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Assessing the Impact of Urban Expansion on Surrounding Forested Landscape Connectivity across Space and Time

Zhouqiao Ren ¹, Jianhua He ² and Qiaobing Yue ^{2,*} 

¹ Institute of Digital Agriculture, Zhejiang Academy of Agricultural Sciences, Hangzhou 310021, China; renzq@zaas.ac.cn

² School of Resource and Environmental Sciences, Wuhan University, Wuhan 430079, China; hjianh@whu.edu.cn

* Correspondence: joyceqb@whu.edu.cn

Abstract: Landscape connectivity is important for all organisms as it directly affects population dynamics. Yet, rapid urbanization has caused serious landscape fragmentation, which is the primary contributor of species extinctions worldwide. Previous studies have mostly used spatial snap-shots to evaluate the impact of urban expansion on landscape connectivity. However, the interactions among habitats over time in dynamic landscapes have been largely ignored. Here, we demonstrated that overlooking temporal connectivity can lead to the overestimation of the impact of urban expansion. How much greater the overestimation is depends on the amount of net habitat loss. Moreover, we showed that landscape connectivity may have a delayed response to urban expansion. Our analysis shifts the way to understand the ecological consequences of urban expansion. Our framework can guide sustainable urban development and can be inspiring to conservation practices under other contexts (e.g., climate change).

Keywords: land-use change; fragmentation; urban development strategy; spatio-temporal connectivity



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1. Introduction

Worldwide, the population boom has resulted in rapid urban expansion [1] and dramatic land-use changes, which are considered as the primary drivers of landscape fragmentation and biodiversity loss [2,3]. An adequate degree of landscape connectivity plays a pivotal role in ecological processes such as colonization and extinction [4], ensuring resilience of metapopulations [5]. Understanding the impact of urban development on landscape connectivity and using suitable connectivity models to assess urban growth scenarios can, therefore, significantly contribute to balancing urban development and biodiversity conservation [6].

Certain relationships have been found between landscape connectivity and the rate [7,8], the form [9–12], and intensity [13,14] of urban growth. For example, dense urban development alleviates the encroachment to habitats but inevitably increases barrier effects of built-up areas [13]. Additionally, compact development maintains more connectivity than urban sprawl [15]. Yet, how different regional urban development strategies (uneven development vs. balanced development) affect landscape connectivity is rarely investigated.

Furthermore, only a handful of studies have provided impact assessments from a spatiotemporal perspective (e.g., refs. [16–19]), mainly due to that most of the connectivity models [20–23] are spatial snap-shots [24], which facilitate impact evaluation by comparing connectivity assessments performed independently at multiple time points. Nevertheless, these purely spatial connectivity models overlook the temporal interactions among habitat patches, such as the facilitation or impedance effect caused by the appearance or disappearance of stepping-stone habitat patches over time [17], so that they may generate misleading assessments (see schematic representation in Figure 1).

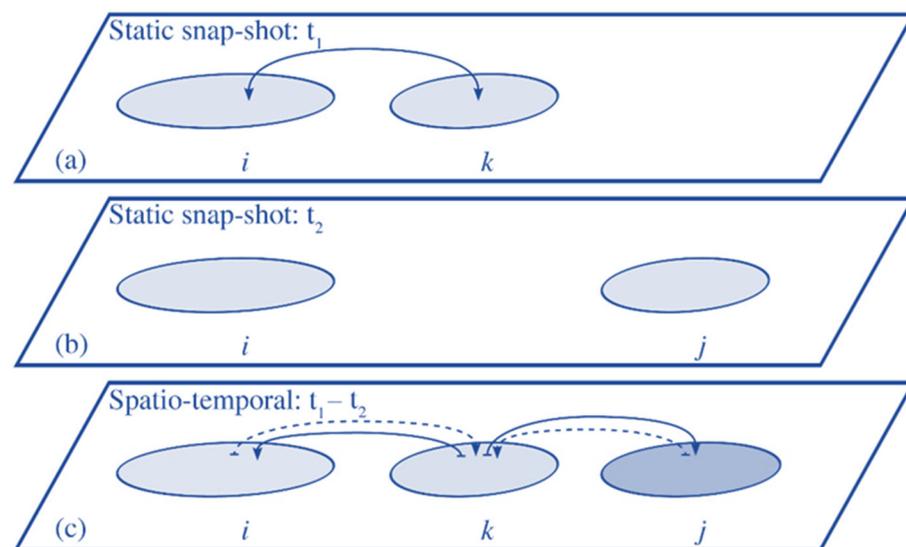


Figure 1. A toy example for the illustration of potential interactions between habitat patches across space and time. At time point t_1 , two patches exist in the landscape and they are connected. Due to land use change, at time point t_2 , patch k disappears while a new patch j appears. Patch j is not connected to i since their distance exceeds dispersal ability of the species. Therefore, from the perspective of static connectivity assessment, landscape connectivity is lost during landscape dynamics. However, from the spatio-temporal perspective, an individual may start its first disperse from patch i to k , then disperse again from k to j before k finally loses habitat. As such, patch i and j can be connected across space and time when considering the temporal stepping stone effect of patch k . This figure is adapted from ref. [16]. (a) the spatial distribution of habitat patches in time point t_1 ; (b) the spatial distribution of habitat patches in time point t_2 ; (c) the potential interactions between habitat patches across time point t_1 and t_2 .

To bridge this gap, here we developed a framework that combines a cellular automata (CA) model with a recent spatiotemporal connectivity model [17]. We aimed to answer which regional urban development strategy is less detrimental to landscape connectivity, and investigate different behaviours of spatial-only connectivity and spatiotemporal connectivity under urban expansion. The CA model supports the design of the three urban development strategies (S1: uneven development that concentrates urban land in the mega-city; S2: balanced development; S3: controlling the mega-city size and put more urban land in other cities). The spatiotemporal connectivity model can capture the effects of temporal interactions of habitat patches. We selected the Three Gorges Reservoir Area (TGRA, SW China) as the study area for its high biological conservation values (one of the richest areas in terms of biodiversity in China; Wu, Huang [25]) and rapid urbanization [8].

2. Materials and Methods

2.1. Study Area and Target Species

The TGRA is located in the middle catchment of the Yangtze River in China (Figure 2). It covers c. 58,000 km² and includes multiple administrative districts of Chongqing City and Hubei Province. According to the national classification of urban size [26], there is one mega-city (i.e., Chongqing main city proper) in the TGRA. The TGRA is one of the richest areas in terms of biodiversity in China, and the biodiversity of genera and families is among the highest globally [25]. The TGRA has experienced fast urban expansion to resettle an enormous population of immigrants during the Three Gorges Dam Project, and the fast rate of urban expansion will continue as it is a key region in the Yangtze River Economic Belt [27]. Meanwhile, the Grain-to-Green Project (GTGP) has been implemented in this region to convert the cropland in the steep slope to the forested land since 2000, which significantly increase the forest area [28].

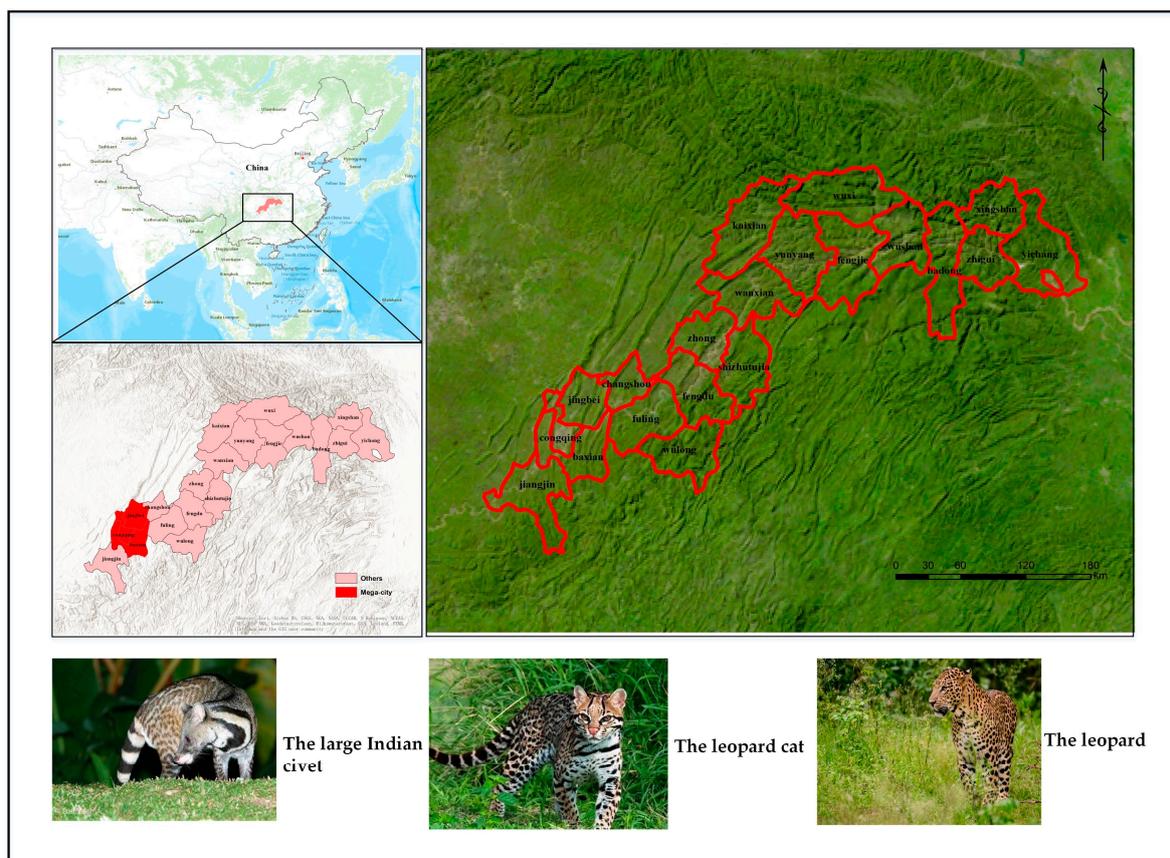


Figure 2. The study area: The Three Gorges Reservoir Area. Species photos credit to Saniakhan, Nicola Scatassi and Saul Flores.

Three nationally protected animals inhabiting the TGRA: the large Indian civet (*Viverra zibetha*, represented by “LIC” hereafter), the leopard cat (*Prionailurus bengalensis*, “LC”) and the leopard (*Panthera pardus*, “L”) were selected as our target species, to represent a wide range of body sizes of local forest mammals. The home range sizes of the three species are 6 km² [29], 12.7 km² [30] and 28.2 km² (the mean value of 5 collared individuals in Odden, Athreya [31]), respectively. As species natal dispersal distance is proportional to the home range size, the natal median dispersal distance of each target species was estimated as [32]:

$$\text{Median dispersal distance} = 7\sqrt{\text{home range area}} \tag{1}$$

Therefore, natal median dispersal distances were estimated as: 14.7 km for the large Indian civet, 25.0 km for the leopard cat, and 37.2 km for the leopard. In addition, the data collected and used in this study are listed in Table 1.

Table 1. The data used in this study. All raster datasets are transformed into the same resolution (250 m) and projection (WGS_1984_Albers) prior to model implementation.

Name	Data Type & Resolution	Source
The information of target species	Html & pdf	International Union for Conservation of Nature (IUCN) Red List
Land use data (2000 & 2010)	Raster, 30 m	CAS (http://www.resdc.cn/ , accessed on 19 December 2020)
Population (2010)	Raster 1 km	
GDP (2010)	Raster 1 km	
DEM	Raster, 90 m	SRTM 90 m Digital Elevation Data [33]
Traffic network	Shapefile	[34]
Ecological redline	Shapefile	Chongqing Environment Protection Bureau
Population statistical data	Pdf & Xls	The statistical yearbook of Chongqing and of Hubei

2.2. Research Framework

An overview of the research framework is displayed in Figure 3. Firstly, future urban expansion was simulated under three different development strategies by the FLUS model. Secondly, the connectivity model that fully takes account of spatiotemporal connections between patches was developed. Thirdly, we evaluated the effects of urban expansion on surrounding forest landscape connectivity based on connectivity metrics.

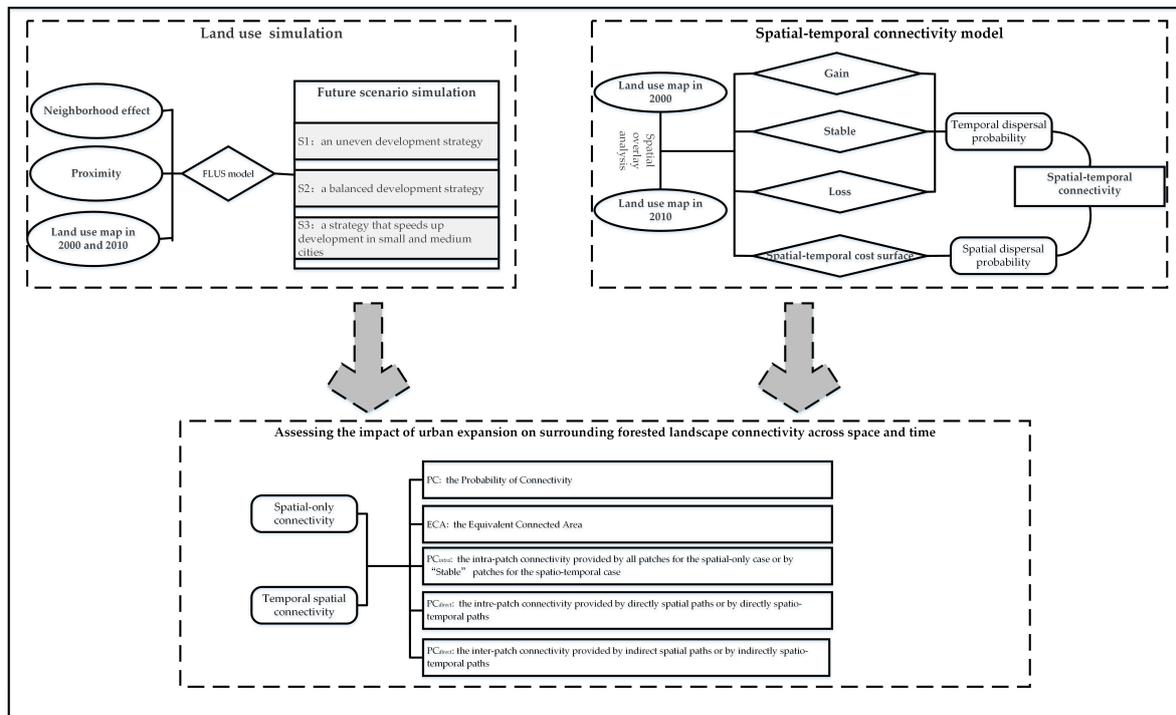


Figure 3. Illustration of the research framework.

2.3. The Future Land Use Simulation Model

The Future Land Use Simulation (FLUS) model [35] is an artificial neuron network [36] (ANN) based CA model. We opted to use the FLUS model as it can better tackle the non-linear relationships in the land-use system than many other CA models [37,38]. First, the probability-of-occurrence of each land-use type on a grid cell is estimated through the ANN training based on a land-use map and other auxiliary geographical information, including terrain factors (elevation, slope and aspect), proximity factors (distance to the mega-city core, distance to common cities, distance to road, and distance to river), and socio-economic factors (GDP and population density). Second, the probability-of-occurrence is multiplied by the neighbourhood effect, inertia coefficient, and the conversion difficulty to obtain the total land-use conversion probability. This is to fully account for factors affecting landscape dynamics and efficiently implement spatial allocation, while also acknowledging that not all grid cells can be converted [39]. Third, based on the total probability, the roulette wheel selection method is applied to determine whether land-use conversion occurs on a grid cell or not. This is to reflect the competition within a land-use system. Please see Supplementary Materials Table S1 or Liu, Liang [35] for detailed information.

2.4. Simulating Different Regional Urban Development Strategies

All grid cells were classified into “mega-city urban land”, “common city urban land” and “non-urban land”, based on the administrative districts which they are located in and the land-use type which the grid cell belongs to. As population growth necessitates the development of urban land [40], we calculated future urban land demands according to the predicted population growth. We assumed that the increase rate of population

declines with the increase in population amount, and thus the logistic model was used (see Supplementary Materials Table S1). Based on the predicted urban land demand, we designed three urban development strategies (S1–S3). S1 is an uneven development strategy that concentrates 75% of the new urban land in the mega-city. S2 is a balanced development strategy that equally places the new urban land in the mega-city and the other cities. S3 is a strategy that speeds up development in small and medium cities (by allocating 75% of the new urban land) while controls urban expansion in the mega-city.

The potential urban expansion under different strategies were simulated by the FLUS model, and were then overlaid on the current land-use map (with six land-use types) to create future land-use maps. This was to ensure that no transitions would occur among other non-urban land-use types, so that the connectivity change is only dependent on urban expansion (i.e., habitat loss and stronger barrier effect caused by conversion from non-urban land to urban land).

2.5. Model Validation

The FLUS model was validated through two aspects: (1) the Area under a Receiver Operating Characteristic curve (AUC) values [41] were applied to quantify the ANN performance in fitting the probability-of-occurrence of the individual land-use type (Figure 4), and (2) the fuzzy Kappa index [42] was used to evaluate the goodness-of-fit of simulation landscape in 2010. For the first aspect, a perfectly fitted result yields an AUC value of 1 while a completely random model yields an AUC value of 0.5. The AUC values of the three land-use types are 0.796, 0.862, and 0.678, respectively, indicating that the fitted probability-of-occurrence of the three land-uses can be well explained by the selected driving forces. For the second aspect, the fuzzy kappa indices of the three land-use types are 0.84, 0.88, and 0.82 respectively; and the overall fuzzy Kappa is 0.85, indicating a considerable high goodness-of-fit of the simulation result. The receiver operating characteristic curve (ROC) curves were obtained through SPSS 23, and the fuzzy Kappa was obtained through Map Comparison Kit [43].

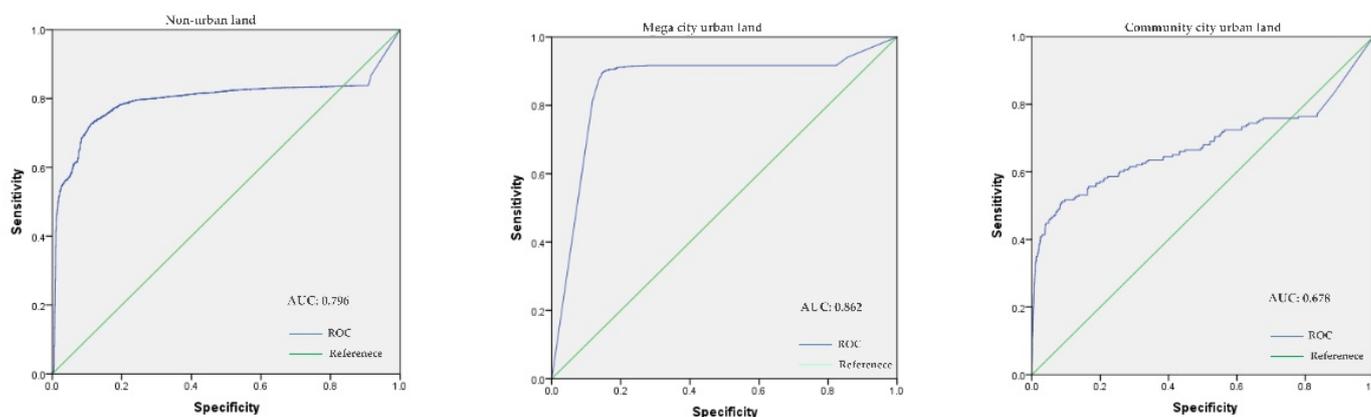


Figure 4. ROC curves and AUC values of the three land-use types fitted by the ANN.

2.6. Spatial-Temporal Connectivity Model

Conceptually, a spatiotemporal path across a habitat network represents the possibility of an individual moving from a given habitat patch (i.e., node in spatial graph terminology) at time t_1 to another patch at t_2 ($t_1 < t_2$). For conservation applications, such a path also indicates the likelihood that an individual will persist from t_1 to t_2 in a changing landscape [17].

We deemed the forest patch whose (1) size is larger than the home range size of a given species and (2) location is 200 m away from urban land and roads as the habitat node of the corresponding species [17]. This selection was to ensure the species' relatively long-term persistence and adequate tolerance to anthropogenic activities. However, tolerance to anthropogenic activities (i.e., distance to construction land) was considered invariable among

the three focal species given that we did not find documents reporting such information. Nodes were attributed to the corresponding patch sizes.

Given two time points (t_1, t_2), all habitat patches in a landscape can be classified into three types by overlay analysis for habitat maps in t_1 and t_2 , including (1) Gain: not habitat in t_1 but habitat in t_2 , (2) Stable: habitat in both t_1 and t_2 , and (3) Loss: habitat in t_1 but not habitat in t_2 . To persist in a dynamic landscape, an individual must stay in a Stable habitat patch, or disperse from a habitat patch at t_1 (i.e., Loss or Stable) to another habitat patch at t_2 (i.e., Gain or Stable).

Temporal interactions between patches can occur if and only if they simultaneously exist in the landscape for a while, that is, having temporal overlap. For example, a Loss patch and a Stable patch must have temporal overlap, since that Loss patch can only lose habitat after an intermediate time point t_x ($t_1 < t_x < t_2$) and Stable patch persists in the landscape through t_1 to t_2 . Similarly, a Gain patch and a Stable patch can also have temporal interactions. In cases where temporal overlap exists, the probability of temporal interactions between these two patches is assigned as 1 (i.e., $p_{ij}^t = 1$). However, for a Loss patch and a Gain patch, they may or may not have temporal interactions since we do not know at time point the Loss patch loses habitat and the Gain patch gains habitat. Therefore, in this case, the probability of temporal interactions is assigned as 0.5 (i.e., $p_{ij}^t = 0.5$).

Additionally, the temporal links can also be classified into two types: (1) the essential link and (2) the auxiliary link [17]. An essential link is a link that, alone, is enough to ensure that an individual can move from habitat node at t_1 to another habitat node at t_2 . An auxiliary link is a link that cannot achieve the transportation for individuals as an essential link does. However, through a path that combines consecutive auxiliary links (and at least one essential link), an individual may be able to indirectly move from a habitat node at t_1 to another habitat node at t_2 . By doing so, more habitats are reachable than by using essential links only. For example, for a path “Loss -> Loss -> Stable”, the first link is an auxiliary link because when dispersing from Loss to Loss, no habitat is available for that individual to ensure persistence. The second link is an essential link because two endpoints have habitat at the beginning and at the end, such that it alone can ensure that individual’s persistence. Thus, a successful temporal path can either be (1) a direct path that consists of a single essential link or (2) an indirect path constituting of any combinations of auxiliary links and essential links, as long as at least there is one essential link. The probability of each movement scenario is listed in Table 2.

Table 2. Probability of movements along temporal links without considering the spatial dispersal probability following ref. [17]. For auxiliary links, an individual can make a first movement in time t_x ($t_1 < t_x < t_2$) to a Loss patch that still has suitable habitat at t_x but will have no suitable habitat at t_2 . In this case, it has to use some other links to move somewhere else after t_x but before t_2 . Alternatively, an individual may also make a movement in t_x from a Gain patch that has habitat at t_x but had no habitat at t_1 . In this case, it has to be located in some other patch with habitat at t_1 , and hence the individual must have previously used some other link in the graph to get to the patch where it is located in t_x .

Source Node: Individual Location at t_1 for the Essential Links or at t_x ($t_1 < t_x < t_2$) for the Auxiliary Links	Target Node: Individual Location after t_1					
	Essential Link (Individual Location at t_2)			Auxiliary Link (Individual Location in t_y , $t_x < t_y < t_2$)		
	Stable	Loss	Gain	Stable	Loss	Gain
Stable	1	0	1	N/A	1	N/A
Loss	1	0	0.5	N/A	1	N/A
Gain	0	0	0	1	0.5	1

For the spatial links, the movement probability from node i to node j (represented as p_{ij}^s) is determined by using an exponential function of the species dispersal capabilities and the distances between patches [17]: $p_{ij}^s = e^{-kd_{ij}}$; where k is a species-specific constant reflecting the dispersal ability, and d_{ij} is the distance between i and j . Here, the distance between patches is the cost-weighted distance derived from the least-cost modelling [17], to consider the spatial heterogeneity of impedance of the landscape (see Supplementary

Table S2 for the cost of each land-use type). Some studies noticed that the landscape impedance may vary with time [44,45], hence such variations were also taken into account. Given that detailed information about when land-use changes occur during t_1 and t_2 is unavailable, we obtained the spatiotemporal cost surface by taking the average between the cost surfaces in t_1 and t_2 . For instance, for a grid cell p belonging to the cropland at t_1 and being converted to the grassland in t_2 , its cost value in the spatiotemporal cost surface is the average between cost values of the cropland and the grassland. The median dispersal distance was multiplied by the median cost value of the dynamic cost surface from 2000 to 2010, and the result determined the dispersal threshold corresponding to a spatial dispersal probability of 0.5 (i.e., to parameterise k ; Gurrutxaga, Rubio [46]).

The ultimately spatiotemporal links and their dispersal probabilities (p_{ij}^{st}) are obtained through multiplying the temporal dispersal probability (p_{ij}^t) by the spatial dispersal probability (p_{ij}^s), which is formulated as:

$$p_{ij}^{st} = p_{ij}^t \times p_{ij}^s \quad (2)$$

By doing so, the connectivity model fully takes account of all possibilities of spatiotemporal connections between patches, in either direct or indirect fashion, while also acknowledging that not all paths will lead to a successful transportation for an individual. The overlay analysis was implemented in ArcGIS 10.2, the least-cost modelling was implemented in Linkage Mapper V1.1 [47].

2.7. Connectivity Metrics

Network theory is a powerful approach to measure connectivity [48], and five network-based metrics: the Probability of Connectivity (PC ; Saura and Pascual-Hortal [23]), the Equivalent Connected Area (ECA ; Saura, Estreguil [49]), and the three PC 's fractions [50] are popular connectivity metrics for conservation planning. These metrics were adapted to spatiotemporal connectivity model by replacing the spatial-only dispersal probability p_{ij}^s in the original formulas with the spatiotemporal dispersal probability p_{ij}^{st} (with the subscript "st"). PC is defined as the probability that two individuals randomly placed within a landscape fall into habitat patches that are reachable for each other across the habitat network [23], and is formulated as:

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}{A_l^2} \quad (3)$$

where a_i and a_j denote the area of patch i and j , respectively; A_l is the area of the study site; p_{ij}^* is the maximum product probability of all possibly spatial paths (p_{ij}^s) for the spatial-only connectivity case (original PC), or of all possibly spatiotemporal paths (p_{ij}^{st}) for the spatiotemporal connectivity case (PC_{st}).

ECA and ECA_{st} indicate the amount of spatially reachable habitat and the amount of spatiotemporally reachable habitat, and are formulated as the square root of the numerator of PC and PC_{st} , respectively.

Moreover, PC 's fractions are formulated as Equations (4)–(6):

$$PC_{intra} = \frac{\sum_{i=1}^n a_i^2}{A_l^2} \quad (4)$$

$$PC_{direct} = \frac{\sum_{i=1}^n \sum_{j=1, i \neq j}^n a_i a_j p_{ij}}{A_l^2} \quad (5)$$

$$PC_{step} = \frac{\sum_{i=1}^n \sum_{j=1, i \neq j}^n a_i a_j (p_{ij}^* - p_{ij})}{A_l^2} \quad (6)$$

where PC_{intra} corresponds to the intra-patch connectivity [51] provided by all patches for the spatial-only case or by “Stable” patches for the spatiotemporal case ($PC_{intra, st}$); PC_{direct} corresponds to the inter-patch connectivity provided by directly spatial paths (for the spatial-only case) or by directly spatiotemporal paths (for the spatiotemporal case, $PC_{direct, st}$) without using stepping-stones; PC_{step} corresponds to the inter-patch connectivity provided by indirect spatial paths (for the spatial-only case) or by indirectly spatiotemporal paths (for the spatiotemporal case, $PC_{step, st}$) that pass through intermediate stepping-stones. We also built a linear univariate model to present the relationship between the amount of habitat change and the contribution of ECA_{st} compared with ECA at t_2 .

3. Results

3.1. Urban Expansion and Habitat Change in Different Urban Development Scenarios

Under S1–S3 at 2020, the urban size is predicted to be 1716 km², which is over twice the size in 2000. The mega-city takes up 59.2% of the total urban land in S1 while only 43.1% in S3. New urban land is put to west and east Chongqing main city proper in S1, while put to cities in northeast TGRA that are close to large and continuous tracts of forests in S2 and S3 (Figure 5). From 2000 to 2010, the three focal species gained more habitats and LIC had the largest habitat increment (+2.99%), but they suffer habitat loss in S1–S3 at 2020. Among all scenarios in 2020, S3 has the severest habitat shrinkage for all considered species while slight habitat loss occurs in S1. Among all target species, L’s habitats are more affected by urban expansion (Table 3).

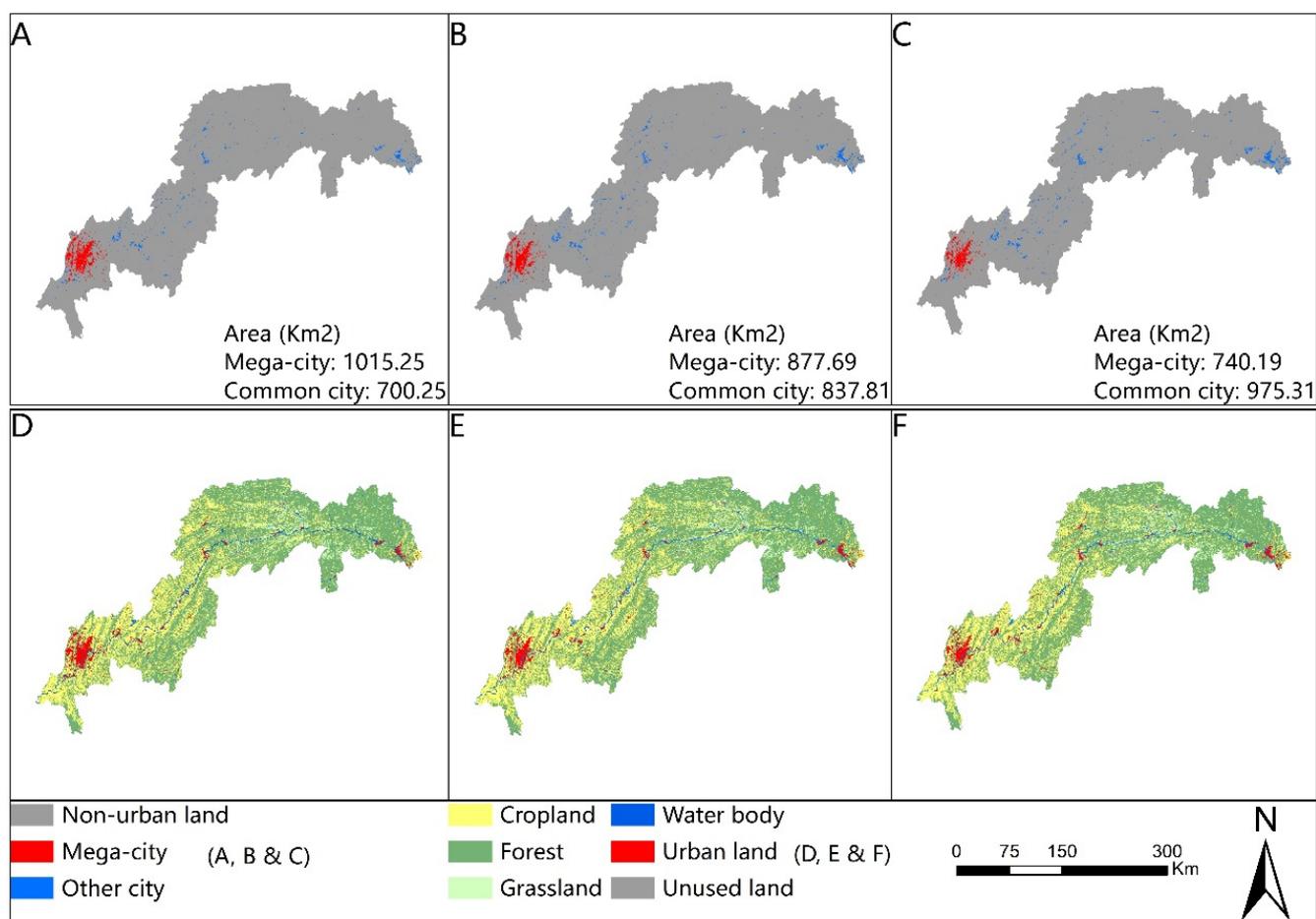


Figure 5. (A–C) present urban land distributions under regional urban development scenarios of S1, S2 and S3 in 2020, respectively; (D–F) present land-use scenarios of S1, S2 and S3 in 2020, respectively, by overlaying (A–C) with the 2010 land-use map.

Table 3. The habitat amount (unit: km²) and the change rate (% , compared to the last time point) of each species under each scenario.

Year	LIC		LC		L	
	Area	Change Rate	Area	Change Rate	Area	Change Rate
2000	27504	N/A	26,843	N/A	26,043	N/A
2010	28241	2.68%	27,509	2.48%	26,823	2.99%
2020 S1	28160	−0.29%	27,414	−0.34%	26,703	−0.45%
2020 S2	28118	−0.43%	27,363	−0.53%	26,679	−0.54%
2020 S3	28045	−0.69%	27,309	−0.73%	26,627	−0.73%

3.2. The Spatial-Only and Spatiotemporal Connectivity in Different Scenarios

During 2000 and 2010, the amount of spatiotemporally reachable habitat (indicated by ECA_{st} , see Methods) is smaller than the amount of spatial-only reachable habitat (ECA) in 2010 for all target species (Figure 6). However, from 2010 to 2020, ECA_{st} exceeds ECA in 2020 and this holds for any species under any scenario. The linear model suggests that, when the amount of habitat increases or decreases by 1%, ECA_{st} will be c. 0.5% lower or higher than ECA at t_2 (Figure 7). Additionally, for each species, ECA increases during 2000 and 2010 due to habitat expansion and decreases during 2010 and 2020 due to habitat shrinkage, while ECA_{st} is higher in the period from 2010 to 2020 than in the period from 2000 to 2010.

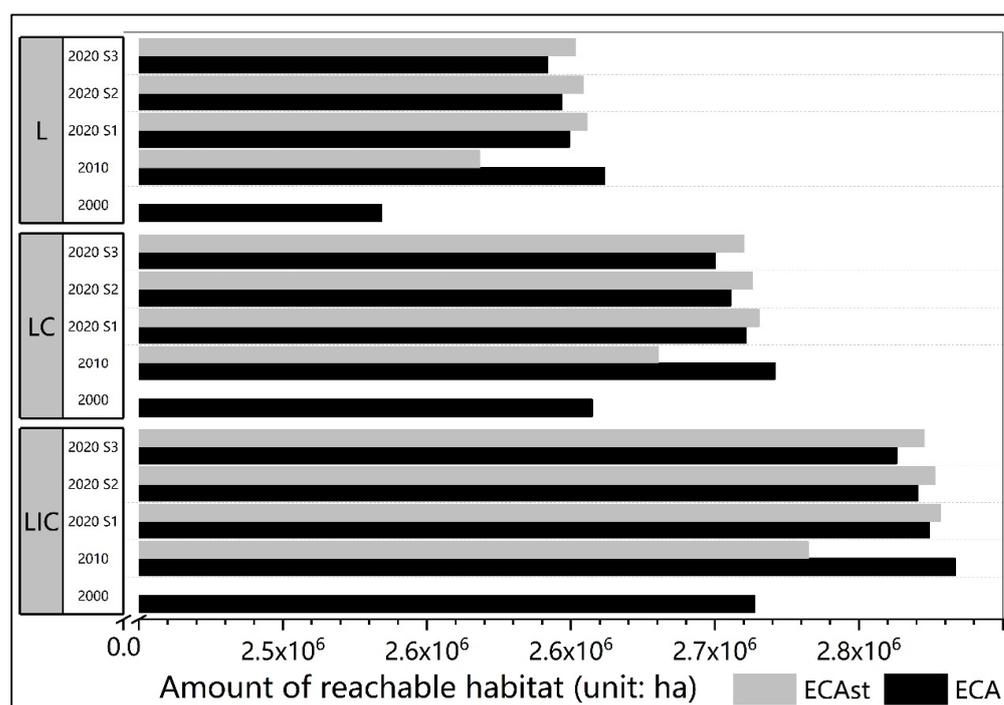


Figure 6. Amount of reachable habitat from the spatial-only and the spatio-temporal perspectives (indicated by ECA and ECA_{st} , respectively) of each species under different land-use scenarios.

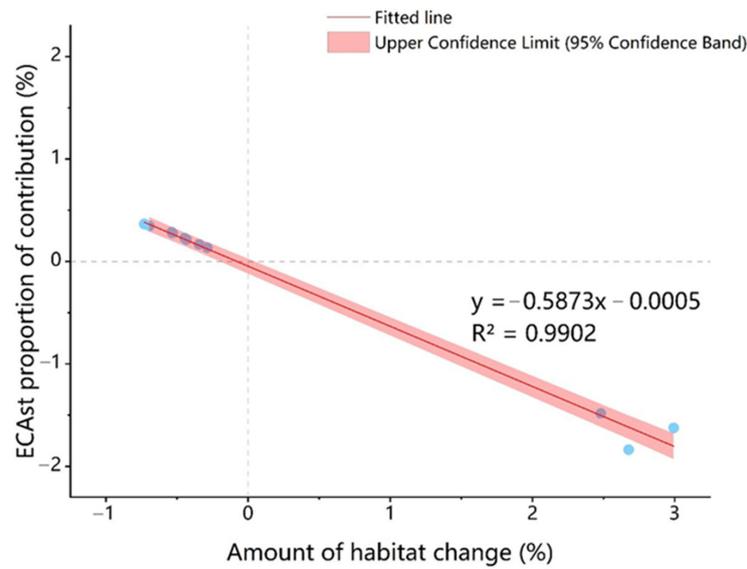


Figure 7. The linear model ($n = 12$) of the contribution of spatio-temporal connectivity ECA_{st} compared with spatial-only connectivity ECA at t_2 (formulated as $100\% * (ECA_{st} - ECA_{t_2}) / t_2$) and the percentage of habitat change.

For contribution of PC_{st} fractions, when habitat area increases by c. 3% (corresponding to the habitat increment during 2000 and 2010), PC_{intra}^{st} is c. 15% lower than PC_{intra} for all focal species, whereas PC_{step}^{st} has relatively large contribution than PC_{step} (Figure 8), which ranges from 9% (for LIC) to 22% (for L). Under S1–S3, PC_{intra}^{st} and PC_{intra} have no difference and PC_{direct}^{st} is slightly lower than PC_{direct} , while remarkable contributions were found in PC_{step}^{st} for LC and L in scenarios with more dramatic habitat losses (i.e., in S2 and S3).

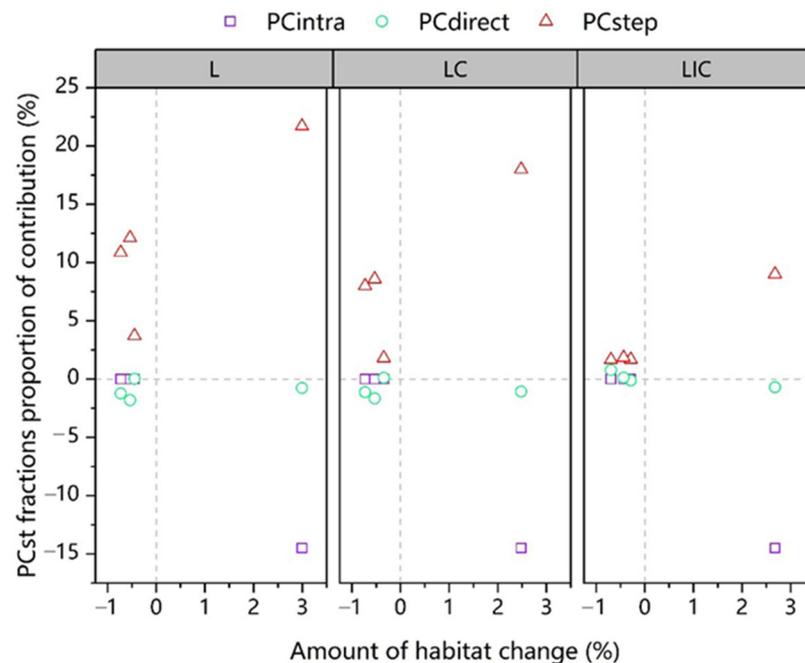


Figure 8. The scatter of PC_{st} fractions contributions compared with PC fractions (formulated as $100\% * (PC_i^{st} - PC_i_{t_2}) / PC_i_{t_2}$, i denotes a fraction) and the percentage of habitat change.

4. Discussion

The simulation results and consequential connectivity changes demonstrate that regional urban development strategies have direct impacts on landscape fragmentation. In

the TGRA, the strategy that concentrates new urban land in the mega-city helps to maintain more connectivity for all target species than other strategies. Natural habitats near the mega-city are much fewer than those near the other cities, so that concentrating urban land in the mega-city reduces the encroachment to habitats. This finding agrees with the Urban-rural Master Planning of Chongqing City, which articulates that the dominant function of the northeast TGRA is biodiversity conservation, rather than urban development.

The impact also varies by species with different dispersal capabilities (Figure 5). Urban expansion seems to have larger negative effects to species with long dispersal capacity, which is contrary to findings in previous studies suggesting that such impact declined with the rise in dispersal capacity [52,53]. However, the previous studies did not account for whether a patch could be viewed as a habitat for a given species or not (i.e., the patch size should be larger than the species home range size), hence the trade-off between the intra-patch and the inter-patch connectivity (i.e., lower intra-patch connectivity provided by fewer habitats vs. higher inter-patch connectivity provided by stronger dispersal ability) was ignored. In our analysed landscape, the higher connectivity decline of long dispersers mainly results from the habitat loss, rather than from the barrier effect and the loss of stepping-stones habitat patches.

Spatiotemporal connectivity and spatial-only connectivity have significantly different responses to urban expansion and the resulting land-use change. Spatial-only connectivity has an immediate rise or fall when habitats are gained or lost (e.g., at 2010 & the three scenarios at 2020). However, the spatiotemporal connectivity may still increase (e.g., ECA_{st} in the period from 2010 to 2020; Figure 5) despite the habitat shrinkage in the period (Table 3). This can be explained by the delayed biodiversity responses to land-use change, which are commonly studied in extinction debt research [54,55]. Landscape connectivity is recognised to play a crucial role in affecting relaxation times (i.e., time lags) and their trajectories [56]. By incorporating temporal connections that do not exist from the perspective of the purely spatial connectivity, habitats are linked in a spatiotemporal fashion. Such dynamics are essential to acknowledge the contribution of connectivity to relaxation times and to capture the lag effect, which cannot be embodied in purely spatial connectivity models. Additionally, in a rapidly changing landscape, more spatiotemporal connected habitat mosaics may be created [17], which can enhance rescue effects [57] or restore local extinctions with recolonizations [55]. Hence, we demonstrated that, the connectivity decline and the risk of species extinction due to urban expansion may be overestimated by previous studies using temporally static connectivity models. The spatiotemporal connectivity can better reflect the lag effect, can exert influences on duration and trajectory of relaxation time, and can help to prevent local and/or global species extinctions through the contribution of temporal connectivity, especially in landscapes where dramatic habitat loss occurs, such as those experiencing rapid urbanization ones.

The significance of the spatiotemporal connectivity is directly affected by the net habitat amount change. We found that the spatiotemporal connectivity exceeds the spatial-only connectivity for the net habitat loss cases, whereas the opposite is true for the net habitat gain cases. This finding agrees with Martensen, Saura [17]. The relationship could be described by a linear model, in which every 1% of net habitat loss or gain could result in nearly 0.5% of spatiotemporal connectivity positive or negative contribution compared with spatial-only connectivity. We further investigated why the spatiotemporal connectivity ends up having no additional contribution when additional habitats are gained, and found that the reason lies in the difference between the spatiotemporally and the spatially intra-patch connectivity. The intra-patch connectivity for the spatiotemporal case is only provided “Stable” patches (see Methods), while for the spatial-only case, it is provided by all patches in the end of term, which include both “Stable” and “Gain” patches in the net habitat gain landscapes. Therefore, the latter case can provide more intra-patch connectivity and further lead to a higher estimated connectivity.

Moreover, we noticed that the spatiotemporal connectivity mainly contributes to improving connectivity through the stepping-stone effect (PC_{step}^{st} , see Figure 8). This

shows that most of spatiotemporal connections occur through habitats that are gained or lost in temporal steps and are used as stepping-stones in temporal paths [58]. This also explains why the spatiotemporal connectivity has higher contribution for long dispersers than for short dispersers, as long dispersers experience more dramatic habitat change in our case, so that the increasing stepping-stone effect over time boosts a higher overall spatiotemporal connectivity.

The spatiotemporal connectivity model should have broad applications in any dynamic landscape, while it also has some limitations. Future research that investigates how to incorporate other species traits, such as longevity, into the current spatiotemporal model will be desired. For example, a long-lived species may better take advantage of spatiotemporal links across the habitat network than another short-lived species, as the former have a longer temporal overlap with patch persistence in its lifespan than the latter.

5. Conclusions

To conclude, our results demonstrated that previous studies had overestimated the impact of urban expansion to landscape connectivity. The analysis also highlighted the need to shift from the spatial-only perspective to the spatiotemporal perspective, as it helps to incorporate the delayed biodiversity response to land-use change in practical urban planning. The spatiotemporal connectivity should find its place in many future sustainable studies, such as biodiversity conservation in diverse climate scenarios.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/land10040359/s1>. Table S1: The terminology, the formula and the description in the FLUE model, Table S2: Movement cost characterizing the impedance effect of each land-use type.

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References

1. Seto, K.C.; Guneralp, B.; Hutyra, L.R. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 16083–16088. [[CrossRef](#)] [[PubMed](#)]
2. Sala, O.E.; Chapin, F.S., 3rd; Armesto, J.J.; Berlow, E.; Bloomfield, J.; Dirzo, R.; Huber-Sanwald, E.; Huenneke, L.F.; Jackson, R.B.; Kinzig, A.; et al. Global biodiversity scenarios for the year 2100. *Science* **2000**, *287*, 1770–1774. [[CrossRef](#)]
3. McKinney, M.L. Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **2006**, *127*, 247–260. [[CrossRef](#)]
4. Bauer, S.; Hoye, B.J. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **2014**, *344*, 1242552. [[CrossRef](#)]
5. Allen, C.R.; Angeler, D.G.; Cumming, G.S.; Folke, C.; Twidwell, D.; Uden, D.R. Quantifying spatial resilience. *J. Appl. Ecol.* **2016**, *53*, 625–635. [[CrossRef](#)]
6. Perkl, R.; Norman, L.M.; Mitchell, D.; Feller, M.; Smith, G.; Wilson, N.R. Urban growth and landscape connectivity threats assessment at Saguaro National Park, Arizona, USA. *J. Land Use Sci.* **2018**. [[CrossRef](#)]
7. Troupin, D.; Carmel, Y. Landscape patterns of development under two alternative scenarios: Implications for conservation. *Land Use Policy* **2016**, *54*, 221–234. [[CrossRef](#)]

8. Huang, Y.; Huang, J.-L.; Liao, T.-J.; Liang, X.; Tian, H. Simulating urban expansion and its impact on functional connectivity in the Three Gorges Reservoir Area. *Sci. Total Environ.* **2018**, *643*, 1553–1561. [CrossRef]
9. Bierwagen, B.G. Connectivity in urbanizing landscapes: The importance of habitat configuration, urban area size, and dispersal. *Urban. Ecosyst.* **2006**, *10*, 29–42. [CrossRef]
10. Mitsova, D.; Shuster, W.; Wang, X.H. A cellular automata model of land cover change to integrate urban growth with open space conservation. *Landsc. Urban. Plann.* **2011**, *99*, 141–153. [CrossRef]
11. Grafius, D.R.; Corstanje, R.; Siriwardena, G.M.; Plummer, K.E.; Harris, J.A. A bird's eye view: Using circuit theory to study urban landscape connectivity for birds. *Landsc. Ecol.* **2017**, *32*, 1771–1787. [CrossRef]
12. Huang, J.L.; He, J.H.; Liu, D.F.; Li, C.; Qian, J. An ex-post evaluation approach to assess the impacts of accomplished urban structure shift on landscape connectivity. *Sci. Total Environ.* **2018**, *622*, 1143–1152. [CrossRef]
13. Aguilera, F.; Valenzuela, L.M.; Botequilha-Leitao, A. Landscape metrics in the analysis of urban land use patterns: A case study in a Spanish metropolitan area. *Landsc. Urban. Plann.* **2011**, *99*, 226–238. [CrossRef]
14. Marulli, J.; Mallarach, J.M. A GIS methodology for assessing ecological connectivity: Application to the Barcelona Metropolitan Area. *Landsc. Urban. Plann.* **2005**, *71*, 243–262. [CrossRef]
15. Tannier, C.; Bourgeois, M.; Houot, H.; Foltete, J.C. Impact of urban developments on the functional connectivity of forested habitats: A joint contribution of advanced urban models and landscape graphs. *Land Use Policy* **2016**, *52*, 76–91. [CrossRef]
16. Huang, J.L.; Andreollo, M.; Martensen, A.C.; Saura, S.; Liu, D.F.; He, J.H.; Fortin, M.J. Importance of spatio-temporal connectivity to maintain species experiencing range shifts. *Ecography* **2020**, *43*, 591–603. [CrossRef]
17. Martensen, A.C.; Saura, S.; Fortin, M.-J. Spatio-temporal connectivity: Assessing the amount of reachable habitat in dynamic landscapes. *Methods Ecol. Evol.* **2017**, *8*, 1253–1264. [CrossRef]
18. Saura, S.; Bodin, Ö.; Fortin, M.-J. Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *J. Appl. Ecol.* **2014**, *51*, 171–182. [CrossRef]
19. Watts, A.; Schlichting, P.; Billerman, S.; Jesmer, B.; Micheletti, S.; Fortin, M.-J.; Funk, C.; Hapeman, P.; Muths, E.; Murphy, M. How spatio-temporal habitat connectivity affects amphibian genetic structure. *Front. Genet.* **2015**, *6*. [CrossRef]
20. Hanski, I.; Ovaskainen, O. The metapopulation capacity of a fragmented landscape. *Nature* **2000**, *404*, 755–758. [CrossRef]
21. Moilanen, A.; Nieminen, M. Simple Connectivity Measures in Spatial Ecology. *Ecology* **2002**, *83*, 1131–1145. [CrossRef]
22. Pascual-Hortal, L.; Saura, S. Comparison and development of new graph-based landscape connectivity indices: Towards the prioritization of habitat patches and corridors for conservation. *Landsc. Ecol.* **2006**, *21*, 959–967. [CrossRef]
23. Saura, S.; Pascual-Hortal, L. A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landsc. Urban. Plann.* **2007**, *83*, 91–103. [CrossRef]
24. Mui, A.B.; Caverhill, B.; Johnson, B.; Fortin, M.J.; He, Y.H. Using multiple metrics to estimate seasonal landscape connectivity for Blanding's turtles (*Emydoidea blandingii*) in a fragmented landscape. *Landsc. Ecol.* **2017**, *32*, 531–546. [CrossRef]
25. Wu, J.G.; Huang, J.H.; Han, X.G.; Xie, Z.Q.; Gao, X.M. Three-Gorges Dam—Experiment in habitat fragmentation? *Science* **2003**, *300*, 1239–1240. [CrossRef] [PubMed]
26. The State Council of the People's Republic of China. *The Notification on Adjusting the Classification Standard of Urban Size*; The State Council of the People's Republic of China: Beijing, China, 2014.
27. Xu, X.; Yang, G.; Tan, Y.; Liu, J.; Hu, H. Ecosystem services trade-offs and determinants in China's Yangtze River Economic Belt from 2000 to 2015. *Sci. Total Environ.* **2018**, *634*, 1601–1614. [CrossRef] [PubMed]
28. Hua, F.; Wang, X.; Zheng, X.; Fisher, B.; Wang, L.; Zhu, J.; Tang, Y.; Yu, D.W.; Wilcove, D.S. Opportunities for biodiversity gains under the world's largest reforestation programme. *Nat. Commun.* **2016**, *7*, 12717. [CrossRef]
29. Rabinowitz, A.R. Behavior and movements of sympatric civet species in HUIAI-KHA-KHAENG Wildlife Sanctuary, Thailand. *J. Zool.* **1991**, *223*, 281–298. [CrossRef]
30. Grassman, L.I.; Tewes, M.E.; Silvy, N.J.; Kreetiyutanont, K. Spatial organization and diet of the leopard cat (*Prionailurus bengalensis*) in north-central Thailand. *J. Zool.* **2005**, *266*, 45–54. [CrossRef]
31. Odden, M.; Athreya, V.; Rattan, S.; Linnell, J.D.C. Adaptable Neighbours: Movement Patterns of GPS-Collared Leopards in Human Dominated Landscapes in India. *PLoS ONE* **2014**, *9*. [CrossRef]
32. Bowman, J.; Jaeger, J.A.G.; Fahrig, L. Dispersal distance of mammals is proportional to home range size. *Ecology* **2002**, *83*, 2049–2055. [CrossRef]
33. Jarvis, A.; Reuter, H.I.; Nelson, A.; Guevara, E. Hole-filled Seamless SRTM Data V4. International Centre for Tropical Agriculture (CIAT). Available online: <http://srtm.csi.cgiar.org> (accessed on 19 December 2020).
34. Center for International Earth Science Information Network—CIESIN—Columbia University; Information Technology Outreach Services—ITOS—University of Georgia. *Global Roads Open Access Data Set, Version 1 (gROADSv1)*; NASA Socioeconomic Data and Applications Center (SEDAC): Palisades, NY, USA, 2013.
35. Liu, X.P.; Liang, X.; Li, X.; Xu, X.C.; Ou, J.P.; Chen, Y.M.; Li, S.Y.; Wang, S.J.; Pei, F.S. A future land use simulation model (FLUS) for simulating multiple land use scenarios by coupling human and natural effects. *Landsc. Urban. Plan.* **2017**, *168*, 94–116. [CrossRef]
36. Openshaw, S.; Openshaw, C. *Artificial Intelligence in Geography*; John Wiley & Sons: Chichester, UK, 1997.
37. Lin, Y.P.; Chu, H.J.; Wu, C.F.; Verburg, P.H. Predictive ability of logistic regression, auto-logistic regression and neural network models in empirical land-use change modeling—A case study. *Int. J. Geogr. Inf. Sci.* **2011**, *25*, 65–87. [CrossRef]

38. Li, X.; Chen, G.; Liu, X.; Liang, X.; Wang, S.; Chen, Y.; Pei, F.; Xu, X. A New Global Land-Use and Land-Cover Change Product at a 1-km Resolution for 2010 to 2100 Based on Human–Environment Interactions. *Ann. Am. Assoc. Geogr.* **2017**, *107*, 1040–1059. [[CrossRef](#)]
39. Liang, X.; Liu, X.P.; Li, D.; Zhao, H.; Chen, G.Z. Urban growth simulation by incorporating planning policies into a CA-based future land-use simulation model. *Int. J. Geogr. Inf. Sci.* **2018**, *32*, 2294–2316. [[CrossRef](#)]
40. He, J.; Li, C.; Yu, Y.; Liu, Y.; Huang, J. Measuring urban spatial interaction in Wuhan Urban Agglomeration, Central China: A spatially explicit approach. *Sustain. Cities Soc.* **2017**, *32*, 569–583. [[CrossRef](#)]
41. Hanley, J.A.; Mcneil, B.J. The Meaning and Use of the Area under a Receiver Operating Characteristic (Roc) Curve. *Radiology* **1982**, *143*, 29–36. [[CrossRef](#)]
42. Vliet, J.V.; Bregt, A.K.; Hagen-Zanker, A. Revisiting Kappa to account for change in the accuracy assessment of land-use change models. *Ecol. Model.* **2011**, *222*, 1367–1375. [[CrossRef](#)]
43. Visser, H.; de Nijs, T. The Map Comparison Kit. *Environ. Model. Softw.* **2006**, *21*, 346–358. [[CrossRef](#)]
44. Bishop-Taylor, R.; Tulbure, M.G.; Broich, M. Surface-water dynamics and land use influence landscape connectivity across a major dryland region. *Ecol. Appl.* **2017**, *27*, 1124–1137. [[CrossRef](#)]
45. Ruiz, L.; Parikh, N.; Heintzman, L.J.; Collins, S.D.; Starr, S.M.; Wright, C.K.; Henebry, G.M.; van Gestel, N.; McIntyre, N.E. Dynamic connectivity of temporary wetlands in the southern Great Plains. *Landsc. Ecol.* **2014**, *29*, 507–516. [[CrossRef](#)]
46. Gurrutxaga, M.; Rubio, L.; Saura, S. Key connectors in protected forest area networks and the impact of highways: A transnational case study from the Cantabrian Range to the Western Alps (SW Europe). *Landsc. Urban. Plann.* **2011**, *101*, 310–320. [[CrossRef](#)]
47. McRae, B.H.; Kavanagh, D.M. *Linkage Mapper Connectivity Analysis Software*; The Nature Conservancy: Seattle, WA, USA, 2011.
48. Dale, M.R.T.; Fortin, M.J. From Graphs to Spatial Graphs. *Annu. Rev. Ecol. Evol. Syst.* **2010**, *41*, 21–38. [[CrossRef](#)]
49. Saura, S.; Estreguil, C.; Mouton, C.; Rodríguez-Freire, M. Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). *Ecol. Indic.* **2011**, *11*, 407–416. [[CrossRef](#)]
50. Saura, S.; Rubio, L. A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography* **2010**, *33*, 523–537. [[CrossRef](#)]
51. Saura, S. Node self-connections in network metrics. *Ecol. Lett.* **2018**, *21*, 319–320. [[CrossRef](#)]
52. Fu, W.; Liu, S.; Degloria, S.D.; Dong, S.; Beazley, R. Characterizing the “fragmentation–barrier” effect of road networks on landscape connectivity: A case study in Xishuangbanna, Southwest China. *Landsc. Urban. Plann.* **2010**, *95*, 122–129. [[CrossRef](#)]
53. Liu, S.; Dong, Y.; Deng, L.; Liu, Q.; Zhao, H.; Dong, S. Forest fragmentation and landscape connectivity change associated with road network extension and city expansion: A case study in the Lancang River Valley. *Ecol. Indic.* **2014**, *36*, 160–168. [[CrossRef](#)]
54. Essl, F.; Dullinger, S.; Rabitsch, W.; Hulme, P.E.; Pysek, P.; Wilson, J.R.; Richardson, D.M. Delayed biodiversity change: No time to waste. *Trends Ecol. Evol.* **2015**, *30*, 375–378. [[CrossRef](#)]
55. Kuussaari, M.; Bommarco, R.; Heikkinen, R.K.; Helm, A.; Krauss, J.; Lindborg, R.; Ockinger, E.; Partel, M.; Pino, J.; Roda, F.; et al. Extinction debt: A challenge for biodiversity conservation. *Trends Ecol. Evol.* **2009**, *24*, 564–571. [[CrossRef](#)]
56. Jackson, S.T.; Sax, D.F. Balancing biodiversity in a changing environment: Extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* **2010**, *25*, 153–160. [[CrossRef](#)] [[PubMed](#)]
57. Brown, J.H.; Kodricbrown, A. Turnover Rates in Insular Biogeography—Effect of Immigration on Extinction. *Ecology* **1977**, *58*, 445–449. [[CrossRef](#)]
58. Wimberly, M.C. Species dynamics in disturbed landscapes: When does a shifting habitat mosaic enhance connectivity? *Landsc. Ecol.* **2006**, *21*, 35–46. [[CrossRef](#)]