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THINK AGAIN

Insights & Perspectives

Modern cities modelled as “super-cells” rather than multicellular organisms: Implications for industry, goods and services

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Funding information

National Science Foundation of China,

Grant/Award Numbers: 31770434, 31870307;

SUTD-ZJU IDEA Seed, Grant/Award Number:

SUTD-ZJU (SD) 201903

Abstract

The structure and “metabolism” (movement and conversion of goods and energy) of urban areas has caused cities to be identified as “super-organisms”, placed between ecosystems and the biosphere, in the hierarchy of living systems. Yet most such analogies are weak, and render the super-organism model ineffective for sustainable development of cities. Via a cluster analysis of 15 shared traits of the hierarchical living system, we found that industrialized cities are more similar to eukaryotic cells than to multicellular organisms; enclosed systems, such as factories and greenhouses, paralleling organelles in eukaryotic cells. We further developed a “super-cell” industrialized city model: a “eukarcity” with citynucleus (urban area) as a regulating centre, and organaras (enclosed systems, which provide the majority of goods and services) as the functional components, and cityplasm (natural ecosystems and farmlands) as the matrix. This model may improve the vitality and sustainability of cities through planning and management.

KEYWORDS

hierarchical living system, industrial systems, scaling, sustainability, urban-rural system

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INTRODUCTION

The most significant feature of industrialized cities (urban-rural complexes) is the emergence of many industrialized functional components such as factories, banks, and wastewater treatment plants. These components carry out the city's processes by providing goods (such as industrial products, food, water, materials), and services (financial regulation, policy control and environmental pollution mitigation) for people.^[1-3] In contrast, pre-industrial cities had only non-industrial handcraft workshops and traditional service facilities such as restaurants and hotels. The first generation of factories emerged in the early 1760s after the Industrial Revolution, marking the establishment of industrialized cities. Nowadays, non-living material mass made by humans exceeds all the living biomass on this planet.^[4] This mass has largely benefited human societies while also concentrating pollutants and degrading land.^[1,5,6]

Fortunately, industrialized functional components of cities have improved by becoming smarter.^[7] The improvements include optimizing functional structure, which is the number of components and their spatial relationships;^[8,9] improving metabolic processes, which are the fluxes and transformation of energy,^[10] water,^[11] food,^[12] building materials and wastes,^[13] as well as reducing environment impacts.^[14] Despite many advances in the science, planning, engineering and management of cities,^[2,15] and the recognition that industrialized cities should enhance sustainability by providing sufficient goods and services while minimizing environmental problems,^[16] most urban planning is still based on trial-and-error. This makes apparent the need to strengthen the theoretical basis for science and engineering in industrialized cities.

Recognizing that cities share traits (such as metabolism) with living systems, researchers proposed a "super-organism" hypothesis.^[5,15] In this hypothesis, wetlands are analogized as the city's kidneys, green spaces as the city's lungs, and streets as its blood vessels. This super-organism model places cities on the hierarchy of living systems (Figure S1) and has inspired disciplines such as industrial ecology and urban metabolism.^[17-19] For example, electricity consumption in response to urban mass follows the power law function $Y = aX^\beta$, in which the allometric scaling exponent β is approximately $5/6$.^[20] This is similar to the sublinear scaling ($\beta \sim 3/4$) of energy metabolism of multicellular organisms (especially animals) to their biomass.^[15] However, the super-organism model is an imperfect analogy because most of the features of multicellular organisms and cities are not comparable. In terms of morphology and structure, for example, a multicellular organism has only a few organs and the quantity of organs is often fixed, while a city can have many functional components of the same kind.^[3] Another structural difference is that cities can optimize the spatial distribution of functional components to improve the provisioning capability of goods and services,^[21] but organs cannot change position in multicellular organisms. In terms of vitality, the walking speed of humans in response to city size is superlinear ($\beta > 1$), while the heart rate of mammals in response to body size is sublinear ($\beta < 1$).^[22] These discrepancies suggest a lack of common principles between cities and multicellular organisms. Meanwhile, engineers and managers have also

argued that such analogies with multicellular organisms provide limited insights for urban planning and management,^[23,24] suggesting the need to build a more accurate and robust model.

Here, we analyse the typical characteristics of industrialized cities and find that enclosed industrial systems—those covered by man-made films such as glass, plastic, cement and other materials—are the essential functional units. We uncover the relationships between industrialized cities and several levels of living systems, including multicellular organisms, organs, single eukaryotic cells and their organelles, in the hierarchical living system (Figure S1). We then propose a conceptual model that both identifies the shared features of cities and living systems and provides a bridge for interdisciplinary studies in ecology, biology and planning. Finally, we propose a bionic approach to improve human well-being, reduce environmental pollution and release more land for the sustainable development of cities.

MATERIAL AND METHODS

Cluster analysis

The quantitative and qualitative traits collection

We chose the shared features of six types of living systems, including industrialized cities, enclosed industrial systems, multicellular organisms, organs, eukaryotic cells and organelles. According to systems science, we identified traits related to the morphology, structure, process and function of cities and enclosed systems, as well as other living systems (Table S1; Table S2). The 15 traits included seven quantitative traits and eight qualitative traits. For the quantitative traits, some traits can be described with a specific numerical value, and some values are expressed as an order of magnitude; other traits are the exponent (β) of a power law in way of expressing the quantity of components or organelles, or metabolic rate in response to the system size. For the qualitative traits, we assigned the attribute values (detail see Table S2).

Clustering

We used a hierarchical cluster analysis with the complete linkage method based on Gower distance to identify relatedness among living systems.^[25]

Assessment of ecosystem services

Frameworks

Ecosystem services include provisioning services, regulating services and cultural services. It should be noted that the calculation of the ecosystem services of natural ecosystems are the sum of all three services (provisioning, regulating and cultural). However, the ecosystem services of artificial ecosystems are divided into

target services and accompanying services separately. For example, the target services of farmlands, greenhouses, and dairy feedlots belong to the larger group of food production, which is equivalent to some of the provisioning services of natural ecosystems; the target services of wastewater treatment plants and constructed wetlands is pollutant removal from wastewater, which is equivalent to the regulating services of natural wetlands. In addition to the target services, the calculation of accompanying services is the same, regardless of whether they are provisioning, regulating or cultural services. Accompanying services are further divided into services (positive) and disservices (negative) in this paper, following the guidelines in ref [26].

Data used in model-building

Data for ecosystem services were collected from the literature. For details, see the Supplementary Information.

Calculations

Ecosystem services for natural ecosystems were calculated following the method in [27]. The provisioning services (ES_p , USD ha⁻¹ year⁻¹) of greenhouses or open farmlands are to produce vegetables, the total value of which is measured by output value.^[28] The provisioning services (ES_p) of dairy feedlots is the economic benefit of milk supply per unit farm area.^[29] The decomposition services (ES_d , USD ha⁻¹ year⁻¹) of wastewater treatment plants and constructed wetlands are calculated as $ES_d = W \times P_w/A$, where W (ton year⁻¹) is the amount of waste treated at wastewater treatment plants or constructed wetlands, P_w (USD ton⁻¹) is price for per unit of waste treated, and A (ha) is the area covered by wastewater treatment plants or constructed wetlands in a city. The provisioning services (ES_p) of a fast-food store, such as Kentucky Fried Chicken, is calculated by dividing the company's total revenue (all stores) in the year divided by the total number of those stores in the country. ES_p is calculated as $ES_p = R_k/N_k/A$, where R_k is the total operating revenue of all stores of the company in 1 year (USD year⁻¹); N_k is the total number of stores belong to the company, A is the average area of a fast-food store (ha). The regulating services (ES_r , USD ha⁻¹ year⁻¹) of a bank are manifest in the management of financial capital, and are calculated by dividing the company's total revenue (all banks) in the year divided by the total number of banks of the same company in the country. ES_r is calculated as, $ES_r = R_b / N_b/A$, where R_b is the total revenue of the company in 1 year (USD year⁻¹); N_b is the total number of banks belong to the same company, A is the average area of a bank (ha). The provisioning services (ES_p) of a thermal power plant is to produce electricity, the total value of which is measured by output value of electricity. ES_p is calculated as, $ES_p = Q \times P_e/A$, where Q is the total power generation of a thermal power plant (kWh year⁻¹); P_e is on-grid price of electricity (USD kWh⁻¹), A is the area of a thermal power plant (ha).

Scaling effect

We chose greenhouses to represent enclosed industrial systems for food production services, and wastewater treatment plants to represent enclosed industrial decomposition systems in cities in order to calculate the scaling effect. The scaling effects are the power law functions ($Y = aX^b$) between the number of a type of enclosed industrial systems (Y) in response of the population (X) in the city. The method follows ref [5].

RESULTS AND DISCUSSION

Enclosed ecosystems emerged in landscape of industrialized cities

In landscapes along rural-urban gradients, the identified entities are the industrial systems embedded in the matrix of ecosystems. In addition to the enclosed non-ecosystems (such as factories, which emerged three centuries ago), the remarkable thing is the recent emergence of enclosed ecosystems (Figure 1A, B). Both enclosed ecosystems and non-ecosystems are industrial systems, and their common features are the outer covers and internal industrial facilities (machines and apparatus). Enclosed ecosystems are unique because they rely on biological processes but are supported by industrial facilities. For example, greenhouses enhance plant production, livestock feedlots improve animal production, and wastewater treatment plants concentrate microorganism activities (Figure S2; Table S1). In contrast, factories, restaurants or banks have no biological components except the people working there. Non-ecosystem components can also provide "ecosystem services" such as cultural services provided by museums and theatres.

The outer membrane greatly increases the efficiency and productivity of enclosed industrial systems (Figure 1C), which yield 2–5 orders of magnitude higher goods and services per land area than open farmlands, and have become productivity hotspots in cities. Multiple types of enclosed ecosystems have emerged worldwide performing functions including food production (e.g., vegetables, meat, milk and eggs), decomposition (e.g., wastewater treatment, waste disposal) and other services (Figure S3; Table S1). In some regions they provide goods and services that cannot be provided by open ecosystems. For example, greenhouses can produce fresh vegetables in very cold areas (e.g., high altitude areas in Tibet, China), while the open farmlands cannot.

Similarities between an industrialized city and a eukaryotic cell

Industrialized cities have characteristics similar to living systems, but they are less similar to multicellular organisms than suggested by the super-organism hypothesis. This raises the question—to which living system in the biological hierarchy model are industrialized cities most similar? We analysed 15 traits of living systems and cities (see Table S2)

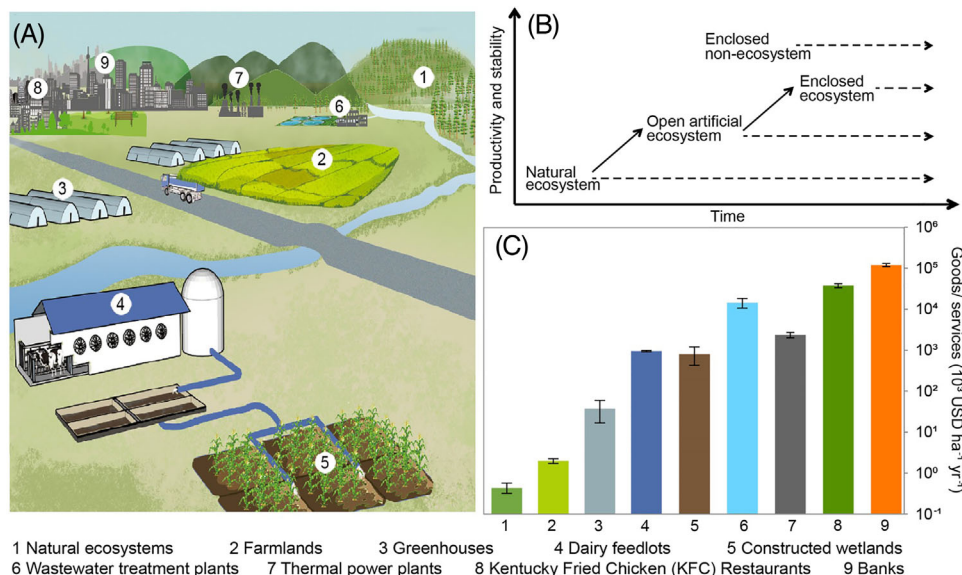


FIGURE 1 Some hotspots of goods and services production in industrialized cities. (A) From exurban, suburban to urban areas, natural ecosystems, open artificial ecosystems, enclosed ecosystems (greenhouses, dairy feedlots, wastewater treatment plants), and enclosed non-ecosystem (factories and other functional components) in the landscape. (B) Evolution from natural ecosystems to enclosed industrial systems. (C) Goods or services (average of the sites globally, Figure S4), number below each bar corresponds to ecosystem types in Figure 1A

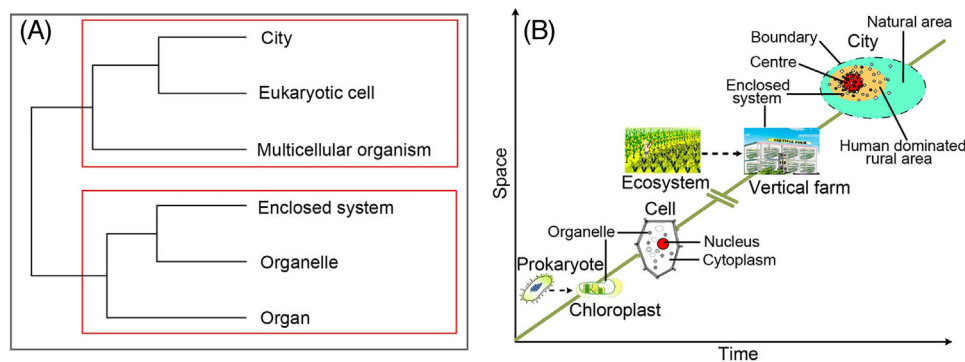


FIGURE 2 The relationships of the systems in the hierarchy of living systems. (A) Clustering tree of six levels of systems in space and time based on 15 traits (see Table S2). (B) The structure composition of a eukaryotic cell and an industrialized city consisting of an urban centre (red) and human dominated rural areas (orange). Dash-dotted line denotes the administrative boundary

to identify relatedness among living systems using a cluster analysis with the complete linkage method based on Gower distance. The clustering results show that industrialized cities are more similar to eukaryotic cells than to multicellular organisms (Figure 2A) in the hierarchy of living systems (Figure 2B). Although industrialized cities (10^5 m) are much greater in size than eukaryotic cells (10^{-5} m), many traits, such as spatial functional structure, metabolism and regulation, are highly similar (Table S2).

A eukaryotic cell has thousands of organelles around the cell nucleus. Each type of organelle is distributed spatially along the centre (nucleus) to the edge (cell membrane) in a eukaryotic cell (Figure 3A). For example, mitochondria in a eukaryotic cell are concentrated near the nucleus while lysosomes are farther away, and many of organelles

frequently move (Figure 3B, C). Similar to eukaryotic cells, there are a great number of enclosed systems around and within the urban centre in industrialized cities (Figure 3D). Enclosed non-ecosystems, such as banks, restaurants and hotels, are concentrated in the urban centre while factories are located on the urban fringe. Enclosed ecosystems, such as greenhouses and wastewater treatment plants, are located outside the urban fringe, while dairy farms are located in exurban areas (Figure 3E). Many studies focus on the two-dimensional pattern of cities,^[5,30] but some argue that living cells are three-dimensional objects and lack strong similarities with cities. In fact, industrialized cities have become increasingly spherical by expanding both above- and belowground,^[9,31] and developing into the third spatial dimension.

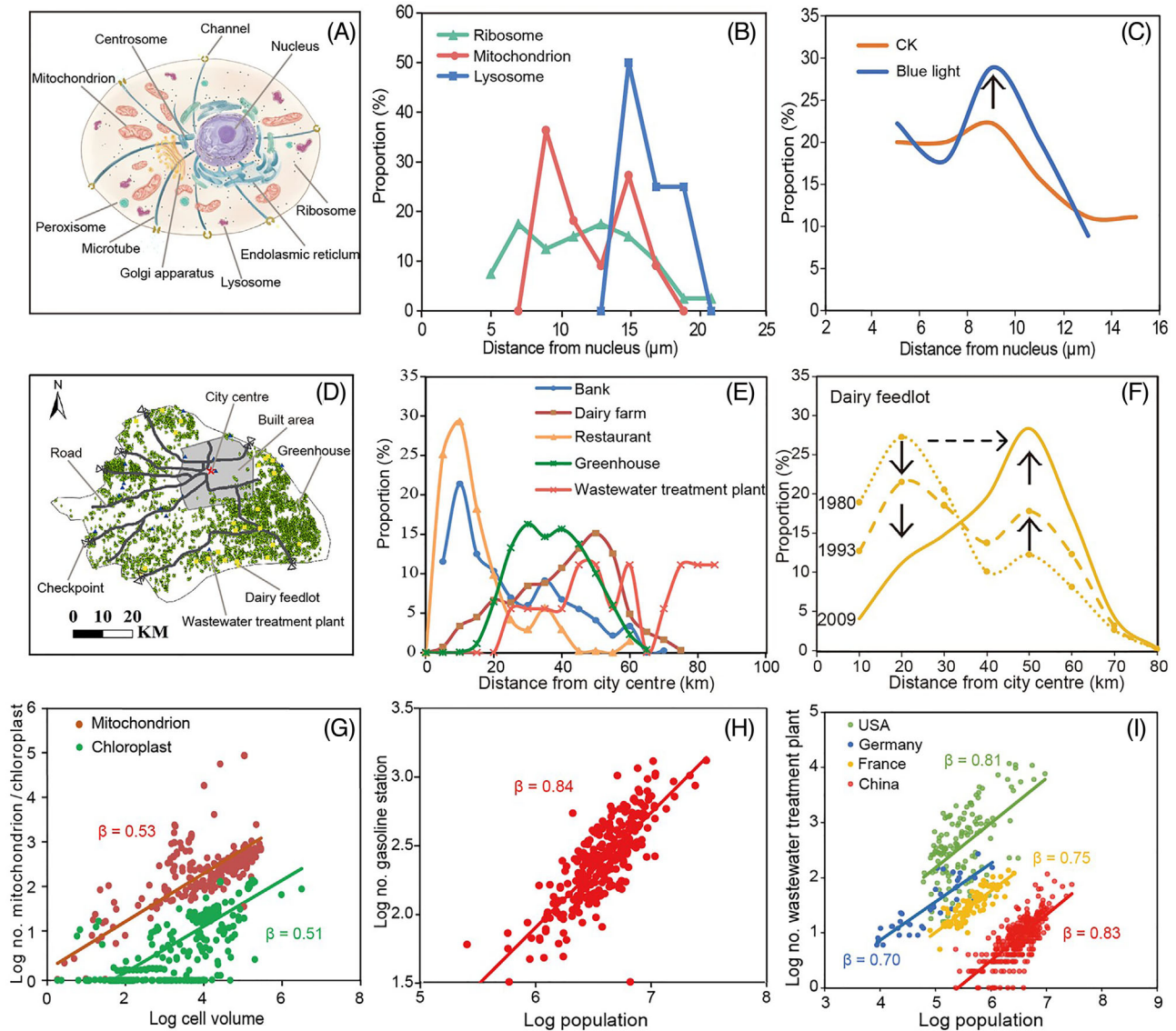


FIGURE 3 Morphology and substructure of industrialized cities and eukaryotic cells. (A) An animal cell with nucleus, organelles and cytoplasm. (B) Distribution of some organelles along the nucleus-edge gradients in a plant cell. (C) Movement of chloroplasts under blue light (CK is the normal state). (D) Greater Shanghai Area, with a city centre and enclosed ecosystems as city components embedded in natural ecosystems and open artificial ecosystems landscape. (E) Density of enclosed ecosystems along the urban-rural gradient in Shanghai in 2010. (F) Distribution patterns of dairy feedlots in Shanghai from 1980 to 2009. (G) The quantity of organelles (chloroplasts and mitochondria) in response to cell volumes (scale effect, $Y = aX^\beta$). (H) The quantity of greenhouses in response to population size in cities of China. (I) The quantity of wastewater treatment plants in response to population size in cities. For data source, see online Supplementary Information

Enclosed ecosystems and enclosed non-ecosystems are frequently relocated for a variety of reasons (Figure 3F). They are moved directly, such as mobile restaurants and railway greenhouses,^[32] or indirectly, such as a factory being dismantled in one place and reconstructed in another. For example, since the 1980s dairy farms in the Greater Shanghai Area have been pushed from the urban fringe to exurban areas many times because they produce high ecosystem disservices. Relocating enclosed systems in cities reflects the change in relative values for net goods and services of the enclosed systems and the changing costs of land leasing due to urban development.

From the perspective of physics, the allometric scale effect of components in response to system size is a general principle for both cities and eukaryotic cells. The number of chloroplasts and mitochondria in response to cell size (volume) is sublinear, with $\beta = 0.51$ for chloroplasts and $\beta = 0.53$ for mitochondria in our compiled data (Figure 3G). Similar allometric scale effects are also found in many industrialized cities: the number of gasoline stations in response to city size (population) is $\beta = 0.84$ in China (Figure 3H) and 0.77 in United State of America;^[15] the number of wastewater treatment plants in response to city population are $\beta = 0.77$ on average across China, United State of America, France and Germany (Figure 3I). In contrast,

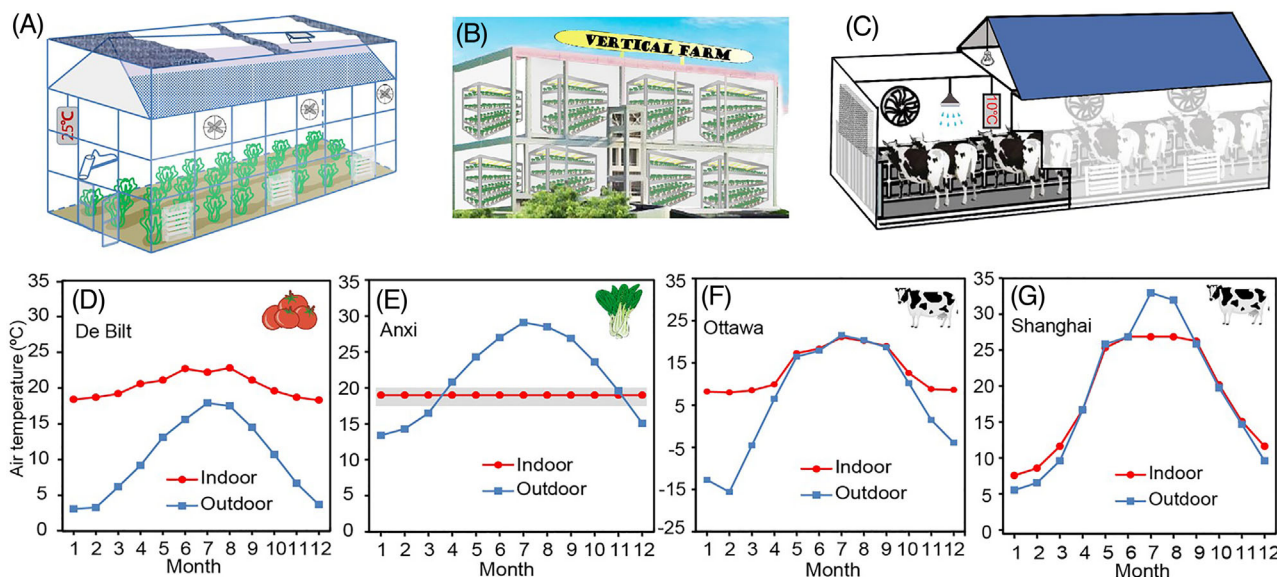


FIGURE 4 Homeostasis of air temperature within enclosed industrial systems. (A-C) Three types of industrial enclosed ecosystems: greenhouse (A), vertical farm (B) and dairy feedlot (C). (D-G) Variations of internal and external air temperature of enclosed ecosystems, including greenhouses in De Bilt, the Netherlands (D), vertical farm (plant factories) in Anxi, South China (E), dairy feedlot in Ottawa, Canada (F), and dairy feedlot in Shanghai, Southeast China (G)

an organism usually has a predetermined number of organs, indicating that there is no such scale effect in response to increased body size.

The metabolic flow and network characteristics of industrialized cities are also similar to those of eukaryotic cells. In eukaryotic cells, organelles are metabolic hotspots;^[33] similarly, enclosed systems are hotspots of biogeochemical metabolism in cities. The nitrogen fluxes passing through enclosed systems are up to three orders of magnitude higher on average than those in open systems (Figure S5a-c). Furthermore, the relationship between the rank of nitrogen pathways (P) and the nitrogen fluxes (F) in the metabolic networks of cities follows the power law $F \sim P^\beta$, and $\beta = -3.5$, indicating that the nitrogen fluxes in Shanghai City are centralized in a few hotspots, and that all of them are enclosed systems (Figure S5d). The nitrogen fluxes in cities have a steeper reduction (the exponent $|\beta| > 3$) than the food webs in natural ecosystem ($|\beta| < 2$; Figure S5d). This reveals that although the nitrogen fluxes (N fixation, N mineralization) in natural ecosystems are highly concentrated in root nodules, animal corpses, and faecal matter decomposition,^[34] cities have a much higher concentration of nitrogen flux than ecosystems.

Similarities between enclosed industrial systems and organelles

The cluster analysis also demonstrates another closely related analogous pair (Figure 2A): enclosed systems are similar to organelles. The crucial feature of this pair is their enclosing structures. Many organelles, such as chloroplasts and mitochondria, have outer membranes to maintain their physical and chemical homeostasis; similarly, enclosed systems are equipped with outer membranes (Figure 4A-C) to

ensure the stability of internal physical and chemical conditions (Table S3). For example, air temperature variations within greenhouses, vertical farms and dairy feedlots are much smaller than ambient environmental variations (Figure 4D-G). With outer membranes, dairy feedlots can keep cooler or warmer and producing milk in extreme climate zones such as subtropical regions and cold-temperate areas that were previously unattainable. In addition, the outer membranes mitigate pollutant leakage, in much the same way as the membranes of organelles play a role in reducing the release of “intermediates” (such as ketones, metal ions) to the cytoplasm. More importantly, organelle membranes have a great number of small “facilities,”^[35] such as channels, ion pumps, glycoproteins, ATPase and receptors, to regulate the physical and chemical conditions. Similarly, the outer membranes of enclosed industrial systems are increasingly fitted with small facilities such as sensors, monitors, air-conditioners, solar batteries, fans, and so on (Figure 4A-C) to improve the conditions for plants, animals and microorganisms. It stands to reason that the development of these fine-scale structures should greatly improve the functions of the enclosed systems.

The internal structures of enclosed systems have also acquired fine structures similar to organelles. For example, a vertical farm uses multi-layer planting to centralize cultivation with 20 to 100 tiers, and uses technology and automation to achieve high yields throughout the year.^[12,36] Similarly, a chloroplast has a multi-layer thylakoid structure that improves photosynthetic efficiency.^[37] Like the fine structure formed by the inner membrane of a mitochondrion,^[38] a cowshed has many stalls, hence efficiently using space and avoiding crowding by designing a trough configuration that gives each cow an equal chance of getting feed: these measures increase the feed utilization efficiency and dairy productivity (Figure S3). Yet, human design of such fine

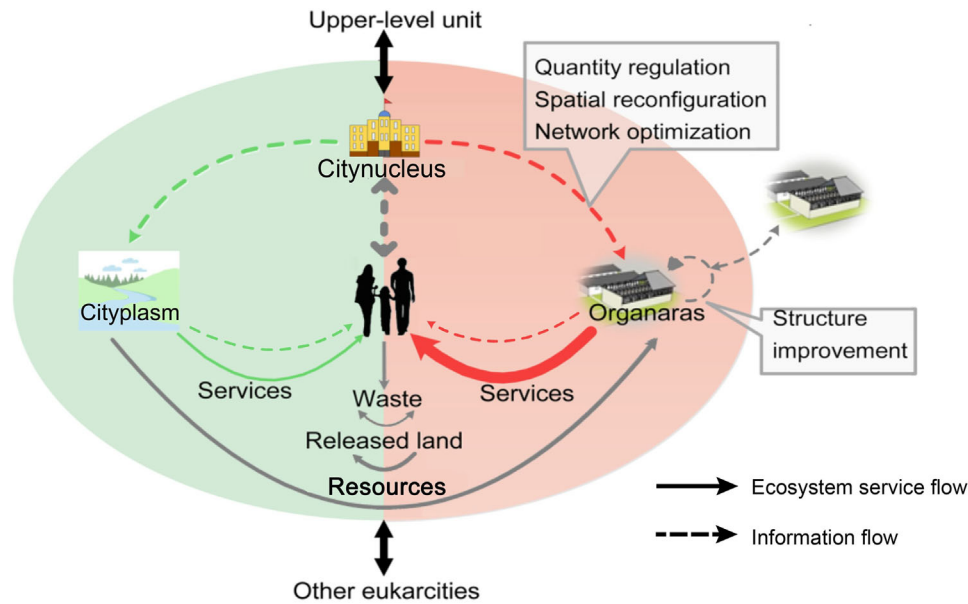


FIGURE 5 The super-cell city model. A eukarcity with the processes dominated by the cityplasm (left, natural ecosystems with no industrial hotspots, ecosystem-based loop) and the processes dominated by organaras (right, organara-based loop). Line thickness indicates ecosystem service intensity; interactions between organaras and the cityplasm are mainly by means of land use change, natural capital, waste production and treatment. The right semicircle dominated by organaras plays an increasing role in eukarcities

structures is in its infancy compared with organelles, suggesting exciting possibilities for further development.

Another similarity between enclosed systems and organelles lies in their information systems. The enclosed non-ecosystems (factories) only have human cultural information systems, such as technology, management and standards. However, the enclosed ecosystems have dual-information systems, that is, human cultural information and biological genetic information. For example, industrial dairy feedlots have biological information systems including the age, sex and genetic structures of cattle populations.^[39] The information collected in enclosed ecosystems and non-ecosystems ensures their self-organization, including technology innovations and updates, in a manner similar to the semi-autonomous DNA genetic of mitochondria and chloroplasts.^[40] For human information, a new field, “culturomics”, has recently emerged as an analogy to genomic research in biology.^[41,42] It has been found that word frequency changes in history also follows rules similar to biological genetics rules. For example, the process of naming a newborn is similar to the process of infinite allele replication of random genetic drift;^[43] the evolution of English grammar is influenced by random drift and selection,^[44] and the evolutionary rate of language can be predicted by population genetic models.^[45] Of course, the evolution of human culture information—whether at the city level or at the enclosed system level—has its own unique characteristics, and requires additional research.

A conceptual super-cell city model

The results of our analysis encouraged us to develop a new hypothesis: an industrialized city is analogous to a eukaryotic cell with respect

to component composition, spatial pattern, and metabolic processes. We henceforth propose a conceptual super-cell city model in which an industrialized city is a “eukaryotic city” or a “eukarcity”, the urban area is “citynucleus”, the enclosed system is “organara”, and the rural ecosystems and open farmlands is “cityplasm” (Figure 5). The term “organara” is similar to “organelles” in etymology, for the suffix “-elle” in means small (via French, from Latin “*ella*”), while “-ara” means big (from Greek -ar / -ara / -aros). The processes in the super-cell city model mimic the biological processes of eukaryotic cells. Organaras provide major goods, such as food production corresponding to “synthesis” in organelles, and they provide services, such as garbage disposal (corresponding to “degradation” in organelles), corresponding to “decomposition” by lysosomes and catalases in eukaryotic cells. The emergence of organaras led to the transformation of traditional cities to eukarcities, just as organelles substantially transformed prokaryotic cells to eukaryotic cells. The “citynucleus” regulates the whole city and integrates urban and rural areas, as well as the number of organaras and their spatial distribution, through policies, science, technology, culture, markets and finance. The cityplasm provides regulating and supporting services such as maintaining air quality, water cycling, soil and biodiversity. Eukarcities and organaras also have many “grey” infrastructures (such as cement, metal, glass, and synthetic plastic polymers) (Table S3) that are non-living materials just as eukaryotic cells have non-living materials such as calcified microtubules, interior materials of some vacuoles, and vacuoles,^[46] as well as collagen. This suggests that non-living components within a living system are a common feature.

The basic processes of a eukarcity couple the ecosystem-based loop with the organara-based loop (Figure 5). The flows of artificial goods, services and cultural information based on organaras are much greater than those based on cityplasm. Organaras interact with the city core

frequently by providing goods and services for people and by receiving feedback from people. Organaras also exchange goods and services, as well as information with other organaras. A eukarcity interacts with other eukarcities and is also constrained by upper organizational level systems (such as province/state and nation). The constraints include policy, culture, economic and environmental standards proposed by provincial or national central governments.

The super-cell city model informs a new management approach

The new principles revealed by the super-cell city model also require new rules to adapt to these new systems, from ecosystem management to organara management. In view of the “super-cell city” model, the new management approach mainly includes three aspects:

(1) Improving organaras following the optimized principles of organelles in terms of structure and function.^[38] First, more tightly closed ecosystems would be expected to increase efficiency and reduce the influence of climate, as well as reduce pollutant leakage. For example, air filters installed on the walls of livestock farms can prevent virus entry.^[47] Of course, closed ecosystems may also bring risks, such as facilitating disease spread and concentrating soil pollution from fertilizer and pesticide use.^[48] Moreover, further development of membrane structures by learning from organelle membranes that have complex structures and important functions^[49–51] could also be envisaged. For example, air temperature sensors, monitors and air-conditioners on the outer membranes of greenhouse improve the production efficiency of vegetables. Internal structures also need to be advanced by learning from organelles such as mitochondria and chloroplasts in which the inner membrane is divided into distinct regions to constitute separate functional domains.^[37,38] Inspired by these traits, organaras can also be compartmentalized by internal membranes into specialized subunits to increase efficiency, such as the multi-layers of vertical farms.^[12,36] The outer membranes and internal structures of organaras are preliminary, and it can be expected that increasing the structural similarities between organaras and organelles will greatly improve organara supply capacity of goods and services.

(2) Optimizing the number of organaras following the scale effects in response to the population size in cities for rational cost and benefit,^[5] which is similar to the number of organelles allocated in eukaryotic cells.^[52] As part of this larger process, the optimization of spatial pattern of organaras by learning from organelles can improve yields and reduce pollution. For example, the intense industrialization of dairy feedlots increases the pollution intensity per unit area of land and increases ecological risk.^[53] Building artificial wetlands near dairy feedlots can recycle and capture waste nutrients and greatly mitigate pollution.^[29] By analysing optimization principles of organelles in eukaryotic cells and by diagnosing existing problems, city functional and spatial structure can be improved to reduce pollution and optimize the spatial distribution and functionality of future cities.

(3) Increasing supply efficiency and robustness by regulating the metabolic networks of organaras according to the high metabolic efficiency and robustness of eukaryotic cells.^[54] The principle of bionic approaches is generally superior to “trial and error” methods^[55] because they are guided by natural selection, and can reduce trial times while increasing efficiency.

There has been much evidence that supports the utility of the super-cell city model in urban design and management. One successful case occurred in Lake Taihu in southeast China, where over the past 30 years water quality deteriorated and then recovered as a result of increasing the number of organaras (Figure 6A–C). The lake had relied on its abundant wetlands for wastewater purification for over 4000 years. After the 1980s, however, industrial waste and farmland fertilization exceeded the purification capacities of the natural ecosystem, and water quality rapidly declined. In Wuxi city, which draws its drinking water from Taihu, a famous drinking water interruption event occurred in 2007, when the water became non-potable. Since the economic upturn (Figure 6D), the number of wastewater treatment plants in all cities around Lake Taihu increased from 5 in 1985 to 331 in 2014 (Figure 6E), and water quality improved even though the population continued to increase (Figure 6F). This case clearly illustrates that optimizing the number of decomposition organaras has been a crucially effective strategy for mitigating environmental pollutions in industrialized cities. Together with industrial non-ecosystems, the industrialization of ecosystems increases the supply of goods and services, and reduces the ecological footprint per unit product.^[56] In China, greenhouse area is increasing while open farmland area is decreasing (Figure 6G). Industrial dairy feedlots are increasing while pasture areas are declining (Figure 6H). In contrast, forests and wetlands are continually being restored as economic development progresses (Figure 6I). These examples suggest that the information provided by the super-cell city model can guide the sustainable development of industrialized cities.

Despite the increasing role of organaras, the cityplasm is crucial in keeping the balance of energy fluxes, material, biological productivity and waste decomposition. The quality of the cityplasm, such as quality of air, water bodies, soil, and ecosystem health is mainly affected by organaras. For example, restaurants and dairy feedlots discharge wastewater causing water pollution.^[29] Now the cityplasm is frequently monitored by people and the data collected are fed back to the citynucleus which then modifies the institutions and policies for optimizing the city through regulating organaras as units. A considerable area of pasture and farmland may be converted into organaras in many cities as populations grow and space becomes scarce and more expensive. However, a substantial portion of land will remain as open farmland and pasture, just as much of the space in most eukaryotic cells is still cytoplasm.^[57] The cityplasm will continue to provide key ecosystem services and some goods in future eukarcities. For example, open farmlands, pastures and forests will continue to provide grain, fibre and raw materials;^[58,59] ocean, forest and wetland provide clean air, water and biodiversity etc. Therefore, the super-cell city model requires serious collaborative management between natural ecosystems and organaras in order to realize city sustainability. Furthermore, the idea that

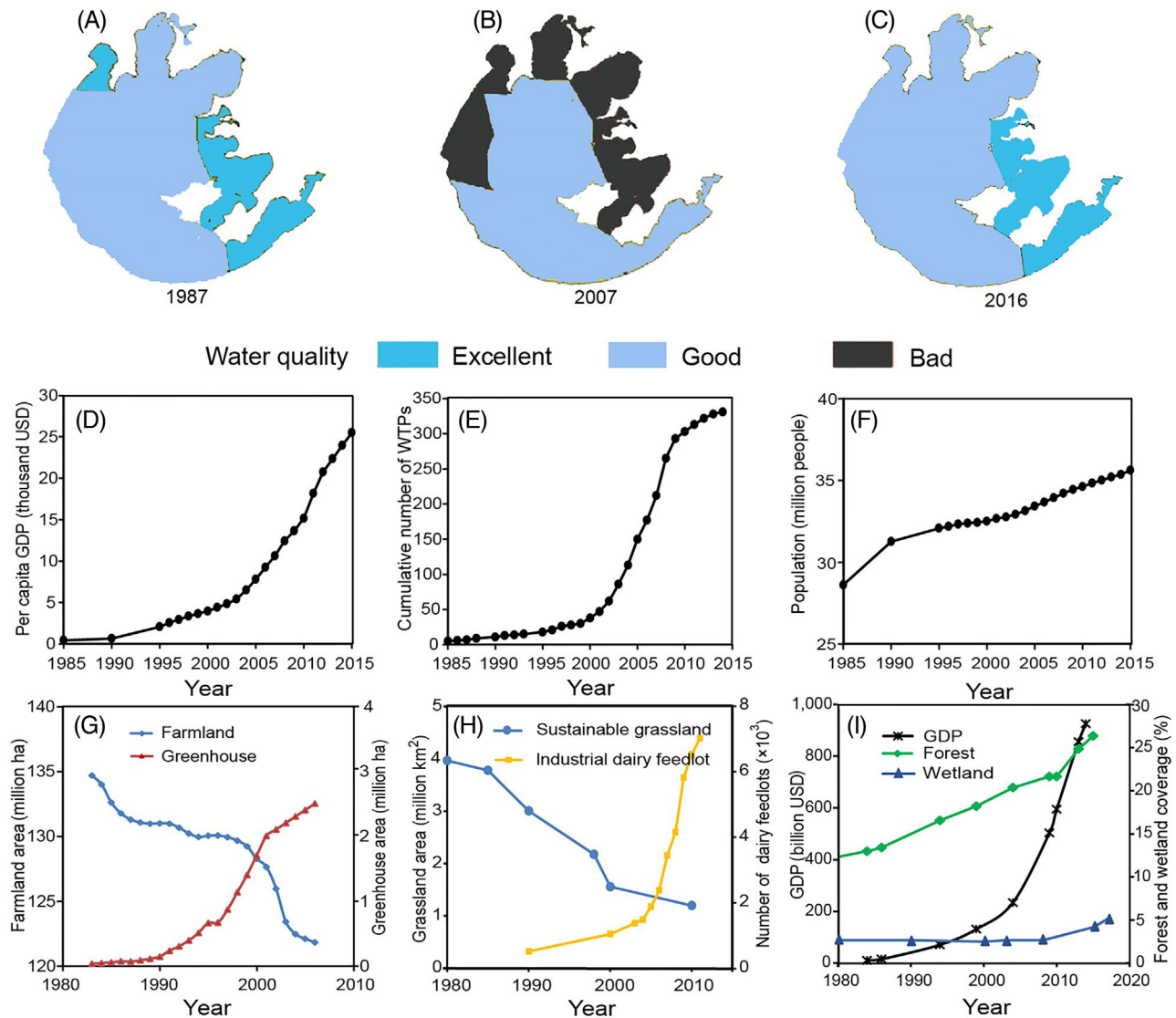


FIGURE 6 Historical trends in the number of organaras and cityplasm in China since the 1980s to 2010s. (A–C) Water quality of Lake Taihu, southeast China in 1987, 2007 and 2016, respectively. (D–F) Historical change of the social-ecological state in Lake Taihu area, including per capita GDP (D), annual increment of wastewater treatment plants (WTPs) (E) and population (F). (G) Decrease of open farmland area and increase of greenhouses. (H) Sharp decrease of sustainable grassland area and increase of industrial dairy feedlots. (I) Synergy between economic development and forest/natural wetland restoration

“cities can save the planet” has enjoyed a recent boon,^[60] and it could be realized through the cooperation of all cities worldwide.

Theoretical significance of the super-cell city model

Filling the gap in the model hierarchy of living systems by adding new living systems

A hierarchical living system model was built from the bio-macromolecular scale to the entire globe but left a sizable gap several orders of magnitude large between ecosystems ($\sim 10^3$ m in size) and the biosphere ($\sim 10^8$ m).^[61] The super-organism hypothesis^[15,17] placed “urban systems” into the hierarchical model at a point that

filled the gap between ecosystems and the biosphere (Figure S6). However, sustainable development requires the coupling of urban with rural areas,^[60] and a coupled urban-rural system (a city) averages $\sim 10^5$ m in size and forms an arithmetic sequence, 10^3 m, 10^5 m and 10^8 m, between ecosystems and global scale (Figure S6). Based on the evidence that we have presented here, we suggest that the super-cell city model should replace the super-organism model. The emergence of organaras forms the basis for eukarcities just as organelles are the basis of eukaryotic cells, revealing that the shared features between cities and cells can be scaled up and down in the hierarchy of living systems (Figure S6). We further suggest that, following the origin of life, the emergence of eukaryotic life^[62] and the appearance of humans, the emergence of the eukarcity is the latest evolutionary event.

Extending endosymbiosis theory from eukaryotic cells to the city level

The super-cell city model extends endosymbiosis theory from eukaryotic cells to the city level. According to endosymbiosis theory, eukaryotic cells were “big vacant cells” that assumed prokaryotic cells, such as cyanobacteria and spirochetes, to form a symbiotic fusion.^[63] There is evidence that some organelles retained their own genes, which can self-duplicate and interact with genes in the nucleus to achieve semi-autonomous regulation.^[40] For example, chloroplasts and mitochondria—besides being controlled by nuclear genes—also have their own DNA.^[63] Inspired by the endosymbiosis theory, we hypothesize that the origin of the eukarcity is a symbiotic fusion of organaras (enclosed ecosystems and enclosed non-ecosystems) with pre-industrial traditional cities. Like organelles, some organaras are also semi-autonomous in that in addition to being controlled by the city nucleus, they also have their own “genetic information” for duplication and operation.^[58] For example, wastewater treatment plants’ information systems include libraries, laboratories and offices that contain technology, records and management files (Figure S3). Cultural information is interpreted, copied, transmitted and modified, and constantly evolves.^[64] The internal structure becomes complex and some organaras start to manifest multi-component nature in their structure: for example, greenhouses have bees that live in symbiosis with crops. In sum, the super-cell city model adopts endosymbiosis theory to explain the evolution of the industrialized city, and also provides a theoretical basis for city research, design and management.

CONCLUSION

1. In this paper, we have envisaged the functional executors of ecosystem processes (such as production and decomposition) as organisms, and the process executors of eukarcity as organaras. Industrialized cities take organaras as the operating units and can optimize urban structures, processes and functions by learning from eukaryotic cells in traits and principles that have been optimized via evolution over billions of years. The rapidly urbanizing world can provide much empirical evidence for such studies.
2. The super-cell city model provides a solid basis in principle and in methodology for finding shared features among living systems and two levels of quasi-living systems (eukarcities and organaras). We present our model as a major theoretical step linking cities and cells and promoting new knowledge generation. In-depth researches on this conceptual model, such as further theoretical and mathematical models, offer intriguing challenges.
3. The super-cell city model encourages transdisciplinary studies and motivates an action-based, problem-driven urban research into university curriculum involving cities and cells. Through analogizing with cytology studies, the planning and management of cities can establish a set of life principles based on eukaryotic cell structure and process, and connect multiple disciplines, including science,

engineering, policy and culture in a coherent manner to promote in-depth research and practices.

4. The analysis in this article is just the tip of the iceberg, and our purpose here is to introduce a methodology for analysing an important feature of the changing world. At present, more and more places are taking cities as governance units worldwide. We suggest that the super-cell city model not only contributes to the development of every city, but also contributes to sustainable global development by guiding all cities towards supporting a model optimized for humans and sympathetic to the environment.

ACKNOWLEDGEMENTS

This work was financially supported by the National Science Foundation of China (Grant No. 31770434, 31870307) and SUTD-ZJU IDEA Seed (Grant No. SUTD-ZJU (SD) 201903). We thank X.Z. Liu, R.H. Xu, W.J. Han, L.F. Shang, S.N. He, B. Luo, G.Y. Luo, L.S. Lin, X. Wang, Q. Wang, Y.Y. Duan, W.L. Gu and Y. Chen, S. Liu, for the data collection and manuscript checking; Y. Geng, S.D. Niu for their comments.

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All data are included in the manuscript and online Supplementary Information.

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How to cite this article: Chang, J., Ge, Y., Wu, Z., Du, Y., Pan, K., Yang, G., Ren, Y., Heino, M. P., Mao, F., Cheong, K. H., Qu, Z., Fan, X., Min, Y., Peng, C., & Meyerson, L. A. (2021). Modern cities modelled as “super-cells” rather than multicellular organisms: Implications for industry, goods and services. *BioEssays*, e2100041. <https://doi.org/10.1002/bies.202100041>