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BIODIVERSITY RESEARCH

Current land use is a poor predictor of hellbender occurrence: why assumptions matter when predicting distributions of data-deficient species

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ABSTRACT

Aim Understanding species distributions is fundamental to effective conservation planning. Data deficiency is common among rare and imperiled species and poses challenges for conservation planning because status assessments become reliant on scant data that can introduce bias. We used occupancy modelling to evaluate support for commonly accepted, but previously untested, hypotheses regarding factors that drive the occurrence of an imperiled and data-deficient amphibian, the eastern hellbender (*Cryptobranchus alleganiensis*). We investigated the potential for mismatch between areas likely to be identified as having high conservation priority based on the common assumption that hellbender occurrence corresponds to areas of high forest cover and those identified by well-informed models.

Location South-west Virginia, USA.

Methods We conducted triplicate surveys to detect *C. alleganiensis* in 49 stream reaches stratified across a land use gradient and two major drainages. We used a Bayesian multimodel framework to investigate factors associated with *C. alleganiensis* occupancy. We used the best-performing models to predict probability of occupancy at the scale of a 50-m stream reach throughout our study area and identify areas most likely to be occupied.

Results Occurrence of *C. alleganiensis* was explained primarily by differences in underlying geology and topography (i.e. physiography) and negative effects of agriculture were only modestly supported. Best-performing models suggested ~ 35% of our study area was occupied. Our findings suggest that predictions from models informed by presence-only data and current land use would likely underestimate *C. alleganiensis* occupancy by as much as one-third and incorrectly classify over half the currently occupied area to be of little importance to the species.

Main conclusion Our study highlights the potential danger of assuming that the distribution of data-deficient species can be approximated using untested, but commonly accepted, species–habitat associations.

Keywords

Bayesian occupancy, *Cryptobranchus alleganiensis*, distribution modelling, hellbender, land use, physiography.

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INTRODUCTION

Reliable knowledge regarding species distributions is fundamental to effective conservation planning. Biodiversity is declining at an unprecedented rate and at a global scale (Hoffmann *et al.*, 2010; IUCN, 2014). Freshwater ecosystems, in particular, are biodiversity hotspots and face losses and threats exceeding those in many terrestrial systems (Sala *et al.*, 2000; Revenga *et al.*, 2005; Strayer & Dudgeon, 2010). A major challenge to conserving freshwater biodiversity is the dearth of knowledge regarding distributions of individual species, which directly limits our ability to reliably identify areas of high conservation priority (e.g. that contain high levels of biodiversity or endemic and imperiled species). The lack of distributional information for species can often be attributed to financial and logistical constraints associated with monitoring rare species that are difficult to detect (Thompson, 2004). As a result, anecdotal accounts, presence-only (as opposed to presence–absence) data, data collected from surrogate species and expert opinion often represent the best available information available to estimate species distributions (e.g. Abell, 2002; Linke *et al.*, 2011) or assess risk (Mace *et al.*, 2007). The class of models (hereafter presence-only models) capable of predicting species distributions from sparse data and readily available spatial environmental data have grown in popularity in recent years, but have been criticized for their potential to both underestimate and overestimate distributions (Hermoso *et al.*, 2015). Underestimates of distribution can result from geographically biased and insufficient survey efforts that often plague sparse data sets (Yackulic *et al.*, 2013). Overestimates of distributions might result due to biases in opinion about environmental variables that are important for species (Donlan *et al.*, 2010) or due to failure to recognize the importance of hierarchical filters (e.g. physiological tolerance, dispersal ability, biotic interactions; Angermeier *et al.*, 2002) that drive biologically relevant discontinuity in species distributions (Hermoso *et al.*, 2015). This is important because species distribution models may be used to inform conservation planning either by identifying critical habitat or assessing species' status, and unreliable predictions can lead to under- or overestimation of a species' extant range and extinction risk (Linke *et al.*, 2011). Therefore, while it may be challenging to test assumptions regarding the occurrence and habitat requirements of imperiled species, doing so has the potential to improve accuracy of status assessments and the effectiveness of conservation strategies (Hermoso *et al.*, 2015).

We used an imperiled and data-deficient amphibian, the eastern hellbender (*Cryptobranchus* alleganiensis, Daudin), to investigate the potential for well-accepted, but untested, species–habitat relationships to introduce bias into predicted distributions for data-deficient species. Hellbenders are stream-dwelling salamanders that make an excellent model for our study, as they are cryptic and difficult to monitor, and their current distribution is poorly understood. Among experts, heavily forested landscapes are considered to be an indicator of suitable hellbender habitat, while sedimentation and water quality alteration associated with intensive land use are commonly suggested as a leading driver of recent precipitous declines (Williams *et al.*, 1981; Wheeler *et al.*, 2003; Briggler *et al.*, 2007; Foster *et al.*, 2009). However, quantitative evidence for land use effects on hellbenders is generally lacking (but see Quinn *et al.*, 2013). Our first objective was to investigate factors associated with hellbender occurrence and explicitly evaluate support for the hypothesis that occurrence at the scale of a 50-m stream reach is negatively influenced by fine sediment within streams and surrounding human land use. Our second objective was to develop a predictive model of hellbender occurrence to investigate how model-based predictions of occurrence might differ from predictions based on well-accepted, but untested, species–habitat relationships.

METHODS

Study species

Hellbenders are large (up to 74 cm total length), fully aquatic, long-lived (25+ years; Taber *et al.*, 1975) benthic stream specialists native to much of the eastern U.S. (Fig. 1). All life stages are highly cryptic and typically remain hidden beneath rocky cover (Nickerson *et al.*, 2003; Bodinof *et al.*, 2012a,b). Given their fully aquatic life history, longevity, highly permeable skin and reliance on cool and well-oxygenated water (Guimond & Hutchison, 1973), hellbenders are often considered an indicator of long-term in-stream habitat quality. Hellbender populations have declined precipitously across the species historic range (Wheeler *et al.*, 2003; Foster *et al.*, 2009; Burgmeier *et al.*, 2011; Graham *et al.*, 2011; USFWS, 2011). Hellbenders are typically associated with cool, swift-flowing streams surrounded by forested landscapes and substrate and water quality alterations associated with deforestation are considered to be primary drivers of declines (Smith, 1907; Nickerson & Mays, 1973; Williams *et al.*, 1981; Wheeler *et al.*, 2003; Briggler *et al.*, 2007). A major challenge for conservation planning is a poor understanding of hellbender status, namely the dearth of information regarding the species distribution. However, studies designed to minimize bias in sampling locations, account for imperfect detection and explicitly test hypotheses of land use effects on the species are lacking.

Study area

Our study took place within the New River and South Fork Holston River drainages in south-western Virginia (Fig. 1). Together, these drainages mark the eastern extent of the hellbender's range in Virginia and a largely unstudied portion of the species' total range (but see Hopkins & DuRant, 2011; Hopkins *et al.*, 2011, 2014, 2016; DuRant *et al.*, 2015). Both drainages overlap portions of the Blue Ridge and Ridge and Valley physiographic provinces of the greater Appalachian

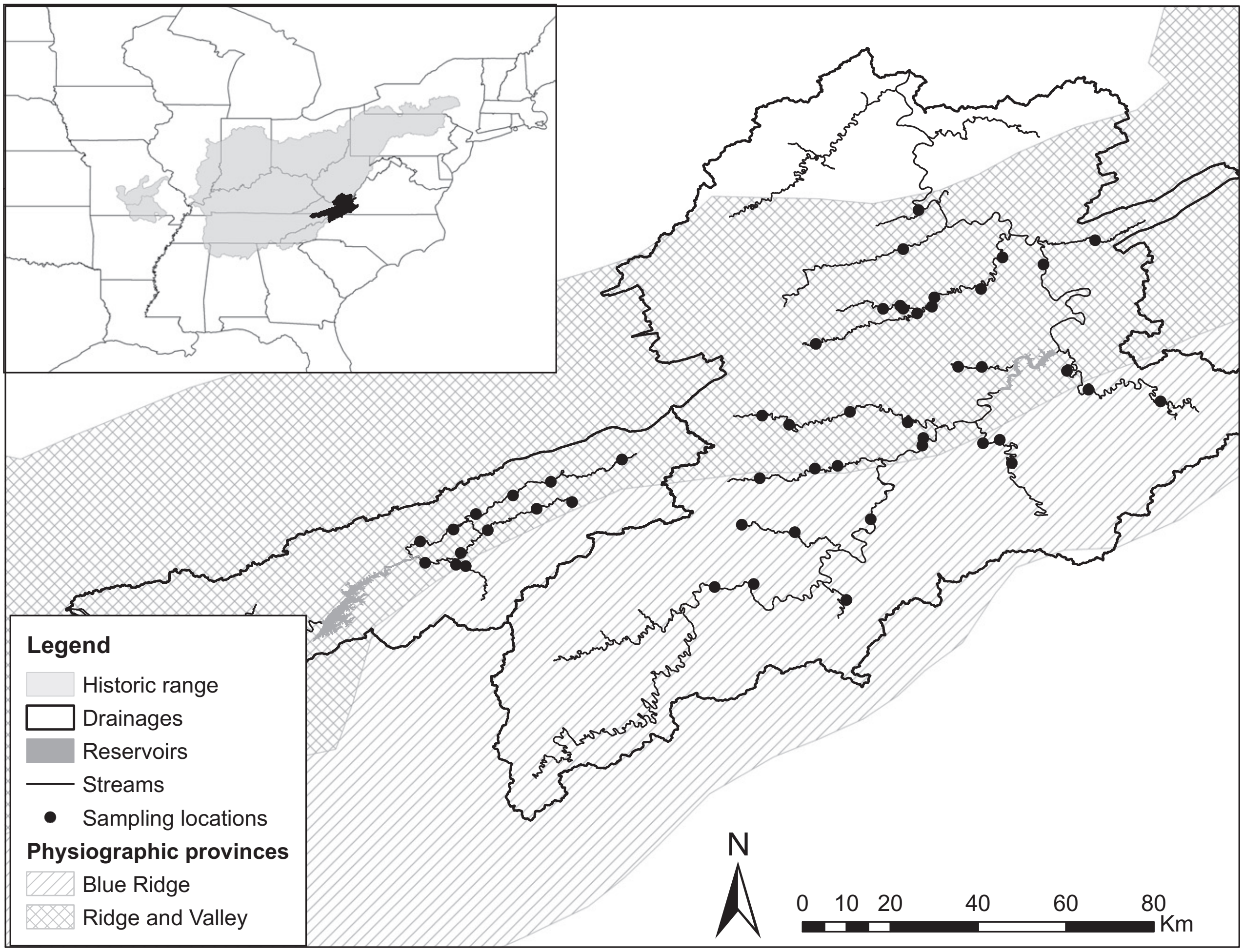

Figure 1 Location of *Cryptobranchus alleganiensis* sampling reaches in south-west Virginia, USA.

Highlands (Fenneman, 1928; Fig. 1). Physiographic provinces are delineated by specific differences in geology and topography and are important determinants of fish communities in Virginia (Angermeier & Winston, 1999). Anecdotal reports indicate hellbenders historically occupied both drainages and both provinces (Mayasich *et al.*, 2003). The Ridge and Valley is characterized by a series of steep ridges paralleled by narrow valleys, bordered on the west by the Appalachian Plateau and on the east by the Blue Ridge. Maximum elevations reach 1400 m and geology consists primarily of sedimentary rock, with uplands composed largely of sandstones and shales and lowlands composed heavily of limestone. The Blue Ridge consists of relatively steep topography bordered by the Ridge and Valley to the west and by the Piedmont to the east. In south-west Virginia, the Blue Ridge widens and forms a broad plateau-like upland hosting the highest elevation (1749 m) in the state and a divide for waters draining to the Atlantic and Gulf of Mexico. In contrast to the Ridge and Valley, geology in the Blue Ridge is relatively impervious, composed primarily of metamorphic and igneous rock, including granites, schist and gneiss, with limestones and shales more common on western slopes. Relative to the Ridge and Valley, Blue Ridge slopes are steep and soils are thin (Nelms *et al.*, 1997).

Sampling design

To investigate effects of land use on hellbender occurrence, we used a spatially balanced random stratified design (Stevens & Olsen, 2004) to select a sample of 49 stream reaches for our study. We considered a sampling pool of all fourth-order or larger stream segments delineated within the National Hydrography Dataset (NHD) Plus version 2.1 (1:100,000 scale; USGS & USEPA, 2012). To ensure our sample represented the full range of land use in our study area, we quantified the percentage of forest (USGS, 2011) in upstream catchments delineated for each of 661 segments in our sampling pool and stratified our sample across bins representing a human activity gradient (Yates & Bailey, 2010) ranging from 50 to 94% forest. While the range of land use in our study area was somewhat narrow, it largely overlaps the range of forested land use among stream reaches in Missouri where hellbenders have declined by an average of 77% (Wheeler *et al.*, 2003; % forest = 46–64% [Big Piney R.];

28–57% [Gasconade R.]; 70–71% [Niangua R.]; 63–64% [North Fork White R.]; 70–79% [Eleven Point R.]). We used a generalized random tessellation stratified (GRTS) approach to reduce spatial autocorrelation among our sample reaches while still employing a true probability design, using the package ‘spsurvey’ (Kincaid & Olsen, 2013) in Program R (Team, 2013). Our final sample of 49 segments represented 16 streams (n = 1–6 segments per stream). For the purposes of our study, we investigated occupancy at the scale of a 50-m stream reach (widths were variable; Table 1). We selected the first 50 m reach that contained at least two boulders (Wentworth, 1922) or at least one irregular bedrock ledge during our first visit to each of the 49 pre-selected stream segments. Hellbenders are highly dependent on rocky cover

Table 1 Summary of covariates considered in modelling detection and occupancy of *Cryptobranchus alleganiensis* in Virginia, USA, 2013–2014.

Covariate	Description	Data source	Median (range)	Predicted effect
Fixed effect covariates				
visibility	Lateral secchi distance (m) while snorkelling; measured prior to each survey	Field measurement	1.6 (0.4–6.0)	+
size	Extent (m^2) of the sampling reach	Wetted width × 50	1450 (400–9400)	±
fine	Proportion of gravel, sand and silt particles (*b*-axis $\leq$ 1.6 cm)	Pebble count	0.34 (0.15–0.83)	–
boulder	Proportion of boulders (*b*-axis > 25 cm)	Pebble count	0.08 (0.01–0.28)	+
riffle	Proportion of 100 stratified sampling locations that occurred in riffles	Field measurement	0.30 (0.00–0.88)	+
pool	Proportion of 100 stratified sampling locations that occurred in pools	Field measurement	0.16 (0.01–1.00)	–
elev	Elevation (m) of the sampling reach	NED (USGS, 1999)	593 (464–797)	+
contr. area	Extent (km^2) of contributing area for the sampling reach	NHDPlus V2	409 (49–7631)	+
physiography	Proportion of the upstream catchment within the Blue Ridge physiographic province	Fenneman & Johnson (1946)	0.60 (0.00–1.00)	±
Catchment land use				
ag.c	Proportion of land use characterized as pasture, cultivated crop, and grassland within the upstream catchment	NLCD 2011	0.29 (0.09–0.41)	–
dev.c	Proportion of land use characterized as medium and high-intensity development within the upstream catchment	NLCD 2011	0.00 (0.00–0.02)	–
Catchment-riparian land use				
ag.cr	Proportion of land characterized as pasture, cultivated crop and grassland within a 50-m buffer on both sides of all delineated streams within the upstream catchment	NHDPlus V2, NLCD 2011	0.30 (0.11–0.47)	–
dev.cr	Proportion of land characterized as medium and high-intensity development within a 50-m buffer on both sides of all delineated streams within the upstream catchment	NHDPlus V2, NLCD 2011	0.00 (0.00–0.02)	–
Immediate-riparian land use				
ag.ir	Proportion of land use characterized as pasture, cultivated crop and grassland within a 50-m buffer on both sides of the sample reach and extending upstream for 300 m	NLCD 2011	0.25 (0.00–0.91)	–
dev.ir	Proportion of land use characterized medium and high-intensity development within a 50-m buffer on both sides of the sample reach and extending upstream for 300 m	NLCD 2011	0.00 (0.00–0.42)	–
Random effect covariates				
RIVER	Random effect variable with 16 levels representing the river in which the sample reach was located			

NED, National Elevation Dataset; NHD, National Hydrography Dataset; NLCD, National Land Cover Dataset.

and are rarely encountered far from shelter (Bodinof *et al.*, 2012b). Thus, our prerequisite for the occurrence of rocky substrate in each reach was intended to avoid sampling habitats that were unavailable to hellbenders, while allowing for high variability in habitat quality among reaches.

We surveyed each reach on three occasions using snorkelling while turning rocks (Nickerson & Krysko, 2003) in 2013 (n = 37 sites) or 2014 (n = 12 sites). On each occasion, we ceased surveys once a hellbender was detected, to limit habitat disturbance. If no hellbender was detected, we ceased efforts once the entire reach had been searched. For detailed survey methodology, see Appendix S1 in Supporting Information.

Predictors

We quantified all in-stream predictors (Table 1) from data collected during our initial visit to each sampling reach and prior to conducting hellbender surveys. To calculate reach size (Table 1), we used a measure of wetted width collected at a point visually estimated to represent average width of the sample reach, using a Nikon Prostaff© laser rangefinder. We quantified meso-habitat (pool, riffle, run) and substrate characteristics from data collected in a modified Wolman (1954) pebble count with 100 observations in each reach.

We quantified landscape-scale predictors (Table 1) from remotely sensed data in ArcMap v.10.1 (ESRI, Redlands, CA, USA). First, we delineated catchments for each sampling reach and used catchments to quantify contributing area (km^2) as a proxy of stream size as per Wenger *et al.* (2008). We quantified the proportion of each catchment that fell within the Blue Ridge and Ridge and Valley physiographic province and quantified land use at three spatial scales (Table 1). We quantified land use at the catchment, catchment-riparian and immediate-riparian spatial scales (defined in Table 1). We used non-forested land use categories (hereafter agriculture and developed), as predictors in our analysis. We pooled crop and grassland categories from the national land cover data set (NLCD; USGS, 2014) to represent agricultural land use, and pooled medium (50–79% impervious surface, typically single family residence) and high-intensity development (80–100% impervious surfaces, typically residential, commercial and industrial) NLCD categories to represent developed land use (Table 1).

Model development

We used single season occupancy models to investigate factors associated with hellbender occurrence and detection while snorkelling. Briefly, occupancy models are hierarchical state-space models that are used to estimate species occurrence while accounting for imperfect detection. Occupancy is defined as the probability that the target species occurs within some area of interest (MacKenzie *et al.*, 2006). Failure to account for imperfect detection (i.e. probability of detecting a species during a single survey is < 1) can lead to negatively biased estimates of occupancy (MacKenzie *et al.*, 2006). Sampling approaches for occupancy modelling are varied (MacKenzie & Royle, 2005; Bailey *et al.*, 2007), but generally entail repeat surveys of sampling units, where the target species is either detected or not during each survey. Models allow for inclusion of predictor covariates and thus the potential to examine support for hypotheses concerning the effect of extrinsic factors on species occurrence or detection (MacKenzie *et al.*, 2002).

We used a multimodel framework, where we investigated relative support for multiple hypotheses concerning factors associated with hellbender occurrence. We considered fixed effects of 15 continuous variables in our analyses (Table 1). We hypothesized positive effects of visibility and either a positive (i.e. as a function of area surveyed) or negative (i.e. due to deep (> 2 m) water) influence of contributing area on detection. We also considered an interaction between contributing area and visibility, where we predicted increased importance of visibility in large rivers, where deep water was more common. We hypothesized negative effects of agriculture and developed land use on detection as a result of decreased local abundance due to altered water quality and increased sedimentation.

We hypothesized effects of physiography on hellbender occurrence, given that physiography corresponds to distinct differences in underlying geology and topography that has been associated with distributions of freshwater fish in the same region (Angermeier & Winston, 1999). We hypothesized positive effects of elevation, canopy cover, boulder substrate, and of riffle over pool, and negative effect of fine substrates and non-forest land use at all scales based on habitat associations reported for hellbenders (Nickerson & Mays, 1973; Humphries & Pauley, 2005; Quinn *et al.*, 2013). We hypothesized a positive effect of contributing area, given that sample reach extent (m^2) increased with contributing area as a function of increasing wetted width. Finally, we considered an interaction between physiography and land use, to represent our hypothesis that susceptibility of reaches to land use effects would vary depending on underlying geology and topography associated with physiographic province.

In addition to fixed effects, we considered random effects of the river where reaches occurred in both detection and occupancy models. While we designed our study to maximize independence between sample reaches, we recognized that stream networks are innately hierarchical in structure. As a result, we considered it likely that reaches within a stream may be more similar to each other than to reaches in other streams. Failure to account for such dependencies can lead to biased estimates in the response of interest and an increase in type I errors (Latimer *et al.*, 2006; Dormann *et al.*, 2007). Therefore, we wanted to investigate the possibility that nesting of reaches within streams may have introduced a problematic level of spatial autocorrelation into our data. On the contrary, we wanted to avoid overfitting models if inclusion of random effects was not warranted, as doing so would be likely to reduce our power to detect effects from covariates of interest. To address our concerns, we fit candidate models both with and without a random effect term for river, in both steps of our analysis. We used model rank along with examination of fitted slope coefficients to determine whether river was an important source of variation in our study. To aid model convergence and interpretation of fixed effects, we standardized $\left(\frac{x-\bar{x}}{sd(x)}\right)$ all continuous covariates other than proportions and multiplied developed land use proportions (due to very small values) by 10 prior to analysis. We screened predictor variables based on Pearson's correlation coefficients to avoid problems associated with coefficient estimation when predictors were collinear. We selectively discarded one of each pair of correlated predictors ($r \geq 0.7$ or ≤ -0.7). Catchment and catchment-riparian land use were strongly correlated (agriculture: $r = 0.87$, $P < 0.001$; developed: $r = 0.84$, $P < 0.001$, df = 47), as were contributing area and size of the sample reach ($r = 0.86$, $P < 0.001$, df = 47). We retained catchment land use over catchment-riparian land use, and contributing area over size of the sample reach based on fit statistics from models that included only one of the pairs at a time.

Given our small sample size relative to the number of covariates considered, we wanted to avoid spurious results due to fitting an overly large set of candidate models (Anderson & Burnham, 2002). To maximize parsimony, we used a two-step approach (MacKenzie *et al.*, 2006), where we examined support for covariates hypothesized to influence detection while holding occupancy constant in step one. In step two, we modelled detection as a function of all covariates that occurred in models that outranked our null model in step one, while examining support for covariates hypothesized to influence occupancy.

Model fitting and selection

We used a Bayesian approach to fit and rank candidate models. Unlike maximum likelihood, Markov Chain Monte Carlo (MCMC) approaches to model fitting can accommodate random effects within hierarchical models (Royle & Dorazio, 2008). We fit all models in OpenBUGS v3.2.3 [originally written as WinBUGS (Lunn *et al.*, 2000)] using the package 'R2OpenBUGS' [originally written as R2WinBUGS (Sturtz *et al.*, 2005)] in program R (Team, 2013). In our model specification, we employed non-informative priors to the extent possible. We specified uniform distributions between -10 and 10 on the logit scale for intercepts. When we specified uniform distributions (e.g. between -10 and 10) for coefficients, posterior distributions for some coefficients appeared 'cut-off' at either the upper or lower end. As a result, we specified diffuse independent normal prior distributions for coefficients that were centred at zero with precision of 1×10^{-2}, after determining that mean estimates and precision were generally insensitive to our choice of prior. We specified priors for the standard deviation of random effects as a uniform distribution between zero and 15. We obtained posterior distributions from every 25th iteration from three independent Markov chains, where each chain contained 20,000 iterations and the initial 2000 iterations were discarded as burn-in. We visually inspected MCMC chains to ensure proper mixing and used the Brooks–Gelman–Rubin diagnostic as a criterion to ensure convergence, where we assumed convergence was reached when R-hat of all parameters reached 1.0 (Gelman & Rubin, 1992). We ranked models using the Wantanabe–Akaike information criterion (WAIC; Wantanabe, 2010) where we calculated WAIC as defined by Vehtari & Gelman (2014). Similar to other model ranking criteria, WAIC represents a measure of model fit corrected by a penalty for model complexity. Unlike other criteria (e.g., Deviance information criteria (DIC); Spiegelhalter, 2002), WAIC assesses fit based on full posterior predictive distributions rather than point estimates and is thus recognized as the only fully Bayesian model ranking criterion (Hooten & Hobbs, 2015). Furthermore, unlike DIC, WAIC is considered valid in hierarchical and mixture models because of the manner in which the penalty term (i.e. number of effective parameters) is estimated for each model (see Hooten & Hobbs, 2015; Vehtari & Gelman, 2014). Currently, methods for handling model selection uncertainty in Bayesian analyses remains unclear, but model averaging approaches are not considered appropriate (Hooten & Hobbs, 2015). We considered models that outranked a null model (hereafter, top-ranked models) as being well enough supported to warrant further consideration. Prior to drawing inference, we subjected each top-ranked model to validation procedures to ensure each was useful.

Model validation

We used k-fold cross-validation (Boyce *et al.*, 2002) and area under the receiver-operating curve (ROC; Metz, 1978) to evaluate model performance. First, we randomly partitioned our original data five times according to Huberty's (1994) rule of thumb, each time excluding 33% of the data for testing. We refit models with each draw of training data and used newly fitted models to predict the parameter of interest (detection or occupancy) for each case in their complementary test data. For validation, we assumed that apparent occupancy after three surveys represented the true state of a reach. We pooled test results for each model to estimate area under the ROC curve using the package 'ROCR' (Sing *et al.*, 2005) in program R (Team, 2013). Briefly, the ROC curve is a plot of sensitivity (probability of correctly classifying a true positive) against specificity (probability of correctly classifying a true negative) across a range of cut-offs between zero and one (Metz, 1978). The area under the curve (AUC) is cut-off independent and defined as the probability that a model will score a randomly drawn positive sample higher than a randomly drawn negative sample. Values of AUC equal to 0.5 indicate a complete lack of predictive power (i.e. random), with values of 1.0 indicating perfect predictive performance (Cumming, 2000). We report posterior mean coefficients and model derived estimates of detection and occupancy along with their 95% credible intervals for our top-performing models based on AUC scores.

RESULTS

We detected hellbenders in both major drainages (New = 7 of 36 reaches; South Fork Holston = 6 of 13 reaches), in eight of 16 rivers, and in 26% of all reaches surveyed. We detected hellbenders during all three surveys in six reaches, during only two surveys in two reaches and during only one survey in five reaches. Most (26 of 27) individuals were sexually mature adults and there was no association between total length (proxy of age) and land use. However, our sample sizes were small ($n = \leq 3$ hellbenders per reach).

Detection

We pooled terms from three detection models that outranked the null model in step one (Table 2) to define the detection model in step two. Posterior distributions for fixed effect detection coefficients and AUC estimates for all models in step two were similar and indicated excellent performance of our detection model (AUC = 0.97; Table 2). Predictions from the model supported our hypothesis that the threshold of visibility necessary to detect hellbenders depended largely on size of the river being surveyed (Table 2). Our model predicted that under average visibility (1.75 m) detection declined exponentially as river size increased (Fig. 2a). Once visibility exceeded about 3 m, detection was predicted to remain extremely high even in large rivers, although uncertainty regarding the effects of visibility was considerable (e.g. Table 3, Fig. 2b). Notably, the river size effect appeared to be driven by a single river (main stem New R.) that contained all of the surveyed reaches with contributing areas > 800 km^2. In contrast to our predictions, the model suggested detection was positively associated with the proportion of the immediate-riparian area classified as agriculture, although uncertainty regarding effects of land use was also considerable (Table 3, Fig. 2c). Although the final model included developed land in the immediate-riparian area as a covariate of detection, the predicted effect of developed land was negligible (Table 3).

Occupancy

Six models met our criteria for further consideration based on model ranking. These included a physiography only model, a physiography × catchment land use model, and the duplicates of both models that included the random effect term for river, all of which performed similarly well (AUC = 0.83–0.86; Table 2). Additionally, two models that included local variables with and without the random effect term for river outranked a null model, but performed relatively poorly (AUC = 0.76–0.79; Table 2). Posterior distributions for fixed effect coefficients in the top-ranked models were virtually identical regardless of whether the random effect term was included (Table 3), suggesting negligible autocorrelation in the occupancy state of each reach as a result of site being nested within the same river. For simplicity, we focus our interpretation of results on the two best-performing models while ignoring random effects.

Collectively, results supported the hypotheses that hellbender occurrence was driven primarily by physiography, and demonstrated modest support for negative effects of agricultural and developed land use when quantified at the catchment scale (Table 2). The most parsimonious model, which included only physiographic province, predicted that reaches with catchments that fell entirely within the Blue Ridge ($\hat{\Psi}$ = 0.67, 0.41–0.88) were about 16 times more likely to be occupied that those with catchments that fell entirely within the Ridge and Valley province ($\hat{\Psi}$ = 0.04, 0.00–0.18; Fig. 3). Extrapolation of the physiography model across our entire study area predicted that only 36% of our study area was occupied by our target species (Table 4).

The equally well-performing but less parsimonious model included an interaction between physiography and catchment land use. However, credible intervals for coefficients associated with land use variables overlapped zero (Table 3), suggesting a great deal of uncertainty regarding effects of agriculture and development on hellbender occurrence. This model predicted that, holding developed land use constant at the mean observed (0.2%), reaches with catchments entirely in the Blue Ridge were twice as likely to be occupied when 10% of land use was agricultural ($\hat{\Psi}$ = 0.93, 0.46–1.00) compared with when 40% of land use was agricultural ($\hat{\Psi}$ = 0.47, 0.13–0.84). Reaches with catchments entirely in the Ridge and Valley were predicted to have extremely low occupancy regardless of land use but were twice as likely to be occupied when agriculture composed just 10% of land use throughout the catchment ($\hat{\Psi}$ = 0.05, 0.00–0.39) compared with 40% ($\hat{\Psi}$ = 0.02, 0.00–0.17; Fig. 4a). The physiography × land use model also suggested a negative effect of developed land use on hellbender occupancy, but only in the Blue Ridge, and uncertainty regarding effects of development was considerable (Table 3). Extrapolation of the physiography × land use model across our entire study area predicted that only 34% of our study area was occupied by our target species (Table 4).

Extrapolation of model predictions across our study area suggested that failing to account for physiography and assuming that high forest cover within a stream catchment functions as a reliable indicator of occurrence would yield numerically and spatially biased estimates of hellbender distribution. For example, our results indicated that over half (53–60%) of the habitat predicted to be occupied by hellbenders consisted of stream segments with catchments currently characterized by only moderate (≤ 65%) levels of catchment forest cover (Fig. 5). Furthermore, our model indicated that the majority of stream habitat characterized by heavily (≥ 70%) forested catchments was of little importance to our target species, given that over half (148 of 223 stream km) of the most heavily forested stream reaches fell within the Ridge and Valley physiographic province where occupancy was

Table 2 Candidate models and area-under-the-curve (AUC) measures of performance used to evaluate support for factors influencing detection (step 1) and occupancy (step 2) of *Cryptobranchus alleganiensis* in Virginia, USA, 2013–2014, ranked from highest to lowest according to a Wantanabe–Akaike information criterion (WAIC).

Model	WAIC	AUC (Ψ)	AUC (*p*)
Step one			
Ψ(.) *p*(visibility + ag.ir + dev.ir + RIVER)	144.65		
Ψ(.) *p*(RIVER)	144.72		
Ψ(.) *p*(visibility + contr. area + visibility*contr.area)	144.73		
Ψ(.) *p*(.)	144.79		
Ψ(.) *p*(visibility + contr. area + visibility*contr.area + RIVER)	145.94		
Ψ(.) *p*(visibility)	146.11		
Ψ(.) *p*(visibility + RIVER)	146.24		
Ψ(.) *p*(visibility + ag.ir + dev.ir)	146.84		
Ψ(.) *p*(visibility + contr. area)	147.42		
Ψ(.) *p*(visibility + contr. area + RIVER)	147.49		
Ψ(.) *p*(visibility + ag.c + dev.c + RIVER)	149.09		
Ψ(.) *p*(visibility + ag.c + dev.c)	149.23		
Step two			
Ψ(physiography) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	133.86	0.83	0.97
Ψ(physiography + ag.c + dev.c + physiography*ag.c+ physiography*dev.c) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	137.83	0.84	0.97
Ψ(pool + riffle + canopy + contr. area) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	138.05	0.76	0.97
Ψ(physiography + RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	139.12	0.85	0.97
Ψ(physiography + ag.c + dev.c + physiography*ag.c+ physiography*dev.c + RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	142.68	0.86	0.97
Ψ(pool + riffle + canopy + contr. area + RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	142.79	0.79	0.97
Ψ(.) *P*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	147.40		
Ψ(ag.c + dev.c) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	149.33		
Ψ(RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	152.03		
Ψ(ag.c + dev.c + RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	153.37		
Ψ(boulder + fine) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	153.76		
Ψ(ag.ir + dev.ir) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	154.43		
Ψ(physiography + ag.c + dev.c + boulder + fine + contr. area) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	154.97		
Ψ(ag.c + dev.c + ag.ir + dev.ir) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	155.35		
Ψ(elev + ag.c + dev.c + contr. area) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	158.73		
Ψ(boulder + fine + RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	158.87		
Ψ(ag.ir + dev.ir + contr. area + RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	159.17		
Ψ(physiography + ag.c + dev.c + boulder + fine + contr. area + RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	159.36		
Ψ(ag.c + dev.c + ag.ir + dev.ir + RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	160.56		
Ψ(elev + ag.c + dev.c + contr. area + RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	162.92		
Ψ(boulder + fine + contr. area) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	163.25		
Ψ(boulder + fine + contr. area + RIVER) *p*(visibility + contr. area + visibility*contr. area + ag.ir + dev.ir + RIVER)	169.92		

extremely low (≤ 0.05). Assuming that stream reaches with heavily ($\geq 70\%$) forested catchments function as a proxy of hellbender distribution in our study area would yield erroneous conclusions for our target species in two ways. First, the proportion of area occupied would be underestimated by about one-third (i.e. 25% vs. 34–36%). Second, over half of the area occupied by our target species (i.e. moderately forested stream reaches) would be misclassified as being of little importance to the species, while a narrow region (i.e. heavily forested Ridge and Valley reaches = 16% of study

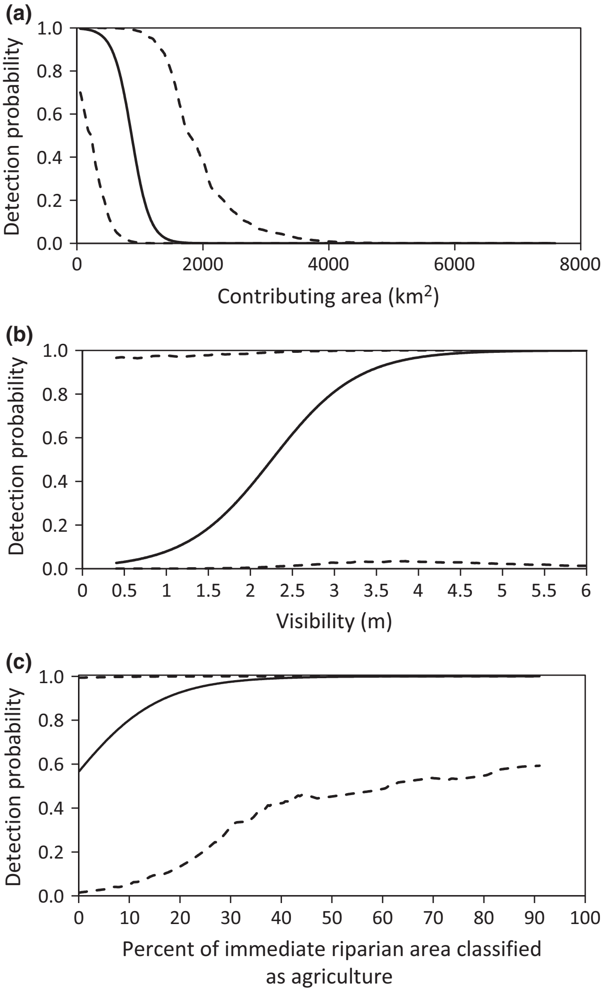

Figure 2 Predicted detection probability for *Cryptobranchus alleganiensis* as a function of (a) contributing area upstream of the reach when holding visibility constant at 1.75 m and as a function of (b) visibility when holding contributing area constant at 1000 km^2, and (c) riparian land use while holding visibility at 1.75 m and contributing area the median observed value (400 km^2). Note the suggested need for visibility ≥ 2 m for even a minimal chance of detection when surveying large rivers (e.g. widths ≥ 50 m). Solid lines represent mean estimates and dashed lines represent 95% credible intervals based on 1000 random samples drawn from MCMC chains.

area) with extremely low occupancy would be misclassified as being of great importance (Fig. 5).

DISCUSSION

We found that the distribution of an imperiled and data-deficient species was better predicted by broadscale patterns in underlying geology and topography, defined by physiographic province, than variables based on well-accepted species–habitat associations. Hellbenders were exceedingly rare in the Ridge and Valley physiographic province relative to the Blue Ridge, even among stream reaches with heavily (≥ 70%) forested catchments. The physiography effect we report is not surprising, as physiography has been shown to be an important determinant of both stream macro-invertebrate and fish distributions in several regions including Virginia (Angermeier & Winston, 1999; Feminella, 2000; Van Sickle *et al.*, 2004; Utz *et al.*, 2009, 2010; Pool *et al.*, 2010). However, the mechanisms by which physiography influences hellbender distribution remain unclear. Physiography is an important determinant of hydrological patterns and physicochemical properties in streams and can directly influence habitat suitability for aquatic species. Ridge and Valley streams are characterized by lower base flows (Nelms *et al.*, 1997), higher levels of dissolved solids, harder water and slightly basic pH relative to Blue Ridge streams, due largely to innate differences in reactivity between water and underlying bedrock (Puckett & Bricker, 1992; Swain *et al.*, 2004). Therefore, although hellbenders were historically reported from many Ridge and Valley streams in our study area (Mayasich *et al.*, 2003), abundance may have always been low in the Ridge and Valley relative to the Blue Ridge due to inherent differences in physiography.

Other than possible differences in inherent habitat suitability variation in hellbender occurrence among among physiographic provinces could be a legacy effect (Foster *et al.*, 2003) of historical land use intensity within each province. Physiography can influence the suitability of the terrestrial landscape for particular human land uses via topography, soil chemistry and vegetation community composition and structure (Godfrey, 1977), and thereby influence exposure of streams to various land use practices (Brown *et al.*, 2005). For example, the Blue Ridge is known to have experienced less exposure to agriculture and intensive logging relative to the neighbouring Piedmont physiographic province (Brown *et al.*, 2005). Agriculture and urbanization have been shown to negatively impact occurrence and abundance of many aquatic species (Barrett & Guyer, 2008; Wenger *et al.*, 2008; Utz *et al.*, 2009, 2010; Ficetola *et al.*, 2010; Pool *et al.*, 2010; Price *et al.*, 2011). Given their high degree of specialization and dependence on benthic microhabitat, it was somewhat surprising that hellbender occurrence did not respond more strongly to current land use or substrate characteristics. However, given longevity of our target species (25+ years), considerable lag could be expected to separate the onset of mechanisms of population decline (e.g. reduced recruitment) and extirpation. Utz *et al.* (2010) reported differential effects of land use on the distribution of fishes from different physiography provinces in Maryland, and hypothesized legacy effects similar to those we discuss here. If the Ridge and Valley province was historically exposed to higher levels of agriculture or logging or if physicochemical conditions in streams responded to land use differently than in the Blue Ridge, historical land use might be an equally strong (or better) predictor of current hellbender distribution than physiography. Unfortunately, high-resolution (≤ 30 m) digitized land use data for our study area that pre-dates the 1990s is lacking, which precluded our ability to investigate the potential role of land use legacy effects.

Table 3 Coefficients and their associated 95% credible intervals for best performing models describing detection and occupancy of *Cryptobranchusalleganiensis* in the New River and South Fork Holston River drainages, Virginia, USA.

Rank	Parameter	Estimate	95% CI		nEff[a]	R-hat[b]
Detection						
1	Intercept	−2.3809	−7.0390	1.5350	54,000	1.0010
	visibility	0.7464	−1.1690	2.8400	54,000	1.0010
	contr. area	−9.1743	−16.4900	−3.3330	16,000	1.0011
	visibility X contr. area	5.9220	0.8489	14.0300	54,000	1.0010
	ag.ir	11.3555	0.4048	24.4603	7000	1.0013
	dev.ir	−0.3474	−19.9700	19.4700	13,000	1.0011
	RIVER	.	.	.	.	
Occupancy						
1	Intercept	−3.2932	−5.7480	−1.5650	14,000	1.0011
	physiography	4.0368	1.7800	6.9910	18,000	1.0011
2	Intercept	−2.5040	−6.5250	0.8027	54,000	1.0010
	physiography	5.9221	1.5060	10.9600	51,000	1.0010
	ag.c	−3.8376	−15.9600	8.0991	54,000	1.0010
	dev.c	0.4034	−15.8000	16.0503	54,000	1.0010
	physiography X ag.c	−5.0249	−19.0000	8.6940	54,000	1.0010
	physiography X dev.c	−2.4834	−21.5703	16.5003	54,000	1.0010
4	Intercept	−3.8036	−7.4640	−1.3590	5200	1.0013
	physiography	4.8044	2.0517	9.0324	3800	1.0014
	RIVER	.	.	.	.	.
5	Intercept	−2.7563	−7.6100	1.3175	15,000	1.0011
	physiography	6.0134	1.3115	11.3900	6700	1.0013
	ag.c	−4.0739	−16.9753	8.6845	33,000	1.0010
	dev.c	−0.0757	−17.2000	16.5000	29,000	1.0010
	physiography X ag.c	−3.3325	−18.3453	12.0400	33,000	1.0010
	physiography X dev.c	−2.6717	−21.9853	16.3453	33,000	1.0010
	RIVER	.	.	.	.	.

[a] Number of effective samples (independent iterations) produced from the MCMC chain

[b] Model convergence criteria, where at convergence R-hat = 1

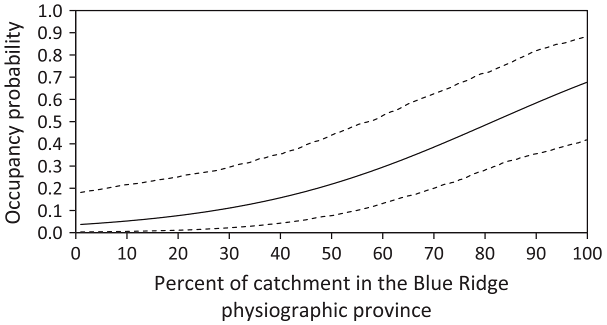

Figure 3 Predicted probability of occupancy for *Cryptobranchus alleganiensis* within a randomly selected 50 m stream reach, based on the proportion of the upstream catchment falling within the Blue Ridge physiographic province of south-west VA, USA. Solid lines represent mean estimates and dashed lines represent 95% credible intervals based on 1000 random samples drawn from MCMC chains.

Table 4 Extrapolated estimates of the total proportion of area occupied (PAO) by *Cryptobranchus alleganiensis* throughout fourth-order and larger streams in the New and South Fork Holston river drainages in south-west Virginia, USA (assuming coarse substrate is present in every 50 m reach).

Estimated occupancy	Ψ (physiography)		Ψ (physiography × catchment land use)	
	Stream km	PAO	Stream km	PAO
0–0.1	371.1	0.04	371.1	0.03
0.1–0.2	0	0	0	0
0.2–0.3	0.4	0.27	25.1	0.26
0.3–0.4	54.4	0.37	74.2	0.36
0.4–0.5	66.2	0.43	128.3	0.46
0.5–0.6	104.3	0.53	107.7	0.54
0.6–0.7	309.5	0.67	80.9	0.64
0.7–0.8			67.8	0.75
0.8–0.9			39.9	0.82
0.9–1.0			11.06	0.92
Total	906.1	0.36	906.1	0.34

Given our findings, we began to speculate that water quality, whether driven primarily by physiography or by more complex interactions between physiography and land use, may function as an underlying mechanism linking physiographic province to current patterns of hellbender distribution. As a post hoc attempt to evaluate this hypothesis, we measured water quality at a subset of 30 stream reaches in December 2015. We found that conductivity

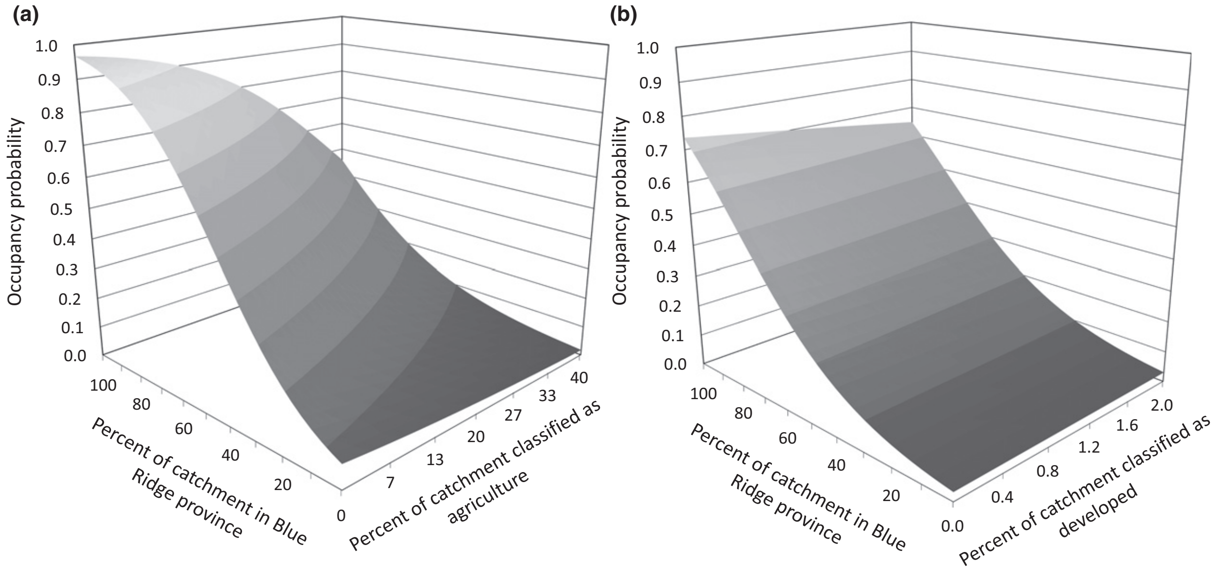

Figure 4 Predicted probability of occupancy for *Cryptobranchus alleganiensis* within a randomly selected 50 m stream reach, based on the proportion of the upstream catchment that occurs within the Blue Ridge physiographic province of south-west VA, USA, and is classified as agriculture (a) or developed (b). Predictions are the result of 1000 random samples drawn from MCMC chains, where effects of each land use type were generated while holding levels of the other category constant at the mean observed (developed = 0.28%; agriculture = 27%).

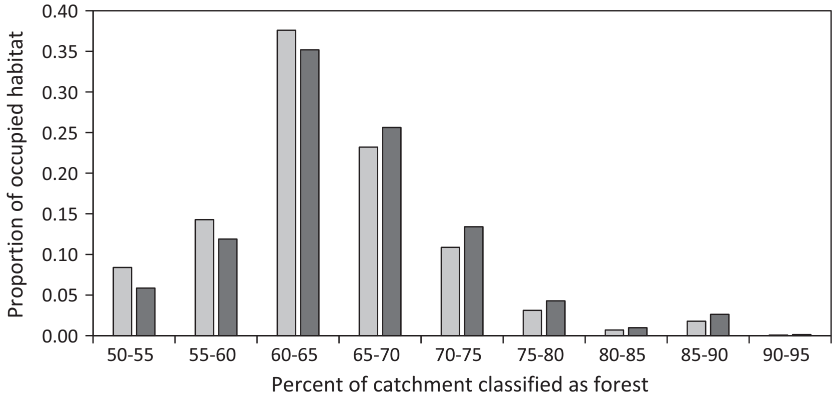

Figure 5 Distribution of the total area predicted to be occupied by *Cryptobranchus alleganiensis* across fourth-order and larger stream reaches subject to varying levels of land use in South Fork Holston and New River drainages, VA, 2013–2014. Predictions are based on best-performing occupancy models (light grey bars = physiography only model; dark grey bars = physiography × land use model). Note that over half of the area predicted to be occupied falls within stream reaches with only moderately forested (≤ 65%) catchments, and only 17–20% of occupied habitat occurs in reaches with heavily (> 70%) forested catchments.

decreased as the proportion of a catchment that fell within the Blue Ridge increased (Fig. 6a) and, regardless of physiography, decreased as forest cover within the surrounding area increased (Fig. 6b–c). Evidence of water quality variation along a physiographic gradient (Fig. 6a) supports our speculation that water quality may function as a contributing mechanism, or strong correlate of other mechanisms, defining current hellbender distribution. However, more comprehensive work is needed to understand effects of land use and physiography on water quality and to determine whether water quality is associated with more sensitive metrics of hellbender population viability (e.g. abundance or reproductive success).

While our results indicate that about one-third of our study area is currently occupied by hellbenders, occurrence is not indicative of abundance or population viability. Occurrence of freshwater species is often less sensitive to land use than abundance (Utz *et al.*, 2009, 2010), particularly over short timescales. Therefore, we caution against assuming probability of occupancy is an indicator of population viability in our study. Rather, given that stream segments subject to moderate or higher (< 65% forest) levels of human land use intensity currently represent the majority of occupied habitat in our study area (Fig. 5), additional research to determine how land use influences population viability may be particularly vital to conservation planning for hellbenders.

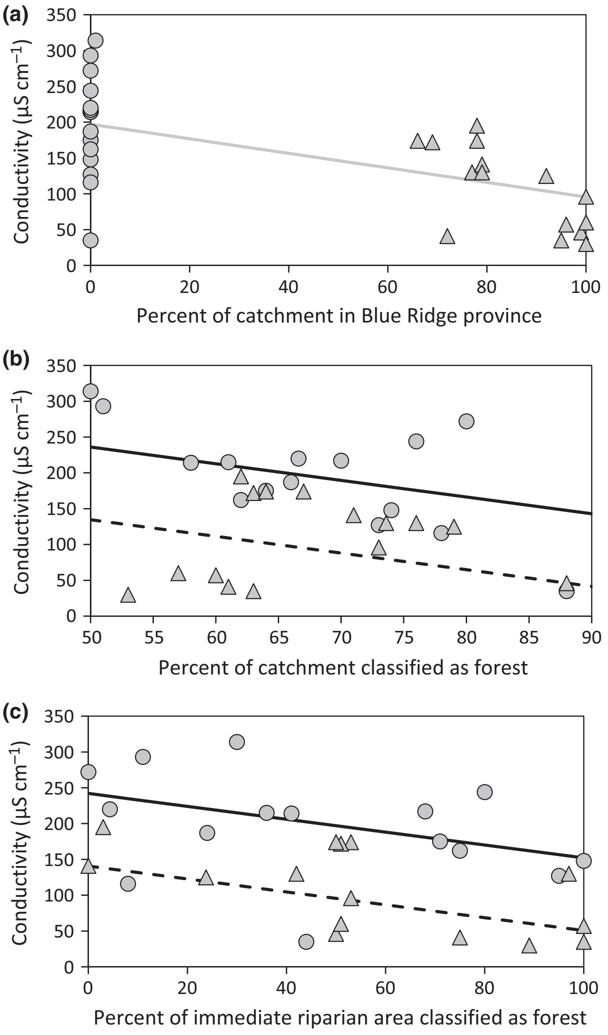

Figure 6 Relationship between water quality, physiography (a) and land use quantified at the catchment- (b) and immediate-riparian (c) spatial scales. Points are observations from a subset of 30 sample reaches with catchments that fell predominantly in the Ridge and Valley (circles) or Blue Ridge (triangles) physiographic provinces. Lines represent predicted effects of covariates, separately for each province (solid black lines = Ridge and Valley; dashed black lines = Blue Ridge), based on results from a least squares regression ($R^2_{\text{adj}} = 0.557$, $F_{1,28} = 13.15$, $P < 0.0001$). Covariate effects were predicted while holding other variables in the model at the mean observed value. Note that conductivity was generally higher in Ridge and Valley streams relative to those from the Blue Ridge (a). Additionally, conductivity decreased as forest cover increased at both the catchment- (b) and immediate-riparian area (c) regardless of physiography.

Our study highlights the potential danger of assuming that the distribution of data-deficient species can be approximated using untested, but commonly accepted, species–habitat associations. Global changes likely to influence species distributions are occurring at an increasing rate. As a result, it is increasingly important to understand the current and potential future distributions for species. Our study focused on an imperiled habitat specialist whose occurrence is often readily assumed to correspond with current indicators of high-quality in-stream conditions (i.e. heavily forested landscapes; Williams *et al.*, 1981). Similar assumptions are likely to exist for many imperiled freshwater species, given that land use has the potential to alter sedimentation input, water chemistry, channel morphology and flow regime (Allan, 2004). For our target species, however, we found current land use to be an unreliable predictor of distribution when physiography was ignored. Our findings are consistent with previous studies suggesting that models informed by presence–absence (rather than presence-only) data can reduce omission (false absence) and commission (false presence) errors when predicting species distributions (Hermoso *et al.*, 2015). Omission and commission errors can lead to inaccuracies regarding the status of species and can reduce the efficiency of conservation planning when conservation targets include protecting discrete habitat units necessary to conserve a species (Hermoso *et al.*, 2015). For many imperiled species, there are likely be important trade-offs between the desire for reliable data and the need to make conservation decisions in a timely manner. We acknowledge that in some cases the risks associated with waiting to acquire presence–absence data may outweigh the benefits. However, when possible, we encourage randomized spatial sampling, multiple site visits and inclusion of absence data (even when only partially available; Hermoso *et al.*, 2015) when modelling distributions of species. Encouragingly, recent advances in molecular techniques to detect freshwater species from water samples (eDNA; reviewed by Goldberg *et al.*, 2015) offer a potentially powerful, more sensitive and relatively low-labour approach to presence–absence sampling in freshwater systems. Pairing presence–absence sampling via eDNA with an occupancy framework has great potential to improve our knowledge of distributions of rare species. However, because extrapolations of occupancy estimates are sensitive to the definition of the sampling unit, such studies should carefully consider and explicitly define the spatial unit represented by a water sample (e.g. see Jane *et al.*, 2015).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Hellbender surveys.

BIOSKETCHES

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