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REVIEW ARTICLE

Potential Effects of Foundation Species Loss on Wetland Communities: A Case Study of Black Ash Wetlands Threatened by Emerald Ash Borer

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Abstract The emerald ash borer (EAB; *Agrilus planipennis*) is an invasive beetle that causes almost complete mortality of ash trees (*Fraxinus* spp.) in North America and Europe. Northern temperate wetlands, where black ash (*F. nigra*) is a dominant and foundation species, will likely undergo dramatic shifts after EAB invasion. Utilizing published knowledge on amphibian and aquatic invertebrate responses to environmental gradients and the effects of ash loss on forest structure and function, we provide a mechanistic framework to discuss how changes in hydrology, canopy structure, and litter inputs could affect wetland communities. Changes in leaf litter could affect primary production and food web structure in the aquatic environment; overall changes in habitat structure might shift the community to species with longer aquatic stages that prefer open-canopy habitats. Amphibians and aquatic invertebrates serve as linkages between aquatic and terrestrial ecosystems. Therefore, understanding how the abundance and functional diversity of these taxa change in response to EAB is necessary to understand whole ecosystem responses. Using a mechanistic framework to formulate hypotheses and predictions is vital for our ability to manage target systems, retain biodiversity, and sustain ecosystem function.

Keywords *Agrilus planipennis* · Amphibian · Aquatic invertebrate · Community ecology · Invasive species · *Fraxinus nigra*

Introduction

While insect pests and diseases are natural parts of ecosystems, epidemic outbreaks of native species and the often uncontrollable spread of exotic invasive species are threatening forests globally (Lovett et al. 2006, 2016; Flower and Gonzalez-Meler 2015). In addition to the high economic costs associated with the loss of timber resources and other forest goods and services (Holmes et al. 2009), severe disturbance by pests can have extensive ecological consequences (Lovett et al. 2006; Flower and Gonzalez-Meler 2015). The magnitude and extent of impact on an ecosystem depends on the virulence of the pest as well as the abundance of the host tree (Lovett et al. 2006). When the host trees are foundation species that modulate the structure and function of the forests they dominate (sensu Ellison et al. 2005), the effects of tree mortality on ecosystem function, as well as plant and animal communities, can be severe. Examples of ecosystems currently threatened by loss of foundation species include forests dominated by eastern hemlock (*Tsuga canadensis*), white-bark pine (*Pinus albicaulis*), bald cypress (*Taxodium distichum*), and mangrove (*Rhizophora* spp.; Ellison et al. 2005).

A direct effect of defoliation and death of dominant trees is altered canopy structure and plant community composition (Lovett et al. 2006, 2016; Flower and Gonzalez-Meler 2015). These changes in vegetation ultimately affect fauna, either directly or indirectly, by altering biogeochemical processes, habitat quality, and resource availability (Lovett et al. 2006; Flower et al. 2013; Nisbet et al. 2015). For example, herbivorous insects that rely on a few species of trees may

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decline or go extinct in response to loss of their host trees (Gandhi and Herms 2010); gap formation caused by tree death can make microhabitats on the forest floor more harsh, and therefore reduce the diversity of ground beetles and favor disturbance-adapted species (Gandhi et al. 2014); and the composition of bird, mammal, and aquatic invertebrate communities may change because of changes in habitat structure and resource abundances (Smock and MacGregor 1988; Wallace et al. 1997; Lovett et al. 2006; Koenig et al. 2013; Flower et al. 2014).

While progress is being made to understand the consequences of the loss of foundation species in terrestrial systems, there is a paucity of studies that focus on wetland ecosystems (but see Smock and MacGregor 1988; Ford and Vose 2007; Nisbet et al. 2015). There are two important processes that will likely be altered by the loss of foundation species and affect aquatic communities: hydrologic cycles and spatial subsidies (e.g., allochthonous detrital inputs). Trees play an important role in regulating hydrology via evapotranspiration (Brooks 2000; Ford and Vose 2007). For example, the loss of eastern hemlock (*Tsuga canadensis*), which is threatened by the hemlock woolly adelgid (*Adelges tsugae*), from the southern Appalachian Mountains in the USA can affect the amount and frequency of runoff into mountain streams, thus altering hydrological regimes (Ford and Vose 2007). Similarly, litter is an especially important source of organic matter to headwater streams and ephemeral wetlands that rely on allochthonous inputs (Wallace et al. 1997). Linked to litter inputs is the amount of light reaching aquatic habitats, which affects algal growth and habitat quality variables (e.g., temperature, dissolved oxygen). Changes canopy structure and the amount and quality of litter fall could affect nutrient cycling and food web dynamics (reviewed in Nisbet et al. 2015, Lovett et al. 2016). Changes in hydrologic cycles and terrestrial subsidies into aquatic habitats may, in turn, affect reciprocal subsidies of nutrients and energy from aquatic to terrestrial systems (Schriever et al. 2014).

The emerald ash borer (EAB; *Agriulus planipennis*; Poland and McCullough 2006) is a wood boring beetle native to east Asia that will dramatically alter temperate forests in North America, especially in forests where ash (*Fraxinus* spp.) is an abundant member of the tree community. Black (*F. nigra*), green (*F. pennsylvanica*), and pumpkin ash (*F. profunda*) are dominant overstory species at sites that are frequently inundated, like swamps and riparian flood plains (Klooster et al. 2014; Wagner and Todd 2015). Of particular concern are black ash dominated wetlands because black ash often grows in pure stands, which can span hundreds of hectares, regulating wetland structure and function (e.g., Slesak et al. 2014; Looney et al. 2015; Telander et al. 2015; Wagner and Todd 2015).

The objective of this paper is to use current knowledge and a mechanistic framework to predict how aquatic wetland communities might respond to changes in forest structure following the loss of a foundation species, black ash. In particular, we focus on amphibian and invertebrate taxa that have terrestrial and aquatic stages because these species are abundant in wetland habitats, are sensitive to changes in terrestrial and aquatic systems, and encompass a diversity of functional feeding groups. Furthermore, these taxa play an important role in linking aquatic and terrestrial ecosystems because they facilitate the reciprocal flow of nutrients and energy (Baxter et al. 2005; Hocking and Babbitt 2014). Collectively, amphibians and aquatic invertebrates provide a comprehensive examination of how an invasive species may alter the ecology and functioning of forested wetlands. We discuss how changes in three major characteristics of forested wetlands—hydrology, canopy structure, and organic matter inputs—could contribute to changes in community composition and alter the structure of wetland food webs (Fig. 1). We focus on changes in species diversity and functional feeding groups as the primary community responses. We also consider how proposed mitigation measures to address EAB could impact these ecosystems. While our study system is black ash wetlands and EAB, our framework is applicable to predicting how disturbance resulting in loss of foundation species may affect taxa across other ecosystems. To our knowledge, this is the first attempt to use available literature to preemptively predict the effects of environmental change on community composition in seasonal woodland wetlands.

The Threat of Emerald ash Borer to Black ash Wetlands

Emerald ash borer was introduced to North America in the 1990s and, as of January 2017, has since been detected in 30 states in the USA, two provinces in Canada, and European Russia (Herms and McCullough 2014; USDA Animal and Plant Health Inspection Service, APHIS 2017). This beetle feeds on the phloem and sapwood of all species of ash, causing over 90% mortality in most species a few years after infestation (Klooster et al. 2014). Further, EAB infested forests have severely reduced potential to regenerate because 1) EAB infests trees before they reach maturity, ultimately resulting in a depleted seed bank and absence of new seedlings and 2) naturally lower rates of regeneration in wetland forests resulting from lower seedling establishment (Kashian and Witter 2011; Klooster et al. 2014). While the ecology, spread, and effects of EAB on host trees have been well studied (Poland and McCullough 2006; Flower et al. 2013; Klooster et al. 2014), the indirect effects of EAB on forest ecosystems are only starting to be investigated (Gandhi and Herms 2010; Flower et al. 2013; Slesak et al. 2014); this need is particularly acute in ecosystems where ash is a foundation species, as is black ash in wetlands of the western Great Lakes region of North America.

Black ash typically grows on hydric soils and frequently occurs in stands ranging in size from small (< 1 ha), isolated

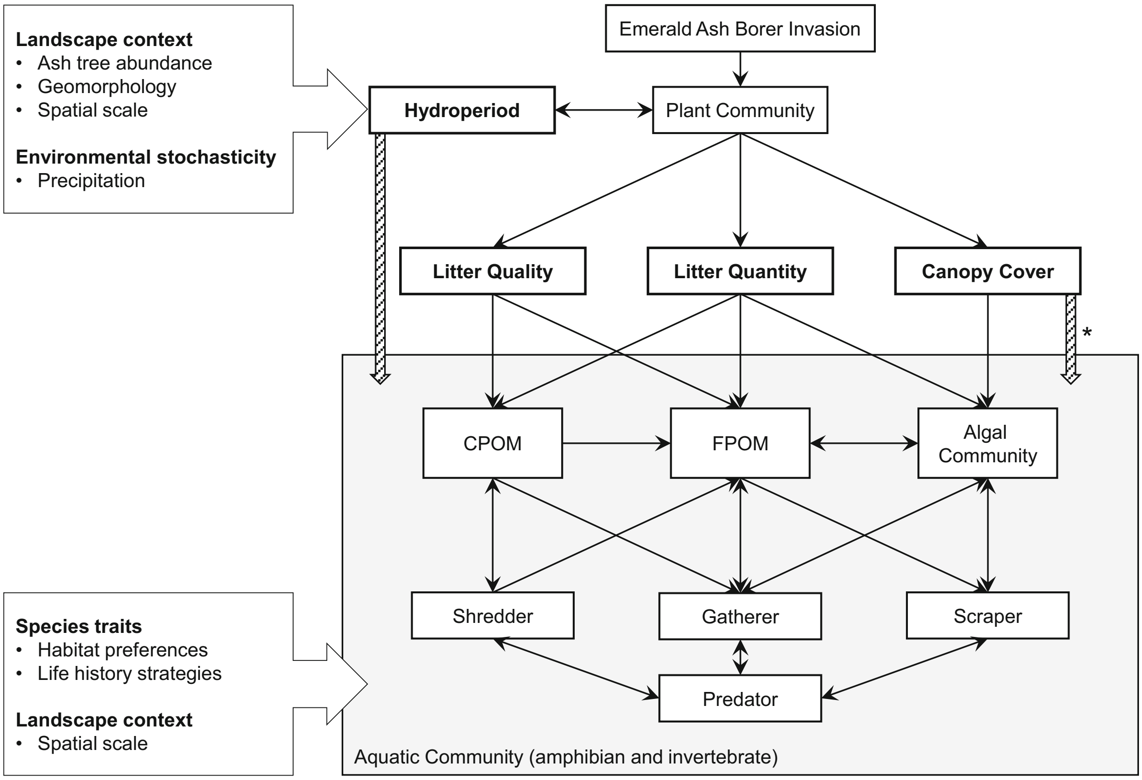

Fig. 1 Conceptual diagram showing the direct effects of key environmental factors on aquatic amphibian and invertebrate communities. The gray box encompasses the aquatic environment; thick boxes indicate functional feedings groups within the aquatic environment. Bolded factors are the focus of this paper: emerald ash borer invasion can alter wetland communities via changes in plant communities that alter hydrology, litter quantity and quality, and canopy cover. Arrows indicate a direct effect between one factor and another without consideration of directionality (positive/negative) or magnitude; thick arrows indicate factors – hydrology and canopy cover – that directly affect all functional feeding groups. The magnitude and direction of changes to hydroperiod, litter, and canopy depend the landscape context and environmental stochasticity; specific changes in community will also depend on species traits and the landscape context. * canopy cover affects the aquatic community via changes in insolation and habitat structure. CPOM: coarse particulate organic matter; FPOM: fine particulate organic matter; algal community includes periphyton/biofilm and phytoplankton

depressional wetlands to extensive swamps covering hundreds of hectares; ash also grows along flood plains and riparian habitats. In forested wetlands, ash comprises 36–80% of the overstory density and can often occur in pure stands (Gupta and Miedtke 2009; Palik et al. 2011; Klooster et al. 2014). These wetlands, where black ash is a dominant or co-dominant species, occur across the north central to north eastern U.S, from Minnesota to Maine and are particularly abundant in the western Great Lakes region. For instance, black ash dominated wetlands occupy 411,018 ha in Minnesota (6% of forest land), 269,257 ha in Michigan (3% of forest land) and 341,206 ha in Wisconsin (5% of forest land) (USDA Forest Service, FS 2016).

Ash plays an important role in regulating the function and biota of these wetlands via hydrology (Slesak et al. 2014; Telander et al. 2015), canopy, and leaf litter (Palik et al. 2006; Batzer and Palik 2007). Black ash is also culturally and economically important to Native American Tribes for basket-making (Benedict and Frelich 2008). Changes in hydrological regimes, resulting from the loss of black ash, coupled with a lack of other canopy species that could replace it, could result in the complete conversion from forested wetland to an open-canopy wet meadow that is dominated by graminoids and shrubs (Fig. 2; Palik et al. 2012; Slesak et al. 2014). Speckled alder (*Alnus incana*) is an abundant understory shrub that may persist after the loss of ash (Palik et al. 2012). Such a dynamic has already been documented following clear-cut harvesting in swamps with extensive black ash cover in the midwestern United States (Erdmann et al. 1987).

Potential Management Responses to EAB Infestation

Freshwater ecosystems are threatened globally and seasonal forested wetland are among the most threatened in the United States (Dudgeon et al. 2006; Dahl 2011). Therefore, conserving the structure and function of these habitat is a conservation priority. A variety of management options have been proposed to halt the spread of EAB, including direct control of EAB with pesticides or biological agents and adaptive silvicultural strategies. One proposed silvicultural technique involve removing ash from forest patches, as pre-emptive timber harvests (Herms and McCullough 2014). However, ash removal may result in similar ecological changes as EAB induced

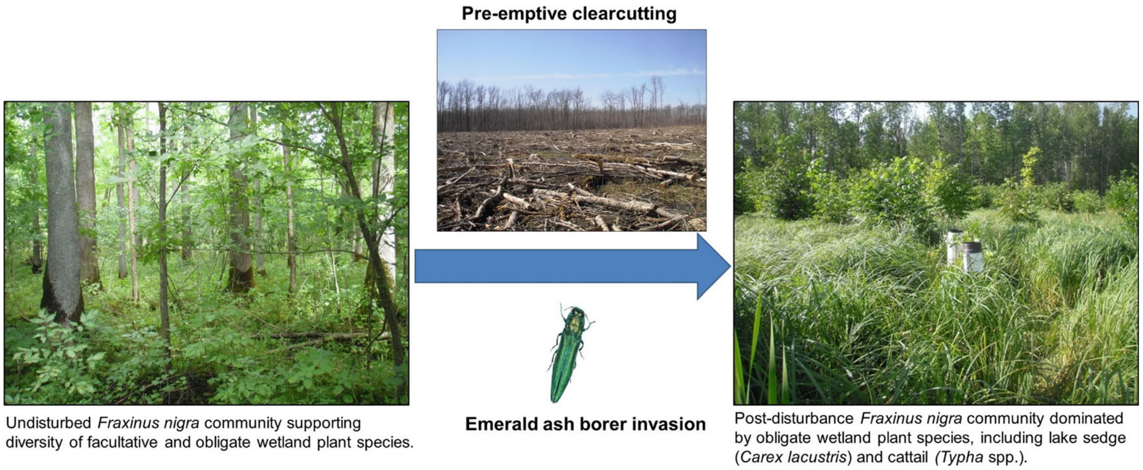

Fig. 2 The loss of overstory black ash due to emerald ash borer or pre-emptive clearcutting in response to this threat can result in dramatic shifts in the structure and composition of understory plant communities. Shift depicted in photos occurred over one growing season following pre-emptive clearcut harvesting in response to emerald ash borer in northern Minnesota. Photo credit: A.W.D

mortality (Fig. 2). Another adaptive management option is to increase forest resilience and maintaining ecosystem structure and function in the absence of black ash by transitioning from ash to species that are not susceptible to EAB (Iverson et al. 2015; Looney et al. 2015). For instance, Looney et al. (2015) found that swamp white oak (*Quercus bicolor*), EAB resistant Manchurian ash (*F. mandshurica*), disease tolerant American elm (*Ulmus americana*), and hackberry (*Celtis occidentalis*) show initial promise as non-host species that may be able to replace locally abundant black ash, for at least some functions, e.g. transpiration, tree productivity, and wildlife habitat.

Amphibian and Aquatic Invertebrate Communities

Reflecting the transitional status between aquatic and terrestrial environments, wetland communities comprise a variety of biota that are uniquely adapted to take advantage of two distinct habitat types. Most pond breeding amphibians are seasonal migrants: they live terrestrially as adults, return to wetlands in the spring to breed, and have an aquatic larval stage. As a group, aquatic invertebrates have highly varied life cycles that reflect their high taxonomic diversity. While all have an aquatic larval stage, some species may be seasonal migrants (e.g., mosquitoes, dragonflies), semi-aquatic (e.g., diving beetles), or fully aquatic (e.g., fingernail clams, small crustaceans).

The structure of amphibian and aquatic invertebrate communities is based on interactive effects of regional and local factors on all life stages (Batzer et al. 2005; Richter-Boix et al. 2007). Within the landscape matrix, adult habitat preferences for breeding, migration and dispersal, and non-breeding habitat dictate the potential local aquatic assemblages (Batzer and Wissinger 1996; Skelly 2001). For example, species preferences for canopy (e.g., open, closed, generalist) and hydroperiod (e.g., short, intermittent, permanent, generalist) determine local species composition. Species that are fully aquatic without a drought resistant stage are excluded from seasonal ponds. Within the aquatic habitat, hydroperiod, predation risk, and food resources influence larval growth and survival and, therefore, filter the community further (Brooks 2000; Skelly 2001; Werner et al. 2007). Dominant vegetation within and around wetlands exert significant control over the suitability of these habitats by regulating hydroperiod, canopy cover, and leaf and woody litter (Fig. 1). Below, we consider how EAB invasion may alter each of these factors individually and the consequences for amphibian and aquatic invertebrate communities.

Throughout this paper, we will consider both taxonomic diversity and functional feeding groups when assessing community responses to changes in black ash forests. We focus on four basic feeding groups: gatherers, scrapers, shredders, and predators. Adult amphibians are generalist predators, feeding mostly on a variety of invertebrates. Anuran larvae are usually omnivores (Whiles et al. 2010). While they feed mostly on detrital and algal food resources (gatherers, scrapers), their diets often include invertebrates and other animal matter (Schiesari et al. 2009). Salamander larvae are generalist predators. Larval and adult invertebrates occupy the full gambit of feeding functional groups. For example, gatherers include mosquito larvae, clams, and crustacean zooplankton; scrapers include some mayfly larvae and snails; shredders include some caddisfly larvae, some beetles, and some dipteran larvae; and predators include dragonfly larvae and some beetles (Merritt et al. 2008).

Hydroperiod

Black ash occurs on a variety of soils, ranging from deep organic peats to mineral soils overlain by shallow layers of muck, but most sites are characterized as having water tables at or above the soil surface during a portion of the growing season (Fig. 3). The primary mechanism contributing to water table dynamics is the balance between precipitation, the primary water source (Lenhart et al. 2012), and outputs via evapotranspiration (ET; Fig. 1). When inputs are high and outputs low, such as early spring during snowmelt and prior to black ash leaf expansion, water tables are generally near the surface and ponding of surface water is common. Following leaf expansion, water tables begin to draw down as black ash ET increases (Fig. 3). Local conditions, such as topographic position and soil and bedrock properties that influence drainage, also influence hydrology (Fig. 1). For instance, black ash wetlands in floodplains (Tardiff and Bergeron 1999), along stream and rivers (Wright and Rauscher 1990), and in topographic low areas within the local landscape, where continuous drainage of surrounding uplands keeps water tables high, are less influenced by ET (Van Grinsven 2015). Thus, while the general pattern of spring ponding and summer drying is common, some sites may never have the water table above the surface, while others may have standing water throughout the year (R. Slesak, pers. obs.). A final consideration is the role of canopy on the accumulation of snowpack and the timing of snowmelt (Varhola et al. 2010), which could indirectly alter the duration of spring hydroperiod. Loss of canopy might increase snow accumulation and melt (Varhola et al. 2010), resulting in faster spring ponding.

Where ET is a main driver of site hydrology, the loss of black ash and reduced transpiration following harvesting or EAB mortality will cause the water table to rise and increase the times when water is at or near the soil surface (Slesak et al. 2014). Because black ash ET is greatest at the wettest sites (Telander et al. 2015) and the risk of prolonged elevated water tables following harvesting (i.e., swamping) is also greatest at the wettest sites (Erdmann et al. 1987), these "wet sites" may have a higher potential for altered hydroperiod and related impacts to wetland fauna. Conversely, loss of ash and opening of the canopy will also increase insolation and air temperature (R. Slesak, unpublished data), which may increase surface evaporation to offset lower transpiration losses (Verry 1986). At "dry sites" or during dry years, increased evaporation could lead to faster dry-down (shorter hydroperiod) and create drier microhabitats though the later summer and fall. Where hydrology is more strongly influenced by geomorphic setting, wetland hydroperiod may be less susceptible to changes following ash loss (Table 1; Van Grinsven 2015).

Most aquatic fauna breed in the spring through early summer and metamorphose early to mid-summer. Therefore, they are most sensitive to early season hydrology: timing of ponding must coincide with breeding and hydroperiod must be sufficient for metamorphosis. Despite expected rises in the water table, the biological influence of changes in black ash ET on early season hydrology may be limited because black ash leaf expansion occurs relatively late (late May to early June; Ahlgren 1957). For example, in a study that compared clearcut harvest and simulated EAB mortality with unharvested stands, there was no effect on the duration of continuous surface water presence in the spring for up to four years after treatments were applied even though water tables were elevated later in the growing season (R. Slesak unpublished data). The dynamics associated with the timing of leaf expansion would be even less pronounced in small isolated wetlands where species other than ash occur (Fig. 1). Another study that examined effects of harvest and riparian buffers on the hydrology of seasonal ponds found that harvest resulted in short-term changes in hydrology but that water depth and hydroperiod returned to pre-harvest levels within five years, after upland regeneration (Kolka et al. 2011). Therefore, if there are effects of EAB induced changes in hydroperiod on wetland fauna, effects will likely be strongest in sites where

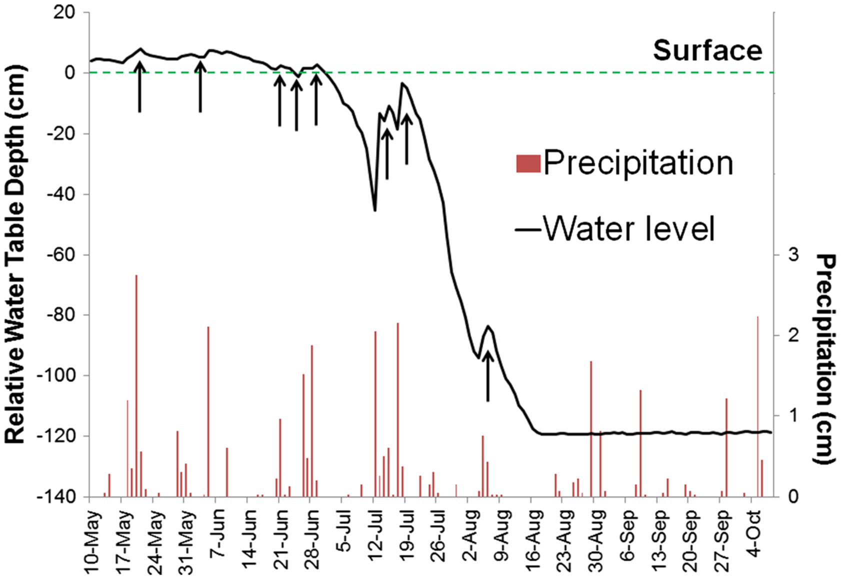

Fig. 3 Typical water table hydrograph for expansive black ash wetland swamps in northern Minnesota. Water tables are typically above the surface in early spring, followed by a drawdown that begins when black ash leafs out and evapotranspiration begins. Arrows indicate the rapid response of the water table to storm events, which is no longer apparent in late summer when soil water saturation is low

ET is a main driver of hydrology and during years with above average or below average precipitation; we expect longer hydroperiods with the loss of ash at sites with poorly drained soils and during wet years (Table 1; Fig. 1).

Amphibian Response to Hydroperiod The composition of local amphibian communities is primarily determined by hydroperiod and trade-offs associated with developmental rate and predation; species may be excluded from aquatic environments either because their larvae cannot metamorphose before wetland drying or they cannot avoid predation by top predators (Batzer et al. 2014). Species richness of pond-breeding amphibians and invertebrates tends to increase with increased duration of ponding, especially in fish-free habitats (e.g., Batzer et al. 2004; Werner et al. 2007); furthermore, communities tend to be nested within hydroperiod classes, such that species found in temporary wetlands are often a subset of those found in wetlands with intermediate or permanent hydroperiods (e.g., Baber et al. 2004; Werner et al. 2007). If the duration of ponding does increase after the loss of ash, especially at wet sites or during wet years, we predict a localized increases in amphibian species richness because species with longer larval periods will be able to persist in the community (Table 1). For example, wood frogs (*Lithobates silvatica*) and toads are generally the only amphibian species able to use very ephemeral wetland habitats; as hydroperiod duration increases, we predict that communities will include salamanders and treefrogs; finally, as hydroperiod becomes semi-permanent other species that have long larval periods may become part of the community (e.g., Werner et al.

Table 1 Summary of possible aquatic community responses to change in hydroperiod, canopy cover, or litter inputs under various scenarios (Variable Affecting Responses x Condition). The effect of each scenario on the community response is considered as independent from any other scenario

Environmental factor	Variable affecting response	Condition	Net community response	Mechanism
Hydroperiod	Vegetation	Sedge dominated	Increase diversity	Loss of canopy can reduce ET, raise water table, and increase hydroperiod
		Sedge dominated	Decrease diversity	Loss of canopy can increase evaporation and speed up dry-down
	Spatial Scale	Smaller wetland	Magnitude of effect smaller	Loss of ash buffered by upland non-ash canopy trees
		Larger wetland	Magnitude of effect larger	Loss of ash not buffered by upland canopy trees
	Precipitation	Higher than average	Increase diversity	More water input to wetland
		Lower than average	Decrease diversity	Less water input to wetland
	Driver of Hydrology	Evapotranspiration	Change in diversity	Changes in ET result in changes in hydroperiod
		Local geology and topography	No change	Changes in ET have muted effect on hydroperiod
Canopy cover	Vegetation	Sedge dominated	Increase diversity	Open-canopy attracts open-canopy specialists, generalists, and forest-associated species
	Insolation	Increased insolation	Increase abundance	Increase algal growth and warm water temperatures
		Decreased insolation	Decrease abundance	Heavy shading by sedge could reduce algal growth and temperature
	Spatial Scale	Smaller wetland	Increase diversity	Most species are attracted to open-canopy wetlands for breeding
		Larger wetland	Shift species composition	Forest specialists may be excluded from expansive open areas
Leaf litter	Vegetation	Sedge dominated	Reduce some shredder abundance	Lower food quality
		Sedge dominated	Increase predator abundance	Decrease quantity of leaf litter increases water quality
		Replacement canopy	Reduce abundance	Lower food quality and secondary compounds affect larval development
		High quality shrubs	No change	Ash replaced with similar-quality litter
	Algal abundance	High	No effects on non-shredders	Increase in algal resources may compensate for reduction in food quality
		Low	Reduce scraper and gatherers	Algal resources cannot compensate for lower food quality
Woody litter	Vegetation	Abundance of ash	Increase diversity	Increased downed woody debris provides habitat and food resources for aquatic taxa

2007). We also predict an increase in survival to metamorphosis and juvenile recruitment with increased hydroperiod duration; an increase in juvenile recruitment could result in increased amphibian abundance in general. We must note, that increased hydroperiod might also increase the presence of vertebrate (e.g., salamander) and invertebrate (e.g., dragonfly) predators. Therefore, under some scenarios species richness might increase but juvenile abundance might decrease (Fig. 1). If replacement canopy trees are pre-emptively planted and maintain hydrological regimes, there may be no change in composition of amphibian communities.

Invertebrate Response to Hydroperiod Most invertebrate taxa found in seasonal wetlands are hydroperiod generalists. Physiological adaptations to variable hydrologic conditions (e.g. drought-resistant eggs or nymphs/larvae, rapid development) and behavioral responses to a drying environment (e.g. burying in moist substrates to diapause, aerial dispersion of adults and nymphs to more permanent aquatic habitats, cyclic colonizers) enable them to inhabit wetlands spanning a broad hydroperiod gradient (Wiggins et al. 1980; Batzer and Wissinger 1996). Invertebrate taxa that are fully aquatic and lack a drought-resistant stage do not survive in seasonal wetlands. Thus, invertebrate communities are sorted along hydroperiod gradients based on species traits and biotic interactions (Fig. 1; Wiggins et al. 1980, Schneider and Frost 1996). Similar to patterns observed with amphibians, increased duration of ponding generally increases invertebrate taxon diversity (Table 1; Wissinger 1999, Brooks 2000). Batzer et al. (2004) reported that hydroperiod was positively related to the number of rare taxa present as well as the abundance of fingernail clams, caddisflies, crawling water beetles, and dragonfly larvae. Similarly, Schneider and Frost (1996) report an increase in taxa diversity and predator abundance in ponds with longer hydroperiods. Predators (e.g., some beetles, water bugs, dragonflies) may be most responsive to increased hydroperiod because they have longer aquatic stages and strong aerial dispersal abilities that would enable them to take advantage of the new aquatic habitat. We predict that if EAB invasion causes the duration and year-to-year predictability of hydroperiod to increase at wet sites or during wet years, then invertebrate diversity will increase. However, amphibian and invertebrate predation on lower trophic levels and intra guild predation may also become more important as hydroperiod duration and permanence increases (Schneider and Frost 1996; Wissinger et al. 2003, 2006) an increase in predator abundance could result in a decrease in prey abundance (Fig. 1). The loss of ash might result in a shift of from gatherer taxa that can develop rapidly (e.g., mosquitos, small crustaceans) to predatory adult and larval invertebrates (Schneider and Frost 1996). Alternatively, if increased insolation results in earlier dry-down or drier falls, the invertebrate community may be dominated by taxa with rapid larval development and with drought resistant stages. At local scales (single wetland) we predict community composition will change depending on the local landscape context and yearly variation in precipitation (Table 1).

Canopy

Canopy cover in black ash forests is generally patchy and lower than most other forests due in part to the comparatively low leaf area of black ash and lower overstory tree densities in these systems (Telander et al. 2015). Natural canopy disturbance regimes are dominated by frequent, gap-scale disturbances associated with wind, drought, and flooding (Tardiff and Bergeron 1999; Palik et al. 2011) with stand-replacing disturbance exceedingly rare occurring at estimated return intervals greater than 1000 years (MNDNR 2003). As a result, natural black ash forests tend to be strongly uneven-aged with canopy tree ages ranging from 200 to 320 years old and diameter distributions characterized by descending monotonic forms with black ash found across all size and age classes (Tardiff and Bergeron 1999; Looney et al. 2016). Loss of overstory American elm (*Ulmus americana*) in many black ash forests due to the introduced Dutch elm disease (*Ophiostoma novo-ulmi*) led to increased levels of canopy disturbance over the latter half of the twentieth century, as this species historically constituted up to 20% of the canopy tree species in these forests (MNDNR 2003).

The high levels of light infiltration and gradation from mesic to hydric conditions occurring in black ash wetland communities results in these forests having the highest levels of floristic diversity of any forest ecosystem in the upper Midwest region of the United States (MNDNR 2003). This diversity is largely expressed in the understory layer, which often contains a mixture of upland forest herbs and facultative and obligate wetland species, including bluejoint grass (*Calamagrostis canadensis*) and lake sedge (*Carex lacustris*) (MNDNR 2003; Looney et al. 2017). Complete mortality of overstory black ash due to clear-cut harvesting or EAB can result in a rapid shift in the structure and composition of these ground-layer communities towards strong dominance and continuous cover by obligate wetland species, including cattail (*Typha* spp.) and lake sedge (Erdmann et al. 1987; Palik and Kastendick 2010; Looney et al. 2017; Fig. 2). However, the exact vegetative community that replaces ash and associated insolation will depend on the local hydrology, degree of canopy disturbance, and available seed bank (Fig. 1; Looney et al. 2017). These vegetation conditions and increases in soil saturation following ash mortality are likely to prevent successful tree establishment in areas impacted by EAB or preemptive clearcut harvests resulting in prolonged periods in which these systems have an open, marsh-like structure.

Amphibian Response to Canopy Cover Many pond-breeding amphibians will select sites that have more open canopies to oviposit because their larvae survive better in open-canopy aquatic habitats, even when the terrestrial stages rely on intact forest (e.g., Binckley and Resetarits 2007; Semlitsch et al. 2009). Open-canopy aquatic habitats are often associated with increased algal resources, temperature, and dissolved oxygen (Sacerdote and King 2009; Plenzler and Michaels 2015). Except for some species like woods frogs, which are adapted to feed on low-quality foods in closed canopy ponds, anuran larvae tend to have faster growth and higher survival with an abundance of algal resources in the open-canopy ponds (Werner and Glennemeier 1999; Schiesari 2006). Therefore, the new sedge-dominated or sedge-shrub habitats might be attractive to species that preferentially breed in open-canopy wetlands as well those that are canopy generalists (Table 1). Assuming intact upland non-ash forest remains, anuran richness may increase locally in wetlands affected by EAB or clear-cutting. However, larval growth (and therefore future adult abundance) might or might not be affected by changes in insolation; shading from increased herbaceous vegetation following canopy loss could result in little difference in algal resources, temperature, and dissolved oxygen between forested and herbaceous wetlands (Table 1). Shading may be particularly likely in sedge dominated habitats because sedge coverage is often dense (Fig. 2). For example, in southeastern depressional wetlands subjected to harvesting around the basin, the conversion of forest to sedge habitat did not result in increased algal growth (Batzer et al. 2000). The effects of vegetation on larval performance will depend on the type and density of vegetation that replaces ash. For salamander species willing to breed in wet-meadow habitats, we predict increased biomass of salamander larvae because invertebrate abundance (i.e., food resources) is generally higher in open-canopy habitats (Palik et al. 2001; Batzer et al. 2004). However, competition with invertebrate predators and lower abundance of preferred prey (e.g., chironomid larvae) could result in higher production of salamander biomass in closed canopy habitats (Earl et al. 2011). Overall, with the opening of the canopy from loss of black ash, amphibian communities may become more species rich because of adult preferences for oviposition sites; depending on local vegetation dynamics and biotic interactions, abundances might increase, decrease, or remain the same.

Invertebrate Response to Canopy Cover Aquatic invertebrate taxa diversity (richness and abundance) also often increases with increasing canopy openness, (Palik et al. 2001; Batzer et al. 2004; Plenzler and Michaels 2015). In particular, predator richness and abundance increases with decreasing canopy cover (Table 1; Batzer et al. 2004, Plenzler and Michaels 2015). One reason for this trend is that, like amphibians, some predaceous beetles preferentially colonize and oviposit in open-canopy habitat (Binckley and Resetarits 2007). We also predict that increased light and warmer temperatures, associated with loss of canopy cover, may favor some scraper and gatherer taxa (Palik et al. 2001); submerged sedge leaves should provide increased surface area for biofilm and fine particulate organic matter, an abundant and nutritious food resource for these invertebrates, to accumulate (Huryn and Gibbs 1999; Eggert and Wallace 2007). However, canopy openness does not generally affect diversity of most functional groups (Palik et al. 2001; Batzer et al. 2004; Plenzler and Michaels 2015) and changes in community composition will most likely be observed at the species level, resulting from species specific traits. For example, species that are closed-canopy specialists may be excluded from these new sedge dominated wetlands. Furthermore, interactions between insolation affecting basal food resources and predator abundance exerting top-down control will affect growth and survival of primary consumers (Fig. 1).

A final consideration is the effect of canopy on dissolved oxygen. Dissolved oxygen can be higher in open-canopy habitat, likely resulting from algal photosynthesis (Sacerdote and King 2009; Plenzler and Michaels 2015). However, if water temperatures become too high and reduce dissolved oxygen concentrations, invertebrate community composition will be limited to those taxa (e.g. mosquito larvae, beetle larvae and adults, water bug adults, pulmonate snails, and tadpoles) that are able to access atmospheric oxygen (e.g., Batzer and Boix 2016). Overall, we predict that changes in canopy cover in black ash wetlands impacted by EAB will have minimal effects on the functional composition of aquatic invertebrate communities; predator diversity and abundance may be the most affected.

Leaf and Wood Litter

In addition to effects on habitat structure, light availability, and water temperature, canopy trees also influence the quantity and quality of allochthonous inputs to wetland ecosystems. With wide-spread and rapid mortality of black ash from EAB or pre-emptive clear cutting, and limited potential for replacement of black ash by other overstory tree species in the near-term (Palik et al. 2012), plant communities will retrogress to dominance by lake sedge or other herbaceous and shrub species (Palik and Kastendick 2010; Slesak et al. 2014). As ash trees die, the quantity of leaf litter inputs may decrease over a period of a few years and remain at reduced levels (Palik et al. 2001; Batzer et al. 2004); however, as dead trees begin to fall, the input of woody debris will likely increase, at least temporarily. The succession from ash-dominated to herbaceous (sedge)-dominated wetlands may be avoided with a concerted effort to establish replacement tree species prior to

EAB arrival (Looney et al. 2015); this scenario would retain leaf litter as a dominant allochthonous input.

The conversion from black ash forests to other tree species or to graminoids could affect the quality of litter (Fig. 1). Litter quality, as measured by the ratio of carbon to nitrogen (C/N) of the litter material, and other chemical factors (lignin and cellulose concentrations) influence litter breakdown (Murphy et al. 1998), nutrient release (Webster and Benfield 1986), and, ultimately, algal and biofilm production (Stoler and Relyea 2011). Generally, litter having high C/N ratios (lower quality) decomposes slower than litter with lower C/N ratios (Melillo et al. 1982). Past research in black ash wetlands has demonstrated that black ash leaf litter has lower C/N ratios compared to other tree species in the regional ecosystem, for instance trembling aspen (*Populus tremuloides*; Palik et al. 2006) and faster rates of decomposition compared to several co-occuring tree species. Therefore, loss of ash will likely result in a decrease in the quality of leaf litter (Palik et al. 2006; Stephens et al. 2013); the exception would be if species like alder (*Alnus* spp.), which have nitrogen (N)-rich litter, become abundant. Alder is an abundant understory tree in black ash wetlands (Palik et al. 2012). As a final consideration, expected hydrologic and water temperature differences in wetlands altered by EAB will also interact with litter quality to modify litter decomposition rates (Murphy et al. 1998; Battle and Golladay 2001; Palik et al. 2006). For instance, dry periods enable fungal colonization, which improves litter quality and enhances biotic breakdown (Bärlocher et al. 1978). Patterns of ponding and drying will affect the plant species that are able to colonize a wetland, the availability and decomposition of palatable resources, and their interaction.

Amphibian Response to Litter Anuran larvae have diverse diets, including phytoplankton, periphyton and biofilms, detritus, and invertebrates (Whiles et al. 2010). While resource quantity may be the primary factor affecting tadpole growth (e.g., Cohen et al. 2012; Rowland et al. 2015), the quality of food resources can also be a significant factor for growth and survival (e.g., Schiesari 2006). In experimental settings, differences in nutritional quality and secondary compounds between litter species can alter tadpole development (Earl et al. 2011; Stoler and Relyea 2011; Stephens et al. 2013). Higher quality litter can benefit anuran larvae directly, as a food source, or indirectly, by supporting more abundant algal and biofilm growth (Fig. 1; Stoler and Relyea 2011). Given the expected decrease in leaf nutrient content associated with the loss of ash (Palik et al. 2006; Stephens et al. 2013; Nisbet et al. 2015), we predict that tadpole growth will be reduced. Of note, is the potential difference in basal resources between two possible plant communities after the loss of ash: retrogression to wet meadow or planting of replacement hardwood species, like swamp white oak (Looney et al. 2015). For example, anuran larvae reared on grass/sedge mixes tend to have higher growth and biomass production compared to those reared on oak/hickory mixes (Earl et al. 2011). Mesocosm studies have also demonstrated that salamander larvae may be affected by litter type (Rubbo and Kiesécker 2004; Earl et al. 2011), however the mechanisms are unknown and likely result from complex species interactions affecting prey availability. Overall, we predict that replacement of black ash by wetland herbaceous species could have minimal effects on the growth of larval amphibians; in contrast, replacement by other hardwoods (i.e., planting a transition forest) could reduce larval growth and survival (Table 1).

Invertebrate Response to Litter Black ash loss could significantly alter a dominant food and habitat resources for invertebrates through changes in quality and quantity of leaf and wood detritus (Nisbet et al. 2015). The relationship between litter and invertebrates in seasonal wetlands is complex (e.g., Batzer and Palik 2007) and likely depends on a variety of environmental factors that affect water quality including hydroperiod, leaf decomposition and dissolved oxygen, secondary leaf compounds, and time since harvest or EAB infestation (Magnusson and Williams 2006; Hanson et al. 2009). Yearly variation in invertebrate abundance, invertebrate traits (i.e., habitat-generalist nature; adult ability to disperse aerially), and within-wetland biotic interactions further obscure direct effects of litter on invertebrate communities. Despite the complexity of these environments, we are able to make some generalized predictions that will depend on the local conditions and species in question (Magnusson and Williams 2006; Batzer and Palik 2007).

With regards to litter quality, we predict that shredders could have the strongest response to changes in litter type because they feed directly on detritus and associated biofilms. For example, larval caddisfly growth and litter processing rates can change in response to litter type and state of decomposition (Bärlocher et al. 1978; González and Graça 2003; Mehring and Maret 2011). The direction of response will be species specific and reliant upon the post-ash community. A shift from the majority of inputs being N-rich black ash leaf litter to lower quality leaf litter (e.g. oaks with higher C/N ratios and secondary compounds) could negatively affect some larval shredder invertebrates. Furthermore, reducing leaf litter breakdown rates will have consequences for nutrient cycling (e.g., nitrogen and carbon assimilation; Peterson and Cummins 1974, Vesterdal et al. 2008). On the other hand, some caddisfly taxa utilize sedge leaves as a food resource and case-building material and may benefit from a transition to sedge-dominated habitat (Huryn and Gibbs 1999). Furthermore, if replacement litter sources such as N-rich alder becomes abundant in open-canopy meadows, then there may be no change or possibly increases in litter breakdown rates and growth of larval invertebrates (González and Graça 2003).

Changes in litter processing rates by shredders and the resulting production of fine particulate organic matter (Fig. 1; Mehring and Maret 2011) may affect gatherers and other taxa that can feed on fine particulate organic matter.

Invertebrates may also be sensitive to changes in the quantity of leaf and woody materials. Large-scale studies have shown that changes in forest composition and the quantity of leaf inputs can alter black ash seasonal pond communities (Batzer et al. 2004; Palik et al. 2006; Batzer and Palik 2007; Hanson et al. 2009). In northern black ash seasonal ponds, Batzer et al. (2004) found that invertebrate taxon richness decreased with increasing litter input. Crawling water beetle and predaceous diving beetle abundances were negatively related to litter input (Batzer et al. 2004). Similarly, experimental manipulations have shown that reducing the amount of leaf litter entering a wetland can result in higher invertebrate biomass – at least in some years for some groups (Batzer and Palik 2007). Therefore, the opening of the canopy and reduction of leaf litter input could increase invertebrate diversity in sedge-dominated wetlands. In contrast to expected decreases in ash leaf litter, the input of large amounts woody materials due to black ash die-off or clear-cutting will likely positively influence aquatic life in the wetlands; woody debris provides additional stable habitat for biofilm development and oviposition and pupation sites (e.g., Benke and Wallace 2003; Eggert and Wallace 2007).

The Landscape Context

Large areas across the Great Lakes Region of North America will lose black ash and the severity of this loss for wetland fauna will depend on the landscape context within which a wetland is situated. This includes the size of the wetland (spatial scale), geology and hydrological regime, the pre-EAB dominance of ash in the forest, and the potential for replacement of black ash by other tree species (Fig. 1). Here we consider two extremes, where the magnitude of change may be minimal or extensive. On one end of the spectrum, where black ash is co-dominant with other tree species, wetlands are primarily small depressional ponds, and hydrology is mostly affected by local geology, the effects of EAB on wetland communities may be minimal (Table 1). In this scenario, ash might not be a foundation species and the overall structure and function of forests within and surrounding ponds will likely be maintained; overstory trees could replace ash – naturally or assisted. Furthermore, if upland forests are generally intact, then terrestrial habitat requirements for forest-associated fauna will be retained; EAB will likely not affect landscape connectivity in this landscape setting.

At the other end of the spectrum, where black ash is dominant in spatially extensive swamps, loss of ash may have more severe effects on community composition (Table 1). Complete loss of black ash and fragmentation of upland forest by wet meadows may result in a shift from a community dominated by forest-associated fauna to a community dominated by disturbance-tolerant and open-canopy faunal species. For example, forest-associated amphibians might only utilize edge habitat for oviposition and, in the extreme, could evacuate the area (Semlitsch et al. 2009). Because some amphibians avoid moving through open habitats (Rothermel and Semlitsch 2002), the loss of ash may negatively affect seasonal migrations and landscape connectivity. However, for invertebrates that disperse aerially, conversion of large areas of forested swamp to sedge-dominated swamp might not affect dispersal and overall diversity could increase. Loss of ash in this landscape could favor invertebrate predators, scrapers, and gatherers.

Our discussion of the effects of EAB on wetland fauna has focused on how community structure might be affected by the loss of ash at a single site rather than the regional community. Regional diversity is maintained when there is diversity of habitat types (e.g., Peterman et al. 2014). Therefore, given the range of contexts within which ash wetlands are found, it is likely that regional amphibian and invertebrate communities will be maintained despite local fluctuations in species assemblages and abundances. The exception is where high-risk ash wetlands (ash is dominant, spatially extensive, and regulates hydrology) are spatially clumped, as in north-eastern Minnesota. Under this scenario, spatially and temporally correlated changes in habitat and community could lead to permanent changes in community structure across multiple wetlands.

Conclusions

Using the growing knowledge of the ways in which environmental factors influence community dynamics in wetlands (Batzer and Wissinger 1996; Batzer et al. 2014; Batzer and Boix 2016), we show how an invasive species might indirectly affect amphibian and aquatic invertebrate communities. Over time, and in the absence of either natural or assisted replacement of black ash by other canopy tree species, EAB invasion might cause a shift in plant community composition to an herbaceous-shrub dominated condition in black ash wetlands. Even in the absence of complete forest loss, changes in dominant overstory species could alter canopy phenology and pond dry-down, canopy cover, amount of leaf litter, and nutritional quality of litter. Over short time periods, species richness may increase in these disturbed forests because many wetland species benefit from reduced canopy cover and increased downed woody debris. However, changes in landscape composition, especially where ash is dominant over large areas, could have long-term negative consequences for forest-associated species. Ultimately, changes in the aquatic community may affect the surrounding terrestrial ecosystem because emerging insects and amphibians transfer nutrients and energy from the aquatic to the terrestrial environment; thus, subsidizing terrestrial food webs (Baxter et al. 2005; Pittman et al. 2013). We acknowledge that there is some uncertainty regarding the magnitude and direction of change, resulting from the complexity of these systems and the many factors affecting the post-EAB wetland environment.

The emerald ash borer is just one example of a single species having direct and indirect effects on entire ecosystems. As more exotic species are introduced, the framework we presented can be used to assess the effects that introduced species could have on other ecosystems and identify processes and communities that are most at risk. Our mechanism-based approach is particularly useful for ecosystems that are not well studied (like black ash wetlands). Finally, a focus on the most likely environmental determinants of species occurrence and population growth might be particularly useful when directing research efforts, making management decisions, and evaluating potential mitigation practices.

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References

Ahlgren CE (1957) Phenological observations of nineteen native tree species in northeastern Minnesota. Ecology 38:622–628

Baber MJ, Fleishman E, Babbitt KJ, Tarr TL (2004) The relationship between wetland hydroperiod and nested patterns in assemblages of larval amphibians and predatory macroinvertebrates. Oikos 107: 16–27

Bärlocher F, Mackay RJ, Wiggins GB (1978) Detritus processing in a temporary vernal pool in southern Ontario. Archiv für Hydrobiologie 81:269–295

Battle JM, Golladay SW (2001) Hydroperiod influence on breakdown of leaf litter in cypress-gum wetlands. The American Midland Naturalist 146:128–145

Batzer DP, Boix D (2016) An introduction to freshwater wetlands and their invertebrates. In: Batzer DP, Boix D (eds) Invertebrates in freshwater wetlands: an international perspective on their ecology. Springer, New York, pp 1–23

Batzer DP, Palik BJ (2007) Variable response by aquatic invertebrates to experimental manipulations of leaf litter input into seasonal woodland ponds. Fundamental and Applied Limnology/Archiv für Hydrobiologie 168:155–162

Batzer DP, Wissinger SA (1996) Ecology of insect communities in nontidal wetlands. Annual Review of Entomology 41:75–100

Batzer DP, Jackson R, Mosner M (2000) Influences of riparian logging on plants and invertebrates in small, depressional wetlands of Georgia. Hydrobiologia 441:123–132

Batzer DP, Palik BJ, Buech R (2004) Relationships between environmental characteristics and macroinvertebrate communities in seasonal woodland ponds of Minnesota. Journal of the North American Benthological Society 23:50–68

Batzer DP, Dietz-Brantley SE, Taylor BE, Debiase AE (2005) Evaluating regional differences in macroinvertebrate communities from forested depressional wetlands across eastern and central North America. Journal of the North American Benthological Society 24:403–414

Batzer DP, Cooper R, Wissinger SA (2014) Wetland animal ecology. In: Batzer DP, Sharitz RR (eds) Ecology of freshwater and estuarine wetlands. University of California Press, Berkeley, pp 242–284

Baxter CV, Fausch KD, Saunders WC (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201–220

Benedict MA, Frelich LE (2008) Site factors affecting black ash ring growth in northern Minnesota. Forest Ecology and Management 255:3489–3493

Benke AC, Wallace JB (2003) Influence of wood on invertebrate communities in streams and rivers. In: Gregory S, Boyer K, Gurnell A (eds) The ecology and Management of Wood in world rivers. MD pp, American Fisheries Society, Bethesda, pp 149–177

Binckley CA, Resetarits WJ (2007) Effects of forest canopy on habitat selection in treefrogs and aquatic insects: implications for communities and metacommunities. Oecologia 153:951–958

Brooks RT (2000) Annual and season variation and the effects of hydroperiod on benthic macroinverbrates of seasonal forest ("vernal") ponds in central massachusetts, USA. Wetlands 20:707–715

Cohen JS, Ng S, Blossey B (2012) Amount of litter determines tadpole performance in experimental microcosms. Journal of Herpetology 46:85–90

Dahl TE (2011) Status and trends of wetlands in the conterminous United States 2004 to 2009. US Department of the Interior; fish and wildlife Service, Washington, DC, p 108

Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny ML, Sullivan CA (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163–182

Earl JE, Luhring TM, Williams BK, Semlitsch RD (2011) Biomass export of salamanders and anurans from ponds is affected differentially by changes in canopy cover. Freshwater Biology 56:2473–2482

Eggert SL, Wallace JB (2007) Wood biofilm as a food resource for stream detritivores. Limnology and Oceanography 52:1239–1245

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486

Erdmann GG, Crow TR, Peterson RM, Wilson CD (1987) Managing black ash in the Lake states. USDA Forest Service General Technical Report NC-115

Flower CE, Gonzalez-Meler MA (2015) Responses of temperate Forest productivity to insect and pathogen disturbances. Annual Review of Plant Biology 66:547–569

Flower CE, Knight KS, Gonzalez-Meler MA (2013) Impacts of the emerald ash borer (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp) mortality on forest carbon cycling and successional dynamics in the eastern United States. Biological Invasions 15:931–944

Flower CE, Long LC, Knight KS, Rebbeck J, Brown JS, Gonzalez-Meler MA, Whelan CJ (2014) Native bark-foraging birds preferentially forage in infected ash (*Fraxinus* spp.) and prove effective predators of the invasive emerald ash borer (*Agrilus planipennis* Fairmaire). Forest Ecology and Management 313:300–306

Ford CR, Vose JM (2007) *Tsuga canadensis* (L.) Carr. Mortality will impact hydrologic processes in southern Appalachian forest ecosystems. Ecological Applications 17:1156–1167

Gandhi KJK, Herms DA (2010) North American arthropods at risk due to widespread *Fraxinus* mortality caused by the alien emerald ash borer. Biological Invasions 12:1839–1846

Gandhi KJK, Smith A, Hartzler DM, Hermes DA (2014) Indirect effects of emerald ash borer-induced ash mortality and canopy gap formation on epigaeic beetles. Environmental Entomology 43:546–555

González JM, Graça MAS (2003) Conversion of leaf litter to secondary production by a shredding caddis-fly. Freshwater Biology 48:1578–1592

Gupta A, Miedtke J (2009) Ash management guidelines for private forest land owners. University of Minnesota Extension and Minnesota Department of Natural Resources. Available at http://www.myminnesotawoods.umn.edu/wp-content/uploads/2009/10/Ash-Management-Guide.pdf. Accessed Oct 2016

Hanson MA, Bowe SE, Ossman FG, Fieberg J, Butler MG, Koch R (2009) Influences of forest harvest and environmental gradients on aquatic invertebrate communities of seasonal ponds. Wetlands 29:884–895

Herms DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annual Review of Entomology 59:13–30

Hocking DJ, Babbitt KJ (2014) Amphibian contributions to ecosystem services. Herpetological Conservation and Biology 9:1–17

Holmes TP, Aukema JE, Von Holle B, Liebhold A, Sills E (2009) Economic impacts of invasive species in forests: past, present, and future. Annals of the New York Academy of Sciences 1162:18–38

Huryn AD, Gibbs KE (1999) Riparian sedge meadows in Maine. In: Batzer DP, Radar RB, Wissinger SA (eds) Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York, pp 363–382

Iverson L, Knight KS, Prasad A, Herms DA, Matthews S, Peters M, Smith A, Hartzler DM, Long R, Almendinger J (2015) Potential species replacements for black ash (*Fraxinus nigra*) at the confluence of two threats: emerald ash borer and a changing climate. Ecosystems 19:248–270

Kashian DM, Witter JA (2011) Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. Forest Ecology and Management 261:480–488

Klooster WS, Herms DA, Knight KS, Herms CP, McCullough DG, Smith A, Gandhi KJK (2014) Ash (*Fraxinus* spp) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). Biological Invasions 16:859–873

Koenig WD, Liebhold AM, Bonter DN, Hochachka WM, Dickinson JL (2013) Effects of the emerald ash borer invasion on four species of birds. Biological Invasions 15:2095–2103

Kolka RK, Palik BJ, Tersteeg DP, Bell JC (2011) Effects of riparian buffers on hydrology of northern seasonal ponds. Transactions of the ASABE 54:2111–2116

Lenhart C, Brooks K, Davidson M, Slesak R, and D'Amato A (2012) Hydrologic source characterization of black ash wetlands: implications for EAB response. Proceedings of the American Water Resources Association Summer Specialty Conference Riparian Ecosystems IV: Advancing Science, Economics and Policy Denver, CO June 27-29, 2012

Looney CE, D'Amato AW, Palik BJ, Slesak RA (2015) Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer threatened *Fraxinus nigra* forests in Minnesota, USA. Canadian Journal of Forest Research 45:1728–1738

Looney CE, D'Amato AW, Fraver S, Palik BJ, Reinikainen MR (2016) Examining the influences of tree-to-tree competition and climate on size-growth relationships in hydric, multi-aged *Fraxinus nigra* stands. Forest Ecology and Management 375:238–248

Looney CE, D'Amato AW, Palik BJ, Slesak RA, Slater MA (2017) The response of *Fraxinus nigra* forest ground-layer vegetation to emulated emerald ash borer mortality and management strategies in northern Minnesota, USA. Forest Ecology and Management 389:352–363

Lovett GM, Canham CD, Arthur MA, Weathers KC, Fitzhugh RD (2006) Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56:395

Lovett GM, Weiss M, Leibhold AM, Holmes TP, Leung B, Lambert KF, et al (2016) Nonnative forest insects and pathogens in the United States: impacts and policy options. Ecological Applications 0: 1–19

Magnusson AK, Williams DD (2006) The roles of natural temporal and spatial variation versus biotic influences in shaping the physiochemical environment of intermittent ponds: a case study. Archiv für Hydrobiologie 165:537–556

Mehring AS, Maret TJ (2011) Red maple dominance enhances fungal and shredder growth and litter processing in temporary ponds. Limnology and Oceanography 56:1106–1114

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626

Merritt RW, Cummins KW, Berg MB (2008) An introduction to the aquatic insects of North America. Kendall Hunt Publishing, NY USA

MNDNR (2003) Field guide to the native plant communities of Minnesota: the Laurentian mixed forest province. Minnesota Department of Natural Resources. St Paul, MN

Murphy KL, Klopatek JM, Klopatek CC (1998) The effects of litter quality and climate on decomposition along an elevational gradient. Ecological Applications 8:1061–1071

Nisbet D, Kreutzweiser D, Sibley P, Scarr T (2015) Ecological risks posed by emerald ash borer to riparian forest habitats: a review and problem formulation with management implications. Forest Ecology and Management 358:165–173

Palik BJ, Kastendick D (2010) Response of seasonal pond plant communities to upland forest harvest in northern Minnesota forests, USA. Forest Ecology and Management 260:628–637

Palik B, Batzer DP, Buech R, Nichols D, Cease K, Egeland L, Streblow DE (2001) Season pond characteristics across a chronosequence of adjacent forest ages in northern Minnesota, USA. Wetlands 21:532–542

Palik B, Batzer DP, Kern C (2006) Upland forest linkages to seasonal wetlands: litter flux, processing, and food quality. Ecosystems 9:142–151

Palik BJ, Ostry ME, Venette RC, Abdela E (2011) *Fraxinus nigra* (black ash) dieback in Minnesota: regional variation and potential contributing factors. Forest Ecology and Management 261:128–135

Palik BJ, Ostry ME, Venette RC, Abdela E (2012) Tree regeneration in black ash (*Fraxinus nigra*) stands exhibiting crown dieback in Minnesota. Forest Ecology and Management 269:26–30

Peterman WE, Anderson TL, Drake DL, Ousterhout BH, Semlitsch RD (2014) Maximizing pond diversity across the landscape: a case study of larval ambystomatid salamanders. Animal Conservation 17:275–285

Peterson RC, Cummins KW (1974) Leaf processing in a woodland stream. Freshwater Biology 4:343–368

Pittman SE, Osbourn MS, Drake DL, Semlitsch RD (2013) Predation of juvenile ringed salamanders (*Ambystoma annulatum*) during initial movement out of ponds. Herpetological Conservation and Biology 8:681–687

Plenzler MA, Michaels HJ (2015) Terrestrial habitat quality impacts macroinvertebrate diversity in temporary wetlands. Wetlands 35:1093–1103

Poland TM, McCullough DG (2006) Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. Journal of Forestry 104:118–124

Richter-Boix A, Llorente GA, Montori A (2007) Structure and dynamics of an amphibian metacommunity in two regions. The Journal of Animal Ecology 76:607–618

Rothermel BB, Semlitsch RD (2002) An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Conservation Biology 16:1324–1332

Rowland FE, Bricker KJ, Vanni MJ, González MJ (2015) Light and nutrients regulate energy transfer through benthic and pelagic food chains. Oikos 12:1648–1663

Rubbo MJ, Kiesécker JM (2004) Leaf litter composition and community structure: translating regional species changes into local dynamics. Ecology 85:2519–2525

Sacerdote AB, King RB (2009) Dissolved oxygen requirements for hatching success of two ambystomatid salamanders in restored ephemeral ponds. Wetlands 29:1202–1213

Schiesari L (2006) Pond canopy cover: a resource gradient for anuran larvae. Freshwater Biology 51:412–423

Schiesari L, Werner EE, Kling GW (2009) Carnivory and resource-based niche differentiation in anuran larvae: implications for food web and experimental ecology. Freshwater Biology 54:572–586

Schneider DW, Frost TM (1996) Habitat duration and community structure in temporary ponds. Journal of the North American Benthological Society 15:64–86

Schriever TA, Cadotte MW, Williams DD (2014) How hydroperiod and species richness affect the balance of resource flows across aquatic-terrestrial habitats. Aquatic Sciences 76:131–143

Semlitsch RD, Todd BD, Blomquist SM, Calhoun AJK, Gibbons JW, Gibbs JP, Graeter GJ, Harper EB, Hocking DJ, Hunter ML, Patrick DA, Rittenhouse TAG, Rothermel BB (2009) Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. BioScience 59:853–862

Skelly DK (2001) Distributions of pond-breeding anurans: an overview of mechanisms. Israel Journal of Zoology 47:313–332

Slesak RA, Lenhart CF, Brooks KNB, D'Amato AW, Palik BJ (2014) Water table responses to harvesting and simulated emerald ash borer mortality in black ash wetlands, Minnesota USA. Canadian Journal of Forest Research 968:961–968

Smock LA, MacGregor CM (1988) Impact of the American chestnut blight on aquatic shredding macroinvertebrates. Journal of the North American Benthological Society 7:212–221

Stephens JP, Berven KA, Tiegs SD (2013) Anthropogenic changes to leaf litter input affect the fitness of a larval amphibian. Freshwater Biology 58:1631–1646

Stoler AB, Relyea RA (2011) Living in the litter: the influence of tree leaf litter on wetland communities. Oikos 120:862–872

Tardiff J, Bergeron Y (1999) Population dynamics of *Fraxinus nigra* in response to flood-level variations, in northwestern Quebec. Ecological Monographs 69:107–125

Telander AC, Slesak RA, D'Amato AW, Palik BJ, Brooks KN, Lenhart CF (2015) Sap flow of black ash in wetland forests of northern Minnesota, USA: hydrologic implications of tree mortality due to emerald ash borer. Agricultural and Forest Meteorology 206:4–11

USDA Animal and Plant Health Inspection Service (APHIS) (2017) Emerald ash borer. https://www.Aphis.Usda.Gov/. Archived by WebCite at http://www.webcitation.org/6nuKTzjvs

USDA Forest Service (FS) (2016) Forests of the Northern Forest Inventory & Analysis Program. Web report. U.S. Department of Agriculture, Forest Service, Northern Research Station, Houghton, MI

Van Grinsven MJ (2015) Implications of emerald ash borer disturbance on black ash wetland watershed hydrology, soil carbon efflux, and dissolved organic matter composition. Michigan Technilogical University, PhD Dissertation

Varhola A, Coops NC, Weiler M, Moore RD (2010) Forest canopy effects on snow accumulation and ablation: an integrative review of empirical results. Journal of Hydrology 319:219–233

Verry ES (1986) Forest harvesting and water: the Lake states experience. Water Resources Bulletin 22:1039–1047

Vesterdal L, Schmidt I, Callesen I, Nilsson L, Gunderson P (2008) Carbon and nitrogen in forest floor and mineral soil under six common European tree species. Forest Ecology and Management 255: 35–48

Wagner DL, Todd KJ (2015) Chapter 2: ecological impacts of emerald ash borer. In: Van Driesche RG, Reardon RC (eds) Biology and control of emerald ash borer. USDA Forest Health Technology Enterprise Team, Morgantown WV, pp 15–64

Wallace JB, Eggert SL, Meyer JL, Webster JR (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104

Webster JR, Benfield EF (1986) Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17:567–594

Werner EE, Glennemeier KS (1999) Influence of forest canopy cover on the breeding pond distributions of several amphibian species. Copeia 1999:1–12

Werner EE, Skelly DK, Relyea RA, Yurewicz KL (2007) Amphibian species richness across environmental gradients. Oikos 116:1697–1712

Whiles MR, Gladyshev MI, Sushchik NN, Makhutova ON, Kalachova GS, Peterson SD, Regester KJ (2010) Fatty acid analyses reveal high degrees of omnivory and dietary plasticity in pond-dwelling tadpoles. Freshwater Biology 55:1533–1547

Wiggins GB, Mckay RJ, Smith IM (1980) Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie Supplement 58:97–206

Wissinger SA (1999) Ecology of wetland invertebrates: synthesis and applications for conservation and management. In: Batzer DP, Radar RB, Wissinger SA (eds) Invertebrates in freshwater wetlands of North America: ecology and management. NY pp, Wiley, New York, pp 1043–1086

Wissinger SA, Brown WS, Jannot JE (2003) Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (USA). Freshwater Biology 48:255–270

Wissinger SA, Whissel JC, Eldermire C (2006) Predator defense along a permanence gradient: roles of case structure, behavior, and developmental phenology in caddisflies. Oecologia 148:667–678

Wright JW, Rauscher HM (1990) Black ash. In: burns RM, Honkala BG (eds) silvics of North America volume 2, hardwoods agricultural handbook 654. USDA, Washington DC, pp 344–347