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Natural and anthropogenic variation in coarse wood among and within lakes

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Summary

1 Residential development is often concentrated near aquatic ecosystems and understanding riparian–littoral zone interactions is therefore critical for assessing its ecological effects.

2 Introduction of wood from riparian forests into the littoral zone, where it becomes habitat for aquatic organisms, is an important, but poorly understood, process. We related the density of littoral coarse wood both among and within 45 lakes in Vilas County, Wisconsin, USA, to forest structure, abiotic drivers and land use.

3 Among all lakes and among a subset of low-development lakes, the best predictor of the density of littoral coarse wood was the density of riparian coarse wood. At the within-lake (site) level, two alternative models explain variability in coarse wood abundance: as a function of exposure to wind and amount of riparian coarse wood or as a function of exposure to wind and land-use intensity.

4 Both among and within lakes, areas more modified by humans had a lower density of littoral coarse wood. Conversely, areas with little (current) human impact were tremendously variable; some sites and lakes had abundant wood and others had virtually none.

5 Contrary to previous studies, there was no relationship between living trees and coarse wood density, suggesting that riparian and littoral coarse wood densities may be strongly influenced by past disturbance, both human and natural.

6 This study highlights the importance of cross boundary subsidies in understanding the impact of development on ecosystems. The concentration of residential development at the boundary between terrestrial and aquatic ecosystems appears to reduce the flow of coarse wood from forests to lakes. Loss of this resource may have negative consequences for lake biota and the aquatic food web.

Key-words: coarse woody debris, coarse woody habitat, cross boundary transfer, land use, land–water interaction, littoral habitat, near-shore ecology, residential development, riparian forest, subsidies

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Introduction

Humans have a disproportionate impact on many ecological processes, and the footprint of these impacts continues to increase in many regions (Vitousek *et al*. 1997; Liu *et al*. 2003). In the United States, rural residential development is increasing in the Great Lakes region (Radeloff *et al*. 2001), the south-east (Turner *et al*. 2003), the west (Hansen *et al*. 2002) and the south-west (Naiman & Turner 2000). Incorporating ecological relationships into land-use planning is critically needed (Dale *et al*. 2000; Hansen *et al*. 2002). Even low-density development can have pronounced impacts on sensitive species (Odell & Knight 2001), habitat connectivity (Turner *et al*. 1996; Crow *et al*. 1999) and ecosystem processes (Radeloff *et al*. 2000).

Understanding terrestrial–aquatic interactions is critical for assessing ecological effects of development because homes are often clustered near lakes and streams (Schnaiberg *et al*. 2002; Walsh *et al*. 2003). Lakeshore modification, e.g. removal of logs and plants

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or construction of docks, although limited to areas less than a metre deep and a few metres out from shore, is of particular concern because of the importance of the littoral zone to lake function (Schindler & Scheuerell 2002; Vander Zanden & Vadeboncouer 2002).

We focused on one component of lakeshore modification: the removal of the littoral coarse wood that is a critical link between terrestrial and aquatic ecosystems (Harmon *et al*. 1986; Naiman *et al*. 2000). What we call coarse wood is often referred to as large or coarse woody debris in stream and terrestrial ecology or as coarse woody habitat by aquatic ecologists. Coarse wood plays a key role in creating habitat heterogeneity in many streams and rivers (Gurnell *et al*. 2002; Webb & Erskine 2003; but see Piégay *et al*. 1999). The pools and riffles created by coarse wood, as well as the logs themselves, are vitally important habitats for fish and other biota in streams (Angermeier & Karr 1984; Benke *et al*. 1984; Piégay *et al*. 1999).

The role of coarse wood in lakes has been less studied, but littoral coarse wood can shelter small fish from predation (Werner & Gilliam 1984; Osenberg *et al*. 1988; Werner & Hall 1988) and it also serves as substrate for insect larvae and algae, particularly in oligotrophic systems (France 1997a; Bowen *et al*. 1998; Vadeboncouer & Lodge 2000). Patterns of predation and the structure of predator and prey populations of fish also differ in lakes with and without abundant littoral coarse wood (Schindler *et al*. 2000; Walters & Kitchell 2001).

Natural dynamics of littoral coarse wood are slow, with inputs and decomposition operating over time-scales of decades to centuries (Harmon *et al*. 1986; Guyette & Cole 1999). As in other systems (DuPouey *et al*. 2002; Foster *et al*. 2003), anthropogenic processes may also leave long legacies for littoral coarse wood dynamics. For example, many of the large white pine (*Pinus strobus*) in an Ontario lake dated from the time of logging (despite investigators' attempts to exclude logging slash) and no large pine had entered the lake in the last 100 years (Guyette & Cole 1999). Simulation studies have also suggested that littoral coarse wood may be enhanced and maintained by natural disturbances (Bragg 2000; Turner 2003), but this has yet to be demonstrated empirically.

Within-lake patterns of littoral coarse wood density may respond differently from whole-lake patterns. Coarse wood is large and heavy, so local factors, such as forest stand structure, bank slope or land use, might determine littoral coarse wood densities at a particular site. However, the tree species found in our study area are buoyant when freshly felled, so wind and water currents could concentrate wood in sections of a lake that do not have high local inputs (Guyette & Cole 1999; Mallory *et al*. 2000). Local and landscape effects are not mutually exclusive; in 16 northern Wisconsin lakes both site factors and the cumulative development of the lake influenced littoral coarse wood (Jennings *et al*. 2003).

Previous studies of littoral coarse wood have focused on contemporary human drivers, with less attention paid to biotic and abiotic processes. However, wood can last for centuries in the littoral zone of lakes (Guyette & Cole 1999), so it is quite plausible that contemporary levels of littoral coarse wood are a legacy of previous forests and past disturbances. To address the relative role of anthropogenic, abiotic and riparian factors at multiple scales, we studied littoral coarse wood in a region characterized by both a high density of lakes and a wide range of lakeshore development, the Northern Highlands Lake District (NHLD) of northern Wisconsin, USA. We explored how a suite of biotic, abiotic and anthropogenic explanatory variables influence coarse wood density both among and within 45 lakes in the NHLD by addressing three major questions: (i) What factors explain variation in coarse wood density among lakes spanning the observed range of recent (1996) building densities in the NHLD? (ii) How does coarse wood density vary among lakes with few houses along their shores and what explains that variation? (iii) What factors explain within-lake variation in coarse wood density?

Methods

STUDY AREA

We studied 45 lakes in Vilas County, the centre of the NHLD (Fig. 1). Vilas County contains over 1300 lakes ranging in size from 0.1 to > 1500 ha and covering 16% of the county's surface area (Black *et al*. 1963). The county is under heavy development pressure, with many lakes surrounded by homes (Wisconsin Department of Natural Resources 1996); however, there are still many undeveloped lakes, providing a good reference for assessing human impacts.

The lakes are largely nutrient poor and many are connected by groundwater rather than surface water flow. A lake's source water (precipitation or groundwater) drives much of the variation between lakes (Kratz *et al*. 1997; Riera *et al*. 2000), with precipitation-dominated lakes being smaller, clearer and less speciose than lakes with significant groundwater input. The soils are derived from glacial outwash and are generally acidic and sandy (Finley 1975).

The most xeric soils support pines (*Pinus banksiana*, *P. resinosa*, *P. strobus*), red oak (*Quercus rubra*) and quaking aspen (*Populus tremuloides*). On more mesic upland sites, sugar maple (*Acer saccharum*) is the clear dominant, with hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*) and American basswood (*Tilia americana*) components. Lowland areas are dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*), with occasional patches of northern white-cedar (*Thuja occidentalis*) and balsam fir (*Abies balsamea*) (Curtis 1959; nomenclature follows Wetter *et al*. 2001).

Currently undeveloped lakes may have been strongly impacted by humans in the past (Cleland 1983; Riera *et al*. 2001). Three historical events may have had strong impacts on coarse wood (CW) levels. First, temporary

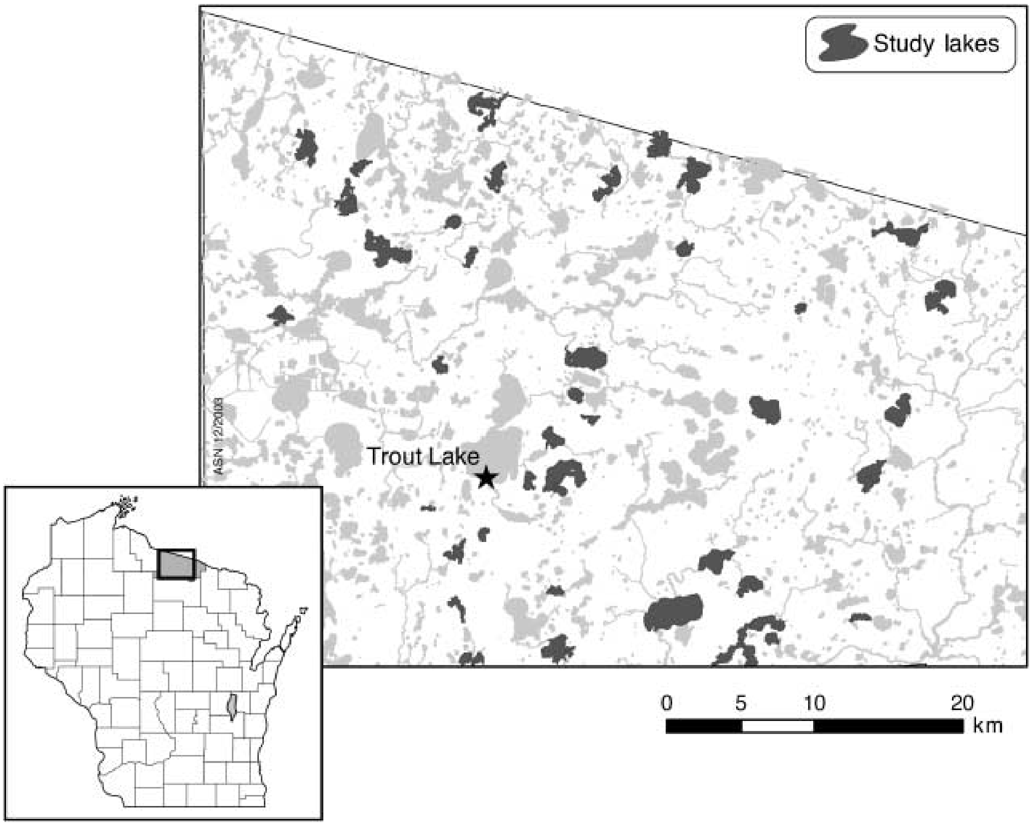

Fig. 1 Location of study lakes within Vilas County, Wisconsin, USA. Trout Lake is located at 46°2′ North and 89°40′ W.

extirpation of beaver (*Castor canadensis*) in the 18th century is likely to have reduced CW abundance. Secondly, forest clear-cutting in the late 19th to early 20th centuries may have increased CW abundance via a temporary pulse of inputs (Fries 1951; Guyette & Cole 1999). Finally, rural zoning laws enacted in 1933 shaped the spatial pattern of vacation cottage development in subsequent decades (Icke 1940; Gough 1997).

FIELD METHODS

We stratified our sampling along two gradients: lake conductivity, a proxy for source-water type (Riera *et al*. 2000), and building density. Using a geographical information system (GIS) and published sources, we compiled a list of the conductivities of 100 lakes in Vilas County that were within a 45-minute drive of our field station and computed the number of buildings within 100 m of each lake (buildings km^{-1} of shoreline) (Black *et al*. 1963; Vilas County Mapping and Land Information Office 1996). We selected 35 lakes that had public boat access, had a maximum depth ≥ 4 m, a surface area ≥ 29 ha, and spanned the range of both gradients. An additional seven lakes that had no public access and three very small (< 20 ha) lakes later used for whole-lake manipulations of coarse wood were also sampled. All 45 sampled lakes were used in this analysis.

For each lake, we divided the shoreline into 50-m segments using a GIS. We then grouped the shoreline segments into four equal-length quadrants based on the ordinal compass directions (north, south, east and west), starting at true north relative to the centre of the lake, and selected two segments at random from each quadrant, for a total of eight sites per lake. We used county tax records to identify landowners, and obtained permission to measure the vegetation on their property. Denials were few and there was no apparent bias by owner type or management; if we could not obtain permission, we moved the site to the adjacent landowner.

Field sampling was conducted during the summers of 2001, 2002 and 2003. To measure the coarse wood in the littoral zone (littoral coarse wood), we established a 50-m transect along the half metre depth contour. An investigator walked the transect wherever possible, but some sites with very soft substrate were sampled from a rowboat.

We recorded every piece of wood that was at least 5 cm in diameter at the point where it crossed the transect and at least 150 cm in length. This line-intersect technique is more efficient than a complete census; however, estimates of volume and surface area of wood are unreliable if, as here (unpublished data), the logs are orientated non-randomly and encounter rates are low (Van Wagner 1968; Gippel *et al*. 1996). We therefore present data on density only. The diverse literature on coarse wood uses several different definitions of ‘large’ so we calculated both the number of logs ≥ 5 cm and the number of logs ≥ 10 cm. Statistical models presented here are for logs ≥ 5 cm. A ln (density + 1) transformation was used prior to analysis to correct for the skewness and heteroskedacity in the data.

We recorded the presumed source for each log (beavers, humans or natural mortality) and then calculated the proportion of logs introduced by beaver and human activity. These values were arcsine-square root transformed prior to analysis. Any log without bite or saw marks was assumed to be natural.

To characterize riparian forest stand structure and human activities along the lakeshore, we extended the 50-m segment of shoreline used in the littoral sampling 10 m upslope into the riparian zone, and divided the enclosed area into five 10 × 10 m plots. We sampled forest structure in the first, third and fifth plots. Within each plot we recorded diameter at breast height (d.b.h.) by species for all living trees ≥ 5 cm d.b.h., counted all logs ≥ 10 cm in diameter at their widest point and tallied the number of snags (standing dead trees) and stumps ≥ 10 cm in diameter (measured at breast height for snags and just above the root line for stumps). We defined logs as dead trees that touched the ground at two or more points. We counted as snags all dead trees that were still upright and connected to their roots, where the main bole reached breast height. If the main bole did not reach breast height, we recorded a stump. Boles that had broken off their stump but were held off the ground by branches of other trees were also counted as logs; boles that were leaning, but had not broken off their stumps were counted as snags. As with littoral coarse wood, we recorded the source of each snag, stump and log and calculated the (arcsine-square root transformed) proportion of logs introduced by beaver and human activity. We summarized the number of living trees by three size cut-offs: 5, 10 or 15 cm at d.b.h. We calculated two measures of downed wood: ln (density of logs ha^{-1}), i.e. riparian coarse wood, and the density of snags and stumps ha^{-1}. Finally, we summed living tree density with the density of snags and stumps to obtain the previous (maximum) forest density.

We recorded the type of ownership (public or private) for each plot. To measure fine-scale human land-use intensity, we noted all natural and human land covers (e.g. wetlands, lawn, beach) and objects (e.g. paths, furniture, stairs) present in each of the five 100 m^2 sections of the site. Up to two land covers or objects were marked dominant in each plot. We summed the plot scores for human activities (0 for absent, 1 for present and 2 for dominant) at each site for the eight most common uses and artefacts we encountered: docks, lawn, boats on shore, stairs, dirt paths, engineered shorelines, beaches and buildings, respectively. This index assumes that the dominant land use had twice as much impact as those uses that were merely present; it has a theoretical range of 0–50 because all eight uses could be present on each of the five plots, and up to two uses could be scored as dominant in each plot.

To assess the abiotic conditions of the site we measured the slope and aspect of the first, third and fifth plots with a hand-held compass and clinometer. The three measurements were then averaged. Aspect was transformed into a linear metric ranging from zero on south-west slopes to two on north-east slopes, using the standard transformation: aspect = cosine (45 – degrees) + 1 (Beers *et al*. 1966).

CALCULATED VARIABLES

Several independent variables were calculated from a GIS or compiled from published data. We used a 1 : 24 000 map of lake outlines to compute lake area and perimeter. Lake shape was calculated by dividing the perimeter (m) by $2\sqrt{[\pi^* \text{area } (m^2)]}$. Although this standard limnological metric is usually called the shoreline development factor (Wetzel 2001), we use the term 'lake shape' to avoid confusion with residential development. We used published values for maximum depth and conductivity (Black *et al*. 1963).

We expected that lakes surrounded by wetlands would have much lower coarse wood densities than lakes surrounded by uplands. We used digitized wetlands data (Gergel *et al*. 1999) to calculate the proportion of each lake's shoreline covered by wetlands, using a 10-m buffer to account for small errors in alignment. These values were arcsine-square root transformed prior to analysis. To examine the effect of wetlands at the site level, we used the land-cover data described above to calculate the presence/absence of wetlands at each site.

To measure how exposed each site was to wave action, we used the empirical relationship between maximum wave height and fetch length (Wetzel 2001), weighted by the proportion of wind from 16 directions: relative exposure (cm) = $\Sigma\,[0.105 \times \sqrt{(\text{Fetch length (cm)})} \times$ proportion of wind from that direction$]$, an approach first suggested by Nonaka *et al*. (E. Nonaka, unpublished data). We used 11 years (1991–2002) of weather data from the Noble F. Lee Memorial Airfield (45.9281° N, 89.7308° W) to determine what proportion of the wind in the open water (ice-free) period came from each direction.

STATISTICAL ANALYSES

To determine what factors explain variation in the density of littoral coarse wood among lakes spanning the development gradient, we used multiple regression, with the number of logs ≥ 5 cm as the dependent variable. We tested 17 independent variables at the whole lake scale: riparian coarse wood ha^{-1}, snags and stumps ha^{-1}, density of trees ≥ 5 cm d.b.h. ha^{-1}, density of trees ≥ 10 cm d.b.h. ha^{-1}, density of trees ≥ 15 cm d.b.h. ha^{-1}, stand basal area ha^{-1}, basal area per tree (cm^2 $tree^{-1}$), tree + snag + stump density ha^{-1}, building density km^{-1}, lake shape, lake area (ha), conductivity (μmohs), proportion of shore in wetlands, proportion of riparian CW chewed by beaver, proportion of littoral CW chewed by beaver, proportion of riparian CW cut by humans, and proportion of littoral CW cut by humans.

We used a 'best' selection technique to determine the best one, two, three and four variable models based on the R^2 values. This approach indicates whether there are multiple models that explain the data equally well, although it does not explicitly test each term in the model for significance. Therefore, models were retained only if each term in the model was significant and none of the terms were correlated, using factor analysis to explore the covariance structure among our independent variables. Models were tested using both the original variables and the factor scores. In all cases, however, the models with the original, rather than synthetic, variables were strongest. Therefore only those results are presented.

Completely undeveloped lakes that meet our size criteria are rare; therefore, to explain variation in littoral coarse wood density in relatively undeveloped lakes, we repeated the analysis described above for the 12 lakes with the lowest building density (0–1.7 buildings km^{-1}, corresponding to the lowest 16% of building densities county-wide). Because the sample size was lower, we restricted the analysis to the best one-, two- and three-variable models.

Within-lake variation in littoral coarse wood density presented two analytical challenges. First, sites on the same lake are not independent. Secondly, preliminary data analysis indicated that many sites had no littoral coarse wood, but the densities at sites with coarse wood were log-normally distributed. To solve the first problem, we used mixed models to model correlation among sites on the same lake as a random effect of the lake. To solve the second, we used a two-step analysis. First, we predicted which sites had coarse wood using logistic regression (SAS macro %GLIMMIX, which implements the approach of Wolfinger & O'Connell 1993). Then we employed a split-plot or ANCOVA approach to model variation in the density of littoral coarse wood where it occurred (n = 214, proc MIXED, SAS version 8, SAS Institute, Cary, NC, USA; Littell *et al.* 1996). For both analyses, we ran all 3213 possible one-, two-, three- and four-variable models using a pool of 17 predictor variables as fixed effects and the lake as a random effect. Building density, lake area, lake shape, lake conductivity, maximum depth and the proportion of the lakeshore in wetlands cannot be computed at the site level and were replaced by land-use intensity, ownership, slope, aspect, relative exposure to wind, and the presence or absence of wetlands. We used Akaike's information criterion (AIC = −2 × log-likelihood + 2 × the number of parameters), to rank the models. A smaller AIC indicates that less information is lost by using that model to approximate reality than if a model with a higher AIC were used. Therefore models with a smaller AIC are considered 'better' (Johnson & Omland 2004). Following Burnham & Anderson's (1998) rules of thumb, models that had an AIC within 4 of the best model were considered reasonable candidates for best model, and subjected to closer examination. We computed two measures of the evidence that each model is the Kullback-Leibler (K-L) best model (given that one of the models in the set must be the best model) for the final set of models: relative AIC ($\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{\min}$) and Akaike weights ($\omega_i = e^{(-0.5\Delta_i)}/\Sigma\, e^{(-05\Delta_i)}$) (Burnham & Anderson 1998). Akaike weights sum to 1 and are dependant on the set of models compared; they can be interpreted as probabilities (Johnson & Omland 2004). A smaller Δ_i and a larger ω_i indicate that it is more probable that that the i^{th} model is the best model than the other n models in the set (Burnham & Anderson 1998). Data from eight sites were excluded because of missing data for one or more variables.

Results

AMONG-LAKE VARIATION ACROSS FULL DEVELOPMENT GRADIENT

The density of littoral coarse wood was quite variable among lakes, even in those that were undeveloped (Table 1a,b). The density of littoral coarse wood (both ≥ 5 cm in diameter and ≥ 10 cm) was skewed towards low values and declined as building density increased (Fig. 2). In addition, the variability among lakes decreased with increasing building density, i.e. lakes that had low levels of development could be either sparse or woody, but lakes with > 9 buildings km^{-1} never had more than 200 pieces of littoral coarse wood km^{-1}. All measured aspects of forest stand-structure (density of living trees, stand basal area, basal area per tree, density of riparian coarse wood, density of snags and stumps, previous stand density) also varied widely among lakes (Table 1a).

Factor analysis of all 17 potential explanatory variables indicated that most of the measures of forest structure loaded on the first axis, while the second axis was a combination of human and biotic variables (see

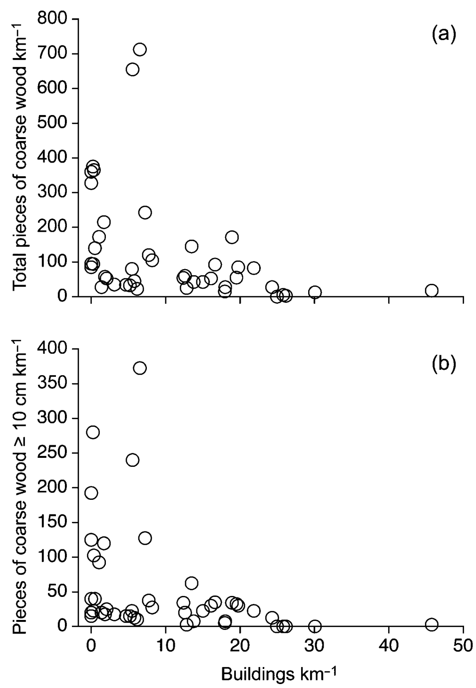

Fig. 2 Relationship between coarse wood at least 5 (a) or 10 (b) cm in diameter and building density in 45 northern Wisconsin lakes. Data points are the mean of eight sites per lake.

Table 1 Distribution of riparian and littoral variables in (a) 45 lakes and (b) 12 low-development lakes in northern Wisconsin

	Median	Minimum	Maximum
(a)			
Littoral variables			
Pieces of coarse wood ≥ 5 cm km^{-1}	57.5	0	712.5
Pieces of coarse wood ≥ 10 cm km^{-1}	22.5	0	372.5
Riparian forest variables			
Trees ≥ 5 cm d.b.h. ha^{-1}	1038	375	1875
Trees ≥ 10 cm d.b.h. ha^{-1}	627	242	983
Trees ≥ 15 cm d.b.h. ha^{-1}	429	179	716
Stand basal area (m^2 ha^{-1})	28.6	14.3	50.8
Basal area $tree^{-1}$ (cm^2 $tree^{-1}$)	318	153	603
Pieces of coarse wood ha^{-1}	225	25	579
Snags and stumps ha^{-1}	225	71	441
Tree + snag + stump density ha^{-1}	1333	588	2313
(b)			
Littoral variables			
Littoral coarse wood ≥ 5 cm km^{-1}	156.3	27.5	375.0
Littoral coarse wood ≥ 10 cm km^{-1}	66.3	15.0	280.0
Riparian forest variables			
Trees ≥ 5 cm d.b.h. ha^{-1}	994	375	1875
Trees ≥ 10 cm d.b.h. ha^{-1}	587	242	858
Trees ≥ 15 cm d.b.h. ha^{-1}	313	200	567
Stand basal area (m^2 ha^{-1})	21.6	14.3	40.9
Basal area $tree^{-1}$ (cm^2 $tree^{-1}$)	249	156	421
Riparian coarse wood ha^{-1}	431	115	579
Snags and stumps ha^{-1}	240	98	438
Tree + snag + stump density ha^{-1}	1365	617	2313

Table S1 in Supplementary Material). The third factor was composed of lake shape and the proportion of littoral coarse wood that had been cut by humans. The fourth factor integrated two abiotic variables (lake area and conductivity), while the final variable, proportion of the shoreline in wetlands, was orthogonal to all other variables. In contrast to previous studies, neither tree density nor stand basal area was correlated with either the density of littoral coarse wood or building density (results not shown).

Parsimonious evaluation of model selection revealed a single best model: the density of littoral coarse wood increased with both the density of riparian coarse wood (partial $R^2 = 0.54$, $P < 0.01$) and with lake shape (partial $R^2 = 0.04$, $P < 0.04$) (Fig. 3).

VARIATION AMONG LOW-DEVELOPMENT LAKES

The density of logs in both size classes in the 12 low-development lakes had larger minimum and median values than those observed in the whole data set, but a smaller total range because the two woodiest lakes (Lynx and Katinka) had > 1.7 buildings km^{-1} and so were not part of the low-development subset (Table 1b). As expected from the lack of correlation between building density and forest structure, the eight forest structure variables had approximately the same distribution in low-development lakes as they did across the whole gradient (Table 1b). The median density of riparian

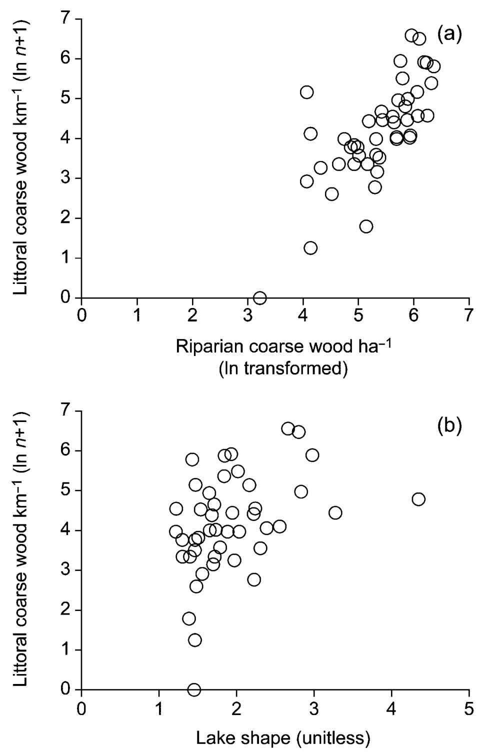

Fig. 3 Relationship between coarse wood density and (a) riparian log density or (b) lake shape in 45 northern Wisconsin lakes. Lake shape is a ratio of the perimeter of the lake to the circumference of a circle with the same area as the lake. Values near 1 indicate almost circular lakes, while larger values indicate more complex shorelines. Data points are the mean of eight sites per lake.

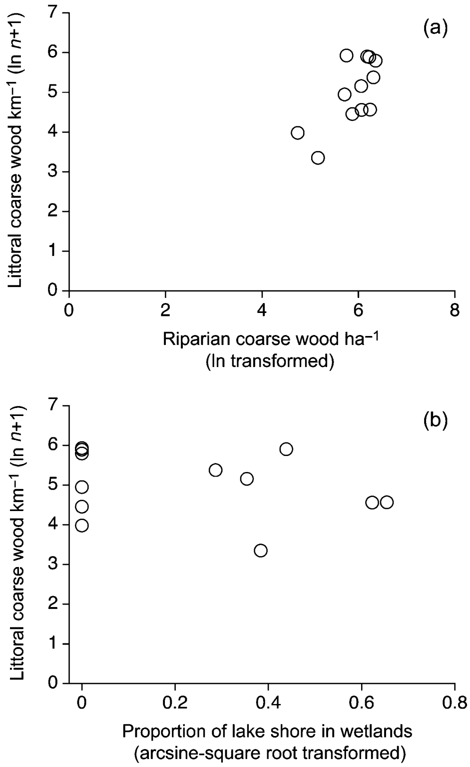

Fig. 4 Relationship between coarse wood density and (a) riparian log density or (b) proportion of the lakeshore covered by wetlands (arcsine-square root transformed), in 12 low-development northern Wisconsin lakes. Data points are the mean of eight sites per lake.

coarse wood and the previous forest density (trees + snags + stumps ha^{-1}), however, were both much higher in the undeveloped lakes. Even though we selected lakes with low levels of development, building density was still correlated with some of our predictor variables: the average basal area per tree ($r = -0.71$, $P = 0.01$) and the proportion of wood on shore that was cut by humans ($r = 0.70$, $P = 0.01$).

As with the full development gradient, there was a single best model for the low-development lakes. Littoral coarse wood was positively related to riparian coarse wood (partial $R^2 = 0.48$, $P = 0.01$) and negatively related to the proportion of the lake surrounded by wetlands (partial $R^2 = 0.21$, $P = 0.03$; Fig. 4). This model had better predictive power than the model for all 45 lakes (adj. $R^2 = 0.69$ vs. 0.58). Riparian coarse wood was still the single best predictor of littoral coarse wood, although it explained slightly less of the variation than in the full data set. Lake shape, which was consistently a part of the models for the whole development gradient, did not appear in any of the potential models for low-development lakes.

VARIATION WITHIN LAKES

Of the 352 sites with complete data, littoral coarse wood occurred at 214 (61%). Only two lakes had wood at one or fewer sites. None of the 17 biotic, abiotic and anthropogenic independent variables explained the presence/absence of littoral coarse wood better than a model fit with just the intercept and a random effect of lake.

At those sites where coarse wood was present, the density varied greatly among sites, ranging from 20 to 4200 logs km^{-1}. Model selection for within-lake patterns of coarse wood did not yield an unambiguously best model. The model with the lowest AIC was (–) exposure + riparian CW + proportion of littoral CW chewed by beaver. However, there were 21 additional models with a $\Delta_i \leq 4$ (See Table S2 in Supplementary Material). All of these models were more credible as the best model ($\Delta_i = 0–4$, $\omega_i = 0.133–0.018$) than a model fit with only the intercept ($\Delta_i = 39.4$, $\omega_i = 3.69 \times 10^{-10}$).

Co-linearity in the predictor variables may explain the large number of 'best' models. All of the final models included the relative exposure to wave action, 68% included the density of riparian coarse wood and 50% included the land-use intensity index, 45% included littoral CW chewed by beaver, 32% included littoral CW cut by humans, 27% included the ownership of the site and 14% included riparian CW chewed by beaver. Riparian CW cut by humans and the presence of wetlands were included in one model each. As expected, the two different measures of beaver activity are correlated ($r = 0.37$, $P < 0.01$). Land-use intensity and riparian coarse wood are negatively correlated ($r = -0.41$, $P < 0.0001$). The similarity in Δ_i values provides little justification for selecting a three- or four-variable model over a two-variable model. Thus, the 22 candidate models can be grouped into two main 'families': (–) exposure + riparian coarse wood and (–) exposure – land use intensity (Fig. 5). The evidence ratio of these two models is just 3.16 (0.705/0.223), providing little evidence for choosing one model family over another (Burnham & Anderson 1998).

Discussion

Our finding that highly developed lakes (> 9 buildings km^{-1}) are uniformly depauperate of coarse wood agrees with the limited literature on the subject (Christensen *et al*. 1996; Jennings *et al*. 2003). In contrast to previous work, the best predictor of littoral woody habitat was not building density *per se*, but riparian coarse wood, which was not measured in earlier studies. We also found little connection between tree density and littoral coarse wood, contrary to previous studies of lakes (Christensen *et al*. 1996) but consistent with most terrestrial studies (Spies *et al*. 1988; Hale *et al*. 1999; Hely *et al*. 2000). The negative correlation of land-use intensity and riparian coarse wood within lakes suggests that riparian coarse wood may be an integrated measure of human and natural disturbance.

Densities of littoral coarse wood in developed lakes were similar to those observed in previous studies, but the maximum density of littoral coarse wood in undeveloped lakes was 200 log km^{-1} lower than reported elsewhere (Christensen *et al*. 1996; Mallory *et al*. 2000). This difference may be due to compositional differences

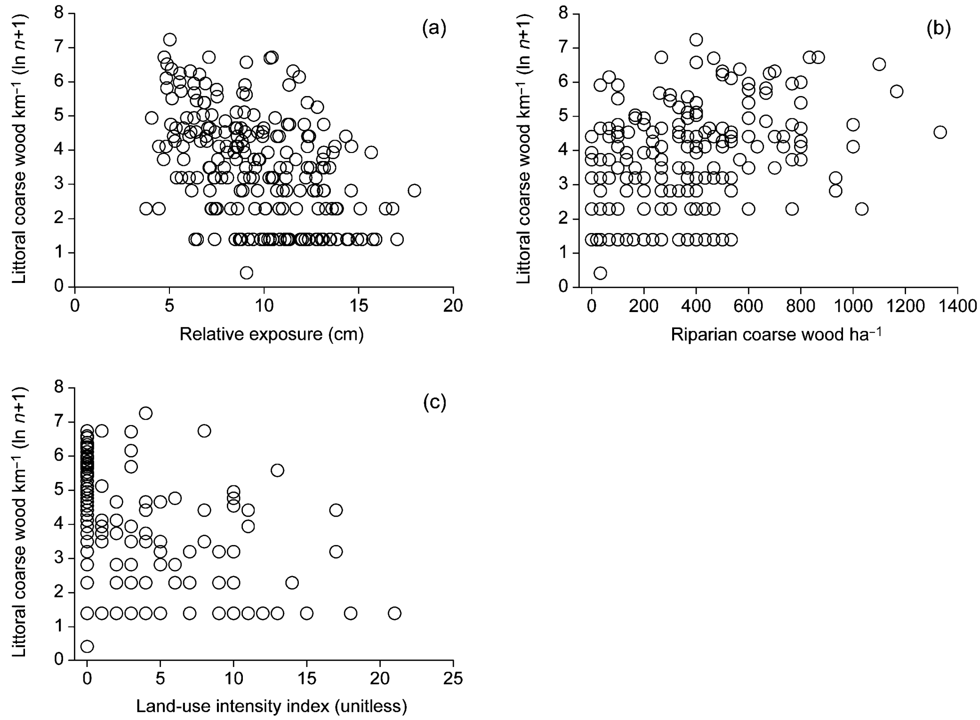

Fig. 5 Relationship between coarse wood density at the 214 sites where it was present and (a) exposure to wind, (b) riparian log density and (c) land-use intensity. Data points represent sites nested within 45 northern Wisconsin lakes.

in the forest surrounding the lakes or differences in land-use history. The undeveloped lakes used in previous studies were very small (< 25 ha) and were located in protected reserves, which was not the case for most of our lakes.

The similarity of the models for the full set of 45 lakes that spanned the development gradient and those for the 12 low-development lakes suggests a consistent relationship between littoral and riparian coarse wood. The factor analysis revealed a significant negative correlation between housing density and riparian coarse wood, suggesting that people may remove downed wood, perhaps for firewood or aesthetics. However, the low levels of riparian coarse wood we observed in some undeveloped lakes must be due to other factors. Disturbance history influences coarse wood in terrestrial forests (Hale *et al*. 1999; Hely *et al*. 2000), and simulation studies suggest that disturbance regime may affect riparian and littoral coarse wood abundance for many decades (Bragg 2000; Turner 2003).

We were surprised by the inability of any of the drivers considered to predict the presence or absence of wood at the site level better than a random effect for the lake itself. This indicates that there might be redistribution of logs once wood enters the lake and, taken together with the decrease in density of littoral coarse wood at more exposed sites, suggests that areas of low exposure may be important areas for littoral coarse wood accumulation and that wood may accumulate at different sites along the lakeshore. Studies designed explicitly to elucidate the mechanisms underlying this relationship and to determine the spatial locations of source and sink habitats for littoral coarse wood are warranted.

Littoral coarse wood varied spatially among sites within a given lake in response to the physical environment and either land-use intensity or the amount of wood on shore. Previous studies have also found lower coarse wood near developed properties (Kratz *et al*. 2002; Jennings *et al*. 2003). The response to local land-use intensity, rather than simply ownership type (public vs. private) or building density at the lake scale, suggests that management choices by individual landowners influence littoral coarse wood.

The results of this study suggest some key new research directions to enhance the understanding of spatial and temporal variability in coarse wood among and within lakes. Long-term studies in which littoral coarse wood inputs, decomposition and losses are measured would be particularly helpful in elucidating why undeveloped lakes have up to a 13-fold difference in coarse wood abundance. The natural disturbance regime of the NHLD is dominated by windthrow, with relatively low frequencies of fire (Canham & Loucks 1984; Frelich & Lorimer 1991). Given that susceptibility to windthrow can vary by species (Canham *et al*. 2001) and that forest composition in the NHLD has changed since European settlement (Stearns 1949; White & Mladenoff 1994), obtaining a thorough understanding of the history of the riparian forests around our study lakes could elucidate the potential influence of disturbance or land-use history on contemporary forest structure and coarse wood.

If natural disturbances and land-use intensity do influence riparian and littoral coarse wood, then these events could also have long-term effects on overall lake function. The density of coarse wood required for the persistence of aquatic organisms is not known and will depend on the fineness of niche partitioning among coarse wood dwellers. Some studies have found that macroinvertebrates are habitat-limited and show no preference for deciduous vs. conifer coarse wood (France 1997b); others have found significant preferences among some species of invertebrates for different species of coarse wood (Bowen *et al*. 1998). Whether coarse wood is sufficient in the NHLD lakes to assure persistence of the populations that use this habitat has not been demonstrated.

Understanding the long-term legacy of historical conditions is increasingly recognized as an important factor explaining variability in many aspects of ecosystem and community structure in forested landscapes (Currie & Nadelhoffer 2002; Foster *et al*. 2003). Furthermore, the potential importance of alteration of natural disturbance regimes in response to increased population density for long-term forest dynamics should also be considered (Turner *et al*. 1989; Grizzel & Wolff 1998; Dwire & Kauffman 2003).

The importance of anthropogenic factors operating at both the lake and local scales has important implications for lake management in the NHLD. At the lake level, a high density of lakeshore development was always associated with very low densities of littoral coarse wood. Within a lake, the intensity of local human land use was strongly and negatively related to abundance of littoral coarse wood. This suggests that lake management for coarse wood might need to be implemented at multiple scales. At the lake level, building density may need to remain below 18 buildings km^{-1} to ensure that the density of littoral coarse wood remains above the minimum observed in undeveloped lakes (*c*. 30 pieces km^{-1}). A more conservative threshold would be needed if the management goal were to match the distribution of coarse wood densities in developed lakes to the range of densities observed in undeveloped lakes. Within lakes, managers should consider how local land-use intensity may interact with sources and sinks for littoral coarse wood.

Interactions between terrestrial and aquatic systems are complex and ecologically important (Naiman & Décamps 1997). As rural landscapes undergo increasing residential development (Dale *et al*. 2000; Naiman & Turner 2000), understanding interactions among anthropogenic, physical and biotic processes and how they affect riparian zones takes on increasing importance. Land–water interactions are central to freshwater research agendas (Naiman *et al*. 1995). This study shows that the processes behind these interactions can be a complex mix of biotic, abiotic and anthropogenic drivers and that the relative importance of these drivers changes from the local to the landscape scale.

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Supplementary Material

The following supplementary material is available online from www.Blackwell-Synergy.com:

Table S1 Results of factor analysis of independent variables.

Table S2 Alternate models of within-lake variation in littoral coarse wood.