

A riverscape perspective on habitat associations among riverine bird assemblages in the Lake Champlain Basin, USA

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Abstract The riverscape perspective recognizes the heterogeneous habitat types within the stream corridor as a single, integrated ecological unit operating across spatial scales. Although there is ample evidence that the riverscape notion is appropriate in understanding the physical phenomena of stream corridors, significantly less attention has focused on its ecological ramifications. To this end, we surveyed riverscape habitat variables and bird community characteristics in the Champlain Valley of Vermont, USA. From the data collected, we used information theoretic methodology (AIC_c) to model relationships between bird community attributes and key habitat variables across the riverscape. Our models with the greatest support suggest that riverine bird communities respond to a suite of characteristics; representing

a variety of riverscape habitats at the in-stream, floodplain, and riparian levels. Channel slope, drainage area, percent conifers, and in-stream habitat condition were among the most influential variables. We found that piscivores are potentially important indicators of riverscape condition, responding to a host of variables across the riverscape. Our results endorse a holistic approach to assessing and managing the mosaic of patches in the riverscape and suggest that a riverscape approach has significant conservation potential.

Keywords Bird communities · Conservation · Floodplain · Information theoretic method · In-stream · Riparian · Riverscape

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Introduction

In recent years, a landscape perspective of streams and rivers [i.e., “riverscape” *sensu* Malard et al. (2000)] has emerged. While the riverscape notion may be applied across multiple spatial scales; it recognizes a stream, its floodplain (i.e., area of land regularly covered with water as a result of stream flooding), and riparian area (i.e., land adjacent to the stream that directly affects the stream; includes woodland, vegetation, and floodplain) as an integrated ecological unit (Wiens 2002). This view builds on documented connections between streams and their riparian zones (Vannote et al. 1980; Amoros and

Roux 1988; Naiman and Décamps 1997), and subsequently explores the importance of physical disturbance (Resh et al. 1988; Junk et al. 1989; Poff 1992; Giller 1996; Poff et al. 1997), interhabitat coupling (McDade et al. 1990; Gregory et al. 1991; White 1993; Johnson et al. 2000; Covich et al. 2004), and non-uniform patchiness (Amoros and Bornette 2002; Ward et al. 2002) to the structure and function of stream ecosystems.

Riverscapes are interactive, open systems, characterized by high levels of natural disturbance and interconnected ecotones (Ward 1989; Ward and Wiens 2001). Channel geomorphology, hydrological flows, and connectivity shape spatial and temporal riverscape patterns (Wiens 2002) and exchanges of particulate and dissolved organic matter, energy, and biota (Hansen and di Castri 1992; Tockner et al. 1999; Ward et al. 2002) across ecotones link various riverscape patches. These exchanges are multi-directional in nature, creating food web dynamics that spatially connect distinct patches within the riverscape. The importance of terrestrial to aquatic transfers of organic material and biota has been well-documented (Wipfli 1997; Nakano et al. 1999; Baxter et al. 2005), and the reciprocal energy transfers from aquatic to terrestrial systems is attracting increasing attention (Ben-David et al. 1998; Nakano and Murakami 2001; Baxter et al. 2005). Bird communities, for example, prey on both terrestrial insects feeding on riparian vegetation and emergent aquatic insects (Jackson and Fisher 1986; Nakano and Murakami 2001; Murakami and Nakano 2002).

Much of our understanding of species–habitat relationships within the riverscape comes from research that independently addresses in-stream-, floodplain-, and riparian-biotic links. Many investigations focus on in-stream habitat characteristics that support benthic macroinvertebrate and fish communities (Gorman and Karr 1978; Karr 1981; Kerans and Karr 1994; DeShon 1995; Deacon and Mize 1997; Inoue and Nunokawa 2002). Floodplains are explored primarily in terms of habitat diversity, biocomplexity, and hydrological connectivity (Copp 1989; Ward et al. 1999; Amoros and Bornette 2002; Ward et al. 2002). The importance of riparian buffers to in-stream ecosystems is also widely-studied (Jones et al. 1999; Boothroyd et al. 2004; Zaimes et al. 2004), as are influences of the extent and quality of riparian vegetation on bird communities (Maloney

et al. 1999; Ammon 2000; Inman et al. 2002; Tucker et al. 2003; Warkentin et al. 2003; Miller et al. 2004). However, the riverscape concept encourages viewing biological communities and connections to their riverine habitats viewed as a single ecological unit. This requires a broader understanding of species–habitat relationships; habitat loss, fragmentation, and degradation; and the range of reciprocal connections between the channel and its surrounding riparian zone.

Bird communities in riverine landscapes

The abundance, distribution, and structure of riverine bird communities may be key factors to an integrative understanding of riverscapes. The mobility of birds and their use of myriad stream corridor habitats suggest that birds operate at a spatial scale appropriate to the riverscape construct. Birds that use both riparian and in-stream resources may be integrators of linkages between the stream, riparia, and watershed.

Because some avian species are highly sensitive to environmental changes at both fine and coarse scales (Saab 1999; Buckton and Ormerod 2002; MacFaden and Capen 2002; Clear et al. 2005), the use of birds as ecological indicators has garnered increasing attention (Collier and Wakelin 1996; Canterbury et al. 2000; O'Connell et al. 2000; Buckton and Ormerod 2002; Feck and Hall 2004). Furthermore, within the stream corridor, riparian-obligate birds might be expected to respond to changes in surrounding habitats before aquatic organisms (Bryce et al. 2002). Many birds occupy high trophic levels and reflect functional impairments at lower levels (Pettersson et al. 1995; Steinmetz et al. 2003; Sullivan et al. 2006). For these reasons, bird indices are used as measures of riparian habitat condition (Croonquist and Brooks 1993; Elias 1997; Loegering and Anthony 1999; Popotnik and Giuliano 2000; Bryce et al. 2002; Inman et al. 2002).

Our objectives were to (1) relate the abundance, distribution, and structure of riverine bird communities to the riverscape unit, (2) assess relationships between reach spatial heterogeneity and bird community characteristics, (3) investigate the utility of bird groups as indicators of riverscape ecological condition, and (4) to define those habitat characteristics whose conservation might result in improved riverscape health.

Methods

Study sites

In 2003 and 2004, we selected 29 reaches in 27 streams in the Champlain Valley, VT. Study reaches were located in various positions within their respective watersheds, capturing a range of drainage area sizes (3.7–509 km², ~10 km²). Reaches represented a range of land cover types and habitat conditions; were predominately pool-riffle, plane bed, and dune-ripple morphologies (see Montgomery and Buffington 1997); and had a mean bankfull width of 18.8 m (± 8.7 SD). Each reach was >10 bankfull channel widths in length (Kondolf and Micheli 1995; Montgomery and Buffington 1997). The matrix of forest patches along reaches included northern hardwood, mixed northern hardwood-conifer, and pure conifer cover types and encompassed a full diversity of successional/seral conditions.

Riverscape variables

We quantified in-stream, floodplain, and riparian habitat characteristics to determine the composition and quality of the riverscape for each reach (Table 1).

We selected in-stream variables to represent stream size (bankfull width and drainage area), geomorphic features (channel slope, mean depth, sinuosity), and

availability and quality of aquatic habitat [Rapid Habitat Assessment (RHA)]. We selected floodplain variables to characterize a stream's access to its floodplain [entrenchment ratio, width to depth ratio (bankfull width/maximum depth)], and the extent and development of the active floodplain (% floodplain forest, number of floodplain waterbodies). Although many variables could potentially be used to characterize riparian vegetation, our variables represented a landscape perspective of stream systems at a scale appropriate to our study (Turner and Gardner 1991; Wiens 1995). Riparian variables represented characteristics of adjacent vegetation structure and composition at both patch (e.g., % floodplain forest, % wet meadow) and within-patch (e.g., % deciduous species, % canopy closure) scales.

Because stream order does not quantitatively capture stream size, we empirically measured stream size using bankfull width and drainage area. We used digital elevation models and the watershed generation algorithm of the Soil and Water Assessment Tool (SWAT, Arnold et al. 1998) to generate drainage area. We estimated bankfull width, mean depth, and floodprone width from cross-sectional surveys. From these measurements, we calculated width to depth and entrenchment ratios (see Rosgen 1996). We calculated channel slope from longitudinal profile surveys of all major features and breaks in slope. We used the straight-line valley distance and the surveyed thalweg distance to calculate sinuosity.

Habitat surveys were based on habitat diversity across the reach. We followed the Vermont Rapid Habitat Assessment protocols (see VTDEC 2003), which yielded an overall habitat evaluation ranging from 0 to 200 for each reach, with higher assessment values indicating better aquatic habitat conditions. We identified the active floodplain according to Rosgen (1996), effectively measuring the width of the stream at flood flows. In each floodplain, we identified all floodplain waterbodies and counted the total number across the entire reach.

To characterize riparian vegetation, we buffered each reach to 50 m on either side of stream banks in a GIS. We then stratified by landform-related patch types: upland forest, floodplain forest, wet meadow, natural non-forest, and agricultural land. We used a supervised classification of polygons to stratify these patch types, ground-truthing these delineations before collecting field data. We quantified the area in each landform type

Table 1 Variables collected at study reaches, representing in-stream, floodplain, and riparian characteristics. (Width to Depth ratio describes aspects of both *In-stream* and *Floodplain* characteristics)

Riverscape variables		
In-stream	Floodplain	Riparian
Bankfull width	% Floodplain forest	% Ag. land
Channel slope	Entrenchment ratio	% Canopy closure
Drainage area	No. of floodplain waterbodies	% Conifers
Mean depth	Width to depth ratio	% Forest
Rapid Habitat Assessment (RHA)		% Hardwoods
Sinuosity		% Natural non-forest
Width to depth ratio		% Wet meadow

in a GIS and aggregated to the site level and by forested versus non-forested. We then distributed sampling plots as a proportionate sample of each patch type, yielding a total of 25–30 plots per site. We sampled forest vegetation in variable radius plots using a ten-factor prism. In each plot, we identified all trees (live and dead) >5 cm diameter at breast height and measured the diameter at breast height (1.37 m). We entered field data into the Northeast Decision Model (NED) (Simpson et al. 1996) to generate stand inventory metrics. From GIS and NED output, we selected variables representing the composition (% forest basal area by conifers vs. hardwoods, % agricultural land, and % wet meadow) and structure (% canopy closure) of the riparian zone for further analysis.

Bird surveys

We conducted all bird surveys from mid-May through mid-June. We selected this sampling period to correspond to the time of peak birdsong in Vermont's Champlain Valley because we anticipated that the majority of detections would be auditory. Because all birds actively select one stream corridor reach over another regardless of its specific use (e.g., breeding territory or migratory stopover site), we did not exclude migrants or other "non-resident" birds from the surveys. We anticipated that different species might use the same reach at different times of the day. Therefore, following the guidelines of the US Fish and Wildlife Service Breeding Bird Survey (USFWS 1990), we conducted 2 surveys of each stream reach at least 10 days apart, with the first occurring in the morning (sunrise to 4 hours after sunrise) and the second in the evening (3 h before dusk to dusk).

To quantify diversity, we summed all bird species that we surveyed at each reach during both the morning and evening surveys. We calculated abundance estimates by adding all individuals surveyed at each reach. To avoid double-counting the same individuals, we used only the larger number of individuals between the morning and evening surveys. For example, if we surveyed two Tree Swallows (*Iridoprocne bicolor*) in the morning, and six in the evening, we entered "six" for that species into the abundance calculation for the reach in question.

Although the objective of our bird surveys was more to characterize bird assemblage composition and relative abundance across a set of stream reaches

than to estimate the densities of bird populations, we remained aware of the potential problems associated with detection probability (e.g., Burnham 1981; Thompson 2002). The potential applicability of using bird assemblages as ecosystem indicators also required the use of a survey protocol that could be easily and accurately reproduced.

To this end, we used the double-observer method (Nichols et al. 2000) along fixed-width line transects. We selected line transects because the geometry of line transects parallels the longitudinal nature of streams. Line transects also yield more detections per unit time (Bollinger et al. 1988) than point counts and tend to minimize potential bias resulting from evasive movements of birds (Rosenstock et al. 2002).

At each reach, we established 250 m parallel transects on each side of the stream at the bankfull width. We centered transects within the reach and flagged them at 25 m intervals. The transect width extended 25 m into the riparian zone on one side and into the middle of the stream channel on the other.

The double-observer method also helped us reduce the number of birds present but not detected (Nichols et al. 2000). To minimize differences among observers' abilities to detect and identify birds, one of the observers was the same individual in all the surveys. The observers walked steadily along each transect at a pace of 100 m/10 min (Ralph et al. 1993). We conducted all bird surveys on days without measurable precipitation or wind. We treated groups of birds as a single observation for purposes of distance and location and did not include immature birds in the count.

Although we considered using distance sampling to address potential differences in detectability of different species, recent literature suggests that detection probability likely approaches 1.0 at distances ≤ 25 m (Diefenbach et al. 2003). The combination of our 25 m transect half-width (which was completely open on the channel side) and the double-observer method gave us confidence that our surveys accurately represented the abundance and composition of the bird assemblage at each site.

Data analysis

We based our data analysis on the information theoretic method (Burnham and Anderson 1998; Anderson et al. 2000). We created a set of *a priori*

models having selected independent variables thought to be crucial to the riverscape notion (Table 2).

All variables included in the regression models carried an F statistic with $P < 0.05$. Each model generated an Akaike's Information Criterion (AIC), which we converted to AIC_c to account for small sample size. The model with the lowest AIC_c is considered the most parsimonious model. Each of the potential models was ranked against the best model ($\Delta_i = AIC_{c,i} - AIC_c$), thus creating the best ($\Delta_i = 0$) and alternate models for each dependent variable. $\Delta_i < 2$ suggests substantial evidence for the model, Δ_i between 4 and 7 suggests the model has considerably less support, and $\Delta_i > 10$ indicates that the model is highly unlikely. We considered all models with $\Delta_i < 4$ to be well supported (Perkins et al. 2003). We calculated Akaike weights (w_i , $w_i = \exp(-\Delta_i/2) / \sum [\min, r = 1; \max, R] \exp(-\Delta_i/2)$) to indicate the probability that a model was the best among all models in its set.

We selected dependent variables to represent bird species richness and abundance of the entire community and of selected groups of birds (Table 3).

We used traditional dietary and foraging guilds based on species' preferences during the breeding season. We also examined the overall bird community excluding waterbirds in order to look at potential differences in habitat associations between water-obligate birds and the remainder of the bird community.

We performed all statistical analysis using JMP[®] 5.0.1 Statistical Discovery Software (SAS Institute, Cary, NC). Transformations were used to normalize data and eliminate heteroscedasticity prior to analysis (Snedecor and Cochran 1967; Zar 1984). We used a correlation analysis to test for highly correlated ($r > 0.80$, Perkins et al. 2003) independent variables, and avoided using any of these correlated variables in the same model (Burnham and Anderson 1998).

Table 2 Independent variables analyzed, their minimums, medians, and maximums in their original units, and their means and standard deviations (SD) (after transformation where appropriate)

	Original data			Values analyzed	
	Minimum	Median	Maximum	Mean	SD
<i>In-stream</i>					
Bankfull width (m)	6.64	14.59	35.18	16.75	7.64
Channel slope	0.05	0.44	2.00	-4.79	5.84
Drainage area (km ²)	3.74	80.86	509.15	4.26	1.03
Mean depth (m)	0.24	0.51	1.19	0.43	0.11
RHA score	82.00	140.00	184.00	138.10	25.24
Sinuosity	0.90	1.22	2.78	-0.81	0.16
Width:depth	11.85	29.06	63.37	31.62	13.40
<i>Floodplain</i>					
% Floodplain forest	0.00	48.39	100.00	0.83	0.76
Entrenchment ratio	0.95	1.39	11.69	-0.64	0.29
No. Floodplain waterbodies	0.00	1.00	8.00	0.83	0.76
<i>Riparian</i>					
% Ag. land	0.00	0.00	1.83	0.37	0.58
% Canopy closure	0.00	51.57	90.00	50.26	22.12
% Conifers	0.00	20.00	75.37	28.06	28.93
% Hardwoods	0.00	46.82	100.00	55.09	30.67
% Forest	0.00	72.00	100.00	67.41	26.57
% Natural non-forest	0.00	8.00	63.00	2.04	1.33
% Wet meadow	0.00	28.00	100.00	32.41	26.54

Table 3 Bird groups and guilds evaluated

Dependent, bird assemblage variables	Description	Examples
<i>Species richness & abundance</i>		
Overall community	All birds within study area	American Goldfinch (<i>Carduelis tristis</i>), Common Yellowthroat (<i>Geothlypis trichas</i>), Common Grackle (<i>Quiscalus quiscula</i>)
Waterbirds	Wading, swimming, and diving birds	Wood Duck (<i>Aix sponsa</i>), Hooded Merganser (<i>Lophodytes cucullatus</i>), Green Heron (<i>Butorides striatus</i>)
Overall community excluding waterbirds	All birds within study area except wading, swimming, and diving birds	Alder Flycatcher (<i>Empidonax alnorum</i>), Yellow Warbler (<i>Dendroica petechia</i>), American Redstart (<i>Setophaga ruticilla</i>)
Piscivores	Birds that prey on stream fish as their principal food source	Belted Kingfisher (<i>Ceryle alcyon</i>), Common Merganser (<i>Mergus merganser</i>), Osprey (<i>Pandion haliaetus</i>)
Waders	Birds that forage in streams and wetlands, feeding on amphibians, macroinvertebrates, fish, and other aquatic foods	Great Blue Heron (<i>Ardea herodias</i>), Spotted Sandpiper (<i>Actitis macularia</i>)
Insectivores	All birds that forage on aquatic insects (in-stream or emergent) as their principal food source	Northern Rough-winged Swallow (<i>Stelgidopteryx ruficollis</i>), Louisiana Waterthrush (<i>Seiurus motacilla</i>)

Results

In all, we recorded 101 bird species (Appendix 1), with a maximum of 28 species at one reach ($= 17.14$, $SD = 4.52$). Abundance estimates ranged from 10 to 64 ($= 34.86$, $SD = 14.62$). We found only a few pairwise correlations with $r > 0.8$: drainage area and bankfull width, percent canopy cover and percent forest, percent forest and percent wet meadow, and percent wet meadow and percent canopy cover (Table 4), and we avoided including both variables from any of these pairwise correlations in the same model. Notably, we found a number of additional correlations among measures of stream morphology: bankfull depth and drainage area ($r = 0.805$), bankfull width and mean depth ($r = 0.492$), channel sinuosity and mean depth ($r = 0.431$), drainage area and channel slope ($r = -0.527$), and drainage area and mean depth ($r = 0.580$) (Table 4).

Our model selections illustrate how bird communities and select bird groups are related to various habitat characteristics of the riverscape, including in-stream, floodplain, and riparian habitat attributes.

Table 5 illustrates these relationships, showing the independent variables for each model, and expressing the AIC_c , Δ_i , w_i , and R^2 for each model in each set.

R^2 values for the best approximating models ranged from 0.19 for Species richness: Waders to 0.64 for Species richness: Overall community (Table 6).

Species richness for the entire bird community generated two models with $\Delta_i < 4$. The Channel slope + % Conifers model was the best approximating model, explaining 64% of the variance. In the alternate model, channel slope alone explained 57% of the variance, but had a relatively small probability ($w_i = 0.15$) of being the most parsimonious model. The best approximating model for overall abundance included channel slope as an important variable, but was complemented by % wet meadow and entrenchment ratio, and accounted for 58% of the variance seen in bird abundance. For overall abundance, Channel slope + % Forest + Entrenchment ratio also explained 58% of the variance, with a small Δ_i (0.265). Channel slope again emerged as an important variable in the species richness and abundance

Table 4 Correlation matrix of independent variables

	Bankfull width	Channel slope	Drainage area	Mean depth	RHA score	Sinuosity	Width: depth	% FP Forest	ER	No. FP WB	% Ag. land	% CC	% Conifers	% HW Forest	% Natural NF	% WM
<i>In-stream</i>																
Bankfull width	1.000	-0.225	0.805	0.492	0.036	-0.207	0.664	-0.020	-0.325	-0.038	0.239	-0.221	-0.378	0.096	-0.025	0.030
Channel slope	-0.225	1.000	-0.527	-0.431	-0.283	0.497	0.004	-0.252	-0.326	-0.135	-0.208	-0.214	0.411	-0.399	-0.283	0.280
Drainage area	0.805	-0.527	1.000	0.580	0.112	-0.354	0.439	0.075	0.045	-0.113	0.227	-0.053	-0.309	0.095	0.111	-0.108
Mean depth	0.492	-0.431	0.580	1.000	-0.063	-0.242	-0.276	-0.185	0.219	-0.057	0.511	-0.308	-0.382	0.029	-0.190	0.191
RHA score	0.036	-0.283	0.112	-0.063	1.000	-0.028	0.131	0.143	0.104	0.252	-0.140	0.526	0.252	0.178	0.647	-0.641
Sinuosity	-0.207	0.497	-0.354	-0.242	-0.028	1.000	-0.062	-0.009	-0.164	0.248	0.001	-0.334	0.156	-0.309	-0.282	0.282
Width:depth	0.664	0.004	0.439	-0.276	0.131	-0.062	1.000	0.222	-0.493	-0.012	-0.159	0.082	-0.161	0.184	0.209	-0.204
<i>Floodplain</i>																
% FP Forest	-0.020	-0.252	0.075	-0.185	0.143	-0.009	0.222	1.000	0.150	0.455	-0.549	0.323	-0.306	0.676	0.405	-0.402
ER	-0.325	-0.326	0.045	0.219	0.104	-0.164	-0.493	0.150	1.000	0.201	-0.074	0.188	-0.108	0.193	0.189	-0.184
No. FP WB	-0.038	-0.135	-0.113	-0.057	0.252	0.248	-0.012	0.455	0.201	1.000	-0.040	-0.133	-0.257	0.383	0.081	-0.086
<i>Riparian</i>																
% Ag. land	0.239	-0.208	0.227	0.511	-0.140	0.001	-0.159	-0.549	-0.074	-0.040	1.000	-0.525	-0.303	-0.248	-0.614	0.616
% CC	-0.221	-0.214	-0.053	-0.308	0.526	-0.334	0.082	0.323	0.188	-0.133	-0.525	1.000	0.379	0.310	0.828	-0.827
% Conifers	-0.378	0.411	-0.309	-0.382	0.252	0.156	-0.161	-0.306	-0.108	-0.257	-0.303	0.379	1.000	-0.604	0.320	-0.326
% HW	0.096	-0.399	0.095	0.029	0.178	-0.309	0.184	0.676	0.193	0.383	-0.248	0.310	-0.604	1.000	0.396	-0.392
% Forest	-0.025	-0.283	0.111	-0.190	0.647	-0.282	0.209	0.405	0.189	0.081	-0.614	0.828	0.320	0.396	1.000	-0.999
% Natural NF	-0.085	0.572	-0.244	-0.230	-0.301	0.182	0.009	0.296	-0.101	0.170	-0.443	-0.190	0.132	-0.008	-0.193	0.190
% WM	0.030	0.280	-0.108	0.191	-0.641	0.282	-0.204	-0.402	-0.184	-0.086	0.616	-0.827	-0.326	-0.392	-0.999	1.000

FP = Floodplain, ER = Entrenchment ratio, WB = Waterbodies, CC = Canopy closure, HW = Hardwoods, WM = Wet meadow

Table 5 Bird groups, habitat model sets ($A_j < 4$), and AIC statistics

Bird response	Habitat model*	AIC _c	A_j	w_i	R^2
Species richness:					
Overall community	Channel slope (-)	121.709	3.425	0.15	0.57
Abundance:	Channel slope (-) + % Conifers (-)	118.284	0.000	0.83	0.64
Overall community	Channel slope (-) + % Wet meadow (+)	195.842	2.744	0.09	0.50
	Channel slope (-) + % Wet meadow (+) + Entrenchment ratio (+)	193.098	0.000	0.35	0.58
	Channel slope (-) + % Forest (-)	196.105	3.007	0.08	0.50
	Channel slope (-) + % Forest (-) + Entrenchment ratio (+)	193.362	0.265	0.30	0.58
	% Conifers (-) + Entrenchment ratio (+) + % Agriculture (+)	195.493	2.395	0.10	0.54
Species richness: Waterbirds	Channel slope (-)	-25.437	0.000	0.88	0.37
Abundance: Waterbirds	Channel slope (-)	9.371	0.000	0.91	0.42
Species richness:					
(Overall community excluding Waterbirds)	Channel slope (-)	91.125	2.432	0.22	0.39
Abundance: Overall community	Channel slope (-) + % Conifers (-)	88.693	0.000	0.74	0.47
(Overall community excluding waterbirds)	% Conifers (-) + % Agriculture (+) + Entrenchment ratio (+)	161.978	0.000	0.45	0.51
Species richness: Piscivores	% Agriculture (+) + Entrenchment ratio (+) + % Floodplain forest (+)	162.540	0.562	0.34	0.50
	Channel slope (-) + RHA (+)	3.695	3.503	0.07	0.39
	Channel slope (-) + RHA (+) + % Natural non-forest (+)	0.192	0.000	0.41	0.49
	Channel slope (-) + % Agriculture (-)	3.389	3.197	0.08	0.39
	Channel slope (-) + % Agriculture (-) + RHA (+)	0.766	0.574	0.31	0.48
Abundance: Piscivores	RHA (+) + Drainage area (+)	10.955	3.151	0.08	0.37
	RHA (+) + Drainage area (+) + % Agriculture (-)	7.803	0.000	0.37	0.47
	RHA (+) + Channel slope (-)	11.342	3.539	0.06	0.36

Table 5 continued

Bird response	Habitat model*	AIC _c	Δ_i	w_i	R^2
Species richness: Waders	RHA (+) + Channel slope (-) + % Agriculture (-)	8.367	0.563	0.28	0.46
	Drainage area (+)	-1.524	0.000	1.00	0.19
Abundance: Waders	Drainage area (+)	18.228	0.000	0.62	0.24
	Bankfull width (+)	19.226	0.997	0.38	0.21
Species richness: Insectivores	% Conifers (-) + Channel slope (-)	-1.825	1.780	0.14	0.53
	Channel slope (-) + % Forest (-)	-0.696	2.909	0.08	0.51
	Channel slope (-) + % Forest (-) + % Hardwoods (+)	-3.282	0.323	0.30	0.59
	Channel slope (-) + % Forest (-) + % Conifers (-)	-3.605	0.000	0.35	0.59
	Channel slope (-) + % Wet meadow (-)	-0.615	2.990	0.08	0.57
	Channel slope (-) + % Wet meadow (+) + % Hardwoods (+)	22.009	0.000	0.47	0.57
Abundance: Insectivores	Channel slope (-) + % Forest (-) + % Hardwoods (+)	22.238	0.229	0.42	0.57

Table 6 Best approximating habitat models for the bird groupings, explanatory variables, and their coefficients in the significant best approximating habitat models

Bird response	Best approximating habitat model	Coefficient	R^2	F statistic
Species richness: Overall community ($P < 0.0001$)	Intercept	16.10		
	Channel slope	-0.49	0.57	24.11
	% Conifers	-0.05	0.64	5.35
Abundance: Overall community ($P < 0.0001$)	Intercept	26.64		
	Channel slope	-1.54	0.34	18.87
	% Wet meadow	0.25	0.50	11.44
	Entrenchment ratio	14.54	0.58	447.65
Species richness: Waterbirds ($P = 0.0004$)	Intercept	0.76		
	Channel slope	-0.05	0.37	16.17
Abundance: Waterbirds ($P = 0.0002$)	Intercept	1.20		
	Channel slope	-0.11	0.42	19.27
Species richness: Overall community excluding waterbirds ($P = 0.0002$)	Intercept	14.70		
	Channel slope	-0.32	0.39	9.81
	% Conifers	-0.04	0.47	4.29
Abundance: Overall community excluding waterbirds ($P = 0.0004$)	Intercept	42.91		
	% Conifers	-0.17	0.27	6.08
	% Agriculture land	9.27	0.39	7.07
	Entrenchment ratio	16.51	0.51	6.27
Species richness: Piscivores ($P = 0.0006$)	Intercept	-1.19		
	Channel slope	-0.05	0.26	13.73
	RHA	0.01	0.39	7.17
	% Natural non-forest	0.14	0.49	5.22
Abundance: Piscivores ($P = 0.0011$)	Intercept	-1.63		
	RHA	0.01	0.24	7.55
	Drainage area	0.23	0.37	8.48
	% Agriculture	-0.31	0.47	4.86
Species richness: Waders ($P = 0.0171$)	Intercept	-0.25		
	Drainage area	0.17	0.19	6.46
Abundance: Waders ($P = 0.0069$)	Intercept	-0.51		
	Drainage area	0.27	0.24	8.54
Species richness: Insectivores ($P < 0.0001$)	Intercept	1.71		
	Channel slope	-0.04	0.33	10.16
	% Forest	-0.01	0.51	3.48
	% Conifers	-0.01	0.59	4.61
Abundance: Insectivores ($P < 0.0001$)	Intercept	0.54		
	Channel slope	-0.07	0.23	12.09
	% Wet meadow	0.02	0.46	18.29
	% Hardwoods	0.01	0.57	6.30

models for waterbirds, explaining 37% and 42% of the variance, respectively.

A variety of factors explained patterns of species richness and abundance in the bird community

excluding waterbirds. Channel slope was an important variable in both the best and alternate models for species richness. Percent conifers combined with channel slope to create the strongest model for

species richness, having a 0.74 probability of being the best model in the set. For abundance models, the best and alternative models both shared % agriculture and entrenchment ratio as important factors. While % conifers was the additional variable in the best model, % floodplain forest was the additional variable of relevance in the alternate model.

Piscivore species richness and abundance models shared many habitat variables: channel slope, RHA, and % agriculture. Across the two groups, RHA was the single most important variable, combining with channel slope, % wet meadow (richness model), drainage area, and % agriculture (abundance model) to explain 49% and 47% of the variance, respectively. Each of these model sets had a number of alternate models. For piscivore species richness, Channel slope + % Agriculture + RHA, with Δ_i of 0.574, was the model subsequently best supported. The drainage area + % Forest model carried a Δ_i of 0.563, suggesting significant support. In contrast, wader species richness and abundance appeared to be controlled by measures of stream size.

Channel slope best explained patterns observed in insectivore species richness and abundance. Channel slope combined with % forest in the best approximating model for insectivore species richness ($R^2 = 0.59$). Channel slope combined with % wet meadow and % hardwoods to explain insectivore abundance ($R^2 = 0.57$).

Discussion

In viewing the river corridor and its adjacent terrestrial areas as an integrated ecological unit, we recognize that component patch habitats and ecotonal zones are intimately linked through exchanges of energy and materials. As in other studies, our results support the importance of habitat heterogeneity at local scales to bird communities (Brotons et al. 2004). Additionally, our models support the riverscape notion in relation to bird assemblages, incorporating a suite of habitat variables that represent a range of characteristics spanning the spatial extent of the stream corridor.

Pairwise comparisons documented how individual variables within the river corridor related to one another (Table 4). Many of these correlations support consistent morphological stream patterns (Leopold

and Maddock 1953; Rosgen 1996; VTDEC 2006). Atypical of common relationships, we found that channel slope and sinuosity were positively correlated ($r = 0.497$). However, as in many areas, human impacts on stream ecosystems in Vermont have led to removal of riparian vegetation, various hydrologic modifications, floodplain encroachments, streambank erosion, and channel straightening (VTDEC 2001), which yield observations such as this that would unlikely be found under natural conditions.

Channel slope was negatively correlated with both overall species richness and abundance and was also critical in explaining patterns in waterbirds (Table 6). Low-gradient, meandering streams are typically found in lower sections of the watershed, and are characterized by larger drainage areas, higher discharge, and greater widths than high-gradient streams. These systems are often associated with large floodplains that maintain a suite of lotic, semi-lotic, and lentic waterbodies, providing a greater variety of habitat types and food sources that support a larger and more diverse avifauna (Spackman 1992). Because of their plane-bed or dune-ripple channel types (see Montgomery and Buffington 1997), such streams are generally deep enough for swimming and diving waterbirds, and support a greater biomass of fish prey (Angermeier and Schlosser 1991; Newall and Magnuson 1999). The high mobility of waterbirds and their ability to use a combination of aquatic and semi-aquatic habitat allows them to exploit the wide array of river corridor resources associated with these low-gradient systems [e.g., Wood Ducks (*Aix sponsa*), Great Blue Herons (*Ardea herodias*), Common Mergansers (*Mergus merganser*)].

Higher entrenchment ratios were associated with a greater numbers of birds in our two top models examining community abundance. In streams with high entrenchment ratios, water breaches the banks during floods and dissipates its energy. Because overbank flows are directly related to the development and persistence of floodplains and the associated diversity of habitat structure, entrenchment ratio is likely a functional link that relates to floodplain habitat complexity. In our study, the site with the highest entrenchment ratio had the greatest lateral hydrologic connectivity as evidenced by a large number of floodplain waterbodies (8) and a high percentage of floodplain forest (65%). At this and other reaches with high entrenchment ratios and

active floodplains, we found numerous birds in floodplain habitats [e.g., Wood Ducks, Tree Swallows, Great Blue Herons, Ringed-bill Gulls (*Larus delawarensis*), etc.] that added to the abundance of the overall reach. Other investigators have also documented the importance of floodplains to bird communities (Knopf et al. 1988; Ohmart 1994; Miller et al. 2004).

Our models indicated that both the overall diversity and abundance of the bird community increased as the percentage of conifers decreased. This result is consistent with previously reported patterns of lower bird community diversity and abundance in coniferous (versus hardwood) forests in the Northeastern United States (James and Wamer 1982; Willson and Comet 1996).

We also examined patterns of abundance and diversity of the overall community excluding waterbirds in order to assess the influence of riverscape variables on non aquatic-obligate birds. The greatest diversity was associated with streams with relatively low channel slope and, to a lesser extent, low percentages of conifers. Percent conifers was also an important variable in predicting community abundance, as were entrenchment ratio and agricultural activities in the riparian zone. Species across a wide variety of habitat and feeding guilds constituted this community. The abundance and diversity of neotropical migrants reinforce the importance of riparian habitats as breeding and stopover areas (Hodges and Krementz 1996; Skagen et al. 1998; Moore 2000; Yong and Finch 2002). Additionally, our models suggest that low-gradient streams with floodplain access and open areas may be of particular value. The abundance and diversity of upland birds in these systems indicates that river corridors are likely providing important supplemental habitat and food resources to a variety of bird guilds, and that energy exchanges between aquatic and terrestrial zones may be far-reaching as terrestrially-based birds transfer this energy to upland habitats.

Piscivores may be the most sensitive to in-stream habitat conditions because of their reliance on fish populations. Of the eight models generated for piscivore richness and abundance, RHA—a composite measure of in-stream habitat condition—was an important variable in seven (Table 5). Piscivores also responded to stream geomorphology (drainage area, channel slope), and riparian vegetation (% agriculture,

% wet meadow). We saw greater numbers of piscivore species and individuals in larger, valley-streams whose riparian corridors were not agriculturally-dominated.

Our use of RHA was intended to help identify the role ecological condition played in bird–riverscape habitat associations. Piscivore models depended on a mixture of habitat characteristics, suggesting that piscivores might have particular promise as an indicator of the condition of the river corridor. Common piscivores—herons, osprey, kingfishers, and mergansers—require a mix of interconnected habitat patches that may only be present in relatively non-impacted riverine systems. The incorporation of the RHA, as well as riparian habitat variables in the models, indicates that piscivores may serve as legitimate integrators of habitat conditions across the stream corridor.

In contrast to the piscivore models, stream size alone accounted for patterns in species richness and abundance of waders. However, because measures of stream size are correlated with channel slope, the composite effects of these factors likely structure piscivore presence and community composition. We commonly found herons and other waders at reaches in larger streams, which is consistent with the habitat and prey requirements of waders: greater fish biomass with larger drainage areas (Newall and Magnuson 1999); larger floodplains, offering a number foraging patches; and wider corridors, with greater visibility for detecting predators.

Insectivores are a unique group because they directly benefit from the energy transfer from the stream to the riparian zone via emergent insects and feed across patch habitats. While swallows, flycatchers, and other riparian-obligate insectivores depend on these subsidies, other non-riparian species may use emergent aquatic insects to complement their diets. For example, many warbler species are associated with a variety of upland habitat types, yet were commonly found at our study sites. These warblers were likely feeding on emergent insects in the riparian zone [e.g., Black-throated Blue Warblers (*Dendroica caerulescens*) predated Lepidopteran and Dipterans (Rodenhouse and Holmes 1992)].

Nakano and Murakami (2001) estimated that emergent aquatic insects contributed up to 26.5% of the annual total energy budget of riparian birds. Other insectivores, such as shoreline birds [e.g., Spotted Sandpipers (*Actitis macularia*)], feed on the larval

stage of aquatic insects. In both cases, insectivores depend on the insect productivity of the stream. In the best approximating model (Table 6), channel slope, % wet meadow, and % hardwoods combined to explain 57% of the variance seen in insectivore abundance. The influence of wet meadow and hardwood coverage suggests that a combination of open-canopied meadow and closed-canopied hardwood forest are important in promoting bird abundance in species selecting this juxtaposition of habitat types.

The strongest model for insectivore species richness argues for similar interpretation, with % forest and % conifers (negative relationships) replacing % wet-meadow and % hardwood (positive relationships). Because of the negative correlations we found between % forest and % agriculture, and between % conifers and % hardwoods, these results indicate that, at least in part, insectivores may prefer more open areas dominated by hardwood stands. However, channel slope was still the most influential variable in the best approximating insectivore richness model, and indicates that in our study area, lower gradient streams support greater insectivore richness. This result is supported by other work that suggests that meandering, low-gradient streams support more insectivorous birds (Iwata et al. 2003).

Conclusions and conservation implications

Stream corridors in temperate systems are often characterized by spatially and temporally heterogeneous habitats (Gregory et al. 1991; Keeton et al. 2005). Because the riverscape notion integrates these habitats into a single landscape perspective, it is particularly valuable in furthering our understanding of how species interact with this unique environment, and how conservation may be focused to maximize ecological gain. Taken together, our findings suggest that river corridors provide important habitat to a broad bird community, including riparian and water-bird communities, as well as upland birds. The diversity and abundance of these communities are enhanced by the mix of habitat patches that comprise the river corridor. Spatial complexity in patch configuration as well as structural and compositional diversity among vegetation patches may provide more suitable habitats for a number of species, as well as a diversity of ecological functions (Gregory et al. 1991).

A consideration of the spatial scale of assessment, and the need for adequate representation across the landscape of multiple riparian habitat configurations, will be necessary for conservation of riverine birds. Habitat variables from different riverscape patches contributed to explaining patterns of richness and abundance across different bird groupings, suggesting that birds are interacting with their environment at a spatial extent that is consistent with the riverscape concept. However, our reach-level assessment is but one of many potential scales at which the riverscape notion may operate. While we attempted to select a feasible and ecologically meaningful scale (e.g., basic entity approach (Jelinski and Wu 1996)), the need for multiscale analyses of riverscapes is necessary to fully understand its ecological value. The results from our study may differ significantly at smaller or larger spatial scales, and the effects of scale dependence of spatial heterogeneity on riverine bird communities remains unknown. However, because stream and river assessments are most often conducted at a reach scale consistent with our study sites (Parsons et al. 2002; VTDEC 2003; USEPA 2006), we feel that our results have particular utility.

Piscivores appear to have the greatest utility as integrative indicators of riverscape condition. The high trophic level of piscivores suggests a number of top-down trophic connections, yielding insights into the condition of the riparian and stream food web that are not captured by direct habitat measurements.

As in other ecological landscapes (Forman 1995), the distinct habitat types of the stream corridor make important contributions to the overall riverscape. The patterns of guild–habitat associations found in our models strongly suggest that the riverscape concept is not merely a physical construct, but a notion that has realized ecological meaning. From a management perspective, our results indicate that simply conserving riparian areas will not sufficiently maintain diverse and abundant bird assemblages. Intact channel geometry, active floodplains, and high-quality aquatic habitat are also important. Functionally, natural flow regimes that enhance hydrological connectivity across the river corridor are crucial in maintaining a productive riverscape ecosystem. Additionally, our results suggest that a mixture of forested and non-forested riparian vegetation types is often crucial for riverine bird communities.

Because of the tremendous diversity in the dietary and habitat needs of riparian bird communities, the shifting mosaic of habitat patches across the riverscape is crucial in supporting a wide variety of species. Therefore, it seems prudent to develop river corridor assessments and conservation strategies that maximize preservation of the whole ecological unit, perhaps focusing first on the habitat linkages that maintain the energy exchange between the river and its corridor. The guild–habitat associations we have highlighted underscore the significance of the riverscape concept and suggest that this more holistic approach might have the greatest conservation benefits.

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Appendix 1

Birds surveyed, common and scientific names, and foraging guilds

Common name	Scientific name	Guild
Alder Flycatcher	<i>Empidonax alnorum</i>	I
American Black Duck	<i>Anas rubripes</i>	WB
American Goldfinch	<i>Carduelis tristis</i>	.
American Redstart	<i>Setophaga ruticilla</i>	I
American Robin	<i>Turdus migratorius</i>	.
Baltimore Oriole	<i>Icterus galbula</i>	.
Bank Swallow	<i>Riparia riparia</i>	I
Barn Swallow	<i>Hirundo rustica</i>	I
Bay-breasted Warbler	<i>Dendroica castanea</i>	I
Belted Kingfisher	<i>Megasceryle alcyon</i>	P, WB
Black and White Warbler	<i>Mniotilta varia</i>	I
Black-capped Chickadee	<i>Parus atricapillus</i>	.
Black-crowned Night Heron	<i>Nycticorax nycticorax</i>	P, W, WB
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	I
Black-throated Green Warbler	<i>Dendroica virens</i>	I
Blue Jay	<i>Cyanocitta cristata</i>	.
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	I
Bobolink	<i>Dolichonyx oryzivorus</i>	.

continued

Common name	Scientific name	Guild
Broad-winged Hawk	<i>Buteo platypterus</i>	.
Brown Creeper	<i>Certhia familiaris</i>	I
Brown Thrasher	<i>Toxostoma rufum</i>	.
Brown-headed Cowbird	<i>Molothrus ater</i>	.
Canada Goose	<i>Branta canadensis</i>	WB
Cape May Warbler	<i>Dendroica tigrina</i>	I
Carolina Wren	<i>Thyrothorus ludovicianus</i>	.
Cedar Waxwing	<i>Bombycilla cedrorum</i>	.
Cerulean Warbler	<i>Dendroica cerulea</i>	I
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	I
Common Crow	<i>Corvus brachyrynchos</i>	.
Common Goldeneye	<i>Bucephala clangula</i>	WB
Common Grackle	<i>Quiscalus quiscula</i>	.
Common Merganser	<i>Mergus merganser</i>	P, WB
Common Nighthawk	<i>Chordeiles minor</i>	I
Common Snipe	<i>Capella gallinago</i>	.
Common Tern	<i>Sterna hirundo</i>	P, WB
Common Yellowthroat	<i>Geothlypis trichas</i>	I
Dark-eyed Junco	<i>Junca hyemalis</i>	.
Double-crested Cormorant	<i>Phalacrocorax auritus</i>	P, WB
Downy Woodpecker	<i>Picoides pubescens</i>	.
Eastern Kingbird	<i>Sialia sialia</i>	I
Eastern Phoebe	<i>Sayornis phoebe</i>	I
Eastern Tufted Titmouse	<i>Parus bicolor</i>	.
European Starling	<i>Sturnus vulgaris</i>	.
Golden-crowned Kinglet	<i>Regulus satrapa</i>	I
Golden-winged Warbler	<i>Vermivora chrysoptera</i>	I
Gray Catbird	<i>Dumetella carolinensis</i>	.
Great Blue Heron	<i>Ardea herodias</i>	P, W, WB
Great-crested Flycatcher	<i>Myiarchus crinitus</i>	I
Great-horned Owl	<i>Bubo virginianus</i>	.
Green Heron	<i>Butorides striatus</i>	P, W, WB
Hairy Woodpecker	<i>Picoides villosus</i>	.
Hooded Merganser	<i>Lophodytes cucullatus</i>	P, WB
House Wren	<i>Troglodytes aedon</i>	I
Least Bittern	<i>Ixobrychus exilis</i>	P, W, WB
Least Flycatcher	<i>Empidonax minimus</i>	I

continued

Common name	Scientific name	Guild
Louisiana Waterthrush	<i>Seiurus motacilla</i>	I, WB
Magnolia Warbler	<i>Dendroica magnolia</i>	I
Mallard	<i>Anas platyrhynchos</i>	WB
Mourning Dove	<i>Zenaid macroura</i>	.
Northern Cardinal	<i>Cardinalis cardinalis</i>	.
Common Flicker	<i>Colaptes auratus</i>	I
Northern Mockingbird	<i>Mimus polyglottos</i>	.
Northern Parula	<i>Parula americana</i>	.
Northern Rough-winged Swallow	<i>Stelgidopteryx ruficollis</i>	I
Northern Waterthrush	<i>Seirus noveboracensis</i>	I, WB
Osprey	<i>Pandion haliaetus</i>	P
Ovenbird	<i>Seiurus aurocapillus</i>	I
Philadelphia Vireo	<i>Vireo philadelphicus</i>	I
Pileated Woodpecker	<i>Dryocopus pileatus</i>	.
Red-bellied Woodpecker	<i>Centurus carolinus</i>	.
Red-eyed Vireo	<i>Vireo olivaceus</i>	.
Red-shouldered Hawk	<i>Buteo lineatus</i>	.
Red-tailed Hawk	<i>Buteo jamaicensis</i>	.
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	.
Ring-billed Gull	<i>Larus delawerensis</i>	WB
Rock Dove	<i>Columba livia</i>	.
Rose-breasted Grosbeak	<i>Phecticus ludovicianus</i>	.
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	.
Scarlet Tanager	<i>Piranga olivacea</i>	I
Song Sparrow	<i>Melospiza melodia</i>	.
Spotted Sandpiper	<i>Actitis macularia</i>	I, W, WB
Swamp Sparrow	<i>Melospiza georgiana</i>	.
Tree Swallow	<i>Iridoprocne bicolor</i>	I
Turkey	<i>Meleagris gallopavo</i>	.
Veery	<i>Catharus fuscescens</i>	.
Vesper Sparrow	<i>Poocetes gramineus</i>	.
Warbling Vireo	<i>Vireo gilvus</i>	I
White-breasted Nuthatch	<i>Sitta carolinensis</i>	.
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	.
White-throated Sparrow	<i>Zonotrichia albicollis</i>	.
Willow Flycatcher	<i>Empidonax traillii</i>	I
Wilson's Warbler	<i>Wilsonia pusilla</i>	I
Winter Wren	<i>Troglodytes troglodytes</i>	I
Wood Duck	<i>Aix sponsa</i>	WB

continued

Common name	Scientific name	Guild
Wood Thrush	<i>Hylocichla mustelina</i>	.
Yellow Warbler	<i>Dendroica petechia</i>	I
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	.
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	.
Yellow-breasted Chat	<i>Icteria virens</i>	.
Yellow-rumped Warbler	<i>Dendroica coronata</i>	I
Yellow-throated Vireo	<i>Vireo flavifrons</i>	I

I = insectivore, P = piscivores, W = waders, WB = waterbird, . = not assigned

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