

Using occupancy modeling and logistic regression to assess the distribution of shrimp species in lowland streams, Costa Rica: does regional groundwater create favorable habitat?

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Abstract: Freshwater shrimps are an important biotic component of tropical ecosystems. However, they can have a low probability of detection when abundances are low. We sampled 3 of the most common freshwater shrimp species, *Macrobrachium olfersii*, *Macrobrachium carcinus*, and *Macrobrachium heterochirus*, and used occupancy modeling and logistic regression models to improve our limited knowledge of distribution of these cryptic species by investigating both local- and landscape-scale effects at La Selva Biological Station in Costa Rica. Local-scale factors included substrate type and stream size, and landscape-scale factors included presence or absence of regional groundwater inputs. Capture rates for 2 of the sampled species (*M. olfersii* and *M. carcinus*) were sufficient to compare the fit of occupancy models. Occupancy models did not converge for *M. heterochirus*, but *M. heterochirus* had high enough occupancy rates that logistic regression could be used to model the relationship between occupancy rates and predictors. The best-supported models for *M. olfersii* and *M. carcinus* included conductivity, discharge, and substrate parameters. Stream size was positively correlated with occupancy rates of all 3 species. High stream conductivity, which reflects the quantity of regional groundwater input into the stream, was positively correlated with *M. olfersii* occupancy rates. Boulder substrates increased occupancy rate of *M. carcinus* and decreased the detection probability of *M. olfersii*. Our models suggest that shrimp distribution is driven by factors that function at local (substrate and discharge) and landscape (conductivity) scales.

Key words: crustacean, detection probability, freshwater, *Macrobrachium*, river, tropical

Freshwater shrimps are functionally important components of tropical streams. For example, shrimps play a key role in foodweb stability and nutrient cycling in island stream ecosystems, where they make up the dominant macroconsumer biomass (Pringle et al. 1993, Covich et al. 1999, Crowl et al. 2001). Because they are migratory, shrimps are vulnerable to changes in river systems, such as damming and landuse changes, which reduce connectivity and alter water quality (Holmquist et al. 1998, Pringle and Scatena 1999, Dudgeon 2000). In Costa Rica, where our study was conducted, hydropower impoundments, non-point sources of pollution (e.g., pesticide runoff from agriculture), and point sources of pollution (e.g., wastewater effluents) alter habitat quality for freshwater shrimps (Castillo et al. 1997, Pringle and Scatena 1999, Anderson et al. 2006).

Low densities and migratory life histories of freshwater shrimp populations in lowland Costa Rica suggest they are potentially vulnerable to alterations in stream habitat quality. Amphidromous shrimp species migrate between fresh and salt water (McDowall 2007, 2009). Some *Macrobrachium* spp. travel the watershed twice: once as larvae drifting passively to the estuarine nursery grounds and again as juveniles migrating upstream to headwater streams where adults reside (Chace and Hobbs 1969). Even though *Macrobrachium* species may have large geographic ranges, extending from Brazil to Florida and including the Lesser and Greater Antilles (Chace and Hobbs 1969, Bowles et al. 2000), their densities in Costa Rica can be low (0.06–0.15 individuals [ind]/m²) (Ramírez and Pringle 2004).

Understanding which freshwater habitat conditions promote survival of shrimps will help managers identify

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sites that could be of high priority for their protection or conservation. High-quality habitats can create areas where source populations of adult shrimps reside, which could be important for maintaining population levels in lower-quality habitat areas. However, the survival, abundance, or even the distribution of low-density species can be difficult to measure. Occupancy modeling is useful for studying distribution and abundance of species with low densities, such as freshwater shrimp, in continental systems. Occupancy modeling has been used to provide knowledge of distribution, occupancy dynamics, and effect of management on species that are rare or of conservation concern (Albanese et al. 2007, Kroll et al. 2010, Wilson and Roberts 2011). Occupancy models relate both presence/absence and detection/nondetection data from temporal or spatial replicate samples to environmental predictor values (MacKenzie et al. 2002, Tyre et al. 2003). These models of species occupancy rates do not directly measure population abundance or survival, but the underlying principle is that changes in occupancy probability are correlated with changes in population size and density.

We used occupancy modeling and logistic regression to identify factors driving shrimp distributions across multiple scales in streams that drain a forested reserve in lowland Costa Rica. Very little information exists on the distribution and habitat requirements of freshwater shrimp species in continental stream systems, where they often occur in low abundance relative to other stream taxa but can occur at relatively high densities in certain regions (e.g., Atchafalaya River, Rio Tarumã-Mirim) (Walker and Ferreira 1985, Bauer and Delahoussaye 2008). Their distribution and abundance are likely to be determined by a combination of local-, network-, and landscape-scale factors because they can migrate long distances (>100 km). Occupancy models have been used in hundreds of peer-reviewed publications to study a variety of organisms, but rarely stream-dwelling invertebrates (Falke et al. 2010). To our knowledge, we are the first investigators to use occupancy modeling to study freshwater shrimp distribution.

The aim of our study was to understand the local- and landscape-level factors that influence distribution of shrimps in streams draining a lowland tropical rainforest where local habitat is relatively unaffected by agriculture or other landuse alterations. In the landscape (1600 ha) of La Selva Biological Station (LSBS), habitat patches of varying quality are created by inputs of solute-rich, regional groundwater high in P (Pringle and Triska 1991). In solute-rich habitat patches, macroinvertebrates have high growth rates and basal resource quality (%P body elemental content) is high (Ramírez and Pringle 2006, Ramírez et al. 2006, Small and Pringle 2010). Solute-rich stream reaches are buffered from seasonal acidification, exhibit more stable pH values, and have higher quantities of Ca (Small et al. 2012) than solute-poor reaches. We examined the effects of natural landscape-scale variation in solute-rich, regional

groundwater inputs on shrimp occupancy rates. We expected that because of the migratory nature of shrimps, landscape-level factors, such as regional groundwater input, would be a positive predictor of their occupancy rates. We also expected that, in addition to landscape-level factors, local-level factors, such as substrate and stream size, would be strong predictors of occupancy rates. We predicted that the effect of substrate size on shrimp occupancy rates would differ by species, but also expected that stream size would positively affect occupancy rates.

METHODS

Study site

This study was conducted at La Selva Biological Station (LSBS) (lat 10°26'N, long 84°01'W), a forested reserve situated on the Caribbean slope of Costa Rica at the intersection of the coastal plain with the Cordillera Central. The geomorphology of the region results in heterogeneous stream chemistry because geothermally modified regional groundwater surfaces at the break in the landform (Pringle 1991). Magmatic outgassing and weathering of volcanic rock creates high levels of solutes (P, Cl, Na, Mg, HCO_3^- , Ca) in regional ground water that range from 13 to 29× more concentrated than solute levels in ground water from local subsurface flows (Genereux and Pringle 1997). Conductivity is positively correlated with the concentration of solutes in the rivers and the percentage of water supplied by regional ground water (Pringle and Triska 1991). We used conductivity as a surrogate for quantity of regional groundwater input and solute concentration. Average annual temperature at LSBS is 25.8°C. Monthly mean daily temperatures range from 24.7°C in January to 27.2°C in August (Sanford et al. 1994). The elevation of LSBS ranges from 30 to 132 m asl.

Costa Rica is home to 15 species of amphidromous shrimp, and 7 of these occur on the Caribbean side (Obregon 1986). We collected data and created models for the 3 most frequently encountered shrimp species (*Macrobrachium carcinus* (Linnaeus 1758), *Macrobrachium heterochirus* (Wiegmann 1836), and *Macrobrachium olfersii* (Wiegmann 1836)) on the Costa Rican Caribbean slope (Chace and Hobbs 1969). Distributions of these 3 species in Costa Rica are not well known, but that they extend from lowland elevations to ≥900 m asl (Obregon 1986).

Data collection

We sampled 360 sites on the Salto, Sura, and Saltito Rivers between June and August 2008. Sampled streams ranged from 1st- to 3rd-order and drained into the Puerto Viejo River. We used modified breeder minnow traps baited with dried cat food in mesh bags to sample for shrimps (Covich et al. 1996). We placed traps in 14 reaches in the 3 streams and distributed them across gradients of longitudinal stream distance and conductivity (Fig. 1). Each

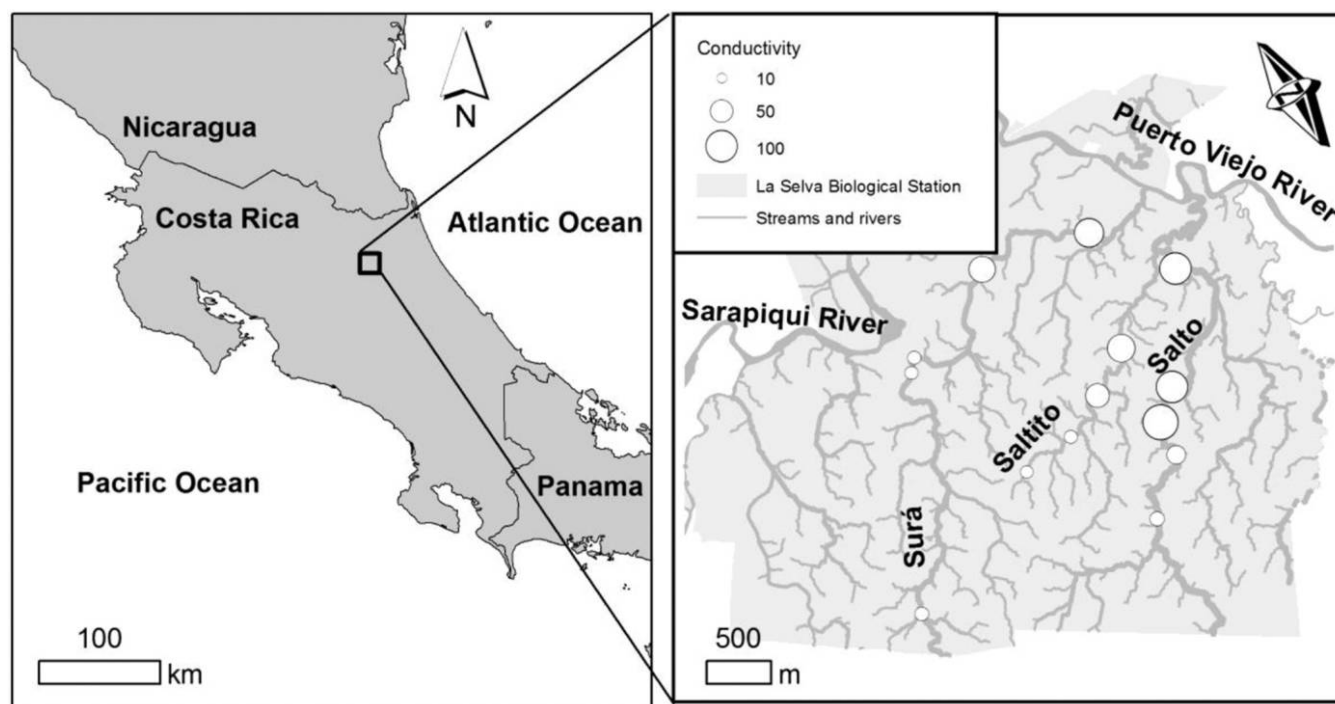


Figure 1. Map showing Sura, Saltito, and Salto Rivers at La Selva Biological Station, Costa Rica. Shrimp were sampled from June–August 2008 in stream reaches varying in solute levels and conductivity ($\mu\text{S}/\text{cm}$). Sizes of the circles are proportional to conductivity at the sampling site.

trap was considered a site. We spaced traps 5 m apart, on average, during the day, left them overnight, and checked them on each of the next 3 days. We rebaited traps each day. We identified shrimp in the field before returning them to the stream. Species were assigned according to Chace and Hobbs (1969) and Obregon (1986).

At each trap site, we categorized the substrate in a 3-m radius around the trap based on prevalence of different size substrates (boulder, sand, clay). We found leaf litter and coarse wood at sites in all substrate categories, but we did not measure it when present or record its absence. We measured conductivity, turbidity, and discharge for groups of trap sites. We measured conductivity ($\mu\text{S}/\text{cm}$) with a hand-held HI9033 meter (Hanna Instruments, Woonsocket, Rhode Island) and turbidity (cm) with a turbidity tube (120 cm) (Carolina Biological Supply, Burlington, North Carolina) each day the traps were checked. We calculated stream discharge (m^3/s) by combining average water velocity measured with a Flo-Mate 2000 flow meter (Marsh–McBirney, Frederick, Maryland) and the cross-sectional area of the wetted channel. We measured water velocity and water depth every 0.10 m along the transect that was used to measure the cross-sectional area. We used stream discharge as a relative measure of stream size.

Data analysis

Our objective was to compare support for alternative models as predictors of shrimp occupancy rates at sites

that varied in substrate characteristics, stream discharge, and conductivity (Table 1). The suite of models predicting occupancy rate and detection probability contained linear combinations of the covariates that represented different a priori biological hypotheses (Table 1). We applied occupancy models to our capture data using maximum likelihood methods with the *unmarked* package (Fiske and Chandler 2011) in R (R Project for Statistical Computing, Vienna, Austria). Occupancy modeling allows one to measure the strength of support for habitat covariates as predictors of the proportion of sites occupied (ψ = occupancy rate) by a species, while accounting for incomplete probability of detection (p = detection probability) (MacKenzie et al. 2002, 2006). In our study, p was the probability of detecting ≥ 1 individual given that a shrimp was present at the trap site ($p_{\text{trap}}|\psi_{\text{trap}}$) and was estimated from capture observations on 3 sequential trap-nights at each site. Capture observations were coded as 1 if shrimp were found in the trap and 0 if no shrimp were detected. We standardized (z -score) discharge and conductivity covariates by subtracting the overall mean and dividing by the standard deviation. We used Box–Cox power transformations to improve normality of turbidity values.

Our approach is based on the assumption that the probability of capture at each site was spatially independent, that sites were closed to changes in occupancy for the entire survey period (3 nights), and that shrimp were not falsely detected. We examined the assumption that the probability of capture at each site was spatially inde-

Table 1. The scale and biological hypotheses developed a priori for predictor variables used in the occupancy and logistic regression models to predict occupancy rates for *Macrobrachium heterochirus*, *Macrobrachium carcinus*, and *Macrobrachium olfersii* at La Selva Biological Station, Costa Rica.

Predictor variables	Scale	Biological interpretation (hypothesis)
Substrate	Microhabitat	The amount of cover from predation and food resources differs by substrate and influences shrimp behavior.
Discharge	Microhabitat	Predator abundance increases as discharge (stream size) increases; food resource availability may increase or decrease as discharge increases, depending on the food resource; habitat diversity increases as discharge increases.
Conductivity	Landscape	Abundance and quality of food resources increase as conductivity increases.

pendent with a runs test (Wald and Wolfowitz 1943) to test for randomness within the trap sequences ($n = 14$) of shrimp presence/absence. The null hypothesis of the runs test is that each trap of the sequence is statistically independent. Traps in a sequence were distributed longitudinally within a stream reach. We tested each species and trap-night sequence separately. If a series of grouped traps had <3 captures, we excluded it from the analysis. Of 42 series of trap presence, 16 were excluded because they had ≤ 2 captures. Only one nightly trap occupancy series of the 42 was significantly spatially correlated ($p < 0.05$). Therefore, in the occupancy models, traps within a sequence were considered spatially independent.

In addition, mean ψ did not differ as a function of trap night, so trap night was not included as a covariate in models of p . Stream identity was included as a covariate to account for influence of stream identity on shrimp ψ . We estimated the correlation strength between explanatory variables with Pearson correlation coefficients, and none was >0.6 .

One of the largest sources of heterogeneity in p can be differences in organism abundance (Royle and Nichols 2003). To address whether p was likely to increase as species abundance increased, we modeled p as a function of site covariates and ψ . To test hypothesized relationships between habitat factors and p , in our first set of models, we held ψ constant and allowed p to vary with covariates ($\psi(.)p(\text{Cov})$) thought to influence abundance (stream identity, conductivity, discharge, substrate) and turbidity, which is thought to influence p but not abundance. Then, to test

hypothesized relationships between habitat factors and ψ , we let ψ vary with covariates and modeled p as constant or allowed it to vary based on covariates from the confidence set of models (ΔAIC_c in the previous model set ($\psi(.)p(\text{Cov})$). This procedure allowed us to determine if including covariates in p and ψ improved model performance. For reference, we used a null model where both ψ and p were constant ($\psi(.)p(.)$). Each species was modeled separately. Because of sample-size limitations, no interaction terms were used, the number of ψ parameters was limited to an intercept plus 3 covariates, and p estimation was limited to an intercept plus 2 covariates. Inclusion of more parameters resulted in models with abnormal fitted boundary probabilities (the fitted probability is equal to 0 or 1) and ambiguous β estimates.

In cases when occupancy models did not converge (*M. heterochirus*), we used logistic regression to test hypothesized relationships between habitat factors and shrimp ψ . We modeled logistic regressions using generalized linear models with binomial distributions and logit links in R. In logistic regression models, a shrimp species was counted as present if it was detected ≥ 1 time at a site during any of the 3 sequential trap-nights and as absent otherwise.

We assessed relative support for occupancy models on the basis of Akaike's Information Criterion (AIC; Burnham and Anderson 2002). The best-supported models were those with the lowest AIC score. We assessed relative support for logistic regression models on the basis of AIC_c , which includes a small-sample size adjustment. We created a confidence set of models by including those with ΔAIC_c scores <2 , suggesting substantial support (Burnham and Anderson 2002). We used the ratio of model weights (w_i) to compare relative likelihood of models to the best-supported model (Burnham and Anderson 2002). w_i is the normalized log-likelihood for all the models in a defined set and is considered the weight of evidence in support of a particular model (Burnham and Anderson 2002). We assessed model fit with a parametric χ^2 test and by calculated \hat{c} (a measure of over-dispersion) for the top-ranked occupancy model (MacKenzie and Bailey 2004). Values of \hat{c} near 1 are indicative of good model fit.

Table 2. Logistic regression models with Akaike Information Criterion for small samples (AIC_c) weights (w_i) > 0.10 for predicting occupancy of *Macrobrachium heterochirus* and model predictor variables for occupancy and values for AIC_c , change in AIC_c (ΔAIC_c), w_i , and number of parameters (k) in each model. Models were included in the confidence set of models if $\Delta\text{AIC}_c < 2$.

Model	AIC_c	ΔAIC_c	w_i	k
Discharge	128.68	0	0.93	2
Null	162.1	33.43	0	1

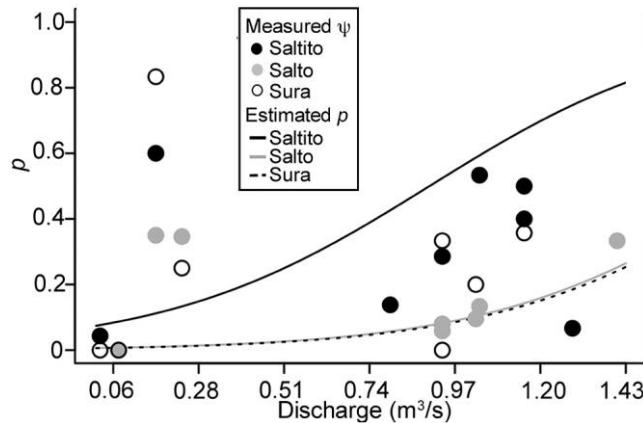


Figure 2. Simulated *Macrobrachium carcinus* probability of detection (p) as a function of discharge across 3 streams at La Selva Biological Station. Each symbol represents the measured occupancy rate (ψ) of a group of traps.

To extrapolate effects of covariates on predicted ψ , we derived model-averaged covariate effect sizes using regression coefficients from the confidence set of models (Burnham and Anderson 2002). We calculated a model-averaged value for β values of predictor variables by adding products of β values multiplied by w_i and dividing them by total combined weight of the confidence set of models (Burnham and Anderson 2002).

RESULTS

We trapped and measured 276 *M. olfersii*, 32 *M. heterochirus*, and 113 *M. carcinus* in 1080 trap nights. Observed ψ (i.e., ψ without correcting for p at a site) ranged from 6 to 34%. The number of shrimp in a trap ranged from 0 to 6. *Macrobrachium heterochirus* was found only in the Salto River. *Macrobrachium carcinus* and *M. olfersii* were found in the Sura, Salto, and Saltito Rivers. *Macrobrachium heterochirus* was present in 21 of 1080 trap sites, *M. carcinus* in 82, and *M. olfersii* in 122 (Appendix).

***Macrobrachium heterochirus*.** Mean ψ was 6% across sites. Occupancy models with covariates for this species did not converge, so logistic regression models were used to model relationships between ψ and habitat covariates. Only 1 covariate could be tested at a time because of the low ψ . Of the 4 occupancy models tested, none were within $\Delta AIC_c < 2$ of the top model. Therefore, the confidence set included only the best model (Table 2). The best model included discharge as a covariate and showed that as discharge increased, ψ increased. The model with the next smallest AIC_c score was 13.3 \times less likely to be the best model ($w_i = 0.07$). The top model accounted for 0.93 of the total w_i .

***Macrobrachium carcinus*.** Observed ψ was 23% across sites. ψ corrected by p was 70% (standard error = 17%). The model \hat{c} values were near 0.75, indicating adequate model fit, so we did not adjust the model standard error values (MacKenzie and Bailey 2004). The χ^2 test also indicated good model fit ($p = 0.8$).

None of the p models in which ψ was held constant were within $\Delta AIC_c < 2$ of the top model. Therefore, only the top model was included in the confidence set of models (Table 3). Covariates that occurred in the best model were discharge and stream. The top model accounted for 0.45 of the total w_i and was 3.3 \times more likely to be the best model than the next most likely model. p increased as discharge increased (Fig. 2), and the estimated mean p was 12%. We used the parameter values from the best model to simulate *M. carcinus* p across a range of discharge and streams (Fig. 2). p increased as much as 4 \times across the range of observed discharge levels and streams (Fig. 2).

None of the occupancy models for *M. carcinus* with covariates on both ψ and p were within $\Delta AIC_c < 2$ of the top model, so only the top model was included in the confidence set of models (Table 4). Covariates that occurred in the top model were discharge, substrate, and stream. The best model was distinguished as the most likely model by the ΔAIC_c score, which was >3.8 . The model with the next smallest AIC_c score was 6.9 \times less likely to be the best ($w_i = 0.1$). The top model accounted for 0.69 of the total w_i . In the best-supported model, p increased with discharge (Table 4).

We used the parameter values from the best model to simulate ψ across a range of substrate types, discharge, and streams (Fig. 3A–C). At the minimum discharge (stream size), ψ was 1.25 \times greater in boulder-dominated sites than in sites with primarily sand or clay. ψ increased with discharge across stream and substrate type, but the size of the influence was mediated by stream and substrate. In all stream sites on any substrate, ψ increased as much as 5 \times

Table 3. Models with Akaike Information Criterion for small samples (AIC_c) weights (w_i) > 0.10 for predicting occupancy (ψ) corrected for probability of detection (p) of *Macrobrachium carcinus* and model predictor variables for ψ when ψ was held constant ($\psi(.)$) and p was allowed to change based on covariates, values for AIC_c , change in AIC_c (ΔAIC_c), w_i , and number of parameters (k) in each model. Models were included in the confidence set of models if $\Delta AIC_c < 2$. $\psi(.)p(.)$ = null model in which both ψ and p were held constant.

Model	AIC_c	ΔAIC_c	w_i	k
$\psi(.)p(\text{discharge, stream})$	629.65	0	0.45	5
$\psi(.)p(\text{discharge, turbidity})$	632.05	2.4	0.14	4
$\psi(.)p(\text{conductivity, substrate})$	632.76	3.11	0.10	5
$\psi(.)p(.)$	636.19	6.54	0.02	2

Table 4. Models with Akaike Information Criterion for small samples (AIC_c) weights (w_i) > 0.10 for predicting occupancy (ψ) corrected for probability of detection (p) of *Macrobrachium carcinus* and model predictor variables for ψ when p was held constant ($p(\cdot)$) and ψ was allowed to change based on covariates and values for AIC_c , change in AIC_c (ΔAIC_c), w_i , and number of parameters (k) in each model. Models were included in the confidence set of models if $\Delta AIC_c < 2$. $\psi(\cdot)p(\cdot)$ = null model in which both ψ and p were held constant.

Model	AIC_c	ΔAIC_c	w_i	k
$\psi(\text{discharge, substrate, stream})$ $p(\text{discharge, stream})$	601.25	0	0.69	7
$\psi(\text{discharge, stream})$ $p(\text{discharge, stream})$	605.05	3.8	0.10	5
$\psi(\cdot)p(\cdot)$	636.19	34.94	0.00	2

across the range of discharge. However, on smaller substrates, the increase in ψ occurred at slightly higher discharge rates

***Macrobrachium olfersii*.** This species was detected at 122 of the 360 sites, and the observed ψ was 34%. ψ corrected by p was 56% (standard error = 7%). The naive estimate of ψ (34%) would have underestimated occupancy by 21%. The χ^2 test indicated good model fit, and the model \hat{c} values were near 1.1, indicating adequate model fit, so we did not adjust the model standard error values (MacKenzie and Bailey 2004).

None of the models of p that held ψ constant were within $\Delta AIC_c < 2$ of the top model, so only the top model was included in the confidence set of models (Table 5). Covariates that occurred in the best model were discharge and substrate. The top model accounted for 0.99 of the total w_i and was 127 \times more likely than the next most likely model. The estimated mean p was 27% and p increased as stream size (discharge) increased. We used the parameter values from the best model to simulate p across a range of discharge and substrate type (Fig. 4). p increased 2.5 \times over the range of discharge (stream size) (Fig. 4). p was lower at sites with sand and boulder than with clay substrates. At maximum discharge, ψ was as much as 2.8 \times higher in primarily clay than in primarily boulder substrate.

Two of the occupancy models with covariates on both ψ and p had $\Delta AIC_c < 2$ and were included in the confidence set of models (Table 6). Covariates that occurred in the top 2 models on ψ were conductivity and discharge (stream size). The model with the next smallest AIC_c score was 4.9 \times less likely to be the best. The top 2 models accounted for 87% of total w_i . All top-ranking models included covariates on p . Models in which p varied with discharge and substrate had better support than models

with a constant p . In the 2 best-supported models, discharge and conductivity increased ψ . Stream identity was included in 1 of the 2 best-supported models.

We averaged the parameter values from the best 2 models by w_i —(ψ [discharge, conductivity], p [discharge, substrate]), (ψ [discharge, conductivity, stream], p [discharge, substrate])—to simulate ψ across a range of conductivity and discharge (Fig. 5A–C). At the mean discharge (stream size), the p increased as much as 3 \times across

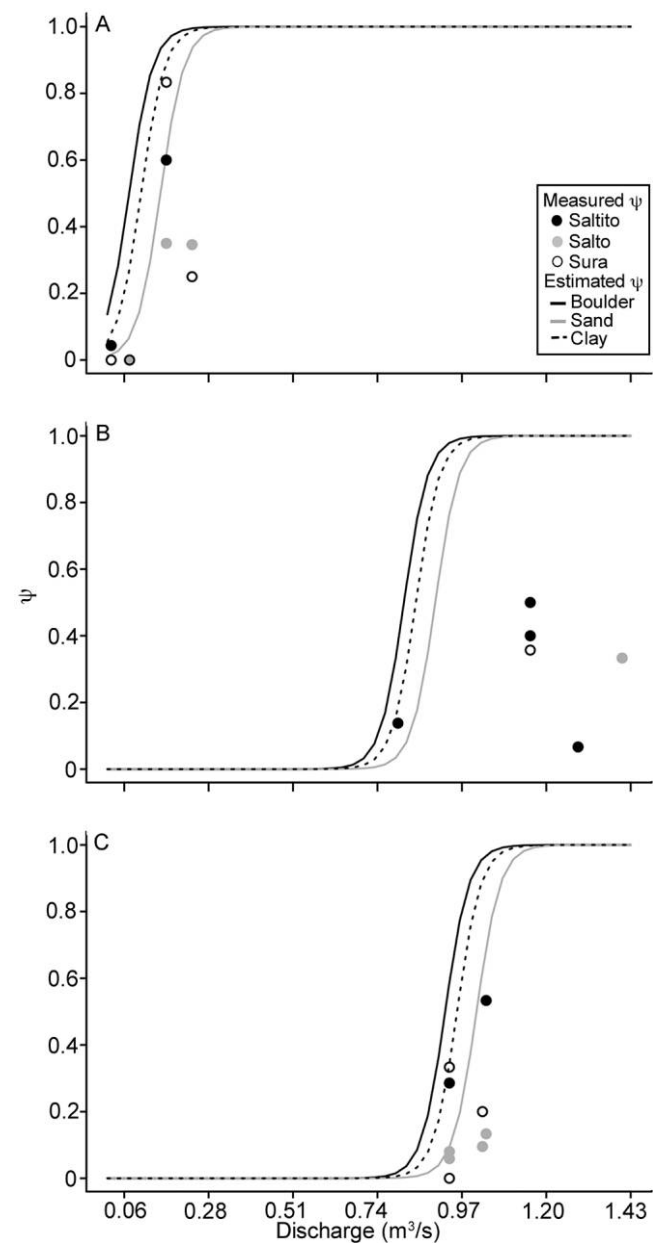


Figure 3. Simulated *Macrobrachium carcinus* occupancy rate (ψ) as a function of discharge across 3 substrate types in the Saltito (A), Salto (B), and Sura (C) rivers at La Selva Biological Station. Each symbol represents the measured ψ subset for a given substrate of a group of traps.

Table 5. Models in which Akaike Information Criterion for small samples (AIC_c) weights (w_i) > 0.10 for predicting occupancy (ψ) corrected for probability of detection (p) of *Macrobrachium olfersii* and model predictor variables for ψ when ψ was held constant ($\psi(.)$) and p was allowed to change based on covariates, values for AIC_c , change in AIC_c (ΔAIC_c), w_i , and number of parameters (k) in each model. Models were included in the confidence set of models if $\Delta AIC_c < 2$. $\psi(.)p(.)$ = null model in which both ψ and p were held constant.

Model	AIC_c	ΔAIC_c	w_i	k
$\psi(.)p(\text{discharge, substrate})$	824.94	0	0.99	5
$\psi(.)p(.)$	895.42	70.48	0	2

the range of observed levels of conductivity (Fig. 5A–C). ψ also increased with stream size (indexed by discharge) by $\sim 1.5\times$ over the range of discharge values. Stream identity mediated the influence of discharge and conductivity on ψ . In the Saltito River, ψ was as much as $1.5\times$ higher in smaller stream sites ($0.5 \text{ m}^3/\text{s}$) than in the Salto or Sura Rivers.

DISCUSSION

Our results suggest that *M. olfersii* distribution is affected by factors at landscape (conductivity) and local (discharge, substrate) scales, whereas *M. carcinus* and *M. heterochirus* are primarily influenced by local-scale factors when stream size, regional groundwater contribution, and substrate size in streams are used to predict shrimp distribution at LSBS. Multiple biological mechanisms may be responsible for the effects of landscape- (conductivity) and local-scale predictor variables (discharge and substrate) in occupancy models for these species (Table 1). For example, if food resources increase with increasing stream size (Vannote et al. 1980), then we would predict that ψ values also would increase. Shrimps were detected in 1st- through 3rd-order streams, but had much higher ψ values in 2nd- and 3rd-order streams overall. Moreover, species-specific effects are possible. All 3 species had higher ψ as stream size increased, but *M. olfersii* ψ was best predicted by discharge, conductivity, and stream identity, whereas *M. carcinus* ψ was best predicted by discharge, substrate, and stream identity.

Macrobrachium carcinus is the largest of the 3 shrimp species in our study and can reach 40-cm total length (TL), whereas *M. olfersii* averages only 14-cm TL. *Macrobrachium carcinus* might have higher ψ in areas with larger boulders because boulders provide higher prey availability and increased refuge from predators for this large species than do clay or cobbles (Table 1). In contrast, *M. olfersii* p was negatively influenced by the presence of larger substrates. Some physical process might decrease p for *M. olfersii* on large substrates, or *M. olfersii* might simply be less abundant in reaches with large sub-

strates. For example, *M. olfersii* could be less abundant in reaches with larger substrates because of a difference in available food resources. More research clearly is needed to understand the biological mechanisms underlying the influence of substrate on ψ and p .

For *M. heterochirus*, the low number of detections limited our logistic regression models to 1 covariate, which reduced our capacity to estimate a relationship between ψ and habitat variables. Our findings were surprising because the top model suggested discharge as the primary influence on *M. heterochirus* ψ . This prediction differs from the findings by Hunte (1978), who observed this species only in high-gradient, boulder-dominated streams in Jamaica. However, some model support existed ($\Delta AIC_c < 8$) for an influence of substrate on *M. heterochirus* ψ , and ψ was higher on primarily boulder substrate (13%) than the other types of substrate (3%).

We could not investigate the relationship between p , ψ , and abundance unambiguously because we did not estimate abundance at our sites. However, metapopulation models of local population dynamics and our personal observations suggest positive correlation between ψ and abundance (Lopez and Pfister 2001). For example, we observed higher maximum counts (3 ind/trap) of *M. carcinus* in larger stream reaches on boulder substrates than in small stream reaches on sand substrate (1 ind/trap). We suggest a positive correlation, but whether the relationship is linear or nonlinear is less obvious (Freckleton et al. 2006).

Our results suggest that larger streams receiving regional groundwater input are high-quality habitat patches for *M. olfersii*. ψ values were predicted to be as much as $3\times$ higher in larger streams with regional groundwater inputs than elsewhere. To the extent that higher ψ values reflect higher density (Bart and Klosiewski 1989, MacKenzie

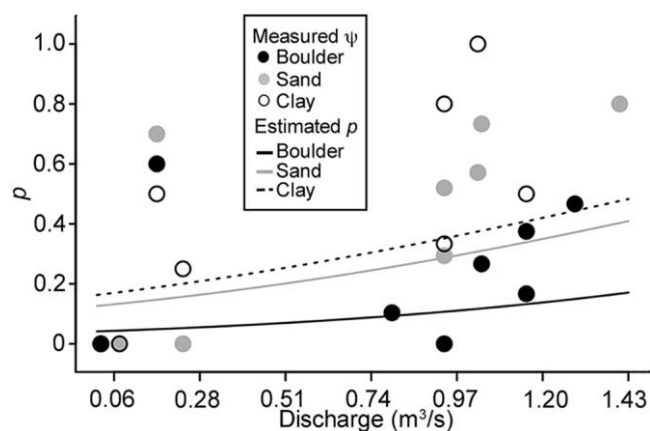


Figure 4. Simulated *Macrobrachium olfersii* probability of detection (p) as a function of discharge across 3 streams at La Selva Biological Station. Each symbol represents the measured occupancy rate (ψ) of a group of traps on boulder, sand, or clay.

Table 6. Models with Akaike Information Criterion for small samples (AIC_c) weights (w_i) > 0.10 for predicting occupancy (ψ) corrected for probability of detection (p) of *Macrobrachium olfersii* and model predictor variables for ψ when p and ψ were allowed to change based on covariates and values for AIC_c , change in AIC_c (ΔAIC_c), w_i , and number of parameters (k) in each model. Models were included in the confidence set of models if $\Delta AIC_c < 2$. $\psi(\cdot)p(\cdot)$ = null model in which both ψ and p were held constant.

Model	AIC_c	ΔAIC_c	w_i	k
$\psi(\text{conductivity, discharge})$ $p(\text{discharge, substrate})$	796.06	0	0.54	7
$\psi(\text{conductivity, discharge, stream})$ $p(\text{discharge, substrate})$	797.05	0.99	0.33	9
$\psi(\text{conductivity, discharge, substrate})$ $p(\text{discharge, substrate})$	799.28	3.22	0.11	9
$\psi(\cdot)p(\cdot)$	895.42	99.36	0.00	2

2005), our results suggest that these areas could be important for maintaining *M. olfersii* populations.

Several mechanisms could be responsible for the positive effects of regional groundwater on *M. olfersii* ψ . One is that higher-quality food resources support higher ψ values in these stream reaches. Shrimps are omnivores that consume periphyton, macroinvertebrates, detritus, and fish (Chace and Hobbs 1969). Other investigators at LSBS have shown that the basal resources (leaf litter, epilithon, and fine particulate organic matter) have up to 4× higher P in high-solute streams than in low-solute streams (Small and Pringle 2010). Moreover, insect macroinvertebrates using these higher-quality basal resources can have 2× higher elemental body P-content and higher growth rates than insects using lower-quality resources (Ramírez et al. 2006, Small and Pringle 2010). Other investigators have found that temporary increases in food resource quality positively influence consumer density and productivity in a variety of aquatic ecosystems (e.g., Slavik et al. 2004). The only research of which we are aware that relates solute levels and distribution of shrimps is that by Thorpe and Lloyd (1999), who found no relationship between shrimp density and solutes in streams that had been converted from forest to agriculture on the island of St Lucia.

High Ca levels in regional groundwater also may have a positive effect on *M. olfersii* and *M. carcinus* ψ values. Low-solute streams at LSBS have Ca levels (0.0–0.7 mg/L) below the recommended values (12–24 mg/L) used in aquaculture production of *Macrobrachium rosenbergii* (Pringle and Triska 1991, New 2002). High-solute streams at La Selva have higher Ca levels (3.0–19.0 mg/L) than low-solute streams, which suggests shrimp in high-solute streams could experience less Ca limitation than those in low-solute streams.

Streams at LSBS exhibit seasonal trends in pH, but high-solute streams are rich in HCO_3^- and exhibit more stable pH values than do low-solute streams (Small et al. 2012). Long-term averages of pH for solute-poor streams (5.33–5.77) are 1.5 pH units below values (6.2–7.4) that have negative effects on growth, molting frequency, and

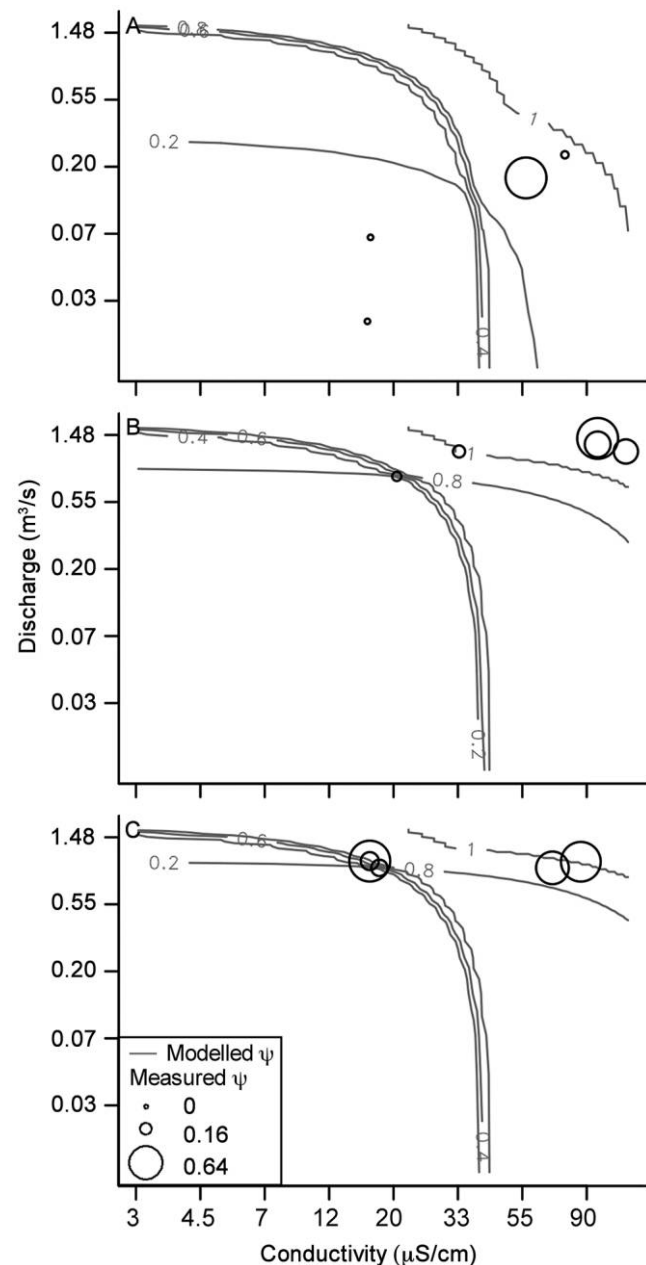


Figure 5. Simulated *Macrobrachium olfersii* occupancy rate (ψ) as a function of discharge and conductivity in the Saltito (A), Salto (B), and Sura (C) Rivers at La Selva Biological Station. ψ contours were estimated using the confidence set of models ranked by Akaike's Information Criterion (Table 6). The size of the symbols represents measured occupancy rates of a group of traps.

biomass accumulation of *M. rosenbergii* (Chen and Chen 2003). The mean long-term pH (6.03–6.34) in high-solute stream reaches is near the lower limit of acceptable pH values from aquaculture studies. Thus, higher *M. olfersii* ψ in stream reaches receiving regional ground water (with high solute levels) suggests these streams may protect shrimp against pH drops.

Estimates of ψ for these shrimp species provided insight into factors influencing their distribution. Regional groundwater input influenced *M. olfersii* distribution positively, whereas stream size and substrate were more important to distribution of *M. carcinus* and *M. heterochirus*. Our results illustrate factors influencing shrimp distribution in high-quality habitat patches in protected watersheds at LSBS, but information on factors affecting shrimp distribution in anthropogenically altered watersheds is lacking. Shrimp in high-quality streams in forested watersheds could serve as source populations for streams where land use change has affected the quality of habitat patches available to shrimps by altering sediment loads, hydrological regimes, and nutrient levels (Pringle and Scatena 1999, Baron et al. 2002). Our occupancy models could prioritize source areas beneficial for these wide-ranging migratory species before landscape changes fragment rivers and alter shrimp access to high-quality habitat patches. In New and Old World tropics, migratory shrimps play an important role in stream food webs and ecosystem function and are important conduits for movement of energy and matter between marine and freshwater systems (Pringle and Hamazaki 1998, Covich et al. 1999, Rosemond et al. 2001). Understanding factors that affect distribution patterns of migratory shrimp is a first step toward conservation of these species.

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LITERATURE CITED

Albanese, B., J. T. Peterson, B. J. Freeman, and D. A. Weiler. 2007. Accounting for incomplete detection when estimating site occupancy of Bluenose Shiner (*Pteronotropis welaka*) in southwest Georgia. *Southeastern Naturalist* 6:657–668.

Anderson, E. P., M. C. Freeman, and C. M. Pringle. 2006. Ecological consequences of hydropower development in Central America: impacts of small dams and water diversion on Neotropical stream fish assemblages. *River Research and Applications* 22:397–411.

Baron, J. S., N. L. Poff, P. L. Angermeier, C. M. Dahm, P. H. Gleick, N. G. Hairston, R. B. Jackson, C. A. Johnston, B. D. Richter, and A. D. Steinman. 2002. Meeting ecological and societal needs for freshwater. *Ecological Applications* 12: 1247–1260.

Bart, J., and S. P. Klosiewski. 1989. Use of presence–absence to measure changes in avian density. *Journal of Wildlife Management* 53:847–852.

Bauer, R. T., and J. Delahoussaye. 2008. Life history migrations of the amphidromous river shrimp *Macrobrachium ohione* from a continental large river system. *Journal of Crustacean Biology* 28:622–632.

Bowles, D. E., K. Aziz, and C. L. Knight. 2000. *Macrobrachium* (Decapoda: Caridea: Palaemonidae) in the contiguous United States: a review of the species and an assessment of threats to their survival. *Journal of Crustacean Biology* 20:158–171.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Castillo, L. E., E. de la Cruz, and C. Ruepert. 1997. Ecotoxicology and pesticides in tropical aquatic ecosystems of Central America. *Environmental Toxicology and Chemistry* 16:41–51.

Chace, F. A., and H. H. Hobbs. 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. Smithsonian Institution Press, Washington, DC.

Chen, S. M., and J. C. Chen. 2003. Effects of pH on survival, growth, molting and feeding of giant freshwater prawn *Macrobrachium rosenbergii*. *Aquaculture* 218:613–623.

Covich, A. P., T. A. Crowl, S. L. Johnson, and M. Pyron. 1996. Distribution and abundance of tropical freshwater shrimp along a stream corridor: response to disturbance. *Biotropica* 28:484–492.

Covich, A. P., M. A. Palmer, and T. A. Crowl. 1999. The role of benthic invertebrate species in freshwater ecosystems: zoobenthic species influence energy flows and nutrient cycling. *BioScience* 49:119–127.

Crowl, T. A., W. H. McDowell, A. P. Covich, and S. L. Johnson. 2001. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. *Ecology* 82:775–783.

Dudgeon, D. 2000. Large-scale hydrological changes in tropical Asia: prospects for riverine biodiversity. *BioScience* 50:793–806.

Falke, J. A., K. D. Fausch, K. R. Bestgen, and L. L. Bailey. 2010. Spawning phenology and habitat use in a Great Plains, USA, stream fish assemblage: an occupancy estimation approach. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1942–1956.

Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:1–23.

Freckleton, R. P., D. Noble, and T. J. Webb. 2006. Distributions of habitat suitability and the abundance-occupancy relationship. *American Naturalist* 167:260–275.

Genereux, D., and C. M. Pringle. 1997. Chemical mixing model of streamflow generation at La Selva Biological Station, Costa Rica. *Journal of Hydrology* 199:319–330.

Holmquist, J. G., J. M. Schmidt-Gengenbach, and B. B. Yoshioka. 1998. High dams and marine-freshwater linkages: effects on

- native and introduced fauna in the Caribbean. *Conservation Biology* 12:621–630.
- Hunte, W. 1978. The distribution of freshwater shrimps (Atyidae and Palaemonidae) in Jamaica. *Zoological Journal of the Linnean Society* 64:135–150.
- Kroll, A. J., T. L. Fleming, and L. L. Irwin. 2010. Site occupancy dynamics of northern spotted owls in the Eastern Cascades, Washington, USA, 1990–2003. *Journal of Wildlife Management* 74:1264–1274.
- Lopez, J. E., and C. A. Pfister. 2001. Local population dynamics in metapopulation models: implications for conservation. *Conservation Biology* 15:1700–1709.
- MacKenzie, D. I. 2005. What are the issues with presence–absence data for wildlife managers? *Journal of Wildlife Management* 69:849–860.
- MacKenzie, D. I., and L. Bailey. 2004. Assessing fit of site occupancy models. *Journal of Agricultural and Ecological Statistics* 9:300–318.
- MacKenzie, D. I., J. D. Nichols, B. L. Gideon, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. Hines. 2006. *Occupancy estimation and modeling*. Academic Press, New York.
- McDowall, R. M. 2007. On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish and Fisheries* 8:1–13.
- McDowall, R. M. 2009. Early hatch: a strategy for safe downstream larval transport in amphidromous gobies. *Reviews in Fish Biology and Fisheries* 19:1–8.
- New, M. B. 2002. *Farming freshwater prawns: a manual for the culture of the giant prawn (Macrobrachium rosenbergii)*. Food and Agricultural Organization of the United Nations, Rome, Italy.
- Obregon, F. C. 1986. *Revision de conocimiento de los camarones de agua dulce de Costa Rica*. MS Thesis, Universidad de Costa Rica, San José, Costa Rica.
- Pringle, C. M. 1991. Geothermally modified waters surface at La Selva Biological Station, Costa Rica: volcanic processes introduce chemical discontinuities into lowland tropical streams. *Biotropica* 23:523–529.
- Pringle, C. M., G. A. Blake, A. P. Covich, K. M. Buzby, and A. Finley. 1993. Effects of omnivorous shrimp in a montane tropical stream: sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. *Oecologia (Berlin)* 93:1–11.
- Pringle, C. M., and T. Hamazaki. 1998. The role of omnivory in a Neotropical stream: separating diurnal and nocturnal effects. *Ecology* 79:269–280.
- Pringle, C. M., and F. N. Scatena. 1999. Aquatic ecosystem deterioration in Latin America and the Caribbean. Pages 104–113 in L. U. Hatch and M. E. Swisher (editors). *Managed ecosystems: the Mesoamerican experience*. Oxford University Press, New York.
- Pringle, C. M., and F. J. Triska. 1991. Effects of geothermal groundwater on nutrient dynamics of a lowland Costa Rican stream. *Ecology* 72:951–965.
- Ramírez, A., and C. M. Pringle. 2004. Do macroconsumers affect insect responses to a natural stream phosphorus gradient? *Hydrobiologia* 515:235–246.
- Ramírez, A., and C. M. Pringle. 2006. Fast growth and turnover of chironomid assemblages in response to stream phosphorus levels in a tropical lowland landscape. *Limnology and Oceanography* 51:189–196.
- Ramírez, A., C. M. Pringle, and M. Douglas. 2006. Temporal and spatial patterns in stream physicochemistry and insect assemblages in tropical lowland streams. *Journal of the North American Benthological Society* 25:108–125.
- Rosemond, A. D., C. M. Pringle, A. Ramírez, and M. J. Paul. 2001. A test of top-down and bottom-up control in a detritus-based food web. *Ecology* 82:2279–2293.
- Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence–absence data or point counts. *Ecology* 84:777–790.
- Sanford, R. L., P. Paaby, J. C. Luvall, and E. Phillips. 1994. Climate, geomorphology, and aquatic systems. Pages 19–33 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (editors). *La Selva: ecology and natural history of a neotropical rainforest*. University of Chicago Press, Chicago, Illinois.
- Slavik, K., B. J. Peterson, L. A. Deegan, W. B. Bowden, A. E. Hershey, and J. E. Hobbie. 2004. Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. *Ecology* 85:939–954.
- Small, G. E., M. Ardon, A. P. Jackman, J. H. Duff, F. Triska, A. Ramírez, M. N. Snyder, and C. M. Pringle. 2012. Climate-driven amplification of seasonal acidification in poorly buffered tropical streams. *Ecosystems* 15:974–985.
- Small, G. E., and C. M. Pringle. 2010. Deviation from strict homeostasis across multiple trophic levels in an invertebrate consumer assemblage exposed to high chronic phosphorus enrichment in a Neotropical stream. *Oecologia (Berlin)* 162: 581–590.
- Thorpe, T., and B. Lloyd. 1999. The macroinvertebrate fauna of St. Lucia elucidated by canonical correspondence analysis. *Hydrobiologia* 400:195–203.
- Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parriss, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications* 13:1790–1801.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130–137.
- Wald, A., and J. Wolfowitz. 1943. An exact test for randomness in the non-parametric case based on serial correlation. *Annals of Mathematical Statistics* 14:378–388.
- Walker, I., and M. J. N. Ferreira. 1985. On the population dynamics and ecology of the shrimp species (Crustacea, Decapoda, Natantia) in the Central Amazonian river Tarumã-Mirim. *Oecologia (Berlin)* 66:264–270.
- Wilson, C. D., and D. Roberts. 2011. Modelling distributional trends to inform conservation strategies for an endangered species. *Diversity and Distributions* 17:182–189.

APPENDIX

Reach-scale mean discharge, conductivity, and number of traps sites/reach on 3 rivers at La Selva Biological Station. Values in *Macrobrachium carcinus*, *Macrobrachium heterochirus*, and *Macrobrachium olfersii* columns are the number of sites in a stream reach with ≥ 1 observation.

River	Discharge (m ³ /s)	Conductivity (μS/cm)	<i>Macrobrachium carcinus</i>	<i>Macrobrachium heterochirus</i>	<i>Macrobrachium olfersii</i>	Trap sites
Saltito	0.24	76	10	0	1	30
Saltito	0.02	16.4	1	0	0	29
Saltito	0.07	16.8	0	0	0	30
Saltito	0.17	56.2	15	0	20	31
Salto	1.16	33.4	12	10	5	30
Salto	1.16	122	13	5	13	30
Salto	0.8	20.6	4	0	3	29
Salto	1.41	98	5	0	12	15
Salto	1.29	98	1	6	7	15
Sura	0.94	69	2	0	17	30
Sura	1.04	16.7	8	0	4	15
Sura	1.04	16.7	2	0	11	15
Sura	1.03	86	4	0	22	31
Sura	0.94	18	5	0	7	30