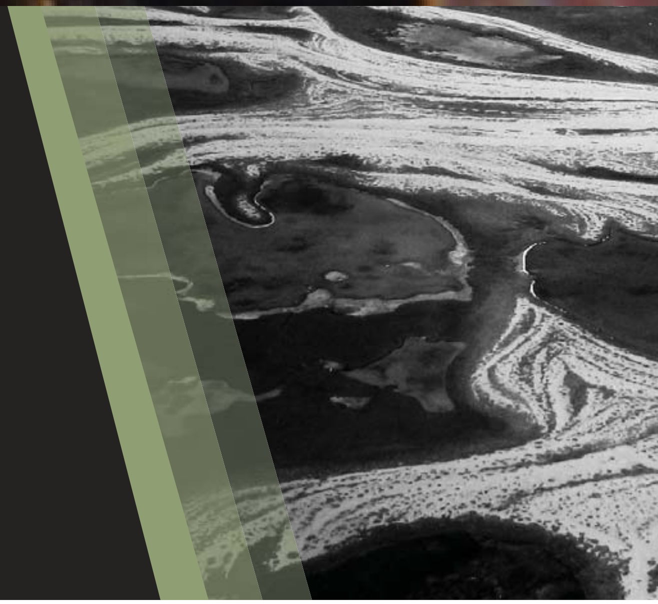
Occupancy of brook trout and brown trout in streams of the Mixedwood Plains Ecozone



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Occupancy of brook trout and brown trout in streams of the Mixedwood Plains Ecozone

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Cover photo: Brook trout in Uxbridge Creek, Ontario. (Photo by Michael Leung)

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Abstract

Understanding which streams might support brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) is valuable to conservation and resource management activities such as assessing habitat; predicting species occurrence; and informing inventory, conservation, and restoration efforts. Species distribution models offer a cost effective way to estimate where fish are without doing an exhaustive inventory across the landscape. Using presence and absence data, we developed models to predict the summertime occupancy of brook and brown trout in the Mixedwood Plains Ecozone in southern Ontario. Our results match those of previous studies and show that the important explanatory variables are mostly topographical and geological (e.g., overburden thickness, elevation), which cannot be changed through management actions. Brook and brown trout prefer streams with high base flows and cold water. Restoration efforts can focus on maintaining/improving cold base flows by reducing water withdrawals, preventing the development of recharge areas, and applying proven green infrastructure and stream restoration methods (e.g., reforestation). Trees keep water shaded and cool, extending the availability of cold water downstream, and provide habitat, stabilize stream banks, and encourage infiltration. Together, these restoration efforts can help to increase brook trout habitat and buffer populations from the effects of climate change.

The competitive success of brook and brown trout varies based on the environmental context (e.g., flow and thermal regimes, water quality, climate, productivity, and network position). Understanding the environmental context and barriers that segregate species is important in assessing species interactions on the riverscape. Reduced aquatic connectivity can lead to increased risk of extinction due to environmental, demographic, and genetic stochasticity. However, increasing connectivity can invite harmful non-native species. Our model predictions about habitat suitability and overlap between brook and brown trout can be used to guide decisions about barrier removal and help balance trade-offs between population isolation and restoring connectivity. Barriers are likely needed in certain locations in stream networks, however, many are likely redundant and could be removed to enhance ecosystem resilience.

Résumé

Occupation des cours d’eau de l’écozone des plaines à forêts mixtes par l’omble de fontaine et la truite brune

La connaissance des cours d’eau abritant l’omble de fontaine (*Salvelinus fontinalis*) et la truite brune (*Salmo trutta*) est essentielle à l’orientation des activités de conservation et de gestion des ressources, comme l’évaluation de l’habitat, la prédiction de la présence des espèces et la documentation des efforts d’inventaire, de conservation et de restauration. Les modèles de distribution des espèces se révèlent rentables pour évaluer où se trouvent les poissons sans dresser un inventaire exhaustif de l’ensemble du paysage. En employant les données sur la présence ou l’absence de l’omble de fontaine et de la truite brune, nous avons développé des modèles de prédiction de l’occupation estivale de ces espèces dans l’écozone des plaines à forêts mixtes dans la partie sud de l’Ontario. Nos résultats concordent avec ceux des études précédentes. Ils démontrent que les variables explicatives d’importance, principalement

topographiques et géologiques (p. ex. l'épaisseur des morts-terrains et l'altitude), ne sont pas modifiables par des mesures de gestion. Les ombles de fontaine et les truites brunes préfèrent les débits élevés et l'eau froide. Les efforts de restauration peuvent se concentrer sur le maintien d'un débit de base froid ou sur son amélioration. Comment? En réduisant les prélèvements d'eau, en empêchant le développement des régions de recharge et en appliquant des méthodes éprouvées de restauration de l'infrastructure verte et des cours d'eau (p. ex. par le reboisement). En procurant de l'ombre, les arbres maintiennent l'eau fraîche, contribuant ainsi à accroître la disponibilité de l'eau froide en aval. Cette condition favorise la préservation de l'habitat, stabilise les berges des cours d'eau et encourage l'infiltration. Ces efforts conjoints de restauration contribueraient à augmenter l'habitat de l'omble de fontaine et à protéger les populations des effets du changement climatique.

La compétitivité de l'omble de fontaine et de la truite brune varie selon le contexte environnemental (p. ex. les régimes de débit et de température des cours d'eau, la qualité de l'eau, le climat, la productivité et la position dans le réseau hydrographique). La compréhension du contexte environnemental et des barrières séparant les espèces importe pour bien évaluer les interactions entre ces dernières dans le paysage fluvial. La réduction de la connectivité aquatique peut accroître le risque d'extinction en raison de la stochasticité environnementale, démographique et génétique. Toutefois, une plus grande connectivité peut faciliter la propagation d'espèces non indigènes nuisibles. Les prédictions de notre modèle sur la pertinence et le chevauchement des habitats de l'omble de fontaine et de la truite brune peuvent orienter les décisions de suppression des barrières et concilier l'isolement des populations et le rétablissement de la connectivité. Des barrières sont probablement nécessaires à certains endroits des réseaux de cours d'eau, mais nombre d'entre elles, vraisemblablement superflues, pourraient être supprimées pour améliorer la résilience de l'écosystème.

Acknowledgements

Many current and former employees of the Ontario Ministry of Natural Resources and Forestry and several conservation authorities in Ontario conducted the stream surveys and provided the data that were used in this analysis. We thank Darren Smith for helping to compile fish data and Michael Thorn for helpful advice on statistical analyses. This manuscript was improved following helpful comments from Helen Ball, Melissa Rose, and Marc Desjardins.

Note: Spatial data including Google Earth and geodatabase files associated with this report are available via GeoHub (geohub.lio.gov.on.ca/). Use the search terms brook trout, brown trout, and occupancy habitat barriers.

Contents

Introduction

Brook trout (*Salvelinus fontinalis*) is a coldwater fish species native to eastern North America that was historically found throughout Ontario (MacCrimmon and Campbell 1969). Though its life history varies substantially across its range (Behnke 1980), this species is a good indicator of cold water of high quality. Brook trout occupancy is typically associated with headwater streams and high amounts of groundwater inflow, which helps maintain cool water temperature and provides essential spawning habitat (Witzel and Maccrimmon 1983, Curry and Noakes 1995, Power et al. 1999, Stanfield et al. 2006, McKenna and Johnson 2011). Brook trout is a prized recreational fish found in both small streams and larger rivers (e.g., Nipigon). Throughout much of its native range, including in many parts of Ontario, populations have been declining or becoming locally extirpated. This decline is largely due to human activities, such as land use change; habitat alteration, destruction, and fragmentation; invasive species; over exploitation; and pollution (Hudy et al. 2008). Estimates suggest that, in southern Ontario watersheds, this species has lost 50 to 80 per cent of its range (Stanfield et al. 2006, Thorn et al. 2016).

Brown trout (*Salmo trutta*) is also a coldwater species, with habitat requirements similar to brook trout, and often resides in sympatric populations (McKenna et al. 2013). Brown trout have been introduced around the world and to Ontario in 1930s. Without doubt, they are one of the most successful aquatic invaders in North America and a very popular gamefish. Through competition and predation, they tend to decrease local fish species diversity and sometimes richness (Townsend and Simon 2006). More specifically, they have displaced brook trout throughout the northeastern and midwestern United States, often restricting them to small cold headwater streams (Nyman 1970; Fausch and White 1981, 1986; Waters 1983). In northern Europe, the pattern of replacement between these species is reversed: when transferred to northern European streams, brook trout spread extensively and partially replaced native brown trout (Korsu et al. 2007). Brook trout excluded native brown trout but only in small, slightly acidic, tributary streams characterized by harsh and variable environmental conditions where brown trout reproduction was poor (Rahel and Nibbelink 1999, Baldigo and Lawrence 2000). In contrast, in larger streams brown trout were largely unaffected by brook trout. On both continents, brook trout ultimately inhabit small cold headwater streams but the replacement process differs.

Like for brown trout, modifications to longitudinal connectivity in streams (e.g., dams, culverts) have also contributed to a decrease in native fishes and biodiversity globally and changed the spatial distributions of species (Poff et al. 1997, Brainwood et al. 2008). Fragmentation restricts the extent and rates of dispersal and, in turn, can lead to species extirpation, smaller populations, and decreased genetic diversity (Frankham 2005a,b). Fragmentation especially affects species that require long movements in stream networks, have low intrinsic growth rate, disperse poorly, and need specialized habitat to complete their life cycle stages (e.g., brook trout, sturgeon; Hughes 2007). Fishes require access to a variety of habitats in which to spawn, feed, and seek refuge from predators and adverse environmental events (Bronmark et al. 2014). Small fragmented populations are more susceptible to the effects of, for example, droughts, floods, spills, or disease. Further, small populations are more strongly affected by random demographic variation (i.e., demographic stochasticity) such as reduced reproductive success or changes in sex ratios (Soulé and Simberloff 1986).

Although demographic stochasticity alone is unlikely to lead to extinction, decreases in population size can increase genetic drift and inbreeding (Lande 1988), which may decrease genetic diversity and cause deleterious traits to accumulate, reduce fecundity and offspring survival, and decrease a populations' ability to adapt to environmental changes. Populations that become too small enter what is known as an extinction vortex, characterized by rapid decline, and eventual extinction, due to the compounding effects of environmental, demographic, and genetic stochasticity (Fagan and Holmes 2006). The effects of demographic and genetic stochasticity can be buffered by the immigration of individuals from sympatric populations, but barriers prevent this movement and further increase the risk of population declines and extinctions (Letcher et al. 2007). Minimum viable populations, a common concept in ecology and conservation biology, describe the number of individuals needed for an isolated population to persist in the face of environmental, demographic, and genetic stochasticity.

Limitations on species' movement and dispersal can lead to ecosystem level effects because species rely on other species for dispersal (e.g., freshwater mussel species; Watters 1996, Brainwood et al. 2008). Many species also rely on nutrient subsidies such as eggs, milt, and carcasses deposited by other species (Childress et al. 2014, Jones and Mackereth 2016). A significant decrease in or absence of nutrient subsidies can affect the abundance, growth, and survival of species that depend on these food resources. In a comprehensive study, Zorn et al. (2019) found that access to the Great Lakes led to greater salmonid density and biomass per unit area; however, the presence of brown trout consistently and negatively affected brook trout density.

Native fishes often face simultaneous threats from habitat fragmentation and invasion by non-native species (e.g., brown trout). Management actions to address fragmentation may allow invasive species to extend their range. Conversely, not addressing fragmentation may lead to local extirpation of a species that is too small and isolated to persist (Fausch et al. 2009). Watersheds often have many barriers but not many are needed for species partitioning and the extra barriers limit the health and resilience of fish populations. A decision process is needed to guide biologists on when and where intentional use or removal of barriers is the most appropriate action. Understanding how environmental variables influence the distribution of brook and brown trout can be used in this decision process.

Species distribution modelling, also known as environmental niche modelling, habitat modelling, and range mapping rely on the use of statistical models and environmental data to predict the distribution of a species across space and time. Species distribution models typically relate the presence-absence or abundance of a species to abiotic and biotic environmental variables at multiple spatial scales (e.g., reach, upstream catchment). These models have many practical applications for conservation and resource management. These applications include assessing the habitat requirements of a species (Buisson et al. 2008), predicting the occurrence of rare or endangered species (Guisan et al. 2006), informing conservation and restoration efforts (Estrada et al. 2011, Oppel et al. 2012), and predicting the effect of future climate change (Wenger et al. 2011). Species distribution models are valuable tools for resource managers because they offer a cost effective way to estimate the distribution of a species without doing an exhaustive inventory across the landscape. Distribution maps may also inform land use planning policies or decisions that avoid or reduce effects and enable the efficient use of resources to assess streams that likely contain trout.

The purpose of this study was to predict the *summertime*[1] occupancy of brook and brown trout in southern Ontario. Using presence and absence data, we modelled how environmental variables influence their occurrence and co-occurrence throughout the Mixedwood Plains Ecozone. Individually, understanding the distribution and habitat of brook and brown trout will help to inform trout conservation, restoration, inventory, and monitoring efforts. When combined, this information can be used to locate potential trout streams and identify overlap in the habitat suitability of brook and brown trout, and the predictions can be used to prioritize barriers for species segregation and enhanced watershed connectivity.

Methods

Trout presence and absence

Brook trout and brown trout presence-absence information was obtained from the unofficial provincial stream fish database. These data were not specifically collected for the purpose of brook trout distribution modelling. Most data were collected for conservation authority monitoring programs and out of convenience often near road crossings. As such, we acknowledge possible inherent biases in the data and that the models may be less informative than those based on a more robust survey design.

This data set was queried to extract samples collected using electrofishing in the Mixedwood Plains Ecozone from 1990 to 2019 (Figure 1). These records were joined to the nearest stream reach from the Aquatic Ecosystem Classification (AEC; Jones and Schmidt 2017). Sites farther than 15 m from the nearest reach were excluded from the final data set. Fish catch data was aggregated at reach level and converted to presence-absence, with the presence of brook or brown trout in any site-year representing occupancy in that reach. Reaches with an upstream catchment area >2000 km^2 were excluded because they are likely to be non-wadeable systems sampled using boat electrofishing techniques.

Environmental data

Environmental data was obtained from the provincial AEC data set (Jones and Schmidt 2017). The AEC summarizes climatic, geological, hydrological, and land cover variables at four distinct spatial scales (Figure 2). Before analyses, several of the landcover classes were aggregated to form 2 new composite variables: treed land cover and open water/wetland land cover. Forty-two ecologically relevant environmental predictor variables were extracted from this data set (Appendix 1). Before modelling, we excluded variables with a correlation >0.7. Beginning with the most highly correlated variable pair, we applied step-wise removal of single variables until all remaining variables were uncorrelated. Unless a variable was particularly relevant to the

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[1] Models reflect summertime distribution because most of the electrofishing surveys are conducted in June, July, and August. For the remaining 9 months, trout are not restricted by high water temperatures and, if barriers do not impede their movement, can use other parts of stream networks.

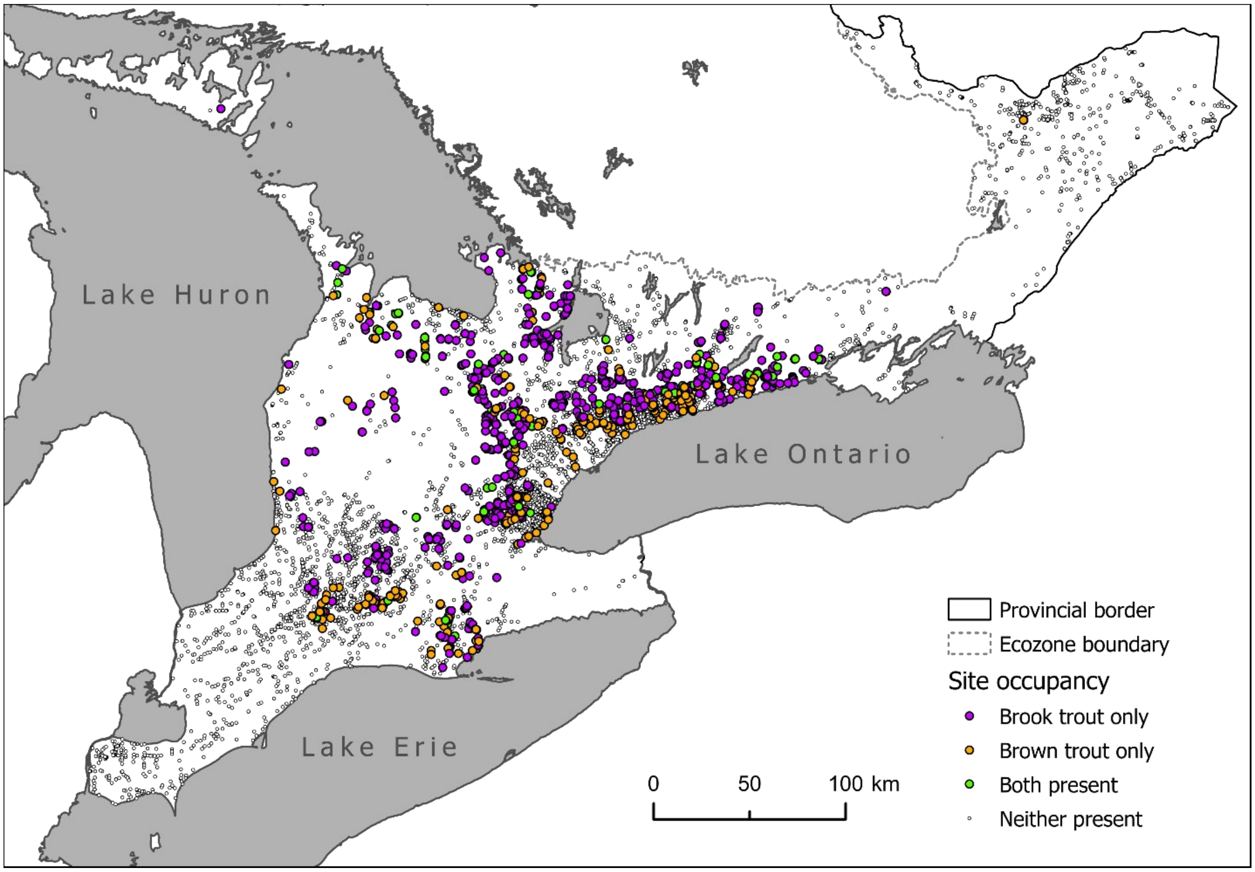


Figure 1. Brook trout and brown trout occupancy in streams based on field surveys in the Mixedwood Plains Ecozone, southern Ontario.

distribution of brook or brown trout, the preferred order of selection was: (1) variables from coarser spatial scales, (2) mean values (e.g., mean elevation before maximum elevation), and (3) raw variables over modelled variables (e.g., channel slope before stream power index). This reduced the number of variables to 17. To reduce collinearity, we chose percentage treed because it was the most informative. Variables that represent land use, such as agriculture, urban, and treed, are often correlated. For example, although urban landcover is not explicitly in the model it is highly correlated with forest cover. Multicollinearity occurs when independent variables in a regression model are correlated. One objective of regression analyses is to isolate the relationship between each independent variable (e.g., land cover) and the dependent

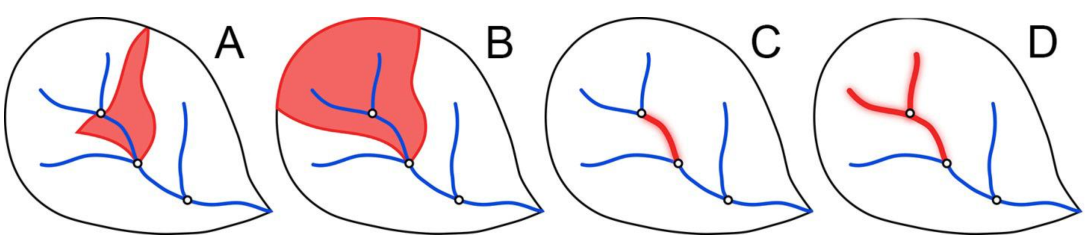


Figure 2. The four scales of variables summary applied to group stream reaches: a) reach contributing area, b) upstream catchment, c) reach channel (30 m raster), and d) upstream channel for the catchment (30 m raster).

variable (e.g., trout presence). The stronger the correlation, the more difficult it is to change one variable without changing another, making it difficult to estimate the relationship between the dependent and independent variables that change in unison. In practice, slightly different models with different degrees of collinearity among variables can lead to very different conclusions.

Occupancy modelling

Occupancy models were developed for brook and brown trout separately with boosted regression trees using the dismo package in R (Elith et al. 2009). Boosted regression tree models (BRTs) are a combination of regression and machine learning techniques. The algorithm works by producing many relatively simple classification trees and combining them to optimize predictive performance (Elith et al. 2009). BRTs have many advantages over other modelling techniques because they are insensitive to scale of measurement, missing data, outliers, and non-normal distributions (Elith et al. 2008).

We first separated the full occupancy data set into training and testing subsets using an 80/20 split. Models were fit to the training data set and validated using 10-fold cross-validation before being evaluated on the testing data set. To determine the optimal parameter combination for each model, we tested different combinations of tree complexity (1, 2, 3, and 5) and learning rate (0.05, 0.01, 0.005, and 0.001) with the bag fraction fixed at 0.5 (i.e., half the data drawn at random without replacement). We then selected the combination of model parameters (tree complexity and learning rate) that maximized the area under the receiver operating curve (AUC; an indication of how well the model distinguishes classes) and deviance explained on the testing data set (Table 1). The final models were simplified using a backwards stepwise procedure that removed variables until predictive performance decreased (Elith et al. 2009). The simplified models were used to predict probabilities of occurrence for all reaches <2000 km^2 in the Mixedwood Plain Ecozone. Occurrence probabilities were converted into presence/absence using a threshold value that maximized the sum of the sensitivity (true positive rate) and specificity (true negative rate). We then divided the presences into low, medium, and high probabilities.

Table 1. Summary of model characteristics and performance for the boosted regression tree occupancy models generated for brook trout and brown trout in the Mixedwood Plains Ecozone, southern Ontario.

Model	Learning rate	Tree complexity	# of trees	AUC[1]	Deviance explained (%)	Occupancy threshold[2]
Brook trout	0.005	5	2700	0.88	37.20	0.19
Brown trout	0.005	5	2950	0.81	27.14	0.13

[1] AUC=area under receiver operating curve as measured on the testing data set.

[2] Occupancy probabilities below this value are absences and probabilities above this value are presences and are divided into equal bins representing low, medium, and high probabilities.

Results

The final data set used for modelling comprised 3,180 reaches, of which 2,544 were used for model training and the remaining 636 for evaluating model performance. In the full data set, brook trout were present in 17.9% of reaches and brown trout were present in 9.6%. This aligned with their prevalence in the testing (brook = 22.4%; brown = 11.9%) and training (brook = 14.9%; brown = 8.9%) data sets.

During summer, brook trout are associated with headwater streams with high channel slopes, thick overburden materials (e.g., moraines), high levels of potential groundwater inputs, and high elevations. These areas contain relatively coarse glaciofluvial ice and glaciolacustrine deposits (e.g., Oak Ridges, Oro, Waterloo, Paris-Galt moraines, and the Norfolk Sand plain). Of less importance were forested reach contributing areas, upstream catchment area, and mean annual precipitation (Figure 3). These streams are mostly natural with minimal adjacent agriculture and urbanization. Flat portions of the relationships in the partial dependence plots indicate minimal data at that level (e.g., no upstream catchment area mean slopes >≈9%; no reach contributing areas >75% treed).

During summer, brown trout were distributed similarly to brook trout but were more strongly associated with larger upstream catchment areas and higher channel slopes that are fed by small headwater streams with high potential for groundwater (Figure 4). Brown trout presence was also associated with mean annual precipitation, mean overburden thickness, treed riparian areas, and high elevations. The predicted distribution is smaller for brown trout than for brook trout.

In longitudinal order, brook trout typically occupied headwater streams followed by both brook and brown trout, and only brown trout in main channel downstream (figures 5 and 6). For mapping, occupancy probabilities were categorized as low, medium, and high (Table 2).

Our models did not produce different results when hindcasted. This outcome is likely because the per cent treed cover did not weigh heavily in the model and did not exceed ≈72% coverage, that is, no watersheds had 100% forest cover (figures 3 and 4).

Table 2. Absence and occupancy probabilities for brook trout and brown trout in the Mixedwood Plains Ecozone, southern Ontario, categorized as low, medium, and high. Occurrence probabilities were converted into presence/absence using a threshold value that maximized the sum of the sensitivity (true positive rate) and specificity (true negative rate).

			Present	
Category	**Absent**	**Low**	**Medium**	**High**
Brook trout	<0.19	0.19–0.46	0.46–0.73	>0.73
Brown trout	<0.13	0.13–0.41	0.41–0.70	>0.70

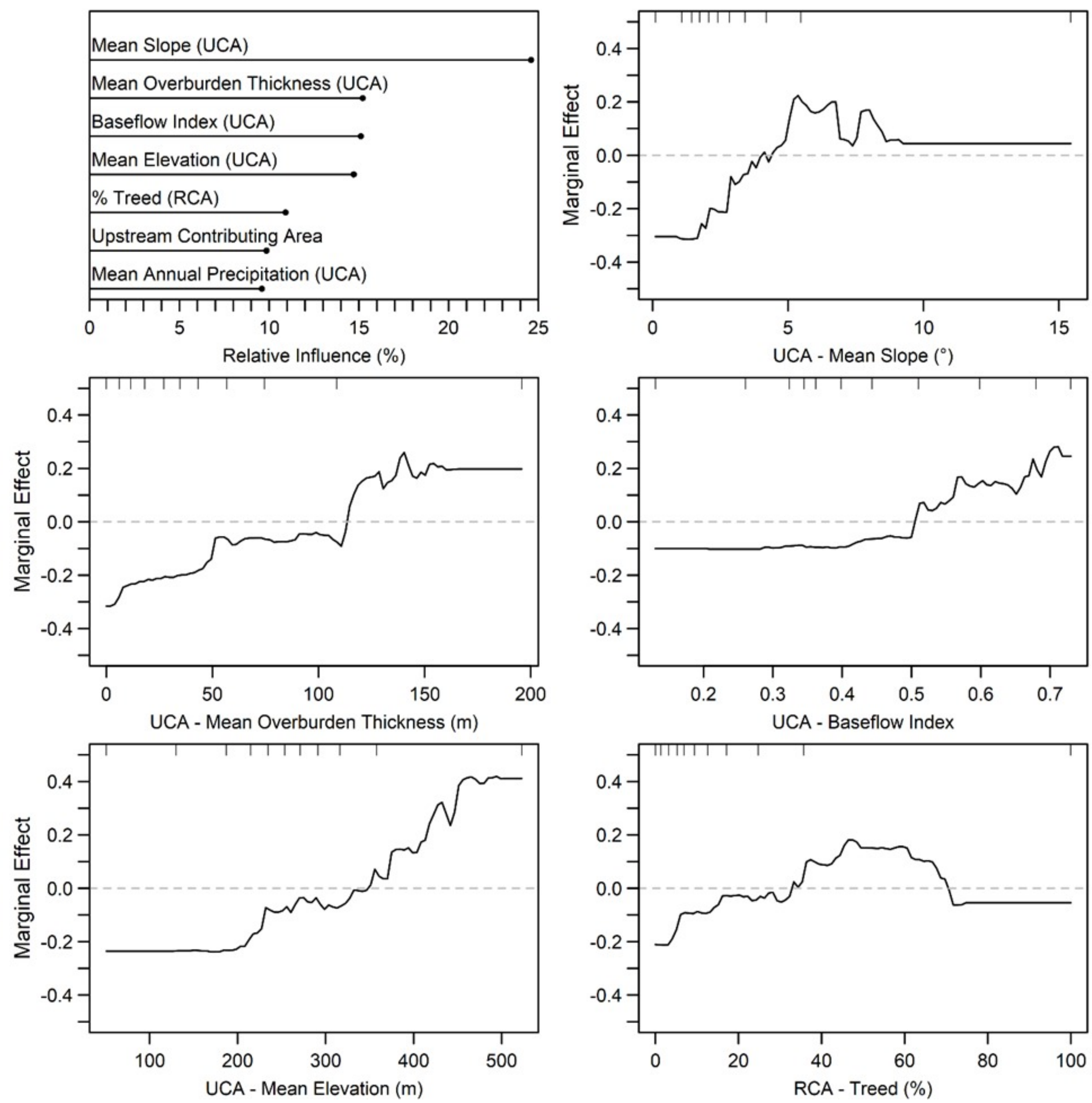


Figure 3. Variable importance and partial dependence plots for the boosted regression tree models of brook trout occupancy in the Mixedwood Plains Ecozone, southern Ontario. (UCA=upstream catchment area; RCA=reach contributing area).

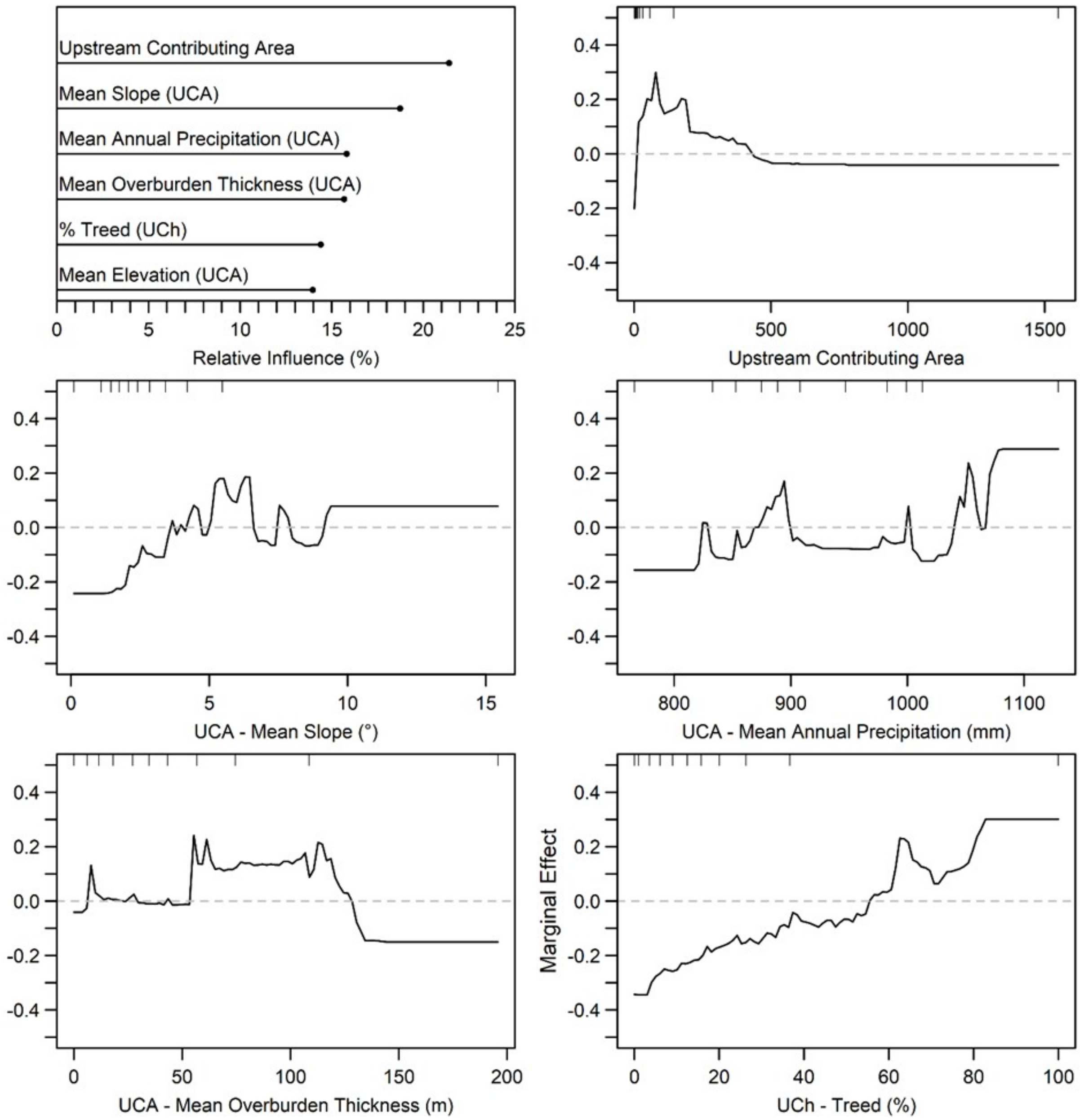


Figure 4. Variable importance and partial dependence plots for the boosted regression tree models of brown trout occupancy in the Mixedwood Plains Ecozone, southern Ontario. (UCA=upstream catchment area; UCh=upstream channel for the catchment).

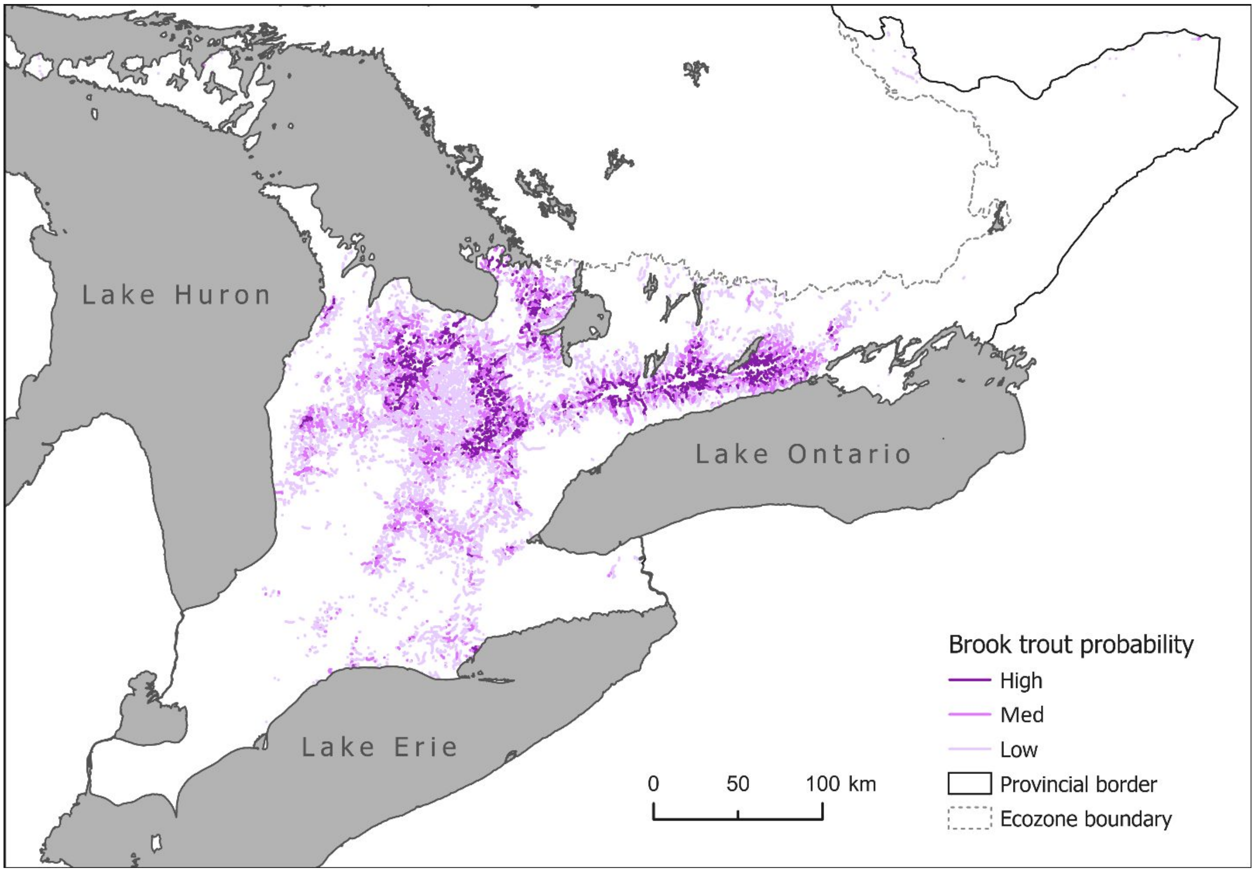


Figure 5. Reach contributing areas and their predicted occupancy probabilities for brook trout in the Mixedwood Plains Ecozone, southern Ontario. The Google Earth KML files, available via GeoHub (geohub.lio.gov.on.ca/), illustrate the distributions at multiple scales for easier interpretation.

Discussion

The summertime, present-day distribution of brook trout was primarily restricted to headwater areas and is consistent with other regions in the species' native range (Stanfield et al. 2006, McKenna and Johnson 2011, Kanno et al. 2015). In longitudinal order, brook trout occupied headwater streams, followed by both brook and brown trout, and only brown trout in main channels downstream (figures 5 and 6). These predictions are based on field data collected in summer (June, July, August) and do not reflect habitat suitability during the remaining months of the year when water temperatures would not restrict fish movement in the stream network to larger mainstem channels (Curry et al. 2002) or into hydrologically connected lakes. Such extensive movements are how fishes exploit their environment to maximize fitness, particularly in environments where their habitat needs vary spatiotemporally (e.g., rivers, spawning, nursery, overwintering, thermal refugia; Northcote 1978).

The maps produced in our study can be used to efficiently guide field efforts to locate stream reaches that may contain trout. Other techniques (e.g., eDNA, efishing) could then be used to verify presence/absence. These maps could also be used to guide stocking of trout and to prioritize restoration efforts on the landscape. For example, streams that have high suitability

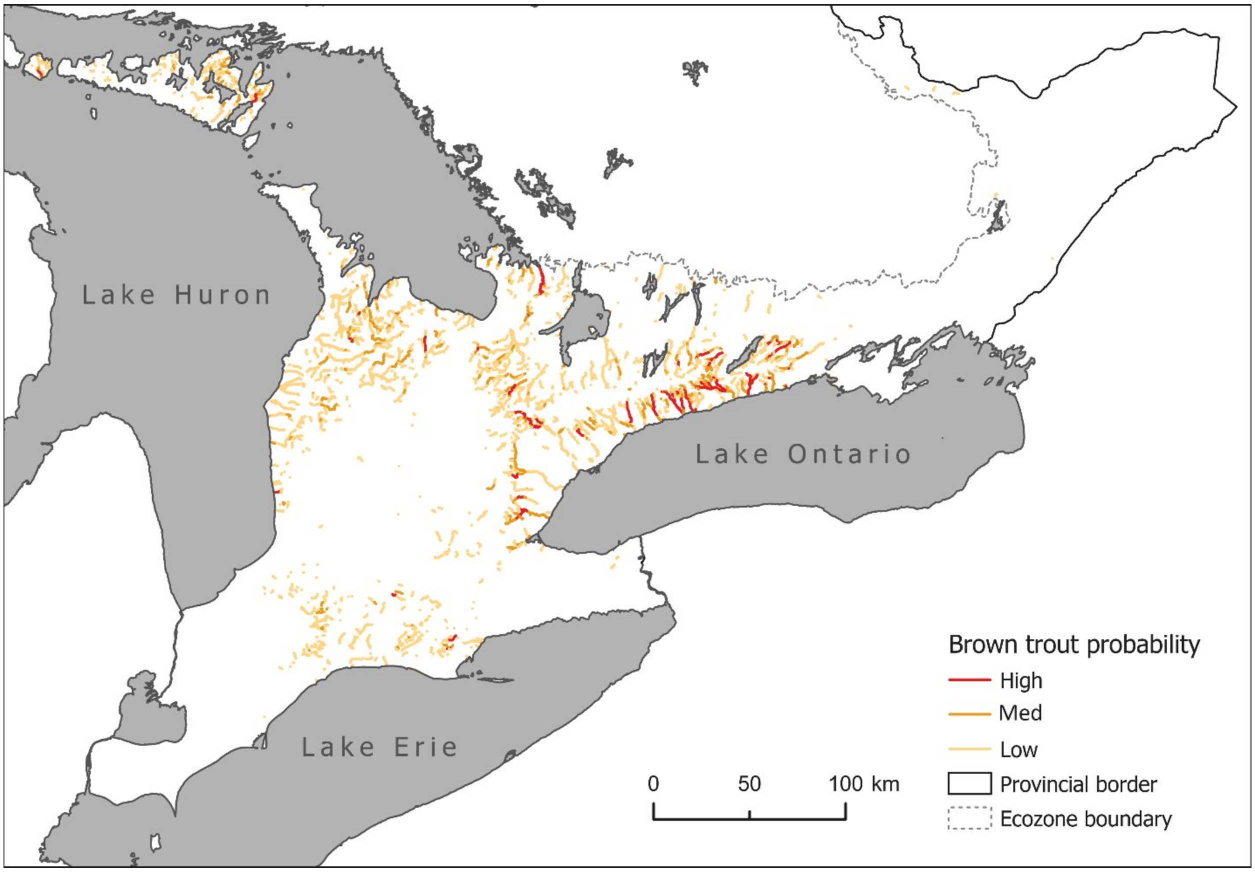


Figure 6. Reach contributing areas and their predicted occupancy probabilities for brown trout in the Mixedwood Plains Ecozone, southern Ontario. The Google Earth KML files, available via GeoHub (geohub.lio.gov.on.ca/), illustrate the distributions at multiple scales for easier interpretation.

for brook trout but do not currently contain trout could be restored and stocked with fish to provide angling opportunities.

Brook and brown trout occurrence were related to overburden thickness, base flow index, channel slope, and elevation. Base flow index is a measure of the ratio of long-term base flow to total stream flow and it represents the slow continuous contribution of groundwater to river flow. Base flow index is divided into 5 classes of quaternary geology including coarse and fine textured sediments, till, shallow bedrock, and organic deposits (Piggott and Sharpe 2007). At large and intermediate spatial scales, the base flow index is a useful surrogate for actual groundwater delivered to a stream and is important in stream hydrology and thermal regime characteristics defining stream habitat. Overburden thickness represents groundwater recession. Thick deposits of overburden, which contain large amounts of groundwater, maintain flow volume even during extended periods without precipitation. In contrast, thin veneers of overburden, even if coarse textured, may not have much water to supply the stream during dry periods (Buttle et al. 2004, Buttle and Eimers 2009).

Our findings match those of Thorn et al. (2016) in that most of the important explanatory variables are topographical/geological (e.g., overburden, base flow index, elevation) and cannot be changed through management actions. Groundwater, represented as base flow index, can be decreased by increasing imperviousness in built-up areas, which influences the proportion of runoff to infiltration. Brook trout prefer streams with high base flows and cold water. Restoration efforts can focus on maintaining/improving cold base flows by reducing water withdrawals in areas identified as potential brook trout habitat, avoiding development in or near recharge areas, and using proven green infrastructure and stream restoration techniques (Bernhardt et al. 2005). The percentage forest cover in a watershed is related to land use and could be managed to provide benefits (e.g., improving groundwater recharge). Loss of vegetative cover in riparian areas due to land use (e.g., development, agriculture, forestry) could benefit from improvements to vegetation cover through restoration/rehabilitation efforts. Trees not only keep water shaded and cool, thus extending the availability of cold water downstream, but also provide habitat, stabilize stream banks, and encourage infiltration of water for groundwater recharge. Together, these restoration efforts can help to increase brook trout habitat and buffer populations from the effects of climate change.

Trout preferred forested riparian and reach contributing areas, but in our models this variable was less important than others (e.g., overburden thickness). Thorn et al. (2016) noted that among their models the proportion of forest was the most consistently selected landscape variable. Forested riparian vegetation shades streams from solar radiation, which leads to less diurnal temperature fluctuation and lower summer maximum stream temperatures (Barton et al. 1985, Johnson and Jones 2000, Cross et al. 2013). The positive relationship between brook trout and forested area is consistent with findings from other studies (Hudy et al. 2008, Wagner et al. 2013, Kanno et al. 2015b). Thorn et al. (2016) found that brook trout occupancy decreased sharply when the amount of forested land decreased below 40%. Wagner et al. (2013) found that brook trout occurrence was highest when >60% of the upstream catchment was forested.

Our model results indicated that brown trout were found in larger upstream catchment areas. However, this might be an artifact of barriers that separate the two species and limit their presence in headwater streams. Habitat suitability is also a product of where brown trout were introduced, strayed, and colonized. The modelled maps show where environmental conditions and landscape characteristics are likely suitable for trout, not where trout are found. For example, the model predicts that many streams on Manitoulin Island are suitable for brown trout but, based on electrofishing data, they are not present on the island. This is also true for West Cobourg Creek, near Lake Ontario.

Our models were created using data collected by various agencies that does not represent an ideal random selection of surveyed streams. Further, the data represents sites from a contemporary distribution in the Anthropocene when little of southern Ontario is pristine. Historically, the Speed River in Guelph was one of the better and larger streams in which to catch brook trout in southern Ontario so model predictions that include this watershed will differ from those that exclude it. Indeed, using hindcasting, Stanfield et al. (2006) estimated that current brook trout distribution in the Lake Ontario catchment area is 21% of its historic range and Thorn et al. (2016) estimated the historical distribution to be 47% larger than present-day distribution in the Lake Simcoe watershed. Our models did not produce different results when hindcasted because the per cent treed cover did not weigh heavily in the model and did not exceed ≈72% cover so no watersheds had 100% forest cover.

Point source factors such as on-line ponds, industrial and sewage discharges, and barriers are not considered in the modelling. The west branch of Bowmanville Creek (Tyrone Creek), east of Oshawa, illustrates how on-line ponds can alter predictions. A pond below Concession 8 is a bottom-draw dam and brook trout are found in high abundance below the dam for 1700 m before flowing into Tyrone Mill pond. This pond is a top-draw dam and brook trout are absent downstream. Their absence is likely due to the high water temperature leaving the surface of the pond and subsequent changes in competition ability of other fish species (e.g., brown and rainbow trout; *Oncorhynchus mykiss*). Removing this pond or converting it to a bottom-draw would likely keep the downstream waters cold enough to support brook trout and may give them the competitive edge over brown trout.

Understanding the environmental context and barriers that segregate species is needed to assess species interactions on the riverscape. Brown trout are a known invasive species introduced around the world. Likewise brook trout, while native to and declining in Ontario, are invasive and introduced in many regions (e.g., western North America and Europe). For example, brook trout replaced brown trout in headwater streams in northern Europe, whereas in North America, headwater streams are the ultimate refuge for brook trout when in the presence of brown trout (Korsu et al. 2007). In Northern Europe, brook trout exclude native brown trout in small, slightly acidic, tributary streams characterized by harsh and variable environmental conditions where the reproduction of brown trout was poor (Grande et al. 1978). In western North America, brook trout displaced cutthroat trout (*Oncorhynchus clarkia*) (Dunham et al. 2002, Peterson and Fausch 2003, McGrath and Lewis 2007) and have since become ubiquitous and abundant. No rules exist to suggest that one species of native or non-native fish will always displace another species: success varies based on the environmental context (e.g., flow and thermal regimes, water quality, climate, productivity, and network position).

Reduced aquatic connectivity can increase the risk of extinction due to environmental, demographic, and genetic stochasticity. Small populations are strongly affected by events such as droughts, floods, spills, or disease. Further, these small populations are affected by random demographic variation (i.e., demographic stochasticity) such as reduced reproductive success or changes in sex ratios (Soulé and Simberloff 1986). Genetically, small populations are at risk of losing genetic diversity via genetic drift and inbreeding. However, increasing connectivity can also invite harmful non-native species.

Our model predictions of habitat suitability can guide which barriers to movement would be most useful for balancing tradeoffs between isolation and restoring connectivity (Fausch et al. 2009) and help prioritize stream reaches for barrier removal or repair. For example, the suitability for brook trout is high from the headwater streams to about 18 km downstream in Lynde Creek (Figure 7). In contrast, brown trout habitat suitability is low in the headwaters to moderate in the mid-reaches. Combining these two probability distributions allows us to see where brook trout will likely do well and where brown trout will do poorly. For example, the dark blue streams indicate that suitability is high for brook trout and low for brown trout. The light blue streams indicate that suitability is high for brook trout and moderate for brown trout. The light green stream reach indicates suitability is moderate for brook trout and low for brown trout. The light or dark blue stream section is where barriers should be maintained to segregate the two species. The green stream reach should have a barrier just below the confluence of the purple streams as this would almost double the size of the connected watershed for brook trout. Other barriers in the watershed are likely affecting fishes and should be removed to enhance ecosystem resilience; however, if other fishes (e.g., rainbow trout and salmons) are of interest this will complicate barrier management considerations beyond brook trout and brown trout interactions.

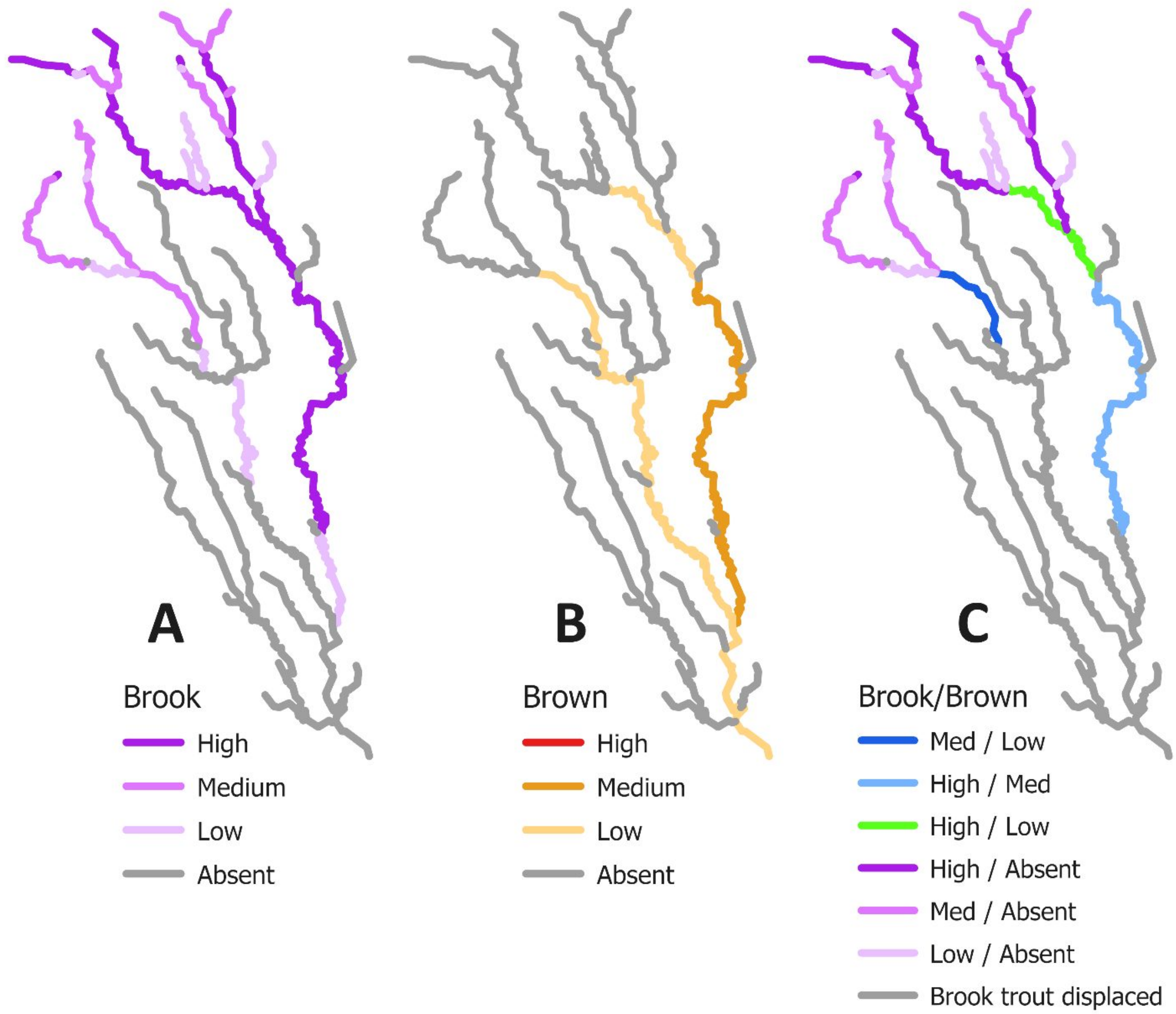


Figure 7. Occupancy probabilities for brook trout (A), brown trout (B), and both (C) are shown for Lynde Creek, Whitby, Ontario, as an example of how model predictions can be used to prioritize barriers for segregation and enhanced connectivity. To preserve segregation between species, barriers should be maintained where brook trout probabilities are high relative to probabilities for brown trout. Under these conditions we assume that brown trout will not exclude brook trout. Grey streams are where brown trout probabilities are med or high and brook trout are med or low. Other barriers in the watershed are likely affecting fishes and should be removed to increase ecosystem resilience. One caveat is we assumed that risk stems only from brown trout and not other species (e.g., invasive species) or diseases. The Google Earth KML files, available via GeoHub (geohub.lio.gov.on.ca/), illustrate the distributions across multiple scales and are easier to interpret.

Next steps

In northern Ontario, before development activities and before forest harvesting occur on Crown land, occupancy models are needed to identify brook trout streams. Surveyors identifying forest values can use occupancy models to prioritize where to look for brook trout. Given the large area of northern Ontario and paucity of available field data, building occupancy models for brook trout will be difficult. Crowdsourcing data from biologists is an option to consider for assessing the presence and absence of brook trout across this vast region.

References

Baldigo, B.P. and G.B. Lawrence. 2000. Composition of fish communities in relation to stream acidification and habitat in the Neversink River, New York. Transactions of the American Fisheries Society 129: 60–76.

Barton, D.R., W.D. Taylor and R.M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. North American Journal of Fisheries Management 5: 364–378.

Behnke, R.J. 1980. A systematic review of the genus Salvelinus. Pp. 441–479 *in* E. K. Balon (ed.). Charrs: Salmonid Fishes of the Genus Salvelinus. Kluwer Boston, Hingham, MA.

Bernhardt E.S., M.A. Palmer, J.D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D, Hart, B. Hassett, R. Jenkinson, S. Katz, G.M. Kondolf, P.S. Lake, R. Lave, J.L. Meyer, T.K. O'Donnell, L. Pagano, B. Powell and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308(5722): 636–637.

Bourne, C.M., D.G. Kehler, Y.F. Wiersma and D. Cote. 2011. Barriers to fish passage and barriers to fish passage assessments: The impact of assessment methods and assumptions on barrier identification and quantification of watershed connectivity. Aquatic Ecology 45: 389–403.

Brainwood, M., S. Burgin and M. Byrne. 2008. The impact of small and large impoundments on freshwater mussel distributions in the Hawkesbury-Nepean River, Southern Australia. River Research and Applications 24: 125–1342.

Bronmark, C., K. Hulthen, P.A. Nilsson, L.A. Hansson, J. Brodersen and B.B. Chapman. 2014. There and back again: Migration in freshwater fishes. Canadian Journal of Zoology 92: 467–479.

Buttle, J.M., P.J. Dillon and G.R. Eerkes. 2004. Hydrologic coupling of slopes, riparian zones and streams: An example from the Canadian Shield. Journal of Hydrology 287: 161–177.

Buttle J.M. and M.C. Eimers. 2009. Scaling and physiographic controls on streamflow behaviour on the Precambrian Shield, south-central Ontario. Journal of Hydrology 374: 360–372.

Childress, E.S., J.D. Allan and P.B. McIntyre. 2014. Nutrient subsidies from iteroparous fish migrations enhance stream productivity. Ecosystems 17: 522–534.

Cross, B.K., M.A. Bozek and M.G. Mitro. 2013. Influences of riparian vegetation on trout stream temperatures in central Wisconsin. North American Journal of Fisheries Management 33: 682–692.

Curry, R. A., and D. L. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 52: 1733–1740.

Curry, R. A., D. Sparks, and J. van de Sande. 2002. Spatial and temporal movements of a riverine brook trout population. Transactions of the American Fisheries Society 131: 551–560.

Dunham, J.B., S.B. Adams, R.E. Schroeter and D.C. Novinger. 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. Reviews in Fish Biology and Fisheries 12: 373–391.

Elith, J., J.R. Leathwick and T. Hastie. 2009. A working guide to boosted regression trees. Journal of Animal Ecology 77: 802–813.

Estrada, A., R. Real and J.M. Vargas. 2011. Assessing coincidence between priority conservation areas for vertebrate groups in a Mediterranean hotspot. Biological Conservation 144: 1120–1129.

Fausch K.D., B.E. Rieman, J.B. Dunham, M.K. Young and D.P. Peterson. 2009. Invasion versus isolation: Trade-offs in managing native salmonids with barriers to upstream movement. Conservation Biology 23: 859–870.

Fausch, K.D. and R.J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38: 1220–1227.

Fausch, K.D. and R.J. White. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. Transactions of the American Fisheries Society 115: 363–381.

Fagan, W.F. and E.E. Holmes. 2006. Quantifying the extinction vortex. Ecology Letters 9: 51–60.

Frankham, R. 2005a. Genetics and extinction. Biological Conservation 126: 131–140.

Frankham R. 2005b. Stress and adaptation in conservation genetics. Journal of Evolutionary Biology 18: 750–755.

Guisan, A., O. Broennimann, R. Engler, M. Vust, N.G. Yoccoz, A. Lehmann and N.E. Zimmermann. 2006. Using niche-based models to improve the sampling of rare species. Conservation Biology 20: 501–511.

Grande, M., I.P. Muning and S. Anderson. 1978. Relative tolerance of some salmonids to acid waters. Verhandlungen des Internationalen Verein Limnologie 20: 2076–2084.

Hughes, J.M. 2007. Constraints on recovery: Using molecular methods to study connectivity of aquatic biota in rivers and streams. Freshwater Biology 52: 616–631.

Hudy, M., T.M. Thieling, N. Gillespie and E.P. Smith. 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. North American Journal of Fisheries Management 28: 1069–1085.

Jones, N.E. and R.W. Mackereth. 2016. Resource subsidies from adfluvial fishes increase stream productivity. Freshwater Biology 61: 991–1005.

Jones, N.E. and B.J. Schmidt. 2017. Aquatic Ecosystem Classification for Ontario's rivers and streams: Version 1. Ontario Ministry of Natural Resources and Forestry, Science and Research Branch, Peterborough, ON. Science and Research Technical Note TN-04. 23 p.

Johnson, S.L. and J.A. Jones. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 57: 30–39.

Kanno, Y., B.H. Letcher, A.L. Rosner, K.P. O'Neil and K.H. Nislow. 2015. Environmental factors affecting brook trout occurrence in headwater stream segments. Transactions of the American Fisheries Society 144: 373–382.

Korsu, K., A. Huusko and T. Muotka. 2007. Niche characteristic explain the reciprocal invasion success of stream salmonids in different continents. Proceedings of the National Academy of Sciences of the United States of America 104: 9725–9729.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241(4872): 1455–1460.

Letcher, B.H., K.H. Nislow, J.A. Coombs, M.J. O'Donnell and T.L. Dubreuil. 2007. Population response to habitat fragmentation in a stream-dwelling brook trout population. PLoS One 2: e1139.

MacCrimmon, H.R. and J.S. Campbell. 1969. World distribution of brook trout, *Salvelinus fontinalis*. Journal of the Fisheries Board of Canada 26: 1699–1725.

McGrath, C.C. and W.M. Lewis, Jr. 2007. Competition and predation as mechanisms for displacement of greenback cutthroat trout by brook trout. Transactions of the American Fisheries Society. 136: 1381–1392.

McKenna, J.E. and J.H. Johnson. 2011. Landscape models of brook trout abundance and distribution in lotic habitat with field validation. North American Journal of Fisheries Management 31: 742–756.

McKenna J.E., M.T. Slattery and K.M. Clifford. 2013. Broad-scale patterns of brook trout responses to introduced brown trout in New York. North American Journal of Fisheries Management 33: 1221–1235.

Northcote, T.G. 1978. Migratory strategies and production in freshwater fishes. Pp. 326–359 *in* S.D. Gerking (ed.). Ecology of Freshwater Fish Production. Blackwell Scientific Publications, Oxford, UK.

Nyman, O.L. 1970. Ecological interaction of brown trout, *Salmo trutta* L., and brook trout, *Salvelinus fontinalis* (Mitchill), in a stream. Canadian Field-Naturalist 84: 343–350.

Oppel, S., A. Meirinho, I. Ramírez, B. Gardner, A.F. O'Connell, P.I. Miller and M. Louzao. 2012. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. Biological Conservation 156: 94–104.

Peterson, D.P. and K.D. Fausch. 2003. Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Oncorhynchus clarki*) habitat. Canadian Journal of Fisheries and Aquatic Sciences 60: 1502–1516.

Piggott, A.R. and D.R. Sharpe. 2007. Geological interpretations of baseflow for southern Ontario. Pp. 394–401 *in* Proceedings of the 60th Canadian Geotechnical and 8th Joint IAH-CNC and CGS Groundwater Specialty Conferences, Ottawa, ON.

Poff, N.L., J.D. Allan, M.B. Bain and J.R. Karr. 1997. The natural flow regime: A paradigm for river conservation and restoration. Bioscience 47: 769–784.

Power, G., R.S. Brown and J.G. Imhof. 1999. Groundwater and fish: Insights from northern North America. Hydrological Processes 13: 401–422.

Rahel, F.J. and N.P. Nibbelink. 1999. Spatial patterns in relations among brown trout (*Salmo trutta*) distribution, summer air temperature, and stream size in Rocky Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 56: 43–51.

Soulé, M.E. and D. Simberloff. 1986. What do genetics and ecology tell us about the design of nature reserves? Biological Conservation 35: 19–40.

Stanfield, L.W., S.F. Gibson and J.A. Borwick. 2006. Using a landscape approach to identify the distribution and density patterns of salmonids in Lake Ontario tributaries. Pp. 601-621 *in* R.M. Hughes, L. Wang and P.W. Seelbach (eds.). Landscape Influences on Stream Habitats and Biological Assemblages. Madison, WI. 25-26 August 2004. American Fisheries Society, Bethusda, MD. Symposium 48.

Thorn, M.W., C. Chu and N.E. Jones. 2016. Influence of environmental variables on the occurrence of brook trout (*Salvelinus fontinalis*) within streams of the Lake Simcoe watershed. Ontario Ministry of Natural Resources and Forestry, Science and Research Branch, Peterborough, ON. Science and Research Technical Report TR-09. 58 p.

Townsend C.R. and K.S. Simon. 2006. Consequences of brown trout invasion for stream ecosystems. *In* Allen R.B. and W.G. Lee (eds.). Biological Invasions in New Zealand. Ecological Studies (Analysis and Synthesis), Vol. 186. Springer, Berlin, DE.

Wagner, T., J.T. Deweber, J. Detar and J.A. Sweka. 2013. Landscape-scale evaluation of asymmetric interactions between brown trout and brook trout using two-species occupancy models. Transactions of the American Fisheries Society 142: 353–361.

Waters, T.F. 1983. Replacement of brook trout by brown trout over 15 years in a Minnesota stream: production and abundance. Transactions of the American Fisheries Society 112: 137–146

Watters, G.T. 1996. Small dams as barriers to freshwater mussels and their hosts. Biological Conservation 75: 79–85.

Wenger, S.J., D.J. Isaak, C.H. Luce, H.M. Neville, K.D. Fausch, J.B. Dunham, D.C. Dauwalter, M.K. Young, M.M. Elsner, B.E. Rieman, A.F. Hamlet and J.E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences 108: 14175–14180.

Witzel, L.D. and H. R. Maccrimmon. 1983. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. Transactions of the American Fisheries Society 112: 760–771.

Zorn, T.G. , J. Hessenauer and T.C. Wills. 2019. Increasing connectivity of Great Lakes tributaries: Interspecific and intraspecific effects on resident brook trout and brown trout populations. Ecology of Freshwater Fish DOI: 10.1111/eff.12527.

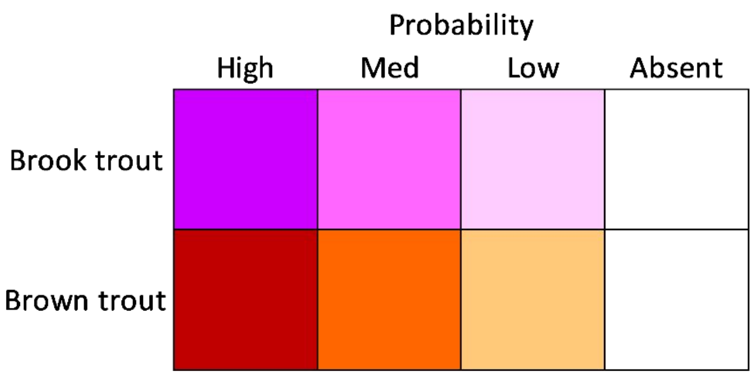
Appendix 1: Environmental predictor variables evaluated in modelling trout presence and absence

Table A1. Ecologically relevant environmental predictor variables for brook trout presence and absence in streams. (RCA is the reach contributing areas scale; RCh is the 30 m raster under the stream line representing riparian conditions; UCA is the upstream catchment area.)

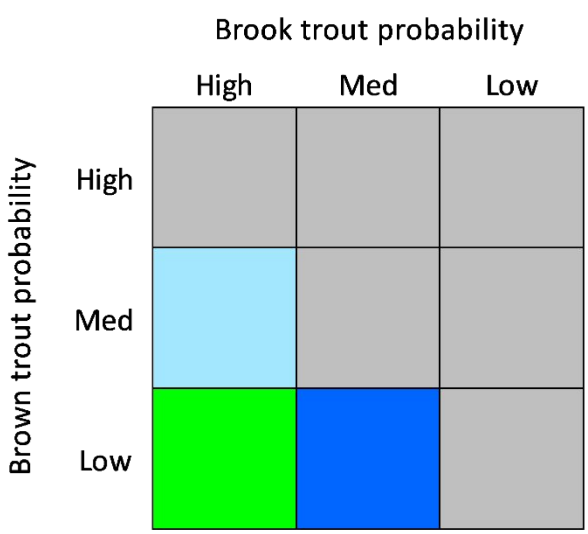
All variables	Units	Uncorrelated variables used in modelling
Strahler	NA	Strahler
RCA	km^2	RCA
RCA Climate Mean Annual Temperature	mm	RCA Landcov Open Water & Wetland
RCA Climate MeanGDD5	NA	RCA Landcov Treed
RCA Climate Mean Annual Precipitation	mm	UCA
RCA Geology Mean Overburden	m	UCA Climate Mean Annual Temperature
RCA Geology mean BFI	NA	UCA Climate Mean Annual Precipitation
RCA Geomorph Mean Elev	m	UCA Geology Mean Overburden
RCA Landcov Open Water & Wetland	%	UCA BFI
RCA Landcov Treed	%	UCA Geomorph Mean Elev
RCA Landcov 27 Community Infrastructure	%	UCA Geomorph Mean Slope
RCA Landcov 28 Agriculture Rural	%	UCA Landcov Open Water & Wetland
RCh Geology Mean Overburden	m	UCA Landcov Treed
RCh Geomorph Channel Slope	degree	%UCA Landcov 27 Com Infrastructure
RCh Geomorph SPI	NA	%UCA Landcov 28 Agriculture Rural
RCh Geomorph TWI	NA	UCh Geomorph TWI
RCh Landcov Open Water & Wetland	%	UCh Landcov Treed
RCh Landcov Treed	%	
RCh Landcov 27 Community Infrastructure	%	
RCh Landcov 28 Agriculture Rural	%	
UCA	km^2	
UCA Climate Mean Annual Temperature	Celsius	
UCA Climate Mean GDD5	NA	
UCA Climate Mean Annual Precipitation	mm	
UCA Geology Mean Overburden	m	
UCA BFI	NA	
UCA Geomorph Mean Elev	m	
UCA Geomorph Mean Slope	degree	
UCA Geomorph TWI	NA	
UCA Landcov Open Water & Wetland	%	
UCA Landcov Treed	%	
% UCA Landcov 27 Com Infrastructure	%	
% UCA Landcov 28 Agriculture Rural	%	
UCh Geology Mean Overburden	m	
UCh Geomorph Mean Elev	m	
UCh Geomorph Channel Slope	degree	
UCh Geomorph SPI	NA	
UCh Geomorph TWI	BA	
UCh Landcov OpenWaterWetland	%	
UCh Landcov Treed	%	
pChan UCh Landcov 27 Community	%	
pChan UCh Landcov 28 Agriculture Rural	%	

Appendix 2. Legends for Google Earth KML files

Keyhole markup language (KML) is a file format used to display geographic data in a browser such as Google Earth. For interpretation purposes be aware that the last file opened overlays on previously opened layers. Google Earth has a ≈10 megabyte limit after which it may stop working. Alternatively, use the geodatabases available via GeoHub [(geohub.lio.gov.on.ca/](geohub.lio.gov.on.ca/)).

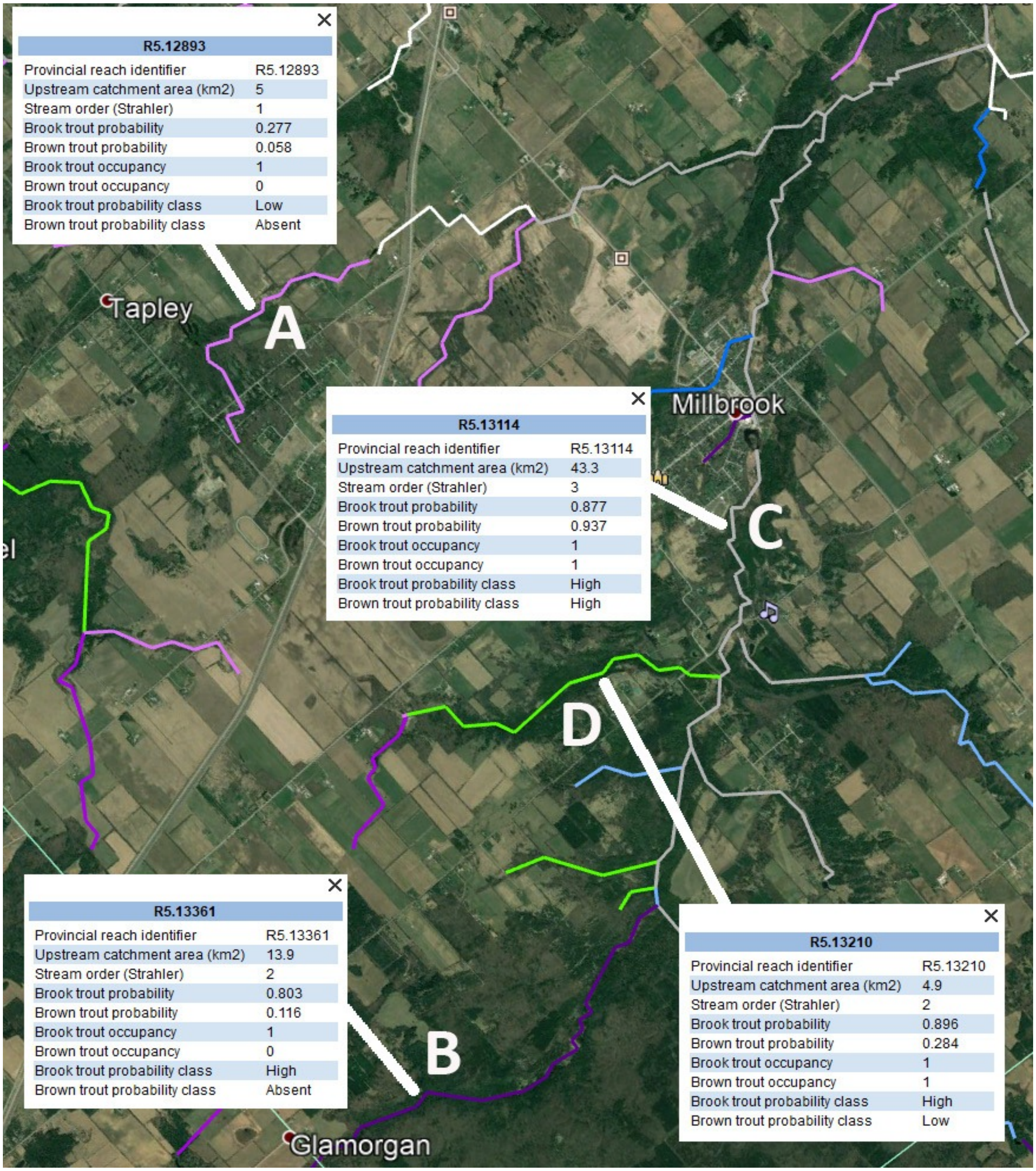


Brook (top row, purple shades) and brown trout (bottom row, red shades) occupancy probabilities.



Occupancy overlap of brook and brown trout. Combinations of occupancy where brook trout may thrive are coloured blue (middle left and bottom middle cells) and green (bottom left cell). We assumed that brook trout will be competitively excluded in the grey colour stream reaches.

Example Google Earth output



This map shows branches of Baxter Creek near the town of Millbrook, Ontario. Reach A (light pink line, ProvID R5.12893) has a low probability of supporting brook trout. Brown trout have an even lower probability, which is below the threshold to declare presence. Immediately downstream the reach (white line) supports neither species. Reach B (dark purple, ProvID R5.13361) has a high probability for brook trout but brown trout are likely absent given a very low probability of occupancy. Reach C (grey line, ProvID R5.13114) has high occupancy probabilities for both fish species. Reach D (green line, ProvID R5.13210) has a high probability for brook trout and a low probability for brown trout.

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