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RIPARIAN COMMUNITIES ASSOCIATED WITH PACIFIC NORTHWEST HEADWATER STREAMS: ASSEMBLAGES, PROCESSES, AND UNIQUENESS[1]

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ABSTRACT: Riparian areas of large streams provide important habitat to many species and control many instream processes – but is the same true for the margins of small streams? This review considers riparian areas alongside small streams in forested, mountainous areas of the Pacific Northwest and asks if there are fundamental ecological differences from larger streams and from other regions and if there are consequences for management from any differences. In the moist forests along many small streams of the Pacific Northwest, the contrast between the streamside and upslope forest is not as strong as that found in drier regions. Small streams typically lack floodplains, and the riparian area is often constrained by the hillslope. Nevertheless, riparian-associated organisms, some unique to headwater areas, are found along small streams. Disturbance of hillslopes and stream channels and microclimatic effects of streams on the riparian area provide great heterogeneity in processes and diversity of habitats. The tight coupling of the terrestrial riparian area with the aquatic system results from the closed canopy and high edge-to-area ratio for small streams. Riparian areas of the temperate, conifer dominated forests of the Pacific Northwest provide a unique environment. Forest management guidelines for small streams vary widely, and there has been little evaluation of the local or downstream consequences of forest practices along small streams.
(KEY TERMS: floodplain; forest; plants; riparian ecology; rivers/streams; wildlife.)

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INTRODUCTION

Several decades ago, scientists and managers began to appreciate the important services that riparian areas provide to streams, and riparian management began primarily to protect aquatic resources (e.g., FEMAT, 1993). In the past two decades, understanding of the value of riparian areas as unique elements of terrestrial ecosystems has increased substantially, largely based on studies of the floodplains of medium to large streams. It is now clear that riparian areas and streams are strongly linked, such that riparian areas can be defined as the terrestrial zone of forest/stream interactions (Gregory *et al.,* 1991; Naiman *et al.,* 2005). Riparian zones are biologically important areas for their diversity, productivity, and habitat complexity (Gregory *et al.,* 1991; Naiman and Décamps, 1997; Naiman *et al.,* 2000, 2005). Among the reasons for this importance are the dynamic nature of riparian zones (Gregory *et al.,* 1991), coupled with high degrees of patchiness resulting in part from topographic heterogeneity and in part from disturbances characteristic of both fluvial (e.g., flood and debris flow) and terrestrial (e.g., fire and wind throw) systems (Swanson *et al.,* 1998; Pabst and Spies, 2001). In addition, the riparian area is transitional from the hydrophilous vegetation at the wetted edge to the terrestrial vegetation of the upslope forest, enhancing the range of physical conditions. Collectively, this leads to a diversity of juxtaposed habitats (Naiman and Bilby, 1998; Nierenberg and Hibbs, 2000). Riparian areas are productive as ground water maintains moisture and brings with it nutrients leached from the watershed, and they benefit from the nutrients and sediments delivered during infrequent overbank flooding. The contrast

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between the upslope vegetation and stream margin conditions depends on regional climate, for example, xeric or mesic conditions (Sarr *et al.,* 2005). Some organisms use riparian corridors as conduits for dispersal and for foraging.

The important links between riparian areas and streams have been discussed previously in studies that have made important advances in understanding and management of riparian areas (e.g., Hynes, 1975; Gregory *et al.,* 1991; Naiman and Décamps, 1997; Kelsey and West, 1998; Naiman *et al.,* 2000, 2005). Much is known about riparian communities in floodplain forests alongside larger rivers; however, less is known about communities and processes associated with riparian zones bordering small streams.

Small, perennial streams (Orders 1 and 2 as assessed on the ground, not from topographic maps) make up more than 80 percent of the length of stream channels in many landscapes, yet are often neglected on maps (Naiman *et al.,* 1987; Sidle *et al.,* 2000; Meyer and Wallace, 2001) and given much less protection from potential impacts from land use than medium size or larger rivers. Nevertheless, these small streams provide important services to fluvial networks, including subsidizing the productivity of downstream aquatic populations (Vannote *et al.,* 1980; Wipfli and Gregovich, 2002) and control of sediment and nutrient fluxes (Swanson *et al.,* 1998). Most of the focus on small streams has been directed toward the aquatic environment, although there has been some study of the physical aspects of the riparian area. Questions yet to be investigated include: Do the riparian areas of these small streams also provide unique and critical habitats and other ecosystem functions in a manner similar to those along larger, floodplain streams? In general, there has been little emphasis on how the habitats or the rates of those processes that link streams and the terrestrial area might vary by stream size and geographic context.

The terms "headwaters" or "small streams" are used here to denote channels that are perennial or intermittent and have no perennial tributaries, usually first-order or second-order, based on field interpretation (Moore *et al.,* 2005). These are the most headward of channels in a drainage network, but there is no generally accepted definition that works in all landscapes. Although many small, permanently flowing streams are not shown on topographic maps (e.g., Meyer and Wallace, 2001), even streams shown on maps may become intermittent in dry years. Most of these channels are less than a few meters in width at bankfull. This review will focus on small streams of the Pacific Northwest (PNW, from southeastern Alaska to northern California and including watersheds draining to the Pacific through that area). In montane regions like the Pacific coast of North America, headwaters are typically steep with large substrate and steep hillslopes and have nearly complete canopy closure (Figure 1). These streams are often physically unstable, and hence disturbance is a common attribute in the dynamics of these riparian areas. Usually headwater streams are more colluvial than alluvial, and thus frequently there is little or no floodplain and associated bankfull bench (Figure 1). Contrast the predominance of the degree of canopy closure predicted along the continuum in channel widths and constraint. Also, note the lack of floodplain (alluvial) development along the headwaters. The development of typical riparian vegetation, especially deciduous species, may be more prominent along small streams of lower gradient or lower hillslope due to a broader zone of contact with the water table. This description may not fit regions with less topographic variation or arid regions, which can also apply to many places in the PNW.

Riparian zones have many definitions depending upon the perspective of the person defining it or the question being asked (Figure 2). A stream ecosystem-centered definition would be the extent of the surrounding forest that affects stream processes such as radiation inputs and outputs, supply and storage of organic matter (wood and litter), and streambank structure (Gregory *et al.,* 1991; FEMAT, 1993; Gomi *et al.,* 2002; Benda *et al.,* 2005). Others may define it based on soil properties. More common is an administrative definition based on stream width to which limits to land use are applied for the purposes of protecting aquatic ecological resources and domestic water supplies, for instance, from forest harvesting. A terrestrial oriented view includes that area of the forest and lower stature vegetation influenced by the microclimate, disturbance regimes, and surface and ground water conditions associated with streams (Brosofske *et al.,* 1997; Moore *et al.,* 2005). For the sake of this review, the last of these definitions will be used (i.e., a terrestrial focus). The contrasts between riparian vegetation and upslope forest in the PNW vary from minor in mesic regions (Acker *et al.,* 2003) to strongly contrasting in xeric areas. For small streams, one must consider the question of how the above processes and patterns are modified by stream size and landscape context.

Many processes associated with forest/stream interactions have not been extensively considered for small streams as defined here, but there is increasing appreciation that differences in the rates of these processes contribute to the often unique physical structure of headwaters (e.g., Moore and Richardson, 2003). Although many of the examples here come from steep, forested landscapes, the discussion will extend to include riparian areas of small streams in other landscapes.

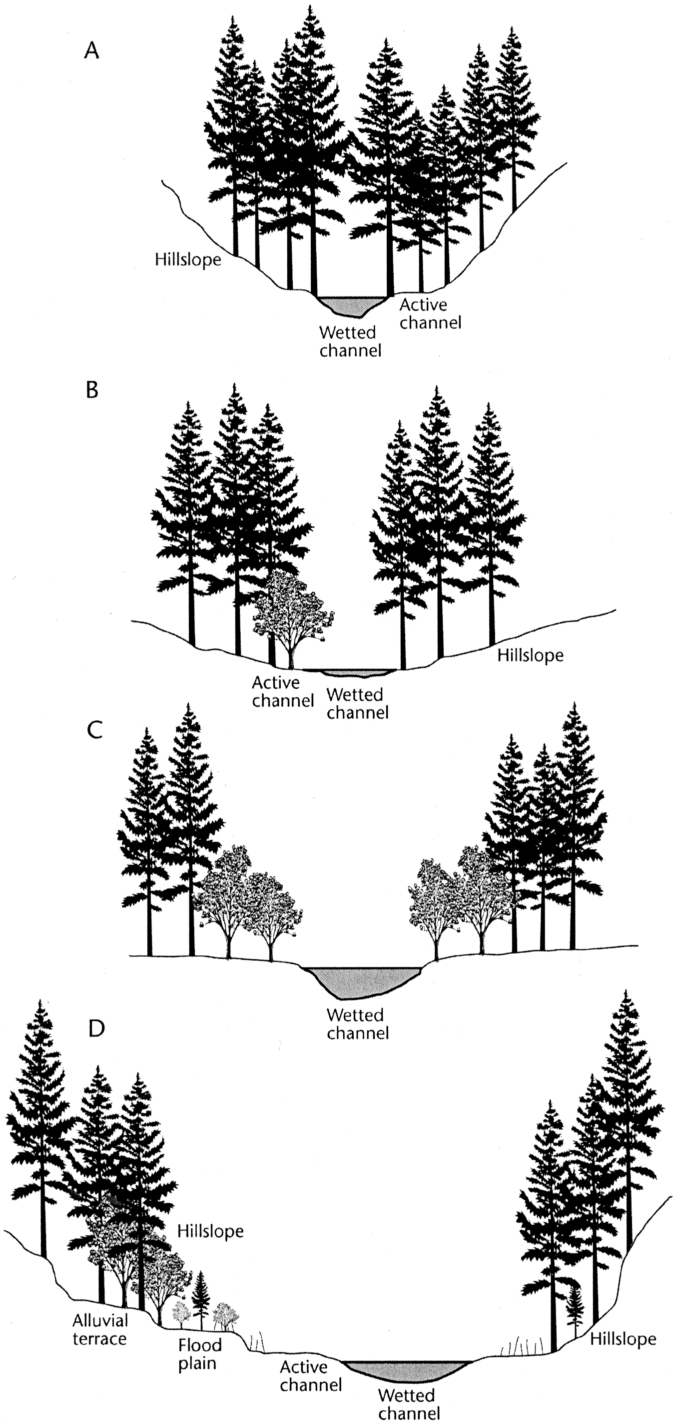

Figure 1. Cross-Section Views of a Range of Channel Types: (A) A Constrained, Steep Headwater; (B) An Unconstrained Headwater; (C) A Plateau Headwater; and (D) An Alluvial Channel Reach Illustrating the Floodplains and Terraces Formed by Alluvial Processes, on Which Riparian Forests Can Develop.

This paper will consider the predominant processes that contribute to the uniqueness of riparian areas and how these processes provide a template for streamside communities. This paper is divided into three parts tied to the questions posed above. That is, are riparian areas of small streams different from those of larger streams, is the PNW different, and does land management affect small streams in ways not characteristic of larger streams?

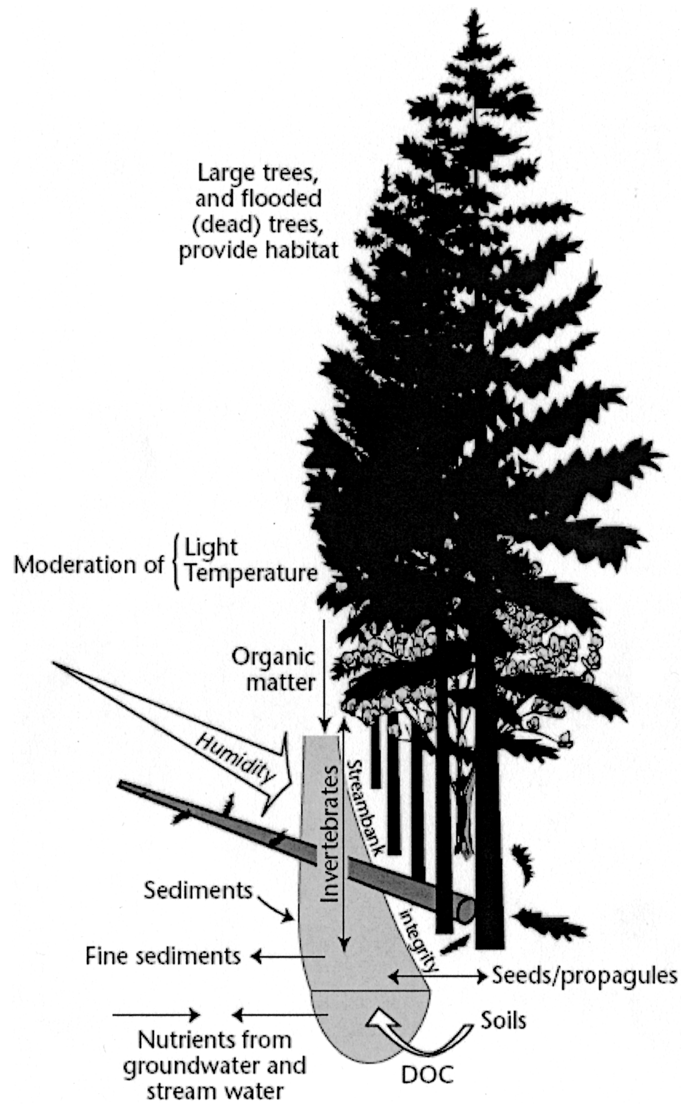

Figure 2. Schematic Drawing of Some of the Processes Linking the Forest and Stream Across the Riparian Zone.

HOW ARE THE RIPARIAN AREAS ASSOCIATED WITH SMALL STREAMS DIFFERENT FROM THOSE OF LARGER RIVERS?

Medium to large rivers have floodplains that support diverse and unique components of terrestrial systems (e.g., Sabo *et al.,* 2005), and these have been extensively studied around the world. Small streams generally lack floodplains and may have narrow riparian areas, but the value of these areas as special habitats has been little studied to date, despite the high density of small streams in forested landscapes (~2.5 km/km^2). Small streams often lack alluvial benches, have steeper hillslopes, and have a closed canopy cover (relative to larger streams), all of which diminish the distinction between their riparian areas and the surrounding forest, especially in mesic environments. For instance, riparian cottonwood (*Populus* spp.) forests provide important habitats for many species (e.g., Davidson and Knight, 2001), but these forests are typical of large floodplains and not small streams. There are differences between large rivers and small streams in riparian areas (Table 1) and their communities, such as degree of canopy shading and depth of the water table relative to the hillslope. Many of these differences are associated with the physical environments that determine processes and process rates affecting the value of these areas as habitat.

Small streams typically experience infrequent but intense disturbances, such as landslides and debris flows, particularly in steeper landscapes (Swanson *et al.,* 1998). These disturbances create a high degree of landscape (stream network) heterogeneity that is critical to maintaining a diversity of habitats. For example, red alder (*Alnus rubra*) is a common riparian tree of the Pacific coast that establishes in disturbed areas. Small streams often have a large component of this deciduous species within a predominantly conifer forest (Swanson *et al.,* 1998; Nierenberg and Hibbs, 2000). The area taken up by this deciduous tree diminishes with time since disturbance (many decades) and does not replace itself on a site, yielding to conifer forest.

Accumulations of woody debris created by fluvial processes are another unique feature of riparian areas. These wood piles may provide valuable habitat to some birds and small mammals (Steel *et al.,* 1999); however, these structures are found mainly in streams competent to move large wood into debris dams. On large streams these occur through moving of wood through floating or debris flows. Wood jams caused by slides and debris flows are most common on small streams where steep topography contributes to the accumulations.

Use of Riparian Areas of Small Streams as Habitat

Riparian communities are shaped by conditions of both the surrounding terrestrial ecosystem as well as the aquatic environment (Nilsson *et al.,* 1994). The structural, microclimatic, and biological aspects of riparian areas provide important habitats for some species, but not all of these species extend to headwater streams while others are found only there (Table 1). Species restricted to riparian areas are typically described as obligates (or riparian dependent) (i.e., requiring the riparian areas for at least some portion of their life cycle, or associates; i.e., found more often in riparian areas but able to complete their life cycles without them). Three factors determine a species' use of riparian areas. First, physical conditions associated with streamsides, such as wetted soils, provide special microenvironments for plants and other organisms and create characteristic physical structures. Second, they are used by consumers of prey resources provided by streams, such as fish or invertebrates (including adults of aquatic insects). Third, food web interactions, such as presence of nonriparian dependent

TABLE 1. Contrasts Between Characteristics of the Riparian Areas of Small Versus Large Streams in the Pacific Northwest.

Attribute	Small Streams	Large Streams
Widths of hydrophilous forest vegetation	Narrow	Narrow to wide, depending on channel confinement
Canopy	Closed	Partly to fully open
Dominance of forest on stream processes	High	Generally low
Frequency of intense disturbances	High	Low to intermediate
Side slope angles	Often steep	Usually low
Alluvial development	Little alluvium, more colluvial	Usually extensive alluvial areas
Microclimate	Cool, dark, humid	More open and less stream influence
Water velocity	Low to high	Low to high
Flow patterns	Sometimes seasonal flow	Less "flashy"

Note: These are generalizations that apply principally to mesic regions, which represent a large fraction of the streams in the region, but not all.

predators consuming prey particular to the riparian areas, may provide for additional species.

Obligate Use. Riparian obligates are well known from larger, alluvial streams. For instance, wetted and recently deposited soils on floodplains can provide critical germination sites for cottonwoods (*Populus* spp.). However, small streams, as defined here, often have very limited alluvial development and hence little evidence of true floodplains and benches. However, riparian obligate species are found there (i.e., terrestrial species associated in some respect with the aquatic environment).

Among these small stream riparian obligates are species that are hydrophilous or require some specific characteristics of the microclimate or physical habitat. For instance, the better known species include vascular plants characteristic of these zones, such as skunk cabbage (*Lysichiton americanum*) and stink current (*Ribes bracteosum*). Many mosses and liverworts also occupy specific microhabitats that are typically found in and along small streams (Dynesius, 2001; Hylander *et al.,* 2002). Many occur at the wetted edges of small streams or on wood and rock in the channel. Not surprisingly, most riparian-obligate bryophytes remain poorly known (Hylander *et al.,* 2002).

Several predator species occur in riparian areas due to their dependence on prey from streams. Those prey include fish and larval aquatic invertebrates and their adult stages. Some of the best known riparian-dependent wildlife species include piscivorous birds and mammals [e.g., kingfishers (*Ceryle alcyon*), mergansers (*Mergus* spp., *Lophodytes cucullatus*), herons (*Ardea* spp.), river otters (*Lontra canadensis*), and mink (*Mustela vison*] (e.g., Loegering and Anthony, 1999). However, most of these species are normally associated with larger, fish bearing streams. Small streams in many landscapes lack substantial fish populations or diversity of fish (Taylor and Warren, 2001; Fagan, 2002), so there may be many fewer species of specialized terrestrial piscivores compared to larger rivers. For instance, in the PNW, cutthroat trout (*Oncorhynchus clarki*) and young coho salmon (*O. kisutch*) are among the few fish species found in small streams. This varies depending upon landscape, the volume of habitat for fish in small streams, and barriers to dispersal. Some species can make facultative use of small streams, such as European river otters (*Lutra lutra*), which may move to small streams when there is sufficient water but move downstream to larger rivers as flows recede seasonally (Prenda *et al.,* 2001). These contrasts in the abundance and diversity of available aquatic prey affect the nature of the communities associated with streams of various sizes.

There are also many benthivorous (feeding on stream invertebrates) vertebrates associated with streams, such as dippers (*Cinclus mexicanus*), harlequin ducks (*Histrionicus histrionicus*), and water shrews (*Sorex bendirii*). Other species, such as swallows, flycatchers, and dragonflies (order: Odonata), depend upon adult aquatic insects (Nakano and Murakami, 2001). Some species, such as those that feed on stream benthos, may be found throughout the fluvial network, including headwater streams. For instance, dippers have been shown to use small streams, which allow them to move further up into steep drainages. The water shrew is found along small and large streams of the PNW (Gomez and Anthony, 1998). The larval stages, and sometimes adults, of salamanders are found in small streams, with adults most commonly found dependent on the riparian area [e.g., giant salamanders (*Dicamptodon* spp.) and torrent salamanders (*Rhyacotriton* spp.)]. In other ecoregions, water voles (*Microtus richardsoni*) and water shrews (*Sorex palustris*) are found along streams of 7 to 14 percent gradient, allowing them to use headwaters (Pagels *et al.,* 1998).

For some species, headwater areas above the limits of fish dispersal may provide a predator free refuge either permanently or seasonally. For example, tailed frogs (*Ascaphus* spp.) are thought to have highest success where they are free of predation by fish or coastal giant salamander (Dupuis and Steventon, 1999; Sheridan and Olsen, 2003). Although not from the PNW, Fraser *et al.* (1999) suggested that the killifish (*Rivulus hartii*) uses headwaters in streams in Trinidad to evade one of its predators, the wolf fish (*Hoplias malabaricus*). The hypothesis of a headwater refuge from predation for some riparian species does not seem to have been explicitly tested to date.

Food web effects may occur that result from dependence of species on other species found only in riparian areas. For instance, some species of monkeyflower (*Mimulus* spp.) are sheltered from herbivory at streamsides by sedges (*Carex nudata*), an example of facilitation (Levine, 2000). There are few examples of such food web effects involving headwater riparian areas, which is not surprising given the detailed research necessary to document such complex interactions. Among the several possible hypotheses for organisms having distributions restricted to headwater riparian areas are that they may be unable to coexist with predators or competitors found associated with larger rivers. However, alternative hypotheses such as specifics of the hydrologic and disturbance regimes would need to be considered to determine the drivers of such patterns.

Riparian areas may be used for different functions by the same species at different times of year (e.g., birds nesting in upslope forest forage in riparian areas during summer and autumn) (Wiebe and Martin, 1998). Adult coastal giant salamanders (*Dicamptodon tenebrosus*), a characteristic species of small stream riparian areas, may spend summer months near streams but move to upslope forest to overwinter (e.g., Johnston and Frid, 2002). These examples illustrate that riparian areas of small streams are at least seasonally critical to the persistence of some species of the fluvial network.

There is relatively little evidence of specific associations of terrestrial invertebrates found uniquely along small streams. However, there have been many studies of invertebrates associated with alluvial riparian areas of larger rivers (e.g., Hering, 1998; Antvogel and Bonn, 2001). Some species [e.g., the carabid beetle (*Bembidion biguttatum*)] were found only at the water margins of an alluvial floodplain of a large river (Antvogel and Bonn, 2001). Prey consumed by carabid beetles along a third-order stream were more terrestrial than along a fifth-order river where 89 percent of prey were of aquatic origin (Hering and Plachter, 1997). Notes from systematics and natural history studies suggest that there are invertebrate species unique to headwater riparian areas, but more specific tests of this hypothesis are needed.

Non-Obligate Use of Riparian Areas. Some species that are not dependent on riparian areas for survival may occur in riparian areas occasionally or even in higher densities or higher frequency than upslope forest. For instance, riparian areas of medium to large streams are the favored habitat of grizzly bears in southeastern British Columbia during autumn (McLellan and Hovey, 2001). Some stream breeding amphibians may occur there because of the steeper stream gradients (Wilkins and Peterson, 2000). Some small mammals may be riparian associates along small as well as large streams, such as the Pacific shrew (*Sorex pacificus*) and long-tailed vole (*Microtus longicaudus*) (McComb *et al.,* 1993; Gomez and Anthony, 1998). Some web building spiders (e.g., *Tetragnatha* spp.) may also be riparian associates and capture large numbers of emergent aquatic insects (Williams *et al.,* 1995). Even bats occasionally forage along very small stream channels (if the canopy is open) in preference to the upslope forest, but less so than near larger streams (Seidman and Zabel, 2001). Commercially harvested mosses are most likely to be found in riparian areas within 50 m of water in western Oregon (Peck and Muir, 2001) but are not necessarily associated with small streams. Such species may occur in higher densities within riparian areas relative to upslope forests.

Species richness of taxonomic groups for which it has been studied is often higher in riparian areas (Pollock, 1998; Pollock *et al.,* 1998; Sabo *et al.,* 2005; Sarr *et al.,* 2005), although for the majority of groups there are either no data along these lines, or the studies were limited to larger channels. In Pacific Northwest forests, riparian areas may have a higher deciduous tree component than the mostly coniferous covered hillslopes (Nierenberg and Hibbs, 2000; Wimberly and Spies, 2001; Sarr *et al.,* 2005). Proportions of plant species in phanerophytes, chamaephytes, and geophytes (mostly bog species) are higher along tributaries than along larger rivers (Nilsson *et al.,* 1994). Riparian areas, especially those with a hardwood component, are hotspots for lichen diversity in western Oregon, where 28 of 117 species were strongly associated with riparian areas (Peterson and McCune, 2003), perhaps because of cold air drainage down steep channels. There are no clear patterns of species richness in riparian areas of small streams, although riparian-area diversity may be inversely related to average discharge (Nilsson *et al.,* 1994).

The degree to which riparian areas of small streams contribute to higher species diversity relative to the upslope forest has not been broadly considered. Sheridan and Spies (2005) found the riparian area in zero-order basins in the Oregon Coast Range contributed significantly to plant diversity of these upland areas. In an example from Belgium, species richness of vascular plants declined significantly up into the headwaters of streams, probably due to difficulty with dispersal upstream for some species (Honnay *et al.,* 2001). Plant species richness below deciduous (red alder) canopy was higher than under conifer canopy (DeFerrari and Naiman, 1994; Hibbs and Bower, 2001), resulting in higher plant diversity along streams with past disturbance contributing to the mosaic of habitat types. The deciduous component of vegetation along small streams tended to be less important along very small streams but still higher than the surrounding forests (Nierenberg and Hibbs, 2000). Large differences in assemblages of riparian plants along tributaries compared to larger rivers are likely to be a consequence of dispersal strategies, disturbance, and habitat suitability.

Other Riparian Associated Processes

There may be species dependent upon the riparian system as conduits for dispersal and for the maintenance of metapopulation structure. As the sources of the fluvial network, headwaters may be relatively isolated from each other for aquatic species and for riparian obligates. This may create patterns of nestedness in species assemblages (e.g., Lock and Naiman, 1998; Taylor and Warren, 2001). This makes the metapopulation dynamics of such species vulnerable to small alterations in those habitats that may not provide ready access to similar habitats if they cannot easily cross drainage divides or move down along the fluvial network and back up to another headwater (e.g., Fagan, 2002; Curtis and Taylor, 2004). This is likely to present a challenge primarily for aquatic species with limited dispersal between headwater habitats. Some species of the riparian areas of small streams may be capable of finding new habitats dispersing across upslope forests: tailed frog juveniles and adults are frequently observed long distances from streams (Matsuda and Richardson, 2005). However, some obligate, hydrophilous terrestrial species may experience the same isolation and dispersal barriers as more aquatic species if they cannot tolerate conditions farther downstream from the headwaters. To date, there has been little examination of dispersal patterns along headwaters, so the importance of this process is not known.

The subsidies of energy and nutrients from riparian areas to small streams are considerable, and these streams depend on such inputs. These inputs have been well studied, particularly in terms of litterfall inputs, nutrients, and dissolved organic carbon in ground water (e.g., Naiman *et al.,* 1987; Richardson, 1991; Wallace *et al.,* 1999). Small, forested streams often receive the largest proportion of their biologically available energy as litterfall (see Richardson *et al.,* 2005). Riparian areas are the sources of large woody debris that have important influences on stream functions. Riparian areas also contribute to the function of stream communities by the inputs of terrestrial invertebrates that drop into streams (Edwards and Huryn, 1996; Kawaguchi and Nakano, 2001) and consumption by salmonids and other fish (Wipfli, 1997). A larger deciduous component to the riparian forest may provide more invertebrates to streams than forests dominated by conifers (Wipfli, 1997). These contributions from the riparian area are clearly substantial.

In larger streams, marine-derived nutrients and energy delivered by anadromous fish such as salmon may provide an important flux to riparian forests (Naiman *et al.,* 2002). However, this flux of nutrients and energy does not extend to the small streams considered here, which are largely upstream of the limits of anadromous fishes. In addition, recent work in the Oregon Coast Range using stable isotopes has found no evidence of marine derived N in riparian vegetation (Scott, 2004), suggesting that riparian areas of small streams are unlikely to benefit from nutrients of marine origin.

ARE SMALL STREAM RIPARIAN AREAS OF THE PNW DIFFERENT FROM ELSEWHERE?

In the mesic forests of the Pacific Northwest, the contrast between riparian areas and upslope forests is minor compared to drier landscapes (Kelsey and West, 1998; Acker *et al.,* 2003). Along small streams with very little in the way of alluvial development and relatively steep banks, the upslope forest may extend to the streambank. Under the latter conditions, one could say that headwaters have very narrow riparian areas. Nevertheless, there are species that use these narrow riparian areas in other temperate regions (Hylander *et al.,* 2004), and it is predicted that the same is true in the PNW.

In some parts of the PNW east of the coastal mountains, small streams drain extensive areas of xeric vegetation from Ponderosa pine (*Pinus ponderosa*) forests to bunchgrass (*Agropyron spicatum*) and sagebrush (*Artemesia tridentata*) grasslands. In these areas of the PNW, the contrast between riparian and terrestrial communities is quite pronounced, and the dependence of riparian associated organisms on small streams may be considerable. For instance, in very dry landscapes the yellow-breasted chat (*Icteria virens*) is found only in riparian areas, whereas elsewhere it is more widely distributed. However, there has been only a very modest amount of research on these systems in drier landscapes.

Headwaters in the PNW normally have a smaller deciduous component on average than the larger rivers, although it may still be locally abundant (Nierenberg and Hibbs, 2000). The small amounts of deciduous vegetation may contribute to lower abundance and species richness of birds along smaller streams (Lock and Naiman, 1998). However, even the "small" streams in Lock and Naiman's (1998) study of birds were 12 to 21 m wide, not small in the context of this review.

The high plant diversity observed in riparian areas around the world is also found in the PNW. The botanical diversity alongside even very small streams is augmented by the addition of unique mesic species, especially in drier landscapes (Pollock *et al.,* 1998; Pabst and Spies, 1999; Sarr *et al.,* 2005). A less distinct pattern can be found along streams in more mesic areas, such as northwestern Oregon (Sarr *et al.,* 2005) and other areas where the moisture gradient is not as sharp.

For groups of vertebrates that have been well studied in the PNW such as birds and small mammals, there appears to be only a minor effect of the riparian areas of small streams on their species richness and abundance. Most bird species found along small streams in Washington were also found along big rivers, indicating that small stream assemblages were a nested subset of those near bigger rivers (Lock and Naiman, 1998). In western Washington and British Columbia, no significant differences were observed in composition or richness of birds in riparian versus upland forests near small streams, despite differences in forest structure (Pearson and Manuwal, 2001; Lance and Phinney, 2001; Haag, 2002; Shirley, 2004); however, for an exception see Anthony *et al.* (1996). Some species of small mammals are more strongly associated with riparian areas than upslope forests in the PNW, but some species actually occur at higher densities away from streamsides (McComb *et al.,* 1993; Cockle and Richardson, 2003). It is interesting that although the beaver is a common, riparian obligate species, it is typically absent from small streams in the PNW (Kelsey and West, 1998), although elsewhere in North America it can be found along headwaters.

Many riparian dependent species found along medium to large streams are decidedly absent from small streams. The absence of some of those species could be a result of the lack of opening in the forest canopy along small streams, since many species, such as flycatchers, bats, and dragonflies, need canopy gaps for foraging. Finally, the constrained nature of such channels in steep landscapes may result in a band of riparian vegetation so narrow that larger species such as birds do not distinguish it from upland forest (Lock and Naiman, 1998; Wiebe and Martin, 1998).

Do riparian areas of small streams of the PNW differ from elsewhere? It is clear that a number of differences exist among regions, but a detailed answer is not possible given the data currently available. Small streams of the PNW are characterized by steep topography and consequently steep hillslopes, which limit the development of alluvial features and communities associated with those features. However, not all small streams in the PNW have high gradients and steep hillslopes – there are also extensive plateau regions with low gradients. The contribution of large diameter trees to canopy cover and other habitat elements is often described as a distinguishing feature of forests of the PNW. As well, the PNW is known for its high amounts of precipitation in places. In addition, conifer dominated temperate forests are rare, and this conifer influence has a profound influence on riparian processes (e.g., light quantity and quality, the quality and quantity of wood and litter, and size of wood). The predominant riparian deciduous species of the PNW, the red alder, as a N-fixing tree, contributes large amounts of fixed N, unlike most other riparian systems. However, there are similarities in other respects to other regions in processes that differ primarily in rates and particular species. Overall, riparian areas of the PNW are distinctive and relatively rare in terms of the proportional area of the planet they represent.

WHAT ARE THE CONSEQUENCES OF FORESTRY AND OTHER LAND USES FOR RIPARIAN AREAS OF SMALL STREAMS IN THE PNW AND BEYOND?

One of the most common measures for the protection of riparian areas from land use impacts involves the maintenance of buffer strips or reserves along streams. Riparian area reserves began primarily with the objective of protecting aquatic resources from forestry or agriculture and expanded to include riparian communities (e.g., FEMAT, 1993) and other land uses. The evaluation of the effectiveness of these conservation measures for riparian communities has been slow to accumulate over the past two decades, but it is clear that riparian buffers can contribute to the maintenance of at least some riparian species. Following is a brief review of how forest harvesting may affect riparian communities of small streams, although it is beyond the scope here to discuss the wide range of types of forest management.

There have been many more studies of the effects of riparian forest reserves on aquatic resources than on streamside communities, and mostly along larger and usually fish bearing streams. The results from retention of riparian leave strips along medium to large streams vary in the PNW and elsewhere, with some terrestrial species increasing in density while others decrease, and there may be lag times of one to a few years before changes were detectable (e.g., Darveau *et al.,* 1995). Most of these studies have examined vertebrates, primarily birds (Darveau *et al.,* 1995, Hagar, 1999; Pearson and Manuwal, 2001; Vesely and McComb, 2002). A minimum width of 30 m seems to result in lower rates of population declines than narrower reserves, but this depends on species, region, and treatment of the reserves (e.g., Darveau *et al.,* 1995). Fixed width buffers are the most common measure but may constrain the degree of habitat heterogeneity in managed forests (Darveau *et al.,* 2001). Riparian organisms of small streams also appear to benefit from riparian reserves.

Guidelines that have been developed by different jurisdictions for the protection of small streams reflect the diversity of management objectives among regions and institutions (Young, 2000; Blinn and Kilgore, 2001; Lee *et al.,* 2004; Naiman *et al.,* 2005). The amount of protection given to streams is often dependent on stream size, and smaller streams typically receive smaller reserves or none at all, depending on jurisdiction (Moore and Richardson, 2003; Richardson, 2004). Few studies have examined the effectiveness of protective measures for small streams. Kinley and Newhouse (1997) found that densities of riparian birds increased with increasing riparian buffer widths along small, mid-elevation streams. Some forest dwelling small mammals, such as red-backed voles and shrew moles, were protected by riparian reserves along small streams in coastal British Columbia, whereas other species increased with the removal of riparian forest, such as the wandering vole (Cockle and Richardson, 2003). The frequent absence of riparian reserves along small streams may be one reason for the limited evidence of whether they could be effective.

It is unclear how long any of the effects described above persist after forest harvesting. Most studies of the effects of harvesting adjacent to streams take place immediately after the harvest and are of short duration, usually less than five years. Riparian reserves along small streams are typically narrower than on larger streams and therefore more susceptible to wind throw, sun scald, and other edge effects that diminish the persistence and effectiveness of the reserve zone. Hibbs and Giordano (1996) looked at a 30-year chronosequence of alder dominated buffer strips in the Oregon Coast Range and found little change in plant species composition or structure with time since buffer creation. However, most studies have been of limited duration following harvesting (or other disturbance), so relatively little is known about the recovery processes. It is expected that the potential for rapid regrowth of shade, even as a shrub layer, should occur at greater rates for smaller streams than for larger streams because of the narrower width. The longer term and watershed scale role and effectiveness of riparian reserves at meeting some of their objectives should be a valuable research area.

Riparian areas also affect many different in-stream processes. Some functions provided by riparian areas include the filtering of nutrients and sediments by shoreline vegetation. The extent of riparian vegetation reserved during forest harvesting can affect light inputs and the supply of large woody debris. Riparian forest canopy removal may shift the primary aquatic source of C from terrestrial litter to algae, especially in summer (Kiffney *et al.,* 2003; Elliott *et al.,* 2004; Richardson *et al.,* 2005). Riparian area management has impacts on streams that may feed back to the availability of prey (e.g., adult aquatic insects) or predators (e.g., coastal giant salamanders) in their riparian areas.

Interruption in the continuity of conduits for dispersal may fragment populations that are riparian specialists restricted to headwaters. Coastal giant salamander populations in southwestern British Columbia show evidence of isolation and genetic bottlenecks potentially caused by forest harvesting (Curtis and Taylor, 2004). The valley elderberry longhorn beetle in California is found in isolated patches of elderberry in riparian areas and apparently cannot easily disperse between isolated riparian forests (Collinge *et al.,* 2001). Some aquatic insect adults disperse along streams and may interrupt their movements if the forest is discontinuous, at least until vegetation begins to regenerate. Species that occur at the tips of a dendritic network may not be able to reach those sites easily by most methods of dispersal because of isolation and downstream directed flow (Honnay *et al.,* 2001). The consequences of forest management that affects dispersal and population sizes of headwater species are not known, but theory predicts that they may be among the most vulnerable of populations associated with the fluvial network (Fagan, 2002).

DISCUSSION

Riparian areas of small streams differ from those of alluvial reaches of larger streams, but there are many gaps in the knowledge of those differences. In forested, montane regions of the PNW, streams and their riparian areas typically have steeper sideslopes, complete canopy closure, and lack alluvial development (Table 1), all of which contribute to a more rapid transition to nonriparian forest alongside small streams. Moreover, the steeper gradients and smaller flows limit the size of the channels and their influence on adjacent vegetation. The reasons to expect differences in riparian communities include the narrow width of the transitional area from the stream to upslope in steep landscapes. Differences in hydrology, sediment transport, microclimate, and other parts of the habitat template provide for a headwater riparian community that should be predictably distinctive. Some areas of research that will benefit the understanding of riparian areas of small streams will include both descriptive studies and process-based studies of the mechanisms contributing to the special nature of these areas (Table 2) (Richardson, 2004). These abiotic drivers probably apply to other forested landscapes in other regions as well, but perhaps less so to nonforested settings. There is also the need to examine taxonomic groups other than vertebrates and vascular plants, as most forest biodiversity is represented in groups such as the bryophytes, invertebrates, and various microbes.

The natural history knowledge for particular taxonomic groups suggests that there are riparian-area specialists alongside small streams. However, the information on each of these taxa is scattered in the

TABLE 2. Knowledge Gaps and Research Questions Regarding the Importance of Small Streams in Providing Unique Riparian Habitats.

Attributes	Question of Gap	Prediction or Requirement
Uniqueness as a habitat	Are riparian areas of small streams any different from those of large, floodplain streams? Detailed studies of organisms likely to occur a the edges of small streams are lacking.	Taxa such as invertebrates, bryophytes and fungi are likely to include species that are dependent on the special characteristics of hydrology and geomorphology of small stream edges.
	Why are some species restricted to (or excluded from) small stream riparian areas?	Species may use riparian areas of small streams as a refuge from predation or competition from species found in more alluvial stream reaches.
Extent of riparian areas	What determines the width of the riparian habitat?	Widths are likely to depend on hillslope gradient, seasonal contingencies of flow, and degree of contrast from wetted edge to upslope vegetation.
Degree of isolation of headwater communities	If species are obligates to headwater riparian areas, how do they disperse?	Special may be highly resistant to variation in the environment due to infrequent dispersal events between locations.
Metapopulation dynamics	If species are isolated, is there evidence of genetic isolation and microevolution?	Species with limited dispersal abilities that are specialists in headwaters may form genetically isolated populations.
Adaptations	If there are species unique to headwater riparian areas, what are they associated with?	Low hydraulic power and low wash loads may render riparian areas of small streams more benign than those of larger streams. Strong association with ground water inputs may provide a moderated thermal and nutrient regime.

Note: Most of these questions apply to small streams in many geographic regions.

literature and not available in any systematic comparison of riparian areas versus upslope vegetation or of small versus large streams. The riparian areas of small streams may support unique assemblages of organisms that are isolated from other headwaters by intervening reaches of larger streams and upslope vegetation. If so, then these populations may form pockets of strong natural selection (Fagan, 2002). Populations of riparian dependent organisms of small streams are also likely to be small and vulnerable to local extinction through demographic and genetic mechanisms.

In mesic forests of the PNW, the contrasts between riparian areas and upslope forest are not as distinct as in drier landscapes (Kelsey and West, 1998; Sarr *et al.,* 2005), particularly along small streams. Concentration of organisms into the riparian forest, as opposed to upslope forests, may depend on the degree of microclimatic contrast, magnitude of canopy opening in the forest, slopes of the adjacent hillsides, heterogeneity of vegetation structure (e.g., Wimberly and Spies, 2001), and mobility of the organisms. Canopy closure may exclude riparian species such as swallows, flycatchers, and bats associated with edges where they can forage for adult aquatic insects. Steep hillslopes in some landscapes may result in narrow bands of hydrophilous vegetation (Pabst and Spies, 1999), which may be insufficient in size to contribute enough to vegetation structure to affect larger terrestrial species with large home ranges. However, there is still the expectation of an assemblage of organisms uniquely associated with headwaters of the Pacific Northwest, but probably mostly smaller organisms with limited dispersal ability of which less is known, such as invertebrates, bryophytes, and lichens (e.g., Peterson and McCune, 2003).

There are differences in the kinds of processes associated with the wetted edge of small streams that contrast with those of larger streams. The banks of small streams may derive some of their stability from the roots of herbaceous plants, whereas larger streams are thought to get this primarily from tree roots. The lower erosive forces of small streams may permit small plants to fill this role, with the consequences of reducing sediment mobilization from the streambank to downstream. However, it may be that shrubs and herbs simply operate at smaller scales to provide this stability and are consequently more important in the stabilization of small stream margins – a hypothesis awaiting testing.

Management Implications

Forest managers have struggled with the appropriate prescriptions for the protection of small streams. Small streams are dependent on surrounding forests for inputs of detritus and invertebrates. The services provided to streams by reserving forest around them (e.g., shade, inputs, structure) have feedbacks to the riparian area in terms of adult aquatic insects and adult stages of stream breeding amphibians and other processes. The riparian areas of small streams themselves may support species dependent on those sites and not found elsewhere in the watershed, but the extent to which the organisms along headwaters are a nested subset of that found downstream cannot yet be answered. The potentially large number of small streams in mesic landscapes raises the question of how many need protecting and how much protection they need. Questions regarding the effects of forest management around small streams on the riparian community are not answered yet. Additionally, the headwater streams provide ecosystem services to larger streams downstream and thereby play essential roles in environmental quality, fish production, etc. Evaluation of this important role and the contribution that riparian assemblages of headwaters make to the character of downstream reaches are important research directions.

Small streams in the Pacific Northwest and elsewhere are likely to differ from larger streams. These communities of small streams will not be merely nested subsets of assemblages farther downstream, where alluvial development is more pronounced. The conifer dominated forests of generally steep topography found in the PNW and the size of wood from those forests create particular conditions that will differ from other regions. The processes that maintain diversity in riparian areas, especially around small streams, are similar in kind to those found elsewhere but differ in rate, especially the magnitude and frequency of mass movements that contribute to heterogeneity in the riparian landscape. Guidelines that recognize the vulnerability of small streams are slow in coming, especially as they lie beyond the usual limits of anadromous salmonids that motivate so much riparian protection. The value of these areas as habitat and the regional differentiation of such habitats continue to present a large gap in the knowledge of riparian areas and small stream systems in general.

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