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DEGRADATION OF LITTORAL HABITATS BY RESIDENTIAL DEVELOPMENT: WOODY DEBRIS IN LAKES OF THE PACIFIC NORTHWEST AND MIDWEST, UNITED STATES

INVASIVE SPECIES, GLOBAL POTENTIAL • SEA-LEVEL RISE, ECONOMIC IMPACT, SINGAPORE • MIRABEL FRAMEWORK, CALCAREOUS GRASSLANDS, EUROPE • EU WATER FRAMEWORK DIRECTIVE, BALTIC SEA

Report

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Degradation of Littoral Habitats by Residential Development: Woody Debris in Lakes of the Pacific Northwest and Midwest, United States

One of the least understood aspects of aquatic ecology is the role of riparian zones of lakes, and how these habitats and their functions are impacted by human development of lakeshores. We investigated the effects of residential lakeshore development on littoral coarse woody debris (CWD) distribution and on riparian forest characteristics by comparing 18 lakes in the U.S. Pacific Northwest with 16 previously surveyed lakes in the U.S. Upper Midwest. Residential development had a strong negative effect on CWD and riparian forest characteristics at both local and whole-lake scales. There was a strong positive correlation between riparian forest density and littoral CWD abundance in both regions. We found regional variation in CWD and riparian forest characteristics, mostly owing to differences in native forests. Our results suggest the role of local processes in determining CWD distribution and point to potential regional differences in littoral habitat structure associated with forest composition and lakeshore development that may have consequences for littoral-pelagic coupling in lakes.

INTRODUCTION

Increasing attention is being drawn in ecology to the linkages between habitats and ecosystems that have traditionally been considered distinct (1, 2). Associations between adjacent habitats are typically defined by inputs or exchanges of material or energy across boundaries which enhance productivity in recipient ecosystems (1). Much of this work has focused on stream, river, and marine coastal systems (3–7), in part because the riparian zone, the transition zone between terrestrial and aquatic habitats, is an especially active area in these systems for exchange of energy and material that is increasingly recognized as vital to recipient ecosystems (8, 9).

More recently, attention has been drawn to habitat coupling in lake ecosystems (10, 11). A well-understood relationship between lakes and their associated watersheds is the input of nutrients that affect in-lake primary productivity (12). In addition, inputs of exogenous particulate (13–15) and dissolved (16, 17) organic material contribute substantially to lake production. Terrestrial insects are deposited in large numbers on the surface waters of lakes, where they can become key components of fish diets (18–21). Another critical allochthonous input to aquatic ecosystems is coarse woody debris (CWD), large pieces of fallen and dead wood that represent essentially permanent features of littoral habitats of lakes in forested regions (22, 23).

The crucial role of CWD in river and stream ecosystems is well recognized (24–28) and is now a major focus of river management and restoration. In riverine systems, CWD provides physical structure that increases channel stability, alters hydrological processes, and controls the spatial distribution and extent of sediment accumulation (28, 29). In addition, CWD plays a key role in creating habitat for fishes and invertebrates by directly providing refuge as well as by forming pools that are a critical habitat for many fish species (24, 26).

Considerably less is understood about the importance of littoral CWD in lakes, though CWD accumulation can be substantial (30) and dead wood is very stable in littoral zones, remaining in standing waters for as long as 800 years (22). In lakes of the Upper Midwest, CWD density was positively correlated with growth rates of dominant fishes (31), and fish preferentially aggregate in littoral zones with CWD as compared with more simplified habitats (32, 33). In addition, CWD can represent substantial surface area on lake bottoms (28) and is a common site of macroinvertebrate colonization (34–36). Although many of its functions in littoral habitats are not fully understood, CWD is likely to be important in lakes because of its occurrence in high densities, its longevity in standing water, and what is known about the key role it plays in river and stream systems.

Human residential development of lakeshores is associated with changes in key ecosystem characteristics, including nutrient levels (37), aquatic vegetation (38), and the spatial distribution (39) and growth rates (31) of fishes. Concomitant with increasing development pressure, for at least a century, humans have systematically removed CWD from aquatic ecosystems, both directly and indirectly. Christensen et al. (30) showed that humans directly simplify the littoral zone by removing CWD and aquatic vegetation in lakes of the Upper Midwest region of the United States. In Europe, where urban areas were developed earlier than in North America, this removal has likely been occurring for much longer. However, as of yet, there has been little systematic comparison of littoral CWD characteristics, and the effects of human lakeshore development on littoral CWD distribution, among geographic regions with different forest characteristics.

Very few studies exist on the distribution and function of CWD in the littoral zones of lakes. Our purpose is to identify general patterns of riparian forest characteristics and corresponding littoral CWD distribution associated with residential development on lakeshores. To do this, we compare results from a survey of lakes in the Upper Midwest (30) with lakes in the Pacific Northwest, two regions in the United States located within distinct biomes and associated forest characteristics. (Figure 1). We expected to find regional variation in littoral habitat characteristics, specifically CWD size and spatial

Figure 1. Map of United States showing Pacific Northwest and Upper Midwest regions.

Table 1. Vegetation characteristics of the riparian zones surrounding study lakes of the Pacific Northwest and Midwest, United States.

Region	Climax dominant	Early- or mid-climax dominants	Other major riparian tree species
Pacific Northwest	Western hemlock *Tsuga heterophylla*	Douglas-fir *Pseudotsuga menziesii* Western red cedar *Thuja plicata*	Big leaf maple *Acer macrophylla* Black cottonwood *Populus trichocarpa* Red alder *Alnus rubra*
Midwest	Eastern hemlock *Tsuga canadensis* Sugar maple *Acer saccharum*	Balsam fir *Abies balsama* Paper birch *Betula papyrifera* Red maple *Acer rubrum*	Northern white-cedar *Thuja occidentalis* Black spruce *Picea mariana* Tamarack *Larix laricina*

Sources: Pacific Northwest, (44); Midwest, (30).

distribution, associated with differences in forest composition. Not only are we interested in the effects of development at a whole-lake scale, but also in riparian-littoral dynamics occurring at more local scales, such as littoral CWD distribution on forested sites of partially developed lakes as compared with deforested sites (i.e., residential sites) on those same lakes, or sites on undeveloped lakes. Finally, we discuss some management considerations for riparian and littoral habitats, particularly in light of regionally unique patterns.

MATERIALS AND METHODS

Our study followed the methods of Christensen et al. (30), who surveyed CWD characteristics in lakes and forest composition in adjacent riparian habitats in the Upper Midwest, a region in the north-central and northeastern part of the United States, and specifically the northern areas of the states of Wisconsin and Michigan. For the current study, we sampled 18 lakes in the Pacific Northwest, a region of the northwestern United States, and specifically areas of western Washington State and southern British Columbia, Canada. The Pacific Northwest lakes are all located in the western hemlock zone of the Cascade Range and Puget Trough regions, and the forests surrounding the study lakes in the Upper Midwest (hereafter "Midwest") are mixed northern hardwood-conifer forests (Table 1). Most of the forests in both regions were cleared by European settlers by the end of the late 19th century and are currently second or third growth (30, 40).

Most of the lakes in the current study are located in the suburban cities surrounding the Seattle metropolitan area. In addition, three lakes were selected as reference systems and are located in the University of British Columbia's Malcolm Knapp Research Forest, British Columbia, Canada. These lakes lack residential development, although their associated riparian forests were also cleared at the end of the 19th century, and therefore are not without human influence. Since the initial deforestation, however, the riparian forests have remained intact and have matured, and the three lakes are therefore categorized as undeveloped.

On each lake, we established 300-m^2 rectangular sample plots measuring 30 m along the shoreline and 10 m into the riparian forest. We also sampled the 30-m stretch of lakeshore adjacent to each riparian plot. This plot size was selected because the standard residential plot on these lakes is approximately 30 m wide, and because approximately 80% of CWD originates from the first 10 m of riparian forest (41). Between four and eight sample plots per lake were selected at random, according to a stratified process such that on lakes that were partially developed, we sampled both forested and deforested sites in equal number, aiming for eight plots total (four of each type). On entirely undeveloped lakes where only forested sites existed and on lakes with fully developed lakeshores where only deforested sites existed, we sampled four plots distributed randomly along the lakeshore.

In each 300-m^2 sample plot, we counted and measured the diameter at breast height of all trees larger than 5 cm in diameter, as in Christensen et al. (30). We also counted and measured the diameter of all pieces of CWD greater than 10 cm in diameter and longer than 1 m (42) intersecting the 0.5-m depth contour in the littoral zone adjoining the sample plot. We calculated basal area for each plot as the sum of all individual tree or log basal areas, defined as basal area $= \pi \times r^2$, where $r =$ radius at breast height (trees), or where the log intersected the 0.5-m depth contour.

We compared CWD and forest characteristics at the whole-lake scale and at the local site scale. Whole-lake means were weighted by the relative amount of shoreline that was forested versus developed. We tested the effect of residential development on mean lake CWD density and basal area by using analysis of covariance with region (Pacific Northwest and Midwest) and development intensity (undeveloped, low, high) as main factors, and riparian forest density as a covariate. We also used linear regression to analyze the relationship between CWD density and basal area and residential development, using whole-lake means. One lake (Langlois Lake) was a consistent outlier in CWD density and basal area, with extraordinarily higher values for both metrics, and was therefore removed from comparisons at the whole-lake scale. At the local site scale, we used analysis of variance with Sheffé's post hoc test ($\alpha = 0.05$) by using site type (undeveloped, developed-forested, and developed-deforested) as main factors and CWD density, CWD size, riparian tree density, and riparian tree size as response variables. To facilitate regional comparisons, we used published data from Christensen et al. (30) for whole-lake mean values and raw data from this earlier survey for tests of site type effects.

RESULTS

Study lakes were selected to span a gradient of residential development intensity (Table 2). Lakes in the Pacific Northwest (PNW) were binned to match the development intensity categories of Christensen et al. (30) according to: undeveloped $= 0$ houses km^{-1} of shoreline ($n = 3$); low $=$ 1–10 houses km^{-1} ($n = 3$); high $=$ more than 10 houses km^{-1} ($n = 12$; Table 2).

We found a significant negative effect of residential development on CWD density and basal area in the PNW, and patterns of CWD distribution were tightly coupled to riparian Forest characteristics at the whole-lake scale, similar to what has been observed in lakes of the Midwest (MW). We found significant covariation between CWD density and riparian tree density in the PNW, as was found previously in the MW.

Table 2. Characteristics of Pacific Northwest lakes sampled for coarse woody debris and riparian forest distribution.

Lake	Location	Surface area (ha.)	Residence density (houses km^{-1})	Development intensity
Gwendoline	British Columbia	13	0	Undeveloped
Loon	British Columbia	48.6	0	Undeveloped
Marion	British Columbia	13.3	0	Undeveloped
Langlois	Washington	15.8	1.1	Low
Fenwick	Washington	9.7	3.7	Low
Armstrong	Washington	12.2	6.2	Low
Neilson (Holm)	Washington	7.7	15.1	High
Silver	Washington	72.9	15.5	High
Wilderness	Washington	27.9	16.6	High
Boren	Washington	7.3	19.1	High
Geneva	Washington	10.5	22.8	High
Beaver #2	Washington	25.1	26.4	High
Shadow	Washington	19.8	27.3	High
Meridian	Washington	60.7	30.8	High
Devils (Lost)	Washington	5.3	36	High
Shady	Washington	8.5	40	High
Star	Washington	14.2	40.6	High
Angle	Washington	40.5	46.6	High

Note: All lakes are located between 47–49N latitude and 121 - 122W longitude. Characteristics of Upper Midwest lakes previously sampled are given in Christensen et al. (30).

Maximum riparian forest density was larger in the PNW than in the MW (Fig. 2). CWD basal area also covaried significantly by riparian tree basal area in the PNW, as in the MW (Table 3 and 4; Fig. 3). CWD density varied significantly by development at the whole-lake scale in both regions (Table 3 and Table 4; Fig. 4). Mean lake CWD densities tended to be lower on undeveloped lakes in the PNW than undeveloped lakes in the MW (Table 4; Fig. 4A). We also found a significant effect of development on CWD basal area in both regions, and CWD basal area covaried significantly with riparian forest basal area (Table 3 and Table 4; Fig. 4B). Maximum CWD basal area was greater in the Pacific Northwest (46.2 m^2 km^{-1} in the Pacific Northwest versus 19.4 m^2 km^{-1} in the Midwest), as was maximum riparian forest density (Table 4; Fig. 4B).

We found negative correlations of both CWD density ($p < 0.001$, $r^2 = 0.60$) and basal area ($p < 0.001$, $r^2 = 0.57$) with residential density in the Pacific Northwest, as has previously been shown in the Midwest (Fig. 4). Riparian forest density was also negatively correlated with lakeshore residence density in both regions (Pacific Northwest: $p < 0.001$, $r^2 = 0.72$; Midwest: $p = 0.002$, $r^2 = 0.50$; data not shown). In general, there was more CWD in Pacific Northwest lakes than in the Midwest (Table 4; Fig. 4A), and CWD persisted at higher development intensities in the Pacific Northwest than in the Midwest (Fig. 4A).

At the local site scale, we found a significant effect of

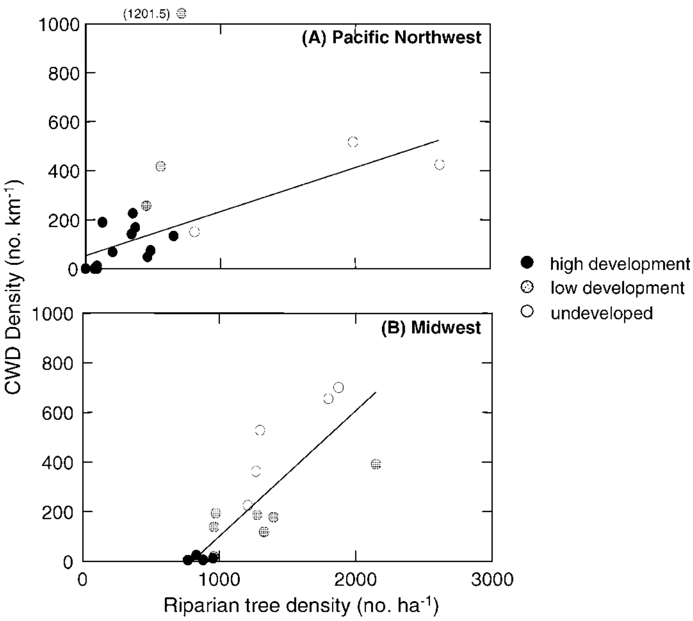

Figure 2. Coarse woody debris (CWD) density as a function of riparian tree density for Pacific Northwest (A) and Midwest (B) lakes. Circles represent whole-lake means. Open circles indicate undeveloped lakes; hatched circles, lakes with low resident density (0.1–10 residences km^{-1}); and solid circles, lakes with high resident density (>10.0 residences km^{-1}). Midwest data are redrawn from Christensen et al. (30).

Table 3. Summary of analysis of covariance results showing effect of human residential development level (high, low, undeveloped) and region (Pacific Northwest, Midwest) on whole-lake coarse woody debris (CWD) density and basal area with riparian tree (RT) characteristics as covariates.

Response	Main factor	Covariate	F ratio	p value
CWD density (pieces km^{-1} of shoreline)	Development		4.2	0.03
	Region		9.6	0.005
	Region × development		15.2	<0.001
		RT density	27.2	<0.001
CWD basal area (m^2 km^{-1} of shoreline)	Development		7.8	0.002
	Region		12.0	0.002
	Region × development		0.6	0.5
		RT basal area	7.4	0.01

Table 4. Least squares means from analysis of covariance showing effects of lake development and region on whole-lake coarse woody debris (CWD) density and basal area, with riparian tree characteristics as covariates, in lakes of the Pacific Northwest and Midwest, United States.

Region	Density (pieces km^{-1} of shoreline)	Basal area (m^2 km^{-1} of shoreline)
Undeveloped	252.4	18.3
Low development	255.1	11.8
High development	128.3	4.6
Pacific Northwest	272.0	16.7
Midwest	151.9	6.4
Pacific Northwest/undeveloped	150.3	24.5
Midwest/undeveloped	354.4	12.0
Pacific Northwest/low development	429.0	18.0
Midwest/low development	81.2	5.6
Pacific Northwest/high development	236.5	7.7
Midwest/high development	20.0	1.6

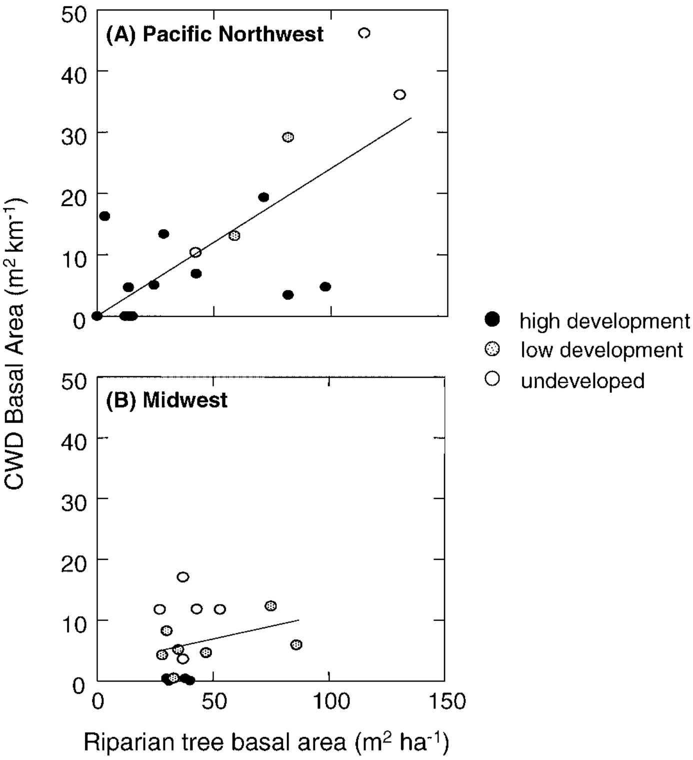

Figure 3. Coarse woody debris (CWD) basal area as a function of riparian tree basal area for Pacific Northwest (A) and Midwest (B) lakes. Symbols as in Fig. 1. Midwest data are redrawn from Christensen et al. (30).

development (undeveloped, developed-forested, and developed-deforested sites) and region on CWD density (Fig. 5; Tables 5 and 6). Post hoc tests showed that in the Pacific Northwest, CWD densities were highest on undeveloped and developed-forested sites, and not significantly different from each other. In contrast, post hoc tests showed that in the Midwest, CWD density on undeveloped sites was higher than on developed-forested sites, and lowest on developed-deforested sites. Riparian tree density also varied by development type in both regions (Tables 5 and 6). Post hoc tests showed that in the Pacific Northwest, riparian forest density was highest on undeveloped sites, whereas in the Midwest, undeveloped sites and developed-forested sites had similar forest densities.

CWD size (basal area) did not vary significantly with local site development in the Pacific Northwest, similar to the pattern previously found in the Midwest (Tables 5 and 6; Fig. 6). Post hoc tests showed that mean CWD size was greater in the Pacific Northwest than in the Midwest. Riparian tree size varied significantly among site types, and between regions (Tables 5 and 6; Fig. 6). Mean riparian tree size was greater on sites with dwellings (developed-unforested) than on either undeveloped or developed-forested sites in both regions (Fig. 6). Riparian trees were significantly larger in the Pacific Northwest than in the Midwest on sites of all development type (Fig. 6; Tables 5 and 6).

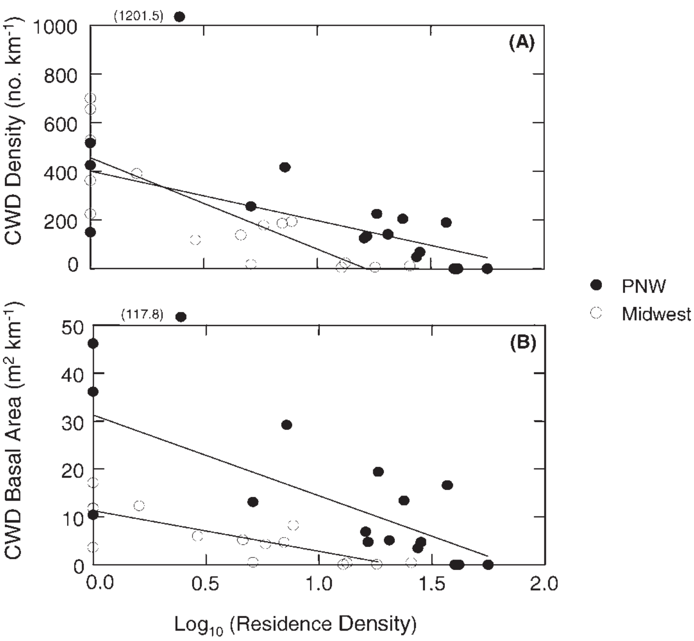

Figure 4. Coarse woody debris (CWD) density (A) and basal area (B) as a function of shoreline residential density (logarithm of number of residences km^{-1} of shoreline). Circles represent whole-lake means. Solid circles indicate Pacific Northwest lakes; open circles, Midwest lakes. Midwest data are redrawn from Christensen et al. (30).

DISCUSSION

Consistent with other published findings for the United States Upper Midwest (30) and Wisconsin State lakes (43), we found that in the Pacific Northwest, residential development around lakeshores is associated with a striking loss of CWD in littoral zones and reduction of riparian forest. As expected, we found that replacement of native forests with homes, lawns, and other residential structures corresponds to lakewide alterations of riparian and littoral habitats. We also found that development impacts littoral and riparian habitats at finer scales, associated with settlement intensity on individual sites. These effects varied between the Pacific Northwest, the focus of the current study, and previously published results for lakes in the Midwest, in ways largely indicative of differences in native forests, human influences on lakeshore habitats, and coupling between riparian and littoral habitats.

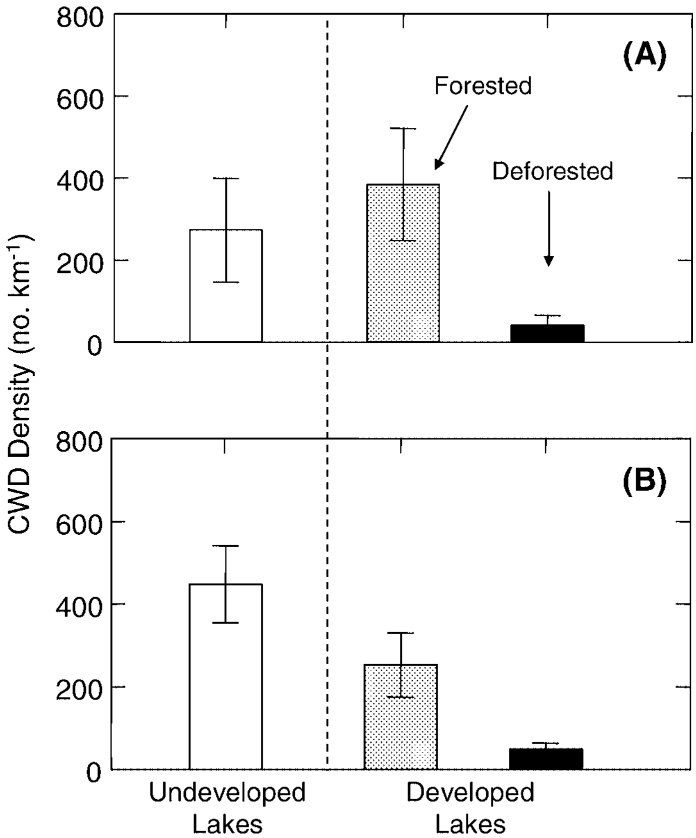

Figure 5. Coarse woody debris (CWD) density in the Pacific Northwest (A) and Midwest (B) for all lakes. Open bars indicate plots on undeveloped lakes; hatched bars, forested plots on developed lakes; and solid bars, residential (deforested) plots on developed lakes. Error bars represent 95% confidence intervals. Midwest data are from Christensen et al. (30).

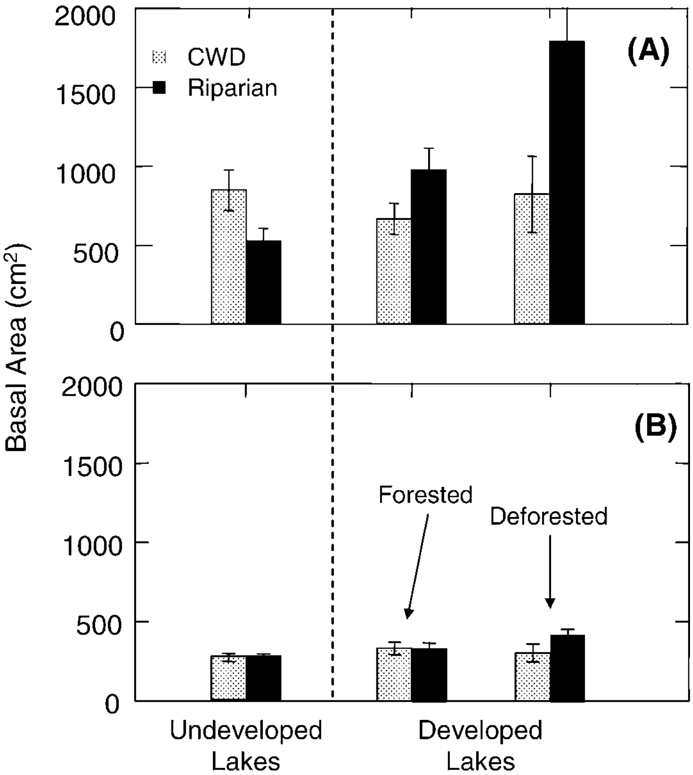

Figure 6. Coarse woody debris (CWD) and riparian tree size in the Pacific Northwest (A) and Midwest (B) for all lakes. Hatched bars indicate CWD; solid bars, riparian trees. Shown are means across all undeveloped lakes, forested plots on developed lakes, and residential (deforested) plots on developed lakes. Error bars represent two standard errors. Midwest data are from Christensen et al. (30).

Table 5. Summary of analysis of variance results showing effects on a local site scale of development (undeveloped, developed-forested, developed-deforested) and region (Pacific Northwest, Midwest) on coarse woody debris (CWD) and riparian tree (RT) density and basal area.

Dependent variable	Effect	*F* ratio	*p* value
CWD density	Region	12.8	<0.001
(pieces km^{-1} of shoreline)	Development	61.5	<0.001
	Region × development	8.0	<0.001
CWD basal area	Region	0.26	<0.001
(cm^2 piece^{-1})	Development	60.8	0.78
	Region × development	1.3	0.27
RT density	Region	13.6	<0.001
(trees ha^{-1})	Development	60.3	<0.001
	Region × development	11.9	<0.001
RT basal area	Region	42.2	<0.001
(cm^2 tree^{-1})	Development	14.9	<0.001
	Region × development	8.9	<0.001

Our results highlight some of the differences in native riparian forests between the Pacific Northwest and the Midwest. We found that riparian forests of the Pacific Northwest have fewer, larger trees, whereas riparian habitats in the Midwest have more, smaller trees. The larger tree size on Pacific Northwest lakeshores is likely due to the dominance in the Pacific Northwest of larger climax tree species, such as Douglas fir and western red cedar (44). Even when excluding Pacific Northwest lakes with higher development intensity than observed in Christensen et al. (30), the same patterns are observed (data not shown), allowing us to dismiss the hypothesis that this is a development-intensity, and not a regional, effect.

In lakes of both the Midwest and the Pacific Northwest, we found strong coupling between riparian forest composition and littoral habitat structure. The regional differences in forest composition we observed translate into regional variation in CWD size and volume, such that forests in the Pacific Northwest generate larger and greater overall volume of littoral CWD. Regionally distinct forest composition may therefore have consequences for aquatic biotic associations limited by availability of CWD surface area, such as aggregations of macroinvertebrates on CWD in response to surface biofilm (34, 45, 46).

We also found significant interactions between region and development in the relationship between CWD density and riparian forest density. In the Pacific Northwest, CWD density was lower than expected on undeveloped lakes, which had the highest riparian stem density of all lakes sampled. In contrast, in the Midwest, CWD density patterns directly reflected riparian forest density patterns, suggesting a strong relationship between riparian and littoral habitats on undeveloped lakes. One potential explanation for this regional variation is that in the Pacific Northwest, riparian stem density of newer growth forests on undeveloped lakes may not yet be reflected in littoral habitats, where the legacy of large old-growth fallen trees is retained in relatively fewer, larger logs. Likewise, smaller riparian trees on Midwest lakes may be more sensitive to mechanisms that generate CWD, such as windthrow and beaver foraging. This is supported by the significant relationship between CWD basal area (i.e., total littoral CWD volume) and riparian forest basal area in both regions. Alternatively, CWD may be lost from littoral habitats in the Pacific Northwest undeveloped lakes more rapidly than in the Midwest. One such mechanism could be size of lake, because larger lakes with greater fetch may generate wave action and displace CWD, although mean surface area for undeveloped lakes in each region was virtually identical (Pacific Northwest 25.0 ha; Midwest 26.0 ha).

Table 6. Least squares means from analysis of variance showing local effects of development and region on coarse woody debris (CWD) and riparian tree (RT) density and size in lakes of the Pacific Northwest (PNW) and Midwest (MW), United States.

Region	CWD density (pieces km^{-1} of shoreline)	CWD basal area (cm^2 piece^{-1})	RT density (pieces ha^{-1})	RT basal area (cm^2 tree^{-1})
Undeveloped	252.4	490.3	1619.4	420.3
Developed-forested	255.1	444.4	1140.9	751.3
Developed-deforested	128.3	484.0	492.3	1230.8
PNW	272.0	715.1	925.0	1214.3
Midwest	151.9	230.7	1243.4	387.4
PNW/undeveloped	150.3	775.8	1805.6	775.8
MW/undeveloped	354.4	204.8	1433.3	554.5
PNW/developed-forested	429.0	622.0	808.8	1110.2
MW/developed-forested	81.2	266.8	1472.9	392.4
PNW/developed-deforested	236.5	747.5	160.7	1978.2
MW/developed-deforested	20.0	220.5	823.8	483.5

In addition to the striking effects of development on littoral and riparian characteristics at the whole-lake scale, we also found localized variation in littoral CWD and riparian forest distribution and size associated with the presence of residential structures. On Midwest lakes, CWD densities on developed-forested sites were intermediate to those on undeveloped and residential sites. In contrast, in the Pacific Northwest CWD densities on developed-forested sites were equivalent to those on undeveloped sites. It is unclear why this variation between regions exists, although it may be associated with higher overall CWD densities in undeveloped Midwest lakes, some hypotheses for which were presented above. In both regions, however, CWD densities on developed-forested sites were higher than on developed-unforested sites. Given the usual persistence of CWD in aquatic ecosystems (22), the highest rates of CWD loss on developed sites most likely occur via direct removal by people. CWD densities on forested sites of developed lakes suggest that CWD continues to be delivered to littoral zones from locally forested habitats, and that individual residents have a local effect on littoral CWD, either directly, through its removal or indirectly, through deforestation. The manifestation of reduced CWD source material may occur on a longer timescale than the direct removal of CWD from littoral zones, but nevertheless, deforesting lakeshores likely results in a reduction of CWD inputs to shallow waters (41) and severely diminishes the future capacity for restoration of these ecosystems.

We found that human development also altered the size distribution of littoral CWD and riparian trees in both regions at the local scale. Riparian trees were largest on residential plots of developed lakes in both regions, although the difference was most dramatic in the Pacific Northwest. This "trophy tree" phenomenon presumably occurs when developers or residents preferentially leave larger trees on lakeshore property for aesthetic purposes. Often, these trophy trees are nonnative, ornamental species with different successional and litterfall patterns than native trees (T. Francis pers. observation). Sociological surveys in these two regions could clarify the mechanisms that produce this difference in land-use patterns between the Midwest and the Pacific Northwest.

Our results suggest several potential disruptions to the coupling between littoral CWD and riparian trees by humans, including deforestation, high grading for larger trees, and directly removing CWD, all of which can potentially alter ecological function in littoral habitats (28, 47). Although all the functions of CWD in littoral habitats are not known, it is clear that CWD provides key habitat for macroinvertebrates and fishes (32, 34, 36, 46). Alterations to littoral structure such as CWD distribution likely affect benthic communities and trophic interactions. Changes in benthic communities may have ecosystem-wide consequences owing to the tight coupling between benthic and pelagic habitats (10). Thus, not only should we expect consequences for littoral and benthic communities associated with residential development, but also natural and human-induced variation in forest and CWD composition raises questions about associated differences in the relationships between riparian and littoral habitats and benthic-pelagic coupling.

The regional differences outlined here have implications for management strategies related to the maintenance of ecosystem functions in lakes. Actions to retain CWD in littoral zones could be designed with targets for either the number of CWD pieces per length of shoreline or the overall volume of wood in littoral zones. Comparison of the data from these two regions demonstrates that this choice could have different implications in each region. Undeveloped lakes in the Midwest had higher densities of CWD than undeveloped lakes of the Pacific Northwest, but lower overall volumes of CWD. A single strategy based on either the density or total volume would not be appropriate for both regions; rather, management schemes should address both metrics of littoral CWD distribution. In addition, management strategies associated with residential development densities should be tailored to the unique associations between residence density and CWD in each region. In the Pacific Northwest, total loss of CWD occurred at residential densities greater than 20 houses km^{-1}. However, the lowest levels of CWD in the Midwest occurred at much lower residential densities (12 houses km^{-1}). Thus, lake management strategies incorporating development targets should also be regionally defined.

Finally, the decoupling of terrestrial-aquatic linkages by residential development of lakeshores has ecosystem consequences that will likely persist for centuries. Most CWD is produced by periodic disturbance (24). Humans have interrupted the inputs of littoral CWD not only by removing riparian sources of CWD, as seen here, but also by disrupting this disturbance cycle (48). On the basis of estimates of CWD input rates to rivers and streams, where such estimates actually exist, returning littoral CWD levels to those observed on undeveloped lakes will take many decades. Furthermore, these estimates are conservative because they assume the presence of intact riparian forest and were calculated for fluvial systems where CWD inputs are greater as a result of the more transient nature of riparian vegetation and steeper riparian slopes. Active restoration practices, such as directly adding CWD to lakes, may accelerate this recovery but such strategies would be financially costly. Rather, given the rapid pace of human development, the most prudent management actions should now focus on active protection of intact littoral habitat where it is still present (49).

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