Role of small wetlands on the regime shift of ecological network in a wetlandscape

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Abstract

Globally, wetlands in many places have been at risk by natural and anthropogenic threats including climate change and land use and land cover change. Because of their significant contribution to providing various ecosystem services, understanding the vulnerability to various threats and the effects of their loss on various scales and aspects is an imminent issue for wetland conservation. On a landscape scale, these wetlands can be distributed in a variety of forms (e.g., by size, bathymetry, geology, etc.) and interconnected by dispersal of inhabiting species. Here, we use the network modeling approach associated with wetland hydrology to analyze potential shifts in an ecological network caused by hydro-climatic and anthropogenic forcings. We focus on the role of small wetlands which are often easily ignored in assessing landscape function because of their minor occupancy in an overall area. Specifically, by manipulating the hydrological status of the small wetlands, an area of which only contributes 0.82\%, we observed the degrading effects on the characteristics (mean degree and network efficiency) of resulting ecological networks. Our results suggest that wetland size does not necessarily correlate with network centralities, and the loss of small wetlands acting as high centrality nodes induce a critical regime shift in network structure and function. Although hypothetically tested, because of their high sensitivity to hydro-climatic conditions and vulnerability to land use and land change along with climate change effects, the persisting functional loss of small wetlands is highly expected which eventually leads to trapping in the undesirable state of an ecological network. Our study is expected to provide a framework to evaluate the importance of small wetlands that can be easily ignored from an area-based point of view in a landscape.

1. Introduction

Across the world, there are many places called wetlandscapes where numerous wetlands with various forms and functions are spatially distributed within a landscape (Bertassello \textit{et al} 2018a, Kim and Park 2020, Åhlén \textit{et al} 2021). A wetlandcape, as an aggregate, supports additional emergent and dynamic ecosystem services which cannot be generated by an individual wetland. That is, a wetlandcape is a complex system composed of numerous components with their own traits and interactions (Thorslund \textit{et al} 2017, Klammler \textit{et al} 2020). Also, a wetlandcape and systems that depend on this often show dynamic and non-linear behavior originating from any change in its components. One critical property of a wetland that drives the whole behavior of a wetlandcape is hydrology. Seasonal fluctuations in hydroclimatic conditions or climate change cause shifts in hydro-period and -regime in a wetland, which eventually alter the structure and function of wetlandcape (Bertassello \textit{et al} 2019).

Here, we focus on an ecological network that is formed by the interconnectedness of wetlands (Kim and Park 2019, 2020). Interlinkages of components depend on spatial distribution and hydrodynamics of wetlands. Therefore, the ecological network is an ever-changing complex system because its components also
continuously shrink and expand. Furthermore, Kim and Park (2020) showed that the smaller the surface area, the greater the sensitivity of water storage of a wetland to the hydro-climatic condition. Similar to other water bodies and natural systems with fractal properties (Rinaldo et al. 1992, 1993, Andrie 1996, Rodriguez-iturbe and Rinaldo 2001), wetland surface area also typically follows a power-law distribution implying that there are numerous small wetlands while extremely large ones also exist with non-negligible probability (Van Meter and Basu 2015, Bertassello et al. 2018b). This suggests that small wetlands may be more susceptible to drier conditions by rapidly losing water resulting in the loss of numerous components and causing severe fragmentation of the ecological network. Not only the natural forcing but also anthropogenic drivers (e.g., drainage for agriculture or clearing for land development) can aggravate already vulnerable components (Janssen et al. 2006, Cui et al. 2012).

Given their greater exposure due to the majority in numbers and higher hydrological sensitivity, we hypothesize that small wetlands, when subject to external disturbances, may play a critical role in characterizing the features of wetlandscape and ecological networks. Moreover, we questioned if there is a critical threshold in the remaining portion of small wetlands, which may cause an irreversible regime shift in the characteristics of ecological networks. The importance of small wetlands has also been recognized for decades (Gibbs, 1993, Blackwell and Pilgrim 2011, Richardson et al. 2015, Biggs et al. 2017, Lane et al. 2022). Thus, we set the purpose of the study as to observe and analyze nonlinear and potential shifts in an ecological network by applying hypothetical scenarios in hydro-climatic and anthropogenic effects. More specifically, we use the random network model developed by Kim and Park (2020) to calculate the mean characteristics of ecological networks and, by manipulating hydro-dynamics of wetlands, analyze how the loss of small wetlands induces critical shifts in properties of ecological networks. While Kim and Park (2020) showed greater hydrologic sensitivity of small wetlands only using past data, our application of anticipative scenarios to explore the potential regime shift in ecological networks provides the novelty of this study. Our results will be especially useful for evaluating the persistence and regime shifts in the state of ecological networks not only by the effect of seasonal hydro-climatic fluctuation and global climate change but also the anthropogenic land-use and land cover (LULC) change.

2. Methods

2.1. Study area

Our study site is located in the Prairie Pothole Region (PPR) in Brookings County, South Dakota, United States. For analysis, we selected a region of $30.5 \times 30.5 \text{ km}^2$ in which 5,534 geographically isolated wetlands are identified (figure 1). This region is categorized as the Level IV Ecoregion, the Big Sioux Basin (ID #: 46m). Limiting the study area within the same ecoregion enables us to assume that an ecological network is formed by a single or similar species as we use a fixed parameter for simulating the dispersal of those species. The dataset of wetlands was obtained from the National Wetlands Inventory (NWI) from the U.S. Fish & Wildlife Service (assessed on October 1, 2017). QGIS 2.18.18 was used for the classification of wetlands (Kim and Park 2020). Due to its sensitivity to hydro-climatic conditions and LULC change, wetlands in this area have been a subject of interest for many studies (Kahara et al. 2009, Niemuth et al. 2010, McLean et al. 2021).

2.2. Wetland hydrology

In this study, we extracted hydro-climatic parameters (rainfall intensity, $P \text{ [mm]}$, rainfall frequency, $\lambda \text{ [day}^{-1}]$, and evapotranspiration, $E \text{ [mm} \text{ day}^{-1}]$) by season based on daily data of 2011 with no missing elements (table 1) from NOAA (National Oceanic and Atmospheric Administration) website (http://www.ncdc.noaa.gov/cdo-web/). We calculated evapotranspiration based on the Thornthwaite equation (equation (1)) (Xu and Singh 2001).

\[
PET = 16 \left( \frac{L}{12} \right) \left( \frac{N}{30} \right) \left( \frac{10T_d}{T} \right)^{\alpha_i} \tag{1}
\]

where PET is the potential evapotranspiration, $L$ is the average day length of the month, $N$ is the number of days in the month, $T_d$ is the average daily temperature (if the temperature is negative, use zero) of the month, and $\alpha_i$ is an index based on the heat with 12 monthly mean temperature (Thornthwaite 1948). There are other ways of estimating PET such as the Penman equations (Penman 1948) and Penman-Monteith equation (Monteith 1965). However, these methods require the rigorous use of local data such as wind speed, air pressure, solar radiation, and vegetated land area, which are not typically readily available. Because an accurate calculation of PET is not the scope of this study and because of its simple form for simultaneous PET calculations for numerous wetlands, we used the Thornthwaite equation.

To enable the description of the nonlinear and simultaneous hydrologic change of a large number of wetlands, we used normalized wetland bathymetry as described in Bertassello et al (2019) and Park et al (2014). This approach transforms the complex shaped wetlands into circular shapes in their surface area with concave- or convex-shaped bowls. We then simulated Poisson rainfall based on the values in table 1 to drive hydrological
change in each wetland (Rodriguez-Iturbe et al 1999, Park et al 2014). In addition, to calculate water loss through exchange with soil and groundwater below the wetted area of a wetland, we used the value of $9.17 \times 10^{-4} \text{cm sec}^{-1}$ for the saturated conductivity $K_{sat}$, 1.4 m of depth to water level, and 2 m of depth to an impervious zone. These values are based on the soil type (Moritz-Lamoure complex) and geological survey provided by the Web Soil Survey (WSS) of the USDA (Kim and Park 2020).

2.3. Dispersal model and ecological network analysis
The network modeling approach is useful for analyzing various aspects (e.g., connectivity) of a complex system by representing it with nodes and edges (Newman 2018). It has been widely used for decades in the field of landscape ecology to analyze the connectivity and fragmentation of patches or habitats within a landscape (Bunn et al 2000, Urban and Keitt 2001, Amezaga et al 2002). Besides using the terrestrial components, this approach has also been adopted in analyzing the connectivity of wetlands since the studies by Wright (2010) and Fortuna et al (2006). Moreover, by using various dispersal models, Kim and Park (2020) constructed and simulated the temporal dynamics of ecological networks driven by hydro-climatic conditions and wetland hydrology.

In this study, we used the heavy-tailed dispersal model among the three models tested by Kim and Park (2020) because it resembles the real world most and it has been rarely used in the wetland network studies. This model allows the movement of extremely long distances, thus providing higher survivability of species especially when wetlands acting as stepping stones are lost. We used a random walk defined by the power-law function as in equation (2) (Bartumeus 2007, Schick et al 2008).

$$ P(x \leq k_b) = \int_{x}^{\infty} \alpha x^{-\beta} \, dx = \frac{\alpha}{\beta - 1} x^{-(\beta-1)} = \left(\frac{x}{x_{\text{min}}}\right)^{-\beta+1} $$

\begin{table}[h]
\begin{tabular}{|c|c|c|c|c|}
\hline
 & Rainfall intensity ($P$) [mm] & Frequency ($\lambda$) [day$^{-1}$] & Potential evapotranspiration ($E$) [mm day$^{-1}$] & Length of the time series [days] \\
\hline
S1 (Dec $\sim$ Feb) & 2.82 & 0.26 & 0 & 90 \\
S2 (Mar $\sim$ May) & 4.90 & 0.52 & 1.05 & 92 \\
S3 (Jun $\sim$ Aug) & 7.62 & 0.37 & 4.20 & 92 \\
S4 (Sep $\sim$ Nov) & 1.29 & 0.16 & 1.27 & 91 \\
\hline
\end{tabular}
\caption{Seasonal hydro-climatic conditions in the PPR region.}
\end{table}

Figure 1. Study area in the prairie pothole region, South Dakota, USA. The blue-colored areas are geographically isolated wetlands distributed within the study area.

Table 1. Seasonal hydro-climatic conditions in the PPR region.
where \( x \) is the distance between wetlands, \( \beta \) is the exponent of the power-law function, and \( \alpha = (\beta - 1)\frac{1}{\beta_{\text{min}}} \) is a normalization parameter that ensures the finite probability (Kim and Park 2020). In this study, we used \( \beta = 3 \) that had the lowest movement probability (Reynolds and Rhodes 2009). Also, when calculating a distance between two wetlands for connecting by the movement of species, we measured the shortest distance between the perimeters of circular-shaped wetlands which temporally fluctuates (Kim and Park 2020).

After building an ecological network on a given hydrological state of wetland, the importance of each node in this network was evaluated by using two metrics: node degree, \( k_i \), and betweenness centrality, \( b_c \). Also, the global characteristics of the network were evaluated by using mean degree, \( \langle k \rangle \), and global efficiency, \( E \) (table 2) (Latora and Marchiori 2007, Estrada and Bodin 2008, Minor and Urban 2008, Kim and Park 2020). These metric values were computed on daily basis with 10 realizations and their average values were used for analyzing the mean behavior of an ecological network.

### 2.4. Evaluating the role of small wetlands

In the existing literature, wide and diverse areal thresholds for differentiating small wetlands have been used. For example, Moreno-Mateos et al. (2012) and Semlitsch and Bodie (2003) used 0.1 and 0.2 ha, respectively, whereas Reiss et al. (2007) used 5 ha. In our study, we examined wetland area distribution to obtain an appropriate size that occupies an extremely low portion of the overall area but is not negligible in the number. Here, we set 400 m\(^2\) of the maximum surface area as a threshold below which were defined as small wetlands. Based on this criteria, 576 wetlands among the total number of 5,534 were small wetlands, which were grouped as \( N_s \) (table 3). Each area of the small wetlands ranged from 138.5 to 398.6 m\(^2\) while the largest area in this wetlandscapes was 375,969.5 m\(^2\). Although the portion of small wetlands by its number was 10.4\%, the sum of their area only occupied 70\% of their maximum area. Also, wetlands with an area between 400 and 1,500 m\(^2\) were assumed to be occupied with water as in table 4. In the first initial condition (IC-1), all wetlands were filled with water to the maximum area while in the second initial condition (IC-2), only small wetlands were completely emptied to emulate the removal by LULC change. In the third initial condition (IC-3), the small wetlands were also assumed to be hydrologically empty while in the fourth initial condition (IC-4), those wetlands were filled with water to occupy 70\% of their maximum area. Also, wetlands with an area between 400 and 1,500 m\(^2\) were assumed to be filled 30\% of the maximum area in IC-3 while it was 70\% in IC-4. To match the total area, wetlands larger than 1,500 m\(^2\) were filled with more water in IC-3 than in IC-4. Our hypothesis for IC-3 and 4 was that, given a fixed total water surface area (2.70 \( \times \) 10\(^7\) m\(^2\)) stored in wetlands, the condition of which the water area in small wetlands is less or empty will significantly modify the resulting ecological networks. With these initial conditions, we simulated the dynamics of water and ecological networks by using seasonal hydro-climatic conditions in table 1. In addition, we applied another set of scenarios using IC-3 in which small wetlands are...

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**Table 2. Mathematical representation of network metrics.**

| Metric         | Mathematical representation | Description                                                                 |
|----------------|-----------------------------|------------------------------------------------------------------------------|
| Degree \((k_i)\) | \( k_i = \sum_{j \neq i} a_{ij} \) | Number of connections of node \( i \) to the neighboring node                |
| Betweenness centrality \((b_c)\) | \( b_c = \frac{1}{N(N-1)} \sum_{i \neq j \neq k} \frac{a_{ij}a_{jk}}{d_{ij}d_{jk}} \) | The number of shortest paths that pass through the node \( i \)              |
| Mean degree \((\langle k \rangle)\) | \( \langle k \rangle = \frac{1}{N} \sum_{i \neq j} k_i \) | Mean value of node degrees                                                   |
| Global efficiency \((E)\) | \( E = \frac{N(N-1)}{\sum_{i \neq j} \sum_{j \neq k} \frac{1}{d_{ij}d_{jk}}} \) | Quantifies the efficiency of movement in the network by calculating the mean value of reciprocals of shortest path lengths |

**Table 3. Information on the set of small wetlands.**

| Node sets       | Number of wetlands | Range of Area [m\(^2\)] | % of total maximum area |
|-----------------|--------------------|--------------------------|-------------------------|
| Set of total wetlands \((N_T)\) | 5,534              | 138.5 \~ 375,969.5       | 100                     |
| Set of small wetlands \((N_s)\)  | 576                | 138.5 \~ 398.6           | 0.82                    |
1,500 \sim \text{Sum of areas} > bci and compared the characteristics of nodes in the set of all 5,545 wetlands as a preliminary step, we constructed a network assuming that all wetlands are full. Then we analyzed and found that these wetlands are removed by LULC change (IC-3). The results are reported as average values after 10 realizations for each case.

The scenarios introduced above assumed that all small wetlands are functioning or not concurrently. Thus, it is difficult to identify which components among the group of wetlands play a critical role in inducing a characteristic transition in the ecological network. Given that the focal system is the network, we hypothesize that the loss of small wetlands with high network centralities may be the major cause for driving the regime shift. To test this idea, we applied two wetland loss scenarios (a) loss by the decreasing order of $k$ and (b) by the increasing order of $k$. Then, we also examined the effect of larger wetlands which comprise the similar surface area of small wetland sets. By removing those large wetlands, which were randomly selected and composed of 16 \sim 56, 136 \sim 151, and 288 \sim 297 wetlands depending on their size, we observed the effect contrasting to the loss of small wetlands.

### 3. Results

As a preliminary step, we constructed a network assuming that all wetlands are full. Then we analyzed and compared the characteristics of nodes in the set of all 5,545 wetlands ($N_f$) with the set of 576 small wetlands ($N_s$). The mean degree, $\langle k \rangle$, of the $N_f$ was 4.57 while that of the $N_s$ was 4.33, and $k$ ranged from 0 to 20 in both node sets (see Table 5). Although there was a huge difference in the size of the two node sets, there was structural similarity measured by $\langle k \rangle$. The maximum value of $k$ was 20 in both node sets implying that even small wetlands can act as hubs.

In both node sets, there was a low correlation between $k$ and $bc_i$ ($r = 0.34$ for $N_f$ and 0.36 for $N_s$) implying that high degree nodes are less likely to be the nodes with high betweenness. The correlations between $k$ and wetland area $A_i$ were also low in both networks ($r = 0.14$ for $N_f$ and 0.037 for $N_s$), which means that large wetlands are not necessarily the hubs and even small wetlands may act as hubs. The correlations between $bc_i$ and wetland area $A_i$ were also low ($r = 0.085$ for $N_f$ and 0.011 for $N_s$) implying that small wetlands can be important stepping stones. These preliminary results indicate that structural and functional importance, measured by $k$ and $bc_i$, is irrelevant to the size of wetlands.

Figure 2 shows inverse cumulative probability distributions of $k$ and $bc_i$ of both node sets. The degree distribution of $N_s$ (Figure 2(b)) compared to $N_f$ (Figure 2(a)) shows that a cut-off occurred at the tail of the distribution in $N_s$ as the number of nodes was reduced. Nevertheless, the node with the highest $k$ ($k_{\max} = 20$)

#### Table 4. Initial conditions for wetland areas.

| Maximum area (m²) | IC-1 | IC-2 | IC-3 | IC-4 |
|-------------------|------|------|------|------|
| <400              | 100% | 0    | 0    | 70%  |
| 400 ~ 1,500       | 100% | 100% | 30%  | 70%  |
| 1,500 ~ 10,000    | 100% | 100% | 73%  | 69.6%|
| >10,000           | 100% | 100% | 85%  | 60%  |
| Sum of areas (m²) |      |      |      |      |
| <400              | 2.70 \times 10^7 | 2.68 \times 10^7 | 1.88 \times 10^7 | 1.88 \times 10^7 |
| 400 ~ 1,500       |      |      |      |      |
| 1,500 ~ 10,000    |      |      |      |      |
| >10,000           |      |      |      |      |

| Scenario description | IC-1 | IC-2 | IC-3 | IC-4 |
|----------------------|------|------|------|------|
| initial conditions   |      |      |      |      |
| All wetlands are fully occupied by water by long and heavy precipitation. | Same as IC-1 but small wetlands are removed by LULC change. | Small wetlands remain empty even after some precipitation by the desiccation of surrounding soil. | Hydrologic processes normally work in all wetlands. |

#### Table 5. Network metrics and their correlations in the entire network ($N_f$) and the node set of small wetlands ($N_s$).

| Node set | $N_f$ | $N_s$ |
|----------|------|------|
| $\langle k \rangle$ | 4.57 | 4.33 |
| Correlation coefficient between $k$ and $bc_i$ ($r_{k-bc}$) | 0.34 | 0.36 |
| Correlation coefficient between $k$ and wetland area $A_i$ ($r_{k-A}$) | 0.14 | 0.037 |
| Correlation coefficient between $bc_i$ and $A_i$ ($r_{bc-A}$) | 0.085 | 0.011 |
still existed even in small wetlands. Moreover, figures 2(c) and (d) also confirm that important stepping stones can exist regardless of wetland size ($b_{max}$ of $N_T = 0.036$, $b_{max}$ of $N_s = 0.031$).

Table 6 shows network characteristics measured at initial conditions. The difference between IC-1 and IC-2 is that at the initial stage, all wetlands are assumed to be full except that, in IC-2, small wetlands ($< 400 \text{ m}^2$) are removed by LULC change and do not have a chance to recover following hydro-climatic conditions by season. Comparing these two initial conditions, $\langle k \rangle$ decreased from 4.57 (IC-1) to 3.80 (IC-2) and $E$ from 0.12 (IC-1) to 0.091 (IC-2) suggesting that the absence of small wetlands clearly diminishes both structural and functional properties of an ecological network. This phenomenon is more prominently observed by comparing IC-1 and IC-3 because, in IC-3, not only small wetlands are initially empty but also other wetlands are only partly full. However, the result of IC-4 ($\langle k \rangle = 4.35$ and $E = 0.12$), in which all wetlands including the small ones are partly full, indicates that the existence of small wetlands, even with small occupation by water surface area, sufficiently maintains the network properties of the healthiest state (IC-1).

Starting from the initial conditions of IC-3 and 4 in table 4, we simulated the temporal change of $\langle k \rangle$ and $E$ over hydro-climatic conditions given in table 1 (figures 3 and 4). We also added another condition from IC-3 (named IC-3$_{rem}$) where small wetlands are not allowed to recover assuming that these wetlands completely lost their functions either by LULC change or complete desiccation of surrounding soil. In all cases, the temporal change of $\langle k \rangle$ and $E$ for IC-3 rapidly recovered and converged to the trajectory of IC-4 while the values for IC-3$_{rem}$ remained stably close to their initial values without recovery. Only in the driest season (S4, figures 3(d)

Table 6. Network characteristics measured at initial conditions.

| Initial conditions | Descriptions$^a$                                                                 | $\langle k \rangle$ | $E$  |
|--------------------|---------------------------------------------------------------------------------|---------------------|------|
| IC-1               | All wetlands are full                                                            | 4.57                | 0.12 |
| IC-2               | All wetlands are full and small wetlands are removed by LULC change             | 3.80                | 0.091|
| IC-3               | Small wetlands are set to be 0 m$^2$ with other wetlands partly full            | 3.54                | 0.087|
| IC-4               | All wetlands are partly full                                                    | 4.35                | 0.12 |

$^a$ See table 4 for details.
Figure 3. Temporal change of $\langle k \rangle$ over seasonal hydro-climatic conditions given in table 1. $\langle k \rangle$ remained in the diminished state when the function of small wetlands was lost (IC-3rem) while it recovered to the original state when small wetlands were allowed to be filled by precipitation (IC-3).

Figure 4. Temporal change of $E$ over seasonal hydro-climatic conditions given in table 1.
and 4(d)), a significant decrease accompanied by large fluctuations in the $\langle k \rangle$ and $E$ for all initial conditions were observed but still, the trajectories of IC-3rem never converged to and remained far from IC-4.

Recognizing that not all small wetlands are equal in their contribution to forming the ecological network, we additionally analyzed the changes in the properties of the network over the portion of small wetlands lost in two different orders with four-node sets when these wetlands are full. In figure 5(a), $\langle k \rangle$ decreased rapidly when the wetlands were removed in the decreasing order of $k$ (wetlands with the highest $k$ were first lost) whereas $\langle k \rangle$ decreased slowly when the wetlands were lost in the opposite order. In the simulation with larger wetlands which comprised a similar area of small wetland sets, the decreasing rate of $\langle k \rangle$ reduced as the wetland components became larger (thus smaller number of wetlands (figures 5(b) ~ (d)). From these results, we could conclude that not only the individual size of the wetland but also the centrality that a wetland poses within a network matters in ecological restoration activity, especially in the view of a large-scale ecological system.

4. Discussion

To understand the ecological importance of small wetlands in wetlandscape, we analyzed the characteristics of ecological networks with different initial conditions in wetland areas and the recoverability of small wetlands. During a dry season, water loss from a wetland exceeds the water input resulting in the compression of the wetland surface area. Because the distance between the perimeters of neighboring wetlands increases, the probability of dispersal of a species to reach another wetland decreases, which eventually forms an ecological network typically having reduced network properties such as mean degree ($\langle k \rangle$) and network efficiency ($E$). Then, when a wet season begins, these network properties recover as wetland surface areas expand. However, when small wetlands lost their recoverability in storing water, our analysis suggests that the network properties do not recover to their original state even though the total water surface area of the wetlandscape is similar to the case when small wetlands still function. Within a wetlandscape, there are also small wetlands which act as main hubs (measured as $k_i$) and critical stepping stones (measured as $bc_i$), the loss of which may cause substantial degradation and fragmentation of ecological networks. Importantly, these small wetlands tend to be more sensitive to a dry climate and can be emptied with a higher probability (Niemuth et al 2010). This is also explained by the higher recession rate in the water stage of a small wetland originating from a higher perimeter/
Moreover, a prolonged dry period may also desiccate the soil surrounding a wetland, which hinders the rising of the pool stage before the soil is sufficiently saturated by subsequent rainfall.

Although we observed how the properties of a network change by the loss of small wetlands through artificially manipulating their hydrological function, this phenomenon can be expected in many regions by the climate change which may lead to a rise in net dryness (Junk 2002, Lauenroth et al. 2014). Small wetlands in PPR are also predicted to change in their numbers due to climate change and LULC change (Niemuth et al. 2010). In this study, we only examined the effect of wetland hydrology (including their permanent loss by LULC change) on an ecological network. However, climate change, which will bring the permanent and non-stationary change in temperature along with shifted frequency and intensity of hydro-climatic events, will not only affect the hydrological processes but also ecological and biogeochemical processes occurring in the wetlandscape resulting in the modification of various ecosystem services, human activities, and the location of ecological hotspots (Johnson et al. 2005, Rashford et al. 2016, Creed et al. 2017, Zhange et al. 2021). Moreover, because of its larger spatiotemporal scale in its forcing, large wetlands with less hydrological sensitivity can also be victims of climate change which will cause a more rapid and aggravated transition in ecological networks with irreversible consequences.

Our analysis suggests that shifting hydro-periods to near or permanently empty wetlands, especially those with critical centralities, may cause a regime shift in an ecological dispersal network from a highly connected and efficient state to a sparsely connected, less efficient, and fragmented state. Although, network centralities and the size of wetlands do not correlate, because of their vulnerability to natural and anthropogenic forcing, small wetlands are the ones that are more likely to be the causal factors that may induce this regime shift in the network.

Our analysis shows only a few examples of changes in ecological network states and how these approach alternative states. Nonetheless, these results provide a clue that changing patterns in the ecological network can vary from linear (figure 6(a)) to non-linear shape (figure 6(b)), and it depends on the numbers and centralities that wetlands pose. Losing large components may not cause a significant shift in a network property (e.g., figure 5(d)). However, during the loss process, when some portions of small wetlands with high centrality are lost simultaneously (e.g., figure 5(a)), our simulation results indicate that it can induce a dramatic shift in network properties (figure 6(c)). Moreover, when these losses stay permanently or for a long period, hydrological recovery of these wetlands will not promptly shift the network properties back to their original state due to the highly desiccated state of the surrounding soil or inappropriate restoration of the wetlands with the same areas. Under typical hydro-climatic conditions, the ecological network will dynamically respond to the fluctuations of the wetland area. So, it may be difficult to clearly identify the shift in network regime caused by the loss of wetlands. However, when strong events or drivers act, losing the functions of wetlands especially those with high centralities may bring the characteristic shift of the ecological network. Accordingly, studies on regime shift and resilience of ecological networks driven by the functioning of small wetlands are more needed.

5. Conclusion

We applied a network analysis framework using a probabilistic heavy-tailed dispersal model to analyze the effect of loss in small wetlands on the characteristics of ecological networks in a wetlandscape composed of hydrologically dynamic wetlands. Our results suggest that, despite their extremely minor contribution to the overall surface water area (0.82%), the mean degree and network efficiency dramatically shifted when these
small wetlands stopped functioning. The main reason for this phenomenon is that wetlands with high centralities can be distributed anywhere in the wetlandscape regardless of the size. However, because of their high sensitivity to hydro-climate conditions (especially to aridity) associated with surrounding soil conditions, as well as higher vulnerability to anthropogenic forcing, the small wetlands are at high risk of losing their function. If some of these small wetlands possessed high centralities, the loss of these wetlands will induce a critical regime shift of the network with degraded structure and function.

Our study is expected to provide a framework to evaluate the importance of small wetlands that can be easily ignored from an area-based point of view in a landscape (Serran et al. 2018, Lane et al. 2022). In the time of increasing effects from natural and anthropogenic forcing, our framework can supplement deciding the conservation priority, especially regarding large-scale ecological dynamics.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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