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An integrative conservation planning framework for aquatic landscapes fragmented by road-stream crossings

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ABSTRACT

Road-stream crossings represent a significant source of habitat fragmentation for global aquatic ecosystems, yet integrative conservation planning frameworks are lacking for most regions. We describe a connectivity conservation planning framework that draws on recent advances in the fields of surveying, modelling, and optimizing removal of crossings that block aquatic organism passage. We demonstrate this framework with a case study involving 1200 crossings surveyed in Florida, USA in which barrier severity was quantified on a continuous scale from 0 (complete barrier) to 1 (no barrier). Using field surveys, we built a boosted regression tree (BRT) model that linked barrier severity to 44 landscape variables representing natural (e.g., stream size) and anthropogenic (e.g., land use) stream conditions. We used a recently developed optimization routine to conduct two scenarios, including (1) surveyed crossings only and (2) surveyed crossings plus crossings modelled at 5545 unsurveyed locations. The BRT model explained 54% of variation in barrier severity scores and showed that the most severe barriers occurred on small, high-elevation streams draining urban and agricultural catchments. Estimates of connectivity gains following remediation were 5.3-times lower when unsurveyed locations were included in the optimization, suggesting inclusion of unsurveyed sites is critical for conservation planning. Results from this framework can be used over short (e.g., planning immediate barrier mitigation) and long (e.g., planning future field surveys) time horizons to benefit aquatic connectivity conservation. The survey protocol and modelling methods used here, combined with global datasets on stream conditions, can be applied to benefit connectivity planning in other regions.

1. Introduction

Structures placed at intersections between road networks and stream networks, termed "road-stream crossings", represent a significant source of habitat fragmentation for aquatic ecosystems (Fullerton et al., 2010). Warren and Pardew (1998) were among the first to recognize the passage challenges that road-stream crossings created for fishes in small streams, and since their work a number of authors have identified ecological consequences associated with crossings that block aquatic organism passage (AOP; Gibson, Haedrich, & Wernerheim, 2005; Perkin & Gido, 2012; Evans, Riley, & Lamberti, 2015). Although fishes receive considerable attention (e.g., Fullerton et al., 2010), road-stream crossings fragment habitat connectivity for organisms ranging from invertebrates to mammals (Trombulak and Frissell, 2000; Foster & Keller, 2011). Still, compared with terrestrial ecosystems, connectivity in stream networks ("riverscapes" hereafter) has received less attention despite clear research challenges (Fuller, Doyle, & Strayer, 2015). Some challenges that face connectivity research in riverscapes include: (1) the fact that habitats are primarily arranged in a linear fashion (upstream-downstream) rather than a two-dimensional matrix in which multiple pathways connected habitats (Campbell Grant et al., 2007; but see Shao, Fang, Jawitz, Yan, & Cui, 2019), (2) road-stream crossings are numerous across riverscapes ($10^{5\text{-}6}$ m) and systematic inventories are lacking (Januchowski-Hartley et al., 2013), and (3) determining the most appropriate conservation actions that provide maximum benefits with minimal costs requires model development and refinement (McKay et al., 2017). Addressing these challenges requires research that combines field inventories, predictive models that use remotely sensed data, desktop assessments of existing data, and development of decision-support tools to aid managers in directing aquatic connectivity restoration programs (Moody et al., 2017; Atkinson et al., 2018).

Comprehensive aquatic conservation planning requires greater effort directed at identifying the locations of road-stream crossings (Januchowski-Hartley et al., 2013). Road-stream crossings far outnumber dams (Perkin, Gido, & Al-Ta'ani, O., & Scoglio, C. , 2013) and block passage by all or some organisms at up to 97% of locations within some riverscapes (Gibson et al., 2005; Poplar-Jeffers et al., 2009). However, the locations of impassable road-stream crossings can be challenging to identify because not all crossings are constructed

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Table 1
Sub-basins included in this study, their 8-digit hydrologic unit code (HUC), the total number of sites surveyed (visited but inaccessible), the number of crossing that had the complete suite of covariates (see Table 3) and therefore were included in distribution model development, and the number of road-steam intersections used to predict barrier locations.

Sub-Basin Name	8-Digit HUC	Surveyed	Model Development	Intersections
Blackwater	03140104	154 (9)	93	568
Chipola	03130012	150	119	515
Escambia	03140305	153 (1)	82	404
Lower Chocatwhatchee	03140203	151 (1)	116	1,062
Lower Ochlockonee	03120003	145 (2)	98	894
Peace	03100101	150	94	1,018
Upper St. Johns	03080101	150	48	824
Withlacoochee	03100208	147	46	260
TOTAL	–	1,200 (13)	696	5,545

similarly, even within a single riverscape. This means that landscape (i.e., involving terrestrial components in addition to aquatic) variables useful for modelling the locations of problematic road-stream crossings that block AOP are required, yet identifying such variables is challenging. To address this challenge, models linking remotely sensed data to road-stream crossing locations and conditions are developed for some regions, but models explain low percentages of variation in the distributions of structures or their conditions (Januchowski-Hartley, Diebel, Doran, & McIntyre, 2014; Collins, 2016; Januchowski-Hartley, Jézéquel, & Tedesco, 2019). These results suggest additional research is necessary to determine the most appropriate response and predictor variables to include in road-stream crossing distribution modeling frameworks.

Once the distribution of road-stream crossings that block AOP are known or estimated, determining which crossings represent high priority candidates for remediation is a further challenge that requires additional local information. Remediation – defined as corrective action aimed at improving ecological conditions – might involve partial or complete replacement by a design that allows movement of aquatic organisms (McManamay, Perkin, & Jager, 2019). Remediation is a costly endeavor, and costs increase as the size and width of roads and streams involved with a particular road-stream crossing increase (Thomson & Pinkerton, 2008). Multiple strategies exist for identifying the most appropriate crossings to target for remediation (see reviews by Kemp and O'hanley, 2010; McKay et al., 2017), and among these is the concept known as optimization (O'Hanley & Tomberlin, 2005; King, O'Hanley, Newbold, Kemp, & Diebel, 2017). Optimization modelling provides guidance for allocation of limited resources such that gains in habitat connectivity are maximized by solving multiple solutions for mitigation scenarios in which the trade-off between the cost of barrier remediation is measured against potential gains in upstream habitat; and this is done simultaneously for all barriers in a network (Kemp and O'hanley, 2010). Recent applications of optimization modelling revealed that implementation across broader spatial scales improve cost efficiencies (Neeson et al., 2015). However, implementing models that improve cost efficiency at broad spatial scales requires knowledge (or at least estimates) of locations, passabilities, and mitigation costs for thousands of unsurveyed crossings distributed across riverscapes (McKay et al., 2017). Additional research is necessary to develop strategies for guiding mitigation planning at broader scales so that return-on-investment is maximized, particularly for regions other than the North American Great Lakes (Neeson et al., 2015).

The goal of this work was to incorporate road-streams crossings into aquatic connectivity conservation restoration and planning while advancing the science of connectivity research. To achieve this goal, we developed three objectives. The first objective was to survey 1,200 crossings across eight sub-basins distributed across the state of Florida. These direct surveys provide valuable information on the distribution and nature of crossings as they exist across riverscapes. Our second objective was to identify landscape variables that might be useful for predicting the occurrence of potential barriers to AOP across large numbers of unsurveyed crossings. This objective directly addresses the need to account for road-stream crossing barriers across broad spatial scales during aquatic connectivity conservation planning (Januchowki-Hartley et al. 2013; Neeson et al., 2015). Finally, the third objective was to optimize barrier mitigation projects by considering trade-offs between costs of barrier mitigations versus benefits of upstream habitat reconnected after organism passage is improved. This work focuses on riverscapes in the state of Florida as a means of providing decision support-tools for aquatic connectivity managers, including identifying locations of barriers that might be targets of mitigation in the short-term (surveyed crossings) as well as locations where future surveys might be targeted to assess occurrence of barriers over longer time scales (modelled crossings).

2. Material and methods

2.1. Study area

We surveyed crossings in eight sub-basins distributed across the state of Florida. Each of these sub-basins were identified using 8-digit hydrologic unit codes (HUCs) from the National Hydrography Dataset (NHD, 2019; Table 1) and were distributed from the western panhandle to central Florida (Fig. 1). The eight sub-basins were distributed so that major gradients in elevation and precipitation were represented (Fig. 1 insets). Elevations in the study area ranged from sea level to 106 m above sea level, and surveyed sub-basins included some of the largest changes in elevation within the state. Long-term averages (1980–2010) for precipitation ranged 976–1721 mm/year across the study area, and surveyed sub-basins included some of the wettest and driest areas in terms of precipitation.

2.2. Crossing surveys

Twelve-hundred randomly selected crossings distributed across the 8 sub-basins were targeted during surveys. We initially used intersections of roads (US Census Bureau, 2017) and stream networks (NHDplus Version 2 medium resolution hydrography) compiled in a geographic information system (GIS; ArcGIS Desktop, version 10.6, ESRI, INC, Redlands, CA) to identify crossing locations, and then selected 150 random locations to survey within each sub-basin. However, this approach proved inefficient during initial surveying because some crossings selected for surveys were inaccessible. Therefore, we modified our approach such that when a randomly selected crossing was inaccessible, a nearby, accessible crossing was surveyed in its place. At each crossing, surveys followed the Southeast Aquatic Resources Partnership (SARP) Southeast Stream Crossing Survey Protocol (SARP 2019). In the field, crossing types were defined as bridge (deck supported by abutments that constrain the stream channel), culvert (single structure buried under the road), multiple culvert (multiple structures buried under

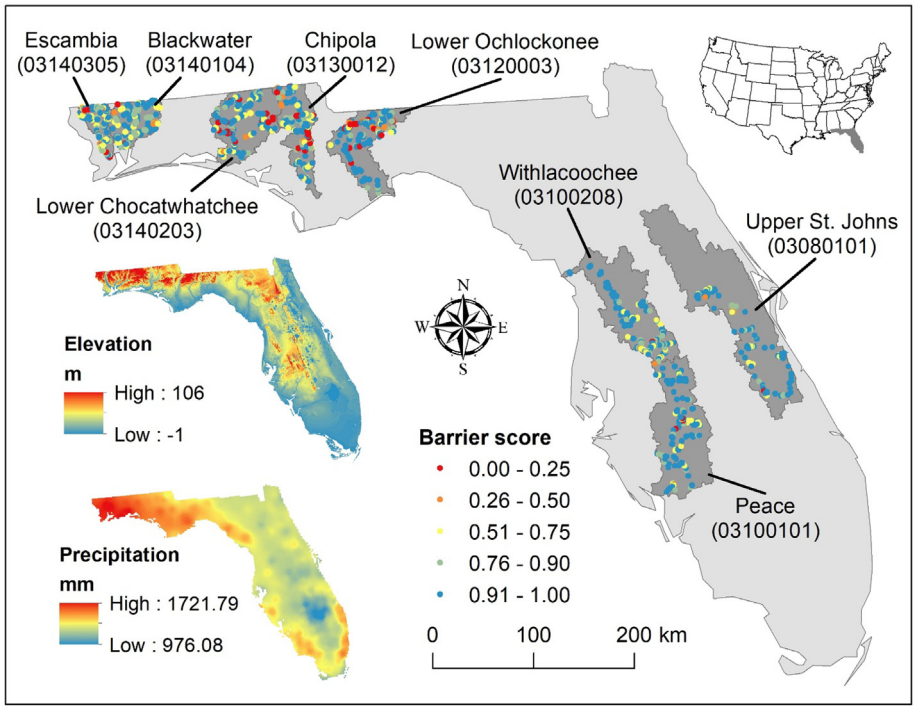

Fig. 1. Map of study area showing eight sub-basins (8-digit hydrologic unit codes; HUCs) included in study surveys and locations of surveyed crossings colored according to barrier severity scores. Insets illustrate gradients for elevation and precipitation covered by survey locations.

road), ford (shallow, open stream crossing), or no crossing because it was removed or no stream channel existed. Bridges that spanned the full channel width and allowed dry passage on either bank were classified as "bridge adequate" because they allowed passage of aquatic and terrestrial organisms underneath the structure. In some cases, crossings were completely inaccessible because of private property or locked gates, and in other cases culverts were partially inaccessible because of fencing or occurrence of dangerous wildlife (e.g., American Alligator *Alligator mississippiensis*) at either the inlet (i.e., where water enters the structure) or outlet (i.e., where water exits the structure). Completely or partially inaccessible crossings were noted but not included in modeling. For accessible crossings classified as bridges (i.e., non-adequate bridges) or culverts (i.e., single or multiple), data on the dimensions of the structure itself and the water in the structure relative to the stream channel at a reference stream reach located upstream from the structure were collected so that a continuous barrier severity score could be calculated.

2.3. Barrier scoring

Field surveys were used to develop a weighted score representing the severity of barriers imposed by road-related structures. This scoring method is based on the North Atlantic Aquatic Connectivity Cooperative numeric scoring system protocol (NAACC, 2019) with small adaptations to represent southeastern-stream dynamics. Each barrier was assigned a barrier severity score ranging 0–1, where 0 represents presumed complete blockage and 1 represents complete passability. To calculate barrier severity, component scores were first assigned to all measured features of crossings according to the NAACC (2019) scoring systems, including values assigned to continuous and categorical variables (Appendix A). Continuous variables such as openness, height, and outlet drop were assigned scores according to equations specific to each variable. Openness component scores were calculated using the equation:

$$(1)\ S_o = a(1 - e^{-kx(1-d)})^{1/(1-d)}$$

where S_o is the component score for openness, $a = 1$, $k = 15$, $d = 0.62$, and $\times$ is the value of openness (Appendix A) recorded in feet. Height component scores were calculated using the equation:

$$(2)\ S_h = min\left(\frac{ax^2}{b^2 + x^2}, 1\right)$$

where S_h is the component score for height, $a = 1.1$, $b = 2.2$, and $\times$ is the value of height recorded in feet. Outlet drop component scores were calculated using the equation:

$$(3)\ S_{od} = 1 - \frac{ax^2}{b^2 + x^2}$$

where S_{od} is the component score for outlet drop, $a = 1.029412$, $b = 0.51449575$, and $\times$ is the outlet drop recorded in feet (NAACC, 2019). Each component score was then weighted according to values NAACC (2019) collected from a panel of experts (Appendix B) and then summed to give a weighted barrier severity score. The final step in scoring crossings included consideration of whether or not the barrier severity score (after weighting) was greater than or less than the outlet drop score (after weighting); the lesser of these two numbers was used as the barrier severity score for the crossing (NAACC, 2019).

2.4. Landscape covariates

Remotely sensed data were used to develop a database of landscape alterations that could be used to predict the spatial distribution of crossings that act as barriers to AOP. The locations of streams were based on National Hydrography Dataset (NHD) plus version 2 medium resolution (NHD, 2019) flowlines that represent inter-confluence segments of stream. A suite of 44 remotely sensed attributes that described stream size, elevation, slope, discharge, velocity, and human alterations within catchments was compiled for each segment (Table 2). Attributes for discharge (Q0001E) and velocity (V0001E) were obtained from the NHD plus version 2 EROM extension and remaining attributes were derived by Herreman, Cooper, Infante, and Daniel (2017). Attributes developed by Herreman et al. (2017) were assessed at multiple spatial

Table 2
Natural and anthropogenic landscape attributes used to model the distribution of crossings among riverscapes in Florida, USA. The attribute for HUCID was developed as a part of this study, Q0001E and V0001E are from the NHD (2019) EROM extension, and all remaining attributes were developed by Herreman et al. (2017).

Abbreviation	Status	Description and units
HUCID	Natural	Identity of 8-digit hydrologic unit code
Q0001E	Natural	Gage-adjusted mean annual discharge estimate (m^3/s)
V0001E	Natural	Gage-adjusted water velocity (m/s)
AREASQKM	Natural	Local catchment upstream area (km^2)
L_SLOPE	Natural	Local catchment slope in degrees
L_ELEVATIO	Natural	Local catchment mean elevation (m)
N_AREASQKM	Natural	Network catchment upstream area (km^2)
N_GWINDEX	Natural	Network catchment percent groundwater contribution
N_PRECIP	Natural	Network catchment mean annual precipitation (mm)
N_TEMPMEAN	Natural	Network catchment mean annual air temperature (°C)
L_POPDENS	Anthro.	Local catchment human population density (#/km^2)
L_ROAD_CR	Anthro.	Local catchment road crossing density (#/km^2)
L_ROADLEN	Anthro.	Local catchment road length density (km/km^2)
L_URBANL	Anthro.	Local catchment percent low development urban land
L_URBANM	Anthro.	Local catchment percent medium development urban land
L_URBANH	Anthro.	Local catchment percent high development urban land
L_PASTURE	Anthro.	Local catchment percent pasture land
L_CROP	Anthro.	Local catchment percent crop land
LB_URBANL	Anthro.	Local buffer percent low development urban land
LB_URBANM	Anthro.	Local buffer percent medium development urban land
LB_URBANH	Anthro.	Local buffer percent high development urban land
LB_PASTURE	Anthro.	Local buffer percent pasture land
LB_CROP	Anthro.	Local buffer percent crop land
N_POPDENS	Anthro.	Network catchment human population density (#/km^2)
N_ROAD_CR	Anthro.	Network catchment road crossing density (#/km^2)
N_ROADLEN	Anthro.	Network catchment road length density (km/km^2)
N_PHOS_YIE	Anthro.	Network catchment anthropogenic phosphorus yield (kg/km/yr)
N_NIT_YIEL	Anthro.	Network catchment anthropogenic nitrogen yield (kg/km/yr)
N_SED_YIEL	Anthro.	Network catchment anthropogenic sediment yield (kg/km/yr)
N_URBANL	Anthro.	Network catchment percent low development urban land
N_URBANM	Anthro.	Network catchment percent medium development urban land
N_URBANH	Anthro.	Network catchment percent high development urban land
N_PASTURE	Anthro.	Network catchment percent pasture land
N_CROP	Anthro.	Network catchment percent crop land
N_TOTAL_WD	Anthro.	Network catchment total water withdrawal (mil. gal./yr)
N_AG_WD	Anthro.	Network catchment agricultural water withdrawal (mil. gal./yr)
N_DOM_WD	Anthro.	Network catchment domestic water withdrawal (mil. gal./yr)
N_IND_WD	Anthro.	Network catchment industrial water withdrawal (mil. gal./yr)
N_THERM_WD	Anthro.	Network catchment thermo-elect. water withdrawal (mil gal./yr)
NB_URBANL	Anthro.	Network buffer percent low development urban land
NB_URBANM	Anthro.	Network buffer percent medium development urban land
NB_URBANH	Anthro.	Network buffer percent high development urban land
NB_PASTURE	Anthro.	Network buffer percent pasture land
NB_CROP	Anthro.	Network buffer percent crop land

scales, including network catchment (total upstream drainage area), local catchment (drainage area for focal inter-confluence stream segment excluding all other upstream segments), network buffer (90 m of land along stream channels for network catchment), and local buffer (90 m of land along stream channels for local catchment). Only land uses were compiled within the 90 m buffer zones and all land use statistics were based on Fry et al. (2011) during calculations by Herreman et al. (2017). Because data compiled by Herreman et al. (2017) were developed using the NHD plus version 1, the version 1 to 2 crosswalk developed by the NHD was used to spatially join these attributes to the NHD plus version 2 flowlines used in this study.

2.5. Barrier modeling

Relationships between barrier locations and landscape correlates were assessed using a tree-based machine learning algorithm. Boosted regression tree (BRT) models have been used to predict the locations of road-stream crossing barriers in the Great Lakes region (Januchowski-Hartley et al., 2014). In this previous study, crossings were classified according to outlet drop height or velocities (i.e., four classes; Januchowski-Hartley et al., 2014). Predictions based on occurrences of barrier classes were then developed using BRT models. We used a regression (rather than classification) tree model to predict the continuous barrier severity score for each surveyed crossing. Boosted regression tree models are built as linear combinations of many trees with boosting used to reweight observations that are modelled poorly (Elith, Leathwick, & Hastie, 2008). These models also provide variable importance plots and partial dependence plots to identify the magnitude and direction of barrier severity in response to natural and anthropogenic landscape alterations. The number of crossings useful for modeling was reduced compared to the total number surveyed because not all landscape correlates were available for all surveyed locations (Table 1). We fit the BRT model using the landscape correlates and subbasin identity as predictor variables (independent variables), barrier severity score as the response variable (dependent variable), 3350 trees, tree complexity = 4, learning rate = 0.001, and bag fraction = 0.70. We evaluated performance using the cross-validated correlation coefficient derived from splitting the data into training and testing datasets and then applying k-fold cross validation. All predictor variables were transformed using $\log_{10}(n + 1)$ prior to analysis and the BRT model was fit using the 'gbm' (Greenwell, Boehmke, & Developers, 2019) package in R version 3.5.2 (R Core Team 2018). Observed versus predicted scores for all crossings including in model construction were plotted as a way of illustrating model performances and partial dependence plots were constructed for natural and anthropogenic landscape variables that best predicted barrier severity. Finally, all intersections between roads and stream segments with the full suite of covariates (n = 5545; Table 1) were identified and included in predictions from the BRT model to predict barrier severity scores at unsurveyed crossings.

2.6. Barrier optimizations

The optimal barriers to mitigate (i.e., remove and replace) are those that fragment the greatest amount of upstream habitat but cost least to mitigate. We identified the optimal barriers for mitigation using the surveyed barrier dataset and the modelled barrier dataset. We first used the barrier assessment tool (BAT; Hornby, 2010) to calculate the upstream length of habitat (km) for each crossing for surveyed crossings (scenario 1) and then all modelled crossings (scenario 2). The BAT provided the upstream length of habitat between the focal crossing and the next upstream crossing (or the headwaters of the stream network if no upstream crossing exists). We included a GIS layer of dams in the BAT analysis so that upstream network distances were reflective of habitats already fragmented by dams. Although other indices of habitat gains associated with barrier removal exist, such as habitat type and quality (Diebel, Fedora, Cogswell, & O'Hanley, 2015), we opted to use the length of stream reconnected because it can be calculated across study areas regardless of habitat data (i.e., a limitation of metrics proposed by Diebel et al., 2015) and because longitudinal length of stream is strongly correlated with biodiversity across a range of systems (e.g., Bain & Wine, 2010; Perkin & Gido, 2011). The BAT also provided the identity of the nearest downstream crossing. The output data from the BAT were then used to develop optimization models using the

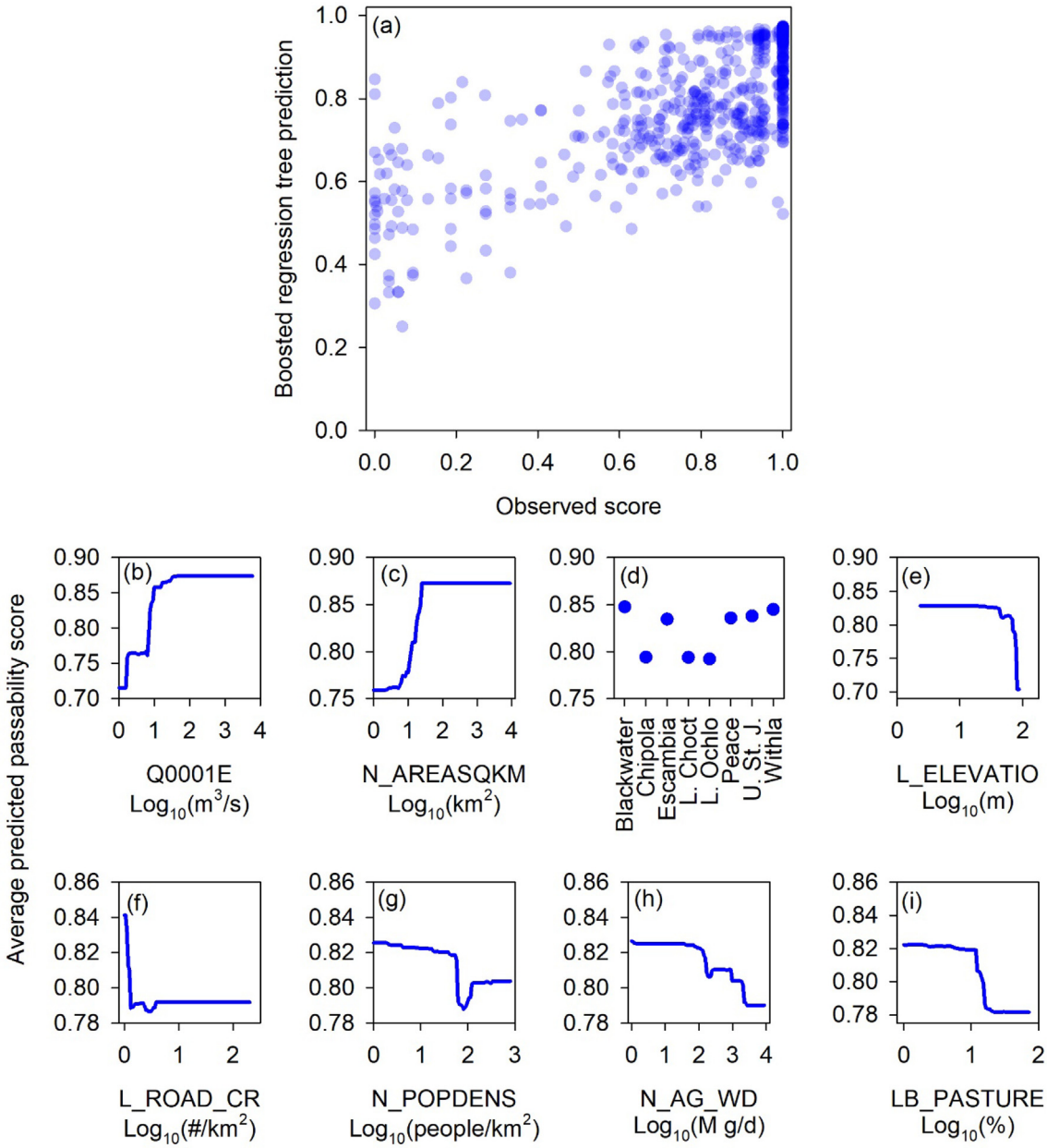

Fig. 2. (a) Relationship between observed and predicted passability scores for boosted regression tree model. Points are partially transparent to show high densities of observations (darker areas in plots). Lower panels show partial dependence plots illustrating the effect of (b-e) natural and (f-i) anthropogenic landscape variables on modelled scores. All continuous predictor variables were $\log_{10}(n + 1)$ transformed prior to analysis. The y-axis shows the average passability score (using all other variables) across landscape variable gradients (see Table 2 for variable descriptions and Table 3 for relative contributions).

program OptiPass (O'Hanley, 2014). OptiPass utilizes a greedy matrix approach in which barriers with the greatest upstream habitat but least estimated costs of removal are assessed across a budget of known magnitude and increment as a means of identifying the best options for mitigation. Similar approaches have been used in other regions to assess the approximate cost of increasing aquatic connectivity as a part of aquatic connectivity restoration programs (Neeson et al., 2015). We assessed all barriers across the study area simultaneously because Neeson et al. (2015) found that regional analyses, rather than finer spatial units such as individual basins, produce greater efficiencies in optimization routines.

Trade-offs in habitat gains versus mitigation costs were optimized using a theoretical budget and remotely sensed data. Budget magnitude = $500,000 and increment = $25,000 were used for optimization modeling, and the cost of removal of individual barriers was estimated using stream size and road size data (Appendix C). We estimated the base cost of barrier removal and replacement (i.e., $25,000) using a review of data from outside our study region (Thomson & Pinkerton, 2008) and costs of previous culvert removals from within the study region (Chris Metcalf, USFWS, *professional communication*). The value of $25,000 was used as the base cost for culvert removal and replacement on an unpaved road crossing a first order stream (Strahler 1957), and doubled or quadrupled depending on road size (paved road or major road) and stream size (order 2 or 3 +). In reality, replacement costs vary on a case-by-case basis with local conditions largely impacting the project costs, but this approach allowed for incorporation of two basic principles that affect project costs: (1) it costs more to modify structures under larger roads, and (2) it costs more to modify crossings over larger streams. Costs were estimated using road size data from the US Census Data (2017) and NHD Plus version 2 medium resolution flowline

attributes (NHD, 2019). Road sizes were classified according to the MTFCC attribute from the US Census Data (2017), including unpaved road (MTFCC = S1500, S1710 or 1740), paved road (MTFCC = S1400 or S1640), and major road (MTFCC = S1100, S1200, or S1630). All crossings with passability scores < 0.5 were included in optimizations to represent those that are most likely to restrict AOP or experience structural failure, and thus might be top candidates for mitigation. Thresholds where large increases in habitat gain occurred over small increases in estimated costs were identified using a chi-squared test assuming a uniform distribution. Each increment or monetary step ($25,000) was tested against the expected value estimated as the mean percent net gain across all monetary steps. Variation partitioning was used to identify thresholds representing monetary steps that combined to represent > 80% of the overall model.

3. Results

3.1. Barrier surveys

We visited 1200 crossing locations across the eight 8-digit HUCs. The most common crossing types encountered were bridge adequate (n = 446), multiple culvert (n = 366), single culvert (n = 258), and bridges that did not span the entire channel (n = 93). However, when culvert and multiple culvert were combined (n = 624), culverts outnumbered bridge adequate crossings. Remaining crossings types were rare, including fords (n = 13), removed crossings (n = 5), crossings where roads did not intersect the stream (n = 3), and crossings with no stream channel (n = 2). We were not able to access structures completely for 14 locations. Among accessible crossings, barrier severity scores ranged 0.00–0.25 (n = 69), 0.26–0.50 (n = 48), 0.51–0.75 (n = 180), 0.76–0.90 (n = 219), and 0.91–1.00 (n = 670; Fig. 1; Appendix D).

3.2. Barrier modeling

The full suite of landscape predictors was available for 696 of the surveyed crossings, and this reduced dataset was used to develop the BRT model. The BRT model had a cross-validated correlation of 0.54, meaning 54% of variation in barrier severity scores was explained by the model (Fig. 2a). The top three most influential variables were natural (Table 3), including discharge (Q0001E; 19.1% of explained variation), network catchment area (N_AREASQKM; 17.6%), and the watershed in which surveys were conducted (HUCID; 7.7%). Modeled anthropogenic covariates that were influential included road crossing density in the local catchment (L_RAOD_CR; 7.4%), network catchment human population density (N_POPDENS; 4.0%), network catchment agricultural water withdrawal (N_AG_WD; 3.7%), local buffer pasture land (3.1%), and network catchment road crossing density (N_ROAD_CR; 3.0%). Partial dependence plots indicated barrier severity was greatest (i.e., scores were lowest) for streams with low discharge (Fig. 2b) and small catchment area (Fig. 2c) in the Chipola, Lower Choctawhatchee and Lower Ochlockonee sub-basins (Fig. 2d) and where elevations were higher (Fig. 2e). Anthropogenic alterations to landscapes were associated with more severe barriers where road crossing densities in the upstream catchment were greater (Fig. 2f), human population density was greater (Fig. 2g), agriculture water withdrawal was greater (Fig. 2h), and pasture land use within the local buffer was greater (Fig. 2i). Model predictions developed for 5,545 unsurveyed sites illustrated geographic areas with greater numbers of crossings with scores ranging 0.51–0.75, and geographically limited regions near urbanized centers (e.g., Tallahassee, Defuniak Springs, Ponce De Leon) with high densities of crossings with scores ranging 0.26–0.50 (Fig. 3).

Table 3
Relative influence measured as percent variation explained for predictor variables included in the boosted regression tree model used to predict locations of barriers at unsurveyed locations. See Table 2 for variable definitions.

Variable	Relative influence (%)	Variable	Relative influence (%)
Q0001E	19.1	L_SLOPE	0.8
N_AREASQKM	17.6	L_URBANL	0.8
HUCID	7.7	N_ROADLEN	0.7
L_ROAD_CR	7.4	NB_CROP	0.7
L_ELEVATIO	6.3	N_DOM_WD	0.6
N_POPDENS	4.0	N_SED_YIEL	0.6
N_AG_WD	3.7	N_URBANM	0.6
LB_PASTURE	3.1	NB_PASTURE	0.6
N_ROAD_CR	3.0	LB_CROP	0.5
V0001E	2.9	N_CROP	0.4
L_PASTURE	2.2	L_ROADLEN	0.4
NB_URBANL	2.0	L_CROP	0.4
L_POPDENS	1.9	N_TOTAL_WD	0.3
N_TEMPMEAN	1.9	N_PHOS_YIE	0.3
N_PASTURE	1.7	L_URBANM	0.2
N_URBANL	1.7	NB_URBANM	0.1
N_GWINDEX	1.1	N_URBANH	0.1
LB_URBANL	1.0	LB_URBANM	< 0.1
N_PRECIP	1.0	L_URBANH	< 0.1
N_NIT_YIEL	1.0	LB_URBANH	0.0
N_IND_WD	1.0	NB_URBANH	0.0
AREASQKM	0.9	N_THERM_WD	0.0

3.3. Barrier optimizations

In total, 721 of the 1200 surveyed crossings (60%) were included in the OptiPass barrier optimization analysis for Scenario 1 (i.e., observed barriers). Crossings excluded from the optimization process were structures that occurred on small stream segments not in the NHD network or segments that were removed in ArcGIS to reduce stream bifurcation during the BAT step of the process. Among the remaining barriers, 79 with passability scores < 0.5 were assigned as potential structures for mitigation. Optimization across a total budget of $500,000 at increments of $25,000 highlighted seven candidate barriers for mitigation among 12 combinations of barriers in which 1–5 barriers were mitigated at estimated costs ranging $50,000-$500,000 and reconnecting 5–86 km of stream (Fig. 4a; Appendix E and Appendix F). The seven barriers identified as candidates for mitigation were located in the Chipola (n = 3), Escambia (n = 1), Upper St. Johns (n = 1), Peace (n = 1), and Lower Chactawhatchee (n = 1) sub-basins (Fig. 5). Crossings identified as candidates during optimization analysis were barriers to AOP based on large vertical drops at their outlets (Table 4; Appendix G). The barrier at one of these structures (i.e., C2) was actually a grade control component rather than the actual culvert itself (Table 4). Threshold increases in habitat gained across small increases in estimated cost were identified at the $50,000 (5 km gained), $100,000 (17 km gained), and $200,000 (51 km gained) budgetary values (Fig. 4), and each of these thresholds represented significant increases in habitat gained relative to increased costs (Appendix F).

Modeled barriers with predicted passability scores < 0.5 were included in the Scenario 2 optimization analysis (i.e., modeled barriers) and resulted in 159 potential mitigation projects. The same $500,000 budget with $25,000 increment was used and 11 potential barriers that should be surveyed for mitigation potential were identified. Optimization results revealed 25 potential combinations of barrier mitigations including 1–9 structures at costs ranging $25,000-$500,000 and habitat gained ranging < 1–16 km (Fig. 4b). Thresholds were identified at three monetary steps, including $25,000 (0.26 km gained), $50,000 (2.44 km gained), and $100,000 (4.51 km gained). Each of these thresholds represented significant increases in habitat gained relative to increases in estimated mitigation costs (Appendix F). These potential barriers occurred in four of the eight sub-basins (Fig. 4), including the Escambia (n = 1), Lower Chochatwhatchee (n = 2),

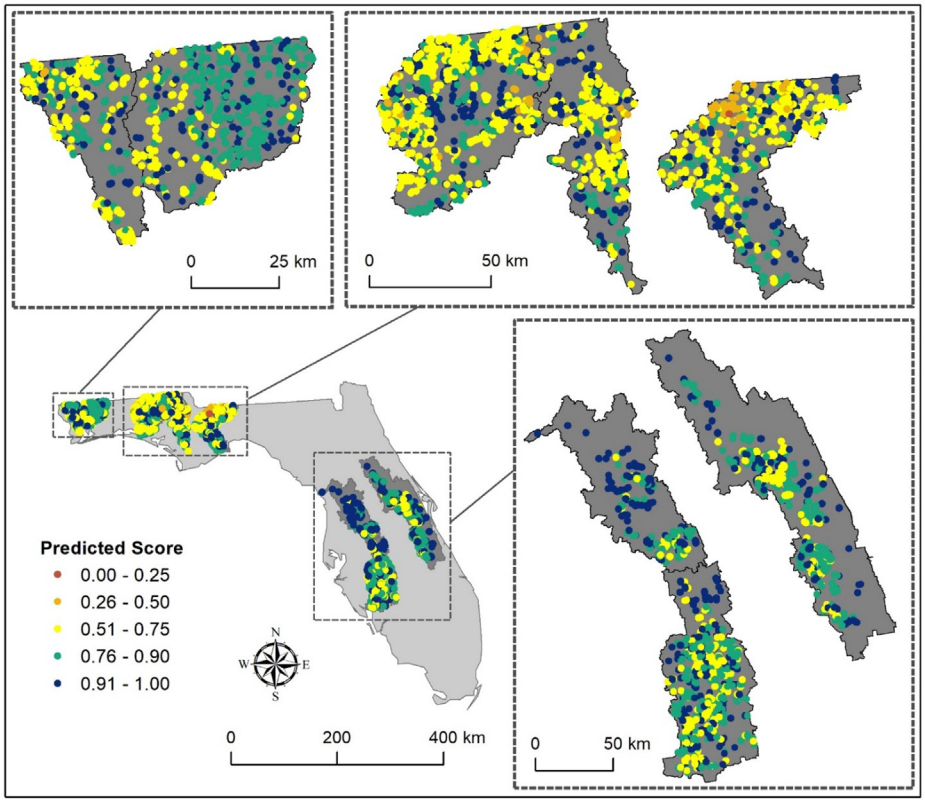

Fig. 3. Map showing predicted crossing locations and passability scores developed using a boosted regression tree model with points colored by barrier severity score values, where 0 represents an unpassable crossing and 1 represents a completely passable crossing.

Chipola (n = 5), and Lower Ochlockonee (n = 3). One crossing was identified in both scenarios (C4; Fig. 5), meaning this crossing is a high priority for mitigation.

4. Discussion

Our survey of 1,200 road-stream crossings across eight sub-basins in Florida revealed culverts (single or multiple) were the dominant crossing type. Barrier severity score was < 0.5 for 117 of the surveyed crossings, meaning AOP was likely strongly affected at approximately 10% of the surveyed locations. When field observations were paired with remotely sensed data in a tree-based modelling framework, we found that landscape variables related to natural (stream size and elevation) and anthropogenic (upstream road crossing density, human population density, agricultural land use) properties explained 54% of variation in barrier severity scores. These landscape variables point to culverts with the strongest effect on AOP occurring on small to medium size streams at higher elevations and where human alterations to land cover such as urbanization and agriculture are prevalent. The ratio between surveyed locations and intersections of roads and streams was 1:5, indicating that inclusion of unsurveyed sites is necessary for aquatic connectivity conservation planning (see also Januchowski et al. 2019). We developed a predictive model that allowed for estimating the number and locations of barriers across the landscape. This allowed for fitting optimization scenarios to both surveyed and unsurveyed locations to identify the highest priority locations to be included in remediation planning. The surveyed barriers identified in optimization scenario 1 represent immediate options for mitigation given that those locations were already visited, whereas barriers identified in scenario 2 represent high priority locations for additional survey work. Our case study identified one crossing at which adjustments to a grade control structure might benefit AOP (potentially without resurfacing roads), meaning costs could be lower than estimated. When we repeated the optimization process for modelled crossings to identify locations for targeted field surveys we found geographic "hotspots" where surveys could be concentrated to identify new mitigation projects. Our work advances the science of aquatic connectivity conservation by addressing challenges related to increasing the spatial scale of mitigation planning, and provides direction for "boots on the ground" survey and mitigation planning over short- and long-term time horizons. Furthermore, out work identified landscape components that contributed to reduced AOP and thus should be included in landscape planning.

Our results suggest both natural gradients in stream size and human alterations to landscapes are correlated with road-stream crossings with greater barrier severity scores. The BRT model identified 45 biotic and abiotic variables that contributed to reduced AOP, but eight anthropogenic and natural variables captured 66% of relative influence (see Table 3). The model identified higher AOP for large (drainage area > 1 $\log_{10}[km^2]$), high discharge (> 1 $\log_{10}[m^3/s]$) watersheds with lower water velocities, fewer road crossings (< 0.2 $\log_{10}[roads/km^2]$), fewer people (< 2 $\log_{10}[people/km^2]$), and less agricultural influence (< 2 $\log_{10}$[M g/d] production; < 1 $\log_{10}$[% pasture land cover]) within the watershed. Potential barriers to AOP, such as culverts, tend to increase in density in both agricultural fields and cities, and are known to create greater water velocities which can lead to a reduction in AOP (Briggs & Galarowicz, 2013, Olsen, Tullis, & ASCE, M. , 2013). This study quantified the thresholds at which these agricultural landscape alterations begin to have an effect on AOP within the region. Road density increases as a population density increases (Glover & Simon, 1975, Hawbaker, Redeloff, Hammer, & Clayton, 2004), which undoubtedly results in road-stream crossings contributing to the degradation of urban streams (e.g., Walsh et al., 2005). However, it is also true that roads are commonplace in agricultural landscapes as a necessity to move products and farming equipment between fields or to distribution centers (Hawbaker et al., 2004). Construction of such barriers to passage are a result of an engineering decision related to

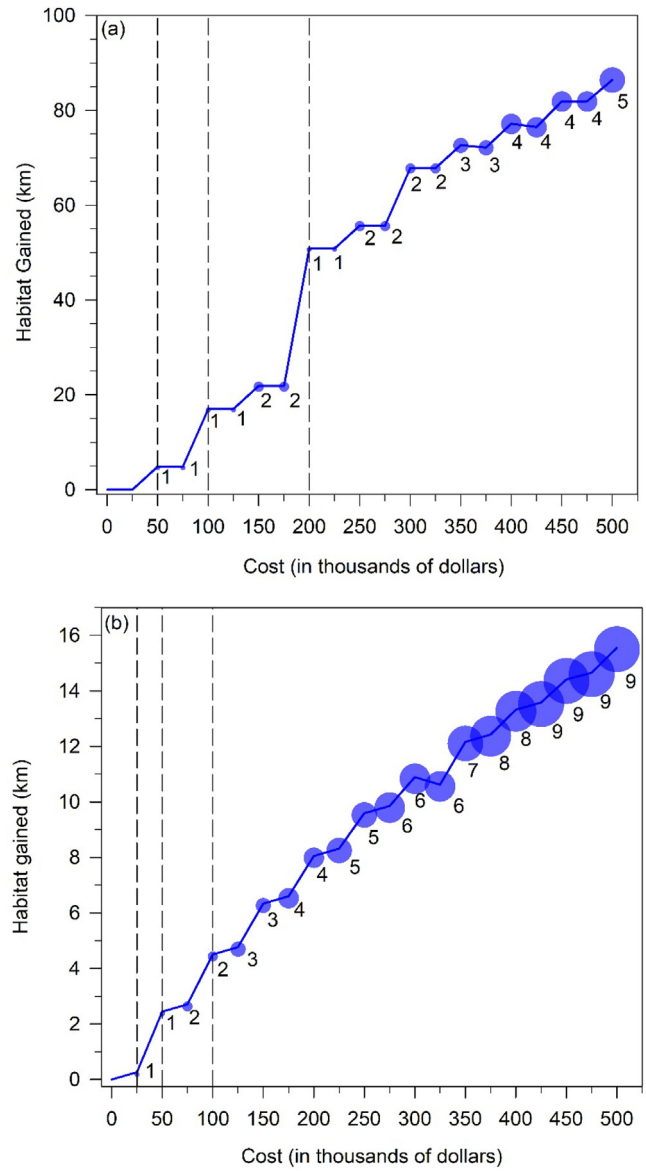

Fig. 4. Relationship between estimated cost of barrier mitigation (removal and replacement) and the length of habitat gained (km) for budgets ranging $0 to $500,000 (USD) incremented by $25,000 for (a) surveyed crossings and (b) modelled crossings. The size of symbols (and numbers near symbols) represent the number of crossings that need to be mitigated to achieve habitat gains (see Table 4 for identity of surveyed barriers, Fig. 5 for their locations, and Appendix G for their photographs). Dashed lines represent thresholds where percent increase in habitat gained was most significant (see Appendix F for threshold results).

stream passage type at road crossings. Culverts, rather than bridges, are typically used as crossing structures on small streams because they are cost efficient, easy to deploy, and can span small to medium channels when multiple structures are installed (Gibson et al., 2005). Our results identify the stream sizes at which the decision to place a culvert versus a bridge could be better planned so that AOP and structure stability might simultaneously benefit. Undersized culverts do not last long on larger streams because they are degraded by high flows (Gillespie et al., 2014), and are therefore unsafe and not cost effective in the long term when placed on streams that are too large. Our findings also highlight the potential for upstream crossings to affect downstream crossings, meaning serial barriers exist along stream corridors perhaps because they exist together in altered landscapes (i.e., spatial autocorrelation). Alternatively, this pattern could be caused by non-independence among crossings such that upstream alterations propagate in an upstream-downstream direction to cause barriers to form at nearby road-stream crossings (e.g., Jones, Swanson, Wemple, & Snyder, 2000). Future research might uncover the mechanism behind the relationship between upstream crossings densities and lower passability scores, but one proposed solution for addressing the effects of flood pulses on crossings involves the installation of crossing designs that simulate natural stream channels and allow for greater passage of aquatic organisms (Gillespie et al., 2014).

Field surveys and modelling work presented here revealed that road-stream crossings were common features in Florida riverscapes. Given the large number of crossings that could be mitigated, conservation planning requires identifying the structures that provide the largest return on investment from mitigation actions. An increasingly applied method for maximizing return on investment is the use of optimization models in which upstream habitat reconnected after mitigation is considered the return while funds required for barrier mitigation are considered the cost (O'Hanley & Tomberlin, 2005; Neeson et al., 2015). These models require input information on barrier locations, upstream habitat length, barrier passability, and mitigation cost. In this study, barrier locations were estimated from field surveys as well as intersections between road networks and stream networks (Januchowski-Hartley et al., 2014), and upstream habitat that could be reconnected was estimated using the BAT (Hornby, 2010). The barrier passability component of the optimization framework can be estimated using a number of methods, including species-specific estimates based on organism swimming, jumping, or climbing ability (reviewed by Kemp and O'hanley, 2010). The barrier severity scores developed by NAACC (2019) range 0–1 as with direct passability estimates, but they do not take into account heterogeneity in organism interpretation of barriers. For example, shallow water might be passable by crayfish but not fish species (Foster & Keller, 2011). Consequently, the barrier severity scores used here should not be interpreted as direct measures of passability, but instead relative condition of crossings. Crossings with low barrier severity scores are likely impassable by most organisms, and future research linking barrier severity scores to organism movement might identify such relationships (e.g., Mahlum, Cote, Wiersma, Kehler, & Clarke, 2014). In the meantime, the barrier severity score represents an excellent measure of relative condition across barriers, shows correlation with landscape variables, and allows use of optimization modeling for conservation planning. The final component to optimization modelling is the cost of barrier mitigation. Barrier removal costs have been estimated based on known structure dimensions (Neeson et al., 2015), stream size, road type, and both stream size and road type (Thomson & Pinkerton, 2008). The approach used here involved using a base cost for replacement of a typical crossing on an unpaved road over a small stream, and adjusting this cost according to increases in road and stream sizes. Although individual project costs will undoubtedly vary from these estimates, this approach did provide a basic framework for incorporating realistic spatial heterogeneity in project costs in optimization modeling. Given that optimization is an iterative process, future work incorporating refined cost estimates can easily be built into the framework presented here. Other improvements to optimization are possible, such as incorporation of ecological information (King & O'Hanley, 2016), and the baseline framework provided here can incorporate these modifications.

Three studies have attempted to model the distribution of barriers associated with road-stream crossings. Januchowski-Hartley et al. (2014) developed a suite of boosted regression tree models that predicted the occurrence of barriers caused by either vertical drops (i.e., anthropogenic waterfalls; one model) or artificially increased current velocities (three models) based on remotely sensed landscape variables in the Great Lakes region. The authors included remotely sensed data representing upstream drainage area and stream segment slope (degrees) or gradient (m/m) in their models. In a separate study, Collins (2016) developed a suite of random forest models to predict the

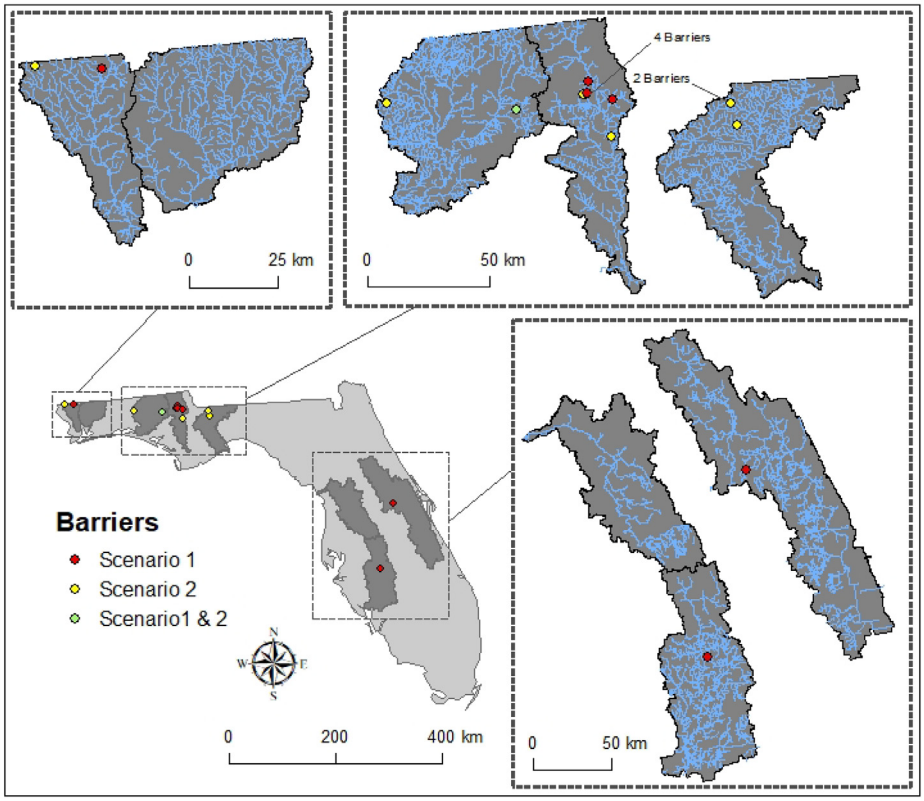

Fig. 5. Map showing high priority crossings identified for mitigation using optimization analysis for surveyed (red points; Scenario 1) and modelled (yellow points; Scenario 2) scenarios across the eight study area sub-basins. The top right panel shows where symbols were too close to appear in the map alone and are indicated by lines and the number of barriers in that location. A single surveyed barrier (Candidate 4; green point) was identified as a high priority for mitigation in both scenarios. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

occurrence of three classes of barriers (i.e., passable, impassable, indeterminate) in the southeastern united states. In the Collins (2016) study, landscape variables included as predictor variables were measures of land cover and use, topography such a slope and gradient, upstream watershed area, and estimates of stream discharge. Model performance measured as the area under the curve (AUC) ranged 0.64–0.69 for Januchowski-Hartley et al. (2014) and 0.61–0.69 for Collins (2016). These model performance metrics fall into the category of "slightly better than random" as described by Hosmer and Lemeshow (2000) and implemented by Pittman and Brown (2011) and Malone et al. (2018). In a more recent study predicting barrier conditions in France, Januchowski et al. (2019) used boosted regression tree models to explain 35–40% of variation in structure heights across the country. Our model explained 54% of variation in barrier severity scores, providing a vast improvement beyond previous studies. This suggests the framework we present here could be used to advance stream connectivity conservation planning world-wide assuming standardized survey protocols and existing datasets are sufficient. Our application of the NAACC outside of the region in which it was developed suggest the methodologies are useful beyond the North Atlantic region, and we hope that future surveys are conducted based on the application described here. Landscape alteration data sources specific to regions not covered by the NHD (e.g., Davies et al. 2005) or a recent global dataset (Linke et al., 2019) mean the framework presented here can be carried out regardless of region.

Our findings operated within a set of contexts that should be considered during interpretation or when applied to new settings. Systematic inventories of road-stream crossings are sparse, yet such inventories are critical for conservation planning (Januchowski-Hartley et al., 2013). Work here represents application of a standardized crossing survey for the southeastern US that is routed in past work in the northeastern US and other areas within the southeast (Southeast Aquatic Resources Partnership (SARP), 2019; NAACC, 2019). Integration of consistent methodologies across such a broad area represents movement in the direction of standardized methodologies across regions; however, the survey protocol in this study varied slightly from other previous works (e.g., regression rather than classification) and consideration of these differences should be made when interpreting findings relative to previous works (Januchowski-Hartley et al., 2014; Collins, 2016). Access to stream crossings was another challenge. Field crews invested considerable time attempting to access crossings identified in our randomization, yet inaccessible crossings were not useful in modeling. Information on inaccessible crossings should still be of interest to connectivity planners given that future field crews might invest

Table 4
Details for surveyed barriers identified as candidates for mitigation during optimization modelling, including candidate ID number, the sub-basin in which crossings occurred, the length of upstream habitat, the condition of the road that crosses the stream, the passability score, and notes on the structure. See Fig. 5 for locations of candidate barriers.

Candidate ID	Sub-basin (HUC)	Upstream habitat (km)	Road Type	Passability Score	Notes
C1	Escambia (03140305)	10.3	Paved Road	0.21	Barrier caused by outlet perch and internal structures
C2	Upper St. Johns (03080101)	22.9	Trail	0.01	Barrier is a grade control structure for a downstream bridge
C3	Chipola (03130012)	1.9	Paved Road	0.33	Barrier is caused by outlet drop
C4	Lower Chocatwhatchee (03140203)	4.8	Paved Road	0.07	Barrier is caused by outlet drop
C5	Peace (03100101)	5.4	Paved Road	0.05	Barrier is caused by outlet drop
C6	Chipola (03130012)	5.5	Paved Road	0.41	Barrier is caused by outlet drop
C7	Chipola (03130012)	4.2	Paved Road	0.00	Barrier is caused by outlet drop

similar amounts of time in attempting to access the same crossings noted as inaccessible in this study. Furthermore, additional follow-up work on these inaccessible crossings could yield accesses and valuable information. Another caveat of this work is that estimated costs of remediation should be validated prior to budgeting projects. The materials and construction methods used for crossings varied substantially among those surveyed, at times seeming entirely random or perhaps a product of the materials available at the time of construction. This means that project costs will undoubtedly differ from estimates and should be carefully re-estimated once high priority candidates for remediation are identified. Although our model for predicting barrier locations outperformed previous models (Januchowski-Hartley et al., 2014; Collins, 2016), these predictions should be validated with future surveys prior to mitigation planning at unsurveyed crossings. Finally, recent works have illustrated that barrier mitigation actions (e.g., partial versus full replacement) or in the quality of habitat they reconnect can strongly influence ecological responses, and that restoration goals should be well-defined prior to mitigation action (Erős et al., 2018; Mahlum, Cote, Wiersma, Pennell, & Adams, 2018; Wellemeyer, Perkin, Fore, & Boyd, 2018).

5. Conclusions

This work highlights the need for greater information on road-stream crossings for aquatic habitat connectivity planning and provides a framework for addressing this need. Although systematic surveys of all crossings within a riverscape will provide the most information, this is logistically infeasible over short time horizons and is a costly endeavor. Surveys at a subset of crossing locations coupled with modelled predictions at remaining crossing locations is an achievable alternative, but development of classification models with high accuracy has been challenging (Januchowski-Hartley et al., 2014; Collins, 2016). This study used a regression-based model and continuous barrier severity scores and found that landscape variables explained over half of the variation in scores. These models might be improved in the future with consideration of other variables, but they do advance the current state of the science of aquatic connectivity planning. Results from the two optimization scenarios modelled here suggest that omitting barriers from consideration during connectivity planning can significantly affect decision making (Januchowski et al. 2019). For example, the amount of upstream habitat that could be gained if barriers were mitigated was reduced by 80% in Scenario 2 (maximum of 15 km) compared with Scenario 1 (maximum of 90 km). Future advances in aquatic connectivity conservation planning could come from iterative implementation of optimization scenarios as new information on barrier locations is collected, estimated costs of mitigation are refined, and existing barriers are mitigated.

CRediT authorship contribution statement

Joshuah S. Perkin: . **:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Matthew R. Acre:** Methodology, Software, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Jessica Graham:** Conceptualization, Supervision, Project administration, Funding acquisition, Writing - original draft, Writing - review & editing. **Kathleen Hoenke:** Conceptualization, Software, Resources, Formal analysis, Writing - original draft, Writing - review & editing.

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Appendix A. Variables measured at crossings designated as culverts (single or multiple) or bridges that constrained the stream channel and therefore could influence organism passage. Scoring weightings are used in conjunction with values in Appendix b to assign passability scores for each crossing.

Variable	Definition	Scoring weight
Outlet drop	Structure outlet relative to water surface; Equation 3	0.161
Physical barriers	Occurrence of obstructions within the structure	0.135
Constriction	Structure width relative to stream width	0.090
Inlet grade	Position of structure inlet relative to stream bottom	0.088
Water depth	Water depth in structure relative to stream	0.082
Water velocity	Water velocity in structure relative to stream	0.080
Scour pool	Occurrence of eroded pool at outlet of structure	0.071
Substrate match	Substrate in structure relative to substrate in stream	0.070
Substrate coverage	Percent of bottom of structure covered by substrate	0.057
Openness	Cross-section area of structure divided by structure length; see Equation 1	0.052
Height	Maximum height inside structure; Equation 2	0.045
Outlet armoring	Occurrence of materials to prevent erosion of outlet	0.037
Internal structures	Occurrence of internal support structures	0.032

Appendix B. Categorical variables and scores for crossings designated as potential barriers to aquatic organism passage. Each variable was assigned a level and score according to the given definition and used in continuous scorings of barrier severity (see text for overview of scoring).

Variable	Levels and definitions	Score
Constriction	Severe – crossing width < 50% of stream width	0
Constriction	Moderate – crossing width 50–99% of stream width	0.5
Constriction	Spans only active channel – crossing width equal to stream	0.9
Constriction	Spans full channel – banks exist within the crossing	1
Inlet grade	At stream grade – inlet of structure level with stream	1
Inlet grade	Inlet drop – water from stream has vertical drop into structure	0
Inlet grade	Perched – inlet of structure is higher than stream	0
Inlet grade	Clogged/collapsed/submerged – physical barriers at inlet	1

Inlet grade	Unknown – the inlet cannot be located	1
Internal structures	None – no apparent structures in inlet	1
Internal structures	Baffles (partial width) or weirs (full width) present	0
Internal structures	Supports – structural supports such a piers or beams present	0.8
Internal structures	Other	1
Outlet armoring	Extensive – non-erosive material covers > 50% of stream width	0
Outlet armoring	Extensive – non-erosive material covers < 50% of stream width	0.5
Outlet armoring	None – No material in place to prevent erosion	1
Physical barriers	None – no physical barriers that block movement in place	1
Physical barriers	Minor – < 10% of structure is blocked	0.8
Physical barriers	Moderate – 10–50% of structure is blocked	0.5
Physical barriers	Severe – > 50% of structure is blocked	0
Scour pool	Large – tailwater pool is > 2-times the size of reference pools	0
Scour pool	Small – tailwater pool is 1–2-times the size of reference pools	0.8
Scour pool	None – No scour pool present	1
Substrate coverage	None – substrate covers < 25% of structure floor	0
Substrate coverage	25% – substrate covers 25–50% of structure floor	0.3
Substrate coverage	50% – substrate covers 50–75% of the structure floor	0.5
Substrate coverage	75% – substrate covers 75–99% of the structure floor	0.7
Substrate coverage	100% – substrate covers the entire floor of the structure	1
Substrate match	None – no substrate is present	0
Substrate match	Not appropriate – substrate size very different from stream	0.25
Substrate match	Contrasting – substrate size contrasts what is in stream	0.75
Substrate match	Comparable – substrate matches what is in the stream	1
Water depth match	No – significantly deeper than stream	0.5
Water depth match	No – significantly shallower than stream	0
Water depth match	Yes – comparable to stream depth	1
Water depth match	Dry – structure and streambed are dry	1
Water velocity match	No – significantly faster in structure compared to stream	0
Water velocity match	No – significantly slower in structure compared to stream	0.5
Water velocity match	Yes – comparable to water velocity in stream	1
Water velocity match	Dry – structure and streambed are dry	1

Appendix C. Estimated costs of barrier mitigation (removal and replacement) across gradients in road size and stream size. The base cost ($25,000) increases 2x and 4x as road size increases because of costs associated with road refinishing, while the base cost increases 2x and 4x as stream size increases because of costs associated with spanning wider streams.

Stream size	Forest road	Paved road	Major road
Stream order 1	$25,000	$50,000	$100,000
Stream order 2	$50,000	$100,000	$200,000
Stream order 3+	$100,000	$200,000	$400,000

Appendix D. Breakdown of crossing types, number surveyed during the study, and the mean (minimum – maximum) barrier severity scores for each crossing type.

Crossing type	Number	Barrier Severity
Bridge Adequate	446	1.00 (1.00–1.00)
Multiple Culvert	366	0.71 (0.01–1.00)
Culvert	258	0.67 (0.00–1.00)
Bridge	93	0.93 (0.21–1.00)
Ford	8	1.00 (1.00–1.00)
Removed Crossing	5	1.00 (1.00–1.00)
No Crossing	3	1.00 (1.00–1.00)
No Upstream Channel	2	1.00 (1.00–1.00)
Natural Ford	1	1.00 (1.00–1.00)

Appendix E. Results of optimization modelling on surveyed crossings showing estimates cost, habitat gains, and candidate barriers for remediation for budgets ranging $0-$500,000 by $25,000 increments. See Table 4 for details on candidate barriers.

Estimated cost	Habitat gain (km)	Candidate barriers
$0.00	0	none
$25,000.00	0	none
$50,000.00	4.85	C3
$75,000.00	4.85	C3
$100,000.00	17.00	C1
$125,000.00	17.00	C1
$150,000.00	21.85	C1 + C3
$175,000.00	21.85	C1 + C3
$200,000.00	50.82	C2
$225,000.00	50.82	C2
$250,000.00	55.67	C2 + C3
$275,000.00	55.67	C2 + C3
$300,000.00	67.82	C1 + C2
$325,000.00	67.82	C1 + C2

$350,000.00	72.68	C1 + C2 + C3
$375,000.00	72.16	C1 + C2 + C6
$400,000.00	77.18	C1 + C2 + C3 + C4
$425,000.00	76.49	C1 + C2 + C4 + C7
$450,000.00	81.90	C1 + C2 + C3 + C5
$475,000.00	81.90	C1 + C2 + C3 + C5
$500,000.00	86.41	C1 + C2 + C3 + C4 + C5

Appendix F. Results from χ^2 tests to identify barrier removal thresholds. Thresholds are represented in bold and were identified as barriers that contribute significant gains in upstream habitat if those barriers were mitigated (i.e., removed and replaced). Scenario 1 (S1) is based on observed barriers and Scenario 2 (S2) is based on predicted barriers. Monetary steps were in increments of $25,000 USD, the threshold column shows which scenario was identified at that monetary step, net gain is represented by linear kilometers (km) gained, the barriers mitigated column is the number barriers altered, percent habitat gained is relative to the previous monetary step, and the % χ^2-value identifies the contribution of each monetary step to the overall model significance.

Scenario 1 – $X^2_{20} = 1054$, $p < 0.001$ ——— Scenario 2 - $X^2_{20} = 906$, $p < 0.001$									
Monetary Step	Threshold	Net Gain (km)		Barriers Mitigated		% Habitat Gained		% of χ^2-value	
		S1	S2	S1	S2	S1	S2	S1	S2
$ -	–	0.00	0.00	0	0	0.00	0.00	1.36	1.86
$ 25,000.00	Scenario 2	0.00	0.26	0	1	0.00	100.00	1.36	45.29
$ 50,000.00	Scenario 1&2	4.85	2.44	1	1	100.00	89.32	48.62	34.40
$ 75,000.00	–	4.85	2.70	1	2	0.00	9.65	1.36	0.34
$ 100,000.00	Scenario 1&2	17.00	4.51	1	2	71.47	39.97	21.63	3.50
$ 125,000.00	–	17.00	4.77	1	3	0.00	5.48	1.36	0.85
$ 150,000.00	–	21.85	6.34	2	3	22.20	24.80	0.41	0.41
$ 175,000.00	–	21.85	6.60	2	4	0.00	3.95	1.36	1.09
$ 200,000.00	Scenario 1	50.82	8.05	1	4	57.00	18.06	12.06	0.01
$ 225,000.00	–	50.82	8.31	1	5	0.00	3.14	1.36	1.23
$ 250,000.00	–	55.67	9.59	2	5	8.71	13.34	0.21	0.08
$ 275,000.00	–	55.67	9.86	2	6	0.00	2.65	1.36	1.32
$ 300,000.00	–	67.82	10.89	2	6	17.92	9.51	0.09	0.35
$ 325,000.00	–	67.82	10.62	2	6	0.00	−2.55	1.36	2.47
$ 350,000.00	–	72.68	12.16	3	7	6.68	12.67	0.39	0.11
$ 375,000.00	–	72.16	12.42	3	8	−0.72	2.10	1.50	1.43
$ 400,000.00	–	77.19	13.32	4	8	6.52	6.74	0.40	0.67
$ 425,000.00	–	76.49	13.58	4	9	−0.91	1.92	1.54	1.46
$ 450,000.00	–	81.90	14.41	4	9	6.61	5.76	0.39	0.81
$ 475,000.00	–	81.90	14.65	4	9	0.00	1.67	1.36	1.51
$ 500,000.00	–	86.42	15.55	5	9	5.22	5.77	0.55	0.81

Appendix G. . Photographs of outlets for surveyed crossings identified by optimization analysis as high priority candidates for mitigation. See Table 4 for details on each candidate crossing. Crossings shown more than once are denoted by lower case letters.

Appendix H. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2020.103860.

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