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Assessing effective hydrological connectivity for floodplains with a framework integrating habitat suitability and sediment suspension behavior

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ABSTRACT

Continual and accelerating declines in hydrological connectivity threaten ecosystem processes, biodiversity, and services throughout the world. Therefore, there is an increasing demand for user-driven tools that assess hydrological connectivity from an effective perspective. We developed the Connectivity ASsessment Tool 1.0 (CAST1.0), which takes the threshold behaviors of focal ecological indicators into account, allows quantifying effective hydrological connectivity and its regime shift. We illustrate the use of CAST1.0 for the case of Poyang Lake, China. It was found that the response of effective hydrological connectivity to inundation depth, flow velocity, and water temperature follows a dynamic threshold effect. The evaluation of connected objects based on specific niches provides a valuable metric for recognizing potential habitat patches and links. This study provides a sound basis for assessing hydrological connectivity in a meaningful way, promising to provide novel insights into maintaining and restoring biodiversity and associated ecosystem services around the world.

1. Introduction

Hydrological connectivity, defined as the water-mediated transfer of matter, energy, and/or organisms within or between elements of the hydrologic cycle, is critical for promoting the formation, development, and stability of natural water systems and the conservation of biodiversity in general (Crooks, Sanjayan 2006; Pringle, 2001). The connectivity of rivers throughout the world has been weakened, affecting many of the fundamental processes and functions characteristic of healthy rivers and leading to the rapid decline of biodiversity and essential ecosystem services (Belletti et al., 2020; Couto et al., 2021; Grill et al., 2019; Su et al., 2021). There is a growing need for more robust and objective quantification of hydrological connectivity to knit together disciplinary interests across hydrologic, geomorphic, and ecologic perspectives (Covino, 2017). However, the structural complexity of most subtropical floodplains and their seasonal inundation patterns creates significant challenges to characterizing or quantifying hydrological connectivity.

Relevant research of hydrological connectivity encompasses three aspects, including structural connectivity, functional connectivity (process-based connectivity), and effective connectivity (Rinderer et al., 2018). Structural connectivity refers to the passage of water from one part of the landscape to another (Lexartza-Artza and Wainwright, 2009), while functional connectivity focuses on how structural elements interact with catchment processes to produce runoff (Bracken et al., 2013). More recently, there has developed a wide consensus that hydrological connectivity is species-specific and should be measured from an effective perspective. That is, not only the spatial arrangement of the adjacency or contiguity characteristics (structural and functional connectivity), but the behavioral response of the focal species and sediment suspension to the physical structure of the continuum (effective connectivity) should also be taken into account (Li et al., 2021). However, the lack of a consensus framework for quantifying effective connectivity has made the operationalization of the concept difficult.

Changes in hydrological connectivity lead to changes in such key hydrodynamic parameters as inundation depth, flow velocity, and water

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temperature, which have a significant impact on the hydrologic cycle, sediment transport, and population dynamic of waterbirds, fish, phytoplankton, and macroinvertebrates (Fig. 1). First of all, hydrological connectivity controls the timing, extent, and duration of flooding (Liu et al., 2020; Tan et al., 2019). Flow velocity and water temperature are the main factors affecting the incipient motion and flocculation of sediment particles (Jiang et al., 2002; Li et al., 2016). Habitat suitability for waterbirds is largely related to their body dimensions (especially the length of their legs, beak, and neck) and the depth of feeding water (Aharon-Rotman et al., 2017). Due to low temperatures and high velocity, juvenile fish born in river mainstreams usually need to enter lakes for food taking advantage of river flooding and backflow, then return to the mainstream after maturity (Abrial et al., 2019; McKey et al., 2016). Water temperature is an essential condition for phytoplankton photosynthesis and is closely related to the rate of intracellular enzyme reaction, plant anabolism, and respiration (Woolway et al., 2020; Zohary et al., 2020). Meanwhile, low flow velocity prolongs the residence time of eutrophic water, providing a long growth and reproduction period for phytoplankton and vice versa (Tian et al., 2021). Moreover, hydrological connectivity directly affects the migration, foraging, and reproductive behavior of macroinvertebrates in a hydrologic and hydrodynamic manner—that is, through flood extent and duration, inundation depth, flow velocity, and water temperature—and reshapes the macroinvertebrate food web by indirectly changing the water environment via nutrients, pollutants, dissolved oxygen, and water transparency (Gallardo et al., 2008). At the same time, the sediment transport and spatial-temporal dynamics of habitat suitability respond to changes in inundation depth, flow velocity, and water temperature following a threshold behavior (Liu et al., 2020). That is, any of the relevant hydrodynamic parameters can trigger strong feedbacks in community structure, biological abundance, and biodiversity when its changes exceed the ecological resilience of the focal species (Saco et al., 2020). In order to successfully integrate habitat suitability and sediment suspension behavior, the assessment of hydrological connectivity should depend on the wet/dry pattern (e.g. distribution of wet and dry patches), inundation depth, flow velocity, water temperature, and so on.

We have developed a new Connectivity ASsessment Tool 1.0 (CAST1.0) that takes the threshold behaviors of key ecological indicators into account and quantifies the effective hydrological connectivity of floodplains. It evaluates as well connectivity improvements provided by new potential habitat sites that may be added in the floodplain through habitat creation or restoration. This study is expected to provide a novel insight into assessing hydrological connectivity in a meaningful way.

2. Study site

A case study of Poyang Lake, the largest freshwater lake in China, was conducted to evaluate the application prospects of CAST1.0. Poyang Lake is located in the middle and lower reaches of the Yangtze River. It receives inflow from five tributaries in the south and empties into Yangtze River via an outlet at its northern extremity. Influenced by the typical subtropical monsoon climate, the lake level, with considerable annual variation (8–22 m), shapes an extensive floodplain of more than 3000 km^2 that consists of seasonally inundated wetlands, sub-lakes, rivers, and the main lake. From April to May, the floodplain is recharged not only by the five rivers upstream but also by the main lake downstream, displaying a two-way hydraulic characteristic. From June to September, all units in the floodplain are submerged and merge into one single water body. From October to November, the water body shrinks from the upland to the lowland of the floodplain, displaying a one-way hydraulic characteristic. From December to the next March,

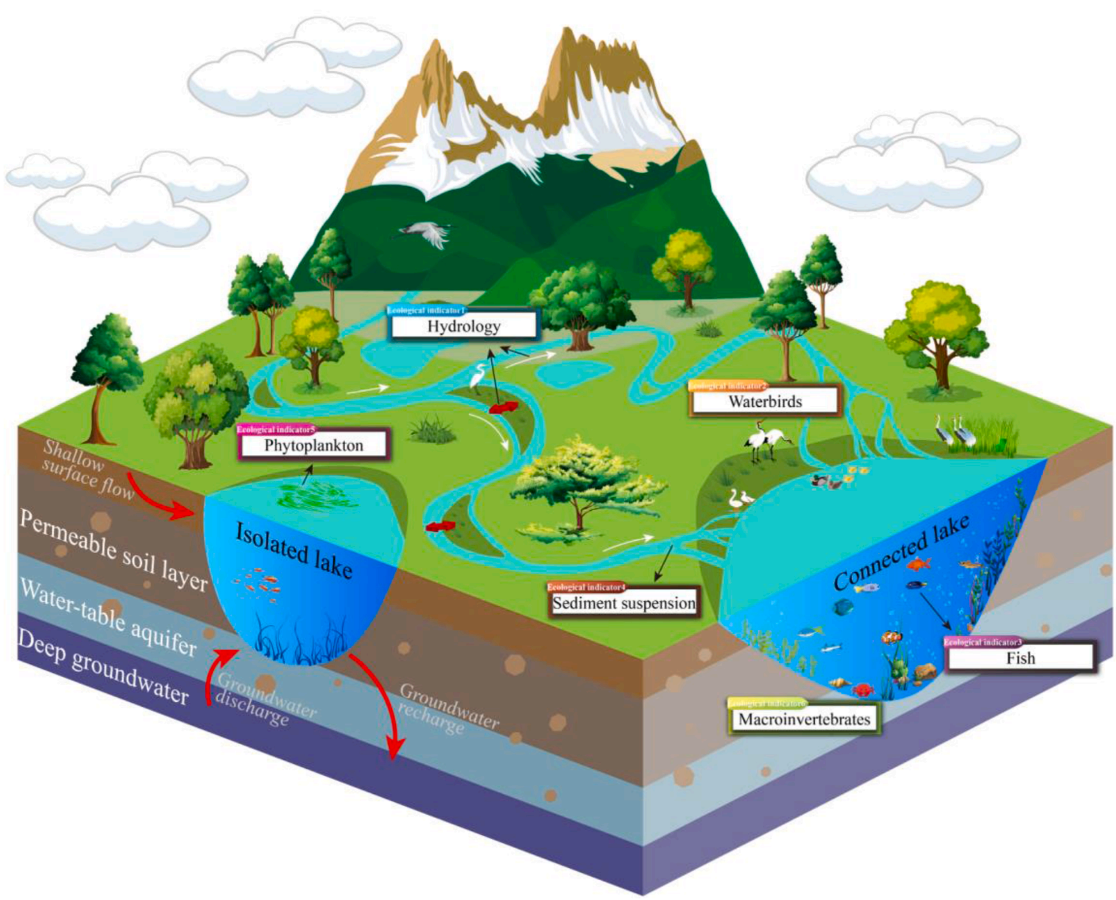

Fig. 1. Schematic diagram illustrating some typical ecological indicators related to hydrological connectivity.

nearly all sub-lakes become isolated, and the water volume is dominated by precipitation, evaporation, and infiltration. These unique hydrologic-hydrodynamic characteristics provide vital habitats for waterbirds, fish, phytoplankton, and macroinvertebrates, making Poyang Lake one of the world's most important wetlands. In recent years, the expansion and shrinkage patterns of the Poyang Lake floodplain have experienced significant changes due to the combined effects of climate change, hydraulic project construction, and sand mining activities. These changes have altered the original habitat suitability, putting degrading wetlands at risk of environmental deterioration, biomass losses, and biodiversity reduction. There is an urgent need to research the spatial variation in hydrological processes that result in the development of habitats and communities from the perspective of effective hydrological connectivity to provide a basis for the delineation of reservoirs and the restoration of degraded wetlands.

3. Methods

3.1. Connectivity assessment tool

The new CAST1.0 software provides quantitative metrics of effective hydrological connectivity (Fig. 2). CAST1.0 was developed using MATLAB, based on a geostatistical analysis script rewritten by Trigg et al. (2013). This geostatistical analysis approach quantifies the probability of connection between each pixel at a specified distance and enables characterization of spatial-temporal patterns of connected objects that can be used to interpret transitions and thresholds in flow processes. We recommend articles by Tan et al. (2019) and Li et al. (2019) for additional information.

CAST1.0 contains five functional modules: the Ecological indicator; User parameters; Input options; Output options; and Results preview. In the first module, six ecological indicators are recommended, including Hydrology, Waterbirds, Fish, Sediment suspension, Phytoplankton, and Macroinvertebrates. Along with the required parameter of Wet/dry pattern, users can choose one or more hydrodynamic parameters from Inundation depth, Flow velocity, and Water temperature as criteria of habitat suitability for the selected ecological indicators and set their thresholds. Georeferenced images (*.tif format) or points with latitude/longitude information (*.xlsx or *.txt format) both meet the input requirement of the source type. Users can process interpolation, projection transformation, clipping, and pixel resampling via the pre-processing function. Except for the interpolation images, CAST1.0 will output two types of results to the specified folder once the calculation is completed. (1) The connected object (CONNOB), which is defined as a cluster of valid pixels with the same attributes (inundation depth, flow velocity, and water temperature). If the attributes of a CONNOB satisfy the requirement of a species, the CONNOB refers to a suitable habitat (patches, cells, etc.) within which all pixels are considered connected. There is no effective connectivity between different CONNOBs. (2) The connectivity function (CF), which quantifies the possibility of a surface hydrological connection between rivers or lakes and their floodplain in the horizontal direction, and enables characterization of spatial and temporal patterns that can be used to interpret transitions and thresholds in flow processes. The probability P expressed in the CF can be calculated by the following algorithm:

$$P(n; z_c) = Pr\left\{ \prod_{j=1}^{n} I(u_j; z_c) = 1 \right\}$$

where $I(u_j; z_c)$ is an index for determining whether the variable $Z(u_j)$ at the position u_j exceeds the threshold z_c. If $Z(u_j) > z_c$, then $I(u_j; z_c) = 1$, or otherwise zero. All positions in the computation domain are estimated from the starting position u_1. The higher the spatial entropy of the computational domain, the faster the $P(n; z_c)$ approaches zero as n increases. Therefore, the value of the connectivity function in any given distance is the proportion of connected points in a specific direction within the distance range.

The last module provides separate previews of CF values going W–E,

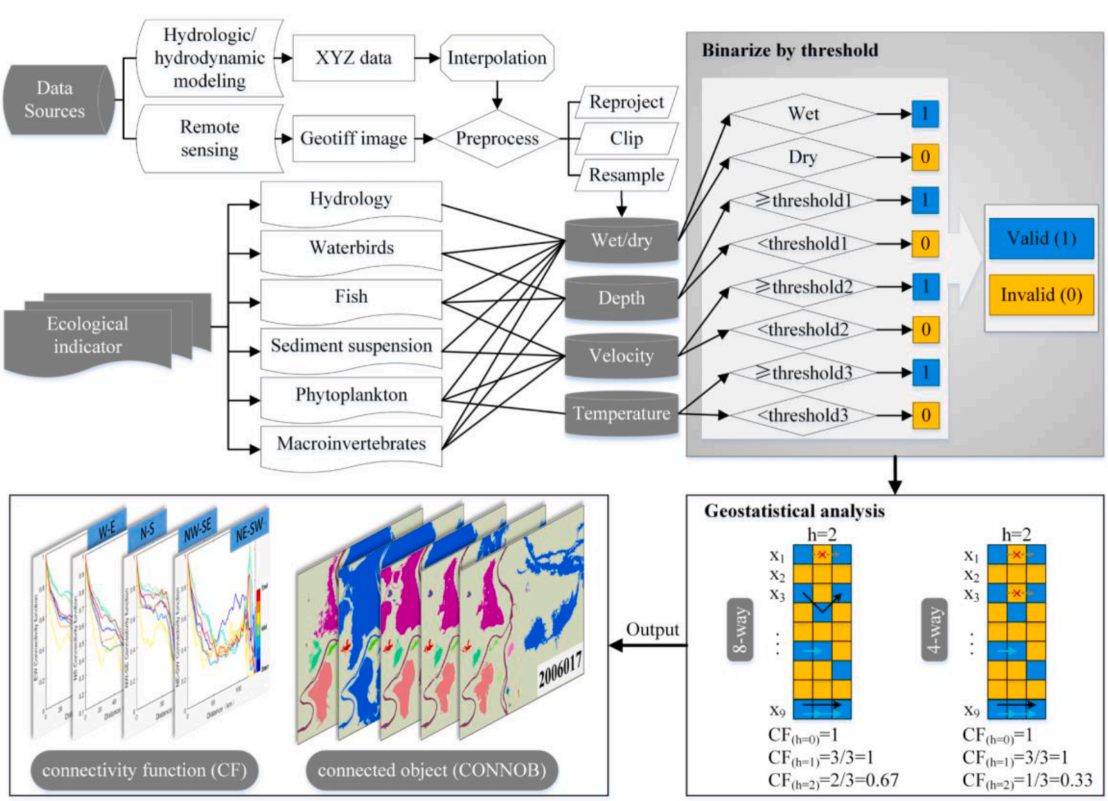

Fig. 2. Schematic outline of the methodology for the analysis of effective hydrological connectivity through the CAST1.0 software.

N–S, NW–SE, and NE–SW. The software is available online.

This framework differs from traditional hydrological connectivity assessment methods, which take into account only the wet/dry pattern. It defines effective units by integrating the flow velocity threshold of sediment suspension as well as the inundation depth, flow velocity, and water temperature thresholds of suitable habitats for waterbirds, fish, phytoplankton, and macroinvertebrates. For example, to assess the potential distribution of phytoplankton, pixels with a flow velocity of 0–0.30 m/s and water temperature from 20 to 30 ℃ are considered effective (defined as 1), otherwise ineffective (defined as 0). Recommended parameters and their thresholds can be found in the software manual. The effective hydrological connectivity can then be calculated based on the binary data. A habitat that is well suited to a species or community should be both abundant and well connected. That is, effective hydrological connectivity may be low if habitat patches are poorly connected, even if their total area is large.

3.2. MIKE 21

Using MIKE 21, a 2D, depth-averaged, finite-volume flow model of Poyang Lake developed by Li et al. (2017), the water level, velocity, and temperature in waterbodies during 2015 were simulated. Observed daily hydrologic data on lake inflows and outlet (discharge and temperature) were used to provide the boundary conditions for the MIKE 21. The hydrometeorological input data included the daily discharge of five tributaries, the water level at the Hukou gage station, precipitation, evaporation, air temperature, relative humidity, solar, radiation, wind speed, and direction. The model was validated with extensive field measurements and remote sensing data in 2015. For the modeled water levels, the Nash–Sutcliffe efficiency coefficient (E_{ns}) varied from 0.95 to 0.99, the determination coefficient (R^2) ranged from 0.97 to 0.99, and the root mean square error (RMSE) was less than 0.5 m, indicating a close agreement with field observations. The water temperatures were also predicted satisfactorily, producing E_{ns}, R^2, and an RMSE within the ranges of 0.92–0.96, 0.94–0.99, and 1.5–1.9 ℃, respectively. There is

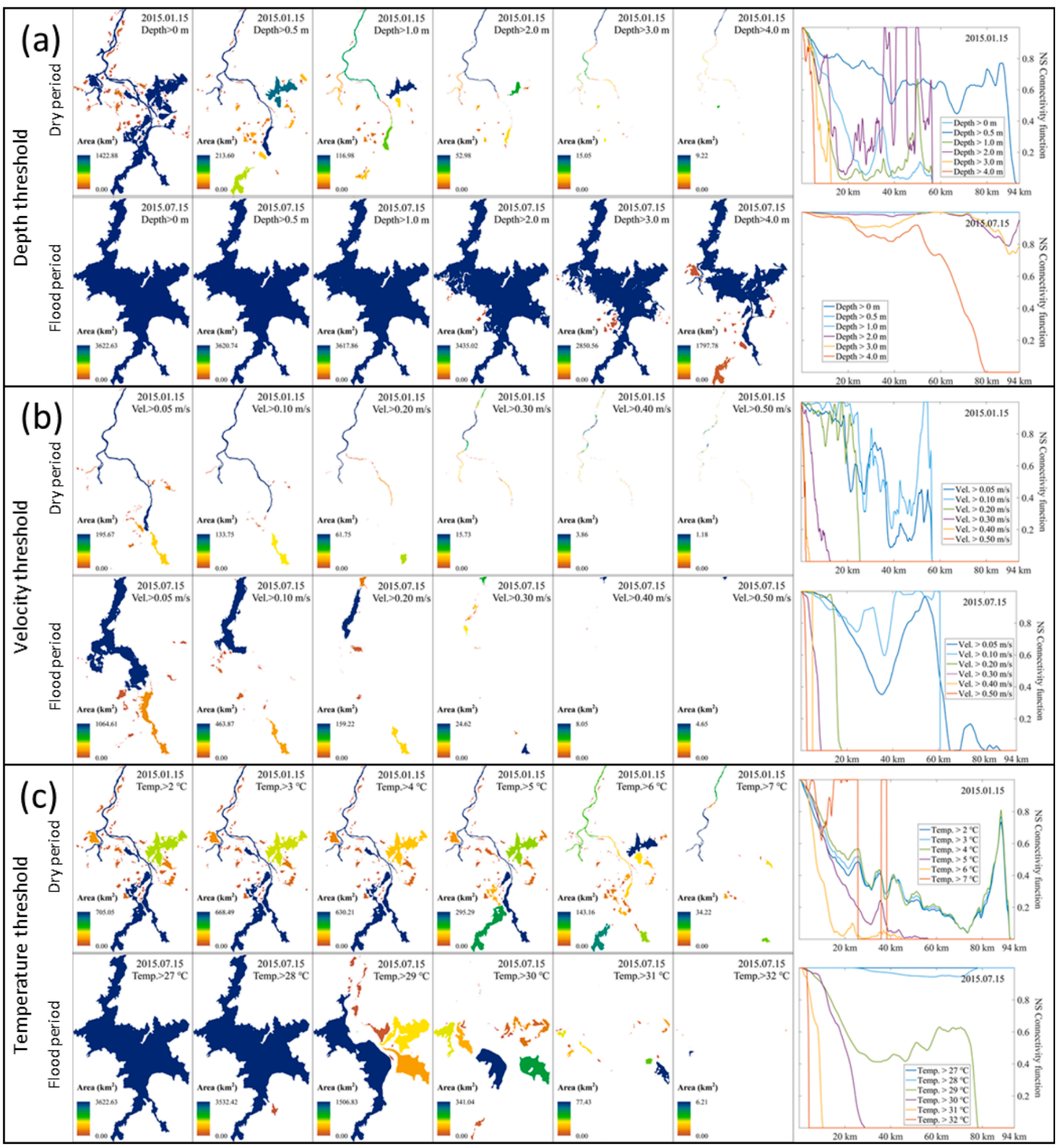

Fig. 3. Connected object plots (left 6 boxes) and associated North–South connectivity function plots. (a) Inundation depth threshold effect. (b) Flow velocity threshold effect. (c) Water temperature threshold effect. Connected object plots show connected objects of different sizes individually, with the largest in blue and the smallest in red. Connectivity function plots show step changes in the maximum distance of the connection. The distance at which the curve reaches zero indicates the connection maximum. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

also a close agreement between the modeled and observed velocity with a relatively low discrepancy (< 0.20 m/s) at a shallow water depth (~2 m below the surface) of the lake (Li et al., 2018). Detailed information on the model setup, calibration, and validation can be found in Li et al. (2017).

4. Results

4.1. Threshold effect

According to the main flow direction of Poyang Lake, an N-S connectivity analysis was conducted using 8-way connectivity (8D), which allows cells connected by an edge and corner vertex. The CONNOB spatial distribution and CF curves are illustrated in Fig. 3.

As shown in Fig. 3(a), the threshold of inundation depth had a greater impact during the dry period on hydrological connectivity than it did during the flood period. During the dry period, large areas of the southern sub-lakes and eastern bays disconnected from the main lake when the depth threshold changed from 0 m to 0.5 m, with the largest CONNOB decreasing from 1422.88 km^2 to 213.60 km^2. As the depth threshold increased, a considerable portion of the valid units became invalid, and the main watercourse was no longer continuous. It can be seen from the CF curve in Fig. 3(a) that an abrupt change of hydrological connectivity was likely to occur when the depth threshold changed from 0 to 0.5 m. The inundation depth had a minor effect on the hydrological connectivity during the flood period. When the depth threshold was 2.0 m, the largest CONNOB was only 187.61 km^2 smaller than when the depth threshold was 0 m. When the threshold was 3.0 m, some valid units in the alluvial delta of the west bank became invalid. The southern sub-lakes were disconnected from the main lake until the threshold was greater than 4.0 m. During a flood event, the regime shift of hydrological connectivity was likely to occur when the depth threshold went from 3.0 to 4.0 m.

Since dish-shaped lakes in the west, the relatively closed bays in the east, and sub-lakes in the south have insufficient water mobility, the impact of flow velocity threshold on hydrological connectivity was mainly manifested in the impact on the central and northern watercourses. The impact on the southern lake was greater than the impact on the northern lake. Whether during a dry event or a flood event, the northern watercourse was disconnected from the central watercourse when the flow velocity threshold was greater than 0.20 m/s. In comparison, when the threshold was greater than 0.30 m/s, the northern watercourse also lost spatial continuity, with the largest CONNOB decreasing by 75% (dry period) and 85% (flood period). From the perspective of CF curves, the hydrological connectivity of Poyang Lake changed dramatically when the flow velocity threshold increased from 0.10 m/s to 0.20 m/s during the flood period.

The temperature threshold had a greater impact on Poyang Lake's hydrological connectivity during the flood period than it did during the dry period. During the dry period, large CONNOBs were mainly located in the main watercourses. The northeastern bay became the largest CONNOB when the temperature threshold reached 6 °C, while the northern and central watercourses maintained upstream-downstream connectivity. The temperature threshold had an obvious impact on the hydrological connectivity during a flood event. When the temperature threshold was greater than 29 °C, for every 1 °C increase, the area of the largest CONNOB decreased on average by 76%. Meanwhile, Poyang Lake is divided into several main CONNOBs—such as the northwestern floodplain, the southwestern floodplain, the northeastern bay, the southeastern bay, and the southern sub-lakes—that are isolated from each other. During the flood period, Poyang Lake's hydrological connectivity underwent a sudden change when the temperature threshold reached 28–29 °C.

4.2. Potential habitat

The sediment incipient velocity and the thresholds of the key hydrodynamic parameters crucial to habitat quality were determined based on literature research (results of which can be found in the shared CAST1.0 user manual). These thresholds were mainly derived from field observations and experiments. Given the variations in the hydrodynamic threshold required by different species and ecological factors with different characteristics, this study broadens the threshold ranges to meet the hydrodynamic requirements of more ecological indicators for suitable habitats, thereby improving the universal applicability of the assessment results. Afterward, the inundation pattern, the possibility of sediment suspension, as well as the appearance of potential habitats for waterbirds, fish, phytoplankton, and macroinvertebrates found at Poyang Lake in 2015 were analyzed, as shown in Fig. 4. As the figure illustrates, the inundation frequency of the eastern bays, southern sub-lakes, and main watercourses was higher, and the sandy hills, alluvial cones, and natural levees in the western floodplain had a lower inundation frequency. Potential waterbird habitats were mainly distributed in the southern alluvial deltas and on the edges of the northern dish-shaped lakes. However, the eastern bays and main watercourses were not suitable habitats for waterbird due to the large inundation depth and difficulty in feeding. Contrary to the distribution pattern of potential waterbird habitats, the eastern bays and main watercourses were the primary habitats for fish. Except for a few dish-shaped lakes, most of the floodplains acted less frequently as fish habitats because they were at suitable inundation depths for only short periods. The lake bed with the highest occurrence of sediment suspension had the same spatial distribution as the lake bed with the most severe erosion (Yao et al., 2018), which was mainly found in the main watercourses, particularly the northern watercourse. Affected by the morphology, the central lake, eastern bays, and southern sub-lakes form relatively closed slow-flow regions, which increase the risk of algal blooms. However, because Poyang Lake is an open and interactive system with frequent water exchange, the overall probability of algal blooms is not high. In addition, the main watercourses are not suitable as macroinvertebrate habitats due to their deep inundation depths and fast flow velocity. Because of their short inundation durations and shallow depths, the highlands in the floodplain and at the edge of the lake also are unsuitable as macroinvertebrate habitats. Although most other habitats are relatively suitable for macroinvertebrates, no region is suitable all year round.

As shown in Fig. 5, the annual change in the area of the potential waterbird habitat is relatively stable except for summer. In the flood period, especially from June to July, the inundation depth of almost all floodplains exceeds the maximum feeding depth of waterbirds, and the potential habitat area is close to zero. Rather, potential fish habitats mainly appear in the flood period, especially from June to July, with an average area of more than 3000 km^2. The average area of fish habitats in other months is only 417.70 km^2, and the smallest area is less than 20 km^2. Influenced by the subtropical monsoon climate, the inflow from the Poyang Lake Basin increases from May to June, accelerating the flow velocity, which is likely to cause sediment suspension. In the dry period from November to December, the area where sediment suspension may occur is also large. It may be due to the emptying effect of the rapid decline in the Yangtze River's water level on Poyang Lake. From May to October, suitable flow velocity and water temperature provide favorable conditions for phytoplankton growth and reproduction. Restricted by low temperatures, it is almost impossible for phytoplankton to appear from December to March of the following year. There is no obvious regularity in the annual changes in the area of potential macroinvertebrate habitat. The area during the dry and flood period is relatively small ($Mean_{area} = 1396.83$ km^2), with large fluctuations ($SD_{area} = 904.98$ km^2); the area during the rising and recession period is relatively large ($Mean_{area} = 2396.43$ km^2), with small fluctuations ($SD_{area} = 421.10$ km^2).

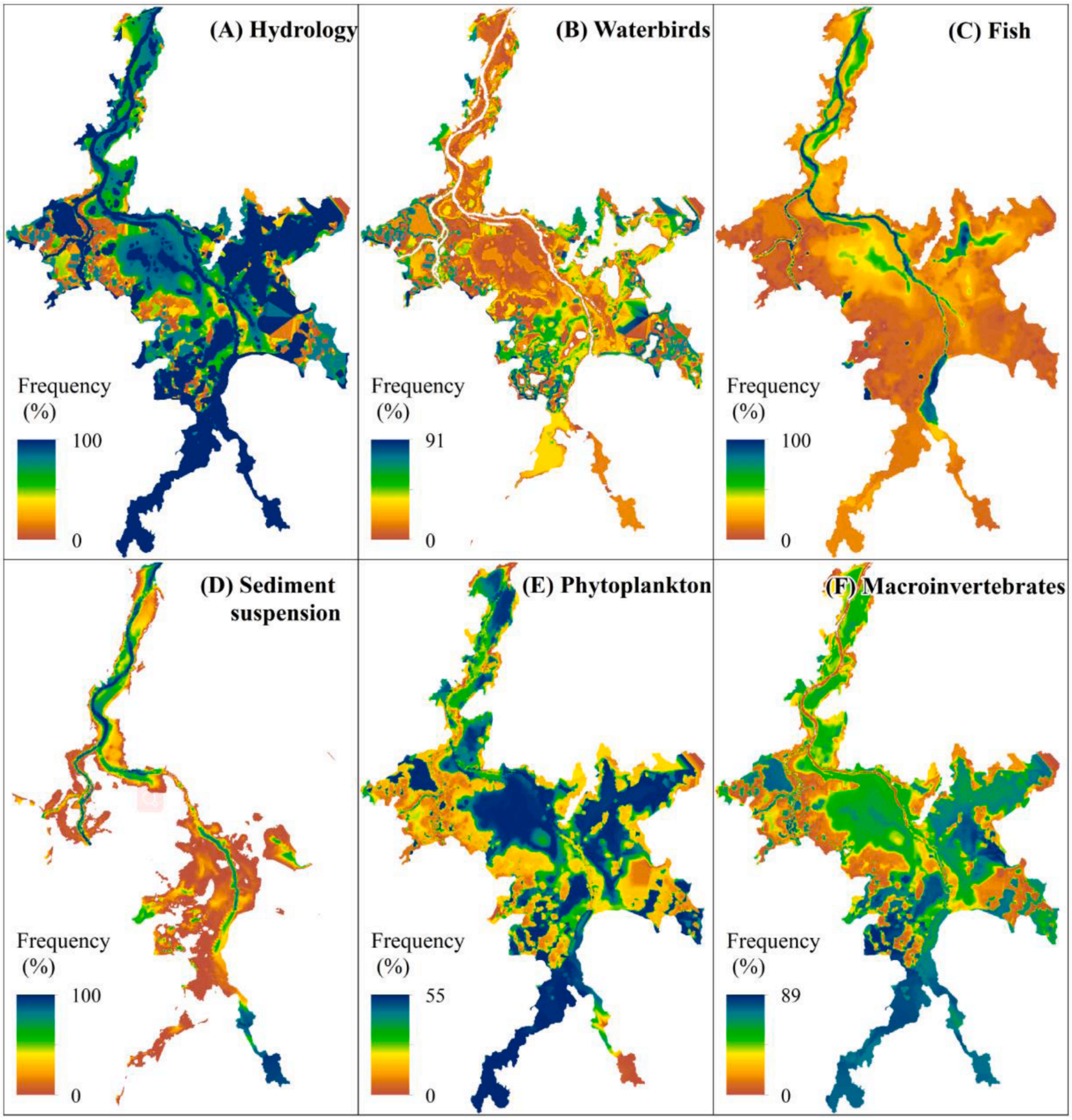

Fig. 4. Inundation pattern (A), the possibility of sediment suspension (D), and the appearance frequency of potential habitats for waterbirds (B), fish (C), phytoplankton (E), and macroinvertebrates (F) at Poyang Lake in 2015. Appearance frequency refers to the percentage of time that a pixel appears as a suitable habitat in the whole year.

5. Discussion

5.1. CAST vs. other tools

The growing demand for ecological protection has motivated researchers to develop many habitat-suitability models to predict the potential habitat distribution of specific species, such as Openmodeller (de Souza Muñoz et al., 2009) and Biomapper (Hirzel et al., 2002). Based on presence/absence data of the focal species in a set of sampled locations and independent ecogeographical variables (these may express topographical features, ecological data, or human superstructures), these models build a presentation of the fundamental ecological requirements for a species and extrapolate these requirements into a geographical region. Sampling the presence/absence data is a crucial part of the process, the following two possible scenarios often increase the uncertainty of this method: (1) the species could not be detected limited by observation methods or timing even though it was present; (2) the species is absent because of historical reasons (such as alien invasion) even though the habitat is suitable. In addition, the most important point is that these models usually do not consider the connectivity among habitats. Some patches presumably were not colonized because of their isolation, or too small to sustain a viable colony in the long term.

Given this, researchers developed a variety of connectivity assessment tools, such as Conefor (Saura and Torné, 2009), Connectivity Analysis Toolkit (Carroll et al., 2012), and FRAGSTATS (Mcgarigal and Marks, 1995). These tools can facilitate the maintenance of demographic flows, genetic flows, nutrient and hydraulic flows, and the resilience of populations to landscape conversion and climate change. Compared with the effective hydrological connectivity in this study, the biggest difference of these tools is that they pay more attention to landscape connectivity assuming that there is a link (corridor) between two nodes (patches), and evaluate the probabilities of direct dispersal between nodes and the link importance to overall connectivity by considering the different movement abilities and mortality risk of a species through different land cover types. This assumption does not apply to aquatic organisms such as fish, phytoplankton, and macroinvertebrates that inhabit the water bodies of the floodplain, while distance is not a limitation for long-distance migratory waterbirds. In

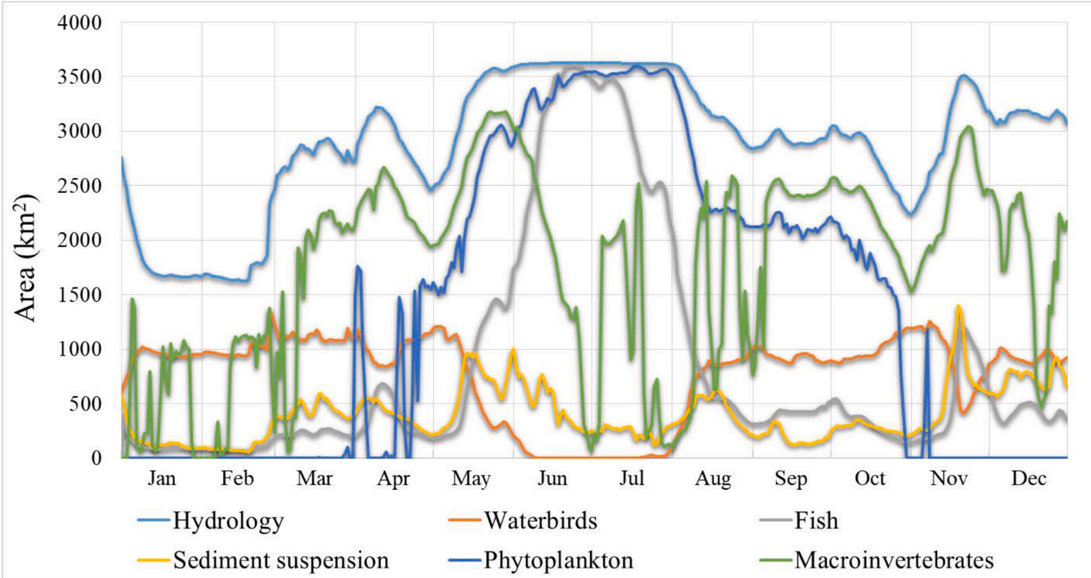

Fig. 5. Annual change of the potential habitat area.

addition, potential habitat distribution is an important output of these tools. Ultimately, whether the predicted habitat belongs to structural, functional, or effective connectivity depends on the evaluation basis and quality of nodes input to the tool.

With the advancement of computer technology, physics-based models such as PHABSIM (Waddle, 2001), Mesohabsim (Parasiewicz, 2001), River2D (Steffler and Blackburn, 2002), and CASiMiR (Benjankar et al., 2011) can also simulate the eco-hydrological process of floodplains and riverine systems. Unfortunately, it usually focuses on a specific species, and requires professional modeling knowledge and a large number of field observations, and is very difficult to realize in ungauged remote regions.

In summary, the CAST1.0 has the following advantages: (1) the whole process from data reading to pre-processing, to geostatistical analysis, and finally to the preview of results can be realized with only one button, without the need for complex parameter adjustment and professional programming foundation; (2) realize effective hydrological connectivity and potential habitat assessment in one tool, because the hydrological connectivity status is an important reference for the evaluation of the habitat quality of aquatic organisms; (3) it couples key hydrodynamic parameters as the basis for the assessment of effective hydrological connectivity (habitat suitability), different from tools that only take the wet/dry pattern into account. The most significant disadvantage of this tool is that our analysis does not investigate fundamental niches, and all thresholds of these key hydrodynamic parameters come from literature research. Although we try to select the results of studies in our study site and similar water systems when conducting literature research, we also consider the habitat suitability of different species (not genera, such as waterbirds) and different attributes of ecological indicators (such as sediment particle size), there is still no guarantee that the assessment has complete universality. Therefore, CAST1.0 provides a methodological framework for effective hydrological connectivity assessment considering habitat suitability of focal species. Which ecological indicators should be selected, and how to determine the thresholds of these indicators relies on the criteria and responsibility of the user.

Although there are deficiencies, CAST1.0 still has great practical value and wide application prospects: (1) As potential habitats, CONNOBs are crucial for the biodiversity conservation, provide a valuable reference for decision-makers to delimit reservoirs and develop specific protection strategies for different species; (2) the CF clustering feature can indicate the water-level threshold at which the overall connectivity may undergo abrupt changes, providing a scientific basis for hydrological regulation with the goal of optimizing effective hydrological connectivity; (3) it is possible to evaluate the possibility of material, energy and information exchanges between important geographic units and recognize the potential connected paths by calculating the connection frequency between key pixels and other pixels. Modifying the attributes of these paths is conducive to maintaining biodiversity and improving water quality.

Water quality is an important indicator for evaluating ecosystem health, and it is often affected by flow velocity. Normally, the greater the flow velocity, the more conducive to the diffusion and elimination of pollutants, and the better the water quality. But for Poyang Lake, the flow velocity is greatest in the dry season, and the water quality is often poor due to the low water volume and environmental capacity. In addition, the impact of basin pollution on water quality is usually greater than the impact of hydrological connectivity. Therefore, this study did not take water quality as a typical ecological indicator for evaluating effective hydrological connectivity. In the future improvement of CAST, we will try to couple the relationship between water quality and other parameters (such as water environmental capacity, vegetation type, and sediment nutrient) considering the variations in different hydrological periods and regions.

5.2. Interpretation of the case study

Inundation depth, flow velocity, and water temperature are key hydrodynamic parameters that affect the quality of aquatic habitats as well as important indicators for effective hydrological connectivity. This study quantified their thresholds for Poyang Lake's typical ecological factors through literature research and analyzed the temporal and spatial dynamics of CONNOB based on these thresholds. These CONNOBs provide potential habitats for ecological indicators. The fragmentation of CONNOBs indicates that the connectivity between habitats is blocked and the material transport, energy flow, and biological migration between patches are restricted, which is detrimental to the survival and reproduction of species or populations. At the same time, the fragmentation of the habitat will also increase the boundary of the patch and produce physical edge effects (Campomizzi et al., 2013). The edge of the habitat patch will show different ecological characteristics from the center, thus changing the spatial distribution of the biological community. For example, different species of waterbirds (such as the little egret, gray heron, and Oriental white stork) have strict minimum area requirements before they will breed. When the habitat patch area is smaller than that minimum, it is unsuitable for these species' reproduction and they will not live in the patch (Jones et al., 2013).

In this paper, the assessment of effective hydrological connectivity based on key hydrodynamic parameter thresholds provides an important basis for wetland biodiversity conservation. However, these thresholds are limited to specific types of water bodies and specific species, and cannot be directly adopted without distinction. For example, the suitable inundation depths for different species of fish or the same fish with different body lengths are not the same (Du et al., 2010). In addition, fish spawning, hatching of fish eggs, fattening of juvenile fish, and migration of adults require different flow velocities and water temperatures (Dadras et al., 2017). Ecological indicators have certain adaptability and survival strategies to respond to environmental changes. For different types of water bodies such as rivers, lakes, and oceans, the environmental factors that stimulate/inhibit the occurrence and development of ecological indicators differ, as do their thresholds. Therefore, inundation depth, flow velocity, and water temperature are not the only parameters for affecting habitat quality and evaluating effective hydrological connectivity. This study provides a new perspective for assessing the hydrological connectivity and predicting potential habitats in Poyang Lake. It is expected that this framework can be promoted to other floodplains by combining more sensitive environmental elements and thresholds of local ecological indicators.

In Poyang Lake, we found that fish habitats and phytoplankton habitats have a large overlapping area during the flood event in July (Fig. 6). There is also a large overlap between phytoplankton habitats and macroinvertebrate habitats in the flood and recession period (October). However, the results of this study cannot completely support these common-sense conclusions. For example, it is difficult to find the predator-prey relationship between waterbirds and fish, phytoplankton, and macroinvertebrates from the overlapping pattern of habitats during the dry period (January). That's because winter's low temperatures inhibit the distribution of phytoplankton and macroinvertebrates; the potential fish habitat predicted in this study is mainly for fish with a body length of more than 20 cm, which generally cannot be preyed upon by waterbirds. On the other hand, in addition to the hydrodynamic parameters, an assessment of the equality of waterbird habitats must consider the distance from human disturbance, the timing and rate of water level recession, and the availability of food sources.

6. Conclusions

This study developed an assessment tool for effective hydrological connectivity that has been successfully used on Poyang Lake. It provides a new perspective for biodiversity conservation and habitat restoration in this region, and is expected to be applied to similar floodplains.

The main conclusions include:

1 The response of hydrological connectivity to inundation depth, flow velocity and water temperature follows a dynamic threshold effect.

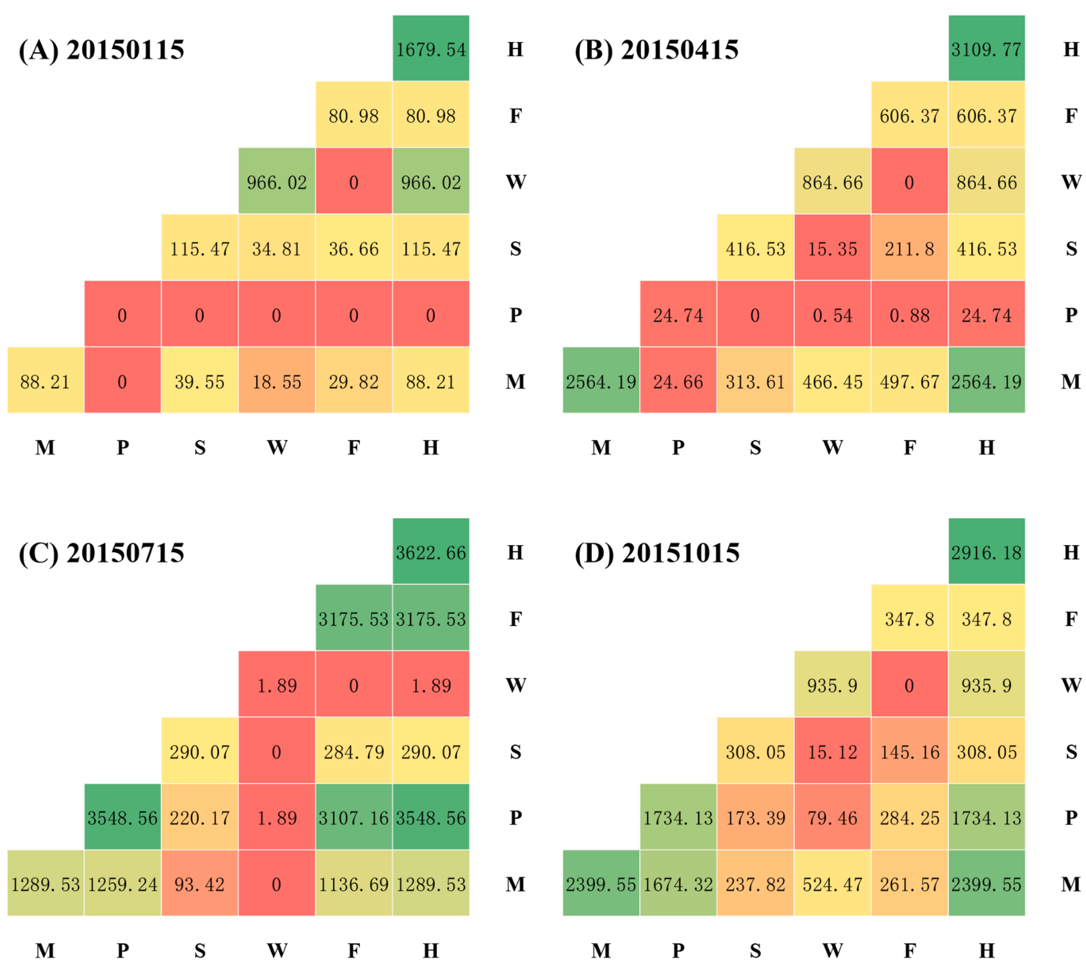

Fig. 6. Spatial relationship between habitats of ecological indicators. Numbers show the overlap areas (km^2) between different habitats (H: hydrology, F: fish, W: waterbird, S: sediment suspension, P: phytoplankton, M: macroinvertebrate), with the largest area green through yellow and red indicating the minimum. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2 The evaluation of connected objects based on specific niche provides a valuable metric for recognizing potential habitat patches and links.
3 The spatial relationship among habitats for different ecological indicators shows evident seasonal variations.

Declaration of Competing Interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the position presented in, or the review of, the manuscript entitled "Assessing effective hydrological connectivity for floodplains with a framework integrating habitat suitability and sediment suspension behavior".

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