RESEARCH ARTICLE

Modeling a cross-ecosystem subsidy: forest songbird response to emergent aquatic insects

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Abstract

Context Resource movements across ecosystem boundaries are important determinants of the diversity and abundance of organisms in the donor and recipient ecosystem. However the effects of cross-ecosystem movements of materials at broader spatial extents than a typical field study are not well understood.

Objectives We tested the hypotheses that (1) variation in abundance of 57 forest songbird species within four foraging guilds is explained by modeled emergent aquatic insect biomass inputs from adjacent lakes and streams and (2) the degree of association varies across foraging guilds and species within guilds. We also sought to determine the importance of emergent aquatic insects while accounting for variation in local forest cover and edge.

Methods We spatially modeled the degree to which distribution and abundance of songbirds in different foraging guilds was explained by modeled emergent aquatic insect biomass. We used multilevel models to simultaneously estimate the responses of species in four different insectivorous guilds. Bird abundance was summarized from point counts conducted over 24 years at 317 points.

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Results   Aerial insectivores were more abundant in areas with high estimated emergent insect biomass inputs to land (regression coefficient 0.30, $P < 0.05$) but the overall abundance of gleaners, bark-probers, and ground-foragers was not explained by estimated emergent insect abundance. The coursing aerial insectivores had the strongest association with emergent insects followed by willow flycatcher, olive-sided flycatcher, and alder flycatcher.

Conclusions   Modeling cross-ecosystem movements of materials at broad spatial extents can effectively characterize the importance of this ecological process for aerial insectivorous songbirds.

Introduction

Resources that move across ecosystem boundaries are important determinants of the abundance and diversity of organisms in a given area (Polis and Hurd 1995; Polis et al. 1997; Gratton et al. 2008). A number of studies have quantified the movements of resources across ecosystem boundaries and how they affect animals in the recipient ecosystem at local sites both observationally and experimentally (Marczak et al. 2007). Local increases in terrestrial predator abundance have been observed in response to increasing prey moving from adjacent ecosystems, including streams and lakes (Gray 1993; Nakano and Murakami 2001; Epanchin et al. 2010). Further, experimental removal of emergent aquatic insect prey decreased growth rates and abundance of terrestrial predators (Sabo and Power 2002; Dreyer et al. 2012). Other effects of cross-ecosystem linkages include fertilization of terrestrial plants from aquatic-derived nutrients and changes in predator–prey dynamics (Henschel et al. 2001; Knight et al. 2005; Hoekman et al. 2012; Bultman et al. 2014). Yet, we are not aware of any studies that have considered the importance of aquatic-derived materials to terrestrial ecosystem structure at broad spatial extents of hundreds to thousands of hectares, likely due to the intensive effort that would be required to measure these movements across a large spatial extent. It is unclear to what degree the transfer of aquatic-derived biomass to adjacent terrestrial areas may affect terrestrial animal diversity or abundance patterns examined across large spatial extents of heterogeneous habitat. In order to understand ecosystem linkages at the spatial extent of landscapes, new approaches are needed that can overcome the spatial limitations of a typical field study.

Recent studies have used models to predict the magnitude and variability of cross-ecosystem movements of material at broader spatial extents. Using empirical relationships between easily measured lake and stream characteristics and benthic secondary production, Gratton and Vander Zanden (2009) modeled the magnitude of the flux of emergent aquatic insects from aquatic to terrestrial ecosystems. Extending this theoretical approach to a real landscape, Bartrons et al. (2013) estimated the magnitude of emergent aquatic insect biomass inputs within 100 m of shore for all of the > 20,000 lakes and streams in Wisconsin, USA. In some localities, the estimated magnitude of carbon transferred through emergent aquatic insects to adjoining terrestrial areas approached or exceeded in situ terrestrial secondary production, suggesting that this cross-ecosystem process could exert strong community and ecosystem effects through localized increases in food abundance for emergent insect consumers. While the results of this model suggest ecological interactions at broad spatial extents, the correlation between consumers and estimates of emergent insect biomass has not been investigated empirically.

Our goal was to use empirical forest bird abundance data to ask whether emergent insect biomass explained variability in bird abundance characterized at a fine-grain across a broad spatial extent. We tested the hypotheses that variation in bird abundance was positively correlated with emergent insect biomass inputs and that the degree of association varied across foraging guilds and species within guilds. We hypothesized that bird species that focus on flying insects for food such as aerial insectivores would be more abundant in areas where there are high estimates of emergent aquatic insect biomass inputs from lakes and streams to land. This is a pressing conservation question, because aerial insectivorous birds have experienced steep population declines of unknown cause (Nebel et al. 2010). Positive associations between aerial insectivores and emergent aquatic insect biomass would indicate that aquatic-derived

insect resources and habitat at the aquatic-terrestrial interface are important for maintaining populations of aerial insectivores. We also hypothesized that local variations in forest cover or the amount of lake perimeter and stream length would affect avian guilds according to their preference for edge habitats in various ways, separately from estimated emergent aquatic insect biomass inputs.

Methods

Study area

The study area was the 270,000 ha eastern "Nicolet" administrative portion of the Chequamegon-Nicolet National Forest (CNNF), (approximately 45.6 °N 88.6 °W), Wisconsin, USA (Fig. 1). Within the CNNF

perimeter, landcover is 87.5% mixed forest, including forested wetlands, 4.0% open water, 3.6% shrubland, grassland, or herbaceous wetland, 2.9% developed, 1.9% pasture or row crops, and the remaining 0.1% barren land (Homer et al. 2007). Logging is the most common disturbance in the forest and the volume of timber extraction declined over the course of the study (Niemi et al. 2016).

Bird data

Birds were tallied at 317 points in the CNNF from June 1989 through 2012 as part of the Nicolet National Forest Bird Survey (NNFBS) (Howe et al. 1995; Howe and Roberts 2006). The points were placed so as to inventory 29 habitat types recognized by the U.S. Forest Service and were constrained to have homogeneous cover within a 125 m radius. Fewer than five
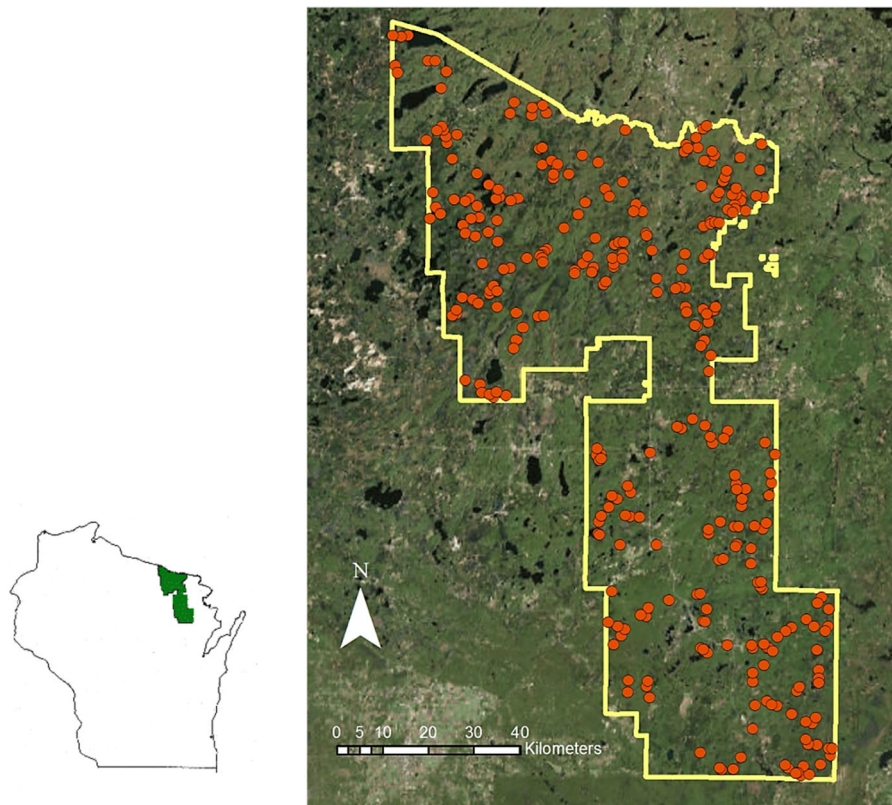

Fig. 1 Location of the NNF section of the Chequamegon-Nicolet National Forest within state of Wisconsin and locations of 317 bird survey points within the National Forest boundary. The Nicolet portion of the CNNF consists of 270,000 ha of predominately northern hardwood-conifer forest located in the

Boreal Hardwood Transition zone. Within the national forest boundaries, 587 privately-owned parcels comprise 31% of the land area with land uses ranging from high intensity management (e.g., agriculture and development) to undisturbed forest

percent of points were located in ecotones. Most points were at least 100–200 m from the nearest road (average 239 m; range 0–1887 m) and marked with a permanent stake. The points were not strictly randomly stratified by habitat but were placed so as to encompass different habitats proportional to their extent of occurrence in the CNNF and to minimize travel time between points (Niemi et al. 2016). Points were surveyed for 10 min by an experienced observer during the June breeding season, and all bird species seen or heard vocalizing were tallied. Most bird species can be detected aurally up to approximately 200 m in northern forests (Wolf et al. 1995). Most points were surveyed biennially. Our data included 278 points surveyed once per year in 12 years, and 39 points surveyed once per year between 8 and 16 years. Raw counts, uncorrected for detection, were used as our abundance estimate.

In our analysis, we included only the subset of detected bird species that are terrestrial, primarily prey on arthropods during the breeding season, and typically breed in or adjacent to forested landscapes. We then classified these 57 species into one of four foraging guilds based on their primary mode and location of prey capture (Online Appendix 1). The guild assignments followed the foraging guild classification developed by Ehrlich et al. (1988) and applied to northern Wisconsin birds by Lindsay et al. (2002). Aerial insectivores (14 species in our study area) primarily capture prey while they are flying in the air. Gleaners (24 species) typically capture insects located on vegetation or woody substrate. Ground-foragers (9 species) procure prey within forest leaf-litter and at the soil surface. Bark-probers (10 species) extract prey from under bark (e.g. black-and-white warbler, *Mniotilta varia*) or by boring into wood (e.g. woodpeckers, Picidae).

Emergent aquatic insect biomass inputs

To examine whether insectivorous bird abundance was related to the potential availability of emergent aquatic insect prey, we first derived estimates of expected emergent insect biomass inputs across the terrestrial landscape, based on a previously published model that was applied to the entire state of Wisconsin (Gratton and Vander Zanden 2009; Vander Zanden and Gratton 2011; Bartrons et al. 2013). The output of the emergent insect model (Bartrons et al. 2013) is a uniform estimated insect biomass per unit area per year (gC m^{-2} year^{-1}) to terrestrial areas up to 100 m adjacent to lakes and streams. For lakes and other lentic waters, the model estimates insect biomass transfer to land based on empirical relationships between benthic insect production, Secchi depth, and lake surface area (radius from the center of the lake). For rivers and streams, insect biomass transfer was estimated from mean annual water temperature and surface area. All of the waterbodies were delineated using Wisconsin Department of Natural Resources 1:24,000-scale hydrography maps (WDNR). Lakes were represented as polygons and streams were represented by two lines, one for each length of stream edge. The insect model is static in time and does not factor in other potential ecological and environmental correlates of insect flux. The model of insect biomass transfer from lakes and reservoirs had an adjusted $R^2 = 0.58$ at the scale of individual waterbodies and uncertainty of insect production estimates ranged from -10 to $+20\%$ in model validation. The adjusted R^2 for streams was 0.79 and insect production estimates ranged from -1 to $+6\%$ in model validation (see Bartrons et al. 2013 for details).

Following the approach of Bartrons et al. (2013), we modeled aquatic insect emergence to produce a uniform estimate for terrestrial areas within 100 m of the shoreline of each lake and the shoreline of each stream. We set aquatic insect biomass transferred to 0 at distances greater than 100 m inland, based on the estimate that 73–100% of emergent insect deposits occur within 100 m of the aquatic-terrestrial interface (Gratton and Vander Zanden 2009). Our model did not include factors such as the structure of the aquatic-terrestrial interface, or the taxonomic composition of the emergent insect community, which would allow us to accurately estimate finer-scale patterns of insect biomass inputs within the 100 m buffer. For ease of further computation, we multiplied the insect biomass value per m^2 by the area of each respective lake or stream buffer so that each lake or stream buffer had one total insect biomass value as an estimate of relative resource availability for birds likely to be foraging in the area.

To quantify the insect biomass associated with each bird survey point, we calculated the proportion of each 100 m lake (L) or stream (S) insect buffer that overlapped a 200 m buffer around each bird survey

point (b) and then calculated the absolute amount of insect biomass based on the proportional buffer overlap. Thus, the total value of aquatic insect biomass for each bird survey point was equal to the insect biomass in any overlapping lake buffers (L_b) plus the insect biomass in any overlapping stream buffers (S_b) (Fig. 2). We performed the spatial calculations using ARCMAP 10.1 (ESRI 2011).

Landscape variables

To determine the importance of emergent insect biomass inputs apart from other factors, we also measured landscape variables that may affect bird abundance and distribution. We measured total lake perimeter and stream length within 200 m of each bird survey point using the WDNR hydrography map (WDNR). Additionally, we estimated percent forest cover within 200 m of each bird survey point using 30 m resolution National Land Cover Dataset 2001 (Homer et al. 2007). We calculated area of each forest type (deciduous forest, coniferous forest, mixed forest, and woody wetlands) in FRAGSTATS (v4.2)

(McGarigal et al. 2012). We grouped coniferous forest, mixed forest, and forested wetlands together as one forest type labeled coniferous in our results and creating two forest types—coniferous and deciduous—as predictors in our model. Most forested wetlands in this region are coniferous, and the presence of conifers can be an important determinant of occupancy for many bird species in this region (Bub et al. 2004). Lake perimeter and emergent insect inputs were moderately correlated (Pearson coefficient = 0.63); however, adding or removing these landscape variables from the model did not change any significant relationships (not shown). We hypothesized that amount of lake perimeter and stream length in the landscape could affect bird abundance by altering habitat so we included them as predictors. We also examined associations of landscape covariates and bird abundance within 100 m and 500 m buffers around each bird survey point and found similar associations, suggesting that the scale of analysis around each bird survey point was not of great importance in determining associations with
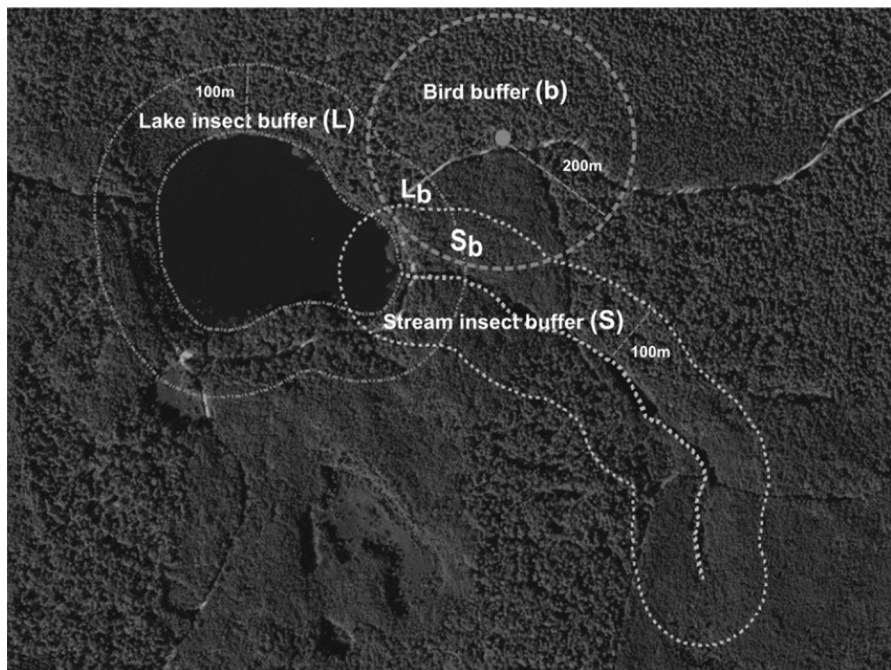

Fig. 2 Aerial photograph of a bird survey point with associated 200 m buffer (b) and 100 m lake and stream emergent insect buffers (L) and (S), respectively. The estimated emergent aquatic insect biomass inputs at each point were calculated based on the area of overlap between the lake insect buffer and bird buffer (Lb) plus the area of overlap between the stream insect buffer and bird buffer (Sb). The emergent insect biomass inputs were assumed to be uniform across the lake and stream buffer areas

landscape variables (results of 100 m and 500 m buffer analyses not shown).

Statistical analyses

Comparison of average guild abundance at survey points with and without insect biomass inputs

We compared the average guild abundances at survey points with estimated insect biomass inputs (survey points within 100 m of lake or stream; N = 153) to average guild abundances at survey points > 100 m inland (N = 164), which we assumed had no insect biomass transferred. We used a t-test to determine whether the average abundance of each guild differed between survey points with and without modeled insect biomass inputs. We $\log_e$-transformed the average guild abundance and the insect biomass input to improve the fit of the data to a normal distribution and improve heteroscedasticity.

Multilevel model of guild and species responses

We used a multilevel model, one for each of our four guilds, to simultaneously examine responses of the guilds and the individual species within the guilds to estimated insect biomass inputs and landscape variables (Gelman and Hill 2006; Jackson et al. 2012). We used a multilevel model because it is an effective way to make inference at both the species and guild levels within one model structure. We hypothesized that variation in response to emergent insect biomass inputs would occur at both levels. Bird counts were collected at the species level, which formed one level in the model. We adopted a Poisson distribution for the bird counts.

Each species' intercept a_i, and slope b_i, where i is a given species, are the sums of the respective guild average intercept α, and guild average slope β, and their respective variances, $\sigma^2_{intercept}$ and σ^2_{slope}, which are treated as Gaussian random variables d and e (Jackson et al. 2012).

$$a_i = \alpha + d_i$$

$$b_i = \beta + e_i$$

$$d \sim Gaussian\left(0, \sigma^2_{intercept}\right)$$
$$e \sim Gaussian\left(0, \sigma^2_{slope}\right) \tag{1}$$

In order to calculate the guild slopes and intercepts, we grouped species' abundances by their respective guilds, creating a second level in the multilevel model. Each guild was modeled separately, for a total of four models each structured as shown in Eq. (2).

The overall guild-level abundance response (λ_g) to each independent variable is the sum of the average of the coefficients for each constituent species from Eq. (1).

$$\lambda_g = \exp(\alpha_i + \beta_{1,i}x_{1,j} + \beta_{2,i}x_{2,j} + \beta_{3,i}x_{3,j} + \beta_{4,i}x_{4,j}$$
$$+ \beta_{5,i}x_{5,j} + \varepsilon_{g,j,t} + j + t_y + \gamma t_q)$$
$$j \sim Gaussian\left(0, \sigma^2_{intercept}\right)$$
$$t_y \sim Gaussian\left(0, \sigma^2_{slope}\right)$$

$$\tag{2}$$

To address over-dispersion we included a random effect, ε, for each unique bird detection in each guild g at point j (named "obs" in Table 3) at time t (labeled "year" in Table 2) (Harrison 2014). The bird survey point j (named "point" in Table 3) and year t_y, where y is a single calendar year, were included as random effects. We also included a fixed effect of year, t_q, where q is a single calendar year and γ is the trend in the number of individuals in each guild over the period of the study. We included year as both a fixed and random effect as a way to account for interannual variation as well as any abundance trends over the study period (Gorzo et al. 2016).

We $\log_e$-transformed the insect biomass and scaled the predictor variables to have mean of 0 and variance of 1 so that the species' coefficients from the multilevel model output could be interpreted as effect sizes. Univariate regressions (not shown) indicated that species abundance generally responded linearly to landscape variables so we modeled the relationships of species' abundances to all predictor variables as linear.

Comparison of guild and species responses

To determine whether insect biomass inputs and other landscape variables explained variation in guild abundance, we extracted each fixed-effect regression

coefficient and tested its significance. To determine whether species responses significantly varied from the guild response, we compared the fit of the full model with the fit of a model with the random effect for each species sequentially removed. For each comparison, we conducted a chi-squared test based on the Maximum Likelihood AIC values of the full and abbreviated model, and tested the significance of each independent variable random effect for a total of five comparisons for each guild (Jackson et al. 2012). Individual species responses to landscape variables were the species-level random effect coefficients.

The multilevel models were implemented using the lmer package in R 3.3.0. We validated the models by bootstrapping for each guild using the bootMer function with 1000 simulations and used the boot.ci function to generate a 95% confidence interval for each model parameter. We considered parameters for which the 95% confidence interval did not overlap 0 to be significant. Significant parameters in our models were consistent with respective bootstrapped models. The original and bootstrapped models had the same significant predictors (R Core team 2013; Bates et al. 2014) (Online Appendix 1 (R code) Online Appendix 2 (bird and landscape data, Online Appendix 3 (conifer cover data). We checked for spatial autocorrelation of model residuals using a semivariogram with 95% confidence envelope generated by 99 random permutations of the residuals (package GeoR in R 3.3.0) (Ribeiro and Diggle 2001; Diggle and Ribeiro 2007). We found no significant spatial autocorrelation in the residuals of a linear regression of average guild abundance as a function of emergent aquatic insect biomass inputs, percent forest cover, stream length, and total lake perimeter for any of the four guilds.

Results

The landcover within the 317 bird survey point buffers was representative of the landcover within the CNNF as a whole. Specifically, 84% of the land cover area was forest (conifer, deciduous, or mixed). Of the 16% that was not forested, most was developed (37.6%) or open water (31.4%) with smaller areas of open, herb-dominated wetlands (16.8%) and shrubland (7.3%). On average, each point buffer was 83.5% forest (SD 20.5%); of this 39% was deciduous and the remainder coniferous or mixed), 6.2% developed (SD 10.1%),

5.2% open water (SD 14.3%), 2.8% herb-dominated wetland, 1.2% shrubland (SD 3.6%), 0.6% grassland (SD 5.0%), and 0.5% pasture or cultivated land (SD 5.0%).

Birds

We analyzed detections of 39,965 individual birds of 57 species (Online Appendix 1). Gleaners were the most frequently detected foraging guild and the average abundance of gleaners per survey point per year was higher than the abundance of any of the other guilds. Ground-foragers were the second most frequently detected guild followed by aerial insectivores and bark probers (Table 1).

Emergent insect biomass inputs

Of the 317 bird point buffers of 12.56 ha, the average buffer had 17.1% (2.1 ha) overlap with a lake or stream buffer (SD 146.2%). While 164 bird point buffers did not overlap with a lake or stream, of the 153 bird point buffers that did, and thus had aquatic insect biomass inputs, the average percent area of overlap was 35.8% (4.5 ha) (SD 66.7%) (Table 2).

The total estimated insect biomass inputs from the 3960 lakes and 11,703 streams and rivers within the CNNF to adjacent terrestrial areas was approximately 2830 metric tons year^{-1}. At the 153 points that had lake and/or stream insect biomass inputs within the 200 m buffer, the total aquatic insect biomass input value across these bird survey buffers was 1797 kg year^{-1} (1.8 metric tons year^{-1}) and the average value per survey point buffer was 11.7 kg year^{-1} (Table 2). Assuming insect biomass inputs are spatially uniform, this represents on average about 0.09 g m^{-2} year^{-1} within the 12.56 ha area of each 200 m radius bird survey buffer.

Comparison of average guild abundance at survey points with and without insect biomass inputs

Aerial insectivorous bird abundance was significantly greater at survey points with higher estimated lake and stream-derived insect biomass inputs (N = 153) compared to survey points greater than 100 m inland, which had no modeled insect biomass inputs (N = 164) ($P < 0.001$). Gleaner and ground-forager average abundances were significantly lower at survey

Table 1 Total number of detections of birds by guild and average abundance of each guild at 317 unlimited-radius survey points

Guild	Total detections	Average abundance per bird survey point
Aerial	4771	1.32
Gleaner	18,811	5.00
Ground	12,960	3.45
Bark-prober	3407	0.91

Table 2 Overlap of emergent insect buffers with bird survey buffers and estimated emergent insect biomass inputs

	Mean percent overlap with lake and/or stream buffers (standard deviation)	Mean areal extent of overlap (ha)	Estimated mean aquatic insect biomass inputs per year (kg year^{-1})	Estimated total aquatic insect biomass inputs per year (kg year^{-1})
All bird survey buffers (N = 317)	17.1 (146.2)	2.1	5.7	1797
Bird survey buffers with overlapping lake and/or stream buffers(s) (N = 153)	35.8 (66.7)	4.5	11.7	1797
Bird survey buffers with overlapping stream buffers(s) (N = 98)	38.1 (64.6)	4.8	1.1	107
Bird survey buffers with overlapping lake buffer(s) (N = 81)	25.7 (65.6)	3.2	20.9	1689

The bird survey buffers are 12.56 ha (200 m radius circular buffers) surrounding bird survey sites. The lake and stream emergent insect buffers extend 100 m inland from the shoreline of the lake and 100 m inland from each side of each stream

points with modeled emergent aquatic insect biomass inputs compared to survey points with none. Bark-prober abundances were not significantly different at survey points with emergent aquatic insects compared to survey points with none. (Fig. 3).

Multilevel model

Inclusion of insect biomass inputs improved model fit compared to a model without insect biomass inputs for all guilds except ground-foragers. Estimated insect biomass inputs significantly explained variation in the abundance of aerial insectivores (fixed effect coefficient 0.303, $P < 0.05$) (Tables 3). Bootstrapping of the aerial insectivore guild also yielded a significant positive correlation ($P < 0.01$) (results not shown). The coefficient of aerial insectivore abundance response to insect biomass inputs was more than four times greater than the coefficient of gleaner abundance response. However, in contrast to results of the t-test

model above, there were no significant relationships between estimated insect biomass inputs and the abundances of gleaners or ground-foragers. In both multilevel and t-test models, variation in the bark-probing guild was not significantly explained by estimated insect biomass inputs.

The percent forest cover within each buffer was the strongest predictor of aerial insectivorous bird abundance, with significantly lower bird abundance in areas with higher coniferous and deciduous forest cover (conifer fixed effect coefficient − 0.769, deciduous fixed effect coefficient − 1.035, $P < 0.001$). However percent coniferous forest positively explained variation in gleaner abundance (fixed effect coefficient 0.280, $P < 0.05$), but not abundance of the ground or bark-probing guilds. Ground-forager abundance decreased as the amount of total lake perimeter within 200 m of a survey point increased (fixed effect coefficient − 0.127, $P < 0.05$) (Table 3).
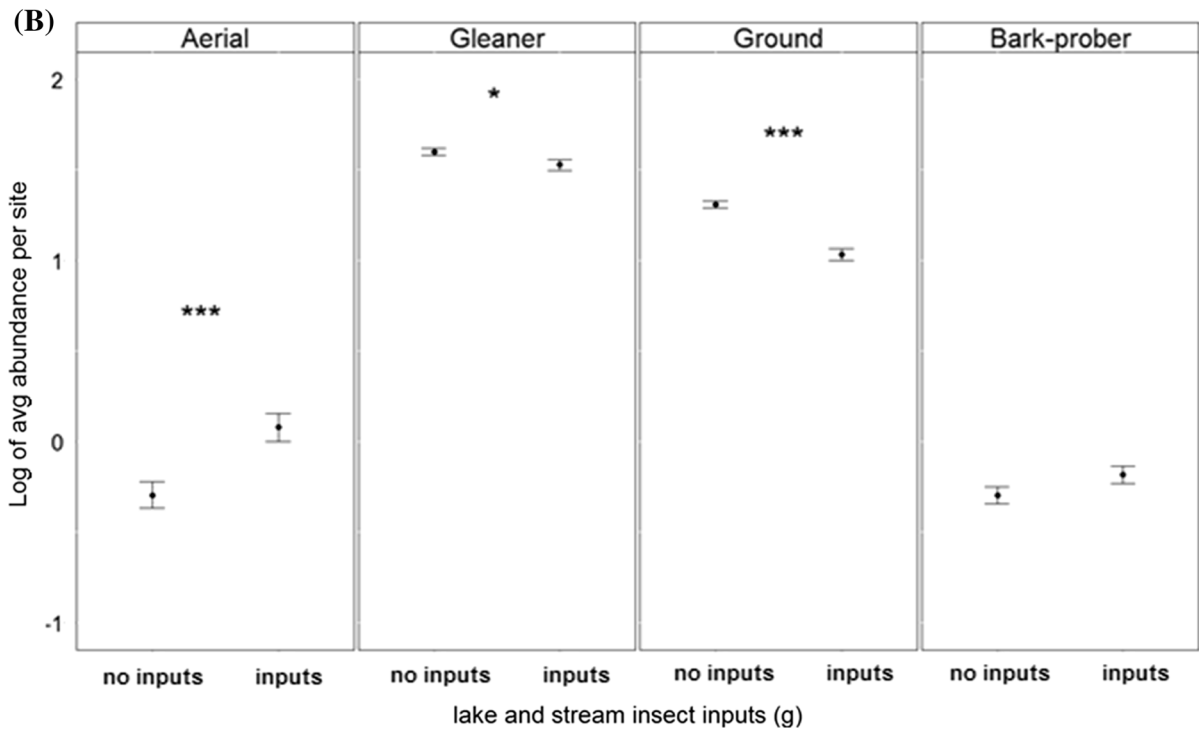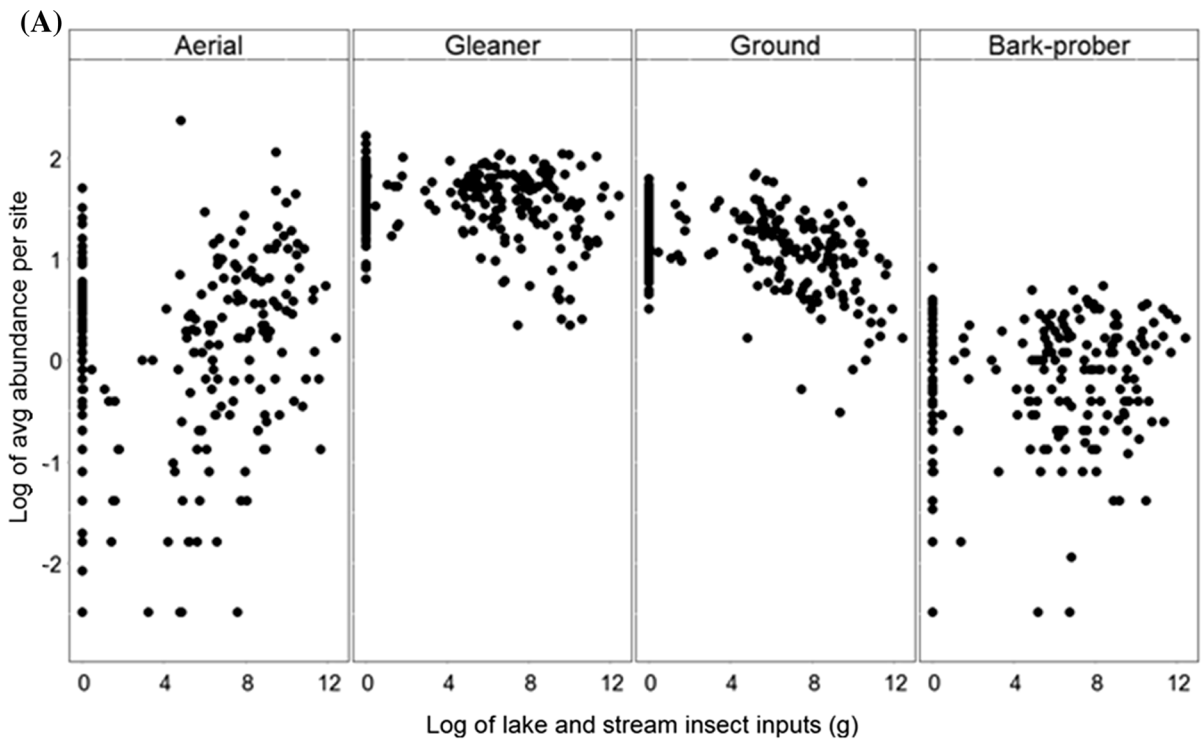
(A)

(B)

◄**Fig. 3 a** Average abundance of birds within four guilds at 317 survey points in the Chequamegon-Nicolet National Forest. Each point represents the average abundance over all bird survey years for that point (8–16 years). See Table 4 for bird species names. **b** Average abundance of birds in each guild at survey points with 0 insect biomass inputs compared to survey points with > 0 insect biomass inputs. Bars indicate standard errors of the mean. ***(p value < 0.001) *(p value < 0.05)

There was a high degree of species-level variance in response to landscape variables, as indicated by the significant random effects of all landscape variables in most guilds, the exceptions being stream length and lake perimeter for the bark-probing guild (Table 3). Most of the variation in the response of guilds to landscape variables was encompassed within species-

specific random slopes within the guild, with lesser portions of the variance attributable to bird survey point differences, and observation-level variance.

Within each guild, species-specific responses to landscape variables ranged widely (Fig. 4, Table 4). Aerial insectivores had the greatest variation in response to lake and stream insect biomass inputs, with many species exhibiting strong positive responses. Only eastern phoebe (*Sayornis sayornis*) had a negative response to increasing insect biomass inputs whereas swifts and swallows had the strongest positive responses. Among the aerial insectivores, percent deciduous forest was the strongest explanatory variable of abundance for 11 of 14 species, with only two of 11 species showing a positive response. Several species responded negatively to stream length and

Table 3 Coefficients of fixed and random effects for each landscape variable in the multilevel model for four avian foraging guilds (average abundance within each guild, over all survey years at a given point)

Guild	Variable	Fixed effects	Random effects
Aerial insectivore	Intercept	− 4.034***	Year 0.000; species 3.132; obs 1.171; point 0.530
	Percent coniferous	− 0.769**	0.981***
	Percent deciduous	− 1.035***	0.957***
	Stream length	0.008	0.082***
	Lake perimeter	− 0.105	0.118***
	Lake and stream insects	0.303*	0.107***
Gleaner	Intercept	− 2.732***	Year 0.000; species 1.935; obs 0.347; point 0.068
	Percent coniferous	0.280*	0.396***
	Percent deciduous	0.057	0.305***
	Stream length	− 0.024	0.057***
	Lake perimeter	− 0.056	0.019***
	Lake and stream insects	0.059	0.017***
Ground	Intercept	− 1.942***	Year 0.00; species 2.208; obs 0.055; point 0.053
	Percent coniferous	0.117	0.425***
	Percent deciduous	0.027	0.434***
	Stream length	0.002	0.026***
	Lake perimeter	− 0.124*	0.022***
	Lake and stream insects	− 0.022	0.008***
Bark-prober	Intercept	− 2.606***	Year 0.000; species 0.962; obs 0.457; point 0.159
	Percent coniferous	0.194	0.110***
	Percent deciduous	0.149	0.159***
	Stream length	0.051	0.002
	Lake perimeter	0.064	0.001
	Lake and stream insects	0.014	0.008*

Year, species, observer [obs], and bird survey point [point] are random intercepts in the model
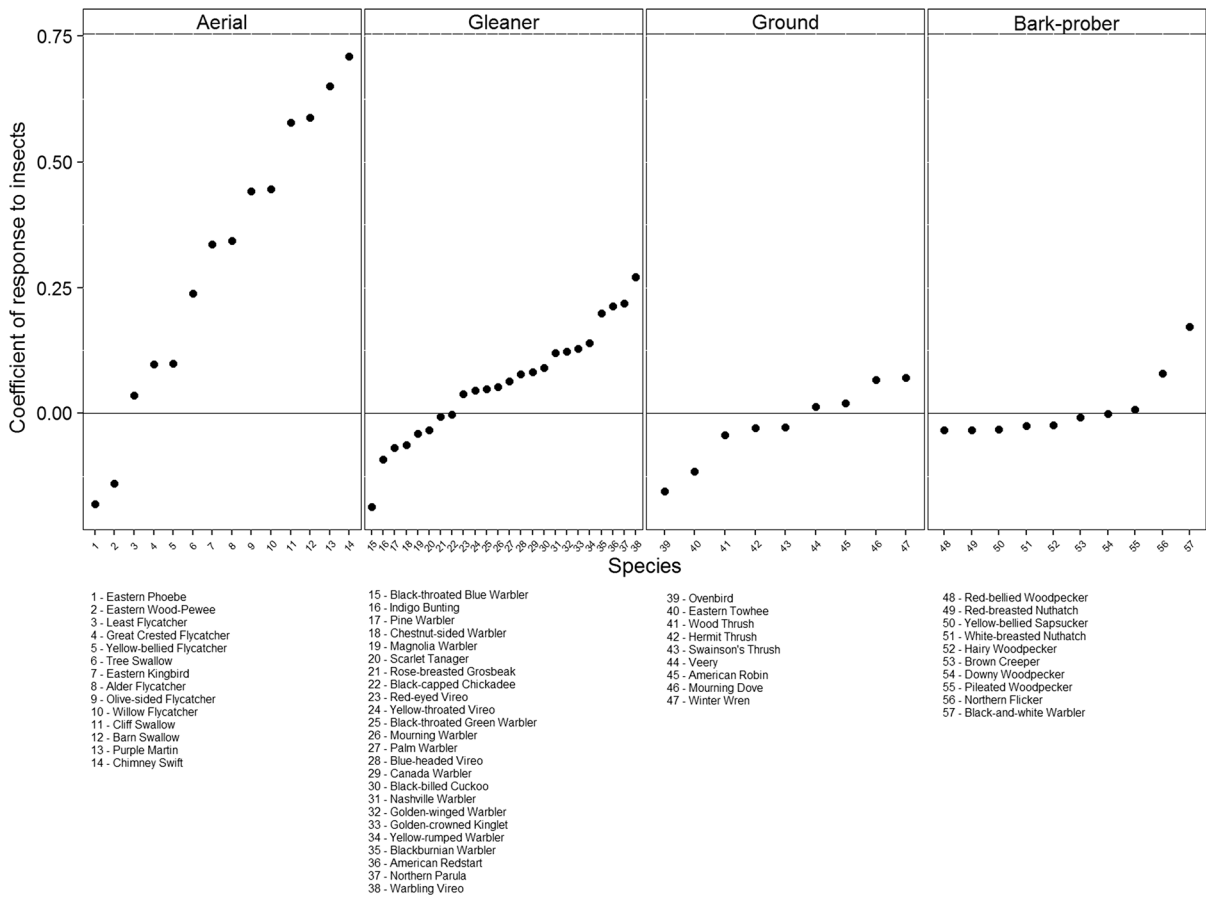
*P < 0.05, **P < 0.01, ***P < 0.001

Fig. 4 Multilevel model coefficient of response to estimated lake and stream insect biomass inputs by each bird species, within guilds. Coefficients are the sum of the fixed and random effects of the species response to each landscape variable. Species are arranged within guilds from lowest to highest coefficient of response to estimated emergent insect biomass

total lake perimeter but positively to lake and stream insect biomass inputs; we interpret this as an affinity for flying insect food resources but not for foraging at habitat edges, particularly the edges of large lakes.

Emergent insect biomass inputs had a positive association with the abundance of 16 of 24 species of gleaning birds. The species with the strongest positive associations with emergent insect biomass inputs were: warbling vireo (*Vireo gilvus*), American redstart (*Setophaga ruticilla*), northern parula (*Setophaga americana*), and yellow-rumped warbler (*Setophaga coronata*). Seven gleaners had slightly negative associations of > -0.070 and the black-throated blue warbler (*Setophaga caerulescens*) had a stronger negative association (-0.186; Fig. 4). Percent coniferous forest in the surrounding landscape was the most important landscape predictor of 14 species (four

negative, ten positive). Within the ground-foraging guild there was not a strong response to emergent aquatic insects. Among the bark-probing species, only the black-and-white-warbler was significantly more abundant in areas where aquatic insect biomass was estimated to be high, although coniferous forest was the most important predictor.

Discussion

Our study has advanced understanding of the importance of resource movements across ecosystem boundaries by combining estimates of emergent aquatic insects with an empirical 24-year dataset of insectivorous bird detections across a 270,000 ha national forest with a high density of lakes and

Table 4 Random effect coefficients for bird species in four foraging guilds of forested landscapes

Guild	Species	Log of estimated insect inputs from lakes and streams	Percent coniferous forest within 200 m	Percent deciduous forest within 200 m	Stream length within 200 m	Lake perimeter within 200 m
Aerial	Chimney Swift	0.710	− 1.536	− **1.579**	− 0.339	− 0.806
	Purple Martin	0.650	− 0.647	− **1.489**	− 0.148	− 0.377
	Tree Swallow	0.239	− 1.446	− **1.659**	0.032	0.110
	Cliff Swallow	0.579	− 2.557	− **2.474**	− 0.315	− 0.523
	Barn Swallow	0.588	− 1.686	− **2.040**	0.067	− 0.168
	Olive-sided Flycatcher	0.442	− 0.147	− **1.276**	− 0.046	0.103
	Eastern Wood-Pewee	− 0.140	0.105	**0.725**	− 0.173	0.166
	Yellow-bellied Flycatcher	0.099	**1.151**	− 0.499	0.025	− 0.081
	Alder Flycatcher	0.343	− 0.457	− **1.122**	0.460	− 0.190
	Willow Flycatcher	0.446	− 0.785	− **1.287**	0.295	− 0.158
	Least Flycatcher	0.036	− 0.283	**0.462**	− 0.280	0.199
	Eastern Phoebe	− 0.180	− 1.119	− **0.945**	0.393	− 0.132
	Great Crested Flycatcher	0.098	0.053	− 0.031	**0.123**	0.106
	Eastern Kingbird	0.336	− **1.415**	− 1.271	0.012	0.277
Gleaner	Black-billed Cuckoo	0.090	0.170	**0.411**	0.200	− 0.040
	Yellow-throated Vireo	0.045	− **0.526**	0.062	− 0.045	− 0.030
	Blue-headed Vireo	0.078	**0.601**	− 0.122	− 0.257	− 0.009
	Warbling Vireo	0.271	− **1.416**	− 1.140	− 0.018	0.014
	Red-eyed Vireo	0.038	0.095	**0.493**	− 0.112	0.028
	Black-capped Chickadee	− 0.003	− 0.013	− **0.372**	0.045	− 0.129
	Golden-crowned Kinglet	0.128	**1.397**	0.212	0.002	0.004
	Golden-winged Warbler	0.123	− 0.182	0.004	**0.418**	− 0.212
	Nashville Warbler	0.120	**0.533**	− 0.266	0.046	− 0.050
	Mourning Warbler	0.052	0.119	**0.310**	0.061	− 0.158
	American Redstart	0.213	− **0.445**	− 0.360	0.061	0.001

Table 4 continued

Guild	Species	Log of estimated insect inputs from lakes and streams	Percent coniferous forest within 200 m	Percent deciduous forest within 200 m	Stream length within 200 m	Lake perimeter within 200 m
	Northern Parula	0.219	**0.422**	− 0.037	0.042	0.103
	Magnolia Warbler	− 0.041	**0.429**	− 0.135	0.199	0.141
	Blackburnian Warbler	0.199	**0.851**	0.291	− 0.315	0.064
	Chestnut-sided Warbler	− 0.063	0.042	0.118	**0.199**	− 0.062
	Black-throated Blue Warbler	− 0.186	0.899	**1.262**	− 0.434	0.029
	Palm Warbler	0.063	**0.883**	− 0.288	− 0.255	0.064
	Pine Warbler	− 0.069	**0.843**	− 0.613	− 0.539	0.134
	Yellow-rumped Warbler	0.139	**0.612**	− 0.464	− 0.106	0.040
	Black-throated Green Warbler	0.048	0.872	**1.225**	− 0.238	0.024
	Canada Warbler	0.082	**0.798**	0.009	0.270	0.123
	Scarlet Tanager	− 0.034	0.230	**0.573**	0.065	− 0.107
	Rose-breasted Grosbeak	− 0.007	− 0.050	**0.270**	0.079	0.064
	Indigo Bunting	− 0.091	**− 0.444**	− 0.065	0.045	− 0.364
Ground-forager	Mourning Dove	0.067	− 0.678	**− 1.002**	− 0.139	− 0.260
	Winter Wren	0.071	**0.788**	0.206	0.143	0.043
	Veery	0.013	0.037	0.310	**0.351**	− 0.166
	Swainson's Thrush	− 0.028	**0.501**	0.209	− 0.095	− 0.031
	Hermit Thrush	− 0.030	**0.512**	0.297	− 0.114	− 0.082
	Wood Thrush	− 0.043	0.773	**0.890**	− 0.007	− 0.104
	American Robin	0.020	− 0.494	**− 0.718**	− 0.033	− 0.138
	Eastern Towhee	− 0.116	**− 0.971**	− 0.716	− 0.032	− 0.389
	Ovenbird	− 0.155	0.588	**0.765**	− 0.060	0.007
Bark-prober	Red-bellied Woodpecker	0.000	− 0.051	**0.233**	0.038	0.065
	Yellow-bellied Sapsucker	− 0.032	0.151	**0.504**	0.085	0.051
	Downy Woodpecker	− 0.001	− 0.084	**0.320**	0.069	0.075
	Hairy Woodpecker	− 0.024	0.104	**0.133**	0.028	0.058
	Northern Flicker	0.079	− 0.251	**− 0.402**	0.072	0.070

Table 4 continued

Guild	Species	Log of estimated insect inputs from lakes and streams	Percent coniferous forest within 200 m	Percent deciduous forest within 200 m	Stream length within 200 m	Lake perimeter within 200 m
	Pileated Woodpecker	0.007	0.039	− 0.031	0.019	**0.065**
	Red-breasted Nuthatch	− 0.034	**0.540**	− 0.332	0.034	0.087
	White-breasted Nuthatch	− 0.025	0.457	**0.573**	0.038	0.042
	Brown Creeper	− 0.008	**0.753**	0.697	0.020	0.046
	Black-and-white Warbler	0.172	**0.280**	− 0.200	0.105	0.078

Coefficients are the random effect plus the estimate for fixed effects. The most important predictor (largest effect) for each species is bold. Estimated insect biomass inputs are modeled from lake and stream characteristics. Percent coniferous and deciduous forest, stream length, and lake perimeter refer to measured values around bird survey points derived from Wisconsin Department of Natural Resources hydrography data and National Land Cover data

streams. We found that one of the four avian foraging guilds we studied, aerial insectivores, were positively related to the modeled biomass of emergent aquatic insects. This result is consistent with more localized field studies that have found positive effects of emergent aquatic insect biomass inputs on insectivorous birds (Nakano and Murakami 1991; Gray 1993). We also found that a number of individual bird species of other foraging guilds exhibited high abundance in areas with higher emergent insect biomass inputs relative to other sites, largely consistent with their specific foraging preferences.

Guild responses

Although inclusion of insect biomass inputs improved model fit compared to a model with only landscape variables for three of four guilds, insect biomass inputs were a significant predictor of abundance only for aerial insectivores. Areas on the landscape where more emergent insect biomass inputs were predicted also had higher average abundances of aerial insectivorous birds. The average response in abundance of aerial insectivores to emergent insect biomass inputs was four times higher than that of gleaners and there were significantly more aerial insectivores at survey points

that had insect biomass inputs compared to survey points that had none. These results are consistent with observational studies of bird responses to emergent insects at local spatial extents, where positive responses of aerial insectivores have been observed (Gray 1993; Nakano and Murakami 2001). Some field studies also have found positive responses of gleaning birds to emergent insect biomass inputs (Gray 1993; Whitaker et al. 2000; Gende and Willson 2001; Iwata et al. 2003; Bub et al. 2004). The fact that in our study the aerial insectivorous guild was positively associated with emergent aquatic insects while other groups were not, suggests that emergent aquatic insects are actively selected as a food source by most species in this guild but by few or no species in other foraging guilds. For example, Gray (1993) found that some gleaners such as black-capped chickadee were more abundant when emergent insect abundance was high, but others, such as common yellowthroat, were not.

The differential response between aerial insectivore and gleaning guilds is consistent with what is known about prey actively selected for by temperate passerine and near-passerine birds during the breeding season: aerial insectivorous birds feed their young aerial insects and the other guilds we studied primarily feed their young other types of arthropods or insects such as

phytophagous caterpillars (Holmes and Schultz 1988). The average estimated annual insect biomass transferred from lakes and streams to land is relatively small on a per meter basis (0.09 g m^{-2}), but assuming that the dry weight of a small emergent insect such as a midge or small mayfly is 5 mg and the average songbird feeding territory is one hectare, this would be an input of 180,000 insects per year within a bird's feeding territory, seemingly enough to influence habitat quality and thus the abundance and distribution of the aerial insectivores that can exploit this food resource. From an energetics perspective the insect input would be 2.23 kJ m^{-2} (Cummins and Wuycheck 1971). A typical songbird, such as a least flycatcher, expends about 75 kJ per day (Holmes et al. 1979). Assuming a foraging area of 10,000 m^2, estimated insect inputs could account for 81% of a single least flycatcher's yearly energy expenditure and greater than 100% during the breeding season.

Individual species responses

Although estimated emergent insect biomass inputs were a significant predictor of guild abundance overall, aerial insectivorous birds also exhibited high variability in species' responses to estimated emergent insect biomass inputs. The high species-specific variability in response to emergent insect biomass inputs may reflect species' plasticity or specialization in foraging on different types of flying insects, such as mostly terrestrial groups like beetles (coleoptera) or ants and wasps (hymenoptera) (Beal 1912). Swallows and larger flycatchers such as olive-sided, great crested, and eastern kingbird, which had greater abundance in areas of high estimated insect biomass inputs may prefer large emergent insect prey such as dragonflies and mayflies (Kennedy 1950; Fitzpatrick 1980). In contrast, eastern phoebe had decreased abundance in areas with higher insect biomass inputs. Eastern phoebe is among the most generalist in diet of aerial insectivorous birds in the study area (Beal 1912). It was not abundant although it is found locally at bridges and in towns, which were included in the forest-wide bird survey. Several forest-associated gleaning species had strong positive responses to emergent insect abundance, including American redstart, blackburnian warbler, northern parula, and yellow-rumped warbler. These species rely more on flycatching to capture prey and eat more emergent

aquatic insects than other species within the gleaning guild (MacArthur 1958; Sherry 1979; Robinson and Holmes 1982), which appears to be reflected in their selection of areas of high expected emergent insect abundance in our study.

We expected that emergent insects would not be a significant predictor of ground and bark-foraging guild abundance because these guilds forage primarily on the ground or by creeping along tree trunks and branches and probing for insects under bark, where they are unlikely to encounter aerial insects. The only species among the ground or bark-foraging guilds for which our models indicated that estimated emergent insect biomass inputs was the strongest predictor of abundance was the black-and-white warbler. While we acknowledge that this is unexpected, we do note that this species, in contrast to other members of the bark-foraging guild, occasionally engages in gleaning and hovering for insects (Morse 1989), and thus their population abundance may respond positively to emergent insects resting on trees near lakes and streams.

Importance of landscape

Of all the predictors we considered, forest cover within 200 m was the most important predictor of bird abundance in our study, with some species having a strong response to any type of forest cover, and others varying in response to coniferous versus deciduous forest cover. Most songbirds are believed to rely on habitat structure, rather than food abundance, as a proximate cue to establish breeding territories (Smith and Shugart 1987; Kristan et al. 2007) and as the bird counts were conducted within a forested landscape, we expected that forest cover would be important. Aerial insectivore abundance was inversely associated with amount of forest cover, which may reflect the need for open foraging areas to pursue flying insect prey. High abundance of aerial insectivores in response to high emergent insect biomass inputs may reflect flexibility in territory boundaries or extraterritorial movements in response to abundant emergent aquatic insect food resources. Some aerial insectivores such as swallow species and swifts do not defend feeding territories, which likely allows them to be more responsive to large pulses of emergent aquatic insects.

We found a moderate degree of correlation between our estimates of emergent insect biomass inputs and

several landscape variables, yet, including emergent insect biomass inputs improved model fit for three of the guilds and was a significant predictor of abundance of abundance of aerial insectivores. Together these findings suggest the importance of food resources in determining bird abundance in addition to habitat (Robinson and Holmes 1982; Gray 1993; Whitaker and Montevecchi 1997; Bub et al. 2004). We found the ground-foraging guild abundance decreased as the amount of total lake perimeter within 200 m of bird survey points increased. This is consistent with knowledge that the most abundant ground-forager in our study, the ovenbird (*Seiurus aurocapilla*), avoids edges, possibly due to their desiccating effects on arthropod prey habitat, such as leaf litter (Burke and Nol 1988). Variations in abundance of certain insect taxa between edges and interior forest also may affect abundance of birds that specialize on particular insects (McCollin 1998; Van Wilgenburg et al. 2001). However in some cases, especially for species with few detections, the effect sizes for predictor variables should be interpreted with caution. For example, the infrequently detected warbling vireo (*Vireo gilvus*) had a strong positive association with emergent insect biomass inputs, yet a smaller negative association with stream length, which is often their typical breeding habitat. Other landscape or habitat variables that we didn't account for such as terrestrial arthropod abundance, forest structure, plant species composition, and groundcover are known to be important determinants of bird abundance in forested landscapes; however these types of data are largely unavailable at large spatial extents.

Limitations of the approach

Although correlative, our study suggests that a cross-ecosystem food resource influences bird abundance and community compositions even when considered over a broad spatial extent. In order to broaden the spatial extent of this question, we made several assumptions about aquatic insect emergence and bird abundance. We assumed that aquatic insect emergence to land is consistent across years, although the magnitude and timing of insect emergence events are likely highly variable both within and between years (Ives et al. 2008). The data set we used only included breeding birds, but emergent insects may also be important to migratory and wintering birds when

other food resources may be scarce. We modeled transfers of emergent insects as uniform up to 100 m inland from lakes and streams rather than declining with distance from water (Dreyer et al. 2015). Finer grain data of bird abundance to go with finer grain insect model outputs could enhance understanding of relationships, however this type of data was not available. Further, we assumed that birds detected from a bird survey point were equally associated with the habitat types within 200 m of that point and were not influenced by other point-level variables. Additionally, bird survey points were not randomly located but placed to survey different habitat types and within several hundred meters of roads to facilitate easy access, which can introduce bias (Veech et al. 2017). However, previous comparisons of bird communities at our survey points compared to roadside points in the same locations suggests that our survey points are not affected by roads (Howe and Roberts 2006). The fact that the guild relationships we found largely conform to theoretical expectations and observational and experimental studies increases our confidence that our model inputs captured the average effect of emergent insect resources and landscape variables on bird abundance in an ecologically meaningful way.

Linkages at a broad extent

Our study moves beyond an observational or experimental spatial extent in contributing to knowledge of ecosystem linkages through cross-ecosystem movement of materials. We show that a model of emergent aquatic insect transfers from lakes and streams to adjacent land derived from easily measured lake and stream attributes such as water clarity and temperature can be used to model a fine-grain ecological process over a broad spatial extent and subsequently explain variation in the abundance of a higher-level consumer, largely in accordance with results of field studies.

Cross-ecosystem processes are important to community and ecosystem dynamics. In this study, our finding that modeled emergent insect prey abundance explained variation in aerial insectivorous bird abundance may be an important consideration in the management of aerial insectivorous birds (Whitaker et al. 2000). Aerial insectivorous birds have declined significantly across the northeastern United States since 1980 (Nebel et al. 2010). Both forest-breeding species and open-country species such as swallows

have declined, suggesting that changes in availability of flying insect prey may be a cause; however, this has received little study, especially at broader spatial extents.

In order to understand ecosystem structure, community dynamics, or even population dynamics, ecologists may need to consider whether ecosystem processes "scale-up" from local scale field studies to broad spatial extents (Pickett and Cadenasso 1995). In the case of aerial insectivorous birds, as we have shown here, even relatively small estimated emergent insect biomass inputs on the order of 0.09 g m^{-2} year^{-1} were associated positively with bird abundance when examined across a broad spatial extent. Our results suggest that protecting habitat at the aquatic-terrestrial interface and emergent aquatic insect populations is beneficial for conserving aerial insectivorous birds.

Author contributions PS analyzed the data and wrote the paper. MB, JVZ, and CG conceived the idea and assisted with writing the paper. JG assisted with data analysis and interpretation of results and assisted with writing the paper. RH contributed the bird data and assisted with writing the paper. AP assisted with the idea, analysis, and writing.

Data availability All data generated or analyzed during this study are included in this published article [and its supplementary information files].

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