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Predicting aquatic habitat connectivity across watershed boundaries: implications for interbasin spread of nonindigenous aquatic species

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Understanding habitat connectivity is critical for managing nonindigenous aquatic species (NAS) spread. Dams and watershed boundaries can be impassable to NAS during typical conditions but may become temporarily passable during flooding. The goal of our project was to develop an approach for identifying locations of aquatic connectivity at a fine spatial scale along watershed boundaries using readily available data. To develop this approach, we focused on the potential for range expansion of invasive fish in the United States via possible cross-boundary habitat connections. First, we developed an index using metrics of elevation, watershed size, and geology at regular points along a watershed boundary to stratify points by likelihood of connectivity during high precipitation (>20 mm of precipitation in a 3-day period). We then used a subset of points across a gradient of connectivity likelihoods to gather Landsat-derived observed surface water data and developed a statistical model to predict surface water presence from landscape characteristics. We applied the model throughout the entire watershed boundary to identify locations of hydrologic connectivity during high-water events. The presence of surface water on watershed boundaries was predicted by the interactions between watershed boundary point elevation relative to the minimum adjacent HUC-12 elevations and watershed boundary point elevation relative to neighboring point elevations (marginal R^2 = 0.94). Our approach can be used to identify potential areas of surface water connectivity between watersheds quickly and easily at a fine spatial scale using readily available, remotely sensed data that can inform conservation and management actions across disciplines.

KEYWORDS

habitat connectivity, biodiversity, dynamic surface water extent, GIS, invasive species, invasive carp, silver carp

Introduction

Habitat connectivity plays a critical role in the persistence of species across the globe, and loss of connectivity may represent a greater extinction risk than habitat loss alone (Tiang et al., 2021). Dams, diversions, and road crossings can interfere with the movement of aquatic organisms and are some of the leading causes of declining biodiversity in freshwater systems (Reid et al., 2019). Rivers and streams are often thought of as linear systems where physical obstructions prevent organisms from moving to new areas. Although this is true during typical water levels, flooding can allow organisms to move into adjacent watersheds or past typical movement barriers (e.g., dams; Lubejko et al., 2017). The focus of many connectivity studies is on longitudinal or floodplain connectivity rather than connectivity across watershed boundaries; however, inter-watershed movements may be important for the natural dispersal or spread of species to new areas or among populations.

Much effort has been expended toward preserving and restoring habitat connectivity to aid in native species conservation, yet understanding and manipulating habitat connectivity can also be important for preventing the spread of invasive species (Rahel and McLaughlin, 2018) and limiting biodiversity loss due to species invasions. For example, potential connections that could allow the spread of invasive species into new watersheds can be modified via behavioral deterrents or physical barriers. Given the importance of watershed connectivity for the conservation of native species and the potential spread of invasive species, it is imperative to be able to quickly predict specific locations where connectivity may allow for interbasin movement so that appropriate preventative actions can be taken.

The objective of our study was to develop a method for predicting locations where surface waters could connect across watershed boundaries or bypass existing barriers during flooding or heavy precipitation events. Our method relies on remotely sensed data products that are easily accessed and represent observed conditions. Geospatial surface water products are useful tools but can be challenging to solely use for assessing connections due to spatial and temporal patchiness. Our method allows researchers to overcome these challenges by using a subset of locations and applying the results across a broader area. Other approaches to assess surface water connectivity can be difficult to implement because of the cost of collecting field-based measurements and processing time limitations when modeling at a region-wide scale (Vanderhoof et al., 2018). We used readily available geospatial data at a broad spatial scale in conjunction with observed surface water data to develop a model that predicted hydrologic connectivity at a fine spatial scale. Our methodology allows resource managers and ecologists to identify potential aquatic connectivity pathways for invasive species management.

Methods

Case study

We developed an approach for assessing potential interbasin connectivity by focusing on routes of aquatic invasive species expansion across watershed boundaries in the north-central United States. Preventing the spread of invasive bigheaded carps, particularly bighead carp *Hypophthalmichthys nobilis* and silver carp *H. molitrix*, is a conservation priority in this region. Bigheaded carps respond to flood pulses with dispersal movements (Coulter et al., 2016), potentially allowing them to invade new areas during periods of temporary connectivity.

Study area

Our study area represented the current extent of bigheaded carp invasion in North and South Dakota, particularly the watershed boundary between the James and Big Sioux rivers and the upper Missouri and Red rivers (Figure 1). This region is dominated by low gradient topography, pothole lakes, and wetlands with high potential for temporary surface water connections. Further bigheaded carp range expansion on the Missouri River is prevented by Gavins Point Dam near Yankton, South Dakota. The James River, a Missouri River tributary, contains bigheaded carp north to the Jamestown and Pipestem dams in North Dakota. Upstream of these dams are the uninvaded upper James River and adjacent Red River of the North. Uninvaded Firesteel Creek is located in the southwestern portion of the James River Basin and shares a watershed boundary with the uninvaded upper Missouri River. Across these basins we collectively analyzed over 3,000 km of watershed boundary for interbasin surface water connectivity.

Approach overview

We first assigned locations along the watershed boundaries a value (hereafter termed ‘Point Selection Index’) based on elevation, stream order, waterbody, and geology, indicating the likelihood of surface water presence following a precipitation event. Next, we subsampled locations along the watershed boundaries to obtain a feasible number of locations for subsequent analyses that represented a gradient in the likelihood of surface water presence (see *Point Selection Index* below). Using these subsampled locations, we developed a statistical model predicting surface water presence (observed via remote sensing) from environmental conditions (e.g., precipitation and elevation data). This model was then applied to entire watershed boundaries to identify specific areas where hydrologic connectivity was likely to occur during high-water events.

Point Selection Index

The Point Selection Index was created to obtain a feasible number of watershed boundary locations for later analyses. We first defined points along watershed boundaries and gathered relevant characteristics including elevation, stream order, watershed size, and quaternary alluvium presence. Watershed boundaries were obtained from the Watershed Boundary Database (United States Geological Survey, 2022). Regular points were then generated along the entire watershed boundary of interest every 0.001° (about 110 m), resulting in 27,417 points. Hydrologic

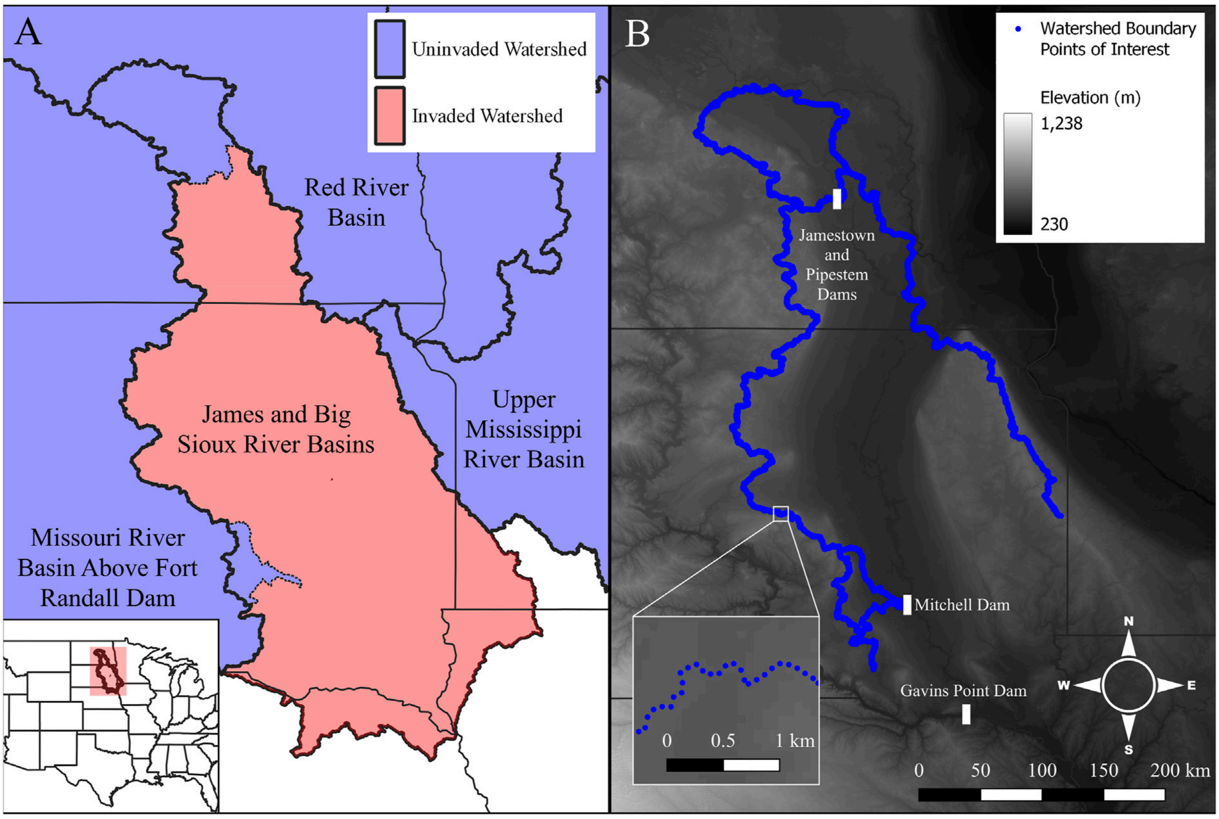

FIGURE 1
Study area in North and South Dakota, United States including **(A)** major river basins and their bigheaded carp invasion status and **(B)** elevation along watershed boundaries. Points of interest are points along the watershed boundaries every 80 m for which connectivity was assessed.

unit code (HUC) 12 watersheds that intersected either side of the watershed boundary of interest were also extracted for later analyses (n = 139). The HUC-12 watersheds that are part of the bigheaded carp-infested James and Big Sioux river basins were termed 'inside' while those of the uninvaded Missouri, James (portions), and Red river basins were termed 'outside' (Figures 2A,B). Elevation data were acquired from the National Elevation Dataset (United States Geological Survey, 2013) at 10 m resolution. Elevations were extracted for each point along the watershed boundary, and mean, median, maximum, and minimum values were calculated for all HUC-12 watersheds on both sides of the boundary. Waterbody and stream shapefiles were acquired from the National Hydrology Database Plus High Resolution (United States Geological Survey, 2017). The presence of quaternary alluvium, a potential historical indicator of hydrologic connectivity, was acquired from the State Geologic Map Compilation geodatabase of the conterminous United States (Horton et al., 2022). Each point along the watershed boundary had a Point Selection Index value calculated based on four components derived from collected characteristics: elevation metric (EM), stream order metric (SOM), waterbody metric (WBM), and geology metric (GM). The EM was calculated from four values. For each watershed boundary point, point elevation minus (1) the inside HUC-12 minimum elevation, (2) the outside HUC-12 minimum elevation, (3) the inside HUC-12 median elevation, and (4) the outside HUC-12 median elevation were calculated, and each was assigned a percent rank (0–1 scale). These four values were then averaged for each watershed boundary point to create EM. The SOM was calculated as the percent rank (0–1 scale) of maximum stream order in each of the intersecting HUC-12s. The WBM was calculated as the percent rank (0–1 scale) of the maximum single waterbody surface area and sum of all waterbody surface areas in the intersecting HUC-12s. The GM was calculated as a binary variable, with 1 representing the presence of quaternary alluvium on the watershed boundary. Finally, each component was weighted based on the complexity and inferred importance of the variable based on the combined professional judgement of the authors. The Point Selection Index value for each watershed boundary point calculated as:

$$Point\ Selection\ Index = (EM*0.4) + (SOM*0.25) + (WBM*0.25) + (GM*0.1).$$

We next selected 50 points along the watershed boundary using a random-stratified process such that each 10th percentile of Point Selection Index values was equally represented. This provided a subset of watershed boundary points that represented a gradient of likely hydrologic connectivity to use in developing a statistical model to predict surface water presence during high-water events. Selecting a subset of points along a gradient of Point Selection Index values minimized the effect of the weights assigned to each variable in the

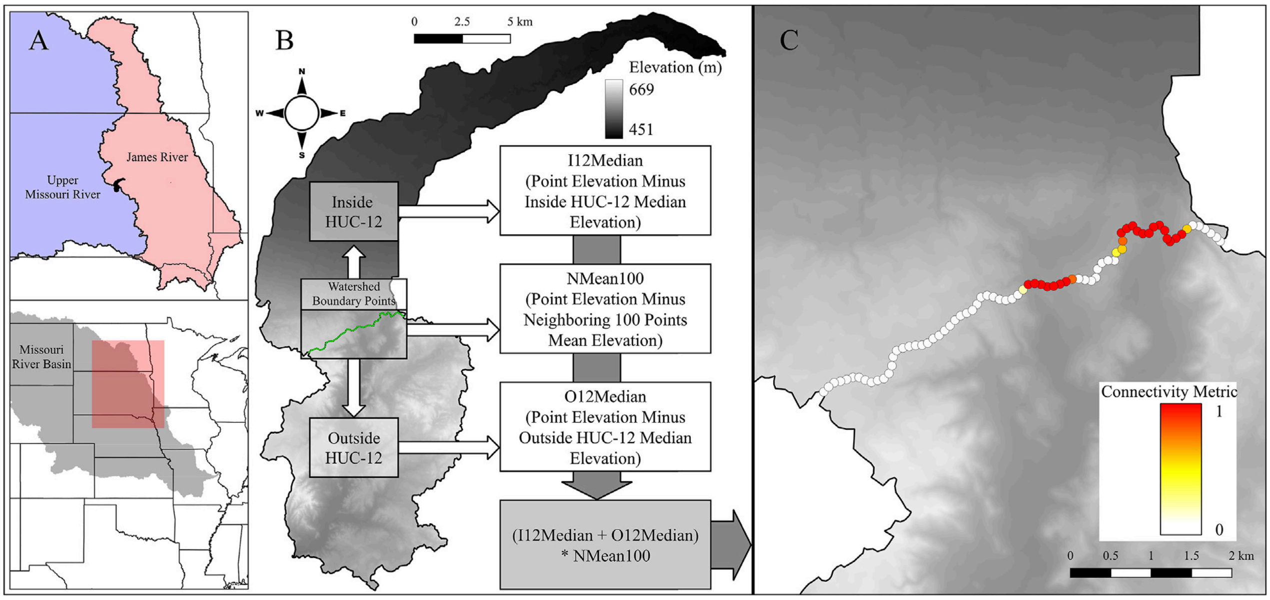

FIGURE 2
Progression of the model workflow. The location of the Hydrologic Unit Code (HUC)-12 watershed pair is first identified **(A)**. Watershed boundary point elevations **(B)** are then used in conjunction with neighboring HUC-12 median elevation to predict the presence of water crossing the watershed boundary following heavy rainfall (>20 mm in 3-day period) on a point-by-point basis. The result **(C)** is a predicted risk value (1 = high) of surface water presence for each point along the watershed boundary.

Point Selection Index calculation. We chose a subset of 50 points as a tradeoff between statistical sample size and the time required to obtain response and predictor variables.

Surface water observations at subset locations

We used dynamic surface water extent (DSWE; Jones, 2019) data products to find observations of water presence on the watershed boundary surrounding points subsampled from the Point Selection Index. The DSWE data uses Landsat imagery to interpret surface water extents. These data are obtained in 5 × 5 km tiles at a 30-m resolution. We used the 'interpreted layer with all masks applied' tiles within the tile packages to identify cloud cover. Surface water presence from the DSWE data were obtained using manual inspection at each subsampled point and the 100 neighboring points (50 on each side) to broaden the area from which data were collected and bring the total number of data collection points to 5,050.

We determined which DSWE tiles represented observations during high-water events using precipitation and cloud cover data. Daily precipitation data were acquired for each point from 1 January 1980 to 31 December 2022 from an online climate database (PRISM Climate Group, 2023). Next, the DSWE tile image dates were cross-referenced with the dates when each subsampled point received more than 20 mm of precipitation within the previous 3 days. The results were then filtered by cloud cover (less than 40% cover) and tile fill (greater than 30%) to increase the likelihood that the points of interest within each DSWE were included in the image and unobscured. We identified 483 DSWE tiles that met these criteria for manual inspection.

Each DSWE tile and accompanying full color images were examined manually to ensure that each subsampled point and the neighboring 100 points were present in the image and unobscured. Cloud cover and associated aerosol radiance obscured some or all points of interest within the DSWE layer, excluding them from further analysis. Cloud-associated aerosol radiance is displayed on the DSWE layers in the same band as water cover which is why we chose to manually inspect DSWE and full color images. Raster values for unobscured points (3-20 tiles per point over time; 40,519 total point values) were then automatically extracted (1 = surface water presence, 0 = surface water absence). All GIS-related methods were performed using spatial analysis software (QGIS Development Team, 2022).

Predicting hydrologic connectivity

We next predicted surface water presence (following a 3-day, >20 mm precipitation event) from climate data and metrics from the Point Selection Index using a binomial generalized linear mixed model. To account for differences in climatic variables between DSWE observations of surface water, we first modeled water presence as a function of daily, 3-day, 7-day, 14-day, 30-day precipitation totals, and the Palmer Drought Severity Index on Google Climate Engine to determine which variables to use as random effects (Matuschek et al., 2017). Fourteen-day precipitation totals alone were found to be the most important factor based on model selection results (Supplementary Table S1) and were then included as a random effect in modeling. Independent

TABLE 1 Comparison of the top five models and the null model predicting surface water presence along watershed boundaries in the north-central United States.

Model	Degrees of freedom	Log likelihood	AICc	ΔAICc
(I12Median + O12Median)*NMean100 + SE	9	−397.1	816.16	0
(I12Median + O12Median)*NMean100	7	−403.7	821.36	5.21
Elevation Metric +SE	4	−413.7	841.49	25.34
I12Median + O12Median +SE	6	−413.1	842.11	25.96
I12Median + O12Median + NMean100 + SE	7	−412.2	842.32	26.17
Null	2	−470.9	945.76	129.61

I12Median: Point elevation - inside HUC-12, median elevation; O12Median: Point elevation - outside HUC-12, median elevation; NMean100: Point Elevation - neighboring 100 points mean elevation; I12Min: Point elevation - inside HUC-12, minimum elevation; O12Min: Point elevation - outside HUC-12, minimum elevation; AICc: Akaike information criterion; SE: spatial eigenvectors.

variables included the four metrics from the Point Selection Index and additional elevation metrics (difference between point elevations and adjacent HUC-12 elevations, and the difference between point elevations and neighboring point elevations; Supplementary Table S2) that were included individually, additively, or as interaction terms. To account for potential spatial autocorrelation, we calculated spatial eigenvectors using location data and included these as additional predictor variables. Prior to modeling, 20% of the data were randomly selected and set aside to perform an area under the curve (AUC) analysis to assess model performance. All candidate models were considered and the top model as determined by Akaike's Information Criterion corrected for small sample size (ΔAICc <2) was then used to predict water presence for the entire watershed boundaries of interest (Figures 2A,B). All statistical analyses were conducted using R statistical analysis software (Program R version 4.2.2; R Core Team, 2022). Binomial generalized linear mixed models were performed using the *glmer* function and R^2 values were calculated using the *r. squaredGLMM* function, both in the LME4 package (Bates et al., 2015). Model selection was performed using the *model. sel* function in the MuMin package (Barton, 2023). Spatial eigenvalues were calculated using the *meigen_f* function in the spmoran package (Murakami, 2017). The AUC was calculated using the *roc* function in the pROC package (Robin et al., 2011).

Results

The survey of 483 DSWE tiles identified 110 incidences of water connectivity across basin or sub-basin watershed boundaries. Water connectivity occurred in 24 DSWE tiles (specific areas in time and space) and on 85 unique watershed boundary points, 16 of which had multiple periods of connectivity. Model selection resulted in a single favored model (Table 1) for predicting connectivity (conditional R^2 = 0.99; marginal R^2 = 0.94). Water presence on the watershed boundary following a rainfall event could be explained as an interaction between the watershed boundary point elevation relative to the two adjacent HUC-12 median elevations and the watershed boundary point elevation relative to the neighboring 100-point elevations, which accounted for spatial autocorrelation with eigenvectors (Figure 2). The top model achieved an AUC of 0.736 on the held-out test data.

The top model to predict water presence across the watershed boundaries of interest identified multiple areas of connectivity spatially spread throughout watershed boundaries (Figure 3). Each of these areas may be composed of tens to hundreds of points. Many of these areas were located in a region with a low elevation gradient in the northern James River Basin adjacent to the Red River Basin which spans nearly 400 km. Areas of likely connectivity which are of high risk for invasive bigheaded carp spread were predicted in narrower low-elevation areas with the neighboring Missouri River basin (Figure 2C).

Discussion

Our approach for predicting locations of watershed connectivity was performed relatively quickly using readily available remotely sensed data. Our approach also incorporated observations of surface water extents, where available, to refine connectivity estimates rather than relying on predictions and associated uncertainty from hydrologic modeling. This is an adaptable technique, similar to other habitat connectivity tools developed for terrestrial conservation purposes (Guo et al., 2018). This tool can be quickly and easily applied to other watersheds as an exploratory step to understand habitat connections between native populations or to assess connectivity should aquatic invasive species be found in new areas and rapid management response is required to control further spread.

Our results indicated that water connectivity across a watershed boundary could be predicted as an interaction between point elevation relative to the median elevations of the two intersecting HUC-12 watersheds and point elevation relative to neighboring points. Essentially, the model identified watershed boundary locations that were in areas of generally lower gradient (i.e., similar elevations across watersheds) and were at a lower elevation than adjacent points. The relatively large number of floodwater occurrences distributed along the watershed boundary was consistent with hydrological patterns in this region. This area has a low elevational gradient and has experienced broad-scale flooding (Todhunter and Rundquist, 2013) and increasing trends in streamflow over the past 30 years (Barth and Sando, 2024). Our case study and predictive model were specific to the study area and may change for other areas due to differing elevation profiles, soil

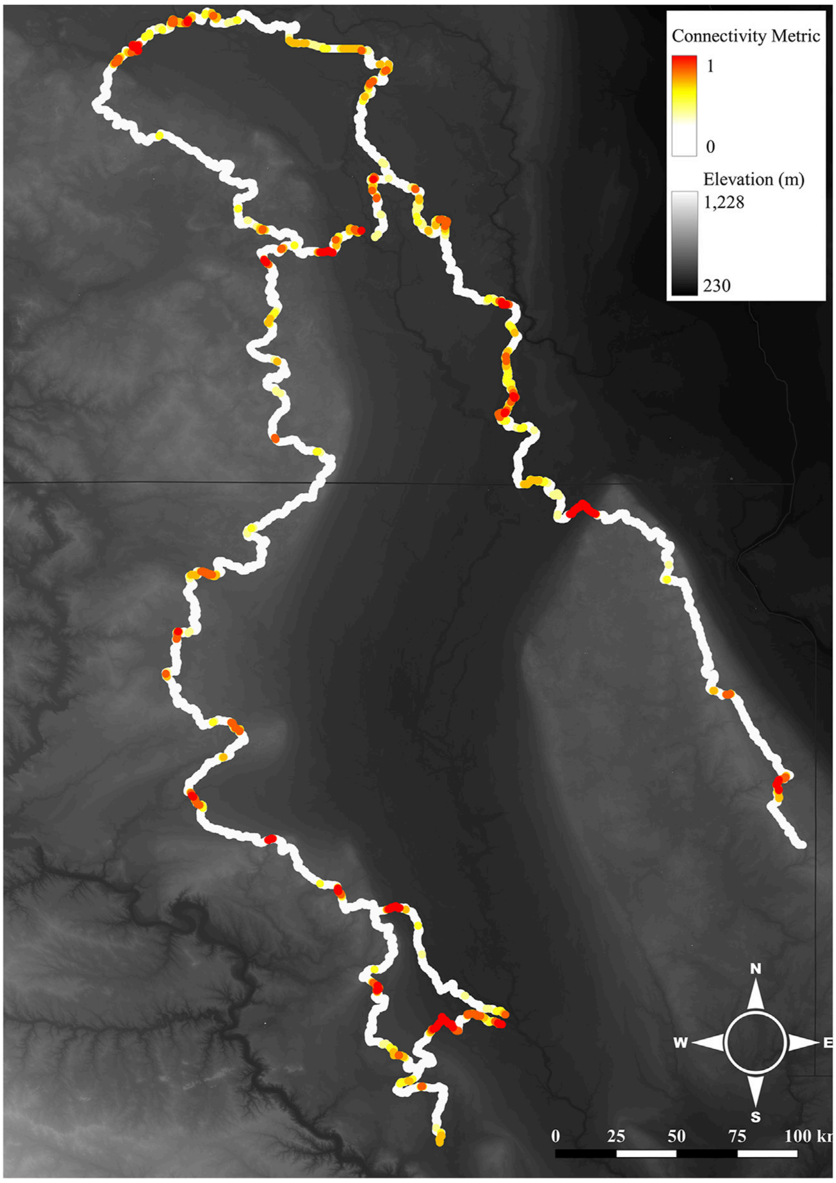

FIGURE 3
Predicted water presence along the watershed boundary in the study area. White points indicate a low chance of water presence while yellow to red represents an increasing likelihood of water presence.

permeability, and precipitation patterns. There may be other variables of interest specific to other areas to include in modeling of surface water presence or in determining the Point Selection Index. Additionally, it could be beneficial, depending on project objectives, to use different remotely sensed floodwater data that has a finer spatial resolution, such as data from Sentinel satellites. This would allow for detections of smaller depressions or channels that can become filled with floodwater and create hydrological connections for invasive species but would require the user to develop methods to identify surface water from raw data (e.g., compared to analysis-ready DSWE data). It might also be useful to alter the number of locations used to develop the Point Selection Index when applying our approach to different areas. Smaller watershed boundaries, for example, could benefit from points spaced every 10 m apart to increase the ability to predict floodwater presence while maintaining reasonable computation times. Although our case study focused on watershed boundaries, this technique could easily be expanded with point clouds to encompass a broader area of the landscape or to examine connectivity within watersheds (e.g., Pander et al., 2018).

Our method also demonstrated the utility of incorporating DSWE data into aquatic invasive species management programs. The locations we identified as having a high risk of floodwater presence can be difficult to otherwise determine due to the erratic and temporary nature of flooding. Once identified, these flood-prone locations can be prioritized for aquatic invasive species prevention efforts, including the creation of temporary or permanent movement barriers, if feasible, or sampling these locations and adjacent waterbodies as part of a proactive surveillance monitoring and rapid response program (Larson et al., 2020). These flood-prone locations could also be prioritized for targeted public outreach efforts to inform recreational users about reporting invasive species, best practices regarding bait disposal, and invasive species regulations (Mulligan et al., 2025). Our results identified a relatively large number of high-priority, flood-prone locations along a large geographic distance. If it is infeasible to take preventative actions at all flood-prone locations, managers could further refine their list of prioritized sites for prevention efforts based on distance to the nearest invaded waterbody or based on the habitat suitability of nearby, uninvaded habitats (Coulter et al., 2022).

Our study demonstrated the ability of this method to predict connectivity across watershed boundaries or other periodically connected aquatic habitats during flooding or heavy precipitation events. By examining relatively few watershed boundary locations, our approach was able to predict watershed connectivity across a regional scale. This information will allow resource managers to quickly and cheaply identify areas of aquatic habitat connectivity to target for conservation actions.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: https://www.usgs.gov/national-hydrography/access-national-hydrography-products, https://www.usgs.gov/the-national-map-data-delivery/gis-data-download, https://www.usgs.gov/national-hydrography/access-national-hydrography-products, https://prism.oregonstate.edu/.

Author contributions

PP: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review and editing. AC: Conceptualization, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review and editing. BS: Conceptualization, Funding acquisition, Investigation, Project administration, Visualization, Writing – original draft, Writing – review and editing. TD: Conceptualization, Funding acquisition, Investigation, Project administration, Visualization, Writing – original draft, Writing – review and editing. SC: Funding acquisition, Investigation, Visualization, Writing – original draft, Writing – review and editing. DC: Conceptualization, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2025.1646017/full#supplementary-material

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