

Comparison of Least-cost Path and UNICOR Cumulative Resistant Kernel Analyses in Mapping Ecological Connectivity Networks in Luohe Region, China

Guifang Wang¹, Samuel A. Cushman², Ho Yi Wan³, Manshu Liu¹, Sándor Jombach¹

¹Institute of Landscape Architecture, Urban Planning and Garden Art/Hungarian University of Agriculture and Life Sciences, Budapest/Hungary · wgf0317@163.com

²USDA Forest Service/Rocky Mountain Research Station, AZ/USA

³Department of Wildlife/Humboldt State University, CA/USA

Abstract: One of the greatest challenges China faces is how to conserve biodiversity during intensive urban and rural development. Ecological connectivity network modelling is a planning strategy that is increasingly used to achieve habitat and biodiversity conservation goals. Often, researchers have not given enough attention to the comparison of different methods for designing and mapping ecological connectivity networks in Chinese cities. In this study, we used least-cost path and UNICOR cumulative resistant kernel analyses to simulate the ecological connectivity network across the Luohe Region of China, and used the results to prioritize ecological connectivity network linkages and core areas. Our analysis produced three main results: (1) Least-cost paths passed through all the core areas because they did not consider species' dispersal limits. (2) Species with dispersal abilities ≤ 2 km, conversely, were predicted by resistant kernel analysis to have highly fragmented functional connectivity networks in the Luohe region, while species with dispersal abilities between 4 km and 8 km were predicted to have moderate levels of functional connectivity, and species with dispersal abilities ≥ 16 km showed high connectivity across most of the study area. (3) We identified the areas of highest functional connectivity by intersecting >75 th percentile of every resistant kernel surface. This identified an area in the Yan-cheng district as the zone of most complete and strong connectivity. The intersection of least-cost paths with the 2 km threshold scenario of factorial least-cost paths was the first protection priority, the intersection of least-cost paths with the 8 km threshold scenario of factorial least-cost paths was the second protection priority, 8 km threshold scenario of factorial least-cost paths without core areas was the third protection priority. Our comparison of methods in mapping ecological connectivity networks is generic and can be performed in any cities with landscape configuration and species information.

Keywords: Dispersal ability, factorial least-cost path, resistant kernel, UNICOR, connectivity network

1 Introduction

Biodiversity conservation in China faces considerable challenges as intensive urban and rural development continues to degrade and fragment species habitats (PENG et al. 2018). Ecological connectivity network (ECN) modelling provides a promising approach to optimally conserve and restore habitat such that it optimizes the effectiveness of networks of habitat core areas and linkage corridors (RUIZ-GONZÁLEZ et al. 2014). The increasing awareness of habitat fragmentation and landscape degradation has rapidly increased demand for modelling tools to simulate and evaluate ECNs. Rudnick and others (RUDNICK et al. 2012) compared modelling methods for evaluating landscape connectivity, and noted that least-cost path (LCP) (ADRIAENSEN et al. 2003) and UNiversal CORridor (UNICOR) cumulative resistant kernel (COMPTON et al. 2007, LANDGUTH et al. 2012) analyses are some of the methods most

frequently used to map ECNs (CUSHMAN et al. 2014, CUSHMAN et al. 2018, KASZTA et al. 2020a). Different input data from different methods generate different outcomes and meet diverse requirements to help planners in mapping ECNs and prioritizing protection orders, which prompts researchers to explore the limitations and advantages of different modelling methods for assessing connectivity networks (e. g., RUIZ-GONZÁLEZ et al. 2014, ZELLER et al. 2018).

While several lines of research have focused developing conservation plans based species-level considerations (e. g., CUSHMAN et al. 2014, 2016, 2018, KASZTA et al. 2019, 2020a) and spatial landscape pattern concern (e. g., PENG et al. 2018, HOFMAN et al. 2018, CUSHMAN & MCGARIGAL 2019), few studies illustrate the interaction and synergy between species conservation and landscape patterns in ecological network design, particularly in the context of urban landscape planning. It is critical to provide practical guidance to city planners to help them to integrate science-based analyses with comprehensive spatial planning. This is of great significance for long-term and healthy growth of medium size cities to enable them to optimize planning designs for multiple objectives including quality of human life and also ecological sustainability and biodiversity conservation.

China, as the world's largest developing country, has been prioritizing wise and sustainable development. Jinping Xi proposed the Two Mountains Theory in 2005: "Mountains of gold and silver are not as good as lucid waters and lush mountains". Therefore, how to protect the resilience and health of ecological systems is identified as a critically important topic in urban planning in China and around the world.

While Luohe is a greening-focused city, relatively little study has illustrated the modelling methods to map and prioritize ECN in this region or elsewhere. Despite their broad usage in ecology, little is known about the differences in the predictions of different connectivity modelling methods and their performance in terms of how well they predict functional connectivity or ecological integrity (e. g., ZELLER et al. 2018), especially in urban settings. We applied LCP and cumulative resistant kernel analyses in UNICOR software (LANDGUTH et al. 2012) to simulate, map and evaluate the functional ecological network in the Luohe region, China, which has seen large-scale intensive land use change. We have two goals: (1) to compare the two methods' predictions of strength, pattern and extensiveness of habitat connectivity, and (2) to develop optimized ecological networks to prioritize protection spatially of habitat remnants and restoration of degraded habitat by identifying areas that are identified as important core areas and linkages across the two methods.

2 Study Area

The area of the Luohe region is situated in the central Henan province, with a total area of 2617 km². The municipal territory of the Luohe region administers three districts (Yuanhui district, Yancheng district and Shaoling district) and two counties (Wuyang county and Linying county) (Figure 1). Luohe city is a "model city for greening" which represents the highest honor of a city's greening achievements. Therefore, Luohe's management of spatial ECN can give an example for other medium sized cities across China and elsewhere in the world.

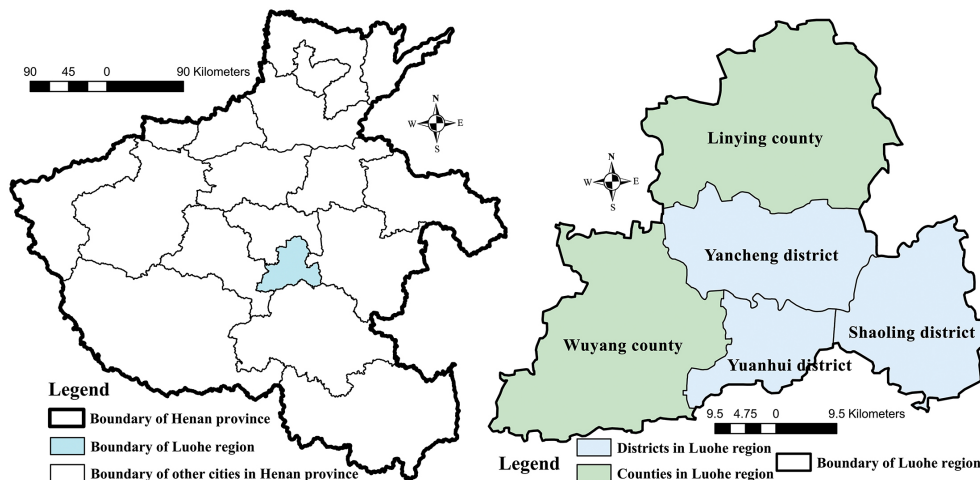


Fig. 1: Luohe region location in Henan Province

3 Methods

3.1 Imagery Acquisition and Preprocessing

We downloaded Landsat images in February 09, 2020 (Coordination: WGS 84 / UTM zone 50N) and in February 16, 2020 (Coordination: WGS 84 / UTM zone 49N) on EarthExplorer – USGS. The acquisition time of the two images is proximal enough to ensure comparable landscape conditions in the two dates without substantial land use and land cover change.

- 1) The functions of Radiometric Calibration and FLAASH Atmospheric Correction were used to normalize the original Landsat images. Next, we classified land use type into water surface, green area (farmland and green space) and built-up area (built-up area and road) by using the Support Vector Machine Classification method in ENVI 5.3.
- 2) We selected 500 ground truth points on Sentinel 2 imagery acquired June 01, 2020 to test the classification accuracy by using the function of Confusion Matrix Using Ground Truth ROIs in ENVI 5.3.
- 3) We calculated several landscape metrics in FRAGSTATS (MCGARIGAL et al. 2012) to assess the structure and composition of the land use map. We chose Percentage of Landscape (PLAND), Patch Density (PD), Edge Density (ED), Radius of Gyration_Area-Weighted Mean (GYRATE_AM), and Aggregation Index (AI) based on previous research that showed these metrics were particularly valuable in ecological connectivity modelling (CUSHMAN et al. 2013a and 2012a). (CUSHMAN & MCGARIGAL 2008, CUSHMAN & MCGARIGAL 2019) illustrated the meaning of these metrics.

3.2 Core Areas Identification

We applied Morphological Spatial Pattern Analysis (MSPA) (SOILLE & VOGT 2009) to divide the green space into Core, Islet, Perforation, Edge, Loop, Bridge, and Branch. The meaning of these seven elements can be found in (SOILLE & VOGT 2009, CARLIER & MORAN 2019). We selected 166 core areas from Core based the size of the Core (the 166 largest).

Then we input the 166 core areas into Conefor 2.6 (SAURA & TORNÉ 2009) to calculate the Degree of Probability of Connectivity (dPC) of every core area to choose the most important core areas. We selected the important core areas whose dPC is larger than 2 (Figure 3).

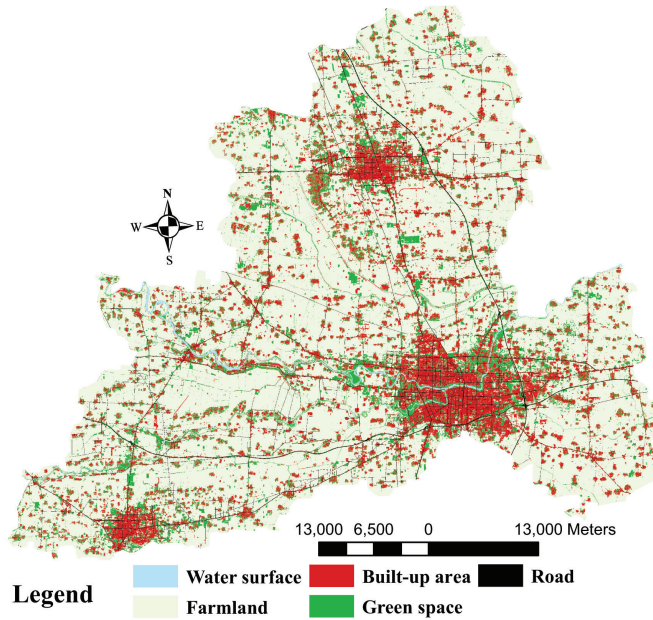


Fig. 2: Land use classification in the Luohe region

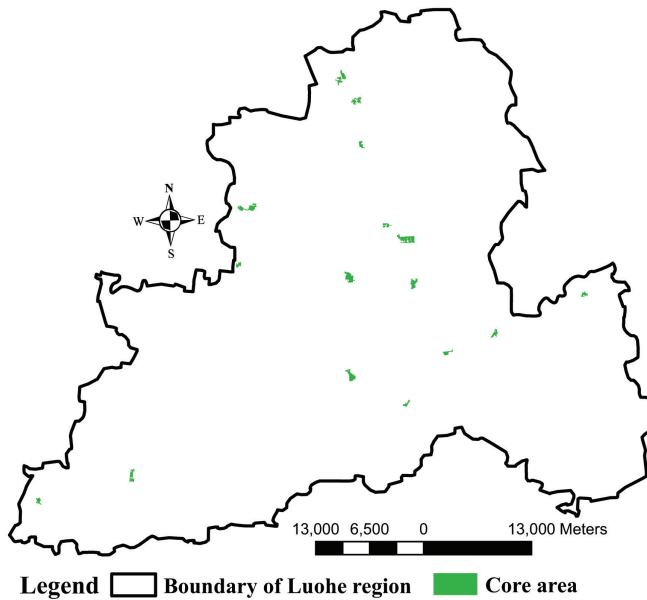


Fig. 3: Location of important core areas in the Luohe region

3.3 Resistance Surface Definition

Resistant surfaces describe the difficulty a species will experience in moving through different locations in the landscape in relation to such things as land use types, topography, barrier features and other landscape characteristics that influence movement (CUSHMAN et al. 2006). Low resistance promotes species movements, high resistance slows down or blocks species movements. Based on expert opinion of relative resistance values of different land cover types for movement of animal species, we set the resistances of green space, farmland, water surface, building and road to 1, 30, 80, 100, 100 respectively.

3.4 LCP Analysis

Linkage Mapper maps least-cost corridors between core areas by using core areas and resistant surface. LCP analysis identifies the lowest cost routes that animal species would move in the region between pairs of core areas, of which can be a patch, park, or conservation area (RUDNICK et al. 2012). We used important core areas and the resistance surface as inputs into the Linkage Mapper Tool (GALLO & GREENE 2018) by using the function of Build Network and Map Linkages to predict the cumulative resistant surface and LCPs among the important core areas.

3.5 UNICOR Cumulative Resistant Kernel Analysis

The UNICOR and network simulation model (LANDGUTH et al. 2012) includes resistant kernel modelling (COMPTON et al. 2007) and factorial LCP modelling (CUSHMAN et al. 2009). Resistant kernel modelling represents the rate of expected movement for every pixel in the region (CUSHMAN et al. 2012b). Factorial LCP modelling predicts the movement corridors of species with different dispersal limits (CUSHMAN et al. 2013b). We applied six dispersal thresholds, including 1 km, 2 km, 4 km, 8 km, 16 km, 32 km (MATEO-SÁNCHEZ et al. 2014) which follows power-2 scaling from highly dispersal limited (1km) to highly mobile (32km species), to simulate multiple connectivity scenarios. We converted the important core areas into raster data at 100 m resolution, then converted raster core areas into 875 points to calculate every core area pixel's resistant kernel and factorial LCP.

3.6 Optimized ecological networks mapping

Evaluation of resistant kernel maps. We used RStudio to calculate the 75th percentile of every resistant kernel surface, then intersected all the kernels above the 75th percentile of every resistant kernel surface in ArcGIS to get the highest connectivity areas.

Evaluation of corridors. We intersected LCP with factorial LCP to get three protection priorities in spatial level. Then we buffered these three protection corridors with 60 m (resolution of Landsat images is 30 m) to calculate the land use type ratio within the corridor buffer.

4 Results

4.1 Land use classification

- 1) **Accuracy assessment** (Table 1). The overall accuracy of the land use classification produced in this analysis was 99.3941%, with a Kappa Coefficient of 0.9867. This illustrates the land use classification is precise and sufficient for the remaining analyses in this study.

- 2) **Fragmentation analysis** (Table 2). The percentage of the landscape (PLAND) of farmland was the largest among land use types. With more than 70% of total land area, farmland is the matrix land use that will dominate the structure and function of this regional landscape, and likely affect the regional ECN. The patch density (PD) and edge density (ED) values of green space were quite large. The correlation length (GYRATE_AM) value of green space was the smallest. The aggregation index (AI) value of green space was quite low as well. Collectively, these metrics indicate that green space in the Luohe region is limited in extent and highly fragmented.

Table 1: Accuracy assessment

Class	Commission (Percent)	Omission (Percent)	Prod. Acc. (Percent)	User Acc. (Percent)
Water surface	0.16	3.12	96.88	99.84
Farmland	0.12	0.03	99.97	99.88
Built-up area	1.09	1.90	98.10	98.91
Green space	8.95	0.43	99.57	91.05
Road	4.03	1.38	98.62	95.97

Table 2: Class metrics of land use classification

Class	PLAND	PD	ED	GYRATE_AM	AI
Water surface	0.6599	0.6420	2.7780	1096.1017	67.3099
Farmland	71.4652	4.7907	62.7221	7032.1139	93.3500
Built-up area	14.5615	5.5365	51.4971	417.9396	73.5571
Green space	11.2809	13.4535	61.7345	220.6607	58.9615
Road	2.0325	1.9101	14.3381	9879.7820	47.2090

4.2 Core area identification

MSPA analysis showed Core green space comprises 1.62% of landscape extent; Islet, indicating isolated green space, accounts for 4.60%; Perforation and Edge (inner and outer green space boundary) are 0.01% and 2.28% respectively, Loop and Bridge (areas connecting green space patches) are 0.29% and 0.64% respectively, and Branch (linkages between main core areas) is 1.83%. 166 core areas were selected by MSPA analysis to calculate dPC value. From these 166 total core areas, 17 important core areas were selected in this study (Figure 3) by dPC value. The core areas were located equally in the Luohe region.

4.3 LCP analysis

The cumulative resistance surface, or cost distance map (e. g., CUSHMAN et al. 2010a) represents the minimum movement cost from any source location to all locations in the landscape. A high-cost distance value means that a given location in the landscape is relatively inaccessible from any source, while a low-cost distance value indicates functional proximity to source locations, based on cumulative resistance. The value of cumulative resistance was defined by the cost-distance from core areas across the resistance map (Figure 4). Areas near to core areas and between two core areas generally had relatively low cumulative resistance. The LCPs produce vector corridors between pairs of source points at a given dispersal distance. They do not show the corridor strength, and passed through all the core areas. That

means LCP analysis only considered the landscape configuration effects and did not consider species' dispersal limits (Figure 4).

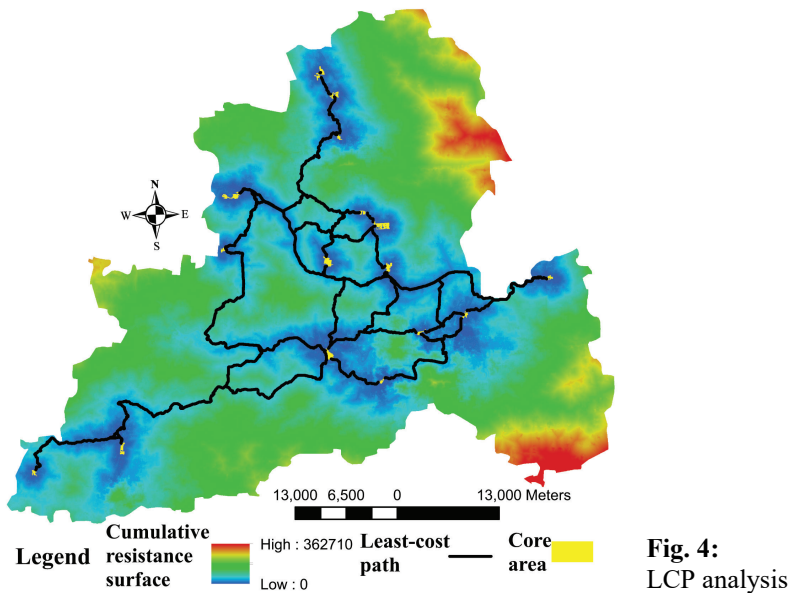


Fig. 4:
LCP analysis

4.4 UNICOR cumulative resistant kernel and factorial least-cost path analysis

Resistant kernels represent the connectivity of species' movement (COMPTON et al. 2007). A high value indicates a high rate of expected movement through that location in the landscape given the source point distribution, density, resistance of the landscape and dispersal ability of the species. A low value indicates low expected rates of movement (e. g., CUSHMAN et al. 2012b, KASZTA et al. 2019, 2020a). The resistant kernels (Figure 5) increased in extent and strength as the dispersal thresholds increased.

Factorial LCPs represent the most optimal potential routes that species would move in connecting all pairs of source points at a given dispersal threshold and on a given resistance surface (CUSHMAN et al. 2009). The number of least cost paths passing through each cell of the network in the factorial LCP analysis increases as the dispersal threshold increased. The factorial LCPs value is a measure of expected relative centrality of each location in the connectivity network, which is related to the rate at which a species would move through that location in the network if moving optimally as a function of resistance among pairs of source points.

The value of cumulative resistant kernels and the number of the factorial LCP (strength) changed markedly with dispersal abilities. The functional connectivity network of species with dispersal abilities ≤ 2 km were very sensitive to the interaction between dispersal ability and the structure of landscape resistance. Species with dispersal 4 km and 8 km showed moderate sensitivity in the factorial LCP and modest resistant kernel value. The value of resistant kernel surfaces and the number of the factorial LCP changed slightly and remained unchanged respectively. That means species with dispersal abilities ≥ 16 km were not highly sensitive

to landscape configuration. This shows a scale dependent effect on network connectivity as a function of dispersal ability, as seen in other studies (e. g., CUSHMAN et al. 2010b, 2016) in which below a certain threshold of dispersal ability the network becomes rapidly attenuated and fragmented.

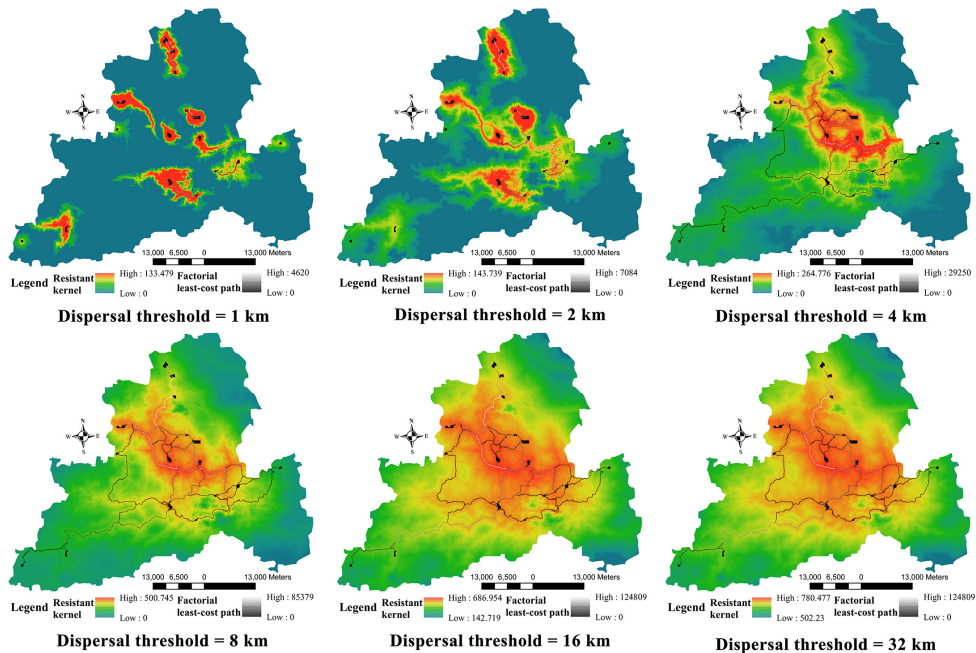


Fig. 5: UNICOR cumulative resistant kernel analysis

4.5 Protection priority

Spatially prioritizing ECN could help planners to optimally arrange green spaces to maximize their ecological resilience and minimize their financial cost (e. g., RUIZ-GONZÁLEZ et al. 2014, KASZTA et al. 2019, 2020b). The overlapping area of all the kernels above 75th percentile of every resistant kernel surface was mostly in Yancheng district (Fig. 6). We intersected LCPs with a 2 km threshold scenario to get the first protection priority, intersected LCPs with a 8 km threshold scenario to get the second protection priority, removed core areas from 8 km threshold scenario to get the third protection priority (Fig. 7). Land use type ratio within the corridor buffer (Table 3) showed most corridors are along green space and farmland.

Table 3: Land use type ratio within the corridor buffer

Land use types	The ratio (%) of first protection priority	The ratio (%) of second protection priority	The ratio (%) of third protection priority
Water surface	2.93	1.74	1.55
Farmland	33.1	35.81	28.56
Built-up area	7.83	8.28	6.2
Green space	53.37	51.97	62
Road	2.77	2.2	1.69

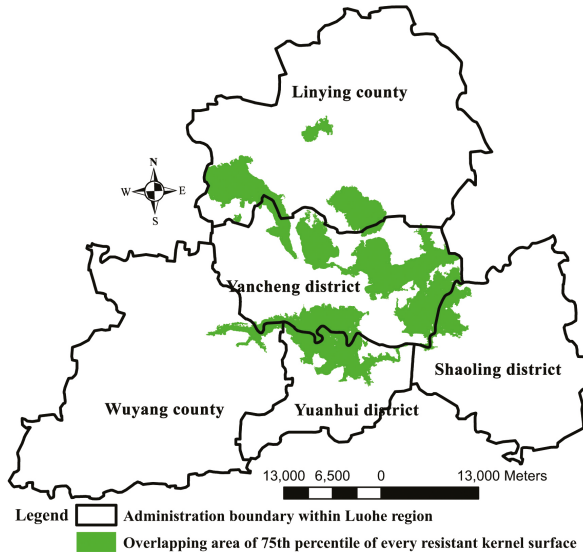


Fig. 6: Overlapping area of 75th percentile of every resistant kernel surface.

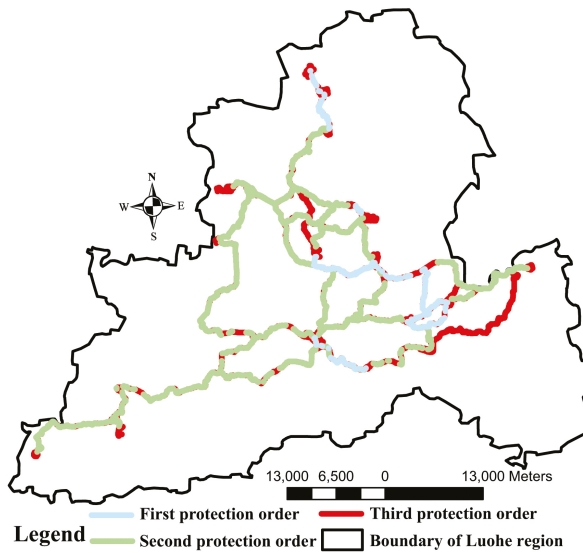


Fig. 7: Protection priority rank in Luohe region.

5 Discussion

The main purpose of this study is to compare two methods frequently used in mapping ECNs to explore the accessibility and applicability of these two methods, and to rigorously prioritize the design of the ECN in the Luohe region. Our main results showed the differences in the predictions produced by cumulative resistant surface, resistant kernel, LCP and factorial LCP across a range of dispersal abilities. An important product of our analysis is a quantitative and objective prioritization of ECN design and protection importance. We identified six specific points for further discussion:

- 1) **Core area and source points.** LCP analysis used individual habitat patches as core areas or linkage zones, resulting in the selection of 17 core areas as sources for the LCP to produce simplified ECNs. UNICOR analyses converted each habitat patch into sets of source points, which has the major advantage of weighting core areas proportional to their size (or the population size of the species that they support). This resulted in the conversion of the 17 core areas into 875 source points, which is a great improvement over the Linkage Mapper approach, as distribution and density of the source population being modelled has dominant effects on predictions of connectivity (e. g., CUSHMAN et al. 2013c, 2016, 2018).
- 2) **Cumulative resistant surface and resistant kernel analysis.** Cumulative resistant surfaces only reflect the total cost of species movement across the landscape from source locations. This is limited given that it doesn't account for the density of source points nor the dispersal ability of the species. Resistant kernel analysis (COMPTON et al. 2007) greatly improves this by explicitly combining the influences of both dispersal ability and the density and distribution of the source population, resulting in the calculation of the incidence function of expected movement rates through every cell in the landscape (e. g., CUSHMAN et al 2014, KASTZA et al. 2018). Similar to CUSHMAN et al. (2016) and (2013c), our results showed very strong dependence of predicted extent and connectivity of the ECN depending on the dispersal threshold employed in resistant kernel analysis. Importantly, our results show that species with dispersal abilities ≤ 2 km cannot traverse among green area patches across most of the landscape, and the connectivity of the green area network increases rapidly and non-linearly with increasing dispersal ability (like seen by CUSHMAN et al. 2016 for lions in Southern Africa).
- 3) **LCP and factorial LCP.** LCPs were vector paths that only showed the spatial pattern of ECNs without the corridor strength, and which passed through all the core areas because they do not consider species' dispersal limits. Factorial LCPs, in contrast, provide much richer information including the strength of corridors and the influence of dispersal threshold on the extent and strength of the corridor network, accounting for the distribution and density of the source population, the dispersal ability of the species and the resistance of the landscape.
- 4) Given the above comparisons we strongly favor the combined use of factorial LCP and resistant kernel analysis over traditional cumulative resistance and LCP analyses (as for example implemented in Linkage Mapper) given they provide much more biologically rigorous, scale dependent predictions that account for the density and distribution of the source population, the dispersal ability of the species and the resistance of the landscape. When applied in combination these two methods enable rigorous prediction of the most important core areas and the strongest corridor linkages among them given particular distributions and dispersal abilities of the target organisms. This combined approach has been used productively in the United States (CUSHMAN et al. 2013c, 2014), Africa (CUSHMAN et al. 2016, 2018), Southeast Asia (KASTZA et al. 2020a) and Western Asia (KHOSRAVI et al. 2018, ASHFRADZADEH et al. 2020).
- 5) The longest dispersal threshold was 32 km in this analysis. We based this on the extent of the factorial LCP network, which spans 76 km from east to west and 64 km from north to south in the Luohe region. The corridor strength and the spatial pattern of factorial LCP stayed unchanged with dispersal thresholds ≥ 16 km; thus, there is no need to explore dispersal thresholds greater than 32 km in this region.

- 6) **Scope and Limitations.** The analysis presented here identifies the most critical, scale-dependent linkages among the main green-space core areas in the Luohe region and prioritizes them based on their importance. This provides an unprecedented quantitative means to guide landscape planning to promote ecological sustainability, human health and biodiversity in urban landscapes. This analysis evaluated connectivity in a synoptic (CUSHMAN et al. 2014), scale-dependent (CUSHMAN et al. 2016) manner. A number of recent research efforts have shown that scale-dependent synoptic analysis is critical to provide rigorous predictions of functional connectivity and evaluation of ECN (e. g., CUSHMAN et al. 2013b, 2014, 2016, 2018, KASATA et al. 2018, KHOSRAVI et al. 2018, ASHFRADZADEH et al. 2020). This is a strength of our analysis. We based our analysis on a classified land use map that was extremely accurate, which is also a strength. However, functional connectivity of ecological processes or biological processes is not the same as structural connectivity of a land cover map. Our analysis assumed expert values for the resistance of different land use classes, which is not ideal and may not reflect the actual resistance experienced by different organisms (e. g., MATEO-SÁNCHEZ et al. 2015a, b, SHIRK et al. 2010, WASSERMAN et al. 2010, ZELLER et al. 2018). It would be desirable, therefore, to conduct empirical optimization of both the distribution and density of the source populations of species of interest (given the dominant effect this has on connectivity predictions; e. g., CUSHMAN et al. 2013c), the resistance of the landscape for their movement (e. g., CUSHMAN et al. 2006, CUSHMAN and LEWIS 2010), and their dispersal abilities (e. g., CUSHMAN et al. 2014, 2016). This would best be done through extensive biodiversity monitoring networks deployed across the green-space network (e. g., LUCID et al. 2018, 2019, 2021, ROBINSON et al. 2017), coupled with telemetry studies of dispersal in focal taxa (e. g., CUSHMAN and LEWIS 2010, ELLIOT et al. 2014) or landscape genetics (e. g., CUSHMAN et al. 2006, SHIRK et al. 2010, WASSERMAN et al. 2010, MATEO-SÁNCHEZ et al. 2015b, ZELLER et al. 2018). These datasets and connectivity analyses based on them would allow for data-driven assessment of ECN effectiveness, as has been done for several species in the United States (e. g., WASSERMAN et al. 2012, 2013, CUSHMAN et al. 2009, 2013b, 2012b) and Europe (RUIZ-GONZÁLEZ et al. 2014). In the present, however, the current analyses provide a robust and informative assessment of the patterns of ECN connectivity in a synoptic, scale dependent manner, enabling localization and prioritization of land use actions to enhance the extensiveness, strength and resilience of the green space network in the Luohe region.

6 Conclusion and Outlook

Overall, our analysis suggested five main conclusions:

- 1) The LCP analysis provided a simple and easy-to-understand illustration of potential paths connecting habitat patches, but grossly underpredicted areas that the species may be using for movement because the results only contained very narrow paths and lacked the consideration of species' dispersal limit.
- 2) Factorial LCP analysis, such as implemented in UNICOR, greatly improves the utility of LCP analysis by enabling it to account for the density and distribution of a source population and the dispersal ability of the species in predicting spatially synoptic patterns of ECN strength.

- 3) Cost-distance or cumulative resistance methods that do not account for source point distribution and density or the dispersal ability of the species are also very limited and potentially misleading.
- 4) Resistant kernel modelling, such as implemented in UNICOR, resolves the limitations of traditional cost-distance and cumulative resistance analysis by enabling explicit accounting for the influences of spatially varying distribution and density of the focal species population as well as the critical influences of its dispersal ability.
- 5) The combination of factorial least cost path and resistant kernel analysis jointly provide complementary and synergistic information that provides a strong suite of methods for comprehensive assessment of ECN extensiveness, effectiveness and prioritization of landscape scenarios to optimize ECN in the future.

References

- ADRIAENSEN, F., CHARDON, J. P., DE BLUST, G., SWINNEN, E., VILLALBA, S., GULINCK, H. & MATTHYSEN, E. (2003), The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning*, 64 (4), 233-247.
- ASHRAFAZADEH, M. R., KHOSRAVI, R., ADIBI, M. A., TAKTEHRANI, A., WAN, H. Y. & CUSHMAN, S. A. (2020), A multi-scale, multi-species approach for assessing effectiveness of habitat and connectivity conservation for endangered felids. *Biological Conservation*, 245, 108523.
- CARLIER, J. & MORAN, J. (2019), Landscape typology and ecological connectivity assessment to inform Greenway design. *Science of the Total Environment*, 651, 3241-3252.
- COMPTON, B. W., MCGARIGAL, K., CUSHMAN, S. A. & GAMBLE, L. R. (2007), A Resistant-Kernel Model of Connectivity for Amphibians that Breed in Vernal Pools. *Conservation Biology*, 21 (3), 788-799.
- CUSHMAN, S. A., MCKELVEY, K. S., HAYDEN, J. & SCHWARTZ, M. K. (2006), Gene Flow in Complex Landscapes: Testing Multiple Hypotheses with Causal Modeling. *The American Naturalist*, 168 (4), 486-499.
- CUSHMAN, S. A. & MCGARIGAL, K. (2008), Landscape Metrics, Scales of Resolution. In: *Designing Green Landscapes*, 33-51. Springer, Dordrecht.
- CUSHMAN, S. A., MCKELVEY, K. S. & SCHWARTZ, M. K. (2009), Use of Empirically Derived Source-Destination Models to Map Regional Conservation Corridors. *Conservation Biology*, 23 (2), 368-376.
- CUSHMAN, S. A. & LEWIS, J. S. (2010), Movement behavior explains genetic differentiation in American black bears. *Landscape Ecology*, 25 (10), 1613-1625.
- CUSHMAN, S. A., CHASE, M. & GRIFFIN, C. (2010a), Mapping Landscape Resistance to Identify Corridors and Barriers for Elephant Movement in Southern Africa. In: *Spatial Complexity, Informatics, and Wildlife Conservation*, 349-367. Springer, Tokyo.
- CUSHMAN, S. A., COMPTON, B. W. & MCGARIGAL, K. (2010b), Habitat fragmentation effects depend on complex interactions between population size and dispersal ability: modeling influences of roads, agriculture and residential development across a range of life-history characteristics. In: *Spatial complexity, informatics, and wildlife conservation*, 369-385. Springer, Tokyo.

- CUSHMAN, S. A., SHIRK, A. & LANDGUTH, E. L. (2012a), Separating the effects of habitat area, fragmentation and matrix resistance on genetic differentiation in complex landscapes. *Landscape Ecology*, 27 (3), 369-380.
- CUSHMAN, S. A., LANDGUTH, E. L. & FLATHER, C. H. (2012b), Evaluating the sufficiency of protected lands for maintaining wildlife population connectivity in the U.S. northern Rocky Mountains. *Diversity and Distributions*, 18 (9), 873-884.
- CUSHMAN, S. A., SHIRK, A. J. & LANDGUTH, E. L. (2013a), Landscape genetics and limiting factors. *Conservation Genetics*, 14 (2), 263-274.
- CUSHMAN, S. A., LEWIS, J. S. & LANDGUTH, E. L. (2013b), Evaluating the intersection of a regional wildlife connectivity network with highways. *Movement Ecology*, 1 (1), 1-11.
- CUSHMAN, S. A., LANDGUTH, E. L. & FLATHER, C. H. (2013c), Evaluating population connectivity for species of conservation concern in the American Great Plains. *Biodiversity and Conservation*, 22 (11), 2583-2605.
- CUSHMAN, S. A., LEWIS, J. S. & LANDGUTH, E. L. (2014), Why Did the Bear Cross the Road? Comparing the Performance of Multiple Resistance Surfaces and Connectivity Modeling Methods. *Diversity*, 6 (4), 844-854.
- CUSHMAN, S. A., ELLIOT, N.B., MACDONALD, D. W. & LOVERIDGE, A. J. (2016), A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change. *Landscape Ecology*, 31 (6), 1337-1353.
- CUSHMAN, S. A., ELLIOT, N. B., BAUER, D., KESCH, K., BAHAA-EL-DIN, L. & BOTHWELL, H. (2018), Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PLoS ONE*, 13 (7), e0196213.
- CUSHMAN, S. A. & MCGARIGAL, K. (2019), Metrics and Models for Quantifying Ecological Resilience at Landscape Scales. *Frontiers in Ecology and Evolution*, 440.
- ELLIOT, N. B., CUSHMAN, S. A., MACDONALD, D. W. & LOVERIDGE, A. J. (2014), The devil is in the dispersers: predictions of landscape connectivity change with demography. *Journal of Applied Ecology*, 51 (5), 1169-1178.
- GALLO, J. A. & GREENE, R. (2018), Connectivity Analysis Software for Estimating Linkage Priority. Conservation Biology Institute: Corvallis, OR, USA.
- HOFMAN, M. P. G., HAYWARD, M. W., KELLY, M. J. & BALKENHOL, N. (2018), Enhancing conservation network design with graph-theory and a measure of protected area effectiveness: Refining wildlife corridors in Belize, Central America. *Landscape and Urban Planning*, 178, 51-59.
- KASZTA, Ź., CUSHMAN, S. A., SILLERO-ZUBIRI, C., WOLFF, E. & MARINO, J. (2018), Where buffalo and cattle meet: modelling interspecific contact risk using cumulative resistant kernels. *Ecography*, 41 (10), 1616-1626.
- KASZTA, Ź., CUSHMAN, S. A., HEARNA, A. J., BURNHAM, D., MACDONALD, E. A., GOOSSENS, B., NATHAN, S. K. S. S. & MACDONALD, D. W. (2019), Integrating Sunda clouded leopard (*Neofelis diardi*) conservation into development and restoration planning in Sabah (Borneo). *Biological Conservation*, 235, 63-76.
- KASZTA, Ź., CUSHMAN, S. A. & MACDONALD, D. W. (2020a), Prioritizing habitat core areas and corridors for a large carnivore across its range. *Animal Conservation*, 23 (5), 607-616.
- KASZTA, Ź., CUSHMAN, S. A. HTUN, S., NAING, H., BURNHAM, D. & MACDONALD, D. W. (2020b), Simulating the impact of Belt and Road initiative and other major developments in Myanmar on an ambassador felid, the clouded leopard, *Neofelis nebulosa*. *Landscape Ecology*, 35 (3), 727-746.

- KHOSRAVI, R., HEMAMI, M. & CUSHMAN, S. A. (2018), Multispecies assessment of core areas and connectivity of desert carnivores in central Iran. *Diversity and Distributions*, 24, (2), 193-207.
- LANDGUTH, E. L., HAND, B. K., GLASSY, J., CUSHMAN, S. A. & SAWAYA, M. A. (2012), UNICOR: a species connectivity and corridor network simulator. *Ecography*, 35 (1), 9-14.
- LUCID, M. K., EHLERS, S., ROBINSON, L. & CUSHMAN, S. A. (2018), Beer, brains, and brawn as tools to describe terrestrial gastropod species richness on a montane landscape. *Ecosphere*, 9 (12), e02535.
- LUCID, M. K., RANKIN, A., SULLIVAN, J., ROBINSON, L., EHLERS, S. & CUSHMAN, S. A. (2019), A carnivores' oasis? An isolated fisher (*Pekania pennanti*) population provides insight on persistence of a metapopulation. *Conservation Genetics*, 20 (3), 585-596.
- LUCID, M. K., WAN, H. Y., EHLERS, S., ROBINSON, L., SVANCARA, L. K., SHIRK, A. & CUSHMAN, S. A. (2021), Land snail microclimate niches identify suitable areas for climate refugia management on a montane landscape. *Ecological Indicators*, 129, 107885.
- MATEO-SÁNCHEZ, M. C., CUSHMAN, S. A. & SAURA, S. (2014), Scale dependence in habitat selection: the case of the endangered brown bear (*Ursus arctos*) in the Cantabrian Range (NW Spain). *International Journal of Geographical Information Science*, 28 (8), 1531-1546.
- MATEO-SÁNCHEZ, M. C., BALKENHOL, N., CUSHMAN, S. A., PÉREZ, T., DOMÍNGUEZ, A. & SAURA, S. (2015a), A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow? *Landscape Ecology*, 30 (8), 1405-1420.
- MATEO-SÁNCHEZ, M. C., BALKENHOL, N., CUSHMAN, S. A., PÉREZ, T., DOMÍNGUEZ, A. & SAURA, S. (2015b), Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data. *Ecosphere*, 6 (4), 1-16.
- MCGARIGAL, K., CUSHMAN, S. A. & ENE, E. (2012), FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. <http://www.umass.edu/landeco/research/fragstats/fragstats.html> (01.10.2021).
- PENG, J., PAN, Y., LIU, Y., ZHAO, H. & WANG, Y. (2018), Linking ecological degradation risk to identify ecological security patterns in a rapidly urbanizing landscape. *Habitat International*, 71, 110-124.
- RUDNICK, D. A., RYAN, S. J., BEIER, P., CUSHMAN, S. A., DIEFFENBACH, F., EPPS, C. W., GERBER, L. R., HARTTER, J., JENNESS, J. S., KINTSCH, J., MERENLENDER, A. M., PERKLE, R. M., PREZIOSI, D. V. & TROMBULAK, S. C. (2012), The Role of Landscape Connectivity in Planning and Implementing Conservation and Restoration Priorities. *Issues in Ecology*.
- RUIZ-GONZÁLEZ, A., GURRUTXAGA, M., CUSHMAN, S. A., MADEIRA, M. J., RANDI, E. & GÓMEZ-MOLINER, B. J. (2014), Landscape Genetics for the Empirical Assessment of Resistance Surfaces: The European Pine Marten (*Martes martes*) as a Target-Species of a Regional Ecological Network. *PLoS ONE*, 9 (10), e110552.
- ROBINSON, L., CUSHMAN, S. A. & LUCID, M. K. (2017), Winter bait stations as a multispecies survey tool. *Ecology and Evolution*, 7 (17), 6826-6838.
- SOILLE, P. & VOGT, P. (2009), Morphological segmentation of binary patterns. *Pattern Recognition Letters*, 30 (4), 456-459.
- SAURA, S. & TORNÉ, J. (2009), Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. *Environmental Modelling & Software*, 24 (1), 135-139.

- SHIRK, A. J., WALLIN, D. O., CUSHMAN, S. A., RICE, C. G. & WARHEIT, K. I. (2010), Inferring landscape effects on gene flow: a new model selection framework. *Molecular Ecology*, 19 (17), 3603-3619.
- WASSERMAN, T. N., CUSHMAN, S. A., SCHWARTZ, M. K. & WALLIN, D. O. (2010), Spatial scaling and multi-model inference in landscape genetics: *Martes americana* in northern Idaho. *Landscape Ecology*, 25 (10), 1601-1612.
- WASSERMAN, T. N., CUSHMAN, S. A., SHIRK, A. S., LANDGUTH, E. L. & LITTELL, J. S. (2012), Simulating the effects of climate change on population connectivity of American marten (*Martes americana*) in the northern Rocky Mountains, USA. *Landscape Ecology*, 27 (2), 211-225.
- WASSERMAN, T. N., CUSHMAN, S. A., LITTELL, J. S., SHIRK, A. J. & LANDGUTH, E. L. (2013), Population connectivity and genetic diversity of American marten (*Martes americana*) in the United States northern Rocky Mountains in a climate change context. *Conservation Genetics*, 14 (2), 529-541.
- ZELLER, K. A., JENNINGS, M. K., VICKERS, T. W., ERNEST, H. B., CUSHMAN, S. A. & BOYCE, W. M. (2018), Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. *Diversity and Distributions*, 24 (7), 868-879.