Diversity and Distributions, (Diversity Distrib.) (2014) **20**, 1414–1424

A Journal of Conservation Biogeography

Diversity and Distributions

BIODIVERSITY RESEARCH

Predicting road culvert passability for migratory fishes

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ABSTRACT

Aim Our goal was to predict road culvert passability, as defined by culvert outlet drop and outlet water velocity, for three fish swimming groups using remotely collected environmental variables that have been shown to influence the passability of road culverts.

Locatio Laurentian Great Lakes Basin, north-eastern North America, on the Canada–USA border.

Methods We generated four boosted regression tree models, one for road culvert outlet drop and one each for the three culvert outlet water velocities, and predicted the probability of impassable road culverts on low-order streams (Strahler 1-4) based on the models. Independent variables in the models included the upstream area draining to the culvert, slope at the culvert, stream segment gradient and stream reach gradient.

Results Gradient of the stream segment was the most important predictor in the outlet drop model, while upstream drainage area was the most important predictor in the three water velocity models. A majority of road culverts on low-order streams are estimated to be passable even for weaker swimming fishes. Moderate to highly impassable road culverts are distributed across many low-order streams throughout the basin, but particular regions are predicted to have higher densities than others due to topography.

Main conclusions Predicted passability of road culverts by migratory fish is related to natural gradients in topography and stream size. While the probability of any particular culvert being impassable is low, the vast number of culverts in the basin means that, together, they could pose a greater challenge to migratory fish than dams. Our modelling framework could be used in any region where culverts are prevalent in the riverscape. The resulting estimates of passability to fishes can guide surveys towards the most problematic hydrological regions and structures and contribute to broad-scale prioritization of barrier removals to restore ecological connectivity.

Keywords

Distribution maps, ecological connectivity, fish passage, Laurentian Great Lakes Basin, remediation.

INTRODUCTION

Engineered in-stream structures such as road culverts and dams impede fish movement within and between aquatic systems around the globe. Although similar in concept to habitat fragmentation in terrestrial ecosystems, barriers are particularly damaging to aquatic ecosystems due to the longitudinal nature of river networks (Fagan, 2002). The negative ecological effects of in-stream structures are becoming increasingly documented (Warren & Pardew, 1998; Poplar-Jeffers *et al.*, 2008; Pépino *et al.*, 2012). Specifically, road culverts have been shown to cause reductions in fish movement compared to other crossing types (e.g. bridges) and unimpaired river reaches (Warren & Pardew, 1998). The pervasiveness of road–stream intersections (herein referred to as road crossings) across the landscape creates a pressing need

DOI: 10.1111/ddi.12248
http://wileyonlinelibrary.com/journal/ddi

to improve or upgrade road culverts to facilitate native fish migrations as well as other ecological processes (Januchowski-Hartley *et al.*, 2013).

It is challenging to determine whether or not a road culvert acts as a barrier to fish movement. Several physical factors have the potential to limit fish passage through culverts, including structure length, water velocity and depth, outlet drop or a lack of velocity refugia in the structure (Love & Taylor, 2003). Fish species vary widely in their ability to move against currents or traverse steep grades (Haro *et al.*, 2004; Peake, 2008), so it is difficult to generalize about structure passability. In addition, most species require passage only at particular times of the year to reach spawning, rearing or overwintering habitats (Lucas & Baras, 2001), so seasonal variation in passability is also an important consideration (Fullerton *et al.*, 2010). Therefore, the passability of a road culvert reflects a complex range of factors, including the natural topography and hydrology of the landscape, the features of the culvert itself, structure installation and maintenance, and the needs and swimming capacity of the fish species in question (Kemp & O'Hanley, 2010).

Whether a road culvert acts as a partial or full barrier for migratory or resident stream fishes is commonly determined through field surveys that assess the physical and hydrodynamic properties of structures (Love & Taylor, 2003), and sometimes by subsequent hydraulic modelling (Furniss *et al.*, 2008). While these methods are useful for estimating the passability of individual culverts or even all culverts within small watersheds (Poplar-Jeffers *et al.*, 2008; Bourne *et al.*, 2011), they are too time-consuming to use across large watersheds or basins containing tens or hundreds of thousands of culverts (Januchowski-Hartley *et al.*, 2013). Alternative metrics based on fish distribution patterns or genetics have been suggested as indirect ways of determining structure passability or disrupted fish dispersal. However, these methods depend on species-specific knowledge of expected distributions, require specialized scientific expertise and can be expensive to undertake. There remains a need for low-cost, transferable methods that can be used to predict road culvert passability for a large number of structures based on limited data from on-ground surveys. Such methods could be used to understand the conditions that are most likely to produce impassable culverts, target regions and specific structures for on-ground surveys, and estimate the frequency of occurrence of passage problems across large regions (Bourne *et al.*, 2011).

The Laurentian Great Lakes Basin (hereafter Great Lakes Basin) is located in north-eastern North America on the Canada–USA border. The Great Lakes and their tributary rivers supply important services and amenities essential to the well-being of regional human populations, but also face numerous threats from human activities (Allan *et al.*, 2013). Two major threats to freshwater biodiversity and ecosystem function in the Great Lakes Basin are road culverts and dams (Januchowski-Hartley *et al.*, 2013; Pearsall *et al.*, 2013) which fragment the riverscape, disconnect native populations of aquatic species and limit dispersal and migration of species between the Great Lakes and their tributaries. Recently, there have been growing efforts to prioritize road culvert and dam remediation projects to maximize longitudinal stream connectivity for both migratory and resident stream fishes (e.g. Januchowski-Hartley *et al.*, 2013; O'Hanley *et al.*, 2013). Road-crossing prioritization assessments have generally been conducted within a single watershed (e.g. Poplar-Jeffers *et al.* 2008; O'Hanley *et al.*, 2013) or several small neighbouring watersheds (e.g. Park *et al.*, 2008), thereby overlooking the system-wide context for restoring habitat access for fish and other aquatic organisms. This could be particularly problematic for migratory species, which often reside in large water bodies but seek distant habitats as breeding grounds.

Here, we expand on previous studies by evaluating road culvert passability on low-order (Strahler orders 1-4) streams across the entire Great Lakes Basin. First, we examine whether remotely collected environmental variables can be used to explain variability in observed road-crossing passability, as defined by culvert outlet drop and water velocity, for three groups of fishes classified by swimming ability. Second, we use the resulting models to predict the probability that unsampled road culverts would pose a passability challenge for fishes in each of the three swimming groups. Third, we map our results across the Great Lakes Basin and characterize the spatial variability of road culvert passability for fishes. Finally, we discuss the implications for broad-scale conservation efforts aimed at restoring ecological connectivity within freshwater ecosystems.

METHODS

Study area

Our study spanned the basins draining to the Great Lakes (769 989 km^2), not including the land area draining directly to the St. Lawrence Seaway. This includes all or part of eight states in the USA and one province in Canada. There are 107 hydrological units on the USA side of the Great Lakes Basin and 53 on the Canadian side (Fig. 1). We represented hydrological units in the USA with HUC8 divisions from the U.S. Geological Survey's Watershed Boundary Dataset (USGS, 2010). Hydrological units in Canada were represented with the watersheds provided through the National Hydrological Network dataset (Geobase, 2013). Hydrological units range in area from 29 to 25 208 km^2 because they are nested within or are equivalent to hydrological subregions, which are defined as a section of river and its tributaries, a closed basin or a group of streams forming a coastal drainage area (USGS, 2010; Geobase, 2013).

We summarized the number and density (km^{-2}) of road crossings within 160 hydrological units based on the 268 818 road crossings identified by Januchowski-Hartley *et al.* (2013). There are several islands in each of the five great lakes for which there are no mapped hydrological regions. Therefore, road crossings on these islands (< 1% of all road

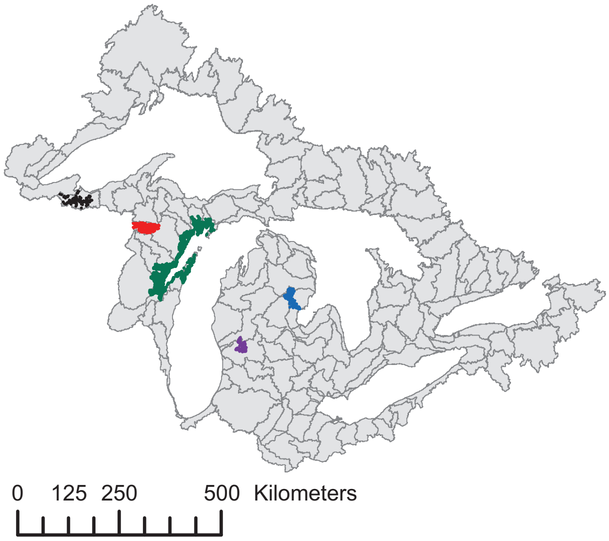

Figure 1 Map of the Laurentian Great Lakes Basin (dark grey area) in north-eastern North America, on the Canada–USA border, and the locations of road culvert field surveys conducted in the Bad – Montreal watersheds (black), Pine – Popple watersheds (red), Green Bay study area (green), Au Gres – Rifle watersheds (blue) and Rogue – Lower Grand watershed (purple).

crossings in the basin) were not considered in our hydrological unit summaries.

Data

Road culverts

Approximately 93% of the 268 818 road crossings identified by Januchowski-Hartley *et al.* (2013) occur on low-order streams (Strahler orders 1-4). We had data from field assessments conducted at 2235 road culverts located across nine hydrological units within the Lake Michigan, Superior, and Huron basins on these low-order streams (Fig. 1). The majority of field assessments were conducted when stream flows were less than or equal to base flow during the summer and fall of 2010–2012. All surveyed structures occurring along streams of Strahler order five and above were identified as bridges or large culverts that would not pose a passability challenge for fishes; therefore, we focused our analyses on road culverts occurring on low-order streams. Based on the range of environments represented by the sampled culverts (Table 1), we believe this sample is adequate for developing a robust model that can be used to predict conditions at unsampled road culverts in the Great Lakes Basin.

Passability criteria

Passability estimates were based on the occurrence of an outlet drop and culvert outlet water velocity. These two factors have frequently been shown to constrain whether fishes can pass through road culverts (e.g. Love & Taylor, 2003; MacPherson *et al.*, 2012). Additional factors that influence passability, such as the presence/absence of substrate in the culvert that can provide velocity refuge, were not considered because the field survey data lacked consistent information on these factors.

Culvert outlet drop was measured as the vertical distance between the lower edge of the structure outlet and the water surface of the stream. Outlet water velocity was measured in the boundary layer of slower velocity where it was expected that an adult fish would swim. If water depth was < 12 cm, velocity was measured at the midpoint of the water depth at the deepest point of the cross section. If water depth was > 12 cm, velocity was measured at 6 cm above the substrate at 2–4 points that were deeper than 12 cm and recorded as the lowest of these velocity values.

Many native fishes in the Great Lakes Basin exhibit some degree of migratory behaviour (McLaughlin *et al.*, 2006; Landsman *et al.*, 2011; Herbert *et al.*, 2012), including several small-bodied species such as river darter (*Percina shumardi*) and spottail shiner (*Notropis hudsonius*). Unlike salmonids, many of the large-bodied migratory species in the Great Lakes such as lake sturgeon (*Acipenser fulvescens*) and walleye (*Sander vitreus)* are not known to leap over barriers to move upstream. Because detailed information on swimming and leaping ability for most Great Lakes native migratory fishes is not available, we used conservative criteria for determining culvert passability. The presence of any drop from the structure outlet to the downstream water surface was considered impassable by all species. We chose three

Table 1 Summary statistics of environmental variables used to characterize both the sampled and all road culverts occurring on low-order (Strahler order 1-4) streams in the Laurentian Great Lakes Basin.

			Sampled culverts			All culverts		
Variable	Reflects	Description	Mean	10%	90%	Mean	10%	90%
Upstream drainage area (km^2)	Stream size, discharge	Area draining to road culvert	9.8	0.5	25.9	5.8	0.2	15.6
Site slope (degrees)	Site-scale topography	Slope of 30 m DEM pixel at site	1.3	0.0	2.7	1.8	0.0	3.9
Stream segment gradient (m m^{-1})	Hydrological regime	Gradient of confluence-bounded stream segment	0.01	0.1	1.0	0.01	0.6	3.0
Stream reach gradient (m m^{-1})	Reach-scale stream energy	Gradient of 300 m stream reach	0.01	0.0	2.0	0.01	0.0	4.0

water velocity thresholds, 0.4, 0.7 and 1.0 m s^{-1}, to represent a range of swimming abilities. The 0.4 m s^{-1} threshold was aimed at identifying road culverts that were impassable in an upstream direction under base or higher flow conditions for young or weak swimming migratory fish species such as the river darter (*Percina shumardi*) (Warren & Pardew, 1998; Anderson *et al.*, 2012). The 0.7 m s^{-1} threshold was aimed at identifying the occurrence of road culverts that would be impassable by migratory species with moderate swimming speeds, such as adult northern pike (*Esox Lucius)*, walleye (*Sander vitreus)* or white suckers (*Catostomus commersonii*) that are moderately strong swimmers (Peake 2008). Finally, the 1.0 m s^{-1} threshold was aimed at identifying the occurrence of structures that would be impassable by strong swimming species during base or higher flows. By modelling outlet drop and velocity separately and considering a range of velocity thresholds, we acknowledge uncertainty about the key factors that determine passability (Mahlum *et al.*, 2014), and produce results that may be interpreted differently as new knowledge on fish swimming performance is acquired.

Environmental predictors

We limited our selection of predictor variables to those that were available for the entire Great Lakes Basin and assembled spatial data for four environmental predictors of passability: (1) upstream area draining to the culvert, (2) stream segment gradient, (3) stream reach gradient and (4) slope at the site of the culvert to represent both broad and local topographical variation that could influence the condition of road culverts (Table 1). Each of these environmental variables has been shown to influence the passability of road culverts based on the association with outlet drops or impassable water velocities (Poplar-Jeffers *et al.*, 2008; Anderson *et al.*, 2012; Pépino *et al.*, 2012). All of our predictor variables were remotely collected and were summarized for each road culvert using ArcGIS 10 (ESRI, 2010).

We extracted upstream drainage area (km^2) and slope (in degrees) at the site of the culvert directly from a 30 × 30 m resolution digital elevation model, which was resampled from the Global Multi-Resolution Terrain Elevation Data (GMTED, 2010). The site slope was aimed at representing the continuity of local topography that could influence culvert hydraulic conditions and to which reach-scale gradient may not be sensitive. Using polylines representing streamlines (at 1:24 000 and 1:20 000 scales in the USA and Canada, respectively), we calculated stream gradient (rise/run) for segments bounded by confluences and for 300 m stream reaches. The hydrological regime of the stream – in particular the magnitude of higher flows, which may contribute to erosion and the development of an outlet drop between the culvert and the stream bottom – was represented by the gradient of the stream segment on which a culvert was located. This gradient of the 300 m stream reach was used to represent the energy of the stream in the local vicinity of each culvert (Park *et al.*, 2008).

Modelling road culvert outlet drop and water velocities

We used boosted regression trees (BRT, Elith *et al.*, 2008) to model the presence/absence of road culvert outlet drops and the presence/absence of road culvert outlets with water velocities equal to or > 0.4, 0.7 or 1.0 m s^{-1}.

To translate the model results into a summary passability index (e.g. O'Hanley *et al.*, 2013), we assigned the absence of an outlet drop as a one (indicating passable) and the presence of an outlet drop as a zero (indicating impassable). We followed the same logic for the water velocities; for each of the three thresholds, water velocities below the threshold were treated as ones (indicating passable), and those above the threshold were zeros (indicating impassable).

Presence/absence data for each of the four response variables were fitted using BRT models with binomial errors. BRT combines a regression tree algorithm and a boosting algorithm to produce an ensemble of trees (Friedman *et al.*, 2000; Elith *et al.*, 2008). The boosting algorithm is a machine-learning approach that improves upon standard regression tree modelling by adding a stochastic component that emphasizes the most poorly explained part of the data space (Friedman *et al.*, 2000; Elith *et al.*, 2008). All BRT models were fitted with a learning rate of 0.001 and tree complexity of five, using the R Statistical Package version 2.15.0, gbm package version 2.1 (Ridgeway, 2013) and code written by Elith *et al.* (2008). The learning rate, also known as the shrinkage parameter, determines the contribution of each tree to the growing model. Tree complexity controls whether interactions are fitted in the model: a tree complexity of one (single decision stump; two terminal nodes) fits an additive model, a tree complexity of two fits a model with up to two-way interactions, and so on.

Introducing some randomness into a boosted model usually improves accuracy and speed and reduces over-fitting (Friedman, 2002), but this can introduce variance in fitted values and predictions between runs. In the gbm package, stochasticity is controlled through a 'bag fraction' that specifies the proportion of data to be used at each step. We used the default bag fraction of 0.5 (Elith *et al.*, 2008), meaning that at each iteration, 50% of the data are randomly drawn from the full training dataset (n = 2235) without replacement. We tested a bag fraction of 0.5 and 0.75 and found little difference in model performance and therefore used the standard 0.5 (see Elith *et al.*, 2008). A tenfold cross-validation was used to identify the optimal number of trees for each model and to subsequently assess predictive performance of the four BRT models (Hastie *et al.*, 2001; Elith *et al.*, 2008).

We aimed to produce a model that not only identifies major environmental factors that differentiate passable culverts from impassable ones, but also predicts the probability of passage by migratory fishes with different swimming abilities for the numerous unsampled road culverts across the study region. BRT models can be used for prediction in the same way as any regression model, and prediction is based on the final BRT model, consisting of the sum of predictions from all trees multiplied by the learning rate. Using our final four BRT models, we predicted the probability that a culvert outlet drop would be absent (passable for fish), and the probability that culvert outlets would have water velocities ≤ 0.4, ≤ 0.7 or ≤ 1.0 m s^{-1}.

Model performance was assessed during cross-validation by comparing model predictions to withheld portions of data (Elith *et al.*, 2008). We report the mean area under the receiver operating curve (and standard error) as a measure of each models performance. The importance of each predictor variable in the four BRT models was evaluated based on the contribution to model fit attributable to each predictor, averaged across all trees (Friedman, 2001; Friedman & Meulman, 2003).

Calculating and summarizing road culvert passability

For each of the 249 310 road culverts on low-order streams, we used the product of the predicted probabilities of no culvert outlet drop and outlet water velocities below the three thresholds to represent the probability that fishes with weak, moderate or strong swimming abilities could pass through a structure. For each of the three water velocity thresholds, we then calculated the average passability within each of the 160 major hydrological units based on both our predicted passabilities for culverts on low-order reaches and assumed passability of 1.0 for road crossings on higher (Strahler order > 4) order reaches.

RESULTS

Both the number and density of road culverts were spatially variable across the 160 hydrological units (Fig. 2). In any single hydrological unit, the minimum number of road culverts was zero (two units), and the maximum was 8634, which occurs on the south-eastern edge of Lake Ontario. Road culvert density also varied across the 160 hydrological units, and those lining the southern end of Lake Erie and Ontario contained the highest density – up to 2.5 culverts km^{-2} (Fig. 2).

Our four BRT models showed reasonable model discrimination and predictive performances, as assessed using cross-validation (Table 2). The final predicted probabilities of road culvert outlet drop absence ranged from 0.30 to 0.94 across the Great Lakes Basin (Table 3). There was lower predicted probability of a road culvert having passable water velocities for fishes with weaker swimming abilities (i.e. water velocities ≤ 0.4 m s^{-1}) than for fishes with moderate to strong swimming abilities (i.e. water velocities ≤ 0.7 or ≤ 1.0 m s^{-1}) (Table 3).

Gradient of the stream segment and upstream drainage area were the most important predictors in the outlet drop model (Fig. 3a). Upstream drainage area made the greatest contribution to the three water velocity models (Fig. 3b–d), while gradient of the stream segment and slope at the road culvert had the second and third highest contributions (Fig. 3b–d). Fitted functions also provide a useful basis for interpreting the types of road culverts that will pose a problem for fish passage (Fig. 3). Our four model fitted functions indicate that low-order streams with an outlet drop are associated with stream gradients > 1%, with upstream drainage areas less than approximately 10 km^2 and with slopes greater than two degrees (Fig. 3a). Impassable outlet water velocities for fishes of all swimming abilities are most common on streams with upstream drainage areas between approximately 10 and 40 km^2 and with higher gradients and slopes at all scales (Fig. 3b–d). Using our four final fitted BRT models and hypothetical combinations of observed values of the four environmental variables, we found that a culvert with a relatively small drainage area (5 km^2) and high gradient (3% segment gradient, 5% reach gradient, 5° slope at the site of the culvert) has a 56% chance of having an outlet drop, and a 60% chance of having water velocities that would not allow weaker swimmers to pass.

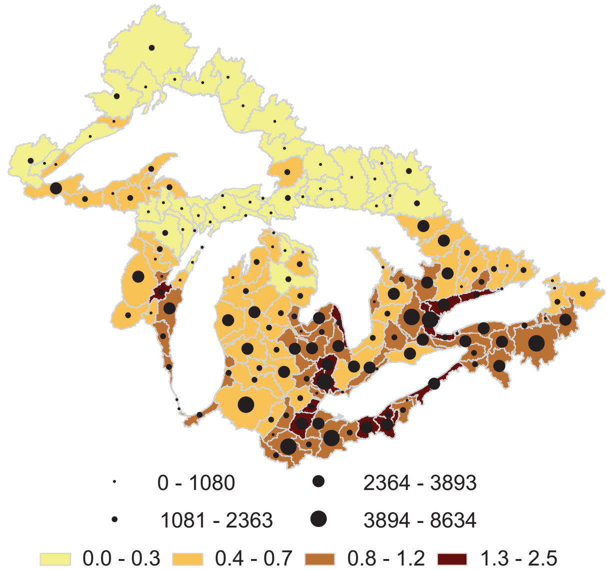

Figure 2 Number (size of dots) and density (km^{-2}) (colour) of road crossings on streams of all sizes (Strahler orders 1-9) within 160 hydrological units in the Laurentian Great Lakes Basin.

Table 2 Summaries of boosted regression tree models for road culvert outlet drop and three culvert outlet water velocities, including the number of trees, the mean area under the receiver operating curve (AUC) and standard error (SE) which were calculated using tenfold cross-validation for each model. AUC and SE indicate the expected model performance when predicting to new sites.

Model	Number of trees	AUC (SE)
Road culvert outlet drop absent	1950	0.69 (0.02)
Road culvert outlet velocity ≤ 0.4 m s^{-1}	2300	0.64 (0.01)
Road culvert outlet velocity ≤ 0.7 m s^{-1}	1250	0.64 (0.03)
Road culvert outlet velocity ≤ 1.0 m s^{-1}	3550	0.67 (0.04)

Table 3 The minimum, mean and maximum predicted probability of an outlet drop being absent from a culvert or outlet water velocities that are ≤ 0.4, 0.7 or 1.0 m s^{-1} for 249 310 road culverts on low-order streams (Strahler order 1-4) in the Laurentian Great Lakes Basin.

Model	Minimum probability	Mean probability	Maximum probability
Road culvert outlet drop absent	0.30	0.81	0.94
Road culvert outlet velocity ≤ 0.4 m s^{-1}	0.33	0.83	0.92
Road culvert outlet velocity ≤ 0.7 m s^{-1}	0.66	0.94	0.97
Road culvert outlet velocity ≤ 1.0 m s^{-1}	0.93	0.98	0.98

The predicted passability (product of predicted probabilities of outlet drop and outlet water velocity) of road culverts on low-order streams ranged between 0.14 and 0.86 for weak swimmers, whereas both the minimum and maximum road culvert passability were higher for moderate (min. = 0.25, max. = 0.89) and strong (min. = 0.28, max. = 0.92) swimmers (Fig. 4). Fourteen per cent of road culverts on low-order streams had a predicted passability < 0.5 for weaker swimmers, whereas only 5% had predicted passability < 0.5 for moderate and strong swimmers (Fig. 4).

The average passability of road culverts varied widely across hydrological units when accounting for both fully passable structures (those occurring on Strahler orders > 4) and potentially impassable road culverts (occurring on Strahler order 1-4). This finding applied to all three fish swimming speed groups. When considering all road culverts, more than 50% of all hydrological units in the Great Lakes had average passability > 0.80, regardless of fish swimming ability. While there was some variability in average passability for individual hydrological units when considering each of the fish swimming speed groups, it was relatively minor, and therefore, we present only the spatial variability of average passability across hydrological units for fishes with weak swimming abilities in Fig. 5a. Hydrological units bordering the south-eastern edge of Lake Ontario (Fig. 5b) and the north-eastern edge of Lake Erie consistently had lower average passability, while hydrological units across central Wisconsin and central and southern Michigan (Fig. 5c) had higher passability. Notably, hydrological units along the south-eastern edge of Lake Ontario with low average passability (Fig. 5b) also contained high numbers of road culverts (Fig. 2).

DISCUSSION

While there is a growing awareness that road culverts inhibit fish movement, until this analysis, there have been no reliable estimates of the prevalence of passability problems across large drainage areas. By estimating the probability that a road culvert could inhibit the movement of fishes with varying swimming abilities, our modelling framework contributes to the growing body of research aimed at understanding and measuring fragmentation of dendritic ecosystems. The influence of natural variation in road-crossing characteristics, including measures of topography and drainage area, on passability indicates that patterns of stream fragmentation are driven by a combination of natural and anthropogenic factors. While our study focused on the Great Lakes Basin, our overall findings and modelling framework can contribute to the challenging task of restoring fish passage in any region of the world that contains a high density of in-stream structures and where conducting on-ground surveys of all structures is infeasible.

Model performance and interpretation

We found that remotely collected environmental variables representing gradient, slope and drainage area can be used to explain the occurrence of road culvert outlet drop and water velocities that cause a passability challenge for fishes. The structures of our models are consistent with basic hydrological and hydraulic principles, field observations and results of previous studies at smaller scales (e.g. Park *et al.*, 2008; Poplar-Jeffers *et al.*, 2008; Doehring *et al.*, 2012). Consistent with finer scale studies (e.g. Park *et al.*, 2008; Poplar-Jeffers *et al.*, 2008), we found that after accounting for variation in stream gradient and landscape slope, culvert outlet drops are most likely to occur on small streams with drainage areas < 5 km^2. The relatively small vertical profile of culverts installed on small streams means the structures can be installed above the grade of the stream bed to maximize hydraulic capacity without requiring adjustments to the road grade, which increases project cost. As a consequence, these structures may have an outlet drop from the time of installation onward (Park *et al.*, 2008; Poplar-Jeffers *et al.*, 2008). In contrast, high water velocities were most common on larger streams after accounting for variation in stream gradient and slope. This finding likely reflects the occurrence of smaller diameter culverts relative to bankfull channel width on larger streams. For example, based on data included in our models from the Rifle River, USA (see Fig. 1), the average constriction ratio (culvert width/stream bankfull width) on larger streams with 3–6 m bankfull widths was 58%, while culverts on the smallest streams with bankfull widths < 2 m were an average of 96% of bankfull width (Huron Pines, unpublished data). Flow constriction has been shown to increase flow velocity through culverts by decreasing the ratio of the perimeter of flow, where friction occurs, to the cross-sectional area. Finally, we found that both outlet drops and high water velocities were more common on streams with high gradients at both the segment and reach scales, a finding consistent with those from road-crossing surveys in Alberta, Canada (Park *et al.*, 2008) and West Virginia,

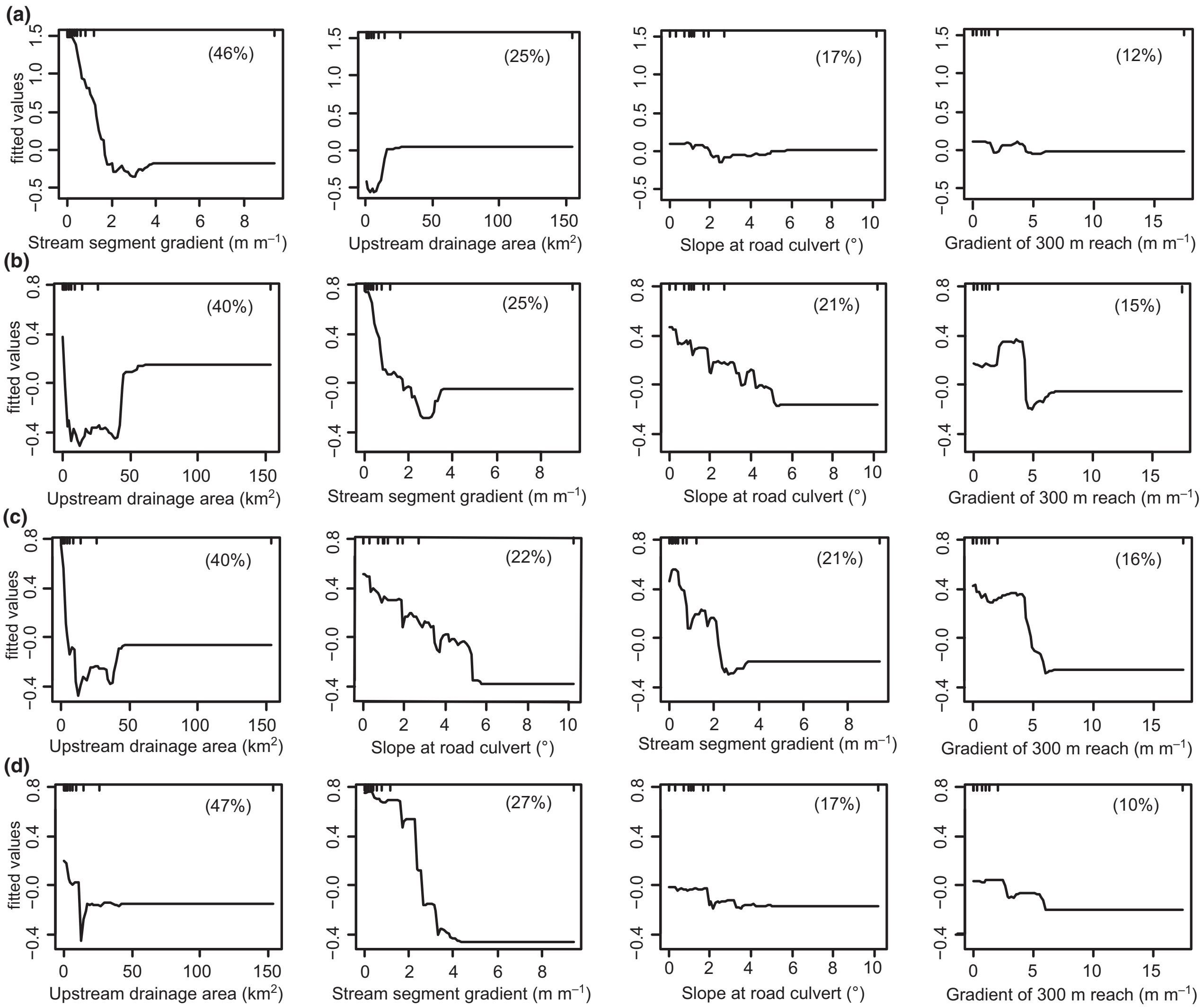

Figure 3 Partial dependence plots for the four influential variables in the models for (a) culvert outlet drop absence, and of culvert outlet water velocity less than or equal to (b) 0.4 m s^{-1}, (c) 0.7 m s^{-1} and (d) 1.0 m s^{-1}. Percentage values indicate the relative importance of the predictor variable in each boosted regression tree model. Rug plots inside the top of each plot show the distribution of observations across the range of that variable, in deciles.

USA (Poplar-Jeffers *et al.*, 2008). High-gradient streams naturally have more energy than low-gradient streams, which leads directly to higher water velocities and may lead indirectly to the formation of culvert outlet drops through erosion of the downstream streambed (Poplar-Jeffers *et al.*, 2008). In high-gradient streams, flow velocities are likely to exceed 1 m s^{-1} in sections of natural channel; in small streams, these sections are typically shorter than a road culvert and often contain areas of lower velocity, such as behind large rocks allowing fishes to move upstream without exhausting themselves (Lonzarich *et al.*, 2011; Doehring *et al.*, 2012).

Our outlet drop and three water velocity models had reasonable discrimination and predictive performance. To be able to predict passability for unsampled road culverts, our models depended on remotely collected data, which are likely to include some error (Januchowski *et al.*, 2010) that could influence model performance. There are also additional influences on outlet drops and water velocities of road culverts that cannot easily be represented using remotely collected data. Factors such as culvert age (Park *et al.*, 2008), installation details and culvert type (Poplar-Jeffers *et al.*, 2008) are not likely to be available or easily generated for large basins, but human population density could be used as a surrogate for infrastructure expenditures, which often reflect culvert type. Two additional factors, the type of road (e.g. is it an interstate or local road; Pépino *et al.*, 2012) and road surface material (e.g. paved or not), might also influence culvert condition and could be generated through remote sensing and geographic information systems in some regions. In the Great Lakes Basin, for example, the Ontario Ministry of Natural Resources has data on whether or not

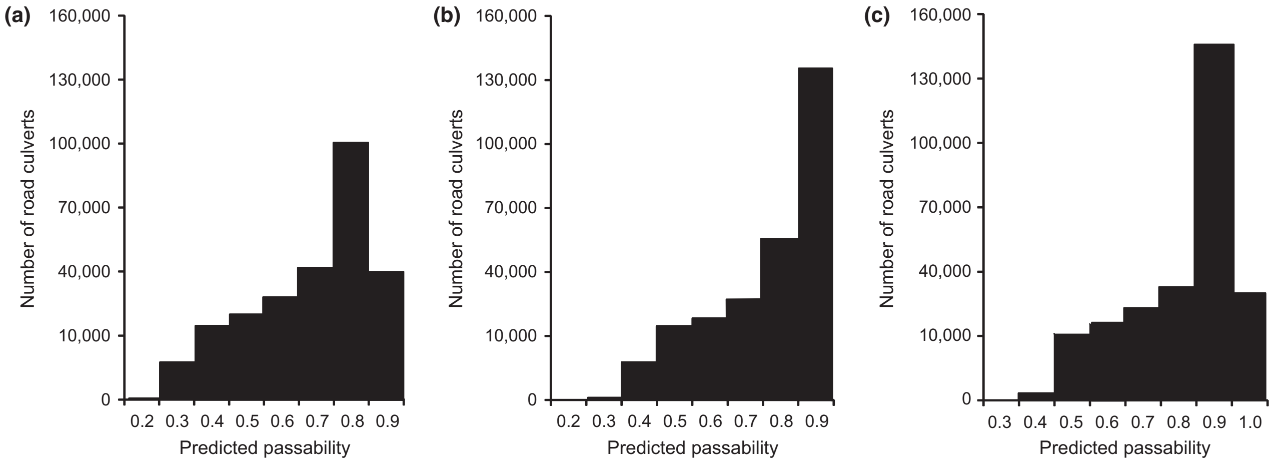

Figure 4 Histograms of passability values for road culverts on low-order stream segments (Strahler order 1-4) for fishes with (a) weak (b) moderate and (c) strong swimming abilities in the Laurentian Great Lakes Basin.

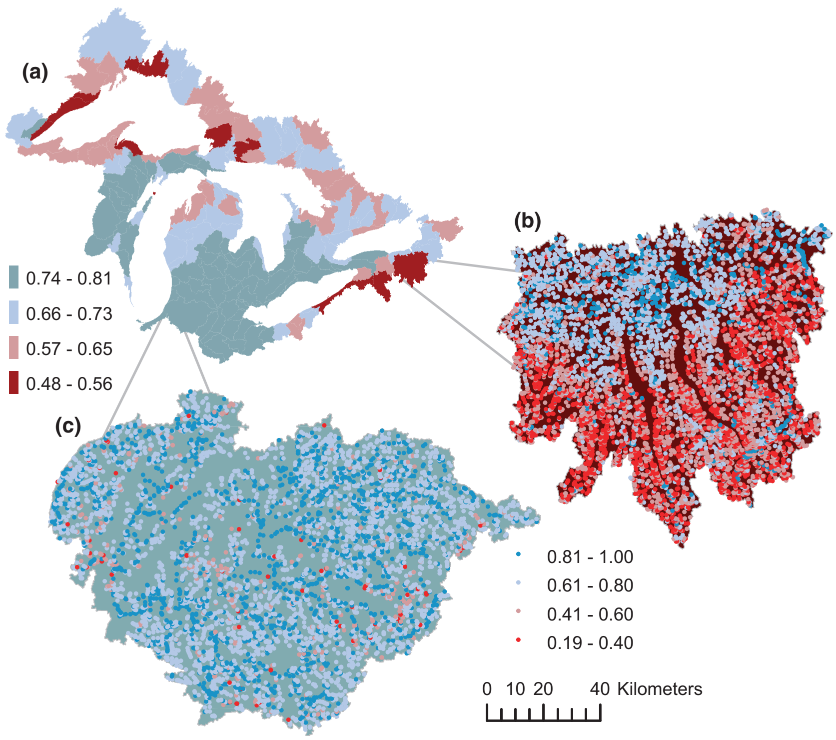

Figure 5 Spatial variability of road-crossing passability across the Laurentian Great Lakes Basin as depicted for fishes with weak swimming abilities. (a) Average road-crossing passability within hydrological units (n = 160) as determined using all road crossings, including those assumed to be fully passable on streams of Strahler order > 4 and those with predicted passability on Strahler orders 1-4. Within unit road-crossing passability for two hydrological units with high (b) and (c) low average passability. Passability is depicted on a cool to warm scale in all cases, where red is lowest and blue is highest passability.

roads are paved, but counterpart data for the USA are not yet available.

Our survey dataset was generally representative of the range of culverts that exist in the Great Lakes Basin, but we acknowledge that it is biased towards lower gradient streams and that further survey efforts could be most valuable in higher gradient systems. Nonetheless, further investment in on-ground surveys will likely have a diminishing return on model performance as relatively small and incomplete datasets have been shown to be effective at identifying where action is needed (Grantham *et al.*, 2008). Finally, given that large river and lake basins often traverse multiple political boundaries, it is likely that the data limitations and imbalances experienced in this study are reflective of other large regions or basins where modelling road culvert passability would be of interest to the freshwater conservation community. The flexibility of our predictive modelling framework makes it easy to refine passability estimates as new calibration or landscape-scale data become available and to ensure model inputs are relevant to the region of interest (additional discussion below).

Implications for conservation decision-making

Our models contribute to conservation decision-making in the Great Lakes Basin and elsewhere in the world in at least three ways. First, quantitative passability estimates for road culverts in the Great Lakes Basin will be made available upon request. Second, our findings could be used to target regions and specific structures for field assessments. Third, our general modelling approach may be replicated wherever adequate data are available, including on-ground passability surveys at a representative sample of road crossings and predictor data for all road crossings. It is important to keep in mind that definitions of passability should be tailored to species of interest and the surrogate variables should be chosen based on data availability, regionally unique natural (e.g. topography) and cultural (e.g. road-crossing construction standards) factors, and hypotheses about what causes variability in crossing performance.

Previous methods developed to assess road culvert passability for native fishes, tended to focus on a particular fish species (e.g. Poplar-Jeffers *et al.*, 2008), or a single passability estimate was determined for complete fish assemblages expected to inhabit the stream where the road culvert is located (e.g. O'Hanley *et al.*, 2013). Our models combine these two approaches and add an element of flexibility that allows users to evaluate and compare system-wide patterns of passability or culvert remediation priorities for fish that differ in swimming capacity. As there could be different interpretations of fish swimming abilities (Peake, 2008; Haro *et al.*, 2004, Mahlum *et al.*, 2014), and empirical knowledge on this topic is likely to grow, we chose to develop parallel models that allow exploration of the implications of alternative water velocity thresholds for a given focal species. Where the goal is to assess passage for an entire fish community, prioritization could be based on passability estimates for the weakest swimming species. If a focal species is believed to not be limited by culvert water velocity, passability estimates could be made solely from the probability of outlet drop. Regardless of the way the individual components are interpreted, estimates of individual road culvert passability are critical for assessing basin-wide stream fragmentation and facilitating spatially explicit decision-making at any spatial scale (O'Hanley *et al.*, 2013).

Road culvert passability predictions derived from our models could also be coupled with data on the amount of upstream habitat that would become accessible after replacing culverts that pose a passability challenge for fishes, thereby elucidating potential return on investment (e.g. O'Hanley 2011). In most watersheds in industrialized nations, a range of potential culvert remediation opportunities exists that vary not only in passability to fishes with different swimming abilities but also in the length of river to be gained from culvert replacement (e.g. Bourne *et al.*, 2011; O'Hanley *et al.*, 2013). Without any additional data or sophisticated prioritization methods, government and non-government groups could combine distance between structures and predicted passability to identify high-return projects based on their particular goal (e.g. Bourne *et al.*, 2011). Ideally, estimates of road culvert passability determined using our modelling framework could eventually feed into spatially explicit prioritizations (e.g. Kemp & O'Hanley, 2010; Bourne *et al.*, 2011; McLaughlin *et al.*, 2013; O'Hanley *et al.*, 2013).

While assessments of road culvert passability are a critical element for understanding how river network connectivity has been reduced, knowledge of passability is only part of the equation for conserving migratory fishes. The passability of road culverts and other potential barriers (e.g. dams or weirs) must be coupled with reliable information on target species distributions and stream habitat quality to achieve successful conservation planning and ecosystem management. Ultimately, combining this benefits-oriented perspective with additional information on economic costs (e.g. culvert replacement cost, dam removals), ecological costs (e.g. control invasive species and contaminant spread; McLaughlin *et al.*, 2013) and sociopolitical constraints (e.g. public sentiment toward particular culverts or dams) could then guide a comprehensive analysis of alternative restoration options (Januchowski-Hartley *et al.*, 2013). For the moment, our work provides a transferable model for estimating road culvert passability, thereby filling a critical gap in the information needed to support sound decision-making to restore ecological connectivity of freshwater ecosystems at broad spatial scales.

ACKNOWLEDGEMENTS

This work was funded by the Upper Midwest and Great Lakes Landscape Conservation Cooperative and The Nature Conservancy's Great Lakes Fund for Partnership in Conservation Science and Economics. We thank M. Fedora, D. Oele, E. Childress, N. DeMol, M. Hudson and P. Ertel for contributing data from on-ground surveys. We also thank M. Khoury, M. Herbert, and the McIntyre Lab for useful discussions and feedback on earlier versions of the manuscript.

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Editor: Kerrie Wilson