

Network Environ Analysis of Spatial Arrangement for Reserves in Wuyishan Nature Reserve, China

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ABSTRACT. The spatial arrangement of reserves within a network is critical to the long-term persistence of dispersing species. In this paper, based on network environ analysis, an approach is presented to explicitly measure such ecological function, in which the dispersal-based interactions between reserves are considered from a holistic view by exploring not only species' direct dispersals but also their indirect ones. The proposed method first defines the ecological function of spatial arrangement of reserves as the probability that a species will survive for long time in a reserve network, and then expands this function by taking the reserve loss into account when evaluating a species' extinction probability at each reserve. A case study for *L. nycthemera* and *M. thibetana* from Wuyishan Nature Reserve, Fujian Province, China, is further conducted. The highest probabilities of long-term survival are identified for both species in the reserve networks that contain several migrations with high successful dispersal probability. In addition, the path number of each common reserve under neighboring scenarios is found to be influenced by the changes of direct dispersal, from which the criteria for protecting and optimizing the spatial configuration of reserves in a nature reserve are derived. For Wuyishan Nature Reserve, these criteria may act as important bases to restrict and guide the development of tourism of surrounding cities and the socio-economic activities of local residents. It is concluded that the proposed method can provide an effective way to examine the ecological function of spatial arrangement of reserve network and contribute to species' long-term persistence in nature reserves.

Keywords: network environ analysis, reserve network, holistic spatial arrangement, long-term persistence, extinction probability, Wuyishan Nature Reserve

1. Introduction

Due to increasing awareness of biodiversity loss (Zhang et al., 2009; Cao and Huang, 2010a, b; Huang et al., 2010), a network of conservation reserves, where lands are protected and managed to maintain species for long, has attracted significant attentions over the past two decades. It is a simple yet effective way to conserve biological diversity (Polasky et al., 2001). However, despite of the conservation need, there are very few studies focusing on reserve networks in nature reserves, within which some emphasize the appropriate representation of the full spectrum of species or surrogates of interest (Wessels et al., 1999; Kati et al., 2004), while the others take the spatial demand of species into account in an implicit manner when satisfying the usual species representation requirement (Zafra-Calvo et al., 2010). The ecological function of spatial arrangement of reserves contributing to species' long-term persistence is therefore often ignored, although it plays an important role by allowing

dispersal (Rodrigues et al., 2000; Cabeza and Moilanen, 2003), especially for a region at small scale (Cabeza et al., 2004a).

The ecological function of spatial arrangement of reserves has been studied in an explicit or implicit way, with or without considering species' specific dispersal ability, respectively. Without any measurement of species' specific dispersal ability, the ecological function of spatial arrangement of reserves is supposed to be implicitly enhanced by keeping sites close together. It will result in aggregated reserves and compact reserve networks that are likely to be more beneficial to species' movements and smaller in the chance of extinctions than scattered ones (Cabeza and Moilanen, 2003). In order to acquire compact spatial configuration, a broad range of implicit spatial criteria has been developed, such as performing adjacent rule (Lombard et al., 1997; Briers, 2002; Fuller et al., 2006; Zafra-Calvo et al., 2010), minimizing the boundary length or a linear combination of boundary length and total reserve area (McDonnell et al., 2002; Fischer and Church, 2003; Onal and Briers, 2003; Cabeza et al., 2004b), minimizing the maximum intersite distance or the sum of pairwise distances among all planning sites (Onal and Briers, 2002), measuring the total distance between neighboring sites (Onal and Briers, 2005; Onal and Wang, 2008) and the summed distance to mandatory sites (Alagador and Cerdeira, 2007), maximizing the sum of the inverse distances

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between pairs of sites (Rothley, 1999), enforcing buffers surrounding selected critical sites (Williams and ReVelle, 1998), keeping sites occurring within the stated proximity distance or the dispersal range of species (Briers, 2002; Van Langevelde et al., 2002; Williams, 2008; Cerdeira et al., 2010) and maximizing the connectivity (Briers, 2002; Siitonen et al., 2003), which are independent of any species' specific dispersal ability. The others, e.g., Van Langevelde et al. (2002), Cerdeira et al. (2005), Fuller et al. (2006) and Onal and Briers (2006), have attempted to fully connect the reserve network. However, it should be noted that the use of these implicit spatial criteria cannot give any definite answer to the important question: how these aggregated or connected reserves are correlated with the persistence of each specific species when considering the variation in the dispersal characteristics of the species? In other words, while successful dispersals between reserves are assumed to be promoted, the ecological function of the distribution pattern of these reserves contributing to each specific species' long-term persistence is still not clear.

In contrast with the adoption of implicit spatial criteria, several studies (Moilanen and Cabeza, 2002; Cabeza, 2003; Moilanen et al., 2005; Van Teeffelen et al., 2006; Rayfield et al., 2009; Bauer et al., 2010) apply species-specific connectivity, which explicitly accounts for species' ability to disperse, as the measure of species' spatial requirements. These studies assume that the spatial location of reserves performs a maximum ecological contribution to the long-term survival of targeted species by maximizing connectivity between pairwise sites, while another study makes use of the probabilities of dispersals between neighboring patches to establish a functional role of spatial arrangements of reserve sites (Jiang et al., 2007). With these two approaches, the ecological function of spatial configuration of reserves facilitating species' long-term persistence is explicitly evaluated by measuring its capacity to maintain species at each site through dispersals from all other or neighboring ones within a reserve network. Thus, for any reserve consisted of contiguous sites, only the direct species dispersals from other or neighboring reserves are considered to support species' long-term survival in it. The fact that when a species migrates from one reserve to another, it may not disperse to the target reserve directly, particularly for reserves that are non-neighboring or far apart, but instead move along an indirect route by taking other reserves as stepping stones, is overlooked in these approaches.

In this study, we present a new approach, in which the extent that the spatial arrangement of reserves favors the permanent survival of a targeted species is assessed by emphasizing the network interactions, embracing not only the direct dispersals but also the indirect ones between reserves. Moreover, compared to the explicit methods outlined above, the proposed method expands the ecological function of spatial arrangement of reserves contributing to the species' long-term persistence by taking into account the reserve loss.

For a reserve network, the network environ analysis (NEA) is used to explore the dispersal-based interactions and measure the ecological function that the spatial distribution of reserves presents to the long-term persistence of a specific species. The

basic concepts of NEA associated with the reserve network and the new holistic assessment approach are introduced in Section 2. In Section 3, we list the main calculation results. Section 4 are the discussions and prospects. Finally, we finish, in Section 5, with a range of conclusions.

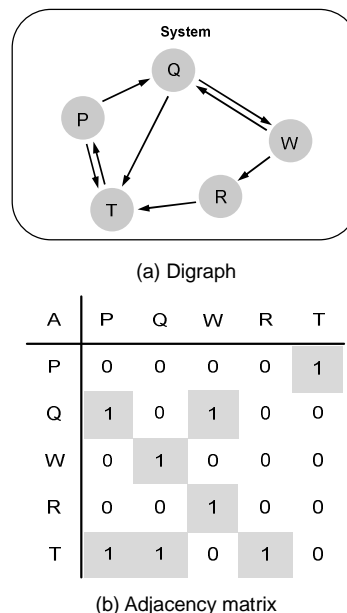


Figure 1. Two isomorphic representations of an example interconnected system.

2. Methods

2.1. Reserve Network Description Based on Network Environ Analysis

NEA is a systematic method developed as an extension of the classic input-output idea and used to investigate interconnected systems conceptualized from the network perspective. System boundary, interacting objects and flow currency should be determined to construct a system model for using NEA (Fath et al., 2007). The interconnected structure can be represented by digraphs and isomorphic matrices (see Figure 1), which are suitable to describe the reserve network within a given region. Corresponding to the network digraph, reserves selected to protect a dispersing species can be regarded as nodes. The species disperses between reserves are the currencies for exchanging, and arcs can be defined by dispersal probabilities, expressing the probabilities that individuals in one reserve could directly reach another. Thus a reserve network can be viewed as a system formed by a collection of interconnected nodes. Boundary of this reserve system is clear once study area is determined. The system is isolated from external environment if there is no species transaction between them. In this system, reserves exhibit three spatial properties related to the mode of species turnover, serving as dispersal sources, sinks for receiving individuals that come from other reserves, and stepping stones to connect reserves. Based on these spatial properties, species in a reserve could disperse to any other reserve directly or indirectly

by taking different paths with different lengths.

In NEA, a specific object's environ refers to its in-system environment, consisting of all the other objects in the system with which that object directly and indirectly interacts (Fath and Patten, 1998, 1999; Bata et al., 2007). Therefore, it is a holistic way to analyze and evaluate how objects are tied to each other. Environ of each object can be divided into two parts, input environ and output environ. For a reserve network, the input environ of a reserve consists of all reserves that offer individuals to it directly or indirectly, and the output environ of a reserve is composed of reserves that receive individuals departing from that reserve.

2.2. Holistic Assessment Method

We assume that, in a network system of N reserves, the dispersal of a species between any pair of reserves is independent of the movements of that species being implemented between other reserves. The contribution of the spatial arrangement of reserves to species' persistence is examined from two aspects. On the one hand, the extinction of a species at any reserve is assumed to occur on condition that no individual leaves from the other reserves can reach that reserve, implying a species inhabiting a reserve could exist for long only if there are successful migrations to the reserve. On the other hand, once a reserve no longer suits the survival of a species due to a stochastic event, such as natural disaster, the individuals live in it will keep in existence if they can disperse to the other reserves, otherwise extinction happens. These assumptions indicate that an isolated reserve would have no ability to maintain a species in the long term, which may be a little bit pessimistic if the scale of the reserve is large enough. However, the assumption is valid since the inner structure of the reserve is omitted in the current study to evaluate the spatial arrangement of reserves. Consequently, the extinction of a species at any reserve depends upon the special relationship the reserve has with the other reserves. The worse this relationship is, the smaller the likelihood that a species survives for long, and the worse the spatial arrangement is.

Probability theory is applied to describe the process of species dispersal between the pair of reserves. The modeling framework implies that local individuals at one reserve can not only directly move to other reserves, but also disperse along indirect routes by reserves as stepping stones and the movements as continuous processes.

By NEA, if dispersals between reserves are independent, the extinction probability p_i of a species at reserve i , considered as the special relationship of the reserve with others, can be defined as the arithmetic product of the probability of no immigration from its input environ E_i^{in} and the probability of no emigration to its output environ E_i^{out} :

$$p_i = \prod_{j \in E_i^{in}} (1 - p_{ij}) \times \prod_{k \in E_i^{out}} (1 - p_{ki}) \quad (1)$$

in which we use the input probability $1 - p_{ij}$ and the output probability $1 - p_{ki}$ to represent the contribution of each reserve in

either the input environ or the output environ of reserve i . j and k denote the reserves included in the input environ and output environ of reserve i respectively. p_{ij} describes the probability that individuals from reserve j succeed in arriving reserve i while p_{ki} expresses the successful dispersal probability from reserve i to reserve k . For the j_{th} or k_{th} reserve, there might be several different paths of dispersing lengths. Thus the extinction probability p_i should be rewritten as:

$$p_i = \prod_{j \in E_i^{in}} [(1 - p_{ij}) \times \prod (1 - p_{ij}^2) \times \prod (1 - p_{ij}^3) \times \dots \times \prod (1 - p_{ij}^m) \times \dots] \times \prod_{k \in E_i^{out}} [(1 - p_{ki}) \times \prod (1 - p_{ki}^2) \times \prod (1 - p_{ki}^3) \times \dots \times \prod (1 - p_{ki}^m) \times \dots] \quad (2)$$

where m is the path length. If $m = 1$, p_{ij} and p_{ki} refer to the probabilities of direct movements between the i_{th} reserve and the j_{th} or k_{th} reserves. If $m > 1$, p_{ij}^m and p_{ki}^m denote the dispersal probabilities through indirect paths of length of m . Note that, according to the assumption that the i_{th} reserve does not suit the survival of a species any more, the indirect paths that take the i_{th} reserve as stepping stone should be excluded from the computation of p_{ki}^m .

The extinction probability of a species across the whole reserve network (EPN), which considers the extinction probabilities at all the reserves, can be expressed as:

$$EPN = \prod_{i \in N} p_i \quad (3)$$

Therefore, the long-term survival probability within the network (LTSPN) supported by the spatial arrangement of reserves can be calculated by:

$$LTSPN = 1 - EPN = 1 - \prod_{i \in N} p_i \quad (4)$$

The direct dispersal probability between pair of reserves is usually calculated as a more or less complex function of the "moving cost", which is generally thought to be closely related to the dispersal distance. Thus some studies directly adopt the exponential function of dispersal distance to characterize the feasibility of direct dispersal (Bunn et al., 2000; Urban and Keitt, 2001; Saura and Hortal, 2007), while the others consider additional factors such as the effective area or the state of occupancy of the sites (Vos et al., 2001; Moilanen and Cabeza, 2002; Cabeza, 2003) and the emigration rate (Moilanen and Cabeza, 2002; Moilanen et al., 2005; Jiang et al., 2007) to simulate the process. In this study, we apply an exponential equation to quantify the dispersal probability p_{ij} that individuals from the j_{th} reserve succeed in arriving the i_{th} reserve directly:

$$p_{ij} = \frac{a_j}{a_{total}} \times \frac{s_j}{s_{max}} \times e^{(-\alpha d_{ij})} \quad (5)$$

in which a_j and s_j denote the area and the habitat suitability of the source j_{th} reserve, respectively, a_{total} is the total area of the reserve network, s_{max} is the maximum reserve suitability value in the network, and $a_j/a_{total} \times s_j/s_{max}$ is used to describe the influence of population size at the j_{th} reserve on direct dispersal probability p_{ij} . It is generally accepted that patches of equal quality will have a carrying capacity which is directly related to their area (Bellamy et al., 1996; Zuidema et al., 1996; Lee et al., 2001). The effect of population size is usually represented as of patch area when there is not complete information about population size (Bunn et al., 2000; Vos et al., 2001; Moilanen and Cabeza, 2002). But, to our knowledge, habitat suitability has not been previously used in the same context. It should be an important factor to consider because of the obvious dependent manner between the quality of a reserve for species' living and its carrying capacity. The s_j is calculated as the average of the habitat suitability values of all sites the j_{th} reserve contains. The negative exponential decay function $e^{(-\alpha d_{ij})}$ is commonly applied to obtain the distance-dependent dispersal probability for each pair of reserves, where α is a species-specific constant that has negative effect of distance on the migration and d_{ij} is the distance between the i_{th} reserve and j_{th} reserve. Following Bunn et al. (2000) and Urban and Keitt (2001), d_{ij} is calculated as the preferable distance termed as least-cost distance to ideally model the actual dispersal route the species in question covers moving from the j_{th} reserve to the i_{th} reserve by incorporating detailed characteristics of the surrounding landscape that may restrict the considered movement process. In this manner, the direct dispersal probability p_{ij} increases with area proportion a_j/a_{total} , and the relative habitat suitability s_j/s_{max} of the j_{th} reserve, while decreases with dispersal distance d_{ij} .

The dispersal probability p_{ij}^m , which denotes the individuals from the j_{th} reserve succeed in arriving the i_{th} reserve through an indirect dispersal path, can be approximated as the product of the probabilities of m direct dispersals contained in that path:

$$p_{ij}^m = p_{i_1j} \times p_{i_2i_1} \times p_{i_3i_2} \times \dots \times p_{im-1} \quad (6)$$

where $i_1, i_2, i_3, \dots, i_{m-1}$ represent the intermediate reserves passed by the indirect dispersal path of length m .

2.3. Study Area and Species

Wuyishan Nature Reserve (WYS) is located at the juncture of Wuyishan City, Jianyang City, Shaowu City and Guangze County in Fujian Province, covering a total area of 565.27 km². It is the largest and the most comprehensive semi-subtropical forest system in the southeast China, with exceptional diverse biological resources. According to the report of Wuyishan Nature Reserve General Planning Project, 2,500 rural residents lived in WYS in 2001 and their socio-economic activities have imposed negative impact on the species' genetic flow.

Two subtropical species, a large primate cercopithecidae, *Macaca thibetana*, and a montane galliformes phasianidae, *Lophura nycthemera*,

are used as indicative species in this paper. *Macaca thibetana*, known as the Chinese stump-tailed macaque, is a large gregarious mammal only found in the central and southern China. It inhabits primarily in subtropical regions of evergreen broadleaved forest, evergreen and deciduous mixed forest or deciduous broadleaved forest at altitude that ranges from 570 to 1,600 meters, but is absent from torrid areas and frigid regions (Xiong and Wang, 1988). *Lophura nycthemera* is an arboreal bird that occupies an elevation range of approximately 500 ~ 2,000 m and has been recorded primarily in the luxuriant evergreen broadleaved forest, ravine rainforest and mixed broadleaf-conifer forest, although sometimes also in bamboo forest (Gao, 1996), deciduous broadleaved forest and shrub forest (Xiong et al., 2003). According to the report of Wuyishan Nature Reserve General Planning Project, both species show widespread geographic distributions in the study area, and each has a relative more number of georeferenced occurrence localities (18 for *M. thibetana*, and 9 for *L. nycthemera*).

2.4. Modeling Species Distribution and Habitat Suitability

Besides the species occurrence records, eight principal environmental variables determined based on the above descriptions and thought to be potentially relevant to the habitats of the two species, at a resolution of 87.22m (consistent with the obtained DEM data), are collected. They are vegetation types, elevation, slope, aspect, distance to water sources, and three human-disturbing variables including distance to roads, distance to construction projects and distance to tourism. Topographic variables such as slope and aspect are chosen instead of climatic conditions due to data availability. This substitution is well explained by the fact that both targeted species prefer the sunny slope in winter but a contrary choice is made by *M. thibetana* in summer (Xiong, 1984; Xiong and Wang, 1988; Xiong et al., 2003). On the other hand, variables representing topography have a direct impact on the species presence. For *L. nycthemera*, habitats with slope below 30° are favored (Xiong et al., 2003). The variable of distance to water sources is selected because habitats close to water sources are apparently preferred by both species (Xiong, 1984; Xiong et al., 2003). Besides, these two species are both sensitive to human activities. It has been recorded that *L. nycthemera* is seldom found within the range of 1 km from roads (Cheng et al., 2009).

By comparing these environmental conditions of each site in the study area with those of sites where a target species has been observed, high probabilities of occurrence of that species are found at suitable sites, while unfavorable ones show low probabilities for the presence of the species. In the present study, the probability of occurrence at each site which, henceforth, is referred to as the suitability of the corresponding geographical location on the landscape to house each target species is estimated with a maximum entropy algorithm (Maxent) and implemented in the Maxent software package (Phillips et al., 2006). The idea of Maxent is to figure out a probability distribution of maximum entropy, subject to a set of environmental constraints. For each species, the input is the sites at which the species are recorded as present, associated

with a suitable set of environmental layers that describe the factors that likely influence the geographical distribution of the species. The resulting distribution also indicates the environmental suitability of each site for the species as a function of the given environmental variables. It gives an estimate between 0 and 1 of habitat suitability value for each site and a high value at a particular site signifies suitable conditions for that species (Phillips, 2005).

In Maxent, linear feature is used when the number of sample localities is 9, while another two features, quadratic and hinge, are added for 18. In this study, we adopt the product feature for both species to take the interactions between each pair of environmental variables into account. Random selections of the occurrence localities for *M. thibetana* and *L. nycthemera* are conducted, by which 14 and 7 of their occurrence localities are chosen respectively as training data, with the remaining 4 and 2 are set aside for testing.

2.5. Reserve Network Construction

2.5.1. Reserve Selection

Using the rarity-complementarity algorithm of the ResNet software package (Garson et al., 2002), we select the reserves to capture the representation goals (corresponding to eight scenarios) from 5 to 75% (at increments of 10%) of the total predicted occurrence across WYS of both species. An adjacency constraint (sites adjacent to ones already chosen will be privileged for selection) in ResNet, serving as a secondary rule to resolve ties among different choices if ambiguities still remain after applying complementarity in the first place, is incorporated into the selection algorithm. For each subsequent scenario, the selecting result of the preceding scenario is introduced as a set of pre-selected sites before running ResNet.

Reserves are finally determined after a second round screening based on the sites selected by the heuristic algorithm. Since the selected sites are usually discontinuous, a reserve composed of contiguous sites will be neglected if its size is less than that of the species' home range, for it is too small to supply enough space for the targeted species. As home range requirements vary between species, screening is separately conducted for *L. nycthemera* and *M. thibetana*. In order to analyze the changes between each pair of neighboring scenarios, we also designate a numerical mark to each fixed reserve where the same marks are given to the common ones identified according to their share of sites included in the preceding scenario.

2.5.2. Direct Dispersal Identification

For each species, direct dispersals, in each scenario, are diagnosed on the basis of least-cost pathways between each pair of qualified reserves. The least-cost pathways analysis contained within Arc GIS 9.3 is used. Least-cost pathways analysis presents a most likely travel route, which may be affected by characteristics of the surrounding landscape, with the minimal cost distance for a dispersing species to move between a source and a target area. A cost value is then assigned to each unselected site according to their facilitating or hindering effects on the

movement process. In this paper, cost value at the unselected site is obtained by calculating the difference between 1 and the habitat suitability for housing targeted species. Therefore, favorable habitats with lower site values express a low cost for species migration, while higher site values correspond to more difficult dispersals. Additionally, streams, roads, construction projects, tourism districts and routes are regarded as strict physical barriers that species dispersal cannot get through. With the visual results exhibited in GIS, two direct dispersals between any pair of selected reserves, which are characterized by their opposite directions and the same migration route, are eventually confirmed if the corresponding least-cost pathways do not pass across the other reserves and the lengths of least-cost pathways are worked out for calculating direct dispersal probabilities.

2.6. Spatial Arrangement Evaluation

The first stage to evaluate the spatial arrangement of a determined reserve network, i.e., the identification of input and output paths of various lengths directed to or from each reserve, requires the application of some techniques developed in NEA. According to the statements made in Section 2.2, how many and which paths between any pair of reserves need to be concerned in the evaluation procedure are obviously affected by the variable m that denotes path length. NEA studies have demonstrated that in a network system with cyclic feedback, the sum of paths of all lengths between two nodes in strongly connected components grows as m increases (Borrett et al., 2007; Fath, 2007). As for the reserve networks we construct, cycles occur even if only two reserves are bi-directional connected by species direct dispersals such that the number of paths with different lengths from a reserve to another, which are considered as input paths lead up to the latter one, diverges as $m \rightarrow \infty$. To facilitate the calculation, therefore, a cut-off value, which is 3 in this paper, is assigned to the variable m before evaluating the spatial arrangement of reserve networks.

Enumerating paths of various lengths between nodes is a basic path analysis problem in NEA, for which the analysis is performed on the adjacency matrix of a network model and the q -th power matrix is generally used to give the number of paths of length q between two nodes (Fath and Borrett, 2006). For each species, with the purpose of finding input and output paths of ordered lengths directed to or from each reserve, an adjacency matrix whose rows and columns are indexed by the selected reserves and whose elements take values 1 if a species direct dispersal from column reserve to row reserve exists is created for each determined reserve network under different scenarios. From power matrixes corresponding to path length of 1, 2, and 3, the reserves that act as dispersal sources or terminuses in the input environ or output environ of a specific reserve are respectively identified as well as the numbers of input or output paths directed from or to these reserves. Specially, before doing a matrix multiplication to determine the number of two- or three- section output paths from a specific reserve, values of the adjacency matrix elements, which represent direct dispersals to this reserve, are transformed into 0 to remove the paths that may take this reserve as stepping stones. The reserves passed by each path, i.e., the detailed routes are there-

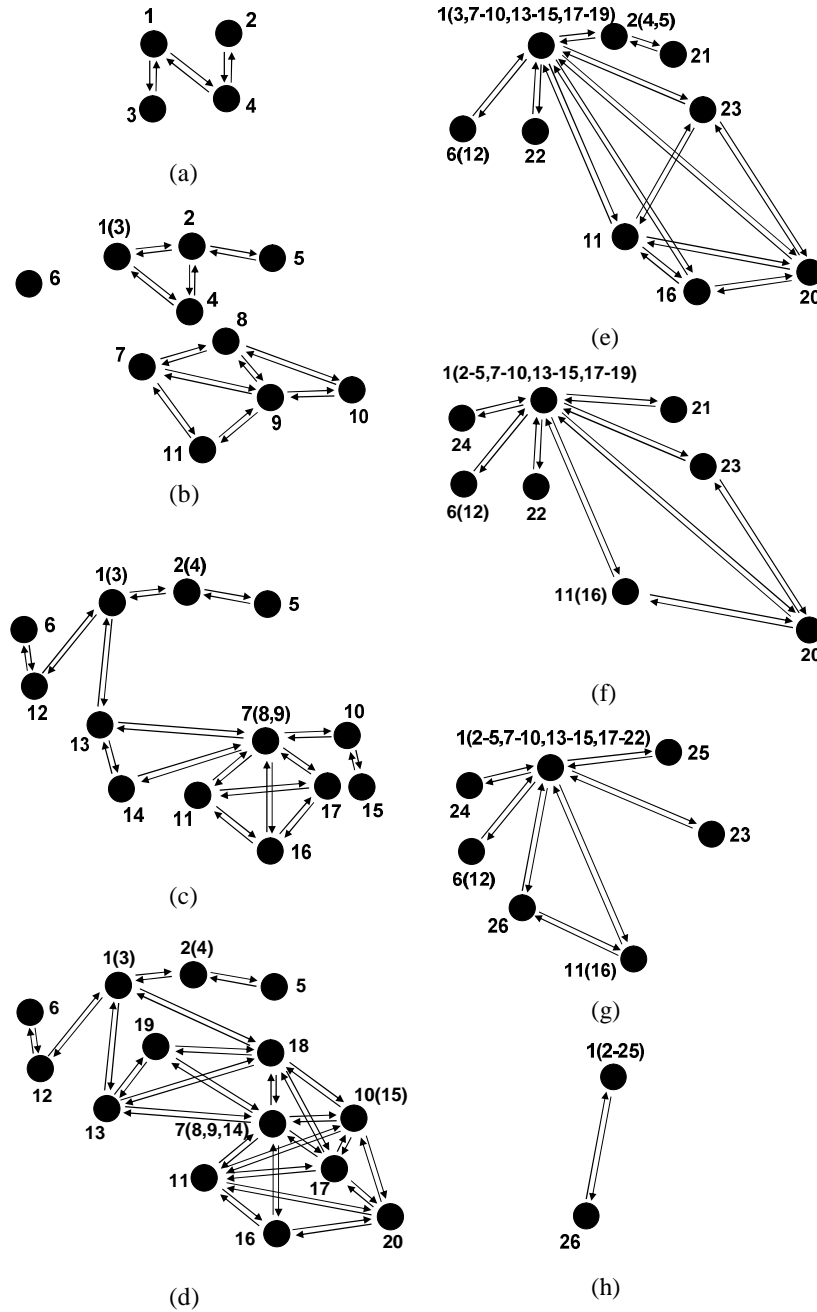


Figure 2. Reserve networks for *L. nycthemera* in eight different representation scenarios: (a) 5%, (b) 15%, (c) 25%, (d) 35%, (e) 45%, (f) 55%, (g) 65%, and (h) 75%.

by searched out with the help of isomorphic digraph so that the ecological function of spatial arrangement of a determined reserve network for a targeted species can be evaluated by the holistic approach.

According to the proposed approach, more paths, no matter input or output, means more chances a species may survival for long in a reserve or a reserve network. In this study, we are also interested in: (1) comparing the number of paths a specific reserve, especially for the common ones, or reserve network

has between the neighboring scenarios for each species, and (2) probing into the causes that may be related with the changes between corresponding reserve networks.

3. Results

3.1. Reserve Networks for Each Species

The numbers of reserves, direct dispersals and structures of networks for each species under different representation

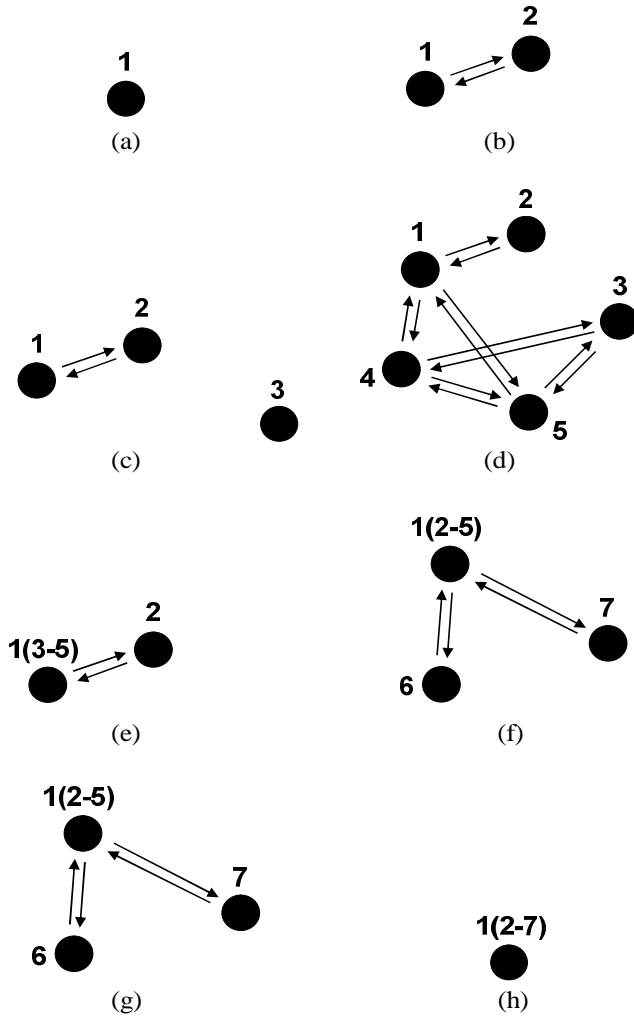


Figure 3. Reserve networks for *M. thibetana* in eight different representation scenarios: (a) 5%, (b) 15%, (c) 25%, (d) 35%, (e) 45%, (f) 55%, (g) 65%, and (h) 75%.

scenarios are respectively given in Figures 2 and 3. By initializing the ResNet with rarity and adjacency for the 5% scenario and selecting reserves in sequence for the other scenarios with an additional pre-selecting constraint, the number of reserves that are finally screened by species' home range varies from 2 (for the 75% scenario) to 14 (for the 35% scenario) for *L. nycthemera* while changes from 1 (for the 5% and 75% scenarios) to 5 (for the 35% scenario) for *M. thibetana*. Furthermore, the number of direct dispersals which is identified based on the least-cost pathways analysis between reserves ranges from 2 (for the 75% scenario) to 52 (for the 35% scenario) for *L. nycthemera* while shows a difference from 0 (for the 5% and 75% scenarios) to 12 (for the 35% scenario) for *M. thibetana*.

For both species, comparing with a preceding scenario, merger between original reserves that results in the reduction of existing direct dispersals, emergence of new reserves that may bring new direct dispersals, and increment or loss of direct dispersals between original reserves, are the three potential causes

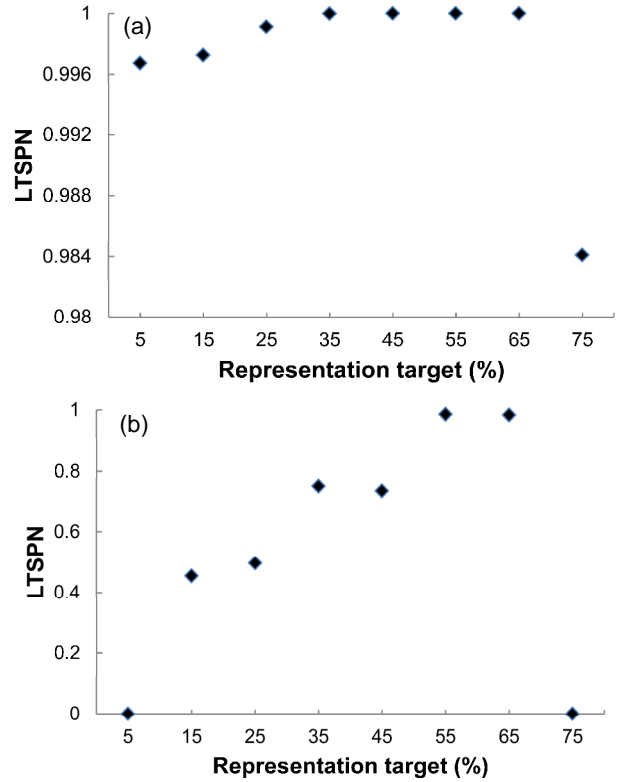


Figure 4. LTSPNs in eight different representation scenarios for species: (a) *L. nycthemera* and (b) *M. thibetana*.

that may impact the formation of the reserve network under the subsequent scenario (Figures 2 and 3).

3.2. LTSPN for Each Species

Figure 4 presents LTSPN for each species under different representation scenarios. The highest values of LTSPN are both in the 55% scenario for the two species and the lowest value obtained in the 75% scenario for *L. nycthemera*, while values of 0 are given to the networks with only one reserve for *M. thibetana* under the 5% and 75% scenarios.

For a reserve network, the number of paths has a positive impact on the evaluation of LTSPN since it is assumed that more paths imply more chances a species has to live for long. By comparing the LTSPN value with the path number in each scenario, as shown in Figure 5, the positive relationship is clearly revealed under the 5, 15, 25, 35 and 75% scenarios for *L. nycthemera* and the 5, 15, 25, 35, 45 and 75% scenarios for *M. thibetana*. The LTSPN values under the 45, 55 and 65% scenarios are higher than those in the 35% scenario for *L. nycthemera* although their path numbers are much smaller. The same situation is also found between the 45% scenario and the 55% scenario for *L. nycthemera* and between the 55 and 65% scenarios and the 35% scenario for *M. thibetana*. Besides, for *M. thibetana*, there is a difference in the LTSPN value between reserve networks with the same number of paths, e.g., the re-

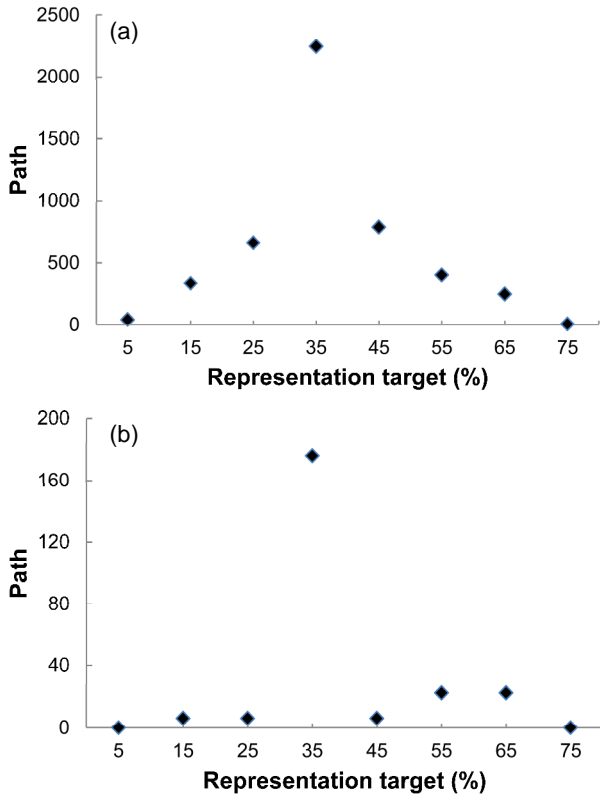


Figure 5. Path numbers of determined reserve networks in eight different representation scenarios for species: (a) *L. nycthemera* and (b) *M. thibetana*.

serve networks under the 15, 25 and 45% scenarios. The fundamental reason for these is the effect of successful dispersal probability between reserves. For example, the highest values of LTSPN found in the 55% scenario for both species result from the existence of a few migrations that are of high successful dispersal probability, e.g., direct dispersals between reserve 1 and reserves 6, 11, 20, 21, 22, 23 and 24 for *L. nycthemera*, and direct dispersals between reserve 1 and reserves 6 and 7 for *M. thibetana*.

Changes of path number, either of each reserve or the whole network, caused by the transformations outlined above between each pair of scenarios are respectively recorded for the two species in Tables 1 to 6. It can be seen that when the effect of new direct dispersals that leads to the increment of paths is greater than those of the lost original ones that reduces paths, common reserves in the subsequent scenario tend to hold more paths, particularly indirect paths, contributing to the long-term survival of species within. Otherwise, the paths will decrease.

4. Discussions

To measure the ecological function of spatial arrangement of reserve network contributing to species' long-term persistence, connectivity and neighboring dispersal probability me-

thods that explicitly account for species' specific dispersal ability have been investigated in previous studies (e.g., Moilanen and Cabeza, 2002; Cabeza, 2003; Moilanen et al., 2005; Van Teeffelen et al., 2006; Jiang et al., 2007; Rayfield et al., 2009; Bauer et al., 2010). Similar to these methods, the proposed method considers the ecological role of direct dispersals to any reserve in relation to the species' persistence in it. The difference is that it concerns indirect dispersals between pairwise reserves, with the purpose of conforming to the reality. The holistic set of network interactions, which allows for both direct and indirect dispersals between reserves, is potentially more important in determining the ecological function of spatial arrangement of a reserve network contributing to the long-term persistence of a specific dispersing species. The problem is to find a way to comprehensively analyze the present dispersals between reserves. NEA is appropriate for this because it captures the reserves' external relationships within a network as input and output environs. With NEA, reserves are regarded as part of an interconnected network. The direct and indirect dispersals of a specific reserve either from its input environ or to its output environ are then identified and quantified according to the assumptions related to species' long-term survival. Specially, the ecological function of spatial arrangement of a reserve network facilitating the long-term persistence of a species is decided by its performance not only to maintain species' internal survival at any reserve, but also to provide refuges if a stochastic event destroys the suitable areas in the reserve.

Eight reserve networks are selected as scenarios for each species under consideration to describe different spatial configurations. By tracing the transformations between each pair of neighboring scenarios, we find that comparing to a preceding scenario, the path number of each common reserve under the subsequent scenario depends largely on the changes, both augment and reduction, of direct dispersals between reserves. This offers a scientific basis for setting conservation criteria to protect dispersing species in nature reserves facing intense economic development pressure like WYS. The areas covered by direct dispersal routes, and identified by the least-cost pathways analysis, should be strictly protected against socio-economic activities and regional tourism to avoid losing more dispersal paths necessary for species' long-term survival. On the other hand, existing human-induced impacts should be minimized by eliminating the obstacles that are passed through by species' direct dispersal routes. For WYS, these conservation criteria can be used as important bases to restrict and guide the tourism of surrounding cities (Wuyishan City and Jianyang City) and the socio-economic activities of local residents. Furthermore, if more than one direct dispersal is needed to be restored, comparing path increment is a way to examine the relative importance of each new direct dispersal and provide a conservation priority to practitioners.

Future efforts could be used to expand the current assessment with respect to other important criteria that are relevant to species' long-term survival via a reserve network, such as reserve shape, population viability and other ecological or non-ecological factors (Williams and ReVelle, 1998; Salomon et al., 2006). Such modified assessment may provide a compre-

Table 1. Path Numbers of Each Reserve or Reserve Network Corresponding to Transformations between Neighboring Scenarios (5, 15 and 25% for *L. nycthemera*)

| Reserve | Representation target (%) | | | | | | |
|---------|---------------------------|------------|----------------|----------------|------------|----------------|----------------|
| | 5 | | 15 | | 25 | | |
| | Total path | Total path | Path increment | Path reduction | Total path | Path increment | Path reduction |
| 1 | 12 | 22 | 15 | 5 | 43 | 36 | 15 |
| 2 | 9 | 23 | 16 | 2 | 22 | 14 | 15 |
| 3 | 9 | | | 9 | | | |
| 4 | 12 | 22 | 14 | 4 | | | 22 |
| 5 | | 15 | 15 | | 11 | 4 | 8 |
| 6 | | 0 | 0 | | 11 | 11 | 0 |
| 7 | | 53 | 53 | | 106 | 98 | 45 |
| 8 | | 53 | 53 | | | | 53 |
| 9 | | 56 | 56 | | | | 56 |
| 10 | | 44 | 44 | | 46 | 39 | 37 |
| 11 | | 44 | 44 | | 83 | 76 | 37 |
| 12 | | | | | 22 | 22 | |
| 13 | | | | | 73 | 73 | |
| 14 | | | | | 64 | 64 | |
| 15 | | | | | 17 | 17 | |
| 16 | | | | | 83 | 83 | |
| 17 | | | | | 83 | 83 | |
| Network | 42 | 332 | 310 | 20 | 664 | 620 | 288 |

Table 2. Path Numbers of Each Reserve or Reserve Network Corresponding to Transformations between Neighboring Scenarios (35, 45 and 55% for *L. nycthemera*)

| Reserve | Representation target (%) | | | | | | | | |
|---------|---------------------------|----------------|----------------|------------|----------------|----------------|------------|----------------|----------------|
| | 35 | | | 45 | | | 55 | | |
| | Total path | Path increment | Path reduction | Total path | Path increment | Path reduction | Total path | Path increment | Path reduction |
| 1 | 124 | 89 | 8 | 139 | 131 | 116 | 83 | 28 | 84 |
| 2 | 38 | 18 | 2 | 52 | 45 | 31 | | | 52 |
| 3 | | | | | | | | | |
| 4 | | | | | | | | | |
| 5 | 13 | 2 | 0 | | | 13 | | | |
| 6 | 13 | 2 | 0 | 49 | 42 | 6 | 35 | 8 | 22 |
| 7 | 295 | 232 | 43 | | | 295 | | | |
| 8 | | | | | | | | | |
| 9 | | | | | | | | | |
| 10 | 257 | 228 | 17 | | | 257 | | | |
| 11 | 233 | 180 | 30 | 128 | 112 | 217 | 56 | 12 | 84 |
| 12 | 38 | 18 | 2 | | | 38 | | | |
| 13 | 188 | 144 | 29 | | | 188 | | | |
| 14 | | | 64 | | | | | | |
| 15 | | | 17 | | | | | | |
| 16 | 161 | 115 | 37 | 113 | 97 | 145 | | | 113 |
| 17 | 257 | 211 | 37 | | | 257 | | | |
| 18 | 264 | 264 | | | | 264 | | | |
| 19 | 171 | 171 | | | | 171 | | | |
| 20 | 192 | 192 | | 128 | 112 | 176 | 67 | 16 | 77 |
| 21 | | | | 19 | 19 | | 35 | 35 | 19 |
| 22 | | | | 49 | 49 | | 35 | 8 | 22 |
| 23 | | | | 113 | 113 | | 56 | 12 | 69 |
| 24 | | | | | | | 35 | 35 | |
| Network | 2244 | 1866 | 286 | 790 | 720 | 2174 | 402 | 154 | 542 |

Table 3. Path Numbers of Each Reserve or Reserve Network Corresponding to Transformations between Neighboring Scenarios (65 and 75% for *L. nycthemera*)

| Reserve | Representation target (%) | | | | | |
|---------|---------------------------|----------------|----------------|------------|----------------|----------------|
| | 65 | | | 75 | | |
| | Total path | Path increment | Path reduction | Total path | Path increment | Path reduction |
| 1 | 56 | 32 | 59 | 3 | 0 | 53 |
| 2 | | | | | | |
| 3 | | | | | | |
| 4 | | | | | | |
| 5 | | | | | | |
| 6 | 27 | 12 | 20 | | | 27 |
| 7 | | | | | | |
| 8 | | | | | | |
| 9 | | | | | | |
| 10 | | | | | | |
| 11 | 40 | 25 | 41 | | | 40 |
| 12 | | | | | | |
| 13 | | | | | | |
| 14 | | | | | | |
| 15 | | | | | | |
| 16 | | | | | | |
| 17 | | | | | | |
| 18 | | | | | | |
| 19 | | | | | | |
| 20 | | | 67 | | | |
| 21 | | | 35 | | | |
| 22 | | | 35 | | | |
| 23 | 27 | 12 | 41 | | | 27 |
| 24 | 27 | 12 | 20 | | | 27 |
| 25 | 27 | 27 | | | | 27 |
| 26 | 40 | 40 | | 3 | 0 | 37 |
| Network | 244 | 160 | 318 | 6 | 0 | 238 |

hensive tool to compare reserve networks offered by a number of alternative reserve selection methods in the nature reserve and to analyze the negative impacts of human activities when more ecological data are available over a longer period. Besides, developing selection approaches with the spatial consideration to design reasonable reserve networks in nature reserves could be another promising direction.

5. Conclusions

The spatial location of reserves is particularly important for maintaining the long-term persistence of species protected by a reserve network, given the fact of species dispersal. Based on NEA, a holistic assessment approach is developed to evaluate the ecological function of the spatial arrangement of reserves. In doing so, two aspects including the probability of no immigration along input paths to a reserve and the probability of no emigration through output paths from that reserve are together studied to measure the extinction probability of a dispersing species at the reserve. The long-term survival probability of the species across the reserve network is also calculated considering

the extinction probabilities in all reserves. Thus, the spatial arrangement of reserves is addressed by incorporating not only the effect of direct dispersals but also that of dispersals through indirect paths on species' long-term persistence. The proposed approach may provide an effective way to evaluate the ecological function of network spatial arrangement in nature reserve, which are constructed and managed primitively for biodiversity conservation.

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Table 4. Path Numbers of Each Reserve or Reserve Network Corresponding to Transformations between Neighboring Scenarios (5, 15 and 25% for *M. thibetana*)

| Reserve | Representation target (%) | | | | | | |
|---------|---------------------------|------------|----------------|----------------|------------|----------------|----------------|
| | 5 | | 15 | | 25 | | |
| | Total path | Total path | Path increment | Path reduction | Total path | Path increment | Path reduction |
| 1 | 0 | 3 | 3 | 0 | 3 | 0 | 0 |
| 2 | | 3 | 3 | | 3 | 0 | 0 |
| 3 | | | | | 0 | 0 | |
| Network | 0 | 6 | 6 | 0 | 6 | 0 | 0 |

Table 5. Path Numbers of Each Reserve or Reserve Network Corresponding to Transformations between Neighboring Scenarios (35, 45 and 55% for *M. thibetana*)

| Reserve | Representation target (%) | | | | | | | | |
|---------|---------------------------|----------------|----------------|------------|----------------|----------------|------------|----------------|----------------|
| | 35 | | | 45 | | | 55 | | |
| | Total path | Path increment | Path reduction | Total path | Path increment | Path reduction | Total path | Path increment | Path reduction |
| 1 | 39 | 36 | 0 | 3 | 0 | 36 | 8 | 8 | 3 |
| 2 | 19 | 16 | 0 | 3 | 0 | 16 | | | 3 |
| 3 | 36 | 36 | 0 | | | 36 | | | |
| 4 | 41 | 41 | | | | 41 | | | |
| 5 | 41 | 41 | | | | 41 | | | |
| 6 | | | | | | | 7 | 7 | |
| 7 | | | | | | | 7 | 7 | |
| Network | 176 | 170 | 0 | 6 | 0 | 170 | 22 | 22 | 6 |

Table 6. Path Numbers of Each Reserve or Reserve Network Corresponding to Transformations between Neighboring Scenarios (65 and 75% for *M. thibetana*)

| Reserve | Representation target (%) | | | | | |
|---------|---------------------------|----------------|----------------|------------|----------------|----------------|
| | 65 | | | 75 | | |
| | Total path | Path increment | Path reduction | Total path | Path increment | Path reduction |
| 1 | 8 | 0 | 0 | 0 | 0 | 8 |
| 2 | | | | | | |
| 3 | | | | | | |
| 4 | | | | | | |
| 5 | | | | | | |
| 6 | 7 | 0 | 0 | | | 7 |
| 7 | 7 | 0 | 0 | | | 7 |
| Network | 22 | 0 | 0 | 0 | 0 | 22 |

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