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Biodiversity at disequilibrium: updating conservation strategies in cities

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Greenspaces represent an ark for urban biodiversity, but understanding their carrying capacity to sustain species remains challenging. Old greenspaces that were fragmented from natural habitats are now overcrowded, while revegetated new greenspaces remain vacant. This is because they have different processes leading towards biodiversity equilibrium, and conservation management needs to differentiate between fragmented and revegetated greenspaces.

Importance of urban greenspaces

Many cities are undergoing rapid expansions, which often involves covering natural, semi-natural, and agricultural lands with hostile impervious surfaces. However, increasing evidence indicates that cities can play a vital role in biodiversity conservation, and the maintenance of urban biodiversity critically contributes to the health and social welfare of urban dwellers [1]. However, cities predominantly harbor wild species in **greenspaces** (see Glossary) that are extremely limited in area, leading to a reduction of biodiversity in urban ecosystems [2]. Therefore, to improve the management of urban biodiversity (https://www.cbd.int/gbo5), it is essential to explore the changing trends of urban greenspaces and the ecological mechanisms determining species richness therein. When compared with natural habitats, the majority of urban greenspaces have been established relatively recently, and thus **biodiversity equilibrium** has not yet been reached. For conservation purposes, it is critical to explore the dynamics of biodiversity in urban greenspaces, but the underlying mechanisms are unclear. This is mainly because of poor understanding of the two opposing processes that contribute to the formation of urban greenspaces: habitat **fragmentation** and **revegetation** [3]. Fragmentation processes usually dominate the greenspace formation during the early stages of a modern city expansion, while revegetation occurs when an established city invests in greenspaces. Nevertheless, the dominant view that urban biodiversity relies on the habitat fragmentation paradigm, overlooks the role of revegetation. Here we elucidate the transitioning importance of these two processes in urban greenspace changes and the underlying dynamics of biodiversity, and propose conservation strategies based on the origin of urban greenspaces.

Greenspace establishment is moving from fragmentation to revegetation

Urbanization covers large areas of natural habitats with impervious surfaces, and remnant habitats become disconnected and fragmented. This fragmentation process dominates urban greenspace establishment, particularly during rapid city expansion [4]. Moreover, the explosive population growth in cities had led to increased demands for housing and associated infrastructure, removing greenspaces and increasing the amount of habitat fragmentation in urbanized regions [5]. For example, in Jakarta, the proportion of greenspace area to the total urban area has declined drastically from 46% to 6% between 1988 and 2014 [5].

Since the 1980s, as a result of modern concepts of urban planning and requirements for better living quality, the reduction in urban greenspaces has been effectively controlled in many metropolises [6]. A trend of increasing urban greenspace has emerged in over half of European cities [7]. Such an increase in greenspace area has also occurred in China in recent years [8]. For example, Shanghai's greenspace has constantly increased since the 1980s, particularly in the central urban area (within the inner ring) (Figure 1A), and the total greenspace area increased from 881 ha in 2000 to 2684 ha in 2020 (Figure 1B).

Although current urbanization still generates greenspaces through the process of fragmentation globally [9], in established cities, the method of generation of greenspaces is moving away from fragmentation processes to processes involving revegetation. Revegetation is dramatically increasing in urban greenspaces and this is expected to increase biodiversity. However, the existing biodiversity in revegetated greenspaces may be much lower than predicted by island biogeography theory (see later for details), because revegetation leads to distinct

Glossary

Biodiversity equilibrium: a state of equilibrium of biodiversity in habitats when the migration rate equals the extinction rate, and the species number remains stable.

Ecological corridors: narrow strips of habitats connecting separated landscape elements, which can facilitate migration of species and delivery of ecosystem functionning.

Extinction debt: the number of species that exceeds the equilibrium of a fragmented habitat due to delayed extinction of long-lived species and/or transiently increased immigration. This debt of the fragmented habitat will be paid off by extinction in the future.

Fragmentation: a process whereby a large and intact habitat is split into many small and isolated patches, usually resulting in a reduction of habitat area and barriers restricting migration of species among patches.

Greenspaces: Urban areas covered by vegetation, e.g., parks, gardens, and green belts.

Immigration credit: the number of species that has yet to reach the equilibrium of a habitat containing vacant niches. This habitat has the capacity (immigration credit) to accommodate future immigrants.

Revegetation: a process to create greenspaces by replanting, transforming disturbed unplanted urban areas such as impervious surfaces into habitats covered with vegetation.

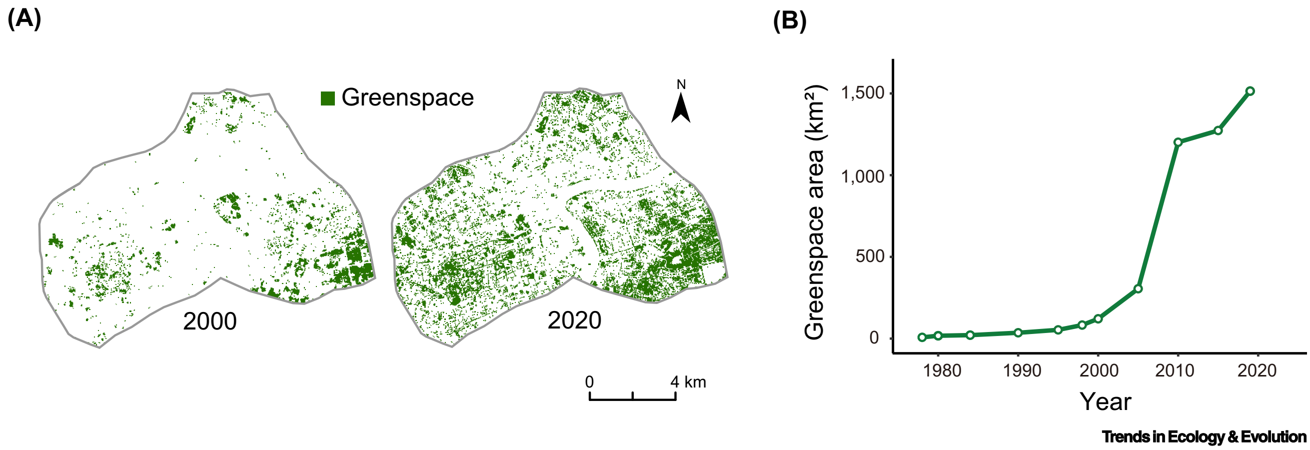

Figure 1. The trend in greenspace area in Shanghai. (A) The increase in greenspace area in Shanghai's central urban district from 2001 to 2020. The green and white parts within the boundary represent the urban greenspaces and impervious surfaces, respectively, and the boundary represents the inner ring of Shanghai. Classification of land use type was performed in ENVI v5.3 (Exelis Visual Information Solutions, Boulder, CO, USA) by non-supervised classification based on remote-sensing images from Landsat 7 in 2000 and Landsat 8 in 2020. (B) The change in greenspace area in Shanghai from 1978 to 2019 (Shanghai Municipal Statistics Bureau 1981, 1984, 1991, 1996, 2001, 2006, 2011, 2016, and 2019).

biodiversity dynamics. Therefore the effects of fragmentation and revegetation on urban biodiversity over time needs to be clearly distinguished.

Biodiversity dynamics varies with fragmentation and revegetation

As greenspaces are scattered within cities and are surrounded by impervious surfaces, island biogeography theory is thought to be the golden rule for examining urban biodiversity [10]. Thus, the total number of species hosted in a greenspace can be predicted by the species–area relationship (SAR) [10]. The SAR predicts that a larger area of greenspace can host a greater number of species, suggesting that increasing the greenspace area will benefit biodiversity conservation. Notably, the SAR predicts that species richness is at an equilibrium between local colonization and extinction; however, the biodiversity of a relatively newly formed greenspace island is still in disequilibrium because of the short time since its establishment. Furthermore, the way species richness approaches diversity equilibrium is different for greenspaces established by fragmentation or revegetation.

After habitat fragmentation, the greenspace island serves as a refuge and local species tend to move into the remnant habitats. Many long-lived species will not go extinct immediately after fragmentation. The rate of colonization is anticipated to increase transiently, exceeding the extinction rate. Therefore, the observed species richness is likely to be higher than the equilibrium predicted by the SAR [11]. Meanwhile, the carrying capacity of fragmented habitats can be reduced by low habitat quality due to edge effects and by the homogeneity of microhabitats [12]. Gradually, the extinction rate increases to counterbalance the increase of colonization, and species richness decreases to equilibrium as expected by **extinction debt** [11] (Figure 2).

After revegetation, a mass of unoccupied niches is available in the greenspace island, allowing more species to colonize it, resulting in **immigration credit** [11]. Species richness is therefore much lower than expected right after revegetation, but will gradually increase to the equilibrium predicted by SAR (Figure 2). The time to reach equilibrium depends heavily on both local landscape configuration and species traits associated with adaptative potential to low habitat quality [13]. Revegetated greenspaces which are located closer to existing habitats can acquire species more easily, and species with stronger dispersal ability can establish earlier in those greenspaces.

Although urban biodiversity should fit the expectations of the island biogeography theory, greenspace islands take a long time to approach the equilibrium species richness predicted by SAR due to either extinction debt or immigration credit. This explains why urban biodiversity does not increase quickly after revegetation and conservation strategies need to be updated to consider these disequilibrium processes of extinction debt and immigration credit.

Distinguishing revegetation from fragmentation improves conservation strategies

Designing an appropriate conservation strategy that can effectively manage urban biodiversity relies on a comprehensive understanding of the underlying processes and their effects. Understanding the distinct impacts of fragmentation and revegetation on urban biodiversity leads the way for improving current conservation strategies. Here, we propose an updated strategy involving the following three points.

First, we must correctly identify how the urban greenspace was established, either

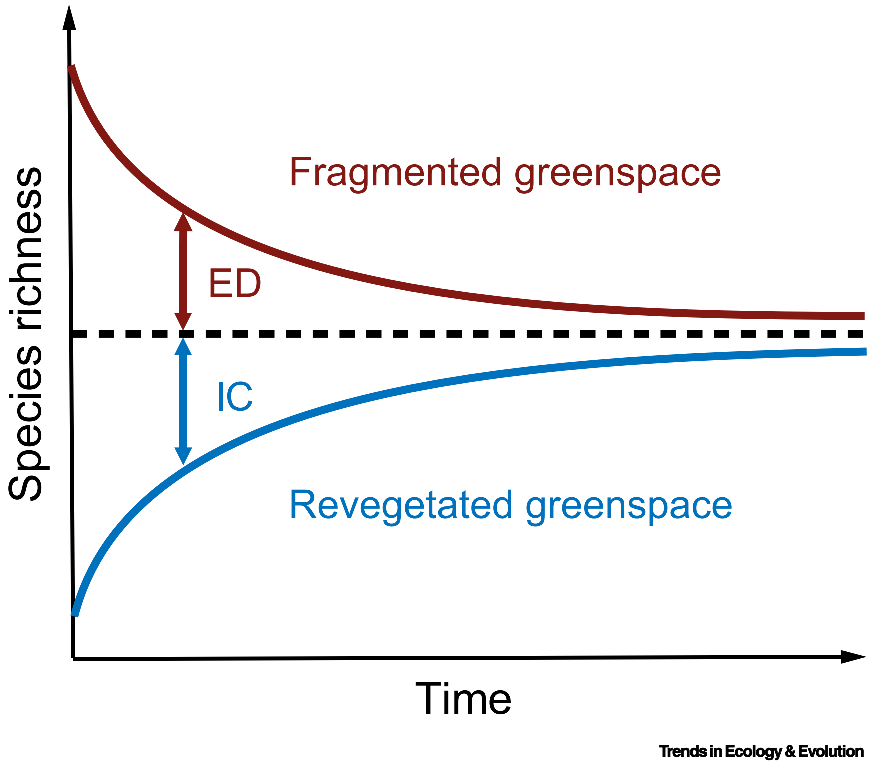

Figure 2. The expected variation of species richness in the scenarios of extinction debt (ED, red line) and immigration credit (IC, blue line) (modified from [11]), compared with the prediction by the species–area relationship (SAR) (dashed line). A decline in species richness due to the high extinction rate is expected in fragmented greenspaces, and species richness is anticipated to increase in revegetated greenspaces because of the high immigration rate. Both types of greenspace will gradually approach the equilibrium predicted by the SAR.

via fragmentation or revegetation, as the confounding of extinction debt versus immigration credit will mislead the evaluation of biodiversity and the entire management design. This identification is often achieved through referring to the history of city development. Generally, it is very difficult to trace the history of older parks because they may have been established for over 100 years without complete records; however, the species richness there may have reached equilibrium irrespective of different underlying processes.

Second, the construction of **ecological corridors** to connect greenspaces and form a meta-community is crucial to maintain urban biodiversity [14]. Furthermore, due to the effects of extinction debt and immigration credit, the urban greenspaces generated by fragmentation or revegetation harbor higher or lower species richness than predicted by the SAR. Therefore, purposely connected greenspaces generated by different processes can establish source–sink dynamics, in which greenspaces formed by fragmentation serve as the source and revegetated greenspaces are the sink. Such targeted source–sink connections can facilitate the migration of excessive species held by fragmented greenspaces into the revegetated ones with vacant niches, avoiding local species extinction and increasing the effectiveness of urban biodiversity conservation. Based on our design of source–sink connections, the locations of future revegetation sites shall be close to the greenspaces established via fragmentation.

Moreover, monitoring and removing invasive species in revegetated greenspaces is needed. Compared with the greenspaces formed by fragmentation, revegetation creates vacant niches, making the greenspaces at high risk of biological invasion. This is because vacant ecological niches provide chances for colonization, and most invasive species are strong long-distance dispersers and colonists [15]. Invasive species can exclude native species and prevent the colonization of native species, threatening the maintenance of urban biodiversity. Furthermore, due to the challenges of removing invasive species after their establishment, prior efforts are necessary to only include native species for vegetation.

Prospects

Urban biodiversity underlines urban ecosystem functioning and is extremely vulnerable. An insufficient understanding of the ecological mechanisms affecting urban biodiversity over time will restrict conservation efficacy. Here we focus on the two processes generating urban greenspaces, and elucidate how the disequilibrium of colonization and extinction drives the species diversity in greenspaces. To update the existing conservation strategies, we propose three aspects: classifying urban greenspaces, establishing source–sink connections, and monitoring invasive species. Overall, our views provide novel insights into urban configuration and address the importance of distinguishing the two processes for urban biodiversity conservation.

To achieve this conservation goal, future urban ecology research is expected to be concentrated on the following points: (i) long-term monitoring of urban biodiversity to provide evidence for extinction debt and immigration credit in the urban greenspaces generated by either fragmentation or revegetation; (ii) characterizing dispersal/behavior traits of native species and evaluating their adaptation to urban greenspaces (e.g., stratifying introduction experiments based on fragmented vs. revegetated greenspaces) [12] to improve the design of greenspaces and corridors; (iii) modeling the biodiversity disequilibrium dynamics caused by extinction debt and immigration credit to determine the optimal network connecting urban greenspaces.

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Declaration of interests

All authors declare no conflicts of interest.

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