologic regimes (more floods and droughts) makes modeling very difficult, particularly with respect to complex phenomenon such as lake stratification and turnover events. The complex ecological networks that move contaminants from aquatic to terrestrial systems will be massively rearranged through species extinction, range shifts, and changes in relative competitive advantages. In general, warmer temperatures can be expected to lead to greater mobilization and biomagnification of contaminants, but even this prediction is not generalizable across contaminants, as mercury biomagnification in aquatic food webs around the globe appears to be greater in colder northern climates (Lavoie et al. 2013). In the end, whether the networks that export contaminants into terrestrial habitats will remain intact is probably the greatest factor in determining the magnitude and direction of effects of climate change on cross-boundary subsidies.

7 Ecological Networks and Contaminant Exposure Risk Can Include Humans

As with ecological systems, networks increasingly have been used to describe social systems. Further, linked social-ecological systems have been studied for a variety of natural- resource applications (Berkes et al. 2003; Armitage et al. 2009). For example, Rathwell and Peterson (2012) combined a social network analysis of water-quality management networks by local Québec, Canada, governments with a social-ecological analysis of water management and ecosystem services. These investigators concluded that strengthening the water-management network will contribute to improving water quality. Social-ecological networks consist of both human/social nodes and nonhuman/ecological nodes, as well as their various connections (which represent the attributes of the network). Janssen et al. (2006) identify three types of primary social-ecological networks (ecosystems connected by people, ecosystem networks fragmented by people, and artificial ecological networks created by people) and their effects on resilience, focusing on two broad network characteristics: the level of connectivity and the level of centrality. Connectivity can be represented by the density of links within the network, or reachability – the extent to which all the nodes in the network are accessible to one another. Centrality is represented by distribution of links among the nodes in the network as well as their structural importance. A highly central network, for example, relies on a limited number of hubs (e.g., key species, critical social positions/leaders; Janssen et al. 2006).

Here, we focus on the potential for social-ecological systems to guide our understanding of contaminant exposure risk to humans from aquatic ecosystems. A classic example comes from the Arctic, where subsistence hunting and fishing are still widely practiced (Suk et al. 2004; Arnold and Middaugh 2004; WHO 1990) (Fig. 5). Hunting for marine species focuses on marine mammals such as seals, walrus (*Odobenus rosmarus*), and whales including narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*), fin (*Balaenoptera physalus*), and minke (*Balaenoptera acutorostrata*). Arctic peoples depend on both anadromous fish species that move

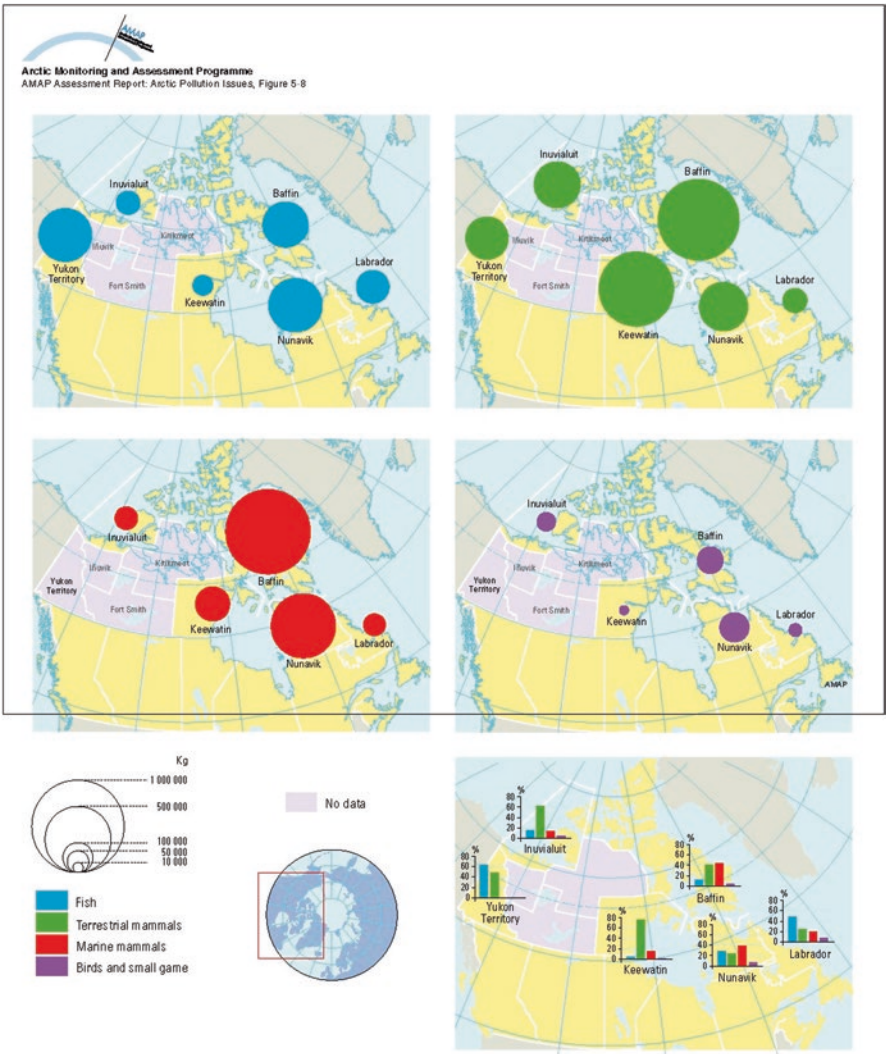

Fig. 5 Annual indigenous subsistence production in Arctic Canada in total kg and percent of harvest, by category. (Source: AMAP 1998)

seasonally from marine to freshwater systems, such as salmon (*Oncorhynchus* spp.) and Arctic char (*Salvelinus alpinus*), and resident species including lake trout (*Salvelinus namaycush*) and northern pike (*Esox lucius*). Harvests from marine and freshwaters provide critical sources of food, clothing, and other products, as well as a cash-economy for local households and communities (Caulfield 2000; Harder and Wenzel 2012).

The relationships between contaminants and human health depend on toxicological effects, as well as broader issues of food security and social and cultural well-being (Jewett and Duffy 2007). For example, in Nunavut children of northern Canada, 95% of mercury intake came from beluga (33%), narwhal (26%), ringed seal (*Phoca hispida*, 20%), and fish (11%) (Stow et al. 2011). Further, mercury levels are rising: a tenfold increase in mercury levels of upper trophic-level marine animals over the last 150 years has been documented. Thus, populations with high intake of traditional foods are at increased risk of chronic methylmercury exposure (Fig. 6). Toxicological effects from elevated mercury exposure range from neurodevelopmental and behavioral effects in infants to increased incidence of cardiovascular disease and diminished IQ in youth and adults (Clarkson et al. 2003; Stow et al.

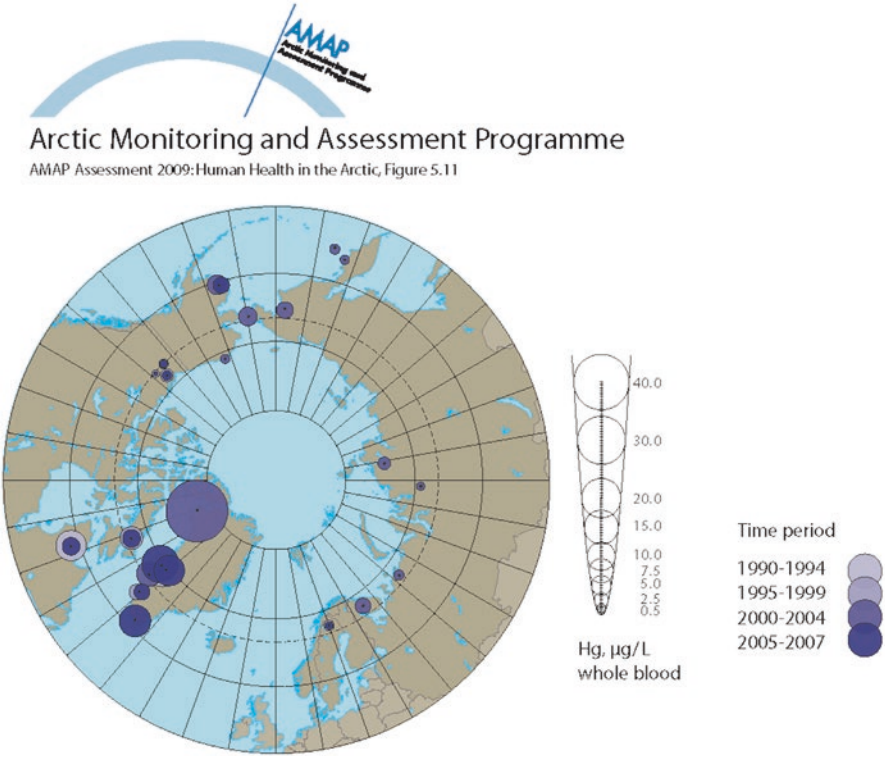

Fig. 6 Total mercury concentrations in blood of mothers, pregnant women, and women of childbearing age in Arctic regions. (Source: AMAP 2009)

2011; Jewett and Duffy 2007). The knowledge of potential risks related to contaminants can dissuade consumption of traditional or local foods and reduce contaminant exposure but also can lead to numerous consequences including the erosion of cultural identity; economic pressure from the relatively high cost of less-healthy, store-bought foods; and nutritional deficits stemming from increased consumption of poor-quality store-bought foods (Stow et al. 2011).

Fishing, along with hunting, herding, and gathering activities, is rooted in social relationships among animals, people, and the environment (Wenzel et al. 2000). Further, indigenous communities increasingly are understood to form complex systems with long-term interactions with their environments (Dowsley 2009). Thus, changes in any one of these factors might be expected to alter transport of aquatic to terrestrial contaminants and their subsequent distribution through human trade and social networks. For example, global climate change, which is comparatively more intense in the Arctic than in other regions (Moore 2006; McBean et al. 2005), may affect assimilation of aquatically derived contaminants via direct and indirect mechanisms (see above). Elevated air temperatures in the Arctic stemming from climate change, for example, may increase re-emissions of mercury deposited from lower latitudes (Stern 2011). Indirectly, a suite of conditions associated with climate change will likely affect subsistence use of aquatic resources: travel and hunting on sea ice (e.g., ability to hunt seal and narwhal), land exposure (altered trade), animal abundance and distribution (challenges to resource harvesting), and harvesting behavior (reduced time and increased danger for hunting and fishing) (Ford et al. 2008). Reduced engagement of younger generations in subsistence practices may also be a critical factor in reshaping the relationships between people and their environment (Moerlein and Carothers 2012) and thus the network characteristics that affect human exposure to contaminants.

Aquatic -to- terrestrial transport of mercury in the Arctic is somewhat akin to Janssen et al.'s (2006) *ecosystems connected by people social-ecological network type*, whereby the acquisition and distribution of traditional, local food items are based on human decisions playing out in a changing environment. Mercury transfer, for example, is regulated by both the density of links on the ecological side via trophic position and degree of biomagnification of mercury in aquatic animals (Fig. 7) and connectivity on the human side via interactions between individuals and communities (e.g., provisioning of aquatic food to family members, economic ties between communities for aquatic food products). Thus, characteristics of the linked social-ecological system will be critical in shaping the extent and magnitude of aquatic- to- terrestrial transport of mercury and other contaminants. The degree of centrality of the network will also be important, particularly for network persistence – e.g., is the network characterized by a variety of exploited species (hubs) or by a highly dependence on one species? Is distribution of fish and other aquatic food dependent on a limited number of relevant social positions (hunters, vendors) or are these roles occupied by a wide variety of people?

Overall, the complexity of the coupled human-natural system components involved in the transfer and assimilation of contaminants from aquatic ecosystems to people demands consideration of both human and ecological network nodes.

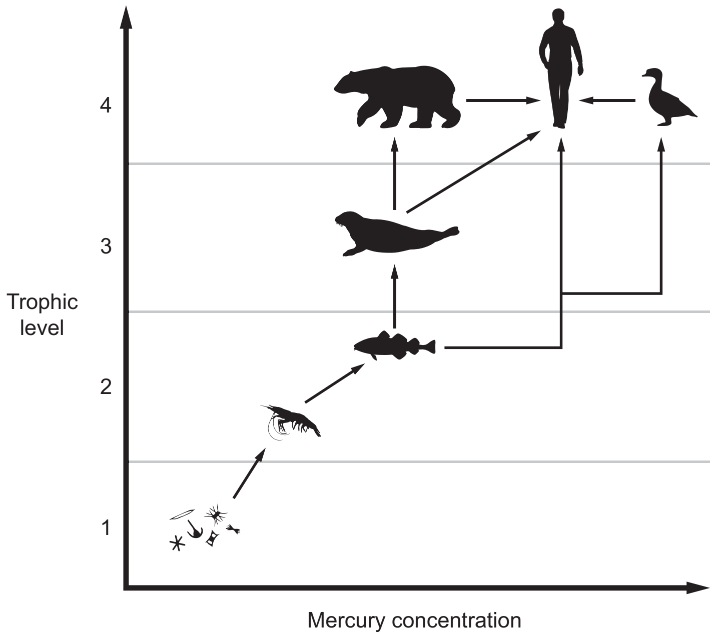

Fig. 7 Mercury flow through Arctic marine food webs in northern Canada. (Modified from AMAP 2011. Figure by Robert Keast)

Further, the majority of network studies focuses on social or ecological systems, treating them as static networks with a large degree of homogeneity among the nodes and lines. However, in the context of contaminant exposure, dynamics, and heterogeneity, it will be necessary to include dynamics and heterogeneity to adequately address resilience (Janssen et al. 2006).

Within this context, the study of social-ecological networks could be helpful in addressing current knowledge gaps related to the fate of mercury entering marine systems, the effects of multiple stressors and nutritional factors on the toxicity of mercury, and the health impacts of mercury in human populations as a function of food choice and availability (AMAP 2011). Although we have presented the Arctic as a case study, transfer of contaminants from aquatic systems to humans is not unique to this area of the world. In fact, this phenomenon extends into temperate and tropical regions and includes both indigenous and nonindigenous peoples, spans a suite of environmental justice issues (Olivero-Verbel et al. 2016; Ha et al. 2017; Lepak et al. 2016; Kalkirtz et al. 2008), and implicates numerous additional mechanisms and pathways that may lead to human intake of aquatic contaminants (Sullivan and Rodewald 2012; see Text Box 2).

Text Box 2: Dam Removal and Ecological Networks: Implications for Cross-Boundary Transfers of Contaminants

S. Mažeika Patricio Sullivan
David W. P. Manning

Low-head, run-of-river dams (< 7.6 m in height) are widespread across streams and rivers of the United States. Many of these dams have become obsolete, expensive to maintain or restore, or dysfunctional, leading to a growing movement of dam removal (see Davis et al. 2017 and references therein). Here, we use fish assemblages from before and after dam removal to show an empirical example of how ecological networks may help us understand and predict shifts in aquatic-terrestrial food-web complexity and lend insight into aquatic-to-terrestrial contaminant transport. In this case, humans using fish as a food resource represent our focal node. Thus, this example illustrates how ecological networks can help describe human health risks associated with bioaccumulation of heavy metals, which are often sequestered in sediments behind dams and can be redistributed following dam removal (see Davis et al. 2017 and references therein).

Dam removal represents an in-stream perturbation that may have cross-boundary consequences (Sullivan et al. 2018); taking an ecological network view of this burgeoning river management tool may aid in predicting these effects, which are likely diffuse and difficult to detect and often challenging to address with traditional hypothesis testing or statistical analyses (Kibler et al. 2011). After dam removal, the impacted river reach previously above the removed dam (i.e., in the reservoir pool; Text Box 2, Fig. 8a, b) was represented by networks that were less complex than the control reach, represented by a reservoir pool above an intact low-head dam (in terms of both linkage density and connectance; Text Box 2, Fig. 8c), suggesting a simplification of the network immediately after dam removal (Text Box 13.2, Fig. 9). Notably, this decrease in network complexity was accompanied by fewer direct links to terrestrial consumers (i.e., humans) suggesting that cross-boundary transfers of energy, nutrients, and contaminants along this pathway were potentially diminished following dam removal. For example, in the impacted reach, the number of links to humans was 11 pre-dam removal, but this decreased to 2 immediately after dam removal and recovered to 8 links after 5 years. In contrast, the number of links to humans remained similar across the years in the control reach (Text Box 2, Fig. 9). The shifts in species composition in the impacted reach were largely related to losses of larger-bodied sport fish (e.g., largemouth bass [*Micropterus salmoides*; node 29], flathead catfish [*Pylodictis olivaris*; node 20]); thus, humans also occupied a lower estimated trophic position in the initial stages post-dam removal (3.79 [post-dam, 2013] vs. 4.18 [pre-dam, 2012]; Text Box 2, Fig. 9) and with concomitant decreases in bioaccumulation.

Fig. 8 River reaches on the Olentangy River, Ohio (USA), a fifth-order tributary of the Scioto River. Ecological networks were derived from fish-assemblage data before and after dam removal at the following river sites: (**a**) reservoir pool, before low-head dam removal; (**b**) previous site of reservoir pool, 4 years following low-head dam removal and channel restoration; and (**c**) intact low-head dam with reservoir pool above dam. (Photo credits: S.M.P. Sullivan)

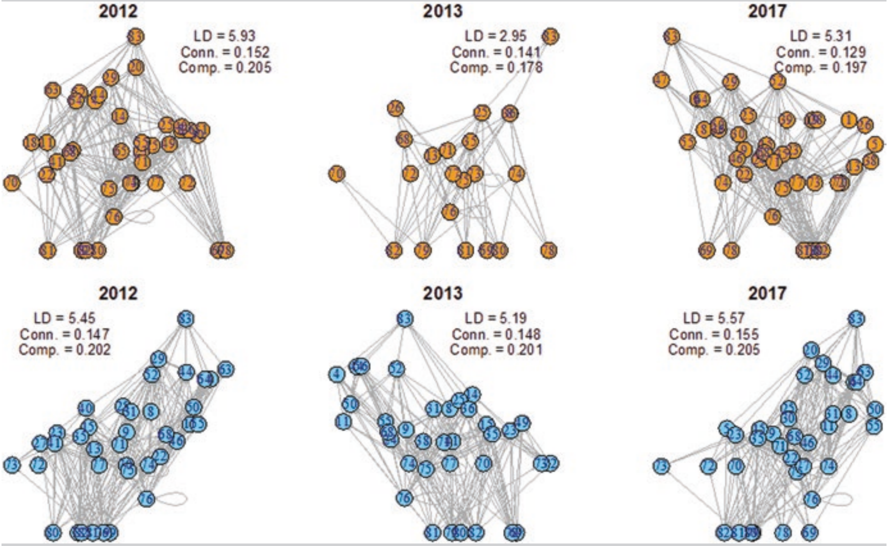

Fig. 9 Ecological networks depicting fish assemblages before (2012), immediately after (2013), and 5 years after (2017) dam removal in the Olentangy River, Ohio, in two distinct sites: one reach was above the former dam and actively restored (orange networks); the other was above an intact dam (light blue networks). Both reaches had similar network indices before dam removal; the reach impacted by dam removal decreased in complexity immediately after dam removal. However other network metrics decreased (connectance) or recovered to pre-dam removal levels by 5 years post-dam removal (compartmentalization). Humans (node "83") represent the potential cross-boundary flux of energy/nutrients/contaminants to the terrestrial zone. In this case, dam removal initially diminished the potential flux of fish-derived nutrition or contaminants, and this pathway appeared to recover 5 years post-dam removal. Note that vertical node positions are according to calculated trophic position from corresponding adjacency matrices

Both the control and impacted reaches showed similar linkage density 5 years post-dam removal, indicating recovery of fish species richness, and network complexity (Text Box 2, Fig. 9). However, the impacted reach exhibited lower connectance compared to the reference reach, highlighting the potential for long-term effects of dam removal on network persistence and resilience. Lower connectance of a network has been linked to diminished overall network stability, owing to fewer species deletions required to "unravel" the interactions within a network. Thus, despite an apparent recovery of network complexity in this example, shifts in species composition (e.g., loss of flathead catfish [node 20], insertion of sauger [*Sander canadensis*; node 47]) were likely associated with changes to network connectivity.

In addition to reduced contaminant flux to terrestrial consumers (in this case, humans) immediately following dam removal, we can also see that dam removal may have led to a regime shift in the impacted reach prompted by the suite of hydrogeomorphic changes in the former impoundment (e.g., substrate grain size distribution, streamflow dynamics, ecosystem size, etc.). While species richness of the network appeared to recover post-dam removal, the accompanying shifts in species composition may have altered the connectivity of the network and thus increased its susceptibility to future perturbations (Dunne et al. 2002a).

8 Conclusions

In this chapter we have argued that contaminants and energy move across ecosystem boundaries through ecological networks comprised of interactions between organisms. Using an ecological network modeling approach is beneficial for understanding and making predictions about movements of contaminants across the land-water interface because network analysis is appropriate for variables that move at different rates, such as contaminants with varying affinities for biotic tissue or variable stability in the environment. Networks also accommodate the varying spatial and temporal scales across which contaminant movement must be considered, some moving only meters and lasting days or weeks, others traveling great distances over decades. Thus, the distance contaminants move from water will be regulated by the interaction of seasonality and the operational scale of networks – local to regional to continental.

The practical value in using network approaches to understanding cross-ecosystem boundary transfers of contaminants is that such models can facilitate predictions for changes in contaminant movement in response to disturbances such as species invasions, anthropogenic intensification of land use, and climate change. The importance of gaining a better understanding of contaminant movements through ecological networks is obvious when one considers that humans are part of such networks, whether urban residents fishing near a dam or indigenous people in the Arctic deriving most of their food from wildlife.

The edge of chaos is a key element of complexity theory that describes the balance point of a system. It has been invoked for termite colonies, financial markets, flocks of birds, mob formation, and recently, by noted historian Niall Ferguson to describe the rise and fall of great historical powers and empires. Ferguson asks, “What if history is not cyclical and slow moving but arrhythmic – at times almost stationary, but also capable of accelerating suddenly, like a sports car? What if collapse does not arrive over a number of centuries, but comes suddenly, like a thief in the night?” Likewise, many ecological systems fluctuate between disturbance and stability – such fluctuations are arguably most evident at the interface between two ecosystem types. Therefore, the edges of aquatic and terrestrial ecosystems constitute a hallmark example of the ways in which complexity of the overall system is driven both by the internal factors and interactions within each contributing ecosystem and the cross-boundary exchanges of matter, energy, and information that link them (Polis et al. 1997; Baxter et al. 2005; Sullivan and Rodewald 2012). In this and other ways, ecological networks might be expected to manifest multiple properties of complex adaptive systems: responding nonlinearly to disturbances, strongly characterized by feedback loop, and undergoing regime shifts marked by tipping points in one or more features (dynamic stability) (Sullivan and Manning 2019).

Although approaches involving analysis of complex networks have been used to describe food webs (e.g., Thompson et al. 2012; Yletyinen et al. 2016), to our knowledge, they have not been considered within the context of contaminant transport. Complex-system approaches have been used successfully to further our understanding of population and community ecology yet have been criticized for failing to take into account key features of ecological complexity such as cross-scale interactions, environmental variability, and diversity (Anand et al. 2010) – aspects that are central to understanding contaminant movement across aquatic-terrestrial borders. Further, emergence is a central feature of complex systems (Mayr 1982), whereby cooperative interactions of the individual components determine emergent properties. At the aquatic-terrestrial interface, transfers of energy and contaminants from the aquatic to terrestrial system might lead to nonlinear, emergent properties such as greater food-web complexity than found in either the discrete aquatic or terrestrial system. As such, individual, small-scale transfers of energy and contaminants (e.g., via emerging aquatic insects) at the aquatic-terrestrial interface might be expected to amplify into macroscale processes and contaminant transport across the landscape.

How do ecological networks at the aquatic-terrestrial boundary interact with each other and other trophic networks over space to regulate contaminant transfer? A focus on *energysheds*, a potential emergent property of aquatic-terrestrial networks that link food webs at the aquatic-terrestrial boundary to trophic networks over much broader spatial scales, may be a valuable construct to address this question (e.g., Power and Rainey 2000). Conceptually, this idea stems from theoretical and empirical evidence that suggests that energetic and contaminant contributions from rivers may extend beyond the aquatic-terrestrial interface well into their adjacent riparian and upland zones (Muehlbauer et al. 2014; Kautza and Sullivan 2016). Thus, cross-boundary energetic transfers and contaminants might be expected to exponentially propagate from the aquatic-terrestrial interface laterally away from the river channel, generating new patterns of network architecture through rising levels of complexity. Hence, the domain of the complex system transcends, for example, the river network, rather encompassing the larger landscape unit of which the river is an embedded and integral part. This new domain may be the watershed itself, or it may prove to be a unique spatial area as defined by the extents of energy and, thus, contaminant transfers. To date, food webs and energy exchanges have been considered aspatially to a large degree. Further, the potentially fundamental contribution of aquatic energetic transfers to the extent and complexity of networks and aquatic-to-terrestrial contaminant transport of the larger landscape has been underestimated. In particular, spatial ecology has not fully embraced the concepts and tools from network theory, yet this is likely to be an important step in understanding and predicting contaminant fluxes. For example, bioenergetic consumer-resource models could be used to simulate species and food-web dynamics (Thebault and Fontaine 2010; Otto et al. 2007) beyond the degree of variability exhibited by real-world study sites to predict hot spots of contaminant flux.

Nature is organized into complex, dynamic networks of species and their interactions. Because contaminant transfer is intimately tied to these interactions, framing contaminant transfer via ecological networks as a complex problem and examining it with the conceptual tools developed in complex-system research could be an effective approach for integrating the multiple facets of contaminant transfer highlighted in this book (also see Sullivan and Manning 2019). This could be a valuable step in extending current knowledge to build on the legacy of Polis and colleagues in relation to contaminant transport, with likely benefits for managing environmental pollution and exposure risk in humans and wildlife. Furthermore, from a practical perspective, ecological networks also offer the advantage of distilling tremendous complexity into relatively simple models (Heleno et al. 2014). As such, we propose that network approaches may be highly advantageous in monitoring and simulating cross-boundary ecosystem contamination. Graphical representations of ecological networks offer the additional benefit of being easily interpretable and could facilitate communication among broad audiences.

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Lead Author Biography S. Mažeika Patricio Sullivan PhD, is an associate professor in the School of Environment and Natural Resources and director of the Ramsar-designated Shiermeier Olentangy River Wetland Research Park at The Ohio State University in Columbus, Ohio, where his research interests lie in watershed and coastal science and conservation. He is a distinguished university teacher and a Fulbright Distinguished Chair on Biodiversity and Sustainable Development. Dr. Sulliván has a deep appreciation for the complexity and beauty of the natural world, which he shares with his wife and four children.

Synthesis: A Framework for Predicting the Dark Side of Ecological Subsidies

Johanna M. Kraus, Jeff Wesner, and David M. Walters

> *Creative thought on [food] webs…supports my optimism that the holy trinity of field observation, controlled experimentation and mathematical exploration can discover some common unity, and in the process provide important guidelines on how to save and even resurrect our increasingly battered natural world.*
>
> Paine (1996)

1 Introduction

Chemical contaminants influence ecological systems and patterns of species distribution at a global scale (Nriagu and Pacyna 1988; Rockstrom et al. 2009; Stehle and Schulz 2015; Beketov et al. 2013). Well-documented examples include pesticides that directly reduce insect biomass and contribute to declines in insectivorous birds (Carson 1962; Hallmann et al. 2014, 2017; Eng et al. 2019), and methylmercury that biomagnifies up the food chain to poison higher-order consumers, including humans (Harada 1995; Lavoie et al. 2010). In fact, chemical pollution resulting from contaminant inputs has such potentially large effects on ecosystem structure and health that it is identified as one of the planetary boundaries needed to maintain a safe operating space for humanity (Rockstrom et al. 2009). Despite these concerns, the use and manufacture of chemicals used in agriculture, manufacturing, medications, and cosmetics have increased exponentially over the past 60 years (Bernhardt et al. 2017). Furthermore, the ecological effects of these inputs of contaminants into the environment have been grossly understudied (Bernhardt et al. 2017). Thus,

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J. M. Kraus (✉) · D. M. Walters
U.S. Geological Survey, Columbia Environmental Research Center, Columbia, MO, USA
e-mail: jkraus@usgs.gov; waltersd@usgs.gov

J. Wesner
Department of Biology, University of South Dakota, Vermillion, SD, USA

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understanding and managing the extent and magnitude of the effects of contaminants on ecosystems will continue to be one of the major challenges of this century.

In this book, we identify two main pathways by which chemical contaminants affect ecosystems. First, contaminants affect ecosystems in contaminant bioaccumulation and biomagnification in food webs (Carson 1962). Contaminants that bioaccumulate within food webs, such as persistent organic pollutants (POPs) and organometals, can increase exposure in higher-order predators. Furthermore, the fate of these compounds may not be limited to the contaminated ecosystem, because dispersing organisms can transport these contaminants to other environments (Walters et al. 2008). The second pathway governs contaminant effects on ecosystems by increasing mortality and altering behavior of specific taxa (Rohr et al. 2006; Clements and Rohr 2009; Halstead et al. 2014), which can indirectly affect other members of the community. For example, contaminants such as trace metals and current-use pesticides reduce prey abundances, alter competitive dominance of sensitive taxa, and cause trophic cascades (Halstead et al. 2014; Rogers et al. 2016). Therefore, both ecological factors and physicochemical characteristics of contaminants determine effects of contaminants on aquatic ecosystems.

Aquatic ecosystems are particularly likely to receive inputs of chemical pollutants as well as allochthonous resources because of their relatively low topographical position in the landscape (Allan 2004). Water, sediment, and detritus tend to move downhill with gravity, along with associated contaminants. This transport of materials from land to water is long recognized to have important effects on ecosystem function, community dynamics, and species distributions. More recently, the movement of animals from water to land as part of their ontogeny (i.e., complex life cycles), or other means of dispersal (i.e., movement by predators or flooding), has been identified as an important conduit of energy and nutrients back to land (Muehlbauer et al. 2014; Schindler and Smits 2017). Theory describing these linkages, which merge paradigms from both landscape and food web ecology, is now being used to answer questions regarding the ecological effects of contaminants and food web structure on contaminant flux (Kraus 2019a, b; Chumchal and Drenner this volume; Sullivan and Cristol this volume).

In this chapter, we review heuristic models useful for predicting the effects of chemical contaminants on ecological subsidies at the land-water interface. These models allow us to generalize empirical findings to new environments; more efficiently utilize time and monetary resources by providing information about what, when, and where to measure effects; and to derive and test hypotheses that separate causal versus correlative agents of ecological change. We focus on effects of contaminants on production of animals with complex life histories, use and quality of terrestrial detritus to aquatic ecosystems, and the flux of contaminants through food webs both within and across ecosystem boundaries. We then construct a synthetic framework using conceptual control (a.k.a. programmatic) and food web models that pull together many of the factors and processes reviewed, including landscape, chemical/ecotoxicological, and ecological factors. Here we define control models as describing how subsidy endpoints are influenced by specific drivers and stressors, while conceptual food web models describe trophic relationships among organisms that drive resource and contaminant flux across ecosystem boundaries (Gentile et al. 2001; Miller et al. 2010). Finally, we use this framework to identify (1) patterns of contaminant effects on ecosystems, and (2) data gaps and areas for future research.

2 Review of Conceptual Models

One of the major patterns evident from efforts to predict effects of aquatic contaminants on linked aquatic-terrestrial food webs is that the physicochemical characteristics of contaminants determine the mechanism of potential effects on consumers (Kraus 2019a). For example, organometals and persistent organic pollutants like polychlorinated biphenyls (PCBs) are more likely to affect aquatic-terrestrial linkages by magnifying in bodies of adult insects and amphibians (i.e., "exposure" pathway, Kraus et al. 2014a; "subsidy drives exposure" sensu Walters et al. this volume). On the other hand, trace metals and some pesticides are more likely to sever aquatic-terrestrial linkages through direct effects on survival of animals with complex life histories through metamorphosis (i.e., "biomass" pathway, sensu Kraus et al. 2014a; "exposure drives subsidy" sensu Walters et al. this volume). As in the organization of this book, we invoke the physicochemical dichotomy of biomagnifying versus toxic contaminants as a heuristic starting point for reviewing the complex suite of factors identified as drivers of contaminant effects on ecological subsidies in linked aquatic-terrestrial ecosystems (Walters et al. this volume).

2.1 Ecology Predicts Ecotoxicology: Subsidy Drives Exposure

Contaminants that accumulate in resource subsidies and biomagnify in food webs can lead to potentially harmful exposures in subsidized consumers. The effects of these contaminants ripple through linked aquatic-terrestrial food webs by disrupting reproduction, endocrine functioning, and metabolism of higher-order consumers, as well as reducing survival of their young (e.g., Custer et al. 1998, 2003, 2005). Aquatic contaminants that biomagnify and persist in subsidies (e.g., adult aquatic insects) but do not tend to directly lower their production include methylmercury as well as many other persistent organic pollutants. For example, Chumchal and colleagues found that adult aquatic insects export methylmercury from ponds to riparian spiders (Speir et al. 2014; Chumchal and Drenner this volume). Methylmercury flux to riparian spiders was mediated by the emergence of small-bodied aquatic insect taxa (Tweedy et al. 2013). Furthermore, the maximum concentration of mercury detected in odonates emerging from these small ponds exceeded wildlife health values for red-wing blackbird nestlings (Williams et al. 2017). Similarly, Walters and colleagues found that PCBs accumulated in a diverse assemblage of riparian insectivores (spiders and herptiles) in proportion to their reliance on aquatic prey (Walters et al. 2008) and that these concentrations reflected PCB concentrations and congener profiles found in nearby river sediment (Walters et al. 2010;Kraus et al. 2017). Maximum total PCB concentrations found in riparian spiders were 14-times higher than risk values protective of bird health for chickadee nestlings (Walters et al. 2010). Finally, Christine and Tom Custer and colleagues have found bioaccumulation of multiple POPs including PCBs, dioxins and dichlorodiphenyl trichloroethane (DDT) and derivatives in diet, eggs, nestlings, tissues, and blood of tree swallows foraging for aquatic insects near industrially polluted rivers (Custer et al. 1998, 2003, 2005). Hatching success declined with summed concentration of dioxins and furans in eggs and newly hatched chicks (Custer et al. 2003).

Contaminants in aquatic ecosystems can be strong drivers of terrestrial food web exposure. However, other factors, besides contaminant type and concentration, can influence subsidy production, contaminant flux, and impacts on recipient food webs. Approaches including field surveys (Walters et al. 2008; Raikow et al. 2011), experiments (Chumchal and Drenner this volume), conceptual models (Chumchal and Drenner this volume; Otter et al. this volume), network models (Sullivan and Manning 2019; Sullivan and Cristol this volume), and meta-community frameworks (Schiesari et al. 2018) have explicitly incorporated ecological factors in predicting exposure resulting from subsidy-mediated contaminant flux. Specifically, these approaches have revealed that organism life history, community structure, ecosystem productivity, landscape structure, and disturbance are important predictors of subsidy-mediated exposure for contaminants that biomagnify and do not strongly reduce subsidy flux. For example, Chumchal and colleagues have shown that adult aquatic insect emergence from ponds and concomitant mercury flux is increased by nutrient enrichment (bottom-up control) but decreased by presence of top predators like fish (top down control; Jones et al. 2013; Tweedy et al. 2013; Chumchal and Drenner this volume). Community structure and composition was also altered by these factors (i.e., nutrient enrichment and predation), which combine with concentration of methylmercury at the base of the food web to influence the flux of methylmercury by adult aquatic insect prey (Tweedy et al. 2013). Sullivan and colleagues found that mercury and selenium body burdens of riparian spiders were more affected by riparian zone width, vegetation structure, and distance from hydrological disturbance than flux of these contaminants in adult aquatic insects (Alberts and Sullivan 2016). In the case of persistent organic pollutants, Walters and colleagues demonstrated that the distance that PCBs penetrate riparian habitats tracks patterns of insect dispersal away from water (Raikow et al. 2011). Thus, ecological factors strongly influence the patterns of contaminant flux, and thus terrestrial food web exposure, for these contaminants.

Certainly, study of the movement of contaminants through food webs is not new. American bald eagle populations famously crashed as a result of DDT accumulation from contaminated fish that caused egg shell thinning and population collapse (Grier 1982). Vultures across the Indian subcontinent met a similar fate as a result of renal failure after exposure to the anti-inflammatory drug diclofenac through eating contaminated dead livestock (Oaks et al. 2004; Green et al. 2004). In fact, the direct exposure effect of biomagnifying contaminants on higher-order consumers has often been the focus of studies on food web–related effects of contaminants, likely because of the similar position of these animals to humans in the food web. However, knowledge of subsidy-mediated exposure to contaminants has lagged. Recent efforts to fill this data gap have borne several conceptual models aimed at synthesizing findings.

Several approaches have been taken to predict the effects of biomagnifying contaminants on cross-ecosystems linkages. Sullivan and colleagues enumerated multiple food web pathways of biologically mediated flux of contaminants across the aquatic-terrestrial boundary (Sullivan and Rodewald 2012). They also tested factors driving the effects of this flux and illustrate how to model these factors using network theory (Sullivan and Rodewald 2012; Alberts and Sullivan 2016; Sullivan and Cristol this volume). For example, they show how changes in fish species composition caused by dam removal can reduce fish-mediated transfer of aquatic contaminants to terrestrial food webs (Sullivan and Cristol this volume). Kraus and colleagues used meta-analysis and qualitative models to look for patterns of transfer of contaminants across insect metamorphosis based on contaminant physicochemical properties (Kraus et al. 2014b, Kraus 2019. Persistent organic contaminants and organometals that are not highly toxic to aquatic insects at concentrations typically found in the environment are likely to affect terrestrial food webs via an "exposure" pathway (sensu Kraus et al. 2014a; Kraus 2019a, b). These compounds accumulate in larval insects and are retained through metamorphosis, in some cases bioamplifying to higher concentrations in adults as they lose body mass during metamorphosis (Kraus et al. 2014b). These increased contaminant concentrations can lead to higher contaminant flux mediated by resource subsidies and to greater toxic effects on consumers (Walters et al. 2010; Chumchal and Drenner 2015; Kraus 2019a, b).

Chumchal and Drenner (this volume) present a conceptual model based on their empirical work showing the preeminence of ecological factors (top predators, nutrient enrichment, and drying disturbance) in driving aquatic-insect-mediated flux of methylmercury from ponds to terrestrial predators. Schiesari et al. (2018) built on these findings using a meta-community perspective to model the role of dispersing organisms in directly or indirectly mediating contaminant flux across ecosystem boundaries. Multiple factors, including other contaminants, can modulate dispersal and alter contaminant fluxes (Schiesari et al. 2018). This pattern has led to several conceptual models showing insect-mediated contaminant flux as being driven by factors altering contaminant retention through metamorphosis and survival to metamorphosis (Chumchal and Drenner 2015; Kraus 2019a; Otter et al. this volume). Finally, Schultz and colleagues included contaminants in their review of environmental alterations propagating from aquatic to terrestrial ecosystems (Schultz et al. 2015). In their conceptual model, they highlighted the potential for cascading food web effects of insect-mediated contaminant flux as well as loss of aquatic insect prey because of aquatic contaminants (Schultz et al. 2015).

2.2 Ecotoxicology Predicts Ecology: Exposure Drives Subsidy

Contaminants affect production of adult aquatic insects and processing of terrestrial detritus in aquatic ecosystems. These impacts ripple through linked aquatic-terrestrial ecosystems, altering subsidies dynamics in food webs and ecosystems. For example, trace metal inputs resulting from widespread hard rock mining can be ubiquitous limiters of aquatic to terrestrial subsidies. Burdon (this volume) describes the role of acid mine drainage (mixtures of elevated concentrations of trace metals, major ions, and low pH) and agricultural land use in driving a productivity gradient in adult aquatic insect emergence from New Zealand streams. Burdon found that emergence was lowest from mining-impacted streams and that the shift in emergence production due to adult aquatic insect biomass explained >20% of the variance in riparian spider densities. Kraus and Pomeranz (this volume) similarly summarize findings from the United States showing a 97% reduction in adult aquatic insect emergence from mountain streams in the Colorado Mineral Belt (USA) resulting from highly elevated concentrations of bioavailable trace metals. This loss of insect prey coincided with a 75% reduction in riparian spider populations (also explaining ~20% of the variation in densities) observed across the landscape. Additionally, Kraus and Pomeranz (this volume) demonstrate how the diet of insectivorous stream trout shifts over this same stream-metal gradient, with consumption of terrestrial arthropod prey increasing 82% in the most contaminated streams (Kraus et al. 2016). Loss of resource subsidy exchange in linked aquatic-terrestrial food webs can lead to reduced frequency of trophic interactions, fewer interacting taxa, and altered food web stability (Sullivan and Manning 2019).

Insecticides and elevated concentrations of nutrients and major ions from salt pollution can also reduce quantity of resource subsidies to land and water. For example, Morrissey and colleagues found that adult aquatic insect emergence was greatly reduced by a commonly used class of agricultural insecticide, neonicotinoids (Morrissey et al. 2015; Cavallaro et al. 2018; Stanton et al. 2018). In a laboratory study of 6 neonicotinoid compounds, Raby et al. (2018) found that percentage of insects to complete adult emergence was the most sensitive life history endpoint for midges and mayfly species (based on EC50 concentrations) for 5 of the 6 compounds. Furthermore, emergence biomass was reduced by >90% at concentrations that killed only 50% of pre-emergent larvae. In a study of contaminant effects on detrital subsidies to streams, Evans-White et al. (this volume) concluded that elevated concentrations of salts and nutrients altered decomposition of terrestrial plant detritus. This change reduced local detrital subsidization of stream life and led to a shift in the community composition of microbial and insect detritivores (Evans-White et al. this volume).

Because of the negative effects of some contaminants on subsidy production, these contaminants can also reduce contaminant flux (the product of contaminant concentration in subsidy and subsidy biomass or production) across ecosystem boundaries (Kraus 2019a; Kraus and Pomeranz this volume). For example, the reduction in aquatic insect emergence caused by trace metal toxicity to larvae, combined with excretion of metals by emerged adults during metamorphosis, leads to lower insect-mediated metal flux from high metal streams (Kraus et al. 2014a). This phenomenon could have important, albeit untested, effects on contaminant flux in ecosystems containing contaminant mixtures whereby biomagnifying contaminants are also present. For example, in the Prairie Pothole Region of North America, wetlands accumulate atmospherically derived methyl mercury (Hall et al. 2009), and large fluxes of methylmercury (mass of methylmercury per surface area of water per day) can be exported from wetlands by adult aquatic insects (Chumchal and Drenner 2015). However, agricultural runoff to these wetlands, specifically inputs of insecticides, is known to directly reduce adult aquatic insect emergence (Raby et al. 2018). As a result, the effects of toxic insecticides on production of adult aquatic insect subsidies (i.e., direct mortality of larvae) could reduce methylmercury flux from these wetlands to linked terrestrial food webs.

Variation in species sensitivity to contaminants leads to changes in relative species abundance and diversity, as well as interactions among aquatic organisms (Clements et al. 2000; Clements and Newman 2002; Clements et al. 2010; Clements et al. 2016). Thus, species sensitivity can alter the effects of aquatic contaminants given the respective characteristics and consumption of resource subsidies in linked aquatic-terrestrial ecosystems (Kraus et al. 2014a; Sullivan and Manning 2019; Kraus and Pomeranz this volume). For example, mixtures of trace metals including Cu, Cd, Zn, and Pb structure stream communities in areas of historic mining such as the Colorado Mineral Belt (Clements et al. 2000). Some species of mayfly are more sensitive to the effects of dissolved metals, and concomitant low pH, compared to other taxa such as dipterans (Clements et al. 2000). As a result, emergence of mayflies drops more precipitously than emergence of dipterans over the same metals gradient (Kraus et al. 2014a). Moreover, riparian spiders that eat adult aquatic insects at these sites decline with availability of dipteran, but not mayfly prey (Kraus et al. 2014a). Thus, relative sensitivity of taxa, as well as their decline over the contamination gradient, affects the response of riparian predators to subsidies.

Sensitivity to contaminants also varies with life stage, which has strong implications for predicting effects of aquatic contaminants on adult aquatic insect emergence. For example, Wesner and colleagues as well as others have shown that effects of contaminants on adult aquatic insect emergence can be stronger than predicted by effects on larvae (Schmidt et al. 2013; Wesner et al. 2014; Henry and Wesner 2018; Wesner 2019; Raby et al. 2018; Kotalik et al. 2019). One potential mechanism responsible for this relationship appears to be enhanced mortality during metamorphosis, in which death occurs disproportionately in the penultimate developmental stage (e.g., pupal stage in holometabolous insects or wingpad stage in hemimetabolous insects) (Wesner et al. 2014; Raby et al. 2018; Wesner et al. this volume). This presents a challenge in using bioassessments based on larval insects alone to infer patterns of emergence, since larval populations may show only subtle changes in response to contaminants even as adult populations show precipitous declines (Schmidt et al. 2013; Raby et al. 2018; Wesner 2019). However, declines in adult abundances do not necessarily lead to declines in larval populations due to high fecundity and immigration of aquatic insects. For example, genetic analyses suggest that only a small number of successful adult matings are needed to sustain robust larval populations (Bunn and Hughes 1997). Future work modeling the stage-specific responses of insects to contaminants, perhaps using recently developed theory in population and community ecology on stage-structured dynamics (e.g., de Roos and Persson 2013), would improve our understanding of ontogenetic changes in contaminant sensitivity.

Several approaches have been developed that could be used to predict the effects of contaminants on resource subsidies. For example, Rohr and colleagues use community ecology theory to derive predictions regarding effects of chemical contaminants on different aquatic ecosystems (Rohr et al. 2006; Clements and Rohr 2009). They predict that in some cases, contaminants act like predators, depressing prey availability and potentially leading to indirect effects such as trophic cascades and apparent competition. An experimental test of these hypotheses uncovered that response of aquatic ecosystems to a mixture of agrochemicals was best predicted by direct effects of contaminant(s), reproductive rates, interaction strengths with other taxa, and links to ecosystem function of each functional group of species included in the experiment (Halstead et al. 2014). Other researchers similarly showed that community level effects of a widely used insecticide (bifenthrin) cascaded through the food web to alter adult aquatic insect emergence, reducing aquatic subsidies available to terrestrial consumers (Rogers et al. 2016).

Also applying community ecology theory to predict effects of chemical contaminants, Clements and colleagues developed hypotheses of how environmental gradients, such as previous chemical exposure, upstream-downstream community variation and disturbances, could shape community responses to contamination (i.e., context-dependency, Clements et al. 2012; Clements et al. 2016). Specifically, they suggested that disturbance would vary longitudinally (although not necessarily in a linear manner) based on the Intermediate Disturbance Hypothesis (Menge and Sutherland 1987). They expected contaminants to have the least effects (greater resilience) on communities within the watershed experiencing intermediate levels of disturbance (Kiffney and Clements 1996; Clements et al. 2016). In support of this hypothesis, they found early successional diatom communities in headwater streams in Colorado to be less sensitive to the direct effects of metal pollution than late successional diatoms in higher-order streams (Medley and Clements 1998). Although implications for aquatic-terrestrial linkages were not discussed, these patterns suggest that position within the watershed could partially determine the effects of contaminants on the production and use of resource subsidies (see Sect. 2.3 Other Considerations below for more on this point).

In contrast to the previous approaches, Kraus and colleagues use physicochemical properties of contaminants to predict the effects of chemical contaminants on aquatic-terrestrial linkages (Kraus et al. 2014b; Kraus 2019a, b). For example, trace metals, PAHs, and current-use insecticides that stress larval aquatic insects during their development drastically reduce emergence of adult aquatic insects (via larval mortality), thereby reducing the quantity of aquatic prey subsidies available to terrestrial consumers (Kraus et al. 2014a; Wesner et al. 2014; Kraus 2019a). Across contaminant classes, except for insecticides, they also suggest that classes more toxic to insects are less likely to persist in insect bodies across metamorphosis (Kraus 2019b). This relationship between direct toxicity and persistence of contaminant classes across metamorphosis drives the effects of aquatic contaminants on subsidized insectivores (Kraus 2019b). For directly toxic contaminants, Kraus' framework suggests that reduction of emergence production, rather than increased exposure, will be the main mechanism by which insectivores of adult aquatic insects are affected by aquatic contamination.

2.3 Other Considerations

Resource exchange between aquatic and terrestrial ecosystems is a well-studied phenomenon in ecology (Minshall 1967; Polis et al. 1997; Baxter et al. 2005; Gratton and Vander Zanden 2009; Muehlbauer et al. 2014, see Collins and Baxter this volume for a brief overview). Theory describing animals with complex life histories and factors affecting timing and success of ontogenetic switch points (i.e., metamorphosis) is also well developed (Wilbur and Collins 1973; Wilbur 1980; Wilbur 1997; Schreiber and Rudolf 2008; de Roos and Persson 2013). Combined, these bodies of research may be usefully applied to predict the effects of aquatic contaminants on aquatic-terrestrial linkages.

As previously discussed, ecological drivers of subsidy production and use by consumers can govern contaminant effects on aquatic-terrestrial linkages. Polis and colleagues introduced the concept that productivity of the ecosystem producing the subsidy (donor) and ecosystem receiving the subsidy (recipient) would drive the direction and effects of resources subsidies across ecosystem boundaries (Polis et al. 1997, 2004). Specifically, they hypothesized that the effects of subsidies on consumers would increase with the ratio of donor to recipient production. In a meta-analysis, Marczak et al. (2007) found empirical evidence that consumer response to subsidies increased with the ratio of resource subsidies to alternative in situ prey. This concept suggests that contaminant flux in resource subsidies may have larger effects on consumers when resource subsidies are relatively more abundant than in situ resources.

Also building on the idea that relative productivity would influence consumer use and response to subsidies, Wipfli and Baxter (2010) presented a framework based on Vannote et al.'s (1980) River Continuum Concept. They predicted that the role of upstream, terrestrial, and marine allochthonous production in salmonid resource use would vary longitudinally within a watershed. They suggested that terrestrial resources would be more likely to support salmonid production in low-order streams, and that marine inputs become more important closer to the ocean. In line with this prediction, we would expect that the effects of aquatic contamination on the use of terrestrial inputs by salmonids would be more important in headwater streams. Several studies have found that reduction of aquatic prey by aquatic pollution can lead to increased reliance by fish on terrestrial insect subsidies in low-order streams (Kraus et al. 2016; Burdon et al. 2019). Thus, longitudinal position in the watershed could influence reliance of consumers on subsidies and increase the propensity of subsidies to mitigate effects of aquatic contamination.

Habitat shape or dimensions also affect subsidy fluxes across the aquatic-terrestrial boundary. For example, secondary production of macroinvertebrates is >5 times higher in streams than in lakes. However, an average-sized lake exports ~10 times higher insect emergence biomass than an average-sized stream in part, because an average stream width is smaller than an average lake radius (Gratton and Vander Zanden 2009). At the landscape scale, stream network geometry generates hotspots of adult aquatic insect flux, particularly at stream confluences (Sabo and Hagen 2012; Kopp and Allen 2019). Integrating the disciplines of freshwater geomorphology and subsidy production at the landscape scale (e.g., Schmidt et al. 2018) represents an exciting opportunity to predict cross-ecosystem contaminant flux.

Finally, for animals with complex life histories, larval conditions and environmental predictability can alter optimal timing and size at metamorphosis (Wilbur and Collins 1973). These factors can affect success of metamorphosis, future fitness, and subsidies to terrestrial consumers (Kotalik et al. this volume; Schreiber and Rudolf 2008; de Roos and Persson 2013). Contaminants can increase timing to metamorphosis if larval conditions are so stressful that animals cannot survive the total reorganization of body tissues (Clements et al. 2000; Kotalik and Clements 2019). Alternatively, if contaminants are pulsed, then naïve larvae that are developmentally mature enough to emerge, emerge earlier than noncontaminated larvae (Lee et al. 2016; Richmond et al. 2016; Rogers et al. 2016). Importantly, these physiological responses are predicated on the history of stress and previous exposure, as well as other interacting factors (including density and resource availability) that affect the timing, size, and ability of immature larvae or nymphs to metamorphose into an adult (Courtney and Clements 2000; Cain et al. 2006).

3 Synthesis Models

Multiple factors contribute to the biologically mediated flux of energy, nutrients, and contaminants across ecosystem boundaries (Fig. 1). To better understand the similarities and differences among these factors, we categorized them into four broad groups. Landscape factors are defined as those that shape the distribution of chemical contaminants and their bioavailability across the landscape. Ecotoxicological factors represent parameters associated with studies of the effects of chemical contaminants on organisms and environmental health including the chemical properties of contaminants and interaction of contaminants with the environment and living organisms. Ecological factors include measurements of organisms and their traits (e.g., both functional traits and physiological sensitivity) at different levels of organization. We group nutrients with ecological factors as they are a commonly measured parameter of ecological studies. To summarize the effects of these multiple factors on adult aquatic insect emergence, contaminant flux mediated by these insects, and impacts on terrestrial consumers, we employed a control

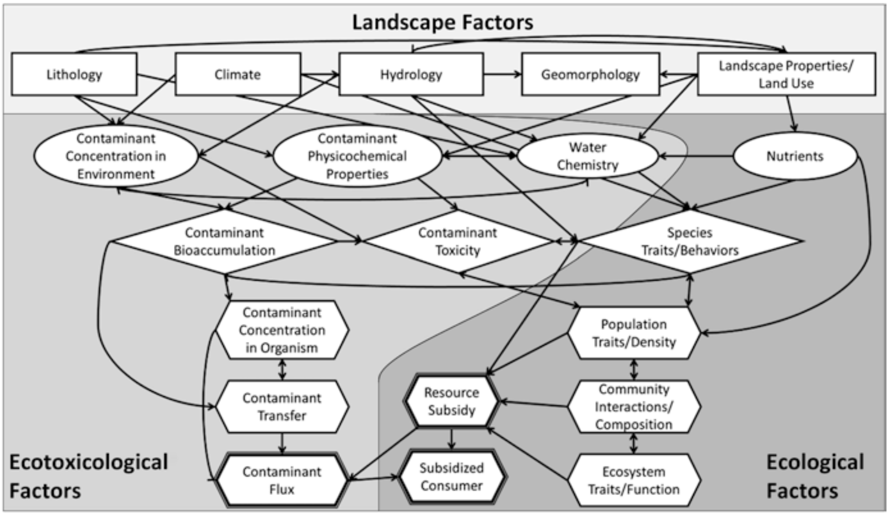
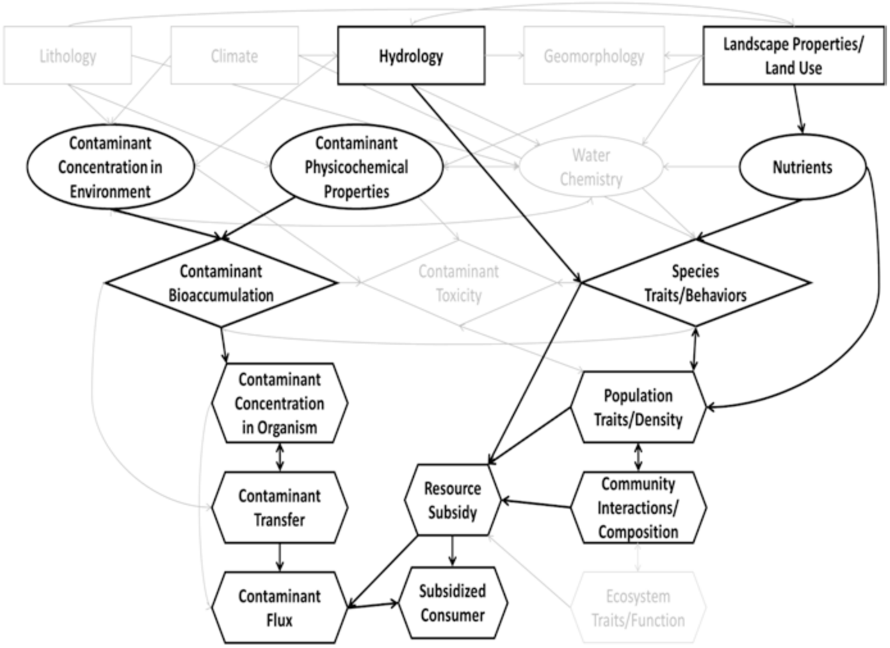


Fig. 1 Conceptual control model of major factors governing effects of aquatic contaminants on resource subsidies and subsidized consumers with a focus on freshwater-terrestrial linkages. Factors are grouped by category including landscape, ecotoxicological, and ecological and variable type. For variable type, squares are landscape drivers, circles are chemical stressors, diamonds are pathways or proximate drivers, and hexagons are endpoints or measured outcomes. Bold hexagons highlight focal endpoints. Arrows represent directionality of control. (See Table 1 for further details)

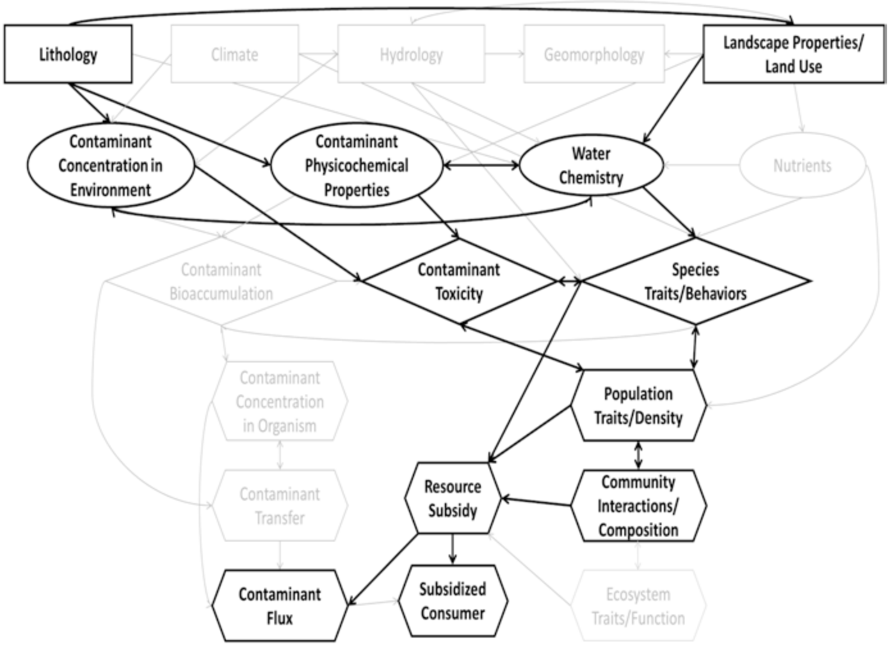
model that expresses the directionality of control by "drivers" on ecosystem "endpoints" (Gentile et al. 2001).

In general, the factors influencing contaminant effects on aquatic-terrestrial linkages are dependent upon the identity of contaminants within the study systems. This pattern arises because contaminants vary in the control pathways that dominate their effects on contaminant flux, subsidies, and consumers (Fig. 2, Table 1). For example, methylmercury does not tend to drive subsidy production but does drive contaminant flux by biomagnifying within the food web. For example, Chumchal and Drenner (this volume) show that pond permanency, nutrients, and predators alter mercury flux to terrestrial systems by changing the community composition, emergence production, and methylmercury concentration of adult aquatic insects emerging from ponds. Specifically, fish reduce emergence of large predatory dragonflies and damselflies (Odonata) but not smaller bodied dipterans, while nutrients increase overall emergence biomass. More ephemeral ponds are less likely to have fish, and thus have higher exports of mercury-laden predatory odonates and odonate-mediated adult emergence mercury flux. Meanwhile, the concentration of methylmercury available for uptake into freshwater food webs is codetermined by atmospheric (Hammerschmidt and Fitzgerald 2006), land-use, and organic factors such as presence of organic matter (dissolved organic carbon, DOC; e.g., Chaves-Ulloa et al. 2016), and anaerobic/redox conditions commonly linked to mercury methylation in freshwater ecosystems (Ullrich et al. 2001). The concentrations of methylmercury

A. Methylmercury



B. Trace Metals



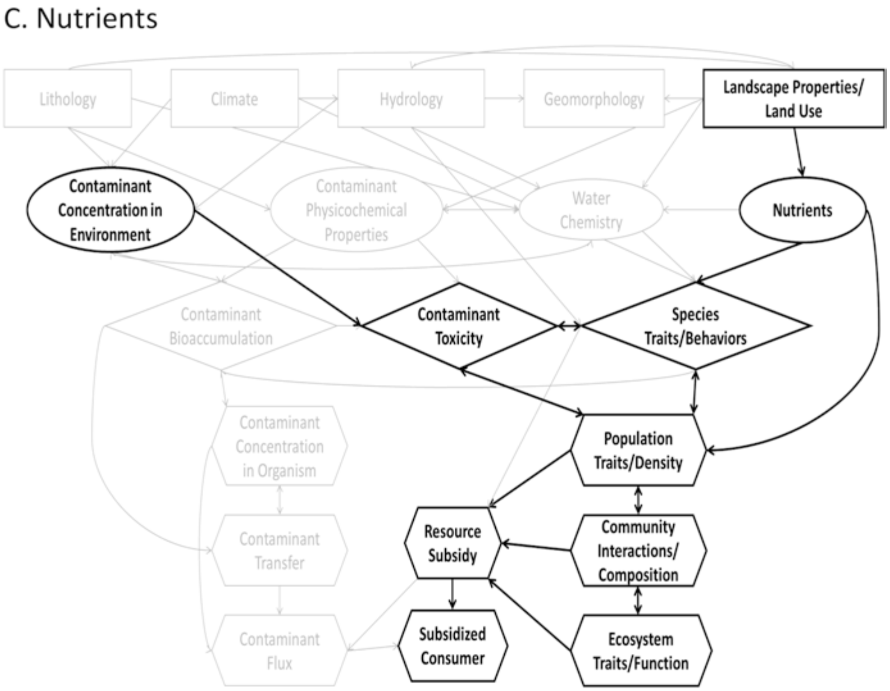


Fig. 2 Conceptual control model highlighting major factors found to govern effects of various aquatic contaminants on resource subsidies and subsidized consumers. Bold arrows and symbols represent pathways shown to be important in driving effects for methylmercury (**a**) as summarized in Chumchal and Drenner (this volume), trace metals (**b**) as summarized in Kraus and Pomeranz (this volume), and nutrients (**c**) as summarized in Evans-White et al. (this volume). Arrows represent directionality of control. (See Fig. 1 and Table 1 for further details)

within food webs is also strongly influenced by trophic biomagnification, which leads to exponentially higher concentrations as the number of trophic levels within a food web increases. Thus, understanding the effects of mercury on cross-ecosystem linkages requires knowledge of the ecological, chemical, and landscape factors affecting aquatic productivity, food web structure, and mercury methylation (Fig. 2a).

On the other hand, at toxic concentrations, trace metals drive subsidy production and thus contaminant flux in mineralized streams in areas mined for hard-rock minerals (Paetzold et al. 2011; Kraus et al. 2014a; Kraus and Pomeranz this volume). Mayfly emergence decreases more rapidly across a concentration gradient of trace metals than emergence of aquatic dipterans (Kraus et al. 2014a). Furthermore, this relationship has been validated using stream mesocosm exposures on representative montane stream benthic assemblages (Kotalik and Clements 2019; Kotalik et al. 2019). The distribution and concentration of trace metals in these streams is

Table 1 Variables included in control model predicting effects of landscape, ecotoxicological, and ecological factors on resource subsidies, contaminant flux, and subsidized consumers, with a focus on aquatic insect subsidies to terrestrial insectivores

Variable	Type of variable	Reason for inclusion
Landscape factors		
Lithology	Driver	Rock type predicts stream chemistry including pH, concentrations, and identity of dissolved solids and acid-neutralizing capacity.[1,2,3] Lithology can also influence land use (e.g., through influencing distribution of extractable minerals).[4]
Hydrology	Driver	Hydroperiod, timing of flow, flooding, and water source (ground vs. surface) alter geomorphology, water chemistry, contaminant concentrations, and species traits with cascading effects on cross-ecosystem movements of resource subsidies.[5,6,7,8]
Geomorphology	Driver	Topographic and bathymetric features of freshwater ecosystems have cascading effects on species traits and magnitude of resource subsidies.[9,10,11]
Land use/ Landscape properties	Driver	Anthropogenic land uses such as resource extraction, urbanization, industrialization, and agriculture can determine the type and form of contaminants transported to aquatic ecosystems, including nutrients.[4,12,13] Land use and landscape properties such as vegetative cover can also influence hydrology, geomorphology, and water chemistry (e.g., inputs of dissolved organic carbon), which alter bioavailability of many contaminants.[5,14]
Climate	Driver	Precipitation, temperature, and atmospheric currents can alter distribution, concentration, and ecological effects of contaminants on aquatic ecosystems, including changes to species distributions, density, phenology, and diversity.[8,12,15,16]
Ecotoxicological factors		
Water chemistry	Driver/ stressor	Chemical characteristics of water such as pH, conductivity, hardness, and dissolved organic matter can alter the physicochemical properties of contaminants, which affects their bioavailability[17,18,19]. They also have direct effects on organism physiology and cellular functioning.[17]
Physicochemical properties of contaminant	Stressor	Characteristics such as lipophilicity, molecular weight, molecular form, elemental components, ionization potential, and softness shape the toxicity and accumulation of these contaminants in organisms.[17,20]
Contaminant concentration in environment	Stressor	Concentration of contaminants in water, sediment, and food interact with their physiochemical properties, water chemistry, and species traits to affect toxicity of contaminants as well as their accumulation in organisms.[17,18,21]
Contaminant bioaccumulation	Stressor/ pathway	Contaminant accumulation by organisms from all sources in the environment (e.g., food, water, and sediment) occurs when uptake and ad/absorption occur at a faster rate than excretion or metabolism. Bioaccumulation is related to contaminant concentrations in organisms and can be related to both the toxicity to the organism and trophic/metamorphic contaminant transfer.[17,21]

(continued)

Table 1 (continued)

Variable	Type of variable	Reason for inclusion
Contaminant toxicity	Stressor/ pathway	Toxicity describes the effects of contaminants on organismal endpoints including reduced survival, reproduction, and population density as well as altered cellular function and behavior. These changes have cascading effects on community composition and ecosystem function. Toxicity is influenced in part by contaminant physicochemical properties, environmental concentration, species traits, and environmental/biological context (e.g., species interactions and other stressors).[21,22]
Contaminant concentration in organisms	Endpoint	Concentration is a measure of contaminant mass per unit body or tissue mass within an organism. This measure differs from bioaccumulation, which is a process, although contaminant concentration within tissues is used to estimate bioaccumulation. Contaminant concentration in resources can affect transfer of contaminants through food webs and, in the case of aquatic insects, the flux of contaminants from aquatic to terrestrial ecosystems.[21,23,24]
Contaminant transfer	Endpoint	Trophic or metamorphic transfer of contaminants through food webs or across ecosystem boundaries can expose consumers in remote locations to contaminants bioaccumulated elsewhere. Transfer is often measured as the ratio of concentrations in predator and prey or adults and larvae. Physicochemical properties of a contaminant often predict its propensity to be transferred from predator to prey or from larvae to adult in animals with complex life histories.[21,24,25]
Contaminant flux	Endpoint	Defined as the movement of contaminant mass from water to land or land to water per unit area per unit time. Contaminant flux is estimated as the product of resource subsidy biomass and contaminant concentration in the subsidy. Thus, it is mediated by the multiple factors that control subsidy production and contaminant concentrations. Contaminant flux may be the best determinant of consumer exposure in cases where other factors such as habitat are not limiting.[6,26]
Ecological factors		
Nutrients	Driver/ stressor	Nutrients have positive physiological effects on organisms, because they comprise important building blocks of cells or cellular processes and historically have been found at low concentrations. Low concentrations can lead to increased organismal growth and reproduction and lower C:N ratios. At high concentrations, nutrients can become contaminants.[27,28]
Species traits/ behavior	Pathway/ endpoint	Physiological (e.g., sensitive vs. tolerant) and functional traits (e.g., consumers vs. producers) of species can determine their responses to contaminants. Species traits such as body size, growth rate, and pollution tolerance influence population densities and growth in contaminated ecosystems.[21,28,29] Behaviors like predator avoidance, habitat selection, resource consumption, and timing of metamorphosis can be influenced by contaminants.[21,30,31] These changes in species traits also directly affect traits of resource subsidies.[6]

(continued)

Table 1 (continued)

Variable	Type of variable	Reason for inclusion
Population traits/ density	Endpoint	Contaminants can change all the demographic parameters of populations including birth, death, immigration, and emigration.[21] These changes can not only directly lower population densities and magnitude of resource subsidies, but also lead to positive indirect effects on other more tolerant organisms mediated by community interactions (e.g., trophic cascades).[31,32]
Community interactions/ composition	Endpoint	Changes in community composition can alter the type and strength of species interactions including predation and competition, as well as emergent properties of communities such as diversity and food chain length.[22] These factors alter subsidy production, contaminant flux, and ecosystem function.[6,28,32] Contaminants affect communities through direct and indirect effects on organism survival, behavior, and traits.[22,33]
Ecosystem traits/ function	Endpoint	Productivity, decomposition, respiration, and nutrient cycling are all functions of ecosystems that are altered by the effects of contaminants on water chemistry, species traits and diversity, and community interactions.[22,28,35] Ecosystem productivity can influence magnitude and direction of resource subsidies.[34]
Resource subsidies	Endpoint	Production, flux, and dietary quality of resource subsidies to consumers can all be altered by contaminants mediated by effects on species traits, population density, community composition, and ecosystem function.[6,24,36]
Subsidized consumers	Endpoint	Resource subsidies can alter physiology, reproduction, behavior, population densities, and community composition of subsidized consumers.[34] In many cases, resource subsidies increase or maintain consumer densities by providing an alternative resource in addition to other food or when in situ resources are not readily available. Because subsidized consumers may exist at densities not sustainable by in situ resources, indirect effects of subsidies on recipient food webs such as apparent competition and trophic cascades may be common.[34] However, when organisms that become subsidies, such as aquatic insects, bioaccumulate contaminants, they can act as contaminant vectors among ecosystems, exposing subsidized consumers to toxic effects of contaminant flux.[6,24,36]

Supporting citations are included
[1]Wanty et al. (2009), [2]Bluth and Kump (1994), [3]Sullivan et al. (2007), [4]Schmidt et al. (2012), [5]Poff et al. (2006), [6]Chumchal and Drenner (this volume), [7]Greenwood and McIntosh (2008), [8]Muehlbauer et al. (this volume), [9]Iwata (2007), [10]Lamouroux et al. (2002), [11]Townsend et al. (1997), [12]Kaushal et al. (2014), [13]Gurnell et al. (2007), [14]Jansson et al. (2008), [15]Debecker et al. (2017), [16]Clements et al. (2012), [17]Hamelink et al. (1994), [18]Hare (1992), [19]Fornaroli et al. (2018), [20]Wu et al. (2013), [21]Newman and Jagoe (1996), [22]Clements and Newman (2003), [23]Deforest et al. (2007), [24]Kraus et al. (2014b), [25]Walters et al. (2016), [26]Kraus (2019a, b), [27]Dodds (2006), [28]Evans-White et al. (this volume), [29]Buchwalter et al. (2008), [30]Vonesh and Kraus (2009), [31]Rogers et al. (2016), [32]Kraus et al. (2014a), [33]Morin (2009), [34]Polis et al. (1997), [35]Rosi-Marshall and Royer (2012), [36]Walters et al. (2008)

determined by rock type, mineralization, and mining history (Wanty et al. 2009; Schmidt et al. 2012). In industrial and urban scenarios, trace metals inputs to freshwaters might be more linked to land use, point sources, and atmospheric sources (Nriagu 1996). However, in all cases, the effects of trace metals on benthic insects are influenced by metal concentration, water chemistry (which affects bioavailability), and species traits (Clements et al. 2000; Buchwalter et al. 2008). Thus, understanding the effects of trace metals on cross-ecosystem linkages requires focusing on lithology, land use, and water chemistry parameters affecting their bioavailability as well as taxon-specific sensitivity (Fig. 2b).

Finally, nutrients can function as both a subsidy and a contaminant in aquatic ecosystems (Evans-White et al. this volume). As previously mentioned, nutrients can increase emergence of aquatic insects, and thus resource subsidies to terrestrial insectivores (Chumchal and Drenner this volume). They can also increase the nutritive value of terrestrial detrital subsidies to aquatic ecosystems by decreasing the carbon to nitrogen ratio (C:N) on biofilms that colonize detritus before and during decomposition (Evans-White et al. this volume). At sufficiently high concentrations, however, nutrients become chemical contaminants of aquatic ecosystems. For example, high nitrogen and phosphorous runoff from agricultural fertilizers increases algal blooms, resulting in anoxic conditions in lakes and estuaries (Dodds 2006). In terms of terrestrial detrital subsidies to aquatic ecosystems, high nutrient concentrations can lead to rapid decomposition of detritus and release of associated carbon into the water column (Benstead et al. 2009; Rosemond et al. 2015; Evans-White et al. this volume). In streams, this pattern leads to increased rates of downstream export of the energy derived from these detrital subsidies, resulting in reduced resources for local detritivores (Evans-White et al. this volume). These effects are especially marked for less labile detritus (Ferreira et al. 2015), which depends in part on the species of plant contributing terrestrial organic carbon to the aquatic ecosystem (Tank et al. 2010). Thus, understanding the effects of nutrients as a contaminant on cross-ecosystem linkages requires knowledge of the landscape factors affecting nutrient concentrations and ecological factors influencing terrestrial plant species composition (Fig. 2c; Cross et al. 2003).

For all contaminants, their influence on aquatic-terrestrial linkages is constrained by traits and behaviors of resource subsidies and their consumers. For example, subsidies that are comprised of living organisms “choosing” to move between aquatic and terrestrial ecosystems, either as part of their development or foraging (i.e., “active” subsidies, sensu Kraus et al. 2011), respond directly to the effects of contaminants. These responses vary among species and can take the form of habitat selection, changed foraging decisions, increased contaminant bioaccumulation, reduced reproduction, and reduced survival through metamorphosis (Custer et al. 2003; Vonesh and Kraus 2009; Schmidt et al. 2013; Wesner et al. 2014; Kraus et al. 2014b, 2016). The effects of aquatic contaminants on active subsidies such as animals with complex life cycles are thus likely to be mediated by behavior, sensitivity to contaminants, and processing of contaminants by the subsidies. On the other hand, subsidies that are passively deposited or moved between ecosystems by factors external to themselves (i.e., salmon carcasses, leaf litter, or accidental input of terrestrial organisms into water) integrate the effects of contaminants on the living organisms that are their vectors of movement or responsible for their processing/consumption (Kraus et al. 2010). The effects of aquatic contaminants on passive subsidies are thus more likely to be mediated by contaminant effects on consumers of those resources. Therefore, predicting the response of subsidies and linked consumers to contaminants depends in part on understanding ecological responses of those organisms/resources.

To further help predict the effects of contaminant physicochemical properties in governing aquatic-terrestrial linkages, we built a food web model that can be applied to multiple contaminants and subsidy types (Fig. 3, Table 2). This model differs from our control model (Fig. 1) in that it shows energy and contaminant flow among focal taxa of the linked aquatic-terrestrial food web (Fig. 3a). Like the patterns illustrated in the control model, we suggest that the pathways of major energy and contaminant fluxes through the food web will be governed in part by contaminant identity and physiochemical properties (see Kraus 2019a, for more details). Specifically, we show how some contaminants can virtually eliminate aquatic prey for terrestrial consumers, leading to prey loss as the mechanism driving effects on terrestrial consumers (Fig. 3b). For detrital inputs, loss of aquatic prey for aquatic consumers can increase consumption and, reliance upon, terrestrial subsidies (Fig. 3b). Lastly, bioaccumulative aquatic contaminants can negatively impact terrestrial consumers of animals with complex life histories (e.g., insects) by exposing consumers to elevated concentrations of contaminants in prey (Fig. 3c). For terrestrial inputs to aquatic ecosystems, bioaccumulative contaminants can increase detrital contaminant concentrations either through adsorption or uptake by biofilms. However, alternative aquatic prey may also be exposed in these environments and accumulate contaminants, making aquatic food web exposure possible through either aquatic or terrestrial prey sources (Fig. 3c).

4 Data Gaps

Mapping these control and mechanistic pathways reveals crucial management foci as well as data gaps in predicting the effects of aquatic contaminants on aquatic-terrestrial linkages. For example, further linking of information on transport of aquatic mercury by adult aquatic insects with information on the distribution and bioavailability of methylmercury in freshwaters would allow derivation of spatial predictions of biologically mediated mercury flux to terrestrial consumers across the landscape. Shape and hydrology of aquatic ecosystems would also influence these predictions. For lotic systems, researchers and managers might need to focus on downstream effects of mercury contamination (Otter et al. this volume), especially since streams and rivers tend to become wider downstream and may export more adult aquatic insects compared to lower-order streams (Gratton and Vander Zanden 2009). For lentic systems, surface area as well as the depth profile could affect flux of aquatic insects, and therefore mercury to land (Gratton and Vander

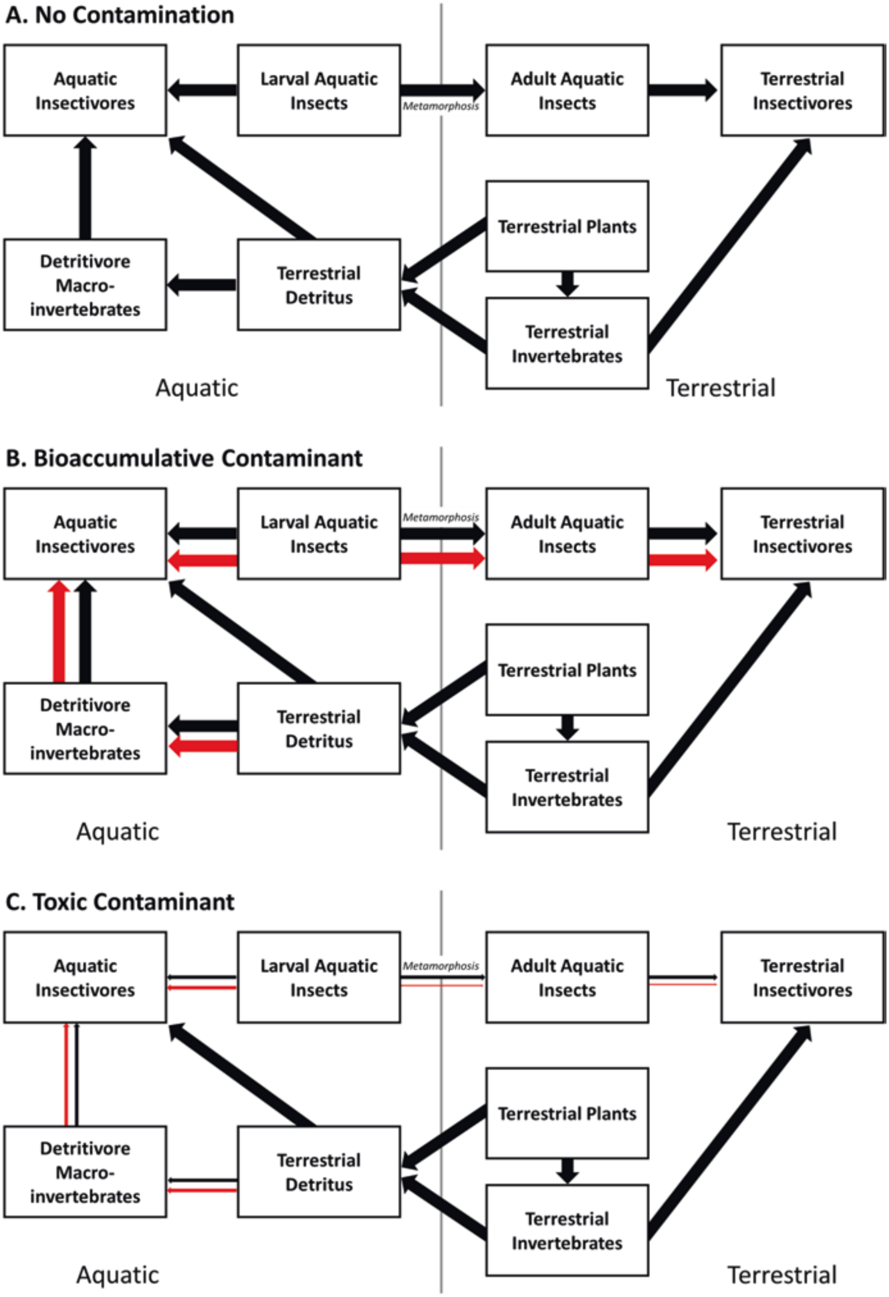


Fig. 3 Simplified food web model of freshwater-terrestrial linkages in reference conditions (**a**) and affected by bioaccumulative (**b**) and toxic contaminants (**c**). Arrows represent directional flux of energy (black) and contaminants (red). Bioaccumulative contaminants are more likely to lead to consumer exposure, while toxic contaminants reduce availability of aquatic resources and may cause consumers to shift diets toward terrestrial prey or suffer population declines. Variation in weights of arrows represents general differences in relative magnitude of fluxes. (See Table 2 for more details)

Table 2 Variables included in simplified food web model predicting effects of bioaccumulative and toxic contaminants on freshwater-terrestrial linkages

Variable	Predicted effects
Aquatic ecosystem	
Larval aquatic insects	Aquatic contaminants reduce densities of larval aquatic insects and accumulate in their tissues.[1,2] Bioaccumulated contaminants can be transferred from larvae to insectivore consumers[3].
Aquatic insectivores	Consumers of aquatic insect larvae can suffer from lack of food when prey densities are reduced by toxic contaminants. Some generalist insectivores consume more terrestrial invertebrate subsidies as aquatic prey availability decreases or bioaccumulation increases because of contamination.[4,5] Insectivores can also see lower reproductive success when exposed to bioaccumulative contaminants in prey tissues.[6]
Detritivore macroinvertebrates	Detritivorous invertebrates in freshwater ecosystems are often subsidized by terrestrial plant and animal detritus.[7] The availability of these resources to consumers can be reduced or altered by toxic and bioaccumulative contaminants.[8] Bioaccumulative contaminants can enter the detrital food web as detritivores consume contaminated bacterial biofilms associated with the detritus.[8]
Terrestrial detritus	Terrestrial detritus is composed of terrestrial animal and plant inputs, such as invertebrates, terrestrial leaf litter, and other sources of terrestrial plant-based carbon falling or washing into freshwaters.[7,9]
Terrestrial ecosystem	
Adult aquatic insects	Aquatic contaminants can reduce density and biomass and alter timing of emergence of adult aquatic insects.[10–12] Because larval insects lose 20–80% of their body mass during metamorphosis, bioaccumulative contaminants that persist in their bodies across metamorphosis become more concentrated (i.e., bioamplification).[13]
Terrestrial insectivores	Terrestrial insectivores can consumer terrestrial invertebrates and/or be subsidized by adult aquatic insects emerging from freshwater ecosystems.[9] Reductions in biomass of prey caused by aquatic contaminants can cause shifts in diet or population decline.[10,14,15] Aquatic insects can be a vector of aquatic contaminant exposure to terrestrial consumers.[13,16]
Terrestrial invertebrates	Terrestrial invertebrates are an important prey source for insectivores.[9]
Terrestrial plants	Riparian and terrestrial plant matter are the basis of production for many terrestrial and aquatic food webs.[7,17] Herbivorous invertebrates can consume multiple parts of living plants, while detritivores eat dead plant matter.

Supporting citations are listed below
[1]Hare (1992), [2]Clements et al. (2000), [3]Walters et al. (2011), [4]Kraus et al. (2016), [5]Ward et al. (2012), [6]Custer et al. (2003), [7]Minshall (1967), [8]Evans-White et al. (this volume), [8]Nakano and Murakami (2001), [10]Kraus et al. (2014a), [11]Rogers et al. (2016), [12]Cavarallo et al. (2018), [13]Kraus et al. (2014b), [14]Graf et al. (2019), [15]Graf et al. (2020), [16]Walters et al. (2008), [17]Hairston et al. (1960)

Zanden 2009; Chumchal and Drenner 2015). Most information regarding the effects of trace metals on aquatic-terrestrial linkages comes from field and mesocosm studies of high elevation montane stream communities with adult aquatic insects and spiders as the focal subsidy/consumer (Kraus et al. 2016; Kotalik and Clements

2019; Kotalik et al. 2019). To understand how these patterns play out in different ecosystems, other ecological drivers such as subsidy production, community composition, and subsidy/consumer traits need to be considered. For example, environmental gradients such as disturbance (e.g., drought and flooding frequency) or longitudinal variation (e.g., low to high stream order) within a watershed can change the relative magnitude of resource subsidies and contaminant flux, as well as their impacts on consumers (Greenwood and McIntosh 2008; Wipfli and Baxter 2010; Schultz et al. 2015; Burdon this volume; Chumchal and Drenner this volume). Finally, while the effects of nutrient enrichment on aquatic ecosystems have generally been well studied, the effects of nutrients on cross-ecosystem linkages are less well known. For example, harmful algal blooms can create anoxic conditions that might lead to reduced emergence as well as increased export of algal toxins in adult aquatic insects (Moy et al. 2016).

The effects of other contaminants such as current-use pesticides, pharmaceuticals, and biotoxins (as well as contaminant mixtures) on aquatic-terrestrial linkages are poorly understood, and there are many gaps in the mapping of their pathways of effects. For example, in the case of current-use pesticides, Morrissey and colleagues have published field and laboratory studies on effects of neonicotinoids on emerging aquatic insects and insectivorous birds in the heavily agricultural Prairie Pothole region of Canada (Morrissey et al. 2015; Cavallaro et al. 2018; Stanton et al. 2018). However, no data have yet been published for other current-use pesticides or on current-use pesticide accumulation and transfer across metamorphosis for these insects. For pharmaceuticals and personal care products (POPs), as well as algal toxins, insect-mediated transfer of these compounds to aquatic and riparian birds and riparian spiders has only recently been documented (Moy et al. 2016; Richmond et al. 2018). However, effects of these transfers on insect consumers or on patterns of adult aquatic insect emergence are not well understood. Finally, Kraus and colleagues synthesized the current knowledge on transfer of contaminants across metamorphosis (Kraus et al. 2014b), but there are many contaminants that were either missing from this synthesis or were incompletely studied. Even metamorphic transfer of mercury, which is a particularly well-studied contaminant, was only measured in a few studies. In fact, transfer of methylmercury, which is the most common organic form of mercury found in animals, was only reported in one study.

In addition to contaminant-specific data gaps, we also lack knowledge about certain aspects of how aquatic contaminants alter aquatic-terrestrial linkages more broadly. In particular, the specific roles of multiple chemical contaminants in driving patterns observed in the environment require further study. For example, agricultural systems and wastewater effluent may contain multiple pesticides, nutrients, trace metals, and other contaminants. We expect that these contaminants will have interactive effects on aquatic-terrestrial linkages. Study of the role of aquatic insects in transferring these contaminants and contaminant mixtures across metamorphosis is in its infancy, as are the effects on detrital processing. But given their near-ubiquitous distribution and their known effects on aquatic ecosystems, greater understanding of their effect pathways on aquatic-terrestrial linkages will be crucial for researchers formulating questions and for resource practitioners managing risks in the environment. Mapping of multiple pathways of exposure and toxicity using our synthetic models could help with generating predictions under these complex scenarios. Other gaps in our knowledge include information on how disrupted aquatic-terrestrial linkages affect a broad suite of consumers. Specifically, what are the effects of shifting diets, contaminated prey, loss of prey, and change in prey taxonomic composition, and are there any generalizations to be made across ecosystems (as in Wipfli and Baxter 2010)? Finally, we lack knowledge about how regional/continental variation in the distribution of contaminants on the landscape impacts aquatic-terrestrial linkages and recipient consumers. Unanswered questions include: what are the effects of different contaminants across the landscape? How do regional patterns in contaminant distribution and bioavailability impact cross-ecosystem linkages? How do the effects of contaminants interact with other global stressors? Ultimately, including aquatic-terrestrial linkages and resource subsidy metrics (such as detrital endpoints and adult aquatic insect emergence) in regulatory and management decisions will be necessary to estimate "safe" contaminant concentrations for linked aquatic and riparian life.

5 Applications and Next Steps

One of the central themes that emerges from our conceptual control model is that understanding contaminant effects across ecosystem boundaries requires expertise from a wide range of scientific disciplines including geology, analytical chemistry, biogeochemistry, hydrology, ecology, physiology, statistical modeling, and landscape ecology, among others. As those of us who have tried to assemble these teams can attest, the most challenging aspect of building interdisciplinary teams is in finding experts who can communicate across disciplinary boundaries (Fiore 2008). We hope that our conceptual control model (Fig. 1) will improve communication by explicitly demonstrating how knowledge, for example, of lithography can help to predict the risk of metal contamination in riparian birds.

We could also view the conceptual model (Fig. 1) as a guide to risk assessment in the face of incomplete knowledge. For example, Dixon (2012, p. 191) used models like ours to derive a risk assessment of agriculturally applied chlorpyrifos, an organophosphate insecticide, to four species of birds without collecting new empirical data. The assessment used conceptual and mechanistic models to build a roadmap of how chlorpyrifos could move from seed coatings in corn fields to tissue concentrations in birds with different foraging traits. Dixon then quantified the risk to birds by assigning literature-derived values to each step along the roadmap, including studies that measured diet composition, consumption rate and foraging time of birds, dissipation rates of chlorpyrifos from plant surfaces, population size of seeds, and concentration-dependent mortality rates of birds to contaminants.

Similarly, we envision scientists using our conceptual and mechanistic models (Figs. 1, 2, and 3) as a roadmap to model cross-ecosystem contaminant flux. By assigning numerical information and associated uncertainty to factors in Figs. 1, 2, and 3, perhaps with a Monte Carlo analysis, teams could prioritize data collection to areas of high uncertainty, thereby maximizing impact and limiting cost. For example, if a monitoring survey revealed that a wetland contained 7 μg/l of total dissolved Se, we would be concerned, because that value is >4 times higher than the US EPA aquatic life criterion. Yet, there is considerable mechanistic uncertainty in the concentrations of Se that will move through food webs or across ecosystems to affect birds receiving subsidies from wetlands. A first step in resolving this uncertainty might be to derive literature estimates of the variation in the fraction of total dissolved Se that becomes bioavailable, Se retention through food webs, and the consumption rates of local birds on adult aquatic insects. In doing so, we might discover large uncertainties in the fraction of bioavailable Se, but lower uncertainties in the fraction retained through metamorphosis (presumably most of it is retained, Kraus et al. 2014b). This would allow researchers to focus sampling on factors that affect bioavailability, such as the fraction of Se that is organic versus inorganic (Wang and Lovell 1997).

Aquatic contaminants affect aquatic-terrestrial linkages in cryptic and nonintuitive ways. Understanding how these contaminants affect aquatic-terrestrial linkages will require the continued use of standard ecotoxicological methods, such as laboratory-based concentration-response testing, community mesocosm exposures, and field surveys. Yet, these approaches are unlikely to keep pace with the volume of new contaminants. As a solution, systematic approaches that combine fundamental principles from multiple disciplines into contextual and predictive models will be essential. Our hope is that the conceptual frameworks we present here, as well as this book, will help researchers and practitioners formulate questions and conduct studies that increase understanding of our complex and increasingly battered natural world (Paine 1996) and aid in efficient and effective management decisions protective of linked aquatic-terrestrial ecosystems.

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