

# Forest succession and terrestrial–aquatic biodiversity in small forested watersheds: a review of principles, relationships and implications for management

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## Summary

Early-successional forest habitat (ESFH), characterized by dense, short-statured woody vegetation, abundant and diverse herbaceous vegetation and high productivity-to-biomass ratios, supports diverse and productive terrestrial faunal communities. In upland forested areas, small watersheds, encompassing ecologically interconnected terrestrial and freshwater habitats, are fundamental units of the landscape for managing and protecting terrestrial and aquatic biodiversity. However, little is known about how the occurrence or abundance of upland ESFHs affects linkages between aquatic and terrestrial species and communities in these small watersheds. It is likely that the presence of ESFH in small watersheds affects the magnitude and direction of aquatic–terrestrial linkages, which may, in turn, affect overall biodiversity. We conducted a literature review of current information on aquatic and terrestrial biodiversity in small watersheds as related to forest age and structure. While the review identifies some fundamental uncertainties and information gaps, there is no evidence of negative effects of the creation and maintenance of upland ESFH on aquatic and riparian diversity. Increased aquatic production, due to higher light and nutrients, and increased primary and secondary production in ESFHs have the potential to increase watershed biodiversity. The review underscores the need for systematic evaluation of these potential outcomes to inform the management community.

## Introduction

Early-successional forest habitat (ESFH), characterized by short-statured vegetation and a high productivity-to-biomass ratio, is critical to terrestrial species in many forested ecosystems. For example, DeGraaf and Yamasaki (2001) list 40 New England wildlife species (12 per cent of the regional wildlife fauna of 338 species) that are restricted to ESFH and only 32 species (10 per cent) as not using ESFH in combination with other forest size classes. However, the area of ESFH in this region continues to decline with each decadal national forest assessments (Trani *et al.*, 2001). A reduction in the scale and intensity of timber management, along with succession of previously abandoned agricultural fields

to mature forest, have reduced the occurrence and extent of ESFH. The importance of ESFH as wildlife habitat, combined with this long-term decline in ESFH resources, has resulted in a large and diverse number of federal and state special-status designations of New England flora and fauna that rely on ESFH (DeGraaf and Yamasaki, 2001).

The forests and streams of first- and second-order headwaters are fundamental units of upland forest landscapes and strongly influence water quality, biodiversity and ecological health of downstream freshwaters (Gomi *et al.*, 2002; Lowe and Likens, 2005). Numerous bidirectional linkages occur between upland forests and embedded aquatic systems (Likens and Bormann, 1974; Nakano and Murakami, 2001; Baxter *et al.*, 2005; Kappes *et al.*, 2011).

For example, the structure and composition of riparian forests are critically important to the geomorphology and functioning of headwater streams (Wallace *et al.*, 1997; Nakano *et al.*, 1999; Cummins, 2002; Mallik *et al.*, 2011). Likewise, headwater streams affect physical, chemical and ecological processes in riparian zones (Naiman and Décamps, 1997; Briers *et al.*, 2005; Gratton and Vander Zanden, 2009) and in turn terrestrial biodiversity (Sabo *et al.*, 2005). However, in contrast to our appreciation of the role of ESFH in maintaining diverse terrestrial communities, there is little understanding of how the presence or abundance of ESFH influences the combined aquatic and terrestrial biodiversity of small watersheds. Consequently, potential benefits of maintaining ESFH are rarely incorporated in management plans for these watersheds.

The influence of upland ESFH on these aquatic–terrestrial linkages is unknown. Many studies have shown the effectiveness of riparian buffers in protecting aquatic systems (Blinn and Kilgore, 2001; Broadmeadow and Nisbet, 2004; Fortino *et al.*, 2004; Clinton, 2011), leaving little question of the importance of maintaining intact forest habitat in the riparian zones of headwater streams. Additionally, studies have shown that forest management activities upland of riparian buffers can affect stream organisms and biochemical processes (Willson and Dorcas, 2003; England and Rosemond, 2004). However, there has been no holistic assessment of the effects of ESFH in the managed portion of the watershed (i.e. upland of the riparian zone) on total biodiversity of headwater streams and their forested watersheds and on the processes maintaining that biodiversity. This information is crucial to management of both private and public lands in the 30 million acre Northern Forest region of the northeastern United States where ESFHs are likely to become increasingly rare under current successional and economic trajectories (Trani *et al.*, 2001; Brooks, 2003).

In this paper, we review and synthesize published studies to provide a clearer understanding of how ESFH affects combined terrestrial–aquatic biodiversity and aquatic–terrestrial linkages in small watersheds and to identify mechanisms underlying these effects. Although we focus on the Northern Forest region, many of the concepts and conclusions emerging from the review apply broadly to upland forested ecosystems. Our objectives are to review (1) the creation of ESFH in small watersheds with respect to underlying disturbance factors, spatial and temporal dynamics and synergies and conflicts with other management targets, (2) species groups and guilds associated with ESFH and small watersheds, (3) key ecological processes and concepts underpinning the role of ESFH and small watersheds in biodiversity conservation and (4) implications of management options for conservation of ESFH and small watersheds, along with the identification of key information gaps.

#### *Creation, maintenance and extent of ESFHs*

Mechanisms of forest disturbance, patterns of occurrence, duration of these disturbances, and resultant patterns of

vegetation composition and structure interact to create distinct categories of ESFH. Lorimer (2001) distinguishes between ‘successional habitat’ dominated by pioneer species and ‘young forest habitat’ dominated by young trees of late-successional species. Both types include low woody vegetation, but they differ greatly in vegetation composition. Successional ESFHs are created by more destructive disturbance events and are initiated by pioneering species, including herbaceous vegetation, on barren or treeless ground. Young forest ESFHs are created by less destructive disturbances, such as fire, insects or wind, and may initiate with seedlings and saplings of mature forest species (Bormann and Likens, 1979; Lorimer, 2001). Consequently, young forests are more transitory than successional ESFH. The distinction between successional and young forest ESFHs has received little attention, but it may be a key consideration in regional conservation planning (Askins, 2001). King *et al.* (2009) reported differences in vegetation structure and avian community assemblage between ephemeral regenerating (young) forest and permanently maintained wildlife openings, dominated by shrubs and herbaceous vegetation, typical of ESFH.

ESFHs are disturbance dependent; the creation, maintenance and/or restoration of ESFHs require periodic natural or anthropogenic disturbance. The temporal and spatial patterns of disturbance events are a matter of considerable debate but are critical to the sustainable supply of these habitats. In turn, ecological theory predicts that the high species diversity of ESFHs is partly a consequence of intermediate levels of disturbance that are sufficiently frequent to prevent competitive exclusion by one or a few dominant species but infrequent enough to allow disturbance-sensitive species to become established (Connell, 1978). In this section, we briefly review: (1) the anthropogenic and natural processes which create ESFH in the Northern Forest region, (2) spatial and temporal dynamics of ESFH and (3) vegetation structure and function.

Both historically and currently, disturbance regimes and patterns vary widely and are spatially non-random (Lorimer, 2001; Lorimer and White, 2003). Disturbance events that create and/or maintain ESFH vary geographically and among major forest types (Lorimer, 2001) and in their severity (Roberts, 2004). Windstorms, ice storms, fires, drought and insect and disease infestations are important agents of natural disturbance in the eastern hemlock (*Tsuga canadensis* L. Carr) – northern hardwood – white pine (*Pinus strobus* L.) type of the Northern Forest region. Effects of these disturbances, other than wind, are more commonly diffuse, causing the death of scattered trees and patches. Catastrophic wind disturbance is a dominant feature in northern hardwood forests, but its frequency is fairly low, except in coastal and near-coastal areas affected by Atlantic hurricanes (Lorimer and White, 2003). Most interior northern hardwood regions were dominated by old-growth forest in pre-settlement times, with ESFH occupying an estimated 13 per cent or less of the landscape (Lorimer, 2001). Management to restore pre-settlement ESFH conditions and maintain or mimic natural disturbance processes are desirable goals, but can, in some cases,

result in forests of differing species composition. For example, recent invasive pest and pathogen-caused declines in ash (*Fraxinus* sp. L.), beech (*Fagus grandifolia* Ehrh.) and hemlock in southern New England may, eventually, change the regional species pool, thus affecting the successional dynamics of ESFH in the Northern Forest region (Lovett *et al.*, 2006).

Fire, whether natural or human-caused, was a dominant disturbance factor in the oak-dominated forests (Lorimer, 2001) of the southern portions of the Northern Forest. While not regionally important, other fire-dependent forest types of the northern forest, such as pitch pine (*Pinus rigida* Mill.) and scrub oak (*Quercus ilicifolia* Wang.) require active management, including controlled burning and mechanical treatments, to sustain them (Jordan *et al.*, 2003).

Flooding can be a canopy disturbance factor in riparian forests by erosion along headwater streams, causing individual trees to fall, creating light gaps and adding large woody debris to the stream (Fierke and Kauffman, 2005; Keeton *et al.*, 2007). However, in most cases, it is unlikely that flooding of low-order streams would be sufficiently destructive or of sufficient duration to affect large forest areas. One major exception is the disturbance associated with beaver dam construction and abandonment and its effects on the frequency, duration and extent of flooding (McMaster and McMaster, 2001; Wright *et al.*, 2003; Bonner *et al.*, 2009).

Native (e.g. spruce budworm (*Choristoneura fumiferana* Clemens) Bouchard *et al.*, 2006) and invasive pests (e.g. gypsy moth (*Lymantria dispar* L.) Davidson *et al.*, 1999) and pathogens can disturb forest canopies sufficiently to allow for the creation of ESFH conditions (Crawley, 1989; Roberts, 2004). Eschtruth *et al.* (2006) documented changes in vegetation composition and structure of two hemlock ravines (Delaware Water Gap Recreation Area, PA) following hemlock woolly adelgid (*Adelges tsugae* Annand) infestation. Average per cent total transmitted radiation more than doubled, resulting in the increase in total per cent cover and species richness of vascular plants and in the occurrence of invasive plant species. Other pest and pathogen disturbances may only cause minor changes in forest structure and composition (Lovett *et al.*, 2006).

Anthropogenic actions can create or maintain ephemeral or longer term ESFH conditions either as the objective of or incidental to management goals. Utility rights-of-way in forested areas are intensively managed by selective herbicide applications, resulting in permanent ESFH conditions (Confer and Pascoe, 2003). Ephemeral openings created by silvicultural operations or permanently maintained wildlife openings result in distinct habitat conditions that support differing avian communities (Askins, 2001; Thompson and DeGraaf, 2001; King *et al.*, 2009; Schlossberg and King, 2009).

Without repeated or chronic disturbance, ESFHs are generally quite ephemeral and rapidly succeed from conditions following disturbance to closed canopy, exclusion stages of development (e.g. 25 years; Schlossberg and King, 2009). Concurrent with successional (i.e. compositional)

development following disturbance, diversity and productivity also follow a temporal pattern. As a general pattern, aboveground net primary productivity reaches a maximum in young forests and then decreases by as much as 76 per cent as stands mature (Gower *et al.*, 1996). Data from headwater riparian zones in New Hampshire suggest that production of soil invertebrates may follow a similar pattern (Greene *et al.*, 2008), and floral diversity has been shown to decrease with time since disturbance in this region (Howard and Lee, 2003). Furthermore, temporal patterns of change following disturbance have been observed in an increase in benthic invertebrate community abundance in streams draining ESFHs (Stone and Wallace, 1998), an increase in the terrestrial component of stream salamander diets with bordering high-density/small-diameter forest stands (Lowe *et al.*, 2005), and in species-specific variation in shrubland bird composition and abundance with time following timber harvesting (Schlossberg and King, 2009; Schlossberg *et al.*, 2010).

The area of ESFH in the northeastern US has declined since standardized forest surveys were begun in ca 1950 (Trani *et al.*, 2001). Over this period, losses of ESFH are greater in the coastal states than among the interior states (Brooks, 2003). The area of ESFH in coastal lands is approaching or below the area estimated to have existed at the time of European settlement (Lorimer, 2001). Selective harvesting, fire suppression, urban sprawl and declines in the rate of agricultural abandonment have contributed to the present imbalance in distribution of young forest. Private forest ownership predominates in the northeastern US and presents a significant challenge to the active management of ESFHs (Trani *et al.*, 2001). Given the current trajectory, the extent of ESFHs will continue to decline without proactive management of private forests.

### *ESFHs in small watersheds: species groups and guilds*

#### *ESFH diversity*

For the most part, flora of the ESFHs of the northeastern US consist of common, opportunistic, early-successional plant species and few rare, endemic species (Latham, 2003). ESFHs with the greatest number of rare plant species include geographically restricted alpine/subalpine dwarf shrub and krumholz, heath-dominated peatlands and 'mesic barrens' (Latham, 2003). Plant species diversity in ESFHs tends to increase rapidly following disturbance, depending on available seed source, to a maximum richness by 15–30 years (Howard and Lee, 2003). Thereafter, floral diversity declines with age, governed by competition for light and the loss of shade-intolerant species.

Terrestrial invertebrate abundance is generally predicted to be greater in ESFH than mature forests (Brown, 1984). Herbivores seek more nutrient-rich, herbaceous vegetation typical of ESFH, resulting in a greater biomass of these insects on regenerating vegetation (Schowalter *et al.*, 1981). Although the direction of taxon-specific terrestrial invertebrate response to timber harvest varies, most evidence indicates that canopy openings result in higher overall

abundances of terrestrial invertebrates (Deans *et al.*, 2005). This effect was demonstrated by Greene *et al.* (2008) who identified a greater abundance of terrestrial invertebrate prey of spring salamanders (*Gyrinophilus porphyriticus* Green) in ESFHs than mature forests. A large number of rare moths and butterflies (Lepidoptera) are associated with shrub-dominated ESFHs in southern New England, especially oak and pine communities (Wagner *et al.*, 2003). In addition to moths and butterflies, many less well-known phytophagous insects are associated with shrub-dominated ESFHs in southern New England, especially oak and pine communities (Wagner *et al.*, 2003). In general, insects favouring ESFH should be highly mobile (e.g. fully winged), with rapid invasion rates and high reproductive potential (Brown, 1984).

It is generally accepted that amphibians tend to avoid ESFHs, but this avoidance is not absolute and there is considerable variation among species and age class (deMaynadier and Hunter, 1995; Renken *et al.*, 2004). This avoidance is believed to stem from increased forest-floor temperatures and decreased forest-floor moisture that follows canopy reduction and exposure of the forest floor to solar radiation (deMaynadier and Hunter, 1995), resulting in increased energetic costs for amphibians (Homyack *et al.*, 2011). However, regrowth of low vegetation (herbaceous, shrubs and tree regeneration) is rapid following canopy disturbance in northern forests, shading the forest floor, and resulting in forest-floor microclimates quickly returning to pre-disturbance conditions (Brooks and Kyker-Snowman, 2008; Homyack *et al.*, 2011).

Broadly, toads (Amphibia: Anura: Bufonidae) tend to be more tolerant of ESFHs than frogs (Anura: Ranidae), and salamanders (Amphibia: Caudata) are the least tolerant. There are no amphibian species in the northern forest that are known to be exclusively associated with old-growth conditions (DeGraaf and Rudis, 1983; DeGraaf and Yamasaki, 2001). Adult amphibians tend to be more tolerant of canopy disturbance than juveniles, but post-metamorphic individuals of some amphibian species are tolerant of open-canopy areas (Patrick *et al.*, 2006).

Reptiles are generally considered more tolerant of forest canopy disturbance than amphibians (Renken *et al.*, 2004). Reptilian species of the Northern Forest are fairly few in number and their use of ESFH has not been well assessed (DeGraaf and Rudis, 1983; DeGraaf and Yamasaki, 2001). However, given that the thermal constraints are likely to be the major limiting factor for the northern distribution of many reptile species, closed-canopy forests are unlikely to be preferred habitats. There are no reptile species restricted to closed-canopy habitats in the northern forest region (DeGraaf and Rudis, 1983).

Mammals, as a group, are not closely associated with ESFHs. Of the 64 mammal species listed for New England (DeGraaf and Yamasaki, 2001), as many as 20 species demonstrate some preference for ESFHs (Litvaitis *et al.*, 1999; Litvaitis, 2001). Bats (Chiroptera) identify and readily use open-canopy ESFHs for foraging, especially larger bodied species that are not adapted to flight in structurally cluttered forest canopies (Brooks, 2009). The New England

cottontail (*Silvilagus transitionalis* Bangs) is the mammal species most closely associated with ESFHs (Litvaitis and Villafuerte, 1996). Due in great part to loss of ESFHs, the species is a candidate for listing under the US Federal Endangered Species Act (71 Federal Register 53756, 53757-58 (Sept. 12, 2006)).

Birds are probably the best documented faunal community of ESFHs. Avian fauna are diverse and express structurally oriented habitat selection (Hunter *et al.*, 2001). Schlossberg *et al.* (2010) identified 41 bird species that regularly breed in ESFHs in New England. Bird species associated with shrublands and ESFHs account for ~15 per cent of the total number of breeding species of the north-eastern US and are experiencing disproportionate declines in regional populations (Dettmers, 2003). Additionally, both adults and young of forest-interior species use ESFHs during the post-fledging period (Marshall *et al.*, 2003).

#### *Riparian and aquatic diversity*

Aquatic and terrestrial environments juxtaposed at riparian zones possess a diversity of species and environmental processes (Naiman and Décamps, 1997; Crow *et al.*, 2000). Sabo *et al.* (2005) report that riparian habitats support species' pools distinctly different than those of adjacent upland habitats. The occurrence of distinct riparian communities has been ascribed to (1) the physical conditions associated with stream presence, such as wetted soil that creates a special microenvironment, (2) the presence of consumers of prey originating from the stream, such as fish and invertebrates and (3) food-web interactions (Richardson *et al.*, 2005). The unique characteristics of riparian zones may also occur along small streams and in moist temperate climates where the contrast between streamside and upland forests is not as strong as in drier environments (Richardson *et al.*, 2005). However, riparian effects on patterns in biodiversity across low-order (e.g. first to third) stream-to-upland forest gradients occur inconsistently, especially in moist temperature environments of the Northern Forest region, and unique riparian microclimates may not be evident in these systems (Brooks and Kyker-Snowman, 2009).

Plant diversity in headwater riparian zones may not differ substantially from that of adjacent upland forest. Hagan *et al.* (2006) found that herbaceous plant diversity in western Maine was greater in the immediate vicinity (0–5 m) of streams, but these differences were subtle and there were no detectable differences in shrubs or tree vegetation. However, the cumulative floral diversity at watershed scales is greater for fluvial landforms of the northern Great Lakes region than for upland forest (Goebel *et al.*, 2003). Also, disturbance of upland forests can indirectly affect floral communities in headwater riparian zones. For example, timber harvesting in the upland forest of small watersheds was shown to affect the riparian herbaceous community and narrow the effective width of the riparian zone through increased light and evapotranspiration (Dieterich *et al.*, 2006).

DeGraaf and Yamasaki (2000) identify 52 species of birds and mammals that are associated with riparian

areas of the northeastern US. They identify three factors that influence animal use of riparian areas: (1) extent of riparian forest and connectivity with adjacent upland land use, (2) lentic versus lotic systems, and (3) vegetation structure. Most riparian-associated species occur along edges of wetlands. In general, animal use increases with extent of riparian forest, and connectivity with adjacent uplands is higher in lentic riparian zones than lotic riparian zones and with increasing structural habitat diversity (Naiman *et al.*, 1993; DeGraaf and Yamasaki, 2000).

#### *Fish*

In fish-bearing streams, disturbance of upland and riparian forest can change abiotic and biotic components of fish habitat. Canopy disturbance from logging can affect stream macroinvertebrates, but the ensuing effects on fish are neither consistent nor uniform, and partial disturbance may have no significant effect (Chizinski *et al.*, 2010). In northern New England, brook trout (*Salvelinus fontinalis* Mitchell) density and biomass were higher in streams draining young recently logged stands than in streams draining mature second-growth stands (Nislow and Lowe, 2003, 2006). This response may have contributed to an increase in overall macroinvertebrate abundance in the recently logged stands. However, the local increases in trout may negatively affect co-occurring fish and amphibian species, as well as downstream conditions. In contrast to these findings in northern New England, brook trout density and biomass were substantially lower in headwater streams bordering selectively logged catchments in Michigan's Upper Peninsula (VanDusen *et al.*, 2005). Streams in logged stands had increased fine sediment content and lower overall habitat quality.

#### *Amphibians and reptiles*

Stream salamanders of the Northern Forest region frequently venture into adjacent riparian and upland forest habitats to forage (Lowe *et al.*, 2005; Greene *et al.*, 2008), behaviour that can be affected by disturbance of these habitats (Willson and Dorcas, 2003; Olson *et al.*, 2007). Population-level effects of forest disturbance on amphibians can occur through impacts on both stream and forest-floor conditions. For example, timber harvesting, even with protected riparian buffers, can result in sedimentation and increased substrate embeddedness and a decline in stream salamander abundance (Lowe and Bolger, 2002; Lowe *et al.*, 2004). The presence of a stream can also affect forest-floor microclimatic conditions in adjacent riparian forest, improving temperature and moisture conditions favourable for amphibians (Olson *et al.*, 2007).

Terrestrial activity for nesting, aestivating or foraging is common in some freshwater turtle species (Bodie and Semlitsch, 2000). The wood turtle (*Clemmys insculpta*, Le Conte), a species with listed status in many state and Provincial jurisdictions throughout its range, uses forest streams more than other turtles of the Northern Forest, which principally use lentic waters (DeGraaf and Yamasaki, 2001). The impact of ESFH creation on the species is unknown, though the species is described as disturbance

dependent, using young, short, low cover, scrub-shrub habitats (Compton *et al.*, 2002; Arvisais *et al.*, 2004). The identification and protection of riparian zones are recommended for the management of freshwater turtles (Bodie, 2001).

#### *Birds and mammals*

Bird and mammal fauna are less closely identified with riparian habitats, possibly as they are more mobile and less likely to be associated with a single habitat type. One exception, the Louisiana waterthrush (*Seiurus motacila*, Vieillot) is closely linked to small streams and associated riparian areas (feeding largely on aquatic invertebrates) to the extent that Mattison and Cooper (2006) suggest that the presence of this species be used as an indicator of stream biotic integrity. In general, where a distinctive riparian avian community along small streams has been recognized, the riparian forest was structurally or compositionally different than the upland forest, with greater conifer or shrub density and dominance (Bub *et al.*, 2004), or the riparian forest had been harvested, creating distinctive ESFH (Hanowski *et al.*, 2007). For example, beaver-created ESFH along small streams provide critical habitat for scrub-shrub birds of regional conservation concern (Chandler *et al.*, 2009).

Mammals are more typically habitat generalists than birds, and home ranges would typically include riparian areas in a larger suite of habitats (DeGraaf and Yamasaki, 2000). Small- and medium-sized mammals associated with small streams and adjacent upland forests (e.g. water shrew (*Sorex palustris*, Richardson)) and/or vertebrate (e.g. mink (*Mustela vison*, Schreber)) that consume invertebrate aquatic prey are linked to forest structure through indirect effects on their prey base, but no studies have explicitly examined these relationships. Bats (Chiroptera) drink from and forage over aquatic systems. Any disturbance to riparian vegetation that affects the production of aquatic insects would impact bat foraging activity (Ober and Hayes, 2008). Small-bodied, clutter-adapted species (e.g. *Myotis* spp.) may also use small streams within continuous forest for daily movements between roosting and foraging habitats (Brooks, 2009).

#### *Invertebrates*

A general conceptual model of small stream ecosystem structure and function views the stream as a subsystem of its watershed (Hynes, 1975) and linkages among aquatic, riparian and upland forest habitats are best documented by impacts on stream and terrestrial invertebrates. Invertebrate linkages between streams and riparian zones are reciprocal (Baxter *et al.*, 2005). Reach-scale observational studies have measured variation in terrestrial insect inputs to streams due to differences in forest structure and composition (Wipfli, 1997; Allan *et al.*, 2003). Fluxes of terrestrial invertebrates to streams are highest from closed-canopy riparian zones with deciduous vegetation and vary markedly with invertebrate phenology and weather (Cloe and Garman, 1996; Nakano *et al.*, 1999; Baxter *et al.*, 2005). Because these studies limit measurement of forest

characteristics to the riparian zone, however, they overlook any watershed-level influence on terrestrial invertebrate supply to streams. However, a predicted increase in biomass of mobile invertebrates within ESFH may cause heavier invertebrate traffic over streams flowing among ESFH patches, leading to increased terrestrial subsidies to aquatic and riparian consumers (Brown, 1984; Greene *et al.*, 2008).

In the opposite direction, benthic production can be exported to terrestrial habitats by the emergence of adult insects from streams and can constitute a substantial energy supply to terrestrial consumers (Gratton and Vander Zanden, 2009; Wesner, 2010). The flux of aquatic invertebrates to riparian zones varies with in-stream productivity and is enhanced by reducing canopy coverage over streams. When no riparian buffer is used, more aquatic insects emerged from streams in clear-cut catchments than in forested catchments (Banks *et al.*, 2007). The abundance of adult aquatic insects in the terrestrial environment declines exponentially with distance from the stream edge (Baxter *et al.*, 2005; Macneale *et al.*, 2005; Gratton and Vander Zanden, 2009; Wesner, 2010). While reduction in riparian canopy cover increases the magnitude of aquatic insect emergence, it is still unclear how timber harvest outside of the riparian zone influences aquatic insect production and emergence when riparian buffers are intact. With no-harvest buffer zones, leaf litter decomposition and aquatic macroinvertebrate community structure differed between clear-cut and reference catchments, suggesting that macroinvertebrates were accurate bioindicators of catchment logging impacts (Kreutzweiser *et al.*, 2008). Effects seem to have been caused by upland logging disturbances, possibly affecting water quality, flow regimes or water temperature.

### *Key ecological processes and concepts*

#### *Aquatic–terrestrial interactions and stream processes*

There are a variety of linkages for energy and nutrient exchange between streams and adjacent upland forests (Likens and Bormann, 1974). The vectors transporting energy and materials may be categorized as meteorologic, geologic or biotic. The biotic linkages of terrestrial and aquatic flora and fauna are the focus of this review but in no way diminish the significance of physical linkages. Ground and surface water inputs of nutrients and particulate matter are one of the most important terrestrial–aquatic linkages (Likens and Bormann, 1974), and research on this topic has played a central role in the growth of stream ecology as a discipline (Cummins, 2002).

#### *Stream processes*

Small forest streams are strongly linked to adjacent forest because of the high canopy closure over the stream and high edge-to-area ratio of these two systems (Richardson *et al.*, 2005). Disturbance in riparian and adjacent upland forest can affect embedded streams in conflicting ways. Disturbance that affects the forest floor can result in increased sedimentation and, consequently, stream embeddedness,

which can decrease biotic abundance and diversity within the stream (Lecerf and Richardson, 2010). At the same time, forest soil disturbance can result in increased nutrient inputs to streams and disturbance of the canopy can increase light penetration, which can increase water temperatures, primary production and litter processing rates, changing in invertebrate composition and increasing invertebrate biomass (Griffith and Perry, 1991; Banks *et al.*, 2007; Stovall *et al.*, 2009).

While closed forest canopies over small streams reduce light transmission and autochthonous production, they increase leaf fall into the stream and the development of allochthonous-based food-webs. The exclusion of litter can have a strong bottom-up effect that is propagated through detritivores to predators; most invertebrate taxa will decline in abundance, biomass or both (Wallace *et al.*, 1997). The lateral extent of allochthonous litter inputs to headwater streams is unknown, but it probably declines exponentially with distance.

Canopy disturbance can reduce amounts of litter fall and allow for the occurrence of early-successional plant species, whose litter is frequently more easily processed than that of mature forest trees (Griffith and Perry, 1991). Enhanced in-stream litter decomposition rates in disturbed riparian forest can be explained by four factors: (1) post-logging nitrate inputs may stimulate microbial decomposition processes, (2) dominance of litter fall by medium and fast processing leaves from the recovering forest, (3) increased sediment loads during storms may hasten breakdown through physical abrasion and (4) interaction of high nutrients and high-quality leaves may be attractive to leaf-shredding invertebrates whose feeding activities may also hasten breakdown rates (Cummins, 2002).

Not every canopy disturbance in riparian zones impacts in-stream processes. Across the eastern US, moderately disturbed early- and mid-successional riparian forests were compositionally similar to late-successional reference conditions (Rheinhardt *et al.*, 2009). Kreutzweiser *et al.* (2004) found that selection-based harvesting, at up to 42 per cent basal area removal with no riparian buffers, did not significantly alter average over-stream canopy cover, leaf litter or other organic matter inputs, benthic particulate organic matter accumulation, or woody debris abundance. Dissolved organic matter fluxes increased slightly for 1 year after harvest and were associated with increased water yield. As harvesting intensity increased above 42 per cent, significant effects on organic matter inputs and accumulation in streams were detected. However, McKie and Malmqvist (2009) detected no differences in macroinvertebrate abundance, diversity or assemblage composition between forested and clear-cut streams.

While canopy disturbance and young forests are associated with elevated litter decomposition rates and associated invertebrate impacts, large in-stream wood is associated with older forests (Keeton *et al.*, 2007; Warren *et al.*, 2009). In an analysis of large wood loading to a chronosequence of 28 streams in the northeastern US, the volume and frequency of large wood and wood accumulations were most closely associated with the age of the

dominant canopy trees in the riparian forest (Warren *et al.*, 2009). Accumulations of large in-stream wood provide a variety of ecological and geomorphic functions in stream ecosystems, such as the retention of sediment and organic material and the formation and complexity in pool habitats, creation of cover and refugia and increasing bank stability (Sweka and Hartman, 2006; Keeton *et al.*, 2007).

#### *Landscape matrix*

Streams are closely connected to the landscapes in which they occur (Cummins and Klug 1979; Fausch *et al.*, 2010) and the interactive effects of streams and upland forests can occur at these landscape scales (Johnson and Host, 2010). As such, one needs to consider landscape elements beyond the boundaries of individual watersheds that might influence terrestrial and aquatic biodiversity (Ficetola *et al.*, 2008). For example, the structure of the stream network can affect the abundance of stream salamanders; spring salamanders were less abundant in isolated headwater streams than in paired streams that allow for greater population connectivity (Lowe and Bolger, 2002). Contiguous 'linkage areas' should be considered for species dispersal among watersheds (Olson and Burnett, 2009; Grant *et al.*, 2010).

The occurrence and amount of non-forest land cover in otherwise forested watersheds can also affect headwater food webs. England and Rosemond (2004) showed that coarse particulate matter decreased with small decreases in forest cover in predominantly forested watersheds (82–90 per cent), independent of the successional stage of existing forest, resulting in greater dependence on autochthonous production among aquatic consumers. The arrangement of habitat elements in a forest-stream landscape is also important to mobile non-territorial species, such as bats. The interspersed streams and open-canopy ESFH facilitates access of travel corridors (streams) to uncluttered foraging habitat (Brooks, 2009). Retention of mature trees and snags for roosting sites could complete bat summer habitat requirements.

#### *Biodiversity management and conservation of ESFHs in small watersheds*

##### *Management principles*

Prior to European colonization, early-successional and shrub-dominated habitats were widely distributed throughout the northeast US (Litvaitis *et al.*, 1999). Guidelines for restoring a more natural forest age structure may require more detailed investigations of historic disturbance regimes that are spatially linked to local habitat and site variation (Lorimer and White, 2003). Current efforts to maintain these communities are not sufficient and they are continuing to decline in abundance (Trani *et al.*, 2001; Brooks, 2003; Buffum *et al.*, 2011). To reverse this trend, an aggressive approach will be required to increase the area and distribution of ESFH and to restore the disturbance regimes to maintain these systems (Litvaitis, 2003). Where forests dominate, efforts should be directed towards

patterns that resemble natural disturbances. The creation and maintenance of ESFHs will require a diverse mix of management interventions; natural disturbance events are too irregular (wind) or potentially destructive (wild fire). Without active management, ESFHs and their unique wildlife communities will continue to decline (Askins, 2001).

Decades of research, much of it accomplished in the Northern Forest region, has yielded a general understanding of the type and extent of management required to conserve many ESFH-dependent terrestrial species in upland forests (King *et al.*, 2011). The retention of minimal populations of ESFH birds could be accomplished by maintaining a minimum of 10–15 per cent of forested land in ESFH (Dettmers, 2003). The most recent estimate, based on stand-size class summaries from forest surveys, is that ESFH constitutes 15.1 per cent of timberland in the northeast (Trani *et al.*, 2001) but is much less abundant (e.g. 5 per cent of timberland) in more populated areas of the region (Brooks, 2003). To support the recovery of declining species would require a greater area of ESFH or at least ending the declines in area experienced over the recent past (Buffum *et al.*, 2011).

Human actions can create or perpetuate ephemeral ESFHs as incidental to or the objective of management actions (Askins, 2001; Thompson and DeGraaf, 2001; Confer and Pascoe, 2003; King *et al.*, 2009). Management alternatives include controlled burning, mechanical thinning or mowing, grazing and silvicultural treatments (Hunter *et al.*, 2001; Litvaitis, 2001; Oehler, 2003; Wagner *et al.*, 2003). In developed landscapes, the indirect benefits of conventional management efforts are likely to be insufficient to maintain viable populations, and intentional large-scale (>10 ha) habitat management to create clustered wildlife openings of ESFH may be necessary (Litvaitis, 2001; King *et al.*, 2009). ESFHs were historically emphasized as important for a number of harvested 'game' species (Leopold, 1933). As the wildlife management profession evolved and began to address all faunal species and biodiversity, the prioritization of game species and their habitats faded in importance within wildlife management programmes. To effectively maintain ESFHs, State agencies will need to develop new funding sources, use alternative and more cost effective management tools and consider expanding technical assistance to private landowners (Oehler, 2003). A concern for managers must be how management for upland ESFH may influence terrestrial-aquatic linkages and aquatic biodiversity (Hutchens *et al.*, 2004). These are vital questions because much of the opposition to forestry management comes from concerns about potential negative effects of harvesting operations on water resources (Hutchens *et al.*, 2004).

The recognition and protection of a riparian buffer have been used as the principal management tool to protect aquatic resources during forest management operations (Broadmeadow and Nisbet, 2004; Fortino *et al.*, 2004). The main functions of the buffers are for sediment removal and erosion control, protection of water quality, moderation of shade and water temperature, maintenance of habitat structural diversity and ecological integrity and

improvement of landscape quality (Broadmeadow and Nisbet, 2004). The ecological delineation of riparian buffers is difficult and can vary by the metrics being considered. Clinton *et al.* (2010) suggest that significant transitions in structural and functional characteristics occur at 10–20 m from southern Appalachian headwater streams and that these transitions could be useful for riparian definition. The maintenance of physical and chemical characteristics of streams generally requires narrower buffers (10 m), whereas the maintenance of ecological integrity requires broader buffers (30 m) to minimize edge effects (Baker *et al.*, 2009).

Riparian management has traditionally emphasized a ‘hands-off’ approach; however, some regulations permit limited forest management within riparian corridors. For example, the Massachusetts Forestry Best Management Practices permit up to 50 per cent basal area removal in filter strips along all water bodies (Kittredge and Parker, 1996). By regulating forest management in riparian zones based principally on water quality, we risk losing key aquatic–terrestrial interactions and adjacent stream and upland forest biodiversity. Benefits are greatest when buffers replicate native forest conditions and processes, including natural disturbances regimes (Sibley *et al.*, 2012).

Selective logging is one category of riparian and stream habitat management that has become widely accepted for facilitating the recruitment of large downed wood to stream channels (Keeton *et al.*, 2007; Nislow, 2010). In addition to directly recruiting downed wood, selective felling creates canopy openings that can increase light and may encourage early-successional vegetation structure. Given that many northeastern US upland streams appear to be light limited (Rand *et al.*, 1992), such activities may increase stream productivity and diversity by adding both light and key physical habitat structure via large wood. At the same time, forest management in the riparian zones brings certain risks. Soil disturbance is particularly problematic, due to potential damage to streambanks and associated sedimentation of stream channels. Soil disturbance also facilitates invasive exotics such as reed canary grass (*Phalaris arundinacea*, L.), which is particularly damaging in riparian areas (Zedler and Kercher, 2004). Finally, increased light may cause stream temperatures to rise. In the Northern Forest region, the optimum level of shade is achieved with 50 per cent of the stream surface open to sunlight and the remainder covered by dappled shade (Keeton *et al.*, 2007; Stovall *et al.*, 2009).

Given the regulatory protection of the riparian zone, negative effects of forest management on aquatic habitat conditions appear to depend on the frequency and magnitude of the disturbance of upslope forest stands. Until thresholds of disturbance are exceeded, riparian buffers tend to be effective in preventing excess sediment, nutrients and light from reaching stream channels. One exception may be the effects of forest harvesting on stream acidification and aluminum mobility, which, due to atmospheric deposition, is a continuing threat to the aquatic ecosystems of the Northern Forest (McHale *et al.*, 2007). Unlike sediment, nutrients and shading, riparian buffers

appear to have little effect on reducing stream acidification (Ormerod *et al.*, 1993). In the Catskill Mountains of New York, streams experienced an increased magnitude and frequency of episodic acidification events when forest basal area removals exceeded ~70 per cent, but with no discernable effects at <30 per cent removal (McHale *et al.*, 2008). If harvest rotations are shortened in order to promote ESFH, this might result in depletion of base cations and soil buffering capacity, but these impacts are unknown for current targets for ESFH (10–15 per cent of forest land area).

Another example of a critical process that could be indirectly affected by management for upland ESFH would be habitat fragmentation and connectivity, particularly if permanent roads are constructed (Marsh *et al.*, 2004; Semlitsch *et al.*, 2007). In such cases, making sure that any associated road crossings allow passage of aquatic and riparian fauna would be critical for maintaining biodiversity (Ward *et al.*, 2008; Nislow *et al.*, 2011).

#### Case studies

Relatively few studies have directly investigated the effects of the presence of ESFH in the watersheds of low-order streams. The scale and logistics required to assess effects across replicated watersheds precludes the easy implementation of these studies.

Lowe and Bolger (2002) and Lowe *et al.* (2004, 2005) investigated the response of spring salamanders to logging history (chronosequence), presence of fish predators (brook trout) and degree of population connectivity (single or paired first-order streams) in 25 headwater streams across New Hampshire. Timber harvest history within the stream drainage was recorded as the number of years since last harvest, with a maximum value of 34 years. All streams were less than 1 km in length and all drainage basins were less than 2 km<sup>2</sup> in area. Riparian buffers were not protected at any of the logged drainages but most harvests were not located in the riparian zone.

In-stream substrate embeddedness declined with time since timber harvest in the watershed and salamanders were less abundant in streams with greater substrate embeddedness (Lowe and Bolger, 2002). Timber harvesting in headwater stream drainages appeared to result in an increase in fine sediment inputs to the streams, an increase in substrate embeddedness and loss of interstitial spaces, and a reduction in salamander abundance. With time since harvest, these additional accumulated fine sediments are resuspended and flushed downstream, and salamander abundance recovers. In a subsequent study, Lowe *et al.* (2004) showed that the sedimentation effect was experienced by adult salamanders and not juveniles. Interestingly, while timber harvest appears to negatively impact in-stream salamander habitat, canopy disturbance and the creation of early-successional forest structure increases the terrestrial-derived prey in stream salamander diets (Lowe *et al.*, 2005).

While stream salamanders were negatively affected by timber harvest in headwater basins, brook trout abundance increased following harvest and then declined with time



(Nislow and Lowe, 2003). The increase in trout abundance may have resulted from increased production of aquatic invertebrate prey in logged streams due to increased light penetration following canopy disturbance and a shift to a grazer-chironomid-dominated macroinvertebrate community (Nislow and Lowe, 2006).

Williams *et al.* (2002) evaluated how timber harvesting in the watersheds of small streams influenced patterns of variation in physical stream features and regional fish and macroinvertebrate assemblages in the Ouachita Mountains, Arkansas. Watersheds that had been harvested had greater proportional area in early-successional forest than reference basins, while basins of unharvested reference streams had greater proportional area of mid- to late-successional forest. Again, the authors fail to mention if protected riparian buffers were used along the harvested streams. Despite the many potential impacts that timber harvesting may have had on the streams, the study determined that harvesting only impacted physical attributes (water chemistry) of the stream, with little impact on fish or macroinvertebrate assemblages. The streams in the study were subject to dynamic natural disturbance, especially in flow regimes, and their biota appeared to be resistant to additional disturbance created by timber harvesting in the drainage basins.

Olson and Rugger (2007) and Rundio and Olson (2007) studied the effects of upslope density management (thinning) with streamside buffers of alternative widths on in-stream and bank-associated amphibians and terrestrial salamanders in managed forests of western Oregon. Pre- and post-treatment surveys were carried out on 68 headwater stream reaches over 3 years (Olson and Rugger, 2007). They detected no negative treatment effect from thinning, with any buffer width, on the more common in-stream and bank species or on in-stream habitat parameters. Terrestrial salamanders were sampled before and during the first 2 years after experimental thinning at two headwater forest sites in western Oregon that differed in the amount down wood (Rundio and Olson, 2007). There was no thinning effect on salamander abundance at the site with high pre-thinning amounts of downed wood, while abundance declined at the site with low amounts of down wood. Based on these findings, the authors concluded that biodiversity management recommendations for headwater drainage basins focus on connectivity among drainages (Olson *et al.*, 2007; Olson and Burnett, 2009). Specifically, they recommended that headwater ridgelines be managed by extending riparian buffer regulations to these areas or by using only low-intensity forest management in these areas.

#### *Key data gaps and information needs*

Research has clearly shown that ESFHs support a unique, and often declining, biotic community that contributes to regional biodiversity. Properly regulated active forest management can be used to create and maintain ESFH while protecting embedded stream habitat and biota. The issues that remain unaddressed concern the occurrence and strength of ESFH-stream linkages when separated by regulated riparian buffers. Specific questions include:

- 1 How does ESFH in upland areas affect the influx of terrestrial invertebrate prey to headwater streams?
- 2 Do changes in aquatic productivity and diversity, associated with the presence of ESFHs, have reciprocal effects on terrestrial wildlife?
- 3 How does the amount and distribution of ESFH in upland areas affect overland dispersal of stream amphibians and aquatic invertebrates between and among headwater streams?
- 4 What are the best practices for creating ESFH in small watersheds while minimizing in-stream sedimentation, soil compaction and introduction of invasive species?
- 5 What are the implications of established management strategies on combined aquatic-terrestrial biodiversity and aquatic-terrestrial interactions in small watersheds?
- 6 Are there novel management strategies for ESFH that can promote combined terrestrial and aquatic biodiversity in small watersheds?

We are currently conducting a multi-year study to quantify the contribution of early-successional habitat to combined terrestrial-aquatic faunal diversity in small watersheds of the Northern Forest and to identify management strategies for maintaining this contribution. The objectives of this study are (1) to examine relationships between forest succession and terrestrial-aquatic faunal diversity at sites across the Northern Forest region, and (2) to expand understanding of the ecological processes that link terrestrial and aquatic components of faunal diversity in small watersheds. We hope that this work will provide land managers with critical information on how to maximize total faunal biodiversity while continuing to derive economic benefits from forest resources on their properties.

#### Conclusions

The individual importance of (1) ESFHs and (2) headwater streams for biodiversity in the Northern Forest region has been thoroughly demonstrated. ESFHs provide a unique habitat structure and composition that is critical to a characteristic faunal community, but ESFHs are ephemeral and require regular disturbance for creation or maintenance. Headwater streams constitute the majority of riverine systems in the region and provide important downstream services as habitat for cold water fisheries and stream-breeding salamanders.

In the Northern Forest region, most headwater streams are embedded within continuous forest landscapes. It is well known that bidirectional aquatic-terrestrial linkages are common and important at the riparian zone of contact between stream and forest. At the present time, however, there is little knowledge of the occurrence or strength of these linkages into more distant upland forest. Furthermore, it is not well known if the presence of ESFH in headwater stream catchments, when separated from streams by regulated riparian buffers, affects aquatic-terrestrial linkages and biodiversity, either positively or negatively, and to what extent.

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### Conflict of interest statement

None declared.

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