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A prioritization metric and modelling framework for fragmented saltmarsh patches restoration

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ABSTRACT

Saltmarsh is a coastal ecosystem providing crucial ecosystem services, and its continued degradation and fragmentation has drawn increasing attention. However, how to effectively restore the connectivity between fragmented saltmarsh patches remains an open challenge. In this study, we developed a metric and modelling framework that prioritised saltmarsh patches for restoration. To demonstrate our approach, we simulated spatially explicit restoration schedules for *Suaeda salsa* patches at the Yellow River Delta National Nature Reserve, China, using three strategies: increasing-patch-area, increasing-number-of-patches and a benchmark unrestrictive prioritization strategy. We prioritised patches for restoration based on a number of widely used graph-theoretic landscape connectivity and metapopulation capacity metrics. Our simulation results suggested the rank connectivity-importance of extant patches was correlated within the group of graph-theoretic connectivity metrics or metapopulation capacity metrics, but unrelated across group. The unrestrictive prioritization strategy clearly outperformed the strategies of increasing-patch-area and increasing-number-of-patches which returned comparable connectivity restoration outcomes. For the more effective unrestrictive prioritization strategy, there were substantial differences in the simulated priority patches between metrics that considered stepping stone effects and those did not. While the former resulted in corridor-building priority patches that led to a more connected landscape throughout the region, the latter led to local clustering. We recommend use of the total probability of connectivity (PC) among the metrics we tested due to similarity of results to other metrics and its simulation efficiency. The proposed framework is readily applicable to prioritise areas for connectivity conservation and restoration in any monospecific ecosystem at the regional scale.

1. Introduction

Improvement of landscape connectivity has become a key target for biodiversity conservation (see the reviews in Luque et al. (2012) and Ayrám et al. (2016), among others), as such connectivity affects species survival, migration, gene flow and other key ecological processes, as

well as adaptation of species to climate change. Habitat creation or restoration can be used to reduce habitat fragmentation by increasing patch size and connectivity, and this is commonly done in many habitats (Donald and Evans, 2006; Molin et al., 2018; Reynolds et al., 2013). The success of restoration activities is highly affected by connectivity with the surrounding landscape, as this influences the ability of species to

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colonize the created or restored sites. Researchers and practitioners are therefore increasingly incorporating landscape connectivity into restoration practice (Proft et al., 2018; Rudnick et al., 2012).

Computational tools, including graph-theoretic metrics (Urban and Keitt, 2001) and the occupancy-based metric of metapopulation capacity (Hanski and Ovaskainen, 2000), can be employed to prioritize areas for restoration in order to improve connectivity. Recent studies have used graph-theoretic connectivity metrics and habitat cover to set priority restoration areas in terms of their importance to the connectivity of the entire network at both local and regional scales (Tambosi et al., 2014). The occupancy-based metric of metapopulation capacity has also been employed to identify connectivity gaps when devising revegetation strategies in fragmented landscapes (Foster et al., 2017). These graph-theoretic connectivity and metapopulation capacity metrics, which combine the attributes of habitat patches with the dispersal behavior of the inhabitant species, provide useful tools for assisting conservation and restoration planning (Rubio et al., 2015).

Many coastal habitats, such as saltmarshes, mangroves and seagrass meadows, are naturally fragmented, being confined to areas of the coast where hydrological and geomorphological processes allow fine sediments to settle and plants to colonise. This fragmentation has been exacerbated by reclamation and other land use changes (Dethier et al., 2017), and will further increase with sea level rise (Kirwan and Megonigal, 2013; Valiela et al., 2001; Waycott et al., 2009). However, the connectivity of these habitats is poorly understood, as most studies investigating functional connectivity have focussed on terrestrial systems (Agram et al., 2016). In response to these threats, there have been increased efforts to create or restore coastal habitats, particularly saltmarshes (Balke et al., 2014; Cui et al., 2009; Mossman et al., 2012; Sullivan et al., 2018; Wolters et al., 2005), but these efforts have been opportunistic, and spatial planning that considers patch connectivity is rare. Studies have primarily focused on structural connectivity (Almeida et al., 2016; Torio and Chmura, 2015). For example, e.g., West and Zedler (2000) assessed the hydrological connectivity between the vegetated marsh surfaces and the interconnecting tidal creeks and ponds as important foraging area for fishes. Studies focused on the functional connectivity of the saltmarsh patches, particularly those intended for restoration planning, are still lacking.

Here, we propose a new metric and modelling framework for prioritizing the location of patches for saltmarsh restoration to optimize restoration efforts. We apply this framework to identify optimal restoration strategies for *Suaeda salsa* (a dominant species) in the saltmarshes of the Yellow River Delta National Nature Reserve (YRDNNR), a global biodiversity hotspot and regional economic hub in Shandong Province, China. *S. salsa* has suffered severe loss and fragmentation in the YRDNNR as a result of direct land use change and altered physical environments, and so restoration of the degraded *S. salsa* marshes has become a pressing issue for the YRDNNR Administration Bureau. We use our framework to test the performance of graph-theoretic and metapopulation metrics of connectivity, and assess whether restoration strategies should aim to increase the patch area or the number of patches. Whilst parametrized for this system in the Yellow River Delta, this framework is readily applicable to other restoration scenarios.

2. Materials and methods

2.1. Metric and model framework

As data on saltmarsh plant dispersal ability are rarely available and hard to gather, we inferred the dispersal distance that maximized the connector fraction of the probability of connectivity (PC) index, i.e., the contribution of stepping stones to connectivity, from a dispersal distance range reported in the literature on similar plants and evaluate the performance of graph-theoretic landscape connectivity and metapopulation capacity metrics in setting priority restoration patches. The proposed metric and modelling framework comprised the following main steps:

(1) schematization of study area and construction of patch network; (2) assessment of functional connectivity of patch network; and (3) simulation of restoration prioritization using increasing-patch-area or increasing-number-of-patches strategy (Fig. 1), as well as a benchmark unrestrictive prioritization strategy. These steps are explained separately in the next subsections (Sections 2.2-2.4), and we conclude the Materials and Methods with specific details of how the framework was applied to our study site (Yellow River Delta National Nature Reserve, in Section 2.5).

2.2. Schematization of study area and construction of patch network

The study area was schematized into grid cells with the cell size selected based on factors including the minimum practical restoration unit, landscape data resolution and simulation cost; 800 m × 800 m grid cell size was selected for the YRDNNR application (see Supporting Information for details). Each grid cell was assigned an attribute value based on its dominant land cover type (accounting for > 50% cell area) as follows: 1) extant saltmarsh plant of *S. salsa*, 2) unrestorable area, e.g., levees, roads, salt ponds and other developed areas that are unsuitable for restoration, as well as patches of other saltmarsh plants that are unnecessary for restoration, or 3) restorable area that comprises the remaining area. Note that elevation, soil salinity and other factors that could affect the habitat suitability of the restorable cells were not considered here, but could be incorporated into the definition of restorable/unrestorable area with sufficient autecological information. Spatial analysis was then performed on all cells classified as *S. salsa* patches (i.e. cell attribute value 1) to delineate the extant target saltmarsh plant patches and determine the shortest path between any two patches.

2.3. Assessment of functional connectivity of patch network

Three commonly used metrics of connectivity were selected to measure the degree of connectivity among the target saltmarsh patches in the study area. These were network-based (graph-theoretic) habitat availability (reachability) metrics, i.e., the probability of connectivity (PC) index and integral index of connectivity (IIC), and the occupancy-based metrics derived from metapopulation theory, i.e., metapopulation capacity (MC). These were selected because they are widely used in conservation and restoration planning (Rubio et al., 2015). Full descriptions of the metrics are provided in the Supporting Information.

The maximum dispersal probability of all possible paths between patches (nodes) i and j , P_{ij}^* , as a key parameter in the calculation of the PC index, is typically computed using a negative exponential dispersal kernel (Hanski and Ovaskainen, 2000; Urban and Keitt, 2001),

$$P_{ij}^* = e^{-k_d \cdot d_{ij}^*} \quad (1)$$

where d_{ij}^* is the shortest distance corresponding to the maximum probability path between patches (nodes) i and j , and k_d is a constant which reflects the dispersal ability of the propagules of the species of interest between patches, and is typically determined by assuming that $1/k_d$ equals to the average dispersal distance (Hanski and Ovaskainen, 2000). As direct measurements of dispersal distance of saltmarsh plants are prohibitively time-consuming and expensive, k_d was instead inferred from a range of the species dispersal distance following the relevant previous studies as detailed in Sec. 2.5.

Based on the principle of patch removal experiment (Bodin and Saura, 2010), we simulated removal of each individual patch one by one, and calculated the variation in the PC index (dPC_k), which represents the importance of the individual patch to the connectivity of the entire network and can be partitioned into three distinct fractions (Saura and Rubio, 2010), namely, the contribution of patch k in terms of intra-patch connectivity (dPC_{intra_k}), the flux fraction (dPC_{flux_k}) and connector fraction ($dPC_{connector_k}$) (see Supporting Information for

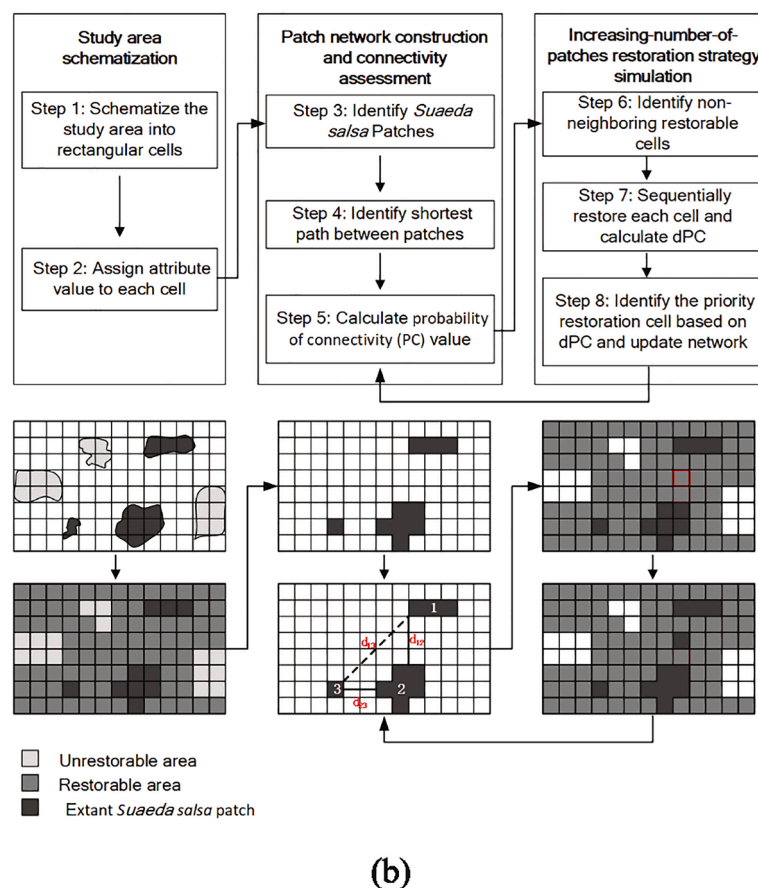
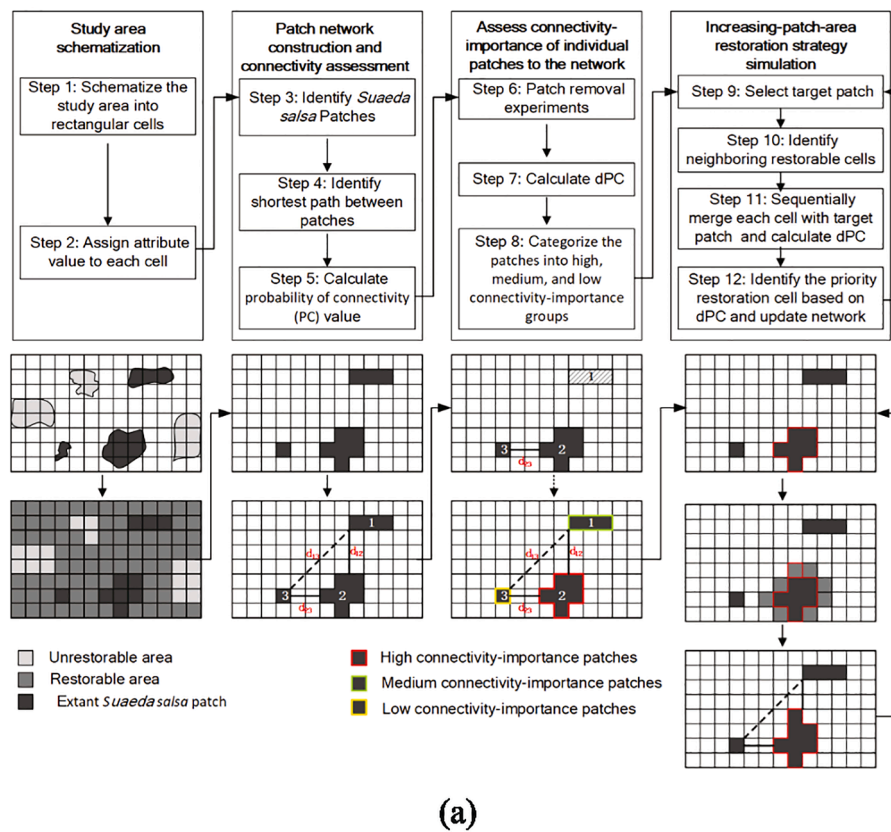
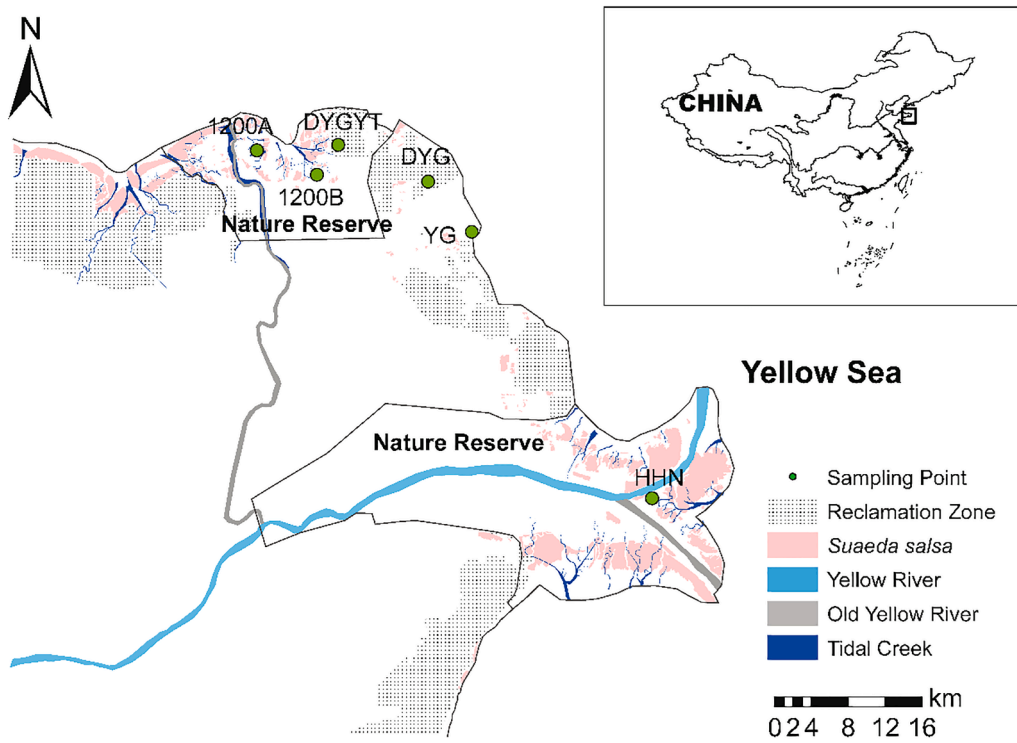


Fig. 1. The main steps of the proposed metric and modelling framework: (a) increasing-patch-area restoration strategy. (b) increasing-number-of-patches restoration strategy.



(a)



(b)

Fig. 2. (a) Location of the case study area – the Yellow River Delta National Nature Reserve (YRDNNR), as well as the distribution of sampling points for gene flow analysis. (b) Up-close view of a *Suaeda salsa* individual in intertidal area. (c) A unique ‘red carpet’ landscape formed at the tidal flats of Liaohe River Delta by expansive distribution of *S. salsa*. (d) Fragmented *S. salsa* patches at the YRDNNR. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



(c)



(d)

Fig. 2. (continued).

details). The total dPC_k was used to categorize the patches into high, medium, and low connectivity-importance groups using Jenks (1967) classification.

In addition to the PC index, we further adopted the integral index of connectivity (IIC) and metapopulation capacity (MC) as the connectivity metric to test the sensitivity of our simulation results on the metric adopted in the simulation. Notably, while both inter- and intra-patch connectivity are considered in the habitat availability (PC and IIC) metrics, the latter is neglected in the metapopulation capacity. To account for this conceptual difference, we also considered a modified metapopulation capacity (MMC) following Schnell et al. (2013) (see

[Supporting Information](#) for the definition of M).

2.4. Simulation of restoration prioritization using increasing-patch-area or increasing-number-of-patches strategy

Our patch prioritization for restoration can either aim to increase the area of existing patches or increase the number of patches. To implement the restoration strategy that focuses on increasing patch area, we first assessed the importance of each individual patch to the connectivity of the entire patch network (its dPC value), and then used an iterative algorithm to sequentially prioritize restoration patches ranked by their

importance for connectivity (Torrubia et al., 2014). Randomly selected representative patches from high, medium, and low connectivity-importance groups were selected for simulation of the restoration schedule. For the selected target patches, all four-connected neighboring restorable cells were first identified. An iterative analysis was then performed to sequentially merge each restorable neighboring cell (with attribute value 3) into the adjacent target plant patch (with attribute value 1) and keep the remaining cells unchanged, and to calculate the updated *PC* and *dPC*. The cell with the greatest *dPC* was identified as the priority restoration cell. These steps were repeated until 10–50 restorable cells were identified (Fig. 1a).

The alternative restoration strategy of increasing the number of patches followed a similar iterative analysis process, except that we converted each restorable non-neighboring cell (with attribute value 3) into a new plant patch (with attribute value 1) and kept the remaining cells unchanged, and calculated the updated *PC* and *dPC*. The cell with the greatest *dPC* was identified as the priority restoration cell. These steps were repeated until the restoration target was reached (Fig. 1b).

2.5. Application in the *Suaeda salsa* patches at the Yellow River Delta

We demonstrate our framework using *Suaeda salsa* patches in the saltmarshes of the YRDNNR, which is located in the northeast of Shandong Province, China (118°33'E – 119°20'E and 37°35'N – 38°12'N, Fig. 2a). The Yellow River Delta National Nature Reserve (YRDNNR) was established in 1992 to protect a key stopover site in the middle of the East Asian-Australasian flyway hotspot, and exceeds 150,000 ha in size. Human activities, including oil and gas exploitation (the YRDNNR is also co-located with a major oil field of China), aquaculture, harbor and levee construction, and reclamation for agriculture and urbanization, have occupied coastal wetlands and resulted in serious habitat loss and fragmentation (Luo et al., 2018), particularly of *S. salsa* saltmarsh (Fig. 2a,d and Table 1). More recently, a number of restoration projects, including the habitat creation and improvement for key species, have been launched at the YRDNNR (Li et al., 2016; Wang et al., 2018).

Suaeda salsa L. (Chenopodiaceae) is an annual herbaceous halophyte native to inland saline soils and intertidal zones in northern China (Fig. 2b). It is highly salt- and waterlogging-tolerant and is a dominant species in the YRDNNR saltmarshes. It has significant economic, biodiversity and cultural value. For example, *S. salsa* marshes are the main habitats for red-crowned cranes (*Grus japonensis*), and the expansive distribution of *S. salsa* at the tidal flats of Liaohe River Delta forms a unique 'red carpet' landscape (Fig. 2c) that is of tremendous recreational and tourism value.

Since the direct measurements of seed or pollen dispersal distance of *S. salsa* are currently unavailable, we assumed it to vary between 0.1 and 10 km, distances typical of pollinator, anemo- and hydro-chorous seeds (Aavik et al., 2014; Dileo et al., 2017), which are the primary propagule types and their external vectors of *S. salsa*. This translated to a dispersal ability constant (k_d) between 0.1 and 10 km⁻¹. Following Rubio et al. (2015), we further determined the dispersal distance among 24 different values that were at 0.1 km increments within 0.1–0.5 km and 0.5 km increments within 0.5–10 km, respectively, at which the contribution of stepping stones to connectivity, as quantified by the connector fraction of the connectivity metrics *PC*, was highest. As shown in Fig. 3, the contribution of $dPC_{connector_k}$ is at its maximum at an intermediate

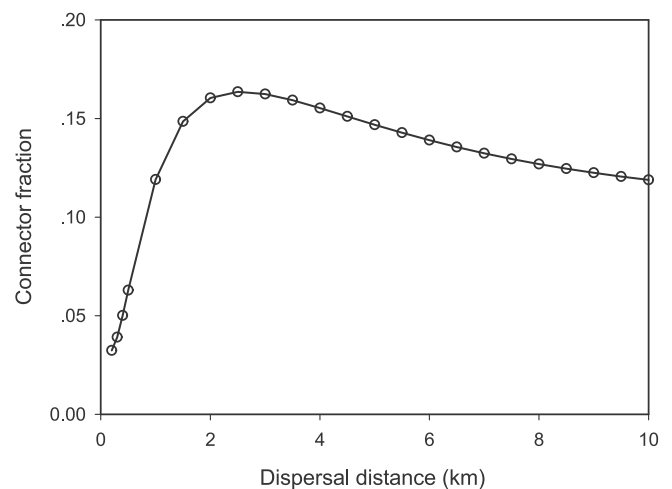


Fig. 3. Sum of $dPC_{connector_k}$ for all patches *k* as a proportion of the total sum of all dPC_k for increasing dispersal distance.

dispersal distance of 2.5 km, and the corresponding dispersal ability constant k_d (0.4 km⁻¹) was used to perform the subsequent analyses.

The study area was gridded into 800 m × 800 m cells. Landsat remote sensing data (dated 5 October 2014) were used to derive the land cover. Spatial analysis was then performed in Matlab on all cells with attribute value 1 to delineate the extant *S. salsa* patches and determine the shortest path between any two patches. The *PC* index value of the extracted patch network with all extant patches was calculated. Three randomly selected representative patches from each of high, medium, and low connectivity-importance groups were selected for restoration schedule simulation.

To further test the efficacy of the strategies to increase patch size or patch number, we compared these approaches to a benchmark restoration strategy that prioritized over all restorable cells including both neighboring and non-neighboring cells (termed 'unrestrictive prioritization strategy' hereafter). In addition, we repeated the patch removal experiments described above for ranking patch connectivity-importance as well as the simulations of the spatially explicit restoration schedule, using different connectivity metrics (integral index of connectivity *dIIC*, metapopulation capacity *dMC*, and modified metapopulation capacity *dMMC*) to test the dependence of the simulation results on the chosen metric.

3. Results

Rank patch connectivity importance was strongly positively correlated among the different variants of the metapopulation capacity metrics (Kendall's Tau rank correlation coefficients 0.48–0.68, Table S1), and there was moderate rank correlation between the graph-theoretic connectivity metrics (*PC* and *IIC*, $T = 0.21$). However, correlations between the two group of metrics were very low (<0.12, see Table S1). The connectivity-importance map for the *PC* index is shown in Fig. 4. The contiguous stretch of patches located inside the southern part of the YRDNNR exhibit greater *dPC* value and hence has greater connectivity-importance. The resultant natural breaks of the *dPC* value,

Table 1

Change of the landscape pattern of *Suaeda salsa* patches at the Yellow River Delta during the 1984–2014 period.

Year	Total Area (<i>TA</i> , km ²)	Number of Patches (<i>NP</i>)	Largest Patch Index (<i>LPI</i> , %)	Average Patch Area (<i>AREA_MN</i> , km ²)	Landscape Division Index (<i>DIVISION</i> , %)	Average Euclidean Nearest Neighbor Distance (<i>ENN_MN</i> , m)
1984	902.01	23	33.31	39.22	0.67	332.61
1994	664.29	66	28.69	10.07	0.79	297.17
2004	277.41	199	17.45	1.14	0.89	259.88
2014	196.93	260	14.89	0.76	0.93	212.35

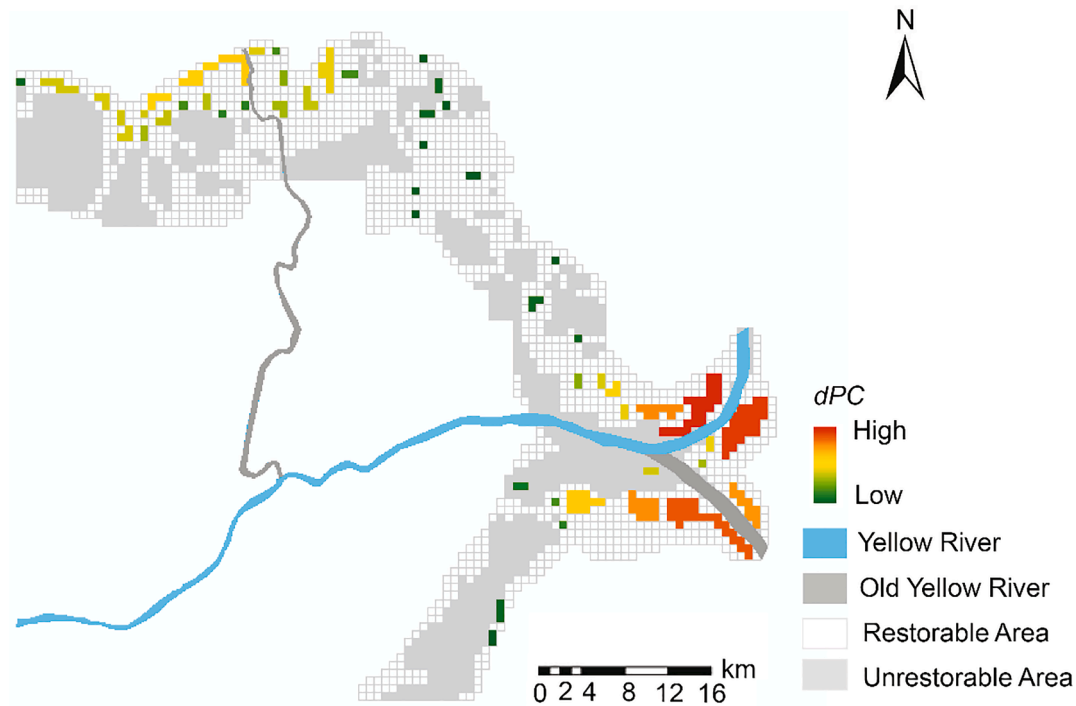


Fig. 4. Distribution of the probability of connectivity difference (*dPC*) of the *Suaeda salsa* patches at the study area. Red and green represent high and low connectivity, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

obtained from Jenks classification, were 4.10% and 15.29%, respectively, which separate the individual patches into high (3 patches), medium (6 patches), and low (44 patches) connectivity-importance groups.

Overall, our simulation results suggest that unrestrictive prioritization produce more effective restoration of connectivity relative to the strategies of increasing patch area and increasing number of patches, which return comparable restoration of connectivity (Fig. 5). For the increasing-patch-area strategy, the improvement of connectivity steadily increases with increasing restoration area, regardless of the connectivity-importance of the patch (Fig. 6a). In addition, focusing on the high and medium connectivity-importance patches appears to be consistently and substantially more effective than low connectivity-importance patches. The steadily increasing trend continues albeit with steeper slope when the patch area increases further, and the

connectivity improvement achieved in terms of *dPC* is ~ 4500%, i.e., more than forty times the original *PC* value associated with the 221 cells initially classified as *S. salsa* patches, when 500 cells (equivalent to 32000 ha, almost all restorable neighboring cells and close to half of all 1260 restorable cells throughout the domain) are added to the representative patches selected regardless of their connectivity-importance category. Moreover, the spatial patterns of patches prioritized are different among different strategies. To showcase the simulated spatially explicit restoration schedules, those for the three high connectivity-importance patches (denoted as patch # 37, 39 and 50) following the increasing-patch-area restoration strategy are shown in Fig. 6b.

For the increasing-number-of-patches strategy using the total *PC* index, the simulated spatially explicit restoration schedule appears to surround the contiguous stretch of patches located inside the southern part of the YRDNNR, i.e., extant patches with large area and higher connectivity-importance, in the first 30 plus steps (Fig. 7a). Afterwards, the priority patches start spreading to the northern part of the YRDNNR. By contrast, the unrestrictive prioritization strategy appears to build a corridor linking the southern and northern parts and form a more connected landscape (Fig. 7b), which may also contribute to the greater improvement of connectivity compared to the strategies of increasing patch area and increasing number of patches (Fig. 5). Spatially explicit restoration schedules based on the flux fraction of the *PC* index ($dPCflux_k$) and connector fraction of the *PC* index ($dPCconnector_k$) are also provided for comparison (Fig. 7c and d), allowing one to specifically rank the restorable cells according to their importance for biological flow (gene flow in this case) or maintaining the connectivity of the entire network, respectively. The two components yield corridor-building patterns that are overall similar to each other and to that based on the total *dPC*, although they appear to prioritize extant patches with large area and higher connectivity-importance inside the southern part of the YRDNNR before building corridor toward the northern part of the YRDNNR where distant clusters of extant patches are located.

To assess the sensitivity of the results to the chosen metric, we re-ran the simulation of the spatially explicit restoration schedule based on the integral index of connectivity (*dIIC*) for restoring 50 cells following the

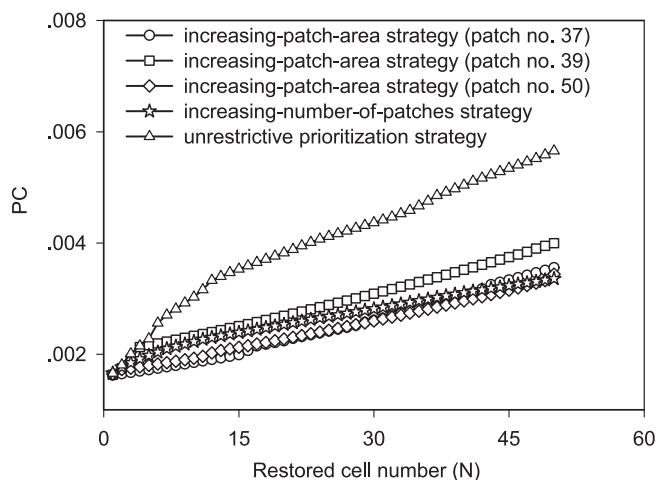


Fig. 5. Simulated optimized restoration processes using increasing-patch-area, increasing-number-of-patches and unrestrictive prioritization strategy.

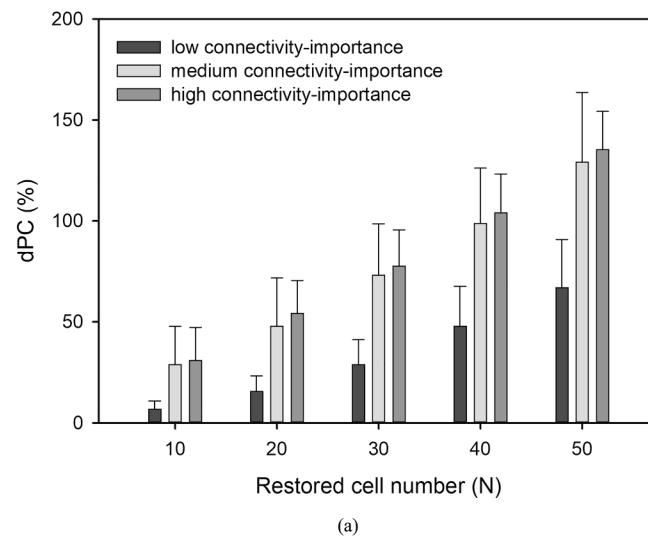


Fig. 6. (a) Simulated improvement of connectivity for optimized increasing-patch-area restoration strategy for patch groups with high-, medium-, and low-importance to the connectivity of the entire network. (b) Simulated spatially explicit restoration schedule for the 3 high connectivity-importance patches (patch # 39, 50 and 37) following increasing-patch-area restoration strategy.

more superior unrestrictive prioritization strategy. The results (Fig. 7e) turn out to exhibit strong local clustering inside the southern part of the YRDNNR. The simulated spatially explicit restoration schedule based on the metapopulation capacity (*dMC*) (Fig. 7f) and modified metapopulation capacity (*dMMC*) (Fig. 7g) exhibit similar and yet more locally clustered zoning pattern, which prioritize entirely on the extant patches with large area and higher connectivity-importance located inside the southern part of the YRDNNR.

4. Discussion

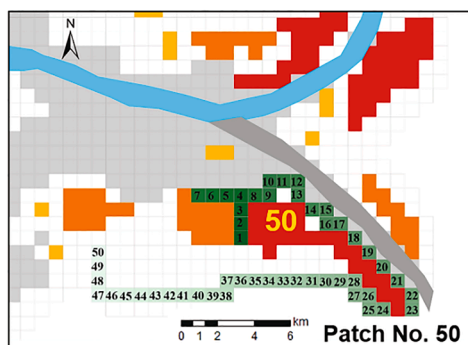
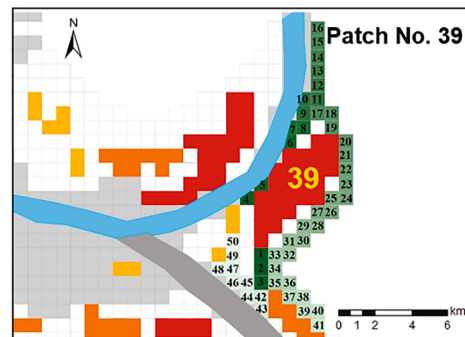
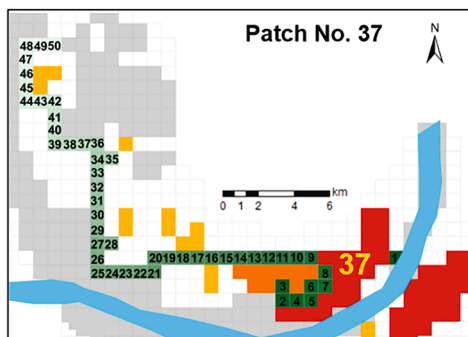
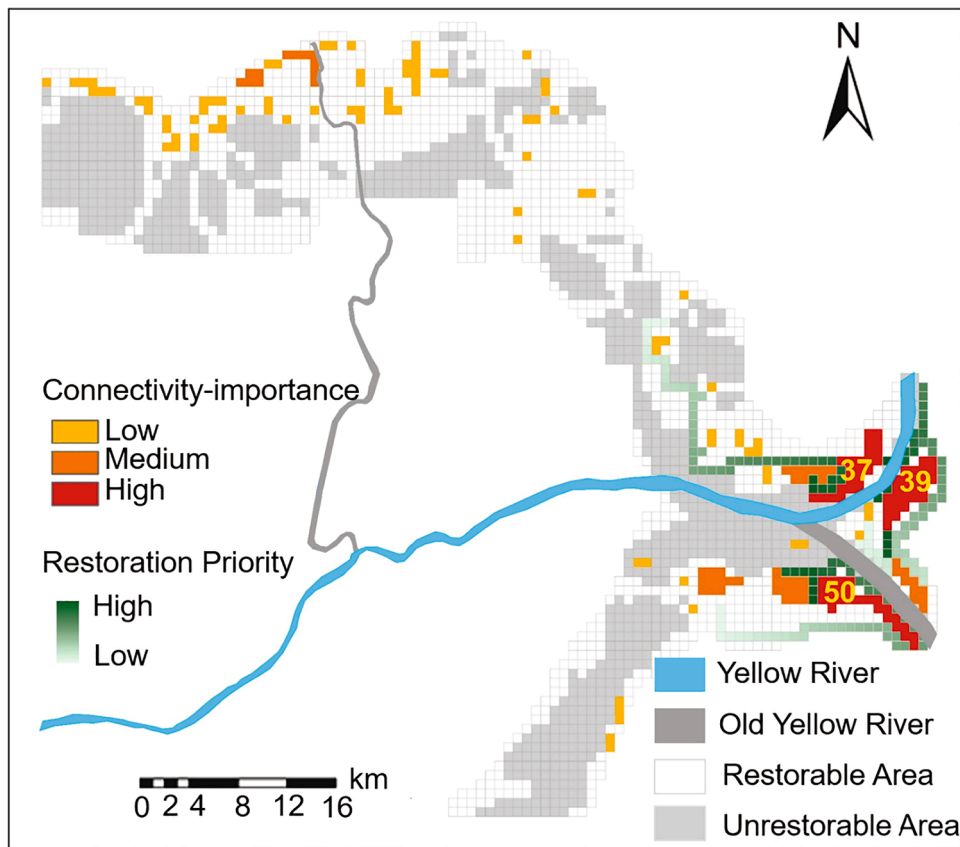
We proposed a new framework for prioritizing monospecific saltmarsh patches to optimize restoration efforts by enhancing functional connectivity for fragmented communities. A range of the species dispersal distance was tested to infer the species dispersal ability and prioritise patches for restoration based on a number of widely used graph-theoretic landscape connectivity and metapopulation capacity metrics. We demonstrated our approach by simulating spatially explicit restoration schedules for a dominant saltmarsh species at a global biodiversity hotspot, i.e., the Yellow River Delta National Nature Reserve (YRDNNR) in Shandong Province, China, following the increasing-patch-area and increasing-number-of-patches strategies, as well as a benchmark unrestrictive prioritization strategy. Overall, the results of this study indicate that an unrestrictive prioritization returns superior connectivity restoration outcomes than the traditional strategies of increasing patch area or increasing number of patches that place more restriction on the candidate cells with respective to a specific target patch or with each other.

Through patch removal experiments, the extracted *S. salsa* patches were ranked by their importance to the connectivity of the entire patch network into low, medium, and high connectivity-importance groups. The simulation results suggested that focusing on the high and medium connectivity-importance patches appeared to be consistently and substantially more effective. Notably, however, Tambosi et al. (2014) have advocated prioritizing patches with intermediate habitat amount and connectivity in the restoration planning of Brazilian Atlantic forest, for its cost-effectiveness compared with other patches, which suggests that depending on the specific prioritization criteria, high connectivity-importance patch may not naturally be the priority.

As direct measurements of dispersal distance of saltmarsh plants are prohibitively time-consuming and expensive, we followed the approach

in Rubio et al. (2015) to infer the dispersal distance that maximized the connector fraction of the *PC* metric, i.e., the contribution of stepping stones to connectivity. The rationale of adopting this dispersal distance is that it can be interpreted as the critical distance at which the ability of species to reach a larger amount of habitats depends most on the spatial configuration among habitat patches (Bodin and Saura, 2010; Rubio et al., 2015). The maximum inter-patch dispersal probability P_{ij}^* calculated using the dispersal constant attains value considerably lower than 1, e.g., $P_{ij}^* < 0.01$ only when the inter-patch distance $d_{ij}^* > 11$ km, which suggests that connectivity between patches becomes minimal when they are located > 11 km apart, and thus negates the bias that the patches identified as most important for connectivity (stepping stones) are generally confined within relatively dense patch clusters (Bodin and Saura, 2010). Notably, as an alternative to direct measurement of species dispersal, spatially explicit, high-resolution genetic data could be used to infer dispersal behavior in relation to landscape features and patterns, as exemplified in some recent applications in other plant species (Aavik et al., 2014; Dileo et al., 2017). Plant species have also been shown to adjust their dispersal to fragmentation (Cheptou et al., 2017), and how to properly account for this variability remains an open question.

Among the various graph-theoretic landscape connectivity and metapopulation capacity metrics adopted in this study, our simulation results suggested that the ranks of the connectivity-importance of the extant patches corroborate fairly well between the graph-theoretic connectivity metrics (*PC* and *IIC*) and among the different variants of the metapopulation capacity metrics, whereas very low correlations exhibited between the two group of metrics. Contrary to the connectivity-importance ranking, the simulated restoration schedules following the unrestrictive prioritization strategy showed wide contrasts between those based on metrics that considered the stepping stone effects (e.g., the total probability of connectivity (*PC*) and its connector fraction) and those based on metrics that neglected the effects (e.g., the integral index of connectivity (*IIC*), the metapopulation capacity (*MC*) and the modified metapopulation capacity (*MMC*)). While the former resulted in corridor-building priority patches that led to a more connected landscape throughout the region, the latter led to local clustering around the the extant patches with large area and higher connectivity-importance, presumably due to the neglect of the stepping stone effects in the latter metrics (Saura et al., 2014). The exception is the flux



(b)

Fig. 6. (continued).

fraction of the *PC* index. Although not incorporating the stepping stone effects, the simulated restoration schedule of this metric is surprisingly similar to the total *PC* index and its connector fraction.

To a varying degree, the priority patches based on the various

metrics all tended to surround the extant patches with large area and higher connectivity-importance. This pattern is similar to other authors' recommendations to prioritize the source population in the restoration of metapopulation structure (for example, the case study of the Mount

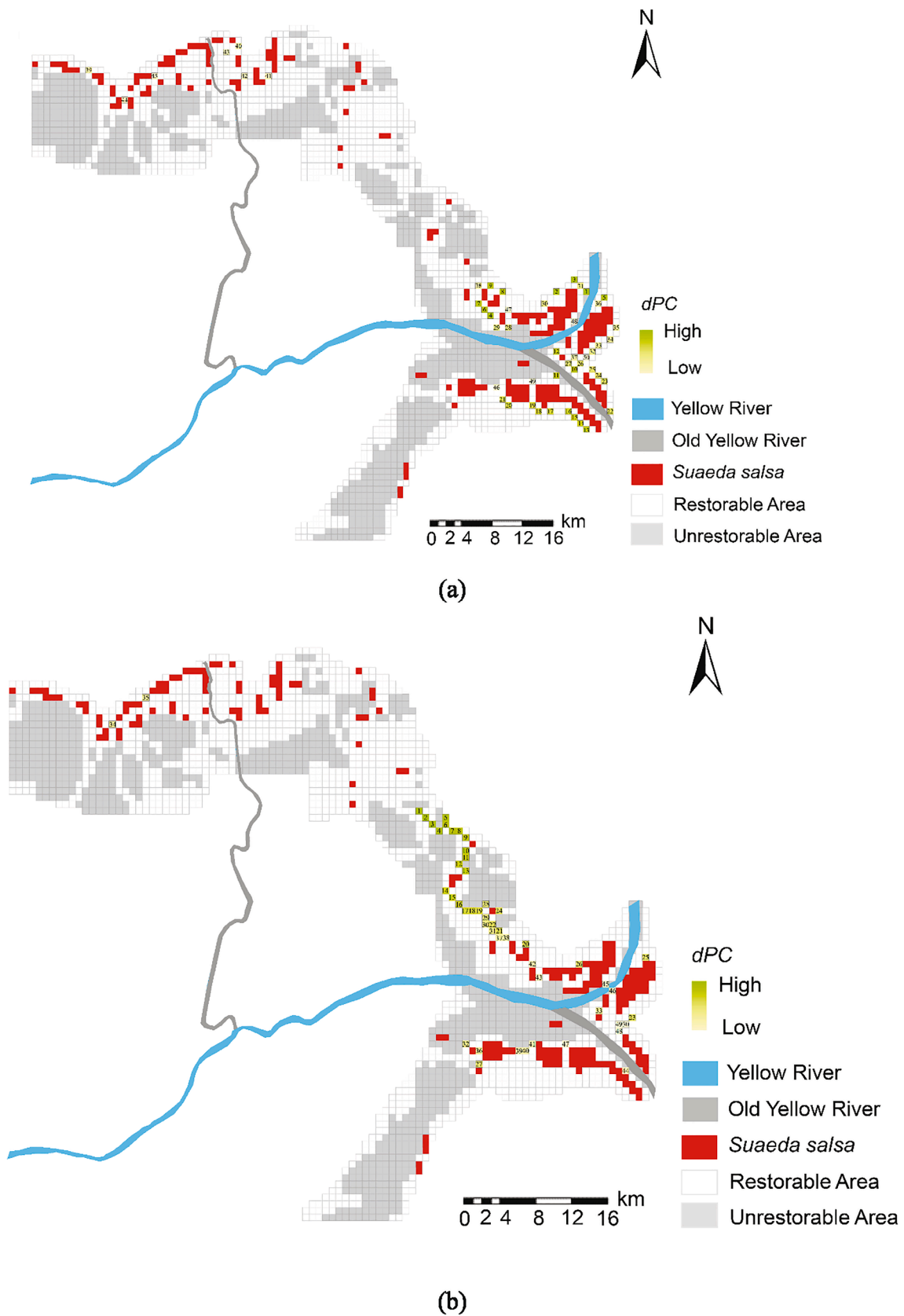
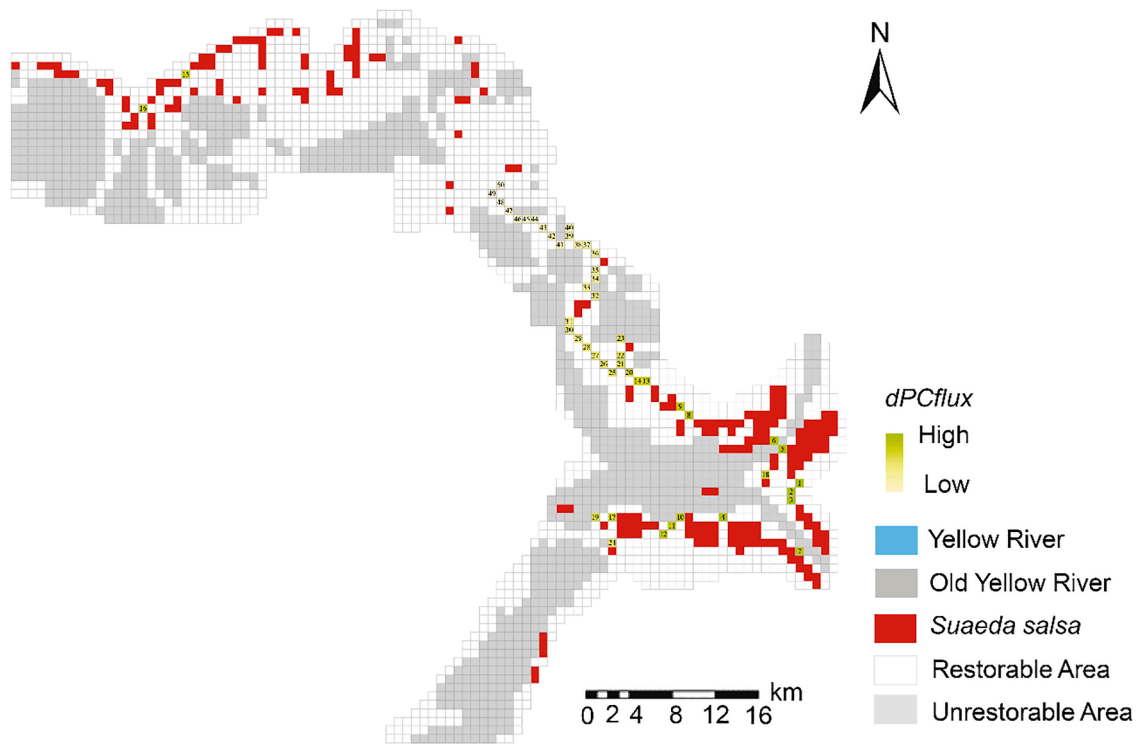
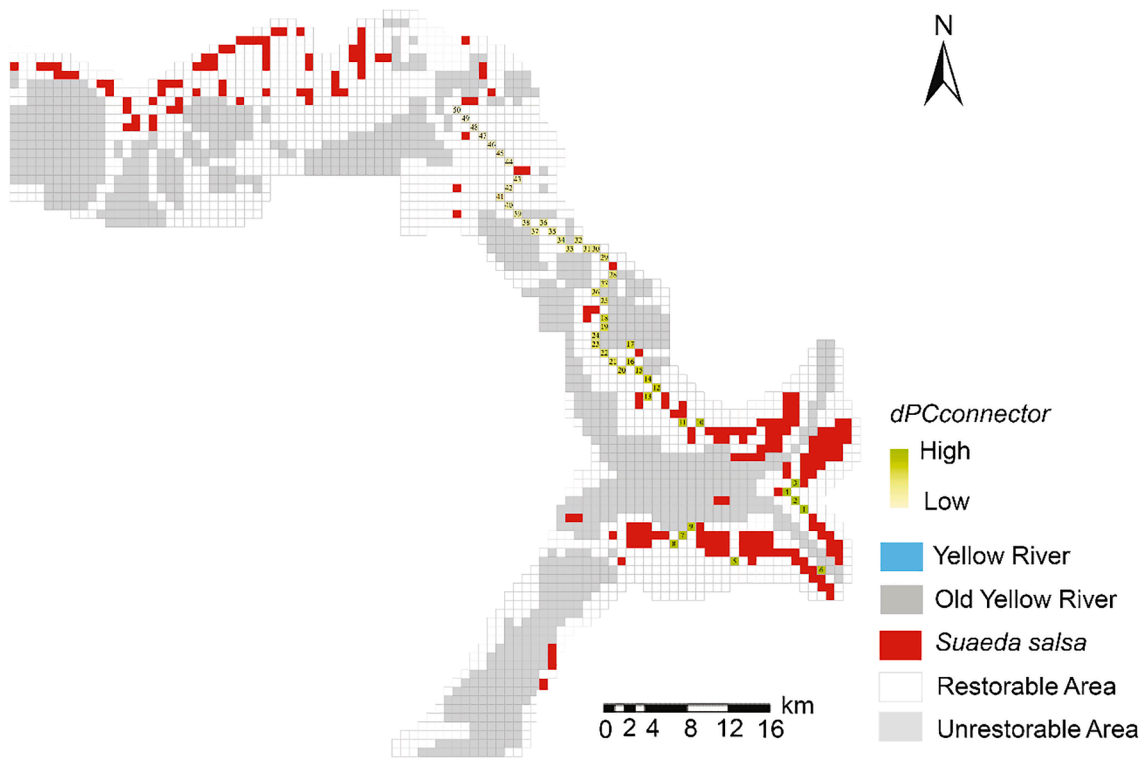


Fig. 7. Simulated spatially explicit restoration schedule for restoring 50 cells: (a) following increasing-number-of-patches strategy and using the total probability of connectivity metric; following unrestrictive prioritization strategy and (b) using the total probability of connectivity metric; (c) using the flux fraction of the total probability of connectivity metric; (d) using the connector fraction of the total probability of connectivity metric; (e) using the integral index of connectivity metric; (f) using the metapopulation capacity metric; (g) using the modified metapopulation capacity metric.



(c)

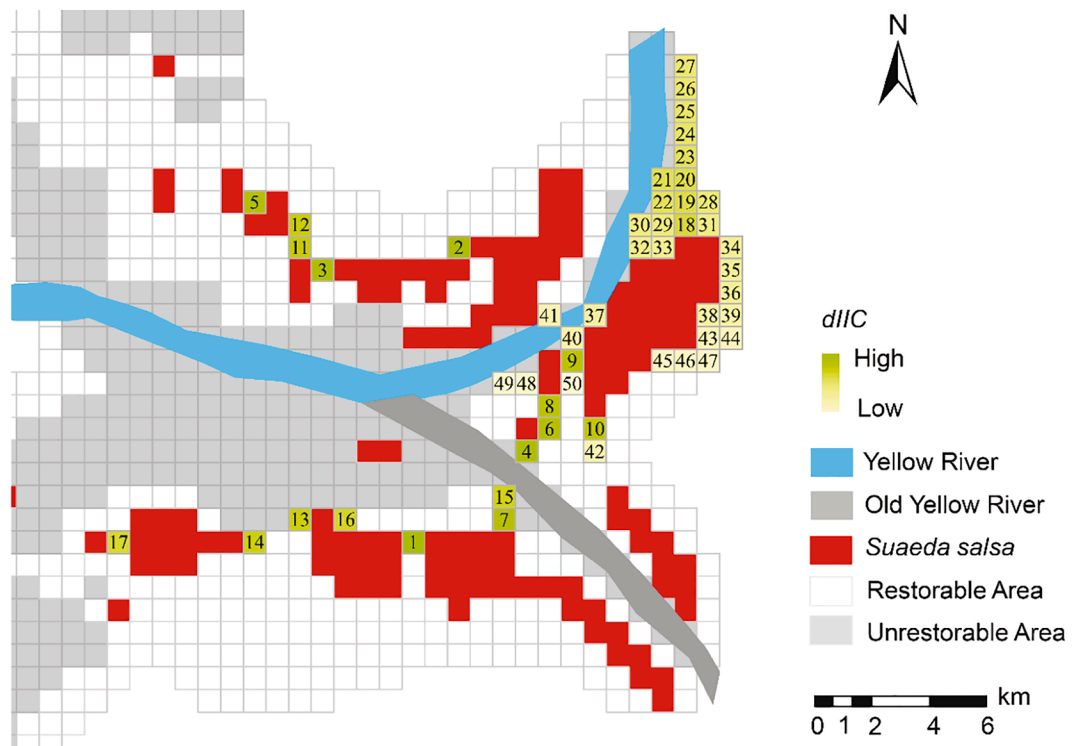


(d)

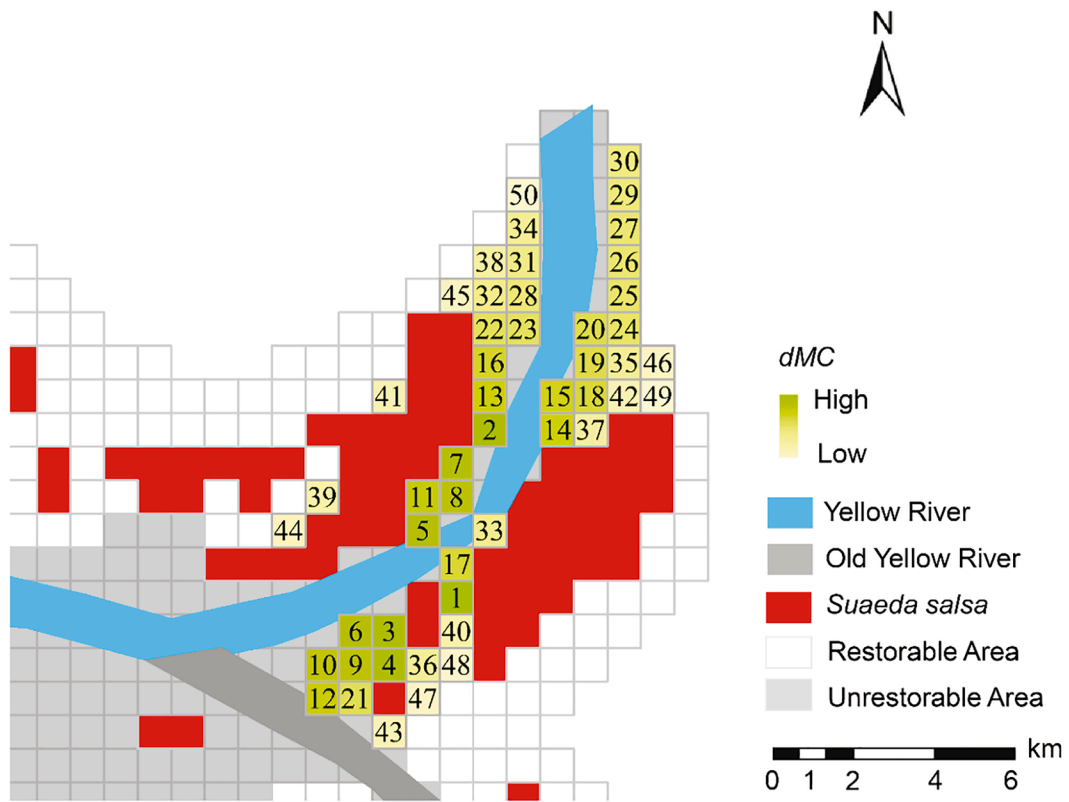
Fig. 7. (continued).

Lofty Ranges Southern Emu-wren in Australia reported by Nicol and Possingham (2010)). Further comparisons between strategies of increasing-patch-area and increasing-number-of-patches suggested that the two strategies return comparable connectivity restoration outcomes to the entire network, whereas the unrestrictive prioritization strategy

appeared to build corridor that effectively links the isolated southern and northern parts of the YRDNNR where the majority of the extant patches are located and hence produced greater connectivity improvement. In the context of restoring fragmented habitat to maximize met-population persistence, while Westphal et al. (2003) and Nicol and

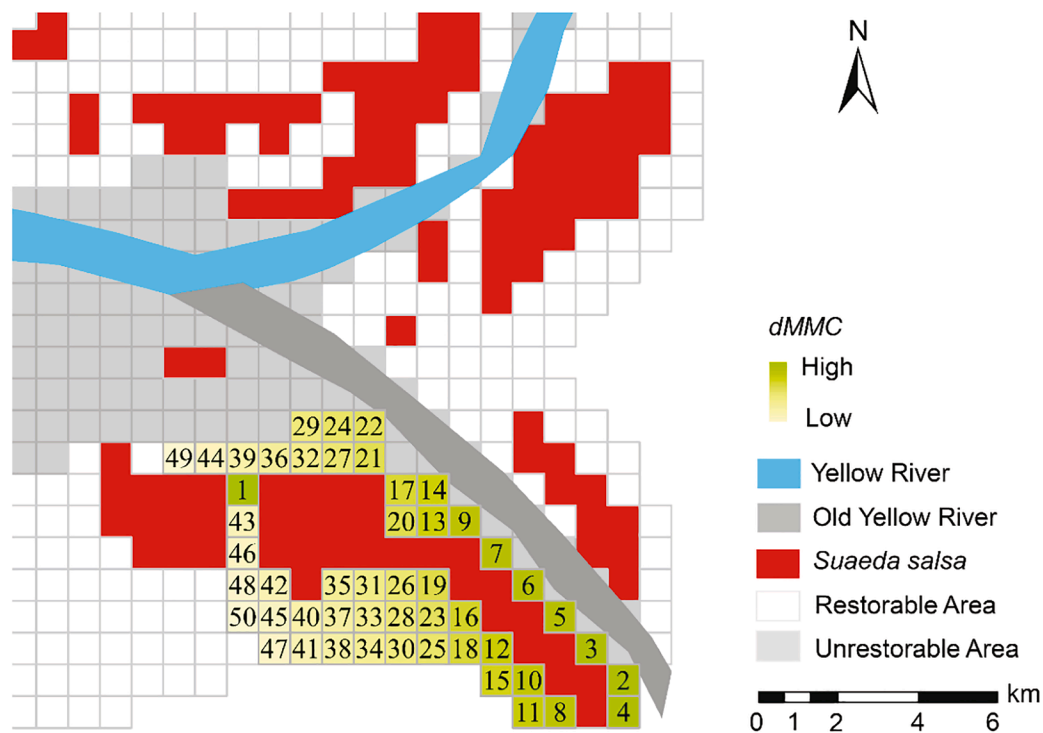


(e)



(f)

Fig. 7. (continued).



(g)

Fig. 7. (continued).

Possingham (2010) both found that it was difficult to make generalizations about the optimal restoration strategy (increasing patch area or number of patches) *a priori* as it depended heavily on the current state of the metapopulation, Ross et al. (2008) showed that protecting patches of habitat from disturbance took priority over creating new patches for metapopulation persistence, in a case study of the greater bilby, *Macrotis lagotis*, in southwestern Queensland, Australia.

Simulation of restoration schedules following the increasing-number-of-patches strategy involves optimization calculation upon all restorable non-neighboring cells (and neighboring cells as well for the unrestrictive prioritization strategy) throughout the entire study area for each prioritization step, and thus is considerably more computationally expensive than connectivity-importance ranking and increasing-patch-area restoration schedule simulations. Furthermore, simulation based on the total probability of connectivity (*PC*) costed 30% less computational hours than the simulation based on the connector fraction (*PCconnector*) when implementing the unrestrictive prioritization strategy. Given the comparison results, total probability of connectivity (*PC*) is recommended as the most computationally cost-effective among the various graph-theoretic landscape connectivity and metapopulation capacity metrics adopted in this study.

As a first step toward building an effective prioritization framework for monospecific saltmarsh patch restoration, the present study is restricted with sequential evaluation of individual cells for restoration. In reality, multiple cells can be added, depending on the resources available. However, that would pose a combinatorial complexity problem for which an exhaustive assessment of all possible combinations would be computationally intractable, and some alternative treatment (e.g., *meta-heuristic* method) might be necessary (Rubio et al., 2015). The graph-theoretic habitat availability (*PC*) metrics are inherently flexible in accommodating different degree of biological and spatial details, and future consideration of patch attributes other than patch area (e.g., habitat quality), effective least-cost path distances through a

resistance surface that accounts for landscape barriers for the focal species (Adriaensen et al., 2003; Tischendorf and Fahring, 2000), as well as the confounding effects of spatial complexity (Papadimitriou, 2020), would be of interest.

The case study on *S. salsa* patches proved its applicability to fragmented saltmarshes with a single flora focal species, complementary to the well-studied counterpart of forest biome with fauna focal species (Tambosi et al., 2014). The general approach to restoration prioritization described here is also readily transferable to other plant species. Although the scope of the present study is on restoration planning, the analysis of the connectivity-importance of the individual patches can be also interpreted as an assessment of their conservation value from a connectivity perspective, thereby providing critical information relevant for conservation planning and prioritization.

CRediT authorship contribution statement

B.S.C., K.L. and D.D.S. conceived and designed the study; K.L. conducted the restoration simulation; D.D.S. conducted the restoration simulation and writing; D.X.L. and Y.Y. contributed to the restoration simulation; and H.L.M., M.P.A., H.F.W. and B.S.C. contributed to the writing. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107833>.

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