

REVIEW

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Reviewing the role of plant litter inputs to forested wetland ecosystems: leafing through the literature

AARON B. STOLER ^{1,2} AND RICK A. RELYEA

¹*Department of Biological Sciences, Darrin Fresh Water Institute, Rensselaer Polytechnic Institute, Troy, New York 12180 USA*

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Abstract. The input of senescent terrestrial leaf litter into soil and aquatic ecosystems is one of the most massive cyclic subsidies on Earth, particularly within forested ecosystems. For freshwater systems embedded within forests, litter inputs provide a vital source of energy and nutrients that allows greater production than in situ resources can provide. In return, freshwater food webs can provide an enormous amount of material to the terrestrial landscape through biotic respiration, photosynthesis, and organism emergence. Most research concerning this important aquatic-terrestrial link has focused on lotic ecosystems (i.e., streams and rivers); far less attention has been given to its role in lentic systems (i.e., wetlands and lakes). A focus on small forested wetlands is particularly important, as these systems account for a disproportionate amount of global carbon flux relative to their spatial coverage, and the decomposition of leaf litter is a major contributor. Here, we review six themes: (1) the evidence for the role of leaf litter inputs as an ecologically important subsidy in forested wetlands; (2) the bottom-up effects of quantitative and qualitative variation in litter inputs; (3) how diversity in litter mixtures can alter ecological functioning; (4) evidence for top-down consequences of litter inputs through toxic effects on predators and parasites, and the alteration of predator-prey interactions; (5) the relevance of our review to other research fields by considering the role of litter inputs relative to other types of subsidies and environmental gradients (e.g., temperature, canopy cover, and hydrology); and (6) the interaction of litter subsidies with anthropogenic disturbances. We conclude by highlighting several high-priority research questions and providing suggestions for future research on the role of litter subsidies in freshwater ecosystems.

Key words: *detritivory; detritus; ecosystem functioning; forest; functional traits; microbial growth; pond; reciprocal exchange; riparian; tadpole.*

INTRODUCTION

Ecosystem attributes are often dependent on external resource inputs to sustain trophic links through time and space (Gratton and Vander Zanden 2009). This is particularly notable for freshwater systems, where reciprocal exchanges of carbon and nutrients across ecosystem boundaries are major drivers of both aquatic and terrestrial productivity (Richardson and Sato 2015). For example, terrestrial inputs such as soil runoff and plant

litter often dominate the basal resources for many small stream communities (Wallace et al. 1997). In return, the movement of organisms (e.g., insect emergence) out of stream systems often occurs in such great biomass that it can substantially fertilize riparian soil (Hoekman et al. 2011). Similarly, terrestrial carbon is a major constituent of consumer tissue composition in larger systems such as rivers and lakes (Carpenter et al. 2005). Indeed, so much evidence has now emerged regarding the aquatic environment as an open system that ecologists may now leave the concept of an isolated system as a relic of ecological literature (Graça and Poquet 2014).

Despite the relatively low nutritional quality of plant litter when compared to other organic and inorganic subsidies (e.g., egesta, carcasses, nutrient runoff; Webster and Benfield 1986), the high quantity of litter inputs in many systems can create an extremely valuable resource.

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¹Present address: School of Natural Sciences and Mathematics, Stockton University, 223 Arts & Sciences, 101 Vera King Farris Drive, Galloway, New Jersey 08205 USA.

²E-mail: aaron.stoler@stockton.edu

Several trophic levels are often responsible for the extraction and remineralization of energy and nutrients from plant litter (Moore et al. 2004). Microbial communities perform most mineralization. In turn, litter and microbial biomass serve as resources for detritivores that further the breakdown and conversion of litter to inorganic matter. These mineralized nutrients provide an essential resource for primary production. As nutrients are recycled into inorganic and organic forms, gaseous byproducts are released such as methane, carbon dioxide, nitrogen gas, and nitrous oxides. The bulk product of these collective processes can be so immense that detrital food webs are increasingly implicated as serving a major part in the global nutrient and carbon budget (Cole et al. 2007, Capps et al. 2014, Holgerson and Raymond 2016).

The relative importance of litter resources to aquatic food webs can be predicted based on a few important gradients. On a global scale, the production of plant litter is positively correlated with rates of actual evapotranspiration, which tend to be highest in tropical, subtropical, and temperate regions (Meentemeyer et al. 1982, Matthews 1997). In addition, the relative contribution of leaf litter to the total pool of aquatic resources necessarily increases with the amount of surrounding terrestrial vegetation and as the surface area-to-perimeter ratio of the water body decreases (Polis et al. 1997). Consequently, litter is a particularly important subsidy among freshwater systems embedded within tropical, sub-tropical, and temperate forests. Although these systems include both lotic and lentic habitats, most attention toward the importance of litter inputs in freshwater environments has focused on forested lotic systems (i.e., streams and rivers), yet there is increasing interest in the role that they play in lentic systems (i.e., lakes, ponds, and wetlands; Fig. 1). Although the reason for this trend is uncertain, we argue that it likely relates to the growing appreciation for the abundance of small, forested wetlands, as well as other permanent or temporary pool communities (e.g., tree holes, tank bromeliads). Unlike their lake counterparts, these smaller lentic systems have a low surface-area-to-perimeter ratio and are much more likely to rely on terrestrial subsidies of plant material. However, such systems have been historically hidden in aerial imagery due to canopy cover or periods of drying (Downing 2010). Extensive field surveys and recent improvements in GIS technology indicate that small pools, ponds, and wetlands occupy a far greater total spatial area than previous estimated (Downing 2010). Indeed, researchers estimate that small, inland lentic ecosystems (i.e., systems $<0.001 \text{ km}^2$) make up only 8.6% of the global inland lentic freshwater area yet account for 15.1% and 40.6% of all carbon dioxide and methane gas emissions from inland lentic freshwaters, respectively (Holgerson and Raymond 2016). A large portion of this carbon cycling is likely a result of reciprocal subsidies across the aquatic-terrestrial interface. Given that leaf litter comprises a major input for

many of these small systems, understanding the ecological effects of litter inputs to wetlands is crucial to elucidating global carbon cycles (Holgerson 2015).

There are numerous similarities between lotic and lentic systems regarding the role of leaf litter inputs. Like streams, forested lentic ecosystems generally occur at the lowest point in the local or regional landscape and are gravitational attractants for terrestrial inputs (Likens and Bormann 1974). Also, like streams, the reliance of aquatic food webs on leaf litter as a source of energy and nutrients is likely to increase as the surface-area-to-perimeter ratio of the water body decreases (Polis et al. 1997). Small streams and wetlands are also both subject to seasonal periods of water drawdown that can lead to cyclic wet and dry periods. The presence of dry periods encourages colonization of organisms capable of aestivating or emerging back to the terrestrial environment, thereby establishing strong aquatic-terrestrial linkages (Williams 2005). However, unlike lotic systems, lentic environments can retain allochthonous subsidies for long periods of time, enabling litter to have a more sustained effect on environmental attributes and provide a less transient source of energy and nutrients (Brinson et al. 1981). This key difference suggests that leaf litter is a major driver of ecological dynamics in forested wetlands, and that these inputs can generate ecological conditions unique from many lotic ecosystems.

To help advance our understanding of the global importance of inland aquatic systems and aquatic-terrestrial linkages, the purpose of this review is to gather evidence for the role of leaf litter inputs as a driver of production, community structure, and evolution in wetlands. Our discussion focuses on forested wetlands because that is the focus of most literature on allochthonous inputs to lentic systems. However, we also present data from other lentic pool communities (e.g., tree holes, tank bromeliads) and we also encompass literature that

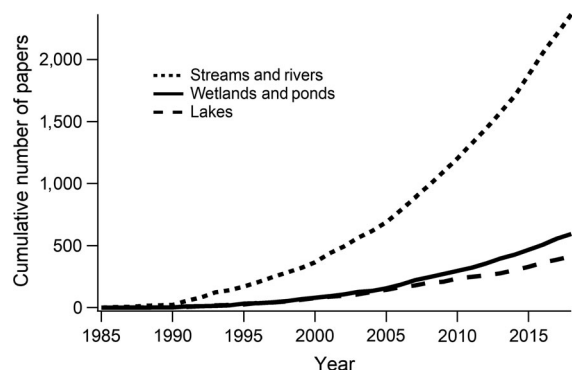


FIG. 1. Cumulative number of peer-reviewed papers discussing the role of leaf litter inputs to streams or rivers (dotted line), lakes (dashed line), and wetlands or ponds (solid line) between 1985 and 2016. Numbers in parentheses refer to the total number of papers published in each type of system. Our search on Web of Science included the terms “leaf litter” OR “plant litter” AND [system type].

suggests a role for litter inputs in freshwater systems where litter might not be the dominant resource (e.g., large lakes). We address six main themes (Table 1). First, we review the evidence for the role of leaf litter inputs as a reciprocal subsidy in forested wetlands, including its role in driving ecological interactions, energy flow, nutrient cycling, and reciprocal exchanges with terrestrial ecosystems. Second, we explore how qualitative and quantitative variation in litter subsidies underlies ecological processes and attempt to generalize the countless specific effects of individual litter species through a trait-based approach (McGill et al. 2006). This discussion provides a framework for our third theme, which discusses the complex effects of litter species mixtures on wetland ecosystems. Next, we move away from the concept of subsidies as a resource and explore top-down effects of litter through changes in predator–prey relationships, parasite abundance, and through changes in physical and chemical attributes of forested wetlands. In our fifth theme, we address the importance of litter inputs in forested wetlands relative to the myriad other subsidies available to these systems, as well as biotic and abiotic factors that are known to drive community dynamics. In our last theme, we provide impetus for the use of this research in management and conservation by examining the interaction between litter inputs and human activities. Finally, we provide direction for the future of litter-subsidy research in forested wetlands by examining outstanding questions and major trends in other areas of research.

THEME 1: EVIDENCE FOR THE ROLE OF LITTER AS A RECIPROCAL SUBSIDY IN FORESTED WETLANDS

Investigations in natural wetlands

The processing of litter inputs is primarily driven by the reciprocal exchange of energy and nutrients between litter, microbes, and detritivores (Fig. 2). Although the importance of this concept has been appreciated since Lindeman's seminal paper (Lindeman 1942), nearly all empirical measures focused on the role of leaf litter have occurred in stream environments. Hodkinson (1975*a, b, c*) provided the first studies on litter inputs to wetlands and indicated that insect communities are largely responsible for the processing of all litter inputs entering beaver ponds. Similarly, detailed energy budgets for wetlands indicate that the exchange of energy between leaf litter and macroinvertebrate grazers accounts for a substantial amount of nutrient and energy flow in woodland ponds (Oertli 1993). Bärlocher et al. (1978) elaborated by demonstrating that microbial growth on litter primes the substrate for digestion by larger consumers and subsequently increases the palatability of litter. Diet analyses of macroinvertebrates in temperate woodland ponds have confirmed that a large fraction of detritivore foraging activity is composed of a

combination of microbial and plant material (Spyra 2011). Moreover, several studies have indicated that most consumers in forested wetlands, including those that are considered herbivores, are generalists capable of processing litter (Skelly and Golon 2003, Schiesari 2006, Altig et al. 2007, Stoler et al. 2016*a*). Consequently, traditional green and brown food webs (i.e., algal and detrital webs) are often intertwined in systems that receive substantial amounts of litter inputs. As the surface-area-to-perimeter ratio of the wetland increases, there is less canopy cover, greater autochthony (e.g., macrophytes, algae), and less overall reliance on terrestrial litter as a resource; consequently, there might be greater differentiation between these food webs as the size of a water body increases. Future research should address this potential gradient.

Experimental exclusions of leaf litter in natural or seminatural wetlands have resulted in increased net ecosystem productivity and lower levels of respiration. This trend indicates that the input of litter leads to reductions in autotrophic production (Rubbo et al. 2006, Earl et al. 2012). However, the effects of litter in wetlands may be context specific. Indeed, comparisons among wetlands in the same ecoregion often reveal different bottom-up effects of litter inputs (Bonner et al. 1997). For example, Palik et al. (2001) measured macroinvertebrate and anuran abundance in wetlands spanning a 120-yr chronosequence of deforestation, where wetland age was positively correlated with amount of leaf litter inputs and inversely related to canopy openness. They found little evidence that wetland age (and, consequently, the amount of litter inputs) was related to community structure. Upon examining two ponds with substantial amounts of litter inputs, Batzer and Palik (2007) found that litter exclusion induced a decline in secondary production within a highly seasonal pond but caused an increase in production for a more permanent pond. They suggested that a layer of litter can retain moisture and protect aestivating macroinvertebrates during dry conditions, whereas organisms in a permanently inundated pond might experience toxic leachates. Indeed, moisture retention by litter can increase local arthropod abundance in wetlands (Levings and Windsor 1984), whereas a growing body of research indicates the potential harm of toxic leachates on freshwater consumers (see *Theme 2*). Hence, the context-specific effects of leaf litter might depend on the interactive effects of litter chemistry with abiotic gradients (e.g., hydroperiod, temperature; see *Theme 5*).

Isotopic approaches continue to provide details for the way that energy and nutrients circulate in freshwater food webs. A large fraction of the internal nutrient and energy pools for any freshwater environment is of terrestrial origin (Carpenter et al. 2005), although the trophic distance between terrestrial plant growth and top aquatic predators might be substantial. However, there can be a close connection between terrestrial vegetation and freshwater primary production; Benetti et al. (2014)

TABLE 1. Summary of major findings associated with the six themes in this review, along with key references.

Theme and major findings	Key references
<p>1: Evidence for the role of litter as a reciprocal subsidy in forested wetlands</p> <p>The majority of consumers in forest wetlands are generalists capable of consuming detritus and contributing to the decomposition process.</p> <p>Experiments and observations in natural systems provide mixed evidence for the importance of litter inputs to wetland food webs.</p> <p>Isotopic analyses indicate that consumers prefer algal resources, but leaf litter can enrich algal-based food webs.</p> <p>Experimental exclusion of litter in mesocosms reveal both positive and negative effects on consumers.</p> <p>Forested wetlands can be both recipients and donors of net nutrient fluxes, but likely have a greater export-to-production ratio than small streams and large lakes.</p> <p>Large, permanent wetlands might promote greater flux of material to land.</p> <p>Heterotrophic wetlands are major sinks for global carbon.</p>	<p>Hodkinson (1975<i>a, b, c</i>), Bärlocher et al. (1978), Skelly and Golon (2003), Schiesari (2006), Altig et al. (2007), Spyrá (2011), Stoler et al. (2016<i>a</i>)</p> <p>Levings and Windsor (1984), Bonner et al. (1997), Palik et al. (2001), Rubbo et al. (2006), Batzer and Palik (2007), Earl et al. (2012)</p> <p>Carpenter et al. (2005), Schiesari et al. (2009), Taylor and Batzer (2010), Benetti et al. (2014), Holgerson et al. (2016), Brett et al. (2017),</p> <p>DeGraeve et al. (1980), Maerz et al. (2005<i>a</i>), Brown et al. (2006), Fey and Cottingham (2012), Stephens et al. (2013), Stoler and Relyea (2016)</p> <p>Boon et al. (1997), Regester et al. (2006, 2008), Cole et al. (2007), Gratton and Vander Zanden (2009), Kraus and Vonesh (2012), Reinhardt et al. (2013), Capps et al. (2015), Fritz and Whiles (2018),</p> <p>Schriever et al. (2014)</p> <p>Cole et al. (2007)</p>
<p>2: Leaf litter quantity vs. quality</p> <p>Effects of litter quantity on forested wetland food webs is not linear.</p> <p>Increased nutritional content accelerates litter breakdown and consumer growth, but very high concentrations can have negative consequences for community stability.</p> <p>Structural compounds inhibit litter breakdown and reduce nutrient availability, but can promote algal growth; effects are not linear.</p> <p>Herbivore defense compounds induce consumer mortality; might have indirect, positive effects on algae and microbes.</p> <p>A chemical trait-based approach to understanding the effects of leaf litter on wetlands can generalize the effects of individual litter species.</p>	<p>Rubbo et al. (2008), Cohen et al. (2012<i>a, b</i>, 2015), Cottingham and Narayan (2013)</p> <p>Ostrofsky (1993, 1997), Knorr et al. (2005), Cohen et al. (2012<i>b</i>), Stephens et al. (2013, 2016), Earl et al. (2014), Fey et al. (2015), Geddes (2015), Martin et al. (2015), Stoler et al. (2016<i>b</i>), Vanni et al. (2017)</p> <p>Rubbo and Kiesecker (2004), Mehring and Maret (2011), Stoler et al. (2016<i>b</i>)</p> <p>Ostrofsky (1993), Maerz et al. (2005<i>a, b</i>, 2010), Ardón and Pringle (2008), Burdett and Watts (2009), Mehring and Maret (2011), Watkins et al. (2011), Martin and Blosssey (2013), Milanovich et al. (2016), Stoler and Relyea (2016), Dodd and Buchholz (2018)</p> <p>Cohen et al. (2012<i>b</i>), Migliorini et al. (2018), Stephens et al. (2013), Stoler and Relyea (2011), Stoler et al. (2016<i>b</i>)</p>
<p>3: Effects of leaf litter mixing</p> <p>Insufficient evidence exists to determine the effects of mixing litter species on total litter decay rates.</p> <p>Higher trophic levels exhibit weak responses to increased litter diversity.</p> <p>Forested wetland food webs exhibit a stronger response to changes in average primary and secondary chemical attributes of litter mixtures relative to changes in litter species or chemical diversity.</p> <p>Consumers exhibit nonlinear responses to changes in litter species evenness.</p>	<p>Gartner and Cardon (2004), Hättenschwiler et al. (2005), Schädler et al. (2005), Schimel and Hättenschwiler (2007), Kominoski et al. (2009), Timov (2009), Gessner et al. (2010), Geringich and Anderson (2011<i>a, b</i>), Stoler and Relyea (2016), Liu et al. (2017), Zhang et al. (2017)</p> <p>Rubbo and Kiesecker (2004), Meier and Bowman (2008), Srivastava et al. (2009), Stoler and Relyea (2011), Zhang et al. (2017)</p> <p>Sternern and Schulz (1998), Cohen et al. (2014), Stoler et al. (2016<i>b</i>)</p> <p>Maerz et al. (2010), Stephens et al. (2015)</p>

TABLE 1. Continued.

Theme and major findings	Key references
<p>4: Top-down effects of litter inputs</p> <p>Litter inputs alter the abundance of wetland parasites and predators, leading to changes in host densities.</p> <p>Predator-mediated reductions of detritivores can increase decomposition rates through microbial fertilization.</p> <p>Litter inputs increase physical refuge space and mediate both visual and chemical communication between predators and prey.</p> <p>Plastic phenotypic responses to litter inputs include changes in consumer development time, growth rate, reproductive output, sexual traits, and metamorphic appendages.</p> <p>Estrogenic and anti-androgenic compounds in litter can alter consumer sex ratios.</p>	<p>Earl et al. (2011), Davidson et al. (2012), Plenzler and Michaels (2015), Stoler et al. (2016c), Stephens et al. (2017), Dodd and Buchholz (2018)</p> <p>Ewers et al. (2012)</p> <p>Richardson (1992), King and King (1991), Brown et al. (2002), Hoverman and Relyea (2008), Hossie and Murray (2010), Stoler and Relyea (2013a), Jabiol et al. (2014), Williams et al. (2007)</p> <p>Reiskind et al. (2009), Tejedo et al. (2010), Cohen et al. (2012), Hofmann et al. (2012), Stoler and Relyea (2013b, 2016), Stephens et al. (2013), Cottrhan et al. (2014), Forsman (2015), Stoler et al. (2015)</p> <p>Hermelink et al. (2010), Lambert (2015), Lambert et al. (2017)</p>
<p>5: Role of litter relative to other subsidies, biotic factors, and abiotic factors</p> <p>Litter abundance and canopy cover provide complementary and only partially overlapping correlates of wetland community composition.</p> <p>Shorter hydroperiod induces both faster and slower litter decay rates, likely dependent on litter quality.</p> <p>Wetland size inversely correlates with the amount of litter inputs per unit area, but all size classes are likely dependent on algal resources.</p> <p>Temperature rise increases decay rate, but relationship is nonlinear and dependent on litter quality and latitude.</p> <p>Animal carcasses, carrion, excretion, egesta, and eggs can serve as valuable subsidies with greater nutrient content than litter; the decay of such subsidies can prime, or be primed by, litter microbial communities.</p>	<p>Werner and Glennemeier (1999), Batzer et al. (2004), Binckley and Reseratis (2007), McCauley et al. (2008), Williams et al. (2008), Earl et al. (2011), Hoyerman et al. (2011), Plenzler and Michaels (2015)</p> <p>Brinson et al. (1981), Warren and Spencer (1996), Battle and Golladay (2001), Inkley et al. (2008), Dell et al. (2014)</p> <p>Wellborn et al. (1996), Batzer et al. (2006), Greig et al. (2012), Holgerson et al. (2016)</p> <p>Graça and Poquet (2014), Follstad Shah et al. (2017), Liu et al. (2017)</p> <p>Regeer et al. (2006), Regeer and Whiles (2006), Nowlin et al. (2007), Pray et al. (2009), Danger et al. (2013), Capps et al. (2014), Earl and Zollner (2014)</p>
<p>6: The interaction between litter inputs and human activities</p> <p>Litter inputs are an important component of created wetlands, but measurements of litter decay might not be an appropriate assessment of created wetland functionality.</p> <p>Variation in the chemical quality of litter inputs interacts with inorganic and organic pollutants to alter decay rates and functionality of higher trophic levels.</p> <p>By altering the environmental conditions of aquatic habitats, litter inputs might also facilitate the invasion or extinction of species.</p>	<p>Fennessy et al. (2008), Gingerich and Anderson (2011a, b), Mackintosh et al. (2016), Holgerson et al. (2017)</p> <p>Benson and Long (1991), Kittle et al. (1995), Haitzer et al. (1998), Lee and Bukaveckas (2002), Rejmánková and Houdková (2006), Batty and Younger (2007), Boone and Sullivan (2012), Kennedy et al. (2012), Stoler and Relyea (2017a), DiGiacopo et al. (2018)</p> <p>Farrer and Goldberg (2009), Vaccaro et al. (2009), Larkin et al. (2012), Eppinga and Molofsky (2013), Kaproth et al. (2013)</p>

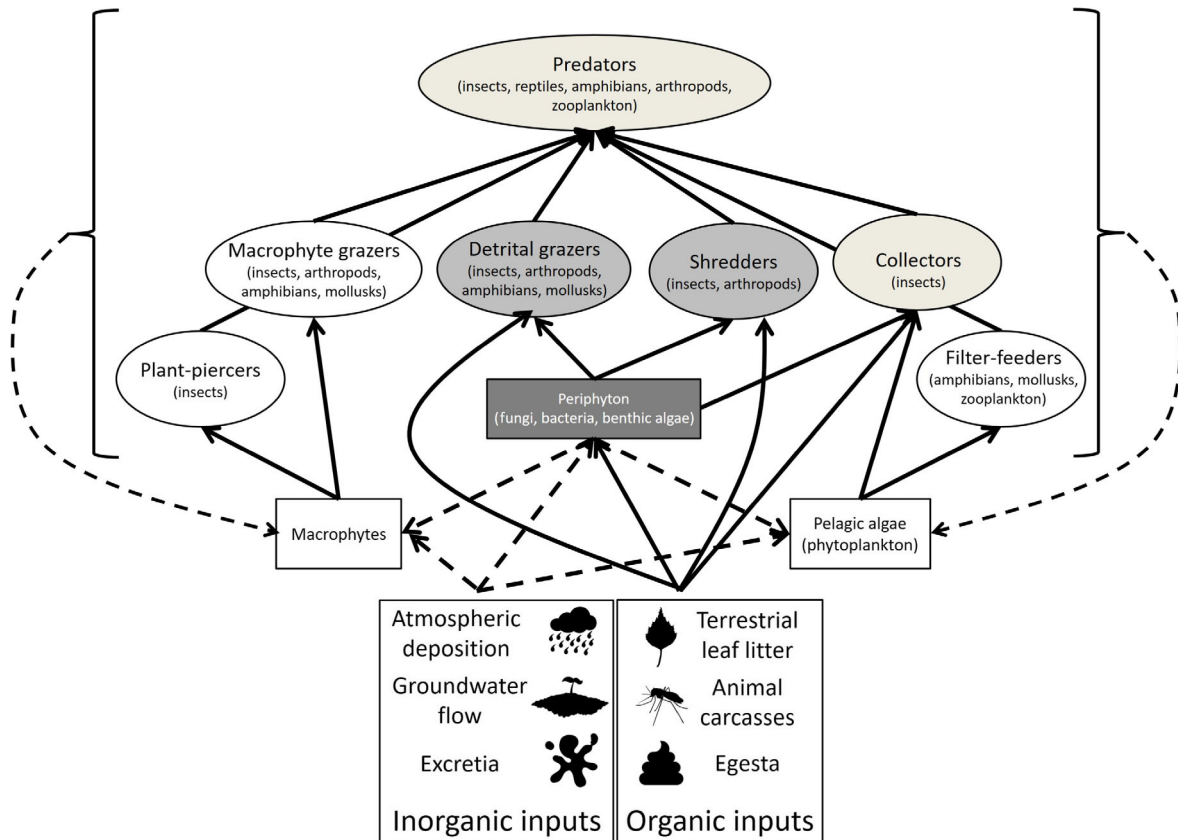


FIG. 2. Conceptualized food web for a forested wetland with inputs of leaf litter. Solid and dashed lines refer to the transfer of organic and inorganic material, respectively. The release of organic fecal material by all consumers and predators is not shown and would constitute straight lines returning to the bacteria and fungi compartment. The gaseous release of inorganic compounds from all organisms (primarily O_2 , CO_2 , CH_4 , N_2 , and N_2O) is also not shown. All primary consumer functional groups are based on Cummins and Klug 1979. The structure of the food web is based on Holgerson et al. 2016.

determined that the bulk of consumer biomass is still derived from riparian vegetation and periphyton even when a pond maintains substantial macrophyte and resources. Moreover, leaf litter predominantly fuels the growth of periphyton, which is, in turn, the dominant resource for consumers in many forested wetlands. Holgerson et al. (2016) traced the flow of ^{15}N -enriched sugar maple (*Acer saccharum*) leaf litter through a single pond in a temperate forest and found that nutrients from terrestrial leaves enriched an algal-based food web. Further, they found that most consumers relied on algae derived from litter resources instead of directly relying on litter or microbes, despite low light and net heterotrophic conditions. A similar result was found by Brett et al. (2017) in a global meta-analysis of litter-fed stream, river, and lake systems. Reliance on algal instead of litter resources is likely a consequence of the relatively high quality of algae relative to leaf litter (Brett et al. 2017). Indeed, isotopic evidence indicates that wetland consumers rely on a mixture of litter fragments, microbes, litter-derived algae, and macrophytes (Schiesari et al. 2009, Taylor and Batzer 2010).

Investigations in experimental mesocosms

Experimental litter addition and removal in artificial mesocosms have further elucidated the role of litter inputs in forested wetlands by removing confounding natural factors (e.g., canopy cover, hydrology). In such studies, the exclusion of leaf litter has generally resulted in increased water clarity, elevated pH, and a decline of phytoplankton and periphyton (Stephens et al. 2013, Stoler and Relyea 2016). The negative effect of litter exclusion is also apparent for both benthic and pelagic consumers (e.g., tadpoles, snails, zooplankton) that compete for these algal resources (Fey and Cottingham 2012, Stephens et al. 2013, Stoler and Relyea 2016). However, the inclusion of litter might also have negative effects, particularly when available litter inputs include plant species that rapidly decompose and subsequently generate hypoxic conditions that prevent the survival of many consumers (Stoler and Relyea 2016). Similarly, litter species that contain toxic leachates (e.g., phenolic acids) can have negative effects on consumer survival (DeGraeve et al. 1980, Maerz et al. 2005a, Stoler and

Relyea 2016). Such negative effects of litter inputs have led to the evolution of several wetland species that exhibit tolerance to toxic leachates and oxygen-poor conditions (Werner and Glennemeier 1999, Schiesari 2006). These organisms can achieve extremely high densities and avoid competition with less tolerant consumers. Consequently, the loss of leaf litter from a previously forested wetland is likely to reduce overall primary and secondary production, alter patterns of consumer succession over a growing season, and lead to substantial turnover of consumer species composition. However, it is important to note the artificiality of mesocosm studies. Mesocosms are often colonized by different types of algae, bacteria, and fungi than natural systems (Brown et al. 2006), which might lead to different results than in nature. In addition, controlled litter exclusion is disassociated with the increase in incident sunlight that would be expected from loss of natural leaf litter. Hence, the reductions in primary production that are observed in mesocosm studies are likely liberal estimates of changes that would occur in nature.

Reciprocal exchanges with terrestrial food webs

Until recently, the emphasis on aquatic-terrestrial linkages has largely focused on the flow of energy and nutrients from terrestrial to aquatic environments, yet increasing evidence demonstrates that energy and nutrient flows in the opposite direction are also ecologically important. From the strict perspective of carbon fluxes, the prevailing view is that small lentic bodies serve as net sinks for carbon (Cole et al. 2007). This view fits well within the concept of a wetland as a transitional ecosystem between inundated aquatic and future terrestrial environments. During this transition, the development of soil inherently involves the buildup and storage of carbon. However, a distinction must be made between wetlands that support either submerged or emergent vegetation and those that do not support such vegetation. Since plants sequester CO₂, wetlands with macrophytes (i.e., floating, emergent, or submerged plants) are more likely to be carbon sinks than sources. In contrast, wetlands without macrophytes are more likely to be a net source of atmospheric carbon (Cole et al. 2007). A further complexity arises when considering the quality of carbon inputs to a non-vegetated wetland; for example, recalcitrant litter might substantially slow processes that release gas to the atmosphere and lead to greater carbon storage. Thus, to fully elucidate carbon budgets for wetland ecosystems, it is essential to consider hydroperiod, wetland area, macrophyte presence, litter quantity, and litter quality.

There is less consensus on whether litter-subsidized systems are net sources or sinks for nutrients. Certainly, the nutritional quality of imports (i.e., leaf litter) is generally lower than the quality of exports (Capps et al. 2015). However, net flux depends on both quantity and quality of exchanges and biomass

export is generally a very small fraction of biomass import (Regester et al. 2008, Reinhardt et al. 2013). Models estimate that wetlands and small lakes likely have a greater export-to-production ratio than small streams and large lakes (Gratton and Vander Zanden 2009). This is particularly likely in litter-subsidized lentic systems where light and primary production is limited (Kraus and Vonesh 2012). Indeed, extensive surveys of anuran inputs and outputs from such systems strongly indicate a net average flux of nutrients from water to land (Capps et al. 2015, Fritz and Whiles 2018). However, the net flux for individual species might be either positive or negative depending on life history, competition, disease, and predation. For example, Regester et al. (2006) found a net influx of nutrients when only considering ambystomid salamanders. Fritz and Whiles (2018) also note that a small subset of surveyed ponds exhibit fluxes in the opposite direction. The net flux of energy and nutrients seems to be dependent on the size and permanence of the ecosystem. Small wetlands might be ecological traps for energy and nutrients if they dry before larvae can emerge (Reinhardt et al. 2013). Short hydroperiods also oxygenate the soil, prevent methanogenesis, and can drastically change the type of carbon efflux from the system (Boon et al. 1997). In contrast, larger wetlands might promote metamorphosis of amphibians and insects (Schriever et al. 2014, Capps et al. 2015). Larger and more permanent systems are also likely to harbor greater amounts of diversity, which generally promotes production and might lead to elevated organic flux to land (Schriever et al. 2014). Such studies suggest that terrestrial subsidies are either buried in wetland sediments, processed into inorganic material that can outflow through groundwater seepage, or emerge as gases. Ultimately, the net flux from any wetland is likely to rely on multiple abiotic and biotic gradients, and comprehensive surveys are needed to elucidate these trends.

THEME 2: LEAF LITTER QUANTITY VS. QUALITY

Subsidy quantity and quality are complementary attributes but are often explored separately. Whereas studies at the ecosystem level have typically focused on subsidy quantity, food web ecologists have noted that the value of any subsidy depends on its nutritional content, caloric value, and overall availability to consumers (Marecchelli et al. 2011). Because ecosystem studies generally have a broader spatial scope than food web studies, this separation between concepts of quantity and quality has led to a poor understanding of how variation in subsidy quality translates from food web dynamics to changes in ecosystem function. This has certainly been true for research concerning stream and lake ecosystems; whereas several large-scale studies have successfully manipulated the quantity of litter falling into freshwater systems (e.g., Wallace et al. 1997), studies have not

manipulated litter quality at the whole-ecosystem level. Both lakes and streams are simply too spatially extensive for such a manipulation, which necessarily requires the replacement of all subsidies with material of differing quality. Moreover, partial manipulations of litter quality within a small lake plot or single stream reach are confounded by the effects of surrounding, non-manipulated area (e.g., from upstream reaches). In contrast, small wetlands are a contained ecosystem that are more easily mimicked using experimental mesocosms. Over the past two decades, an increasing number of studies have explored how qualitative differences in litter inputs can affect lentic communities. Although most of these studies have focused on the most heavily subsidized system types (e.g., temperate forest ponds), there is also growing amounts of research for less subsidized systems (e.g., large lakes).

Effects of litter quantity

Although the addition of litter to lentic systems generally increases primary and secondary production (Rubbo et al. 2006, Earl and Semlitsch 2012), this trend is not necessarily linear with increasing amounts of litter inputs. For example, Rubbo et al. (2008) and Cohen et al. (2012a) found that litter inputs induce greater tadpole growth and development rate, but these effects only became significant beyond a threshold of litter biomass. Using a range of litter inputs similar to the study by Rubbo et al. (2008), Cottingham and Narayan (2013) found that moderate amounts of litter inputs can stimulate photosynthetic growth and subsequently increase zooplankton densities. However, higher amounts of litter inputs can become detrimental to algae and zooplankton, owing to excessive leaching of dissolved carbon, acids, and shading of the benthos. Beyond this threshold of litter inputs, resources might become more available to other, less-sensitive consumers (e.g., tadpoles). Collectively, these few studies indicate that variation in the quantity of litter, as might occur during growth and succession of a forest, can alter the species composition of wetlands.

Effects of litter quality

The response of food webs to litter quantity is also mediated by litter quality. Plant material exhibits tremendous interspecific and intraspecific chemistry, owing to different growth strategies and available resources (Cornwell et al. 2008). Fast-growing and short-lived plants invest more effort in accruing nutrients (e.g., nitrogen, phosphorus) whereas slow-growing and long-lived plants invest more in carbon-rich structural compounds (e.g., lignin, cellulose; Wright et al. 2004). Such variation in living plant tissue chemistry results in substantial interspecific variation in the nutritional value of plant litter (Ostrofsky 1993, 1997). Elevated nutrient content accelerates the breakdown of

litter and availability of the litter to consumers, particularly when lignin content is low (Melillo et al. 1982, Knorr et al. 2005). In turn, elevated nutrient concentrations are also positively correlated with the abundance of algal resources, consumer development rate, and consumer growth (Cohen et al. 2014, Stephens et al. 2013, Earl et al. 2014, Martin et al. 2015, Stoler et al. 2016b).

Increases in litter-nutrient content do not always benefit consumers. For example, an increase in the concentration of a nutrient might not alter consumer growth due to interspecific and temporal variation in consumer stoichiometric demands (Vanni et al. 2017). To demonstrate this, Stephens et al. (2016) exposed detritivorous tadpoles to artificial diets fortified with nitrogen (as protein), phosphorus, or both. They found that tadpoles experienced nitrogen limitation throughout their entire development, but substantially increased phosphorus demands during periods of rapid bone development. Elevated litter-nutrient content (i.e., above a certain threshold) can also have negative consequences on consumer growth through changes in water chemistry; higher quality litter tends to decompose faster, increase microbial biomass, reduce dissolved oxygen, leach soluble chemicals, darken the water column, and reduce algal growth. Fey et al. (2015) found that this effect was enough to reduce cladoceran zooplankton densities within three weeks. In addition, elevated nutrient content in leaf litter might produce large oscillations between consumers and prey, particularly among organisms that reproduce several times during the season, such as zooplankton, phytoplankton, bacteria, and fungi. Geddes (2015) demonstrated that elevated energy resources lead to rapid increases in both phytoplankton and zooplankton populations, and subsequent crashes of both over a relatively short time period (~40 d). From these studies, it is apparent that consumer growth is not necessarily a linear function of litter-nutrient levels.

The effects of litter-nutrient content are often confounded by the effects of carbon-rich structural compounds, such as lignin and cellulose. The compounds provide the leaf with a rigid and protective structure but can also inhibit decomposition by binding nutrients in a chemical matrix (Webster and Benfield 1986). This matrix must be cleaved by specialized enzymes found only within a subset of fungi (Graça et al. 2005). The additional time needed for these enzymes to activate lengthens the time required for litter decay. Litter species with slow decay rates (e.g., *Quercus* spp., *Plantanus* spp.) provide few resources for microbes and detritivores, although the lack of soluble leachates can also increase light availability and algal growth (Stoler et al. 2016b). In contrast, litter species with moderate decay rates (i.e., containing moderate amounts of structural compounds; e.g., *Acer* spp., *Ulmus* spp.) can promote microbial growth on the litter surface that assimilates nutrients from both the leaf matrix and the water column (Rubbo and Kiesecker 2004, Mehring and Maret 2011, Stoler et al. 2016b). Litter species with rapid decay rates, which

have relatively fewer structural compounds (e.g., *Liriodendron* spp., *Tilia* spp.), have fast decay rates and can provide a readily available resource for consumers, but they can also have a substantial number of negative effects as discussed above. For these reasons, the nutritional quality of litter is often expressed as a ratio of nutrients to lignin, as this ratio better predicts the decay rate of litter inputs (Melillo et al. 1982).

The effects of litter-nutrient composition are further confounded by variable concentrations and chemical structures of herbivore defense compounds found in plant tissue (Ostrofsky 1993). A substantial amount of research has demonstrated that these defense compounds can have dramatic, negative effects on aquatic communities when leached from litter. For example, mesocosm studies reveal that tadpoles and zooplankton experience impaired predator recognition and high mortality when provided with phenolic-rich litter inputs, even when nutrient content is high (Maerz et al. 2005a, b, 2010, Burdett and Watts 2009, Watkins et al. 2011, Milanovich et al. 2016, Dodd and Buchholz 2018). Different defense compounds have varying effects on wetland organisms. For example, saponins have a more adverse effect on larval amphibian survival and development than tannins (Martin and Blossey 2013). Moreover, the toxic effects of these defense compounds are likely due to direct toxicity rather than indirect, bottom-up pathways. Whereas phenolic acids seem to have neutral or positive effects on the productivity and biomass of microbial and algal resources (Ardón and Pringle 2008, Mehring and Maret 2011), they can rapidly bind to and disable the functioning of gill cells. Not surprisingly, the presence of litter inputs containing plant defense compounds serves as an environmental filter in wetlands that selects for more tolerant organisms (Cohen et al. 2012b, Stoler and Relyea 2016).

Trait-based approach to understand effects of litter quality

Although an increasing number of studies have questioned how interspecific variation in leaf litter inputs alters wetland communities, few have explicitly identified the effects of the individual chemical components. Such a trait-based approach is an important step toward understanding the general effects of litter, without limiting our knowledge to a subset of studied plant species. The most common approach toward this goal is to simultaneously scan the effects of multiple litter species varying widely in chemistry while also examining the trends associated with single chemical components (Stoler and Relyea 2011, Stephens et al. 2013, Stoler et al. 2016b, Migliorini et al. 2018). For example, Stephens et al. (2013) exposed wood frog tadpoles in artificial mesocosm communities to 10 different species of plant litter, including tree species and emergent wetland vegetation. Tadpole performance was positively related to the amount of nutrients in the litter and negatively

related to the amount of phenolic acids, regardless of litter species identity. Similarly, we explored the effects of litter from 10 different tree species on identical wetland mesocosm communities over a 4-month growing season (Stoler and Relyea 2016). We found that variation in concentrations of phenolic acids and soluble carbon was primarily responsible for changes in wetland community composition, regardless of litter species identity. Litter species that rapidly leached soluble carbon (e.g., red maple [*Acer rubrum*]) initially darkened the water column and decreased oxygen availability, which led to substantial consumer mortality. Later in the growing season, dilution and transformation of leached carbon elevated water clarity, increased energy availability, and benefitted those consumers that either survived the initial conditions or colonized the system later in the season. In contrast, litter species containing high concentrations of phenolic acids had a strong negative effect on consumer survival and growth rate. Field analyses of wetlands with litter of contrasting chemistry further confirms the negative effects of lignin, cellulose, and phenolic acids on consumers, but also indicates substantial positive effects of nutrient availability (Cohen et al. 2012b, Migliorini et al. 2018). Although taking a trait-based approach to understanding the effects of litter in lentic systems remains in its infancy, it promises a pathway toward generalizing the role of litter quality and ultimately providing a tangible link between concepts of subsidy quantity and quality.

THEME 3: EFFECTS OF LEAF LITTER MIXING

Over the past two decades, understanding the effects of mixing litter species in freshwater systems has emerged as a major challenge, in parallel with a rise in the broader question concerning how biodiversity correlates with ecosystem functioning (Gessner et al. 2010). Researchers have applied theory from this body of research to provide hypotheses for what might occur when litter species of varying chemistry are mixed. Such studies have primarily focused on changes in litter decay rates with different litter mixtures. Assuming no interactions among litter species in a mixture, decomposition should respond additively to changes in litter species composition, provided that the total quantity of litter remains the same (i.e., substitutive changes; Gessner et al. 2010). Empirically, this should result in the total mixture decomposition rate equaling the average decomposition rate of individual litter species in proportion to their representative biomass in the mixture.

However, positive, nonadditive (i.e., synergistic) effects on total litter decomposition might result when nutrient-poor and nutrient-rich litter species are combined. This could occur because of nutrient transfer from nutrient-rich to nutrient-poor species, either through active transfer of nutrients by fungal hyphae or passive transfer of nutrients through leaching (Tiunov 2009). Subsequently, microbes and consumers can colonize and

break down both litter types. The presence of nutrient-rich litter near nutrient-poor litter might also attract more detritivores to the latter and increase overall leaf breakdown (Schimel and Hättenschwiler 2007). In contrast, negative, nonadditive (i.e., antagonistic) effects might result from the presence of inhibitory compounds (e.g., phenolic acids) in litter mixtures that either dissuade grazers from the vicinity of litter inputs or prevent microbial growth on the litter surface (Hättenschwiler et al. 2005, Gessner et al. 2010).

Evidence from terrestrial and stream ecosystems indicates that litter mixing generally results in synergistic effects on litter decay rate, although few studies have explicitly tested mechanisms underlying this effect (Gartner and Cardon 2004, Kominoski et al. 2009). Among the few lentic studies to address this question, results have demonstrated additive, synergistic, and antagonistic outcomes (Schädler et al. 2005, Gingerich and Anderson 2011a, b, Stoler and Relyea 2016, Liu et al. 2017, Zhang et al. 2017). Currently, an insufficient number of studies exist to provide a generalized understanding of litter mixing effects on decay rates in wetlands.

When mixing litter species has synergistic effects on decay rates, it should have significant effects on higher trophic levels that utilize litter as a resource. Mixtures of leaf litter with contrasting chemical profiles are hypothesized to benefit microbes and consumers by providing a more varied and complete diet, thereby increasing total decomposer biomass and accelerating decomposition (Meier and Bowman 2008, Gessner et al. 2010). However, a meta-analysis of stream and terrestrial studies by Srivastava et al. (2009) noted that leaf litter diversity generally has weak effects on higher trophic levels. Similarly weak effects of litter diversity have been documented in wetlands. At least one study found that a mixture of two litter species increased microbial activity as measured by respiration (Zhang et al. 2017). However, Rubbo and Kiesecker (2004) found that combining phenolic-rich maple litter with recalcitrant oak litter resulted in antagonistic effects on amphibian and algal growth and synergistic effects on zooplankton densities, although the effects on algae and zooplankton reversed at the end of the growing season. Similarly, Stoler and Relyea (2011) examined mixtures of eight broadleaf litter species, four coniferous litter species, and a mixture of all 12 litter species, and found almost entirely neutral effects of litter mixing on periphyton, phytoplankton, zooplankton, and tadpoles. Such weak effects of litter diversity might occur if litter chemistry has both positive and negative effects on food webs, and if organisms exhibit a stronger response to average chemistry instead of total litter species diversity. To test this hypothesis in wetlands, Cohen et al. (2014) explored the effects of chemical diversity on the performance of two tadpole species and found that individuals only responded to the average chemical composition of litter mixtures (i.e., additively). Similarly, Stoler et al. (2016a, b, c) found that increased chemical diversity of leaf litter accelerated

litter decay rates but had no effect on any other part of the communities. In both studies, all organisms responded more strongly to average litter chemistry rather than litter diversity, suggesting that biodiversity does not support increased ecological function in litter-driven wetland ecosystems.

Changing litter diversity refers to variation in species and chemical richness, as well as variation in evenness. Stephens et al. (2015) found that tadpole performance increased in response to average nutrient content of litter mixtures, but the response became saturated at very high levels. This result is not without precedent. According to stoichiometric theory, elevated nutrient supply can only benefit consumers as the ratio of carbon to that nutrient approaches the stoichiometry of the consumer (Sterner and Schulz 1998). Assuming a fixed biomass of resources, this occurs at a positive, saturating rate with elevated nutrient content. Maerz et al. (2010) examined the effects of multiple litter species on tadpoles and found a similar effect. These results indicate that the role of litter evenness is likely important when considering the effects of litter mixture inputs and has real-world consequences. Natural shifts in the composition of riparian vegetation composition will often consist of incremental changes in species dominance, with associated changes in the dominance of litter species.

THEME 4: TOP-DOWN EFFECTS OF LITTER INPUTS

Effects on predator–prey interactions

Although the conceptual role of leaf litter inputs for primary consumers is largely one of bottom-up changes in resource quantity and quality, leaf litter inputs can also mediate top-down effects by altering the chemical attributes of the water. For example, leached chemicals can alter parasite survival and predator–prey interactions. Phenolic-rich litter leachates can acutely decrease the abundance of *Batrachochytrium dendrobatidis* (Stoler et al. 2016c), which is a chytrid fungus that infects and kills larval and adult anurans. Moreover, amphibians bathed in leachates from phenolic-rich litter experience reduced parasite loads (Davidson et al. 2012). This phenomenon might explain why Dodd and Buchholz (2018) found that ovipositing *Hyla chrysoscelis* amphibians exhibited greater attraction to dark and tannic-rich waters despite the negative effects of such conditions on individual survival in laboratory conditions. However, those same leachates might also slow host development, increase the duration of parasite exposure, and subsequently increase parasite loads (Stephens et al. 2017, Dodd and Buchholz 2018). Research indicates that the composition and chemistry of leaf litter inputs to a forested wetland might act as an environmental filter that selects for specific species and ecological interactions (Earl et al. 2011).

Litter can alter ecological interactions by modifying the physical attributes of the space that organisms

inhabit. Research in streams indicates that macroinvertebrates use leaf litter as a microhabitat for both foraging and refuge, and an increase in the physical integrity of the litter can afford consumers better shelter (Richardson 1992, Jabiol et al. 2014). Similarly, wetland consumers are well known to take shelter under leaf litter when threatened by predators (Hoverman and Relyea 2008). Increased quantities of leaf litter can provide more physical refuge for prey, consequently making visual location of prey more difficult and altering the functional response of predators from a hyperbolic to a sigmoidal curve (i.e., type II vs. type III curve; Hossie and Murray 2010). Litter leachates might also interrupt predator–prey interactions by interfering with visual and chemical sensation of prey. For example, some acid-rich litter species can lower pH by an entire unit (Stoler and Relyea 2013a). Such a change can dampen the response of small fish species to predators (Brown et al. 2002). Leaf leachates can also darken the water column, which might prevent predators or prey from visually detecting each other, although Stoler and Relyea (2013a) found no evidence to support this. Instead, we found that litter inputs have a strong effect on predator–prey interactions by promoting growth of periphyton resources that allow prey to grow faster and achieve a size refuge from predation (Stoler and Relyea 2013a). However, dark water might also serve as a visual indicator of high resource abundance, which can attract ovipositing insects that act as predators in their aquatic stage (Williams et al. 2007). In turn, some prey can mimic the color of litter in wetlands to avoid predation (King and King 1991). As the quality or quantity of litter inputs changes within a wetland system, such subtle effects are likely to alter the diversity and composition of food webs and ecosystem function.

It is also worth noting that the effects of leaf litter on higher-level trophic interactions might ultimately have a cascading effect on litter decomposition and the rate at which leaf litter can change aquatic chemistry. Studies in stream systems indicate that predator-induced reductions in detritivore abundance lead to a reduction in leaf breakdown rates (Rodríguez-Lozano et al. 2016). Wetland food webs might exhibit a different response due to the lack of flow. In contrast to streams, predation in wetlands releases nutrients that remain near the site of release and subsequently fertilize local microbial communities with the result of increased litter decomposition rate (Ewers et al. 2012). This suggests that variation in leaf litter could have substantial, indirect top-down effects on major ecosystem processes, particularly if predators and prey differentially respond to changes in litter inputs (e.g., predators experience greater survival than prey).

Phenotypic changes

Leaf litter can impose other subtle and sublethal effects on biota that might alter ecological interactions. In response to fluctuations of resource quantity and quality,

many organisms exhibit phenotypic changes that are thought to optimize fitness within different environmental contexts (Agrawal 2001). Phenotypic plasticity in life-history traits might provide a means for dampening the size fluctuations of producer and consumer populations in response to variation in resource inputs. For example, instead of leading to malnutrition and mortality, low resource availability might simply induce a slower growth rate and longer developmental time, as has been repeatedly shown for several species of amphibians (Cohen et al. 2012b, Stephens et al. 2013, Stoler and Relyea 2013b). Given that leaf litter inputs can vary substantially in nutritional quality, it is reasonable to also expect inducible life-history changes in response to variation in litter quality. Responses might be both species and environment specific; organisms that must develop within a fixed time are more likely to opt for faster developmental rates at the cost of lower growth rates (Newman 1992). Such a response is likely to occur in temporary wetlands, where a shorter hydroperiod necessitates fast development. Alternatively, organisms that are faced with size-dependent predatory threats might opt to increase growth rates at the expense of slower development in order to reach a size refuge (Newman 1992).

Aquatic consumers are also known to exhibit morphological plasticity in response to declining food resources (Tejedo et al. 2010). Many of these responses appear to be adaptations that allow increased resource consumption and assimilation (e.g., greater numbers of teeth, longer intestines; Relyea and Auld 2004, 2005). Similar adaptive responses have been found among consumers exposed to reduced leaf litter quality, such as the development of longer intestines among tadpoles exposed to leaf litter with low nitrogen content (Stoler and Relyea 2013b). However, the adaptive nature of other responses is not entirely clear. For example, tadpoles exposed to leaf litter of lower quality also developed into terrestrial amphibians with more massive intestines relative to body mass and longer limbs relative to body length (Stoler et al. 2015). It is unknown whether such post-metamorphic changes offer any improvement in fitness. Maximum jump distance is logarithmically correlated with hind limb length, such that greater than a 10% difference in newly metamorph limb length is needed to achieve any difference in hopping ability (Emerson 1978). Given that observed phenotypic variation is typically less than 10%, it is unclear whether litter-induced phenotypic plasticity would have any adaptive effect. Alternatively, observed phenotypic plasticity might be a non-adaptive byproduct of other developmental processes, such as runaway hormonal regulation during extended larval periods (Emerson 1986).

Other plastic responses more clearly benefit fitness. For example, lower litter-lignin-to-phosphorus ratios in litter-induced greater investment into male amphipod (*Hyallela* sp.) sexual traits (Cothran et al. 2014). Exposure to litter leachates with high carbohydrate content also increased body size and reproductive output of a zooplankton species, *Moina macrocopa* (Hofmann et al.

2012). Studies have also found that increases in leaf litter quality can increase body size at metamorphosis for both mosquitoes and larval amphibians, which is important because greater body size generally leads to elevated reproductive success and reduced predation risk (Reiskind et al. 2009, Stoler and Relyea 2016). It is worth noting that such phenotypic changes within generations might lead to the canonization of phenotypes in future generations or speciation (Forsman 2015), yet research relating litter inputs to evolution is entirely lacking.

Evidence for effects of litter on internal physiology is also emerging. Some species of litter contain estrogenic phytochemicals that can induce changes in vertebrate sexual development (Hermelink et al. 2010, Lambert 2015). In particular, leachates of some oak species include estrogenic and anti-androgenic compounds (Hermelink et al. 2010). Lambert et al. (2017) demonstrated that leachate of black oak (*Quercus velutina*) increased the number of females within a population of wood frogs by 10% relative to wood frogs reared with the leachate of red maple litter. Since survival of frogs was similar within the two leachate treatments, this result appears to be due litter-induced sex changes. To our knowledge, this effect of litter leachate has only been demonstrated for a single vertebrate species; thus, further research is warranted to determine whether this is a common effect.

THEME 5: ROLE OF LITTER RELATIVE TO OTHER SUBSIDES, BIOTIC FACTORS, AND ABIOTIC FACTORS

Effect of litter inputs relative to canopy cover, hydroperiod, wetland size, and temperature

Establishing litter inputs as an ecologically important driver of forested wetland processes requires comparing their effects to the relative to the myriad other abiotic and biotic factors that characterize freshwater ecosystems. For example, canopy cover determines a suite of environmental attributes such as light availability, rates of erosion, habitat for emergent organisms, and attractiveness of the wetland for ovipositing consumers (Binckley and Resetarits 2007, Werner et al. 2007a, b, McCauley et al. 2008, Mokany et al. 2008, Hoverman et al. 2011). Studies focused on the relative roles of litter and canopy cover have found contrasting results. A survey of 15 temperate wetlands demonstrated that canopy cover explains far more variation in macroinvertebrate species richness and composition than depth or amount of leaf litter (Plenzler and Michaels 2015), whereas a larger survey of 66 temperate wetlands found mass of litter inputs and canopy cover were both negatively correlated with macroinvertebrate taxon richness (Batzer et al. 2004). Although canopy cover is positively correlated to mass of litter inputs (i.e., more shaded wetlands receive greater inputs of leaf litter), high amounts of canopy cover do not necessarily translate to qualitatively nutritional litter inputs or optimal growth conditions for all species. As evidence of this, several species of tadpoles

exhibit reduced growth and survivorship in closed-canopy wetlands, yet their growth typically increases when their diets are supplemented with high-quality food (Werner and Glennemeier 1999, Williams et al. 2008, Earl et al. 2011). However, other species of tadpoles are well-known for tolerating the conditions generated by canopy cover and litter inputs (e.g., low oxygen, reduced light) and exhibit equal survivorship in both closed- and open-canopy systems (Werner and Glennemeier 1999, Williams et al. 2008). Boes and Benard (2013) even demonstrated that wood frog metamorphs emerging from close-canopied systems are physically larger and exhibit greater locomotory performance than individuals emerging from open-canopy systems. Hence, litter abundance and canopy cover provide complementary, but only partially overlapping, correlates of wetland community composition.

The relationship between litter inputs and wetland hydroperiod is less clear. Cyclic wet and dry periods might aerate the microbial community and subsequently promote microbial activity on the litter surface (Battle and Golladay 2001). Greater microbial activity should provide increased resources for higher trophic levels and might explain why Warren and Spencer (1996) found that periodically dried pond mesocosms had a greater biomass of consumers relative to permanent pond mesocosms. However, there is no consensus on whether wetland permanence increases or decreases leaf decay rate, and studies show a range of effects (Brinson et al. 1981, Inkley et al. 2008). One possible explanation for this is that the detrital communities colonizing periodically dry litter inputs are unique in composition and function relative to communities colonizing permanently dry or wet litter (Dell et al. 2014). In addition, decay rate of periodically inundated litter is likely dependent on its chemical quality. For example, periodic drying might accelerate the decay of labile litter that maintains copious amounts of microbial activity whereas drying might have no effect on the decay of recalcitrant litter. Experimental comparisons of litter decay among species of contrasting quality along a hydrological gradient will certainly provide some novel insight into this area of study.

The size and shape of a wetland are strongly related to both canopy cover and hydroperiod. Small, canopy-covered wetlands typically receive tremendous amounts of terrestrial plant inputs per unit area and have little observable primary productivity due to light limitation (Wellborn et al. 1996). Nevertheless, many small wetlands can maintain algal communities that persist under low-light conditions (Holgerson et al. 2016), and it has been suggested that these algal communities are extremely important to wetland communities due to their high nutrient concentrations relative to litter inputs (Batzer et al. 2006). Moreover, canopy-covered wetlands among northern latitudes are often exposed to sunlight during the earlier parts of the growing season due to a delay in leaf-out and can subsequently support low levels of algal growth for early-breeding organisms. In

contrast, large, forested wetlands, excluding swamps, which are wetlands with trees in the inundated zone, necessarily have less canopy cover relative to their total surface area, receive higher amounts of sunlight, and contain substantial amounts of submerged and emergent plant production (Wellborn et al. 1996, Werner and Glennemeier 1999, Hoverman et al. 2011). Food webs in such large wetlands are less reliant on aquatic-terrestrial linkages and largely driven by autochthonous energy flows (Polis et al. 1997). Moreover, large and permanent wetlands often harbor large-bodied predators (e.g., fish) that tend to decouple aquatic-terrestrial linkages by consuming insects responsible for grazing and breaking down litter inputs (Greig et al. 2012).

Temperature is also a strong driver of ecosystem processes, and its positive effect on litter decomposition has been well documented in streams and riparian areas (Follstad Shah et al. 2017). Among the few studies that have explored the effects of temperature in wetlands, warming also has a positive effect on decay rates (Liu et al. 2017). However, the effects of temperature might not be linear, for at least three reasons. First, the breakdown of recalcitrant litter generally has higher activation energy due to the metabolic costs of degrading lignin and cellulose (Follstad Shah et al. 2017). Consequently, it is likely that substantially greater amounts of thermal energy are needed to accelerate the decay rate of recalcitrant litter, whereas small increases in temperature will immediately elicit the same response for labile litter (Fig. 3). Second, the role of macroinvertebrates in lower latitude streams appears to be greatly diminished relative to higher latitude streams, likely because shredding insects are evolutionarily adapted to cool waters and because of lower palatability of leaf litter in the tropics (Boyero et al. 2011). Third, elevated temperature can also have the effect of altering intraspecific litter chemistry by increasing the carbon-to-nutrient content of foliage, resulting in poorer quality litter and slower decomposition (Graça and Poquet 2014). Hence, although short-term warming generally increases the rate of energy and nutrient release from litter, the long-term net effect of temperature remains unclear. While we begin to understand these complex effects of temperature streams and terrestrial environments, parallel work must be conducted in wetlands to fully integrate these systems into a global carbon and nutrient cycle.

Comparison of litter with other subsidies

Because of the overwhelming biomass, inputs of leaf litter have generally been regarded as underlying the food webs of small, freshwater systems. However, litter offers relatively little in nutritional value when compared to other potential sources of nutrients and energy entering wetlands. For example, periodic cicadas in eastern North America provide a massive pulse of insect biomass to both streams and wetlands, which is an order of magnitude more nutrient rich and labile than leaf litter inputs

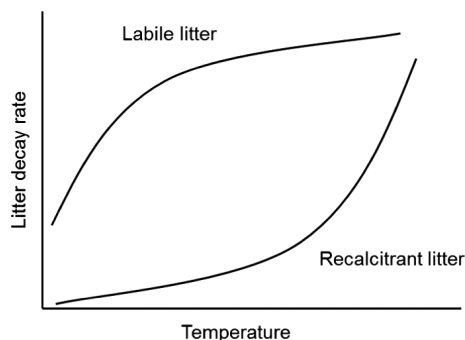


FIG. 3. Conceptual graph showing predicted change in decay rate of labile (top curve) and recalcitrant litter (bottom curve). Recalcitrant litter contains many complex compounds that are broken down by specialized enzymes with high activation energies, and is unlikely to experience any noticeable change in decay rate until a temperature threshold is achieved. In contrast, labile litter is relatively easy to break down without specialized enzymes or additional inputs of energy.

(Nowlin et al. 2007). Although cicada deposition only occurs in a discrete and relatively rare pulse, wetlands typically receive some level of terrestrial insect deposition throughout the growing season (Pray et al. 2009). Consequently, insect deposition is likely to provide immediate benefits to wetland food webs, whereas leaf litter persists for a much longer period of time, can serve as a physical substrate for wetland-dwelling organisms, and is likely to influence long-term, seasonal, wetland dynamics.

Animals larger than insects might also serve as a major source of terrestrially derived energy and nutrients. Although a relatively rare occurrence, deposition and throughfall of rodents and birds can provide a nutrient-rich resource pulse for multiple trophic levels. Such resource additions have received little attention in wetlands, yet the large role of decaying anadromous salmon in Pacific stream ecology provides a substantial precedent to explore the importance of this subsidy in freshwater wetlands (Naiman et al. 2002). Egestion and excretion by birds, bats, adult amphibians, reptiles, and other animals probably provide a more common source of energy and nutrients to wetlands, particularly for those organisms that do not typically travel far from aquatic-terrestrial boundary (Earl and Zollner 2014). Similar to observations in stream systems (Bretherton et al. 2011), the availability of carcasses, carrion, egesta, and excreted material is likely to accelerate the decomposition of leaf litter by providing a nutritional resource to subsidize microbes on the litter surface. Conversely, the presence of microbes on decaying leaf litter might also serve as a means of initiating the decomposition process of animal material, although we do not know of any research that has specifically explored this phenomenon. Excreta and other sources of inorganic subsidies are also likely to increase algal growth, which primes bacteria and fungi on leaf litter and accelerates decomposition (Danger et al. 2013). The deposition of

eggs by terrestrial animals such as insects and amphibians can also provide a major subsidy of energy and nutrients to wetlands (Capps et al. 2015). In one estimate, oviposition by salamanders in a temperate North American wetland provided up to 5.5 g ash-free dry mass·m⁻²·yr⁻¹ (Regeister et al. 2006). In the same study, the biomass of larval emergence was 10% of larval production, with the remainder of biomass accounted for by larval mortality. In addition, a substantial proportion of eggs and new hatchlings can be inviable or succumb to disease. Dead eggs and hatchlings decompose fairly rapidly and can increase rates of litter decomposition by providing a labile source of nutrients in close proximity to decomposing litter (Regeister and Whiles 2006).

THEME 6: THE INTERACTION BETWEEN LITTER INPUTS AND HUMAN ACTIVITIES

Role of litter in created wetlands

Given that the process of litter decomposition underlies a large part of ecosystem processes in forested wetlands, litter decay rate is often employed as an indicator of successful remediation (Gingerich and Anderson 2011a, b). In a survey of created and natural wetlands, Fennessy et al. (2008) revealed that litter decay rates were higher in natural systems, which they attributed to higher concentrations of nutrients in natural systems. In contrast, Mackintosh et al. (2016) surveyed 16 constructed wetlands along a gradient of urbanization and found that both leaf decay rate and nutrient concentrations increased with urbanization. In a similar survey, Holgerson et al. (2017) found that nutrient concentrations did not change across an urbanization gradient, but did find lower levels of canopy cover, more algae, and a greater percentage of algae in the diet of aquatic consumers. Hence, protocols for monitoring the functionality of created and urban wetlands might find more utility in measures of the abundance and diversity of detritivorous consumers, since the presence or absence of tolerant taxa indicates how much the wetland has been impacted by human activities (Mackintosh et al. 2015). In addition, the diversity of consumers more closely aligns with the ability of a wetland to support fauna at higher trophic levels (Moore and Hunt 2012). Nevertheless, litter inputs are still an important basal resource in such systems, and results of experimental manipulations of litter quantity and quality might aid land managers in forming the surrounding terrestrial landscape.

Interactions between litter inputs and pollutants

Experimental assays can also determine how pollutants alter litter decomposition and food webs associated with litter inputs. Microbial-mediated decay of leaf litter appears to be resilient to some molecularly complex

chemical stressors such as pesticides, either because the pesticide has little effect on microbial physiology or because the microbial community is capable of rapid turnover toward more tolerant assemblages (Kennedy et al. 2012, Talk et al. 2016). In contrast, contamination of ecosystems by simpler chemicals such as inorganic nutrients and salts seem to have a much stronger effect. Salt contamination, which is becoming an increasing problem throughout the world (Cañedo-Argüelles et al. 2016), tends to inhibit microbial function (Schäfer et al. 2012, Cook and Francoeur 2013) leading to a reduction in litter decay rates (Rejmánková and Houdková 2006). Contamination from acid mine drainage and coal mining can also interact with litter inputs, primarily due to the propensity for low pH to reduce decay rates (Chamier 1987, Kittle et al. 1995, Lee and Bukaveckas 2002, Batty and Younger 2007). It is worth noting that variation in litter quality can also reduce wetland pH (e.g., due to the presence of phenolic acids; Stoler and Relyea 2011). This is significant, since the breakdown rates of many pesticides decline with pH (Ferrando et al. 1992, Relyea 2006), and the activity of most chemical contaminants is strongly dependent on pH. Consequently, variation in litter quality is likely to alter the persistence and ecological effects of human-associated pollutants. As more studies emerge regarding the effects of contaminants on litter decay in wetlands, it will be important to consider the interaction of contaminants with litter quality.

The stresses and benefits that litter provides to wetland food webs are likely to interact with contaminants in ways that both harm and benefit organisms. Some contaminants (e.g., pesticides) can bind to litter substrates, become part of grazer diets, and lead to significant grazer mortality (Moore et al. 2007). Alternatively, contaminants can adsorb to dissolved humic compounds (Wershaw et al. 1969, Benson and Long 1991, Haitzer et al. 1998). However, there is little evidence to support that this benefits consumers. For example, zooplankton species exposed to elevated salinity exhibited relatively high survival in the presence of oak litter but exhibited a decrease in survival only with maple leaf litter, which contains substantial amount of soluble carbon and phenolic acids (Stoler et al. 2017a). Similarly, tadpole survival and mass were either unchanged or reduced in the presence of both maple litter and insecticides (Stoler et al. 2017b). In contrast, the combination of insecticides and recalcitrant leaf litter increased tadpole performance, likely because insecticides killed apparent competitors for basal nutrients (Boone and Sullivan 2012). Because inputs of leaf litter and contaminants are not likely to occur at the same time, there is potential for these factors to temporally interact. For example, DiGiacopo et al. (2018) found that inputs of invasive leaf litter inputs with high amounts of dissolved organic carbon (measured as turbidity of water) induced a faster hatching time of leopard frogs; this change in development timeline led to a reduced tolerance for larval exposure to sodium chloride contamination.

Collectively, these studies reiterate the strong effect of litter chemistry on wetland consumers and suggest that interactions between contaminants and litter inputs rely on the tolerance of exposed organisms as well as the chemical quality of the litter inputs.

Facilitation of invasions and extinctions

By altering the environmental conditions in aquatic habitats, litter inputs might also facilitate the invasion or extinction of other species. For example, the accumulation of an invasive cattail litter (*Typha x glauca*) on hydric wetland soils is associated with increases in nitrogen mineralization, lower light levels, and a decreased abundance of native plant species (Farrer and Goldberg 2009). Moreover, the accumulation of invasive cattail litter generated conditions that further promote the growth of cattail seedlings (Vaccaro et al. 2009, Larkin et al. 2012). A similar story has emerged regarding the spread of the invasive reed canary grass (*Phalaris arundinacea*), where high amounts of reed canary grass litter generate conditions favoring its own growth (Eppinga and Molofsky 2013, Kaproth et al. 2013). It is also possible that invasive litter species might lead to loss of native consumers. For plants, one strategy of invasion is to maintain or increase foliar concentrations of defense compounds to prevent herbivory (Müller-Schärer et al. 2004). As discussed above, those chemical defense compounds are known to reduce the survival of native wetland consumers when leached from litter (e.g., Maerz et al. 2005a, b, Barrett et al. 2017, Burraco et al. 2018). Niche space opened by the loss of native consumers might facilitate invasion by consumers that are more tolerant to the conditions generated by invasive plant litter. This is certainly a possibility given the range of tolerance to leached secondary compounds exhibited by wetland consumers, and it would be an intriguing avenue of future research.

OUTSTANDING QUESTIONS AND SUGGESTED RESEARCH DIRECTIONS

In this review, we have provided substantial evidence that quantitative and qualitative variation of leaf litter inputs can drastically alter lentic freshwater ecosystems, particularly forested wetlands. As more researchers explore the effects of leaf litter, we expect a continued exponential rise in the number of studies detailing this phenomenon (Fig. 1). The manifestation of this trend will include both applied and conceptual questions that concern local, regional, and global patterns. In this section, we provide suggestions to steer the direction of future research.

Generalizing through functional traits

First and foremost, we suggest that there should be a greater attempt to generalize the effects of litter species on ecological processes. The majority of leaf litter

studies in wetland systems have concerned the effects of a small number of individual litter species. Although such specific research is certainly relevant for specific issues (i.e., local land management), the global field of ecology would greatly benefit from studies that generalize the effects of plant subsidies across multiple plant species, habitat types, and latitudes. As mentioned above, one method of attaining generality is by characterizing plant species according to their inherent functional traits and not their taxonomic epithet (McGill et al. 2006). Studies would further benefit from a priori manipulations of functional traits. Moreover, the use of multidimension trait indices can be used to simultaneously consider multiple relevant functional traits when considering the functional similarity between two or more species (Schleuter et al. 2010, Stoler and Relyea 2016). Community studies involving higher trophic levels will equally benefit and become broadly useful if the effects among interacting species (e.g., leaf litter, detritivores, and predators) are generalized by functional traits of consumers and predators.

The determination of relevant functional traits must be given substantial consideration. Regarding the traits of leaf litter, studies have characterized species according to their major chemical components, including the most abundant primary (i.e., nutrients) and secondary (i.e., structural and defense) compounds. Given that microbial mineralization of litter is strongly affected by the ratio of primary-to-secondary compounds (Aerts 1997), this is a very useful starting point to generalize the effects of leaf litter on aquatic systems. However, attention is rarely given to the composition of micronutrients in leaf litter (e.g., calcium, potassium, silicon). For example, silicone might be highly limiting to microorganisms such as diatoms and fungi, and low levels of calcium in leaf litter might limit the growth of mollusks and vertebrates that require the nutrient for shell and bone growth, respectively. Physical characteristics of leaf litter (e.g., shape, structure, and color) are also likely important functional traits. For example, aquatic systems with darker colors attract more mosquitoes seeking sites for oviposition (Bentley and Day 1989, Li et al. 2009), and leaf litter with more complex physical structure (e.g., a greater three-dimensional representation) might afford greater spatial refuge for prey organisms. Future studies should address the relative importance of both physical and chemical litter traits, including both abundant and rare chemicals, on wetland ecosystems. Because individual traits are likely to affect each trophic level in a different manner, such research would further benefit from studies that manipulate food web complexity.

Consideration of consumer functional traits in addition to litter traits might also afford a greater understanding regarding the bottom-up effects of leaf litter. As discussed above, many wetland organisms are generalist consumers capable of herbivory as well as detritivory. However, consumers vary widely in ingestion rate, assimilation efficiency, growth rate,

permanence (i.e., emergence rate), reproduction, and stoichiometric requirements (Poff et al. 2006, Vanni and McIntyre 2016). The functional similarity of individual consumers can be quantified according to these functional traits in much the same way that chemical and physical traits can be used to quantify the functional similarity of plant litter species. Questions concerning effects of functionally different consumers on the process of leaf breakdown will greatly aid our ability to predict the consequences of litter inputs to any lentic ecosystem. Given that individual consumer traits benefit from certain types of resources (e.g., vertebrates are likely to benefit from phosphorus-rich litter), another important area of research should consider the interaction between litter and consumer functional traits.

Effects of functional trait diversity

Once the relevant functional traits of both litter and consumers are determined, a logical next step is to quantify the effects of functional trait diversity. As reviewed above, several studies have begun to explore the bottom-up effects of chemical dissimilarity of leaf litter mixtures in wetlands. However, most of these studies did not design experiments that specifically manipulated chemical dissimilarity; rather, they invoke chemical dissimilarity as a possible explanatory mechanism. Nevertheless, the results of these studies can now provide insight regarding what chemical traits are likely to be most important, and how these traits affect individual organisms. Using such knowledge, future experiments can finely hone manipulations of litter trait diversity to include or exclude traits that might have more or less importance for ecological function within a given system. Statistical methods for estimating and manipulating functional trait richness are rapidly improving (Laliberté and Legendre 2010, Schleuter et al. 2010, Stoler et al. 2016b), and this advancement will greatly aid in the development of creative and informative future studies. Manipulations of litter trait diversity can also incorporate variation in trait evenness to help move toward a more realistic understanding of how natural litter assemblages alter wetland food webs. Moreover, experiments can manipulate either litter trait diversity, consumer trait diversity, or both factors to understand top-down and bottom-up interactions in food web. In addition, mesocosm experiments can increase or decrease the reticulation and structure of wetland communities to explore how factors such as food web connectance and number of trophic levels influence the bottom-up effects of leaf litter inputs.

Interaction of litter inputs with contaminants

To date, the interaction between leaf litter inputs and chemical contaminants are limited to only a few studies.

As reviewed above, those studies demonstrate interactions that can either decrease or increase the negative influence of contaminants on wetland food webs. Expanding on these interactions is of critical importance for the future of freshwater conservation and management. Numerous questions must be addressed, such as which chemical components of litter are most likely to react with contaminants and the reaction of individual contaminants. This is a daunting task, considering the vast number of contaminants commonly found in freshwater systems, such as pesticides, pharmaceuticals, personal care products, volatiles from construction, and inorganic salts (Pal et al. 2010). Moreover, sublethal effects are often equally important to lethal effects, given that phenotypic changes can dramatically alter ecological interactions and organismal evolution (Agrawal 2001). Despite the complexity of the problem, an improved understanding of the chemical mechanisms underlying molecular interactions between litter inputs and contaminants might aid in deriving generalized effects. Indeed, chemical contaminants often fall into discrete categories with common modes of activity (e.g., endocrine disruptors, serotonin uptake inhibitors, chloride salts), and chemicals within categories are likely to have similar effects on ecosystems (Hua et al. 2013). Hence, it might be possible to link litter inputs with contaminant effects with a relatively few number of studies.

Latitudinal trends

At a global scale, temperature, precipitation, and land use are the primary factors determining rates of litter inputs, overlap between stages of decomposition, and propensity for litter to accumulate in wetlands (Aerts 1997). Most research regarding litter inputs to wetlands have occurred in temperate systems, where litter inputs generally occur in a single, seasonal pulse. Moreover, the decomposition of litter inputs in temperate wetlands occurs primarily during warm periods when there are substantial rainfall and sufficient activation energy to mineralize compounds. Since the full decomposition of litter is often a longer process than the duration of warm periods, litter tends to accumulate in temperate environments. This trend is exacerbated at higher latitudes, which have shorter warm periods and more recalcitrant litter inputs, although there is far less input biomass (Malhi et al. 1999). As one moves toward tropical latitudes, litterfall and decomposition become more continuous and year-round occurrences, although more litterfall is likely to occur during dry seasons, whereas decomposition is likely to accelerate during the wet seasons (Malhi et al. 1999). Although this trend might lead to less accumulation of litter in tropical forests, the residence time of detrital carbon stocks is approximately equal between tropical and temperate forests (Malhi et al. 1999). Another explanation might be that there is a lower number of macro-consumers available to accelerate the process of litter decomposition in tropical

systems. Indeed, this trend was demonstrated through in a global survey of streams by Boyero et al. (2012), who also demonstrated that there are relatively constant rates of litter decomposition across most latitudes. To date, no such cross-latitudinal comparison has been conducted in wetlands, and this area is certainly ripe for discovery.

Improved energy and nutrient budgets

We also need to develop more intricate carbon and nutrient budgets for wetlands. Among the few partial budgets that currently exist (Regester et al. 2006, Capps et al. 2015, Fritz and Whiles 2018), a description of energy and nutrient cycling is largely limited to the confines of the wetted boundary (i.e., the line where standing water stops, and land starts). As discussed earlier, the carbon and nutrient budget extends beyond the wetland's boundaries, because it depends on the migration patterns of emergent organisms and the flow of released gases. Given that many organisms can hop, crawl, or fly a substantial distance beyond the aquatic-terrestrial boundary, it is unlikely that all of the organic material provided to the wetland by surrounding vegetation will recirculate back into the vegetation of origin. Such complex spatial dynamics are logistically challenging to document, although advances in isotopic approaches will certainly aid in this endeavor.

Improved spatial and temporal wetland budgets that elucidate the flow of organisms into and out of wetlands also address the role of leaf litter inputs in aquatic and terrestrial species assembly. Certainly, the presence of a wetland plays a large role in attracting organisms to the local area. However, our review demonstrates that terrestrial diversity surrounding a wetland also plays a large role in determining what organisms can survive within a given wetland. As the terrestrial plant composition changes through processes of succession or disturbance, a major question is how this change will affect wetland community composition and ecological function. Similarly, it is important to understand the extent to what existing wetland communities determine the process of terrestrial species turnover. For example, a vector for seed dispersal might be drawn to a wetland due to the resources provided around that ecosystem. The extent to which that vector then determines the succession of the surrounding landscape through the dispersal of new seeds is an important question that can lead to a far greater understanding concerning the role of wetlands in future ecological growth.

CONCLUSIONS

The evidence put forth in this review suggests that terrestrial plant subsidies can be vital to the functioning of forested wetlands and likely play an ecologically significant role in all wetlands that receive these inputs. From an ecological perspective, the composition, quantity, and quality of litter inputs can dramatically alter

biotic interactions and community composition. From an ecosystem perspective, the input of litter to wetlands has been implicated as playing a major role in global carbon and nutrient fluxes due to the myriad aquatic-terrestrial linkages that stem from litter resources. The importance of these subsidies parallels the long-studied and crucial role of litter inputs to streams. Although stream studies can be informative about expectations regarding litter inputs to wetlands, studies specific to wetlands have yielded several unique insights. As indicated in our first theme, wetlands are generally considered to be net sinks for global carbon but are also likely to have a greater export-to-production ratio than small streams and large lakes. As discussed in our second and third themes, qualitative and quantitative variation in litter subsidies can substantially alter rates of ecosystem processes, and these effects are likely more pronounced in wetlands relative to streams due to the retention of leached and mineralized chemicals. Retention of substances in wetlands can also alter ecological interactions by interfering with predator-prey interactions and eliciting phenotypic responses among consumers and predators that can both benefit and harm fitness, as discussed in our fourth theme. Throughout our fifth theme, it is apparent that the effects of litter inputs in wetlands are complemented, as well as modified by other well-known environmental gradients, including temperature, canopy cover, hydroperiod, habitat size, and other sources of terrestrial subsidies. Our last theme indicates that litter subsidies are an important component of created wetlands, not only because they provide essential resources for colonizing organisms, but also because they can both mitigate and exacerbate the effects of anthropogenic contaminants. Given continued human encroachment and disturbance of natural ecosystems, further studies concerning the effects of litter subsidies in wetlands will provide insightful and exciting discoveries that will be important for both conceptual and applied ecological research.

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