

Partitioning the multi-scale effects of human activity on the occurrence of riparian forest birds

Robert J. Fletcher Jr. · Richard L. Hutto

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Abstract Conservationists, managers, and land planners are faced with the difficult task of balancing many issues regarding human impacts on natural systems. Many of these potential impacts arise from local-scale and landscape-scale changes, but such changes often covary, which makes it difficult to isolate and compare independent effects arising from humans. We partition multi-scale impacts on riparian forest bird distribution in 105 patches along approximately 500 km of the Madison and Missouri Rivers, Montana, USA. To do so, we coupled environmental information from local (within-patch), patch, and landscape scales reflecting potential human impacts from grazing, invasive plant species, habitat loss and fragmentation, and human development with the distribution of 28 terrestrial breeding bird species in 2004 and 2005. Variation partitioning of the influence of different spatial scales suggested that local-scale vegetation gradients explained more unique variation

in bird distribution than did information from patch and landscape scales. Partitioning potential human impacts revealed, however, that riparian habitat loss and fragmentation at the patch and landscape scales explained more unique variation than did local disturbances or landscape-scale development (i.e., building density in the surrounding landscape). When distribution was correlated with human disturbance, local-scale disturbance had more consistent impacts than other scales, with species showing consistent negative correlations with grazing but positive correlations with invasives. We conclude that while local vegetation structure best explains bird distribution, managers concerned with ongoing human influences in this system need to focus more on mitigating the effects of large-scale disturbances than on more local land use issues.

Keywords Exotic species · Grazing · Habitat fragmentation · Patch width · Riparian birds · Species distribution · Urbanization · Variation partitioning

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R. J. Fletcher Jr. · R. L. Hutto
Avian Science Center, Division of Biological Sciences,
University of Montana, Missoula, MT 59812, USA

R. J. Fletcher Jr. (✉)
Department of Wildlife Ecology and Conservation,
University of Florida, P.O. Box 110430, 110 Newins-
Ziegler Hall, Gainesville, FL 32611-0430, USA
e-mail: robert.fletcher@ufl.edu

Introduction

Conservationists, managers, and land planners are faced with the formidable task of needing to prioritize and balance many issues concerning the impacts of humans on natural systems. These impacts can

manifest themselves in diverse ways, including increased habitat loss and fragmentation (Fahrig 2003), habitat degradation (Fleishman et al. 2003), the proliferation of invasive species (With 2002), and direct effects of development and urbanization (e.g., road mortality; Forman and Alexander 1998). While numerous investigations have documented these impacts, many of these issues covary across landscapes (Ewers and Didham 2006; Fletcher et al. 2007). That is, increased human disturbance can simultaneously lead to a variety of anthropogenic effects, such as humans directly or indirectly increasing the spread of invasive species while increasing habitat loss and urbanization (e.g., Borgmann and Rodewald 2004). Consequently, we know relatively little about the independent effects of different kinds of human impacts on biodiversity. This is unfortunate, because managers and conservationists need such information to guide difficult decisions regarding where to allocate limited resources for preservation, restoration, and mitigation.

Riparian forest habitats in the western United States illustrate this problem especially well. Riparian forests comprise an extremely small physical area, amounting to less than 1% of the West (Knopf et al. 1988a), with as much as 90–95% of cottonwood-willow riparian habitats having been lost in some areas (Johnson and Carothers 1982). Although riparian systems are restricted in area, these areas harbor a wide diversity of plants and animals, with species often occurring at exceptionally high densities (Knopf et al. 1988a). Riparian systems have nonetheless been severely affected by a variety of anthropogenic factors, including river damming and changes in hydrology, human recreation, grazing, and invasive plants (Rood et al. 1995; Miller et al. 2003; Scott et al. 2003).

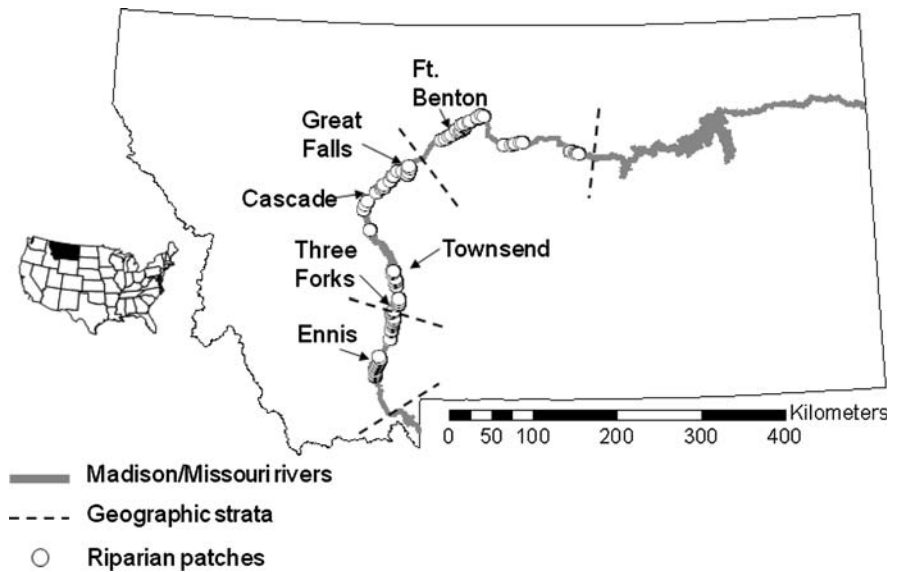
Impacts on riparian forests, however, occur at many spatial scales. At a local scale, degradation of riparian habitats occurs through changes in land use, such as grazing or through a proliferation in invasive species (Miller et al. 2003). At a patch scale, habitat loss and fragmentation can influence riparian forest area and width, which are widely known to influence the diversity of species (e.g., Stauffer and Best 1980; Scott et al. 2003). At a landscape scale, agriculture, urbanization, and development associated with increasing exurban sprawl have been shown to influence species composition in remaining forests (Rottenborn 1999; Miller et al. 2003; Smith and

Wachob 2006). Because these impacts can be correlated across scales ('cross-scale' correlations; Battin and Lawler 2006), there is a growing need to isolate the unique impacts that may occur at different spatial scales, which will help to better interpret how humans influence biodiversity and will help focus potential conservation and management strategies.

We estimated the relative effect of spatial scale and anthropogenic disturbances on bird distribution in riparian forests across a large region along the Madison and Missouri Rivers, Montana. We had two overarching objectives: (1) to determine the relative importance of local (microhabitat within patches), patch, and landscape scales on bird distribution of 28 species; and (2) to partition the effects of humans that occur at different spatial scales, spanning from local land use effects, including grazing and invasive plant species cover, to larger-scale patterns of habitat loss, fragmentation, and urbanization/development (development hereafter). For our first objective, we expected that local vegetation structure would be more influential in explaining species distribution than would information from other spatial scales, because local vegetation is highly variable in riparian forests (Scott et al. 2003; but see Saab 1999). We expected that patch-scale effects would be stronger than landscape-scale effects, based on the known relationships between patch width and bird diversity in riparian systems (e.g., Rottenborn 1999; Shirley and Smith 2005). Yet we also expected that patch and landscape scales would exhibit strong cross-scale correlations, with each scale explaining similar components of variation in bird distribution. For our second objective, we expected that local human disturbances from grazing and invasive species encroachment would affect species distribution less than other large-scale disturbances, because both local disturbances primarily influence only ground cover in this system. We also expected that landscape measures of habitat loss and fragmentation would have negative effects on most species. Finally, we expected that development would influence the occurrence of residents, avian nest predators, and avian brood parasites positively, but would have negative effects on other species (Saab 1999; Rodewald and Bakermans 2006).

To address these objectives, we extend previous approaches that partition variation in general linear models (Whittaker 1984) to models with hierarchical structures that can accommodate multi-level dependencies. Our approach allows investigators to make

Fig. 1 Locations of riparian forest patches ($n = 105$) across three geographic strata along the Madison and Missouri Rivers, Montana. Bird communities were surveyed in each site from 25 May–10 July during either 2004 or 2005. Towns and cities located along the river system are noted



appropriate inferences on species–environment relationships (e.g., appropriate estimates and measures of precision) while still identifying confounding and the potential for cross-scale correlations. Further, our approach partitions multi-scale effects on individual species, which allows not only understanding the relative effect of different scales in explaining species distribution, but also the consistency in directionality of those effects across species.

Methods

Study area and site selection

The study area encompassed deciduous riparian patches along approximately 600 km of the Madison and Upper Missouri Rivers, Montana, May–July, 2004 and 2005 (Fig. 1). Riparian patches were dominated by narrowleaf cottonwood (*Populus angustifolia*), plains cottonwood (*P. deltoides*), and a variety of willow species (e.g., *Salix amygdaloides*, *S. exigua*). Other tree and shrub species included black cottonwood (*P. trichocarpa*), water birch (*Betula occidentalis*), mountain alder (*Alnus incana*), box elder (*Acer negundo*), red osier dogwood (*Cornus stolonifera*), rose (*Rosa* spp.), and snowberry (*Symphocarpus albus*). Common invasive species included leafy spurge (*Euphorbia esula*), hound's tongue (*Cynoglossum officinale*), Canada thistle (*Cirsium arvense*), and Russian olive (*Elaeagnus angustifolia*).

To select patches for sampling, we stratified the river into three geographical sections: the Madison River, the Missouri River between Three Forks and Great Falls, and between Great Falls and Fred Robinson Bridge (Fig. 1). The location of stratification points along the Missouri River was based on the extreme environmental changes that occur along the river at Great Falls, where five dams occur. Within each geographical section, we randomly selected 35 deciduous riparian patches for surveying, based on digital orthophoto quarter quadrangle images (DOQQ) taken in the mid-1990's. The only constraints on the site-selection process were that sites were at least 50-m wide, sites were separated by >500 m, and landowners granted us permission to survey birds on their property. We used a 50-m width criterion to facilitate site identification on DOQQ maps and >500 m distance based on semivariogram analyses from pilot data of common species collected in 2003, which suggested that locations in continuous riparian habitat >500 m apart were independent (Fletcher, unpublished). For each patch selected, we identified the maximum number of potential sampling locations available within the patch, with the constraint that samples were 150 m apart, by overlaying a 150 × 150 m grid, parallel to the main axis of the riparian patch, where the center of each grid cell was considered a potential sampling unit. Within each patch, we sampled all potential locations (1–8 points/patch) to ensure adequate sampling across the entire patch. Overall, 105 patches were sampled, with

223 sampling locations (points; see section 'Point count surveys').

Point count surveys

We surveyed birds using a standard point-count protocol (Hutto et al. 1986). For each point count, we surveyed birds within 50 m of the survey point twice between 25 May–10 July. Each patch was surveyed during only one of the two years of the study, with 75 patches surveyed in 2004 and 30 patches surveyed in 2005. We chose to sample new patches in 2005 rather than repeating surveys at patches sampled in 2004 to increase the total amount of variation sampled across the region and the number of patches sampled, which also eliminates the issues of non-independence from repeated measures through time. However, this design does mask the potential that year effects could have occurred in our investigation. Some sites that were surveyed in 2004 were re-visited in 2005 for an experiment on behavioral aspects of habitat selection (Fletcher 2007). Based on control plots used in Fletcher (2007), 9 sites visited in 2004 were revisited in 2005. Twenty-three of the 28 species modeled here occurred in at least 3 of these sites in one year, with only 1 of the 23 species (Warbling Vireo; see Table 2 for scientific names) exhibiting any evidence for a year effect ($\chi^2 = 4.27$, $P = 0.04$). Consequently, results for Warbling Vireo should be interpreted cautiously.

Two observers surveyed each point, with each observer surveying the point once; these repeated surveys within each breeding season were collapsed into one summary measure of detection/non-detection for each point (see below). Surveys were conducted between sunrise and 5 h after sunrise and were not conducted during high wind velocities (≥ 20 km/h) or during precipitation. During surveys, observers recorded all birds seen or heard, including how individuals were detected (song, visual, or call), sex of individuals, and distances of birds from the center point. To ensure accurate delineation of birds within or outside plots, distances to birds were estimated using a laser rangefinder.

Vegetation sampling

At each point-count station, we measured vegetation after one of the two bird surveys. Vegetation was measured at 4 sampling locations within the point-

count area: one surrounding the survey point and three at locations 25 m from the survey point, at 0°, 120°, and 240°. At each sampling location we measured vegetation composition and structure within a 5-m and a 11.3-m radius plot. Within the 5-m plot, we estimated shrub cover (by species), ground cover, and exotic species cover (by species), based on overlapping ocular percentages. Ground cover categories included woody, grass, forb, and litter. We used fecal counts of cattle within each 5-m plot as an index of recent grazing intensity (sensu Beever et al. 2003). Within the 11.3-m plot, we counted the total number of trees (by species) and snags by size, based on three dbh categories: small (8–23 cm), medium (23–38 cm), and large (>38 cm). We measured tree height (using a clinometer), and shrub height (shrubs > 1 m) at each location. We estimated canopy cover by averaging 4 densiometer readings at each sampling location (one in each cardinal direction). From these measurements, we estimated a variety of metrics related to vegetation structure and diversity (Table 1).

Patch metrics

Using aerial photographs taken in 2005 (1-m resolution), we calculated four metrics to quantify patch structure: patch size, patch width, a shape index (shape = circumference/circumference of a circle of the same area; Laurance and Yensen 1991), and the average distance to edge from each point within a patch. Patch size and width were incorporated based on the known strong relationships of patch width and avian species diversity in riparian systems (but see Rodewald and Bakermans 2006), which are thought to vary primarily from anthropogenic habitat loss and fragmentation. Both distance to edge and the shape index provide measures related to the potential for edge effects (Laurance and Yensen 1991; Fletcher et al. 2007).

Landscape metrics

We calculated measures related to the potential loss (habitat amount) and fragmentation (configuration of forest for a given amount of habitat remaining) of riparian forest surrounding patches and the potential impact of human development within 1 km of each patch. Consequently, our sampling design can be

Table 1 Explanatory variables considered in the analysis of bird distributions in riparian forests, Montana, 2004–2005

Variable/scale	Description
Local (within 5 m or 11.3 m)	
Grass ground cover	Percent cover of grasses
Forb ground cover	Percent cover of forbs
Litter ground cover	Percent cover of litter
Shrub cover ^a	Percent cover of total shrubs
Shrub diversity	Simpson's diversity index for shrub cover
Canopy cover ^a	Average canopy cover, based on a densiometer
Canopy height ^a	Maximum canopy height (m)
Deciduous trees ^a	Total number of deciduous trees
Conifer trees	Total number of conifer trees
Tree diversity	Simpson's diversity index for trees
Snags ^a	Total number of snags
Grazing index	Fecal counts of cattle
Exotic cover	Percent cover of invasive exotics
Variable/scale	Description
Exotic diversity	Simpson's index of diversity for invasive exotics
Patch	
Width ^a	Maximum width (m) of each riparian patch
Shape	Patch irregularity index (perimeter/perimeter of a circle of equal area)
Landscape (within 1 km)	
Forest area ^a	Total area (%) of riparian forest surrounding patch
Forest patch density	Number of patches/forest area surrounding patch
Distance to nearest patch	Minimum distance (m) to the nearest riparian forest patch
Area of nearest patch	Area (ha) of the nearest riparian forest patch
Development ^a	Total area (%) of houses/buildings surrounding patch

^a Nonlinear effects considered in model development

considered a 'patch-landscape' design (McGarigal and Cushman 2002). Estimating metrics within 1 km for riparian systems is warranted based on strong correlations from other investigations on birds using riparian forests in the western U.S. (Saab 1999). To quantify riparian forest structure surrounding patches, we estimated the total area of riparian forest to reflect habitat loss (Fletcher and Koford 2002), the distance to the nearest riparian patch and its size to reflect potential connectivity (cf. Moilanen and Nieminen 2002), and patch density (No. of riparian patches/area of riparian forest) and edge density (length of riparian edge/area of riparian forest) to reflect configuration of remaining riparian forest habitat (Fletcher and Koford 2002). For indices of development, we calculated the density of roads and the area of buildings (e.g., homes, businesses, etc.).

Model building and variation partitioning

We developed occurrence models for all species detected in >10% of the points sampled (28 species), except for yellow warbler (*Dendroica petechia*), which occurred at every point sampled. We initially screened data using a modified removal model for species occurrence to estimate probabilities of detecting each species (Farnsworth et al. 2002). Because average detection probabilities for songbirds ($\hat{p} = 0.974$) and all birds combined ($\hat{p} = 0.938$) were consistently high, and because the movement of some individuals (Fletcher, unpublished data) suggests that populations are not closed within the breeding season (a necessary assumption of most current methods; MacKenzie et al. 2002), we did not adjust for detection probability in occurrence models.

We chose to model occurrence rather than abundance for two reasons. First, detection probability for estimating species occurrence is inevitably greater than estimating species abundance/density, such that modeling abundance would require estimating detection probabilities. Second, we were interested in understanding the importance of within-site variation for the entire breeding bird community, and for all but the most common species, density estimates are probably not accurately estimated for individual points within patches.

We used a variation partitioning approach to compare the relative independent (conditional) and total (marginal) variation explained at local, patch, and landscape scales (Whittaker 1984), focusing specifically on potential anthropogenic disturbances from grazing, invasive species, habitat loss and fragmentation at patch and landscape scales, and human development (Fig. 2). Variation partitioning uses multiple model comparisons for decomposing variance into the unique and joint (or confounded) variation explained from different variables or spatio-temporal scales (Cushman and McGarigal 2002). In statistical terms, this approach identifies potential multicollinearity among variables and/or scales, sometimes referred to as cross-scale correlations (Battin and Lawler 2006; Lawler and Edwards

2006). For the purposes of our study, we focused on the total (marginal) variation explained, derived from univariate models for each factor of interest, and the unique (conditional) variation explained, estimated from determining the change in variation explained when the factor of interest was removed from the full (or global) model (Whittaker 1984, Cushman and McGarigal 2002).

Prior to partitioning, we first identified a hierarchical model structure using generalized linear mixed models:

$$\text{logit}(y_{ij}) = \alpha + X_{ij} + Y_j + Z_j + \gamma_j$$

where y_{ij} is the detection/non-detection of a species at point i in patch j (compiled across the two visits), X_i is a vector of local measures for each point i within patch j influencing species occurrence, Y_j is a vector of measures describing patch j , Z_j is a vector of measures describing the surrounding landscape structure for patch j and γ_j is a random site effect ($\gamma_j \sim N(0, \sigma_\gamma^2)$), which provides hierarchical structure to the modeling process by considering points within patches as correlated sampling units (cf. Thogmartin and Knutson 2007). Models were fit by directly maximizing an approximation of the marginal likelihood (i.e., the likelihood integrated over random effects) using the package ‘glmm.admb’ in R (Otter Research Ltd., Sidney, BC, Canada). This approach uses Laplace approximation, which, unlike some other methods (e.g., penalized quasi-likelihood), allows for direct comparisons of likelihoods, and thus information criteria (e.g., Akaike’s Information Criterion, AIC) and estimates of R^2 , across different models (Skaug and Fournier 2006). Note that our interest was in population-level effects, not cluster effects, such that conventional AIC measures for model comparison were appropriate (Vaida and Blanchard 2005).

Prior to model development, we screened explanatory variables within each spatial scale for strong correlations and removed variables with correlations $|r| > 0.6$. At the local scale, total shrub cover and woody ground cover were highly correlated ($r = 0.6$), so we dropped woody ground cover from further analyses (Table 1). At the patch scale, area and width were highly correlated ($r = 0.7$) as was area and distance from edge ($r = 0.69$) and width and distance from edge ($r = 0.82$). We dropped area and

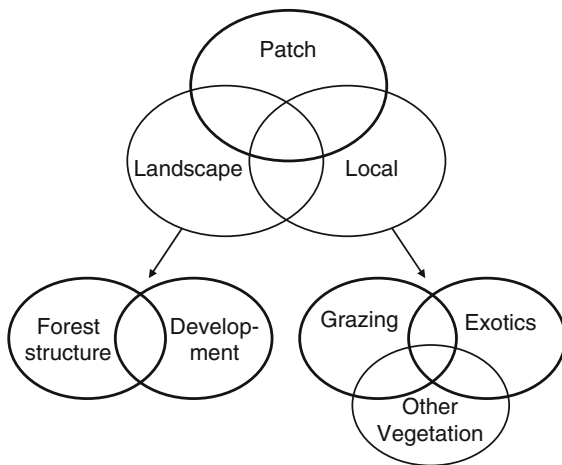


Fig. 2 Conceptual Venn diagram that identifies the investigated hierarchical associations of potential local, patch, and landscape effects on bird distribution in riparian forest habitats in Montana, 2004–2005. Bold ellipses highlight the specific human impacts emphasized in analyses aimed to identify the unique and joint effects of each factor

distance from edge from further analyses, thereby retaining patch width (Table 1), which has been commonly used as a patch measure in other investigations on riparian birds. At the landscape scale, patch density and edge density were highly correlated ($r = 0.87$) as was road density and the area of buildings/houses ($r = 0.88$); for further analyses we dropped edge and road density (Table 1). Each explanatory variable was transformed using a standard normal transformation (mean of zero, variance of 1), to allow coefficients among explanatory variables to be directly compared for interpreting relative effects of each variable and to improve convergence of models. We initially ran a series of models to determine the most parsimonious model to use for further analyses to describe effects of local vegetation, exotics, patch structure, and landscape measures of forest structure, based on Akaike's Information Criterion, adjusted for sample size (AIC_c) (cf. Lawler and Edwards 2006). For local vegetation, models were developed and compared for each species based on knowledge of nest location, nest height, and foraging tactics of each species (supplementary material). For models at patch and landscape scales, we assumed that patch and landscape factors could influence each species and thus considered all explanatory variables (supplementary material).

Given these models, we used variation partitioning to address two issues. First, we addressed the relative influence of spatial scale by partitioning the variation explained at local, patch, and landscape scales (Fig. 2). Second, we focused on the relative influence of specific human impacts at different scales. At the local scale, we focus on two components: grazing and invasive exotic cover. We then compared these to patch structure and two components at the landscape scale, surrounding forest structure and development (Fig. 2).

Variation explained (R^2) for occurrence (logistic) models was derived from a deviance-based measure of the likelihood function, which has a strong theoretical foundation in Kullback-Leibler information (Cameron and Windmeijer 1997; Agresti 2002). A limitation of this measure of variation explained for logistic models (and other R^2 measures for non-Gaussian models) is that the likelihood function is not on an easily interpreted scale, relative to R^2 for ordinary least squares regression. Nonetheless, this

measure is useful for comparative purposes of different models and variables (Agresti 2002). Directionality and significance of effects were inferred based on 95% CI of conditional (partial coefficients from full models) and marginal (coefficients from univariate models) parameter coefficients.

Results

The 28 bird species were detected on an average of 39% of the point counts ($SD = 0.24$). The average variation explained was 27.5% ($SD = 13.0\%$; range = 7.2–58.0%) for the full models that included local, patch, and landscape factors, with the Song Sparrow having the most variation explained, and the Spotted Towhee the least.

Scale and bird distribution

As expected, across all species the total variation explained by local-scale measures (19.1%) was greater than for patch or landscape measures (5.1% and 6.3%, respectively). Similar patterns arose when considering only the unique variation explained by each scale, the only difference being that patch measures explained on average half as much unique variation as did landscape measures (Fig. 3). Overall, the predominant cross-scale correlation occurred between patch and local scale measures (Fig. 3). Counter to our predictions, the cross-scale correlation of patch and landscape measures were low (Fig. 3).

Human disturbance

When partitioning potential human disturbances correlated with bird distribution, patch width/shape explained more total variation than other metrics, yet landscape measures of forest structure (loss, fragmentation, connectivity) explained more unique variation (Table 2, Fig. 4). Unlike the general scale effects described above, local measures of disturbance consistently explained the least variation in distribution (Fig. 4). When comparing the total (marginal) to unique (conditional) variation explained, patch width/shape metrics tended to have larger cross-scale correlations than did other metrics. Interestingly, conditional and marginal coefficients from models suggest when species did respond to

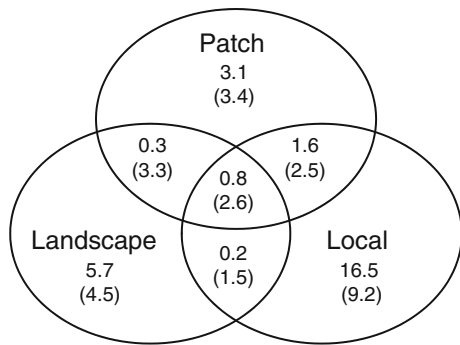


Fig. 3 Venn diagram identifying the mean variation explained (%; SD across species in parentheses) at local, patch, and landscape scales on bird distribution of 28 species in riparian forest habitats in Montana, 2004–2005. Note that ellipses do not scale with the variation explained

potential human disturbances, the most consistent effects (in terms of direction of correlations) were from local disturbances and development, where grazing and development tended to have consistent negative correlations with distribution, while invasives had consistent positive correlations. Note, however, that all observed development effects were highly non-linear (Table 2), with probabilities of occurrence generally highest at moderate levels of development, but the net effects (based on probabilities of occurrence at minimum and maximum levels of observed development) were consistently negative.

Discussion

Scale and bird distribution

Landscape ecologists and conservation biologists are increasingly interested in identifying the influence of spatial scale on the distribution and abundance of organisms. Yet in many circumstances effects that occur at different scales tend to be correlated, such that it is difficult to interpret the unique and confounded effects of spatial scale on observed patterns. For example, in our study area, patch width was positively correlated with the amount of riparian forest surrounding the patch ($r = 0.38$, $P < 0.0001$). Thus, investigators who consider patch-level measures only could be deceived because any potential observed patch width effects could be explained, at least in part, by surrounding landscape effects.

Overall, our analysis revealed that more unique variation in bird distribution could be explained from local measures, particularly local vegetation structure, than from patch or landscape measures. This was not surprising. Local vegetation structure is known to have strong effects on riparian bird diversity and distribution along many river and floodplain systems (Scott et al. 2003; Miller et al. 2004). For example, Scott et al. (2003) recently found that bird communities along part of this same river system were highly correlated with the complexity of local vegetation—where complexity increased, so did diversity and the total number of birds using riparian areas. Our results further support those found by Scott et al. (2003), by partitioning local vegetation effects from effects at other scales across a larger region of Montana.

Patch width and area have been prominent factors influencing riparian management and conservation. Recently, Rodewald and Bakermans (2006) questioned whether this paradigm was the most useful paradigm for riparian forest conservation, arguing that perhaps management would be more fruitful if focused at the landscape scale. On the one hand, our results further support this claim because landscape factors tended to explain more total and unique variation in the distribution of a wide suite of species than did patch metrics (Fig. 3). Yet on the other hand, because local measures consistently explained more variation than did landscape measures, our results could be interpreted as evidence for local measures being most important in conservation (note that Rodewald and Bakermans 2006 did not consider local measures in their investigation). We argue, however, that when weighing management and conservation of riparian and other systems, the variation explained at any given scale should not be the only means for developing strategies. Instead, conservationists, managers, and planners may need to focus more on identifying pressing human disturbances and their potential impacts on biodiversity (see below).

Our approach to partitioning the effect of different scales centered on variation partitioning, an approach that has been used successfully in estimating effects of different scales (Cushman and McGarigal 2002; Heikkinen et al. 2004) and in partialling out spatial structure from datasets (Borcard et al. 1992). Yet other approaches are possible (Graham 2003).

Table 2 The unique and total variation explained (unique/total) for significant effects (based on 95% CI of parameter estimates), with positive (+), negative (-), or mixed (±) effects from increased human disturbances noted (NS = not significant), based on variation partitioning of potential human disturbances on each of 28 species investigated along the Madison and Missouri Rivers, Montana, 2004–2005

Species	Local		Patch	Landscape	
	Grazing	Invasives		Forest	Development
American goldfinch (<i>Carduelis tristis</i>)		0.03(+)/0.02(+)	0.04 (+)/0.05(+)		
American robin (<i>Turdus migratorius</i>)					0.09 (-)/ 0.08 (-)
Black-billed magpie (<i>Pica hudsonia</i>)			NS/ 0.07 (+)	NS/0.08(-)	0.03(-)/ 0.04 (-)
Black-capped chickadee (<i>Poecile atricapilla</i>)			0.06(-)/0.12(-)	0.07(-)/0.11(-)	
Brown-headed cowbird (<i>Molothrus ater</i>)				NS/ 0.08 (±)	0.07 (-)/ 0.05 (-)
Black-headed grosbeak (<i>Pheucticus melanocephalus</i>)				0.11(+)/0.11(+)	
Bullock's oriole (<i>Icterus bullockii</i>)					
Cedar waxwing (<i>Bombycilla cedrorum</i>)	0.05(-)/0.05(-)		NS/0.01(+)	NS/0.01(+)	
Common yellowthroat (<i>Geothlypis trichas</i>)			NS/0.06(-)	NS/0.04(-)	
Downy woodpecker (<i>Picoides pubescens</i>)	0.03(-)/NS		NS/0.04(+)	NS/+0.08(+)	
Eastern kingbird (<i>Tyrannus tyrannus</i>)		NS/0.05(+)	NS/0.05(+)	0.06(+)/0.05(+)	
European starling (<i>Sturnus vulgaris</i>)			NS/0.03(-)	NS/0.05(-)	
Gray catbird (<i>Dumetella carolinensis</i>)	0.03(-)/0.06(-)	0.07(+)/0.04(+)	0.05(-)/0.08(-)		0.09 (-)/ 0.08 (-)
House finch (<i>Carpodacus mexicanus</i>)			0.08(+)/0.13(+)	0.05(-)/NS	
House wren (<i>Troglodytes aedon</i>)			0.05(-)/0.10(-)	NS/0.05(-)	NS/0.03(+)
Least flycatcher (<i>Empidonax minimus</i>)			0.09 (±)/0.09(±)	0.11(+)/NS	0.03(-)/0.03(-)
Mourning dove (<i>Zenaida macroura</i>)			NS/0.03(-)		
Northern flicker (<i>Colaptes auratus</i>)			0.01 (+)/NS	0.01(-)/0.01(-)	
Red-naped sapsucker (<i>Sphyrapicus ruber</i>)			0.14(±)/0.11(±)	-0.15(-)/NS	
Red-winged blackbird (<i>Agelaius phoeniceus</i>)			0.06(-)/0.16(-)	0.04(-)/0.15(-)	NS/0.03(-)
Song sparrow (<i>Melospiza melodia</i>)					
Spotted towhee (<i>Pipilo maculatus</i>)		0.05(+)/0.08(+)		NS/ -0.04 (-)	
Tree swallow (<i>Iachycineta bicolor</i>)		NS/0.06(-)	NS/0.05(-)	0.10 (±)/ 0.09 (±)	
Warbling vireo (<i>Vireo gilvus</i>)					
Western wood-pewee (<i>Tyrannus verticalis</i>)			0.05(-)/0.13(-)	0.04(+)/0.05(+)	
Willow flycatcher (<i>Empidonax traillii</i>)				0.01(+)/0.02(+)	
Yellow-breasted chat (<i>Icteria virens</i>)		0.02(+)/0.05(+)			

Shown are deviance-based R^2 values derived from generalized linear mixed models. Mixed effects (±) occurred when two factors had different effects on occurrence. Non-linear effects highlighted in bold, with the net effects determined from predicted probabilities at minimum and maximum values of explanatory variables. Empty cells highlight non-significant effects, based on 95% CI of parameter estimates overlapping zero

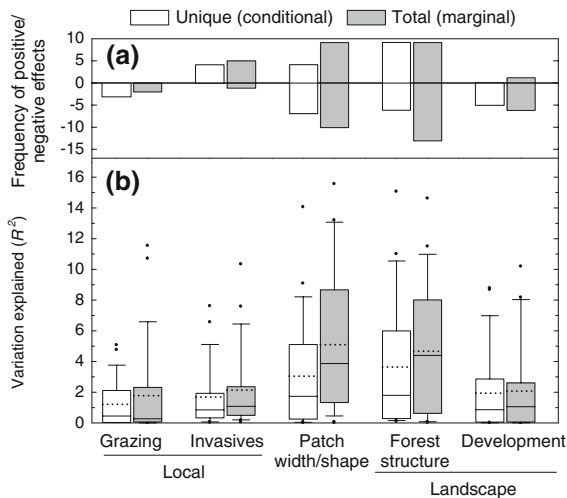


Fig. 4 Partitioning of human impacts at different spatial scales on the distribution of birds in riparian forests, Montana, 2004–2005. **(a)** The frequency of positive and negative effects across 28 species, based on marginal effects from univariate models and conditional effects from the global model (local + patch + landscape). Positive and negative effects were inferred if the 95% CI of coefficients did not overlap with zero, where a positive effect represents a species being more likely to occur with increasing disturbance (e.g., increased development, decreased patch width, increased patch density). **(b)** The unique and total (unique + joint) variation explained (%) for each human impact. Boundary of boxes indicates the 25th and 75th percentile, solid lines within boxes mark the medians and dotted lines the means, and whiskers indicate the 90th and 10th percentiles

Variation partitioning is useful for statistically decomposing variance and interpreting how different variables may explain similar components of variation in the data (joint or confounded variation); thus, in statistical terms, variation partitioning can explicitly identify multicollinearity within and among scales. Notably, joint variation explained across scales was relatively weak in our system, a result that is considerably different than other recent investigations using this approach (Heikkinen et al. 2004; Battin and Lawler 2006; Lawler and Edwards 2006). This result is encouraging, but it likely stems from the statistical hierarchical model structure we imposed throughout the modeling process, which has not been considered previously. In all models we included site as a random effect, which causes within site information to be considered correlated samples. In doing so, our model structure limits the potential for pseudo-replication, but it also captures some of the ‘confounded’ variation in the random component.

Variation captured in this random component could also be partitioned when warranted. In any case, we believe that such minimization of pseudo-replication improves inference and far outweighs any potential limitations for modeling species distributions and interpreting species-environment relationships.

Overall, our models tended to explain only relatively small portions of variation in bird occurrence both within and across spatial scales. Measures of variation explained for logistic models are known to often be low relative to least squares regression (Zheng and Agresti 2000), but other factors not included in the modeling process, such as biotic interactions, could help to explain remaining variation within and among scales. For example, in a recent habitat selection experiment in this region, 79% of the variation in Least Flycatcher density was explained by flycatchers using conspecific and heterospecific cues (Fletcher 2007), whereas in this study, environmental covariates only explained 32% of the variation in occurrence. While incorporating biotic interactions into species distribution models may be difficult and not warranted in some situations (Guisan and Thuiller 2005), incorporating such information does hold promise and should be considered when possible, particularly when developing models at fine resolutions.

Human disturbance

Identifying how humans directly and indirectly influence plants and animals is a crucial aspect of conservation biology and landscape ecology. We provide a unique comparative example among numerous species that illustrates the contrasting effects of multiple human disturbances occurring on different spatial scales, in terms of both the variation explained and the consistency of the directionality of effects. Our example emphasizes that while some scales (patch and landscape measures of habitat loss and fragmentation) may explain more variation in bird distribution, such variation explained may be a bit idiosyncratic, with species responding in different ways to patch and landscape disturbances. In contrast, those factors that explained less total variation in bird distribution—grazing, invasives, and development—had more consistent effects on birds.

At a local scale, disturbances from grazing had consistent negative impacts on bird distribution,

whereas, surprisingly, invasives had positive effects. Numerous investigations have shown negative effects from grazing on riparian birds (Mosconi and Hutto 1982; Knopf et al. 1988b; Tewksbury et al. 2002; Scott et al. 2003). Yet because grazing is often correlated with changes in local vegetation structure (Knopf et al. 1988b; Stanley and Knopf 2002), it becomes difficult to interpret whether such effects are from grazing per se or from changes in vegetation structure. For example, grazing intensity was negatively correlated with shrub density in our study area ($r = -0.17$, $P = 0.01$), but in a ‘ceiling’ sort of relationship, which makes intuitive sense. Grazing likely puts an upper limit on shrub density, with other factors explaining why some areas have sparse vegetation density in the absence of grazing (e.g., succession; see Scott et al. 2003). Our results further expose grazing effects by identifying that grazing can explain unique amounts of variation in bird distribution. Invasive species cover can also be correlated with grazing and other local vegetation measures (Miller et al. 2003), but we found that the unique contribution of invasives tended to be a positive effect. Fleishman et al. (2003) found no strong correlations between measures of bird diversity/abundance and invasive plants in riparian areas in the Mohave Desert. In addition, Rottenborn (1999) found that bird species richness and density increased with declining native vegetation in riparian areas in California. While these investigations suggest a positive effect of invasives on bird occurrence and community structure, we emphasize that numerous other investigations have documented negative effects of invasives on reproductive performance of birds (Schmidt and Whelan 1999; Borgmann and Rodewald 2004; Lloyd and Martin 2005; Ortega et al. 2006).

Indices of habitat amount and configuration at patch and landscape scales explained more variation in bird occurrence than other indices of human disturbance, yet these effects were more variable on species distribution than were other human disturbances. This variation among species can be largely explained by whether or not a species used habitats that surrounded riparian forest patches. Species that had higher probabilities of occurrence in narrower patches and in more heterogeneous landscapes tended to be resident species that are habitat generalists (e.g., American Robin, Mourning Dove, Brown-headed

Cowbird) and use surrounding habitats, such as pastureland. Those species showing lower occurrences in narrower patches or in landscapes comprising less, or more fragmented, forest were more riparian forest-dependent species in this region (e.g., Least Flycatcher, Red-naped Sapsucker). These patterns are similar to those described elsewhere in the western U.S. (e.g., Saab 1999) and underscore that understanding habitat associations of species and the availability of such habitats in a landscape are crucial for interpreting patterns of distribution.

Increased development had consistent negative effects on the occurrence of birds in our study area, but these effects were highly nonlinear. Smith and Wachob (2006) recently reached a similar conclusion for riparian birds breeding outside of Jackson, Wyoming. While we expected that development would have variable effects, with some species (e.g., residents, nest predators, and nest parasites), being more likely to occur in developed landscapes (Tewksbury et al. 2002; Rodewald and Bakermans 2006), we did not find strong support for this hypothesis. Most significant associations with development were non-linear, showing elevated occurrence with moderate development. For example, the Black-billed Magpie, the primary avian nest predator surveyed, exhibited the highest probability of occurrence at moderate levels of development, with the lowest predicted occurrence at the highest levels of development. Consequently, for some species thought to prefer urban landscapes (e.g., Black-billed Magpie; Saab 1999), such relationships may depend on the degree of development and urbanization.

Conclusions

Riparian systems in the western United States are critical habitats that are becoming more disturbed from increased agriculture, housing development, and subsequent fragmentation. Such increased anthropogenic pressures operating at multiple scales pose challenges for managers because these pressures can often covary. Our approach isolates potential effects of scale and disturbance and identifies the directionality of effects, while addressing statistical issues that arise when isolating effects on species distribution. Results suggest that while local vegetation structure

best explains bird distribution, managers concerned with ongoing human impacts need to focus more on mitigating the effects of large-scale disturbances than on local land use issues.

Identifying how humans directly and indirectly influence the distribution and abundance of organisms will continue to be important for managers and conservationists that are forced to allocate limited resources to management. Managers also need to balance whether information on species distribution alone is enough for making prudent conservation decisions. For instance, there is some evidence that landscape context and housing development can have important impact on reproductive performance of riparian birds (Tewksbury et al. 2006). Nonetheless, understanding habitat relationships of species and how those relationships are potentially influenced by humans at different scales will provide an important first step to developing sound land use, management, and conservation strategies of riparian areas.

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