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Patch occupancy of stream fauna across a land cover gradient in the southern Appalachians, USA

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Abstract We modeled patch occupancy to examine factors that best predicted the prevalence of four functionally important focal stream consumers (*Tallaperla* spp., *Cambarus* spp., *Pleurocera proxima*, and *Cottus bairdi*) among 37 reaches within the Little Tennessee River basin of the southern Appalachian Mountains, USA. We compared 34 models of patch occupancy to examine the association of catchment and reach scale factors that varied as a result of converting forest to agricultural or urban land use. Occupancy of our taxa was linked to parameters reflecting both catchment and reach extent characteristics. At the catchment level, forest cover or its conversion to agriculture was a major determinant of occupancy for all four taxa. Patch occupancies of *Tallaperla, Cambarus, and C. bairdi* were positively, and *Pleurocera* negatively, correlated with forest cover. Secondarily at the reach level, local availability of large woody debris was important for *Cambarus*, availability of large cobble substrate was important for *C. bairdi*, and stream calcium concentration was important for *P. proxima*. Our results show the abundance of stream organisms was determined by the taxon-dependent interplay between catchment- and reach-level factors.

Keywords Appalachians · Consumers · Land use · Patch occupancy · Stream chemistry

Introduction

Across a landscape, variation in the occupancy of stream organisms among reaches reflects the integration of processes occurring from local to catchment

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extents. Locally, the occurrence of animals within a patch depends on proximate conditions such as microclimate, food availability, presence of shelter, and water depth and velocity (Morris, 1987; Grossman et al., 2006). However, processes occurring at broader spatial extents influence factors shaping local conditions. For example, as forest is converted to agriculture, or urban and suburban residential use within watersheds, water flow, and the amounts of sediment, detrital inputs, anthropogenic nutrients, and other pollutants are altered (Sovell et al., 2000; Allan, 2004; Webster et al., 2012). Within catchments, flow of nutrients and water from surrounding terrestrial and hyporheic linkages as well as in-stream physical and biological processes help determine stream chemistry (Poole, 2010). Locally, riparian vegetation stabilizes channel morphology, mediates the flow of nutrients and water into stream systems, decreases light penetration, and increases leaf standing stocks and large woody debris available for stream consumers (Jackson et al., 2001; Allan, 2004). While the relationship between local and landscape processes may be intuitive and well-understood, highlighting the interdependence and interaction of local and landscape processes to the local abundance of stream communities are important. Because there is a spatial hierarchy of processes affecting stream systems, focusing solely on local parameters will fail to identify how activities distributed over larger extents influence stream organisms. Ultimately, the goal is to identify the factors and extents that best predict the distribution and abundance of species to better inform conservation and management of stream communities and processes.

Regional landscapes in the southern Appalachians are changing, driven by high population growth, and limited restrictions on human development in steep terrain (Gragson & Bolstad, 2006). The majority of the region is well forested (80% of landscape; Webster et al., 2012), but some catchments have been more intensively developed than others. Historically, it was agricultural development that transitioned to low-density residential development of valley-bottom land; however, between 1970 and 2000, rapid exurbanization has increased mountainside development (US Census Bureau, 1900–2000; Kirk et al., 2012; Webster et al., 2012). Exurbanization is the demographic process in which people move to rural locations while maintaining urban accessibility. The rapid expansion of residential communities from proximity to rapidly growing urban centers such as Atlanta, Charlotte, and Asheville (Pollard, 2005) has intensified potential human impacts on adjacent streams. This scenario also offers an opportunity to investigate the hierarchical nature of land use effects on streams by examining forested and developed reaches within watersheds that differ in the extent of development (forested, valley-bottom development, mountainside development, and urban; Gragson & Bolstad, 2006).

We examined the occurrence of stream organisms in relation to reach and catchment level characteristics within the upper Little Tennessee River basin. We selected sites along a gradient of land cover from heavily forested watersheds to increasingly agricultural, residential, and urban-dominated watersheds. Over a large spatial extent, we examined sites at different stages of development along the land cover development trajectory, using a space-for-time framework to capture much of the variability in regional land cover during a short sampling period (Pickett, 1989; Fukami & Wardle, 2005; Carter et al., 2009). The objectives of the study were to: (1) investigate the relationships of reach and catchment level factors affected by human land use to the occupancy of four focal taxa: *Tallaperla* spp. (stonefly), *Cambarus* spp. (crayfish), *Pleurocera proxima* Say, 1825 (snail), and *Cottus bairdi* Girard, 1850 (mottled sculpin); and (2) evaluate the relative performance of predictive models using reach and catchment level factors to explain the observed occupancy of our focal taxa.

Materials and methods

Site description

The Little Tennessee River originates in northeast Georgia, flows north and west through southwestern North Carolina, and empties into the Tennessee River in eastern Tennessee. Monthly mean air temperatures ranged from 3 to 22°C, and mean annual precipitation ranges from 1.8 to 2.5 m (Swift et al., 1988). Soils were generally classified as Inceptisols in the valleys and weathered Ultisols on the slopes. Our study region was predominately forested (approximately 80% forest cover over the 1,130 km^2 region; Webster

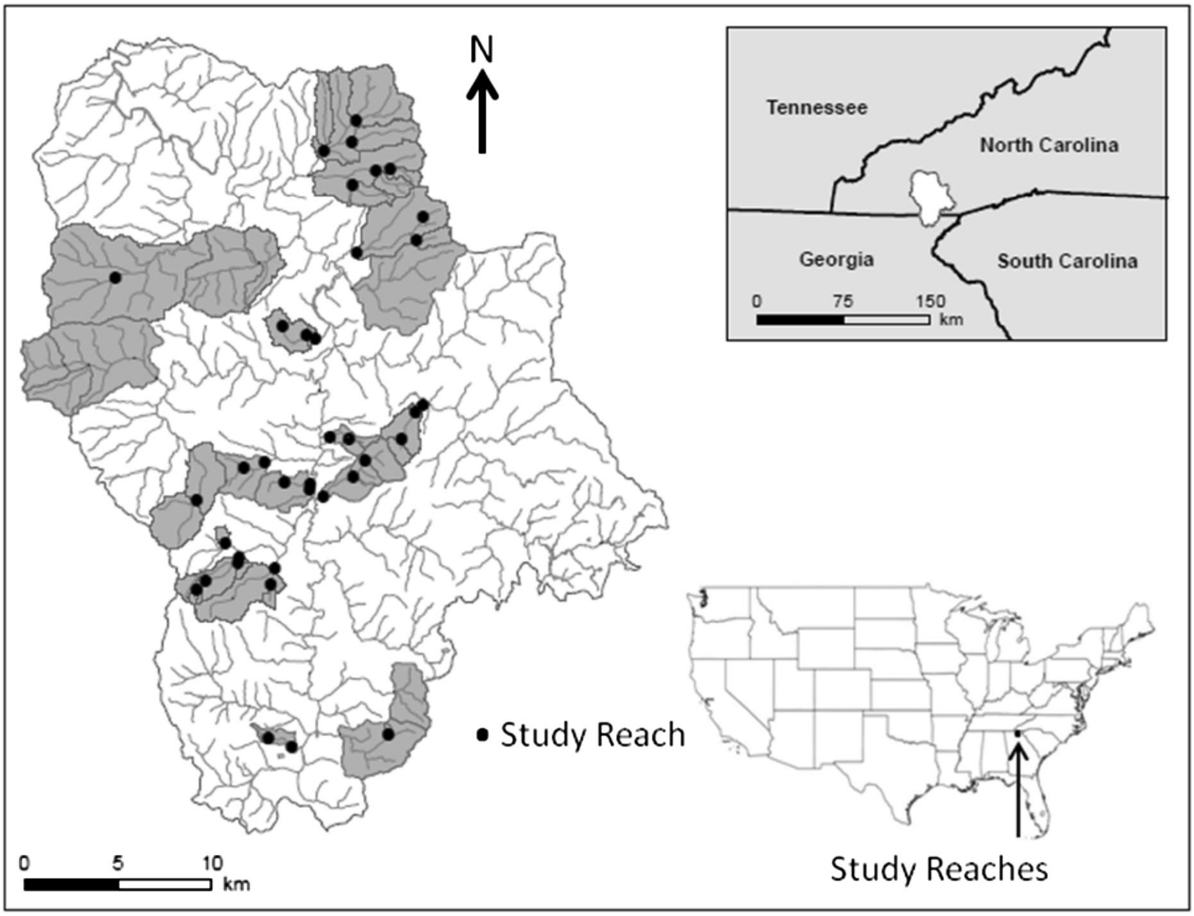

Fig. 1 Location of study sites within the Little Tennessee River basin, Georgia, and North Carolina in the southeastern United States (1,130 km^2)

et al., 2012) but stream valleys featured a mix of small-scale agriculture, rural residences, forests, as well as commercial, urban, and highway land cover. Thirty-seven study reaches were selected in the upper Little Tennessee River basin in the Blue Ridge Physiographic Province (Fig. 1). Our study reaches were a wadeable subset (first through third Strahler stream order) of fifty-eight reaches/catchments that were selected to be representative of different contemporary land use within the region and close to road access (Webster et al., 2012). Sampled reaches all drained an area less than 17 km^2, and land cover varied among these reaches (Table 1). Although stream reaches were not randomly selected, they were selected with no prior knowledge of stream chemistry, habitat, or species occurrence.

Selection of focal taxa

Our four focal taxa were chosen based on both their prevalence and functional importance in the southern Appalachians (Table 2). Common taxa are often influential in ecosystem function (Schmitz, 2010; Gaston, 2010). Our focal taxa are important as shredders (*P. proxima*; Dillon, 2000; Dillon & Robinson, 2009; *Tallaperla*; O'Hop et al., 1984; and *Cambarus*; Schofield et al., 2001; Creed & Reed, 2004), grazers (*P. proxima*; Dillon, 2000; Dillon & Robinson, 2009 and *Cambarus*; Schofield et al., 2001; Creed & Reed, 2004), and benthic insectivores (*C. bairdi*; Grossman et al., 2006). Each taxon was relatively easy to identify in the field, which facilitated larger numbers of rapid surveys.

Table 1 Statistics for covariates included in occupancy models quantified from surveys of 37 sites within the Little Tennessee River basin

Covariate	Mean	SD	Min.	Max.
Forest (%) in catchment (FOREST)	88.56	15.55	43.2	100
Agriculture (%) in catchment (AGRIC)	3.96	6.29	0	29.2
Urban (%) in catchment (URBAN)	5.87	9.80	0	40.7
Rhododendron (%) in reach (RHODODENDRON)	45.87	46.24	0	100
Catchment Drainage Area (km^2) (DRAIN)	2.74	3.99	0.18	14.38
Conductivity (µS/cm) in reach (COND)	26.91	12.84	9.3	63.5
Calcium (mg/l) in reach (CA)	1.46	0.84	0.26	3.15
Total dissolved nitrogen (mg/l) in reach (TDN)	0.14	0.12	0.02	0.52
Total dissolved phosphorous (mg/l) in reach (TDP)	0.007	0.004	0.003	0.02
Slope in reach (SLOPE)	0.04	0.03	0.001	0.2
Channel width (m) in reach (CHANNEL WIDTH)	3.04	1.32	0.78	6.96
Large Woody Debris Frequency (No./m) in reach (LWD)	0.06	0.11	0	0.5
Pool (%) in reach (POOL)	5.64	9.00	0	46.00
Riffle (%) in reach (RIFFLE)	58.21	35.12	0.53	99.24
Median bed particle size (mm) in reach (PEBBLE)	35.95	20.6	5.0	85.5

SD Standard deviation, *Min.* minimum value, *Max.* maximum value

Table 2 Selected focal taxa, relevant taxonomy, feeding guild and type of organism, distribution, and selection considerations for inclusion in this study

Taxon	Taxonomy	Guild and organism type	Distribution and selection considerations
Tallaperla spp.	Insecta: Plecoptera: Pteronarcyoidea: Peltoperlidae	Shredding Stonefly	Found throughout Appalachians Detectable during summer when other insect taxa are in winged form and absent from streams O'Hop et al. (1984), Huryn, (1986); important in leaf decomposition and represents substantial percentage of insect biomass in forested streams Woodall & Wallace (1972), Stout et al. (1993), Hutchens & Wallace (2002)
Cambarus spp.	Crustacea: Decapoda: Astacidea: Astacoidea: Cambaridae	Omnivorous Crayfish	Found throughout eastern & central U.S., most widely distributed and prevalent crayfish in Little Tennessee basin Simmons & Fraley (2010) Leaf shredder that contributes substantially to leaf decomposition Schofield et al. (2001)
Cottus bairdi	Actinopterygii: Scorpaeniformes: Cottoidea: Cottidae	Insectivorous Sculpin	Found throughout Appalachian, Great Lake, Rocky Mountain, and northern Cascade states Most common fish in southern Appalachians & displays high territorial fidelity Grossman et al. (2006), Petty & Grossman (2007) which make ideal for occupancy modeling
Pleurocera proxima	Gastropoda: Cerithioidea: Pleuroceridae	Grazing/ Shredding Snail	Common in southern Appalachian streams from GA to VA Important stream grazer with limited dispersal ability; can significantly regulate nutrient cycling, algal community structure and biomass (Dillon & Robinson, 2009)

Field sampling

Field sampling occurred between May and July 2009. For each reach, we surveyed and sampled focal taxa within a 150 m reach upstream of any nearby road crossing. In each reach, thirty-one 1 m^2 patches were delineated along the stream bank, each located 5 m upstream from the previous patch. To improve detection, we used two different techniques to detect animals at all sites (following Mattfeldt & Grant,

2007) and combined detections with both techniques in analyses. First, we actively surveyed each patch by turning cover objects and searching leaf litter. Second, we used rectangular leaf litter bags (25 by 40 cm) constructed with 1 cm^2 plastic mesh. At each reach, we collected adjacent streamside leaf litter or litter from the nearest upstream source to fill each bag. One litter bag was placed within each patch in shallow water near the riverbank and allowed to sit for 48 h before our first sampling. Litter bags were held in place using a piece of cobble as a weight. The two survey methods were intended to be complementary, as the active surveys could detect larger animals that could potentially be restricted by the mesh size of the rectangular bags, and the rectangular litter bags could serve as attractive microhabitats to improve capture rates.

In order to estimate detection probabilities, we surveyed each patch daily for three consecutive days. We checked leaf litter bags by rapidly lifting them from the stream into a bin and pouring water through the litter bag before gently agitating the litter bags to dislodge animals. Water and any dislodged organisms were filtered through a dip-net. On the first and second day, we returned litter bags to the same location and returned all organisms into the litter bag after anchoring the litter bag. Releasing animals into the litter bags was essential because the failure to capture animals in a bag on a subsequent day would be the result of animals voluntarily leaving the bag and not because we had displaced the animal from the bag. Following sampling on the third day, we removed all litter bags from the reach.

Catchment and reach measurements

During field sampling, the presence/absence of rhododendron adjacent to each patch was noted, to calculate the percent rhododendron for each reach. We also used previously collected water chemistry and land cover data (data from Webster et al., 2012). Reaches were sampled in June 2009 over 3 day periods of stable weather and discharge. Conductivity was measured in the field (YSI Model 30), while calcium, nitrogen, and phosphorous concentrations were determined by laboratory analysis of one to four liter stream samples collected in the field (data from Webster et al., 2012). Total dissolved phosphorous was determined by persulfate in-line UV digestion with a Lachat QuickChem FIA+ instrument, total dissolved nitrogen was determined with a Shimadzu TOC-VCPH TN analyzer, and calcium concentration was determined with a PerkinElmer Analyst300 Atomic Absorption Spectrometer (Webster et al., 2012). We also used previously collected reach data of large woody debris greater than 10 cm, median pebble size (from 100 pebbles), percent pool, percent riffle, channel width, and slope (data from Jackson et al., 2014). Visual assessment of study reaches classified riparian zones as no forested riparian zone (occasional or no trees), single-tree riparian zones less than 3 meters in width, narrow forested riparian zone 3–10 m in width, or riparian forest greater than 10 meters in width (data from Jackson et al., 2014). Catchment drainage area was calculated and land cover data were classified into forest, urban, and agricultural classes from 2006 NASA Landsat Thematic Mapping Imagery after delineation of catchment boundaries (from Webster et al., 2012).

Estimating patch occupancy

We estimated the proportion of patches in each study reach that were occupied by each focal taxon, with the assumption that the estimated proportion of patches occupied was a measure of taxon prevalence in each reach. We then fit occupancy models relating covariates to the proportion of patches occupied by each focal taxon (MacKenzie et al., 2003). Since biota were detected with less than 100% certainty, this had the potential to confound our models of taxon occupancy. To account for incomplete detection, we fit occupancy models as

$$P(d) = P(d|\Psi) * \Psi,$$

where $P(d)$ is the proportion of patches where a taxon was detected, Ψ is the true proportion of patches occupied by a taxon, and $P(d|\Psi)$ was the probability of detecting the taxon at a patch, given it was present (single season model; MacKenzie et al., 2003). Detection probability was modeled as a function of habitat, detailed below.

Modeling patch occupancy factors

Taxon-specific occupancy (Ψ) was modeled as a logit linear function of landscape-level characteristics, water chemistry, and habitat (parameters from

Table 1), and the probability of detection $P(d|\Psi)$ was modeled as a function of habitat. We used Markov Chain Monte Carlo (MCMC) as implemented in WinBUGS software, Version 1.4 (Lunn et al., 2000) to fit models. Models were fit using 1,000 k iterations, 500 k iteration burn in (i.e., the first 500 k MCMC iterations were dropped), and diffuse priors based on Gelman and Rubin diagnostic test results. The number of iterations needed for convergence was estimated using the Gelman and Rubin diagnostic test (Gelman & Rubin, 1992) based on three Markov chains derived from 1,000 k iterations of the global model for each taxon. The Gelman and Rubin diagnostic test was conducted using CODA analysis in program R (Plummer et al., 2006; R Development Core Team, 2010). For each taxon, goodness-of-fit (GOF) was assessed for the global models using a simple discrepancy measure and 1000 simulated data points (Gelman et al., 1996). This method compares deviances of simulated and observed data and fit is considered adequate when the GOF statistic is close to 0.5.

Prior to analyses, catchment land cover measures of percent forest, percent agriculture, percent urban, as well as percent rhododendron, percent pool, and percent riffle in a reach were arcsine transformed. All covariates that were not categorical or percent data were standardized to a mean of zero and a standard deviation of one. To avoid multicollinearity, we ran Pearson correlations on all pairs of predictor parameters prior to modeling. Preliminary evaluation of model fit indicated that the data for each taxon were overdispersed. To account for the overdispersion, we included random effects that corresponded to study reaches. The random effects were assumed to be normally distributed with mean of zero. The random effect variance was counted as an additional parameter in the calculation of Akaike Information Criteria (Akaike, 1973) with small sample bias adjustment (AICc; Hurvich & Tsai, 1989), discussed below.

Our primary objective was to evaluate hypotheses about the relative influence of landscape-level features, water chemistry, and reach habitat on taxon occupancy while accounting for the potential effects of incomplete detection. Therefore, we initially fit a global occupancy model (i.e., all parameters) and evaluated the relative fit of the detection model, $P(d|\Psi)$, using all combinations of the stream habitat characteristics: channel width, large woody debris frequency, percent pool, percent riffle, and median bed particle size. The best approximating detection model was selected using AICc, allowing detection probability (P) to vary with habitat characteristics instead of remaining constant, and was used during the evaluation of the factors affecting taxon occupancy described below.

We used an information-theoretic approach (Burnham & Anderson, 2002) to evaluate the relative fit of candidate models relating the proportion of patches occupied to environmental parameters. We developed a set of thirty-four models representing hypotheses about the relative influence of landscape-level features, water chemistry, and reach habitat on taxon occupancy. We then evaluated the relative fit of the candidate models using AICc and by calculating Akaike weights (w) that can range from ‘0’ to ‘1,’ with the best approximating model having the greatest Akaike weight (Akaike, 1973; Burnham & Anderson, 2002). Because the MCMC methods produce a distribution of AICc values, we used the mean AICc from the 1,000 k iterations for all inferences (Fonnesbeck & Conroy, 2004). The ratio of Akaike weights for two candidate models can be used to assess the degree of evidence for one model over another (Burnham & Anderson, 2002). Thus, we expressed model selection uncertainty by constructing a confidence set of models, which is analogous to the confidence interval of a mean, by including models with Akaike weights that were within 10% of the best approximating model weight. This is similar to the general rule-of-thumb (i.e., 12%) suggested by Royall (1997) for evaluating strength of evidence. The precision of parameter estimates was estimated by computing 95% credible intervals (Congdon, 2001), which are analogous to 95% CI. We also calculated odds ratios (Hosmer & Lemeshow, 2000) for each predictor parameter to facilitate interpretation. For each taxon, we also calculated cumulative detection probabilities for the three sampling dates: $1 - (1 - P)^3$, where P is the average estimated detection probability for a single sampling date (following MacKenzie et al., 2006).

Results

Percent forest, percent agriculture, and percent urban cover in a catchment were highly correlated (Pearson correlation $r < -0.90$), therefore we only used one of these three parameters in each of our candidate models to avoid models with redundant variables. Percent forest in the catchment was also negatively correlated with total dissolved nitrogen ($r = -0.81$), conductivity ($r = -0.76$), and calcium ($r = -0.75$) in the reach. Because we wanted to model catchment and reach-level factors, we included both land cover and water chemistry in our models, and considered the correlations in our inferences. AIC approaches are generally robust to multicollinearity as parameter estimates remain unbiased although sampling variances increase (Burnham & Anderson, 2002; Freckleton, 2011). Remaining correlations were generally small ($|r| < 0.45$). The global (all parameter) occupancy models had goodness-of-fit (GOF) statistics ranging from 0.44 to 0.62, indicating that there was adequate model fit. Therefore, we assumed that the fit was adequate for candidate occupancy models (following Burnham & Anderson, 2002).

Tallaperla

Tallaperla patch detection probability was positively related to large woody debris density and was relatively high and averaged 0.54 for a single sample day and 0.90 for detecting this taxon on at least one of 3 days. The best *Tallaperla* patch occupancy model included percent forest cover in the catchment and total dissolved nitrogen ($w = 0.990$), and every other model had Akaike weights less than 0.04 (Table 3). Therefore, our confidence set contained only the best approximating model. *Tallaperla* patch occupancy was positively related to percent forest cover in the catchment and negatively related to total dissolved nitrogen based on parameter estimates and odds ratios (Table 4). *Tallaperla* exhibited a threshold response to forest cover, essentially only occurring in reaches within catchments with greater than 85% forest cover.

Cambarus

Cambarus patch detection probabilities were negatively related to median pebble size and averaged 0.36 for a single day and 0.73 for 3 days. The best *Cambarus* occupancy model contained percent agricultural cover in the catchment and large woody debris per meter of reach ($w = 0.863$) and was 7.2 times more likely than the next best model that only included large woody debris per meter ($w = 0.119$) (Table 3). These two models comprised the confidence set. Large woody debris per meter was positively related to *Cambarus* occupancy in both models and the parameter estimates were relatively precise based on parameter estimates (Table 4). *Cambarus* occupancy was negatively related to agricultural cover in the catchment, but the parameter estimates were imprecise and overlapped zero (no effect). *Cambarus* patch occupancy had a strong negative association with percent agriculture cover in the catchment and a strong positive association with large woody debris in the reach based on the odds ratios (Table 4).

Cottus bairdi

Cottus bairdi patch detection probabilities were negatively related to percent riffle at a site and were relatively low and averaged 0.23 for a single sample day and 0.55 for three sample days. The best model for predicting *C. bairdi* patch occupancy included percent forest cover in the catchment and median pebble size ($w = 0.552$). There was no clearly best supported candidate model for *C. bairdi*, as the confidence model set ($w > 0.04$) contained four additional models that contained various habitat parameters (Table 3). The parameter estimates for these effects were all imprecise, with wide confidence limits that included zero. Therefore, we present parameter estimates for the best model. *C. bairdi* occupancy was positively related to pebble size and percent forest in the catchment based on parameter estimates, although the confidence interval for forest did overlap zero (Table 4). *Cottus bairdi* patch occupancy had strong positive associations with percent forest cover in the catchment and median pebble size in the reach based on the odds ratios (Table 4).

Pleurocera proxima

The probability of detecting *P. proxima* was not related to any of the stream habitat features considered and was greatest of all four taxa and averaged 0.65 for a single day and 0.96 for 3 days. The best approximating *P. proxima* occupancy model contained the parameter calcium concentration ($w = 0.24$) and was only slightly better supported than the second best model that contained percent forest cover in the

Table 3 Predictor parameters, number of parameters (K), ΔAICc, and Akaike weights (*wi*) for best performing occupancy models (i). Akaike weights are interpreted as relative plausibility of candidate models for *Tallaperla*, *Cottus bairdi*, *Cambarus*, and *Pleurocera proxima*. Models with Akaike weights (*wi*) less than 0.04 were considered highly improbable and were omitted

	AICc	K	ΔAICc	*wi*
Tallaperla candidate model				
Ψ(FOREST + TDN), *P*(LWD)	1,998.99	6	0	0.990
Cambarus candidate model				
Ψ(AGRIC + LWD), *P*(PEBBLE)	3,683.77	6	0	0.863
Ψ(LWD), *P*(PEBBLE)	3,689.75	5	3.95	0.119
Cottus bairdi candidate model				
Ψ(FOREST + PEBBLE), *P*(RIFFLE)	1,394.46	6	0	0.552
Ψ(FOREST + LWD + PEBBLE), *P*(RIFFLE)	1,394.93	7	2.50	0.158
Ψ(RIPARIAN CODE), *P*(RIFFLE)	1,399.75	5	3.28	0.107
Ψ(FOREST), *P*(RIFFLE)	1,399.77	5	3.29	0.107
Ψ(RHODODENDRON), *P*(RIFFLE)	1,401.68	5	5.20	0.041
Pleurocera proxima candidate model				
Ψ(CA), *P*(.)	1,711.34	4	0	0.243
Ψ(FOREST), *P*(.)	1,712.33	4	0.99	0.148
Ψ(FOREST + TDP), *P*(.)	1,710.25	5	1.59	0.110
Ψ(FOREST + CA), *P*(.)	1,710.32	5	1.66	0.106
Ψ(COND + CA + TDN + TDP), *P*(.)	1,704.43	7	1.70	0.104
Ψ(FOREST + COND + CA + TDN + TDP), *P*(.)	1,701.72	8	2.27	0.078
Ψ(TDN), *P*(.)	1,714.56	4	3.21	0.049
Ψ(FOREST TDN), *P*(.)	1,712.23	5	3.57	0.041

Ψ is estimated occupancy, *P* is detection probability, *P*(.) is constant detection probability, FOREST is percent forest in a catchment; AGRIC is percent agriculture in a catchment; RHODODENDRON is percent rhododendron in a reach; TDN is total dissolved nitrogen in a reach; COND is conductivity in a reach; CA is calcium concentration in a reach; TDP is total dissolved phosphorous in a reach; LWD is large woody debris per meter in a reach; PEBBLE is median pebble size in a reach; RIFFLE is percent rifle in a reach; RIPARIAN CODE is classification by riparian forest width

catchment ($w = 0.15$) (Table 3). There was no clearly best supported candidate model for *P. proxima*, as the confidence model set ($w > 0.04$) contained seven additional models with various combinations of covariates. The parameter estimates for these effects were all imprecise, with wide confidence limits that included zero. Therefore, we report parameter estimates for the two best approximating models. Calcium concentration was positively related to *P. proxima* occupancy, whereas percent forest cover in the catchment was negatively related based on parameter estimates (Table 4). *Pleurocera proxima* patch occupancy had a strong positive association with calcium concentrations in the reach and a weaker negative association with forest cover in the catchment based on the odds ratios (Table 4).

Discussion

Occupancy of our focal taxa shared an association with land cover at the catchment level (Fig. 2). This association indicated that large-extent processes (i.e., forest cover and loss of forest cover) influenced the suitability of local habitat for stream organisms. Catchment land cover likely represents a suite of integrated processes that, when coupled with local processes, influenced local environmental conditions (e.g., water chemistry, median pebble size, woody debris inputs, each also associated with patch occupancy for one of the focal taxa). Percent forest cover in the catchment was also identified as the most important factor predicting fish (Kirsch, 2011) and salamander (Cecala et al., in review; Cecala, 2012) patch

Table 4 Parameter estimates, standard deviation (SD), lower and upper 95% credible intervals, and odds ratios (OR) for best approximating *Tallaperla, Cambarus, Cottus bairdi,* and *Pleurocera proxima* occupancy models

Taxon	Parameter	Estimate	SD	Lower	Upper	OR
Tallaperla	*Occupancy* (Ψ)					
	Intercept	−1.654	1.192	−3.953	0.676	
	Forest	1.311	0.677	0.003	2.668	3.712
	Nitrogen	−4.117	1.042	−6.181	−2.197	0.016
	Random effect	3.031	0.499	2.082	3.918	
	Detection (*P*)					
	Intercept	0.163	0.061	0.043	0.282	
	Large Woody Debris	0.238	0.053	0.137	0.341	
Cambarus	*Occupancy* (Ψ)					
	Intercept	2.897	0.563	1.906	4.127	
	Agriculture	−1.616	1.537	−4.571	1.451	0.199
	Large Woody Debris	1.636	0.794	0.258	3.313	5.133
	Random effect	1.903	0.522	1.095	3.151	
	Detection (*P*)					
	Intercept	−0.590	0.053	−0.693	−0.486	
	Pebble	−0.054	0.047	−0.144	0.039	
Cottus bairdi	*Occupancy* (Ψ)					
	Intercept	0.847	1.101	−1.118	3.147	
	Forest	1.441	0.858	−0.374	2.867	4.23
	Pebble	1.550	0.576	0.459	2.750	4.71
	Random effect	3.041	0.541	1.984	3.934	
	Detection (*P*)					
	Intercept	−1.197	0.244	−1.650	−0.695	
	Riffle	−0.210	0.233	−0.685	0.229	
Pleurocera proxima	Best occupancy model					
	Occupancy (Ψ)					
	Intercept	−3.070	1.106	−5.205	−0.843	
	Calcium	1.074	0.439	0.166	1.907	2.49
	Random effect	3.664	0.266	3.019	3.989	
	Detection (*P*)					
	Intercept	0.620	0.064	0.494	0.746	
	Second best occupancy model					
	Occupancy (Ψ)					
	Intercept	0.785	1.255	−1.695	3.194	
	Forest	−1.916	0.902	−3.606	−0.146	0.83
	Random effect	3.687	0.252	3.068	3.990	
	Detection (*P*)					
	Intercept	0.623	0.064	0.497	0.750	

The second best *Pleurocera proxima* occupancy model is included because it contained forest cover, while the best model did not. The random effect is an estimate of the extra binomial variance

Forest is percent forest in a catchment; Agriculture is percent agriculture in a catchment; Nitrogen is total dissolved nitrogen in a reach; Large Woody Debris is Large Woody Debris per meter in a reach; Pebble is mean pebble size in a reach; Riffle is percent riffle in a reach; Calcium is calcium concentration in a reach

occupancy among the same reaches. Collectively, these studies demonstrate the strong control of catchment scale forest cover on native stream biota within southern Appalachian streams.

The greater predictive power of forest cover may be related to ecological mechanisms and in part methodological. Conditions within a stream reach are the integration of terrestrial and in-stream processes in the entire catchment above the reach (Poole, 2010). As a result, larger landscape processes such as forest loss within the catchment may better represent the integrated effects of changes within the catchment on reach scale conditions. Although organisms interact with conditions locally, it can be difficult to determine relative cause-and-effect in hierarchical systems (Morris, 1987). Nonetheless, we do have an understanding of some of the principle drivers for changes in streams due to catchment land cover change. We know that conversion of forest land cover to agriculture, residential, and urban land cover within catchments affects local conditions for stream biota via processes occurring over multiple spatial and temporal scales (Allan, 2004). Catchment land cover change increases sediment loading, which leads to in-filling of gravel habitat, and loss of riparian cover leads to decreases in litter/wood inputs, which can lead to a decrease in habitat/predator cover (see Allen, 2004 for review). Altered hydrology can reshape channel morphology and hydraulics, leading to flashier streams and increased scouring (Roy et al., 2005; Carter et al. 2009; Barrett et al., 2010). Development and loss of forest also alters nutrient levels in streams through loss of vegetative nutrient retention, which combine with increased light and temperature to accelerate leaf litter decomposition (Stout et al., 1993; Allen, 2004). Thus, the ultimate cause of change is likely the influence of multiple drivers acting at multiple temporal and spatial scales.

Large spatial extent models have several inherent properties that could help explain why our catchment models performed better than our local models. Factors measured singly at large spatial extent tend to have higher predictive value than repeated measures at smaller extents (Guisan & Zimmermann, 2000). Thus, integrative measurements at the catchment extent (e.g., forest cover) are less variable than repeated measurements at a site (e.g., channel width, large woody debris per meter). Large-extent measurements are integrative of measured and unmeasured processes occurring at smaller extents (Borcard et al., 2004). Forest loss within a catchment alters the amount of large woody debris, nutrients, and sediment entering streams, as well as the quantity, type, and quality of leaf litter. Furthermore, loss of riparian trees raises stream temperatures, which impacts environmental conditions for aquatic organisms (Sovell et al., 2000; Allan, 2004). Forest loss also causes a shift from heterotrophic stream systems with almost all production derived from a detritus base to a more autotrophic system, which incorporates more plant/algal production (Webster & Meyer, 1997). Thus, processes occurring at the catchment level can directly or indirectly influence reach dynamics.

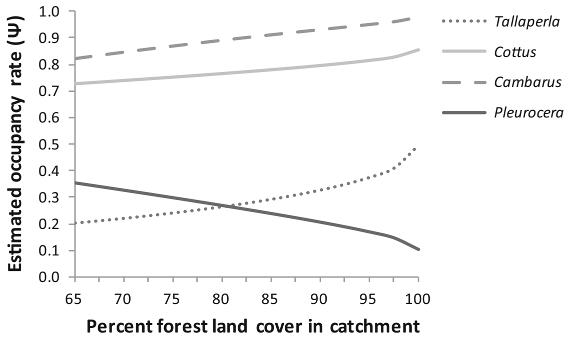

Fig. 2 The relationship between predicted patch occupancy (Ψ) of the four focal taxa and percent forest land cover in a catchment. Figure was generated using parameters estimated by occupancy models after inverse log transformation. *Note x*-axis values from 65 to 100% forest cover in catchment are displayed, representative of forest cover values for most of the catchments in this study, from which the relationships were derived

Our data show that percent forest cover in a catchment was a useful metric for predicting occupancy of stream taxa in the upper Little Tennessee River basin. Similarly, catchment parameters were superior to reach parameters in predicting fish (Kirsch, 2011) and salamander (Cecala et al., in review; Cecala, 2012) occupancy in the upper Little Tennessee River basin. As intensification of human land use in adjacent terrestrial systems is integrated into changes in stream systems, catchment metrics (e.g., percent forest cover in catchment) can help inform planning efforts in the southern Appalachians by providing evidence of how much conversion of land cover can occur in a catchment before detrimental effects on stream communities can be expected.

Given the complexities of natural systems, models are useful tools (MacKenzie et al., 2006). Although some of the complexities of the system are lost due to model simplification, underlying patterns may be detected; however, the limitations of the model need to be kept in mind. In this study, we utilized the natural variation in catchment land cover and local habitat parameters among stream sites instead of manipulative experiments; thus, our results must be interpreted as correlative rather than causative, and it is difficult to deduce process from observing patterns (MacKenzie et al., 2006; Freckleton, 2011). In addition, although we measured many catchment and reach parameters that we expected to have significant impacts on the occupancy of our focal taxa, undoubtedly we failed to assess some parameters that influenced occupancy (i.e., channel morphology and stream temperature).

Within the southern Appalachians, study catchments varied in current land use and expected future development trajectories. We examined the influence of land cover on stream organisms in catchments with varying land use at a single point in time, representing different points along a historical development trajectory, a study framework commonly referred to as space-for-time. One concern with use of space-for-time frameworks is an inability to distinguish historical legacies from current conditions, with potential to mistakenly attribute environmental effects to current instead of historical factors (Harding et al., 1998; Carter et al., 2009). Historical legacies impact this study, but different legacies among watersheds are minimized by consistent region-wide trends including clear-cut logging leading to the elimination of almost all old growth forest in the 1920s and 1930s (Swank & Crossley, 1988; Gragson & Bolstad, 2006). Our results indicated that regional conversion of forest cover to urban, residential, and agricultural land use has measurable effects on the occupancy of stream consumers in the southern Appalachians.

Conclusion

Our results illustrate the fundamental need to consider the effects of natural processes occurring on different spatial extents, which influence local environmental conditions, and the consequent distribution and abundance of stream consumers important to ecosystem function. Findings presented here highlight an association of occupancy of stream consumers with land cover in a catchment and local factors at the reach extent. Since our focal stream consumers are important in ecosystem processes and as predators and prey within food webs, decline or extirpation of these stream consumers likely reflects altered stream ecosystem processes and food web dynamics. Regional development trends are expected to decrease forest cover, which would be expected to maintain or enhance habitat for *P. proxima*. Therefore, as a conservation priority, we recommend maintaining forest within Little Tennessee River basin catchments in order that aquatic taxa associated with forested catchments, such as *Tallaperla*, *C. bairdi*, and *Cambarus,* persist and remain common. Finally, we stress the importance of assessing both reach and catchment level factors, and correcting for incomplete and imperfect detection, when investigating the occupancy patterns of stream taxa.

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