Proceedings of the 14th International Space Syntax Symposium

#27.

Constraints on the City

How convergent evolution can improve our understanding of urban development.

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ABSTRACT

Convergence – the phenomenon where the same features develop independently in unrelated systems – is observed to occur in both biological evolution and the construction of human settlements. In biology, different species on separate evolutionary pathways are seen to repeatedly arrive at the same adaptive solutions to functional problems. Likewise, tools for analysing urban morphologies from the field of space syntax have uncovered a set of invariant forms which developing settlements tend towards, independent of cultural similitude. This paper assesses how applicable biological approaches to convergence are to space syntax research by exploring how each field uses the phenomenon to inform theoretical frameworks for understanding their objects of study. Specifically, it is shown that both fields see convergence as evidence for a kind of material logic underlying the autopoietic processes from which cities and organisms emerge. This logic can be interpreted in both cases as a set of constraints that restrict a vast range of morphological possibilities to the limited forms seen in reality. Having established these mutual perspectives, we apply Bill Hillier's hypothesis that universal laws of construction govern the morphogenesis of urban invariants to George McGhee's more general framework of functional and developmental constraints on evolution. This synthesis is the foundation from which a number of theoretical and analytical approaches to convergence found in evolutionary science are introduced that have potential utility for space syntax's research into urban form, demonstrating that convergent evolution as an interdisciplinary concept has multifaceted potential value for generating new knowledge in the study of cities.

KEYWORDS

Hillier, McGhee, convergence, morphogenesis, evolution

1. INTRODUCTION

In Chapter VI of On the Origin of Species (1859), Darwin sought to explain cases of remarkable similarity between distantly related organisms. His solution would come to be known as convergent evolution, when different lineages independently evolve the same or similar traits. To introduce this idea, he chose to illustrate it via an anthropomorphic analogy:

> I am inclined to believe that in nearly the same way as two men have sometimes independently hit on the very same invention, so natural selection, working for the good of each being and taking advantage of analogous variations, has sometimes modified in very nearly the same manner two parts in two organic beings, which owe but little of their structure in common to inheritance from the same ancestor.
>
> (Darwin, 1859, pp. 193–194)

Over a century later, evolutionary biologist George McGhee opened with this quotation in his contribution to a book compiling the proceedings of the 33rd Altenberg Workshop in Theoretical Biology (O'Brien, Buchanan and Eren, 2018). The workshop's goal was to explore the interdisciplinary value of convergent evolution when applied to archaeology, which McGhee remarked was a reversal of Darwin's endeavour to explain convergence by comparing it to human technology. In his chapter, McGhee outlined how perspectives on convergent evolution might be utilised to understand the culturally independent invention of morphologically similar stone tools. This paper has comparable ambitions, looking to apply convergent evolution as an interdisciplinary concept for studying cities, an artefact of an entirely different nature.

Pioneered in the 1970s by Bill Hillier and his colleagues at the Bartlett School of Architecture, space syntax is a field of study that seeks to understand the relationship between human societies and the spatial structure of the environments they construct (Bafna, 2003; van Nes and Yamu, 2021). For Hillier (2016, p. 200), one of the "most unexpected outcomes" of space syntax analysis at an urban scale was "the discovery that spatially speaking, and at a deep enough level, cities seem to be the same kind of thing". In other words, space syntax research has revealed certain morphological consistencies that developing cities appear to independently converge upon (Penn, 2021).

This paper will discuss the similarities between the phenomena, implications, and purported causes of convergence in urban and biological systems. It will be shown that, according to both evolutionary biology and space syntax, the phenomenon of convergence suggests there are influences restricting the morphological possibilities of their respective objects of study to the limited number of forms seen in reality. This connection will justify a synthesis of these two perspectives, where Hillier's hypothesised mechanism for the morphogenesis of urban invariants will be understood through McGhee's generalised framework of evolutionary constraints. From this, a number of novel analytical and theoretical approaches to urban convergence will be proposed, adapted from biology, demonstrating that convergent evolution is an interdisciplinary concept with strong potential applicability to urban studies.

2. CONVERGENCE AS A PHENOMENON

2.1. Convergent evolution

In biology, convergence occurs when two unrelated species independently evolve the same or similar traits. The existence of convergent evolution has historically been self-evident to biologists, manifesting as visually identifiable similarities between organisms whose phylogenetic distance is too great to presume shared inheritance. Such similarities include wings for flight in bats and birds and the fusiform body shape of fish and porpoises (Seed, Emery and Clayton, 2009; McGhee, 2011; Stayton, 2015). Although recent literature has called for the use of more rigorous statistical measures to verify convergence, the consensus appears to be that these classic examples remain valid case studies (Stayton, 2015). Convergent evolution is widespread: analogous traits are observed between species across multiple kingdoms of life and at scales ranging from body plans to the folding structures of proteins (McGhee, 2011; Stayton, 2015). Finally, the phenomenon can be a valuable resource for research in evolutionary science. The independent development of a trait on multiple occasions can allow researchers to undertake comparative analysis, inferring the shared processes that may have led to its repeated evolution (Stayton, 2015).

2.2. Urban convergence

This paper establishes the term *urban convergence* to refer to the tendency of cities to independently develop morphological similarities in spite of geographic and cultural differences. Unlike convergent evolution, which often produces visually apparent likenesses, the similarities that arise in cities are less immediately detectable. The phenomenon was first demonstrated via axial map analysis, a method used in space syntax to investigate the built environment at an urban scale (Hillier, 2002). An axial map is created by drawing a settlement's least and longest straight lines of accessibility and visibility (axial lines) until all of its open spaces are covered (Hillier and Hanson, 1984; Hillier, 1985), generating a reproducible model that conveys, and thereby supports the comparative analysis of, the structural properties of a street network (Weissenborn, 2022).

In recent years, the use of axial maps has diminished in space syntax's urban analysis. The field now tends to view segment maps – a derivation wherein axial lines are further divided wherever they intersect one another – as a preferable representation of the street network (Griffiths, 2014; Weissenborn, 2022). Though this method allows for more nuanced analyses of the relationship between human behaviour and space, these ramifications lie outside the scope of this paper. We will thus focus our attention on the axial map, as it is the foundational method of urban analysis in space syntax and remains an effective technique for illustrating emergent structures in urban morphology.

Fig. 1 shows the axial maps of two cities: Manchester (UK) and Hamedan (Iran). To Hillier, these are both instances of the most common type of settlement structure: deformed grids (Hillier, 2002; 2012). Found across the world, these settlements are characterised by islands of buildings surrounded on all sides by linearised open space, forming a structure resembling a grid that has been subjected to spatial distortion. This distortion occurs axially, meaning no streets strike through the entire network, and convexly, in that irregularities in the dimensions of convex space produce a "pattern of wider and narrower spaces" (Hillier, 1999a, p. 92). The deformed grid's prevalence across small-scale hamlets suggests that it is the result of an unplanned, bottom-up development process enacted by many spatiotemporally distributed agents (Hillier, 1989; 2002; 2012). It is thus especially surprising to find that, as deformed grid settlements grow, similar structural patterns emerge.

Axial maps demonstrate similarities in the morphology of deformed grids at multiple scales of emergent complexity, with the simplest being those found in the geometric properties of axial lines. The axial maps of Hamedan and Manchester are found to be composed of a "small number of long lines and a large number of short lines", a dynamic that can be expressed as a near-logarithmic distribution of line length (Hillier, 2002, p. 157). This pattern is shared across all instances of deformed grids, yet is more pronounced in larger cities, indicating a convergence towards morphologies with fewer, longer lines as settlements grow (Hillier, 2002; Weissenborn, 2022). Another invariant can be observed in the angles of incidence, those measured at the intersections of axial lines. Across deformed grids, there are many intersections at near-right angles and many so obtuse as to be almost straight, but very few between these two extremes (Hillier, 1999). These two improbable distributions are correlated in axial maps, creating a pattern where long lines generally connect with other long lines at highly obtuse angles, whereas shorter lines are more likely to connect almost orthogonally to one another (Hillier, 1999b; Weissenborn, 2022). This has an organising effect on the street network of deformed grids, resulting in the emergence of larger-scale invariant structures.

The most immediately apparent emergent structure in large deformed grid networks has been termed the generic city. Here, the clustering and sequencing of axial lines with shared geometric properties structures the street network as a “dual system” consisting of “two interrelated sub-networks” (Hillier, 1999b; 2014, p. 101). These are the “foreground network”, composed of fewer, longer lines whose obtuse intersections form a sense of “route continuity”, and the “background network”, which is made up of shorter lines with orthogonal intersections giving rise to more localised, grid-like structures (Hillier, 2014, p. 101). Within this dual system, there are convergences as well as dissimilarities: though the background network appears more variable, reflecting the spatial culture of the region in which it is built, the form of the foreground network remains consistent across cities (Hillier, 2002; 2012; Weissenborn, 2022). Given the foreground network’s overlap with the background network, this structure is often obscured in axial maps, and must be highlighted using integration analysis.

Integration is one of several measures used in space syntax to analyse axial maps. It is derived from the measurement of depth, the minimum number of intermediary axial lines to walk from one line to another. Naturally, each axial line in a network has a certain depth value with respect to every other one. Integration is thus a function of all of these depth values; an axial line with a higher integration value means that from there it takes fewer steps on average to reach any other line in the network (Hillier, 1989). In calculating integration, the elements of a space are analysed as if they were interconnected nodes on a graph, thereby omitting any information about the axial lines’ metric qualities. It is therefore a configurational, or topological, measure concerned only with the connectivity of a spatial part to its whole, irrespective of properties such as distance or angle of incidence (Hillier and Hanson, 1984; Penn, 2021).

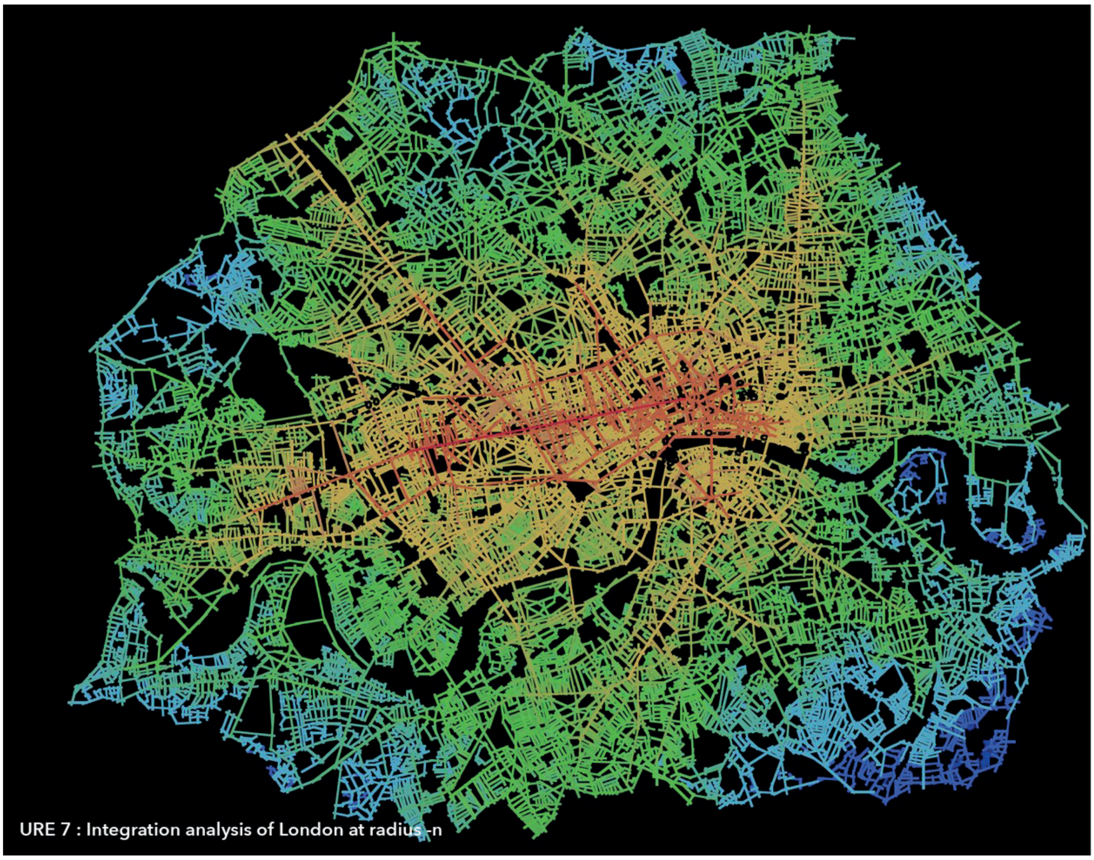

Figure 2: Axial map of London, UK, subjected to integration analysis (Hillier, 1999a, Plate 2).

Calculating the integration value of every line in a city allows us to colour-code the axial map. Fig. 2 is an integration analysis map for London (UK), where more integrated lines are presented with a warmer colour. The foreground grid is thus illuminated and its form revealed to be reminiscent of a deformed wheel, a city-wide structure made up of the most integrated lines in the street network. It features a central integration core that stretches out linearly in multiple directions, forming spoke-like "radii [that connect] the centre of the [city] with its periphery" (Hillier, 2002; 2012; Weissenborn, 2022, p. 637). Remarkably, the deformed wheel structure is found so consistently across all urban systems that it has been described by Hillier (2012, p. 26) as a "near-universal form in self-organised cities".

The comparative analysis of axial maps demonstrates a range of features that cities independently converge upon as they develop, such as the "pervasive geometric construction" (Hillier, 1999b, p. 174) of the street network. But perhaps more striking are the global forms that arise from this, particularly the deformed wheel structure of the foreground grid. Throughout space syntax literature, the word 'genotype' is frequently used to describe these global structures as typological invariants, a term borrowed from biology originally referring to an organism's genetic composition (Hillier, 1985; 1989; 1999a). The counterpart of this concept in biology is the phenotype, which is the set of traits an organism displays in reality and the physical embodiment of a genotype's encoded description (Steadman, 2008). Importantly, two organisms may share very similar genotypes but, due to different environmental conditions, exhibit variations in their phenotypes. Thus, when space syntax describes the deformed wheel as a 'genotype', this emphasises that although individual examples of deformed wheel cities display "phenotypic" differences in topography and size, they share a deep structure that is expressed configurationally (Hillier, 1999a; Penn and Turner, 2018, p. 7).

The genotype/phenotype framework was first authoritatively stated in space syntax by Hillier and Hanson (1984). Here, they insisted that the distinction between universal abstractions and varied particulars should be the limit of the concept's resemblance to its biological counterpart, because attempting to integrate additional features from biology caused the analogy to break down. Perhaps symptomatic of this limitation, the 'genotype' concept becomes troublesome when considering the parallels between urban and evolutionary convergence. The problem stems from the essential mechanism of genetic inheritance; DNA, the organic material that constitutes biological genotypes, is transmitted to an organism's progeny in reproduction. Therefore, if we were to say that two species possess the same trait as a result of *genotypic* likeness, we would be asserting that their similarities are the result of shared ancestry and therefore not convergent. As such, describing two settlements which both exhibit the deformed wheel structure as having the "same genotype" (Hillier, 1989, p. 10) suggests that this similarity is the product of something other than independent, and thus convergent, urban growth. Due to the term's inadvertent implication of the absence of convergence, we will later propose an alternative term to 'genotype', also borrowed from biology but with less conflicting conceptual baggage. Until then, phrases such as 'invariant morphologies' or 'convergent structures' will be used in its place.

3. THE IMPLICATION OF CONVERGENCE

Maturana and Varela (1980; 1998) make a distinction between two types of system, hinging on the causal relationship between its functioning and the organisation of its components. Autopoietic systems are those whose organisation arises as a product of their functioning: the components and their arrangement develop continually as a result of the operation of the system, rather than being conceived of a priori. For Maturana and Varela (1980), this category encompasses all living systems, which evidently self-organise through two interrelated development processes: ontogeny for individual organisms and evolution at a species-wide scale. In contrast, the organisation of allopoietic systems are not the product of their functioning. Most artefacts – things made by humans – are included in this category: for example, a clock's functioning is a process entirely independent of the production and arrangement of its constituent parts by an "(external) designer" (Riegler, 2002, p. 344). However, there undoubtedly are a set of artefacts that are not designed, but instead develop through a process of self-organisation, or autopoiesis. In Hillier's words (1985, p. 164) these are the "artificial systems [that have] the curious property of being both man-made and not understood by man", such as "languages, cities and societies". The autopoietic nature of cities is an accepted premise in space syntax, having been stated explicitly by Weissenborn (2022; p. 631), and implicitly – "self-organised cities" – by Hillier (2012; p. 26). This categorisation lets us perceive urban growth and biological evolution as kindred phenomena: non-teleological developmental processes characterised by self-organisation. This, in turn, facilitates the comparison of the significance of convergence to both.

In both space syntax and evolutionary biology, the presence of convergence implies that there is a material logic (Weissenborn, 2022) underlying the autopoietic development processes of their respective objects of study. In biology, this is characterised as limitations which restrict the possible designs that evolution can exploit, from which McGhee has established a framework of two constraints to understand convergence in more general terms. Correspondingly, it is hypothesised in space syntax that the invariant forms found across human settlements are the result of two interacting factors dictating the organisation of urban systems. These perspectives will be synthesised by interpreting space syntax's theory of urban morphogenesis through the generalised framework of evolutionary constraint, demonstrating a strong link between the disciplines and justifying the application of biological approaches to convergence in urban studies.

3.1. How organisms converge

To McGhee, the pervasiveness of convergent evolution demonstrates the existence of limitations to the possible forms that evolution can generate. McGhee (2011) proposes that these limits can be discriminated into two categories, which generate convergence in different ways. The first are functional constraints, which are imposed by the species' external environment and include the laws of physics (McGhee, 2022, p. 17), the requirements of high metabolic cost-effectiveness (Speed and Arbuckle, 2017), and selective pressures specific to the species' habitat (Thomas and Reif, 1993). These constraints prevent organisms with poorly functional morphologies from reproducing, thereby restricting evolutionary possibility and producing convergence.

The second form of evolutionary constraint is developmental. These are internal to the adaptor and relate to an organism's possible evolutionary trajectories being restricted by its previous adaptations and current form. A specific case of this can be observed in the convergent evolution of the camera-type eye in cephalopods (e.g., squid) and vertebrates, the product of independent modifications to the same shared gene: *PAX6*. This gene, an ancestral trait in both cephalopods and vertebrates, would have been more susceptible to certain modifications than others. This gave way to the convergence of camera-type eyes because the possible adaptations to *PAX6* were, in both taxa, equivalently restricted to those that were 'developable' (McGhee, 2011; 2022). More universally, all organisms are subject to the same "principles of organisation" that derive from the physical properties of their shared elemental building blocks and their combinatorial structures: "carbon, L-amino acids, peptides [and] cells". These principles "determine the internal geometry and structural design potentials of the fabrics they can form", identically limiting the possible traits that all organisms can develop (Thomas and Reif, 1993, p. 350; McGhee, 2011). Developmental constraint is thus a more absolute form of constraint than its counterpart. As McGhee (2015, p. 4) states, if a certain trait cannot be developed, then "the question as to whether [it is] functional or non-functional is moot". It is only after the internal developmental constraints have been imposed that the functionality of possible forms in their external environment becomes relevant.

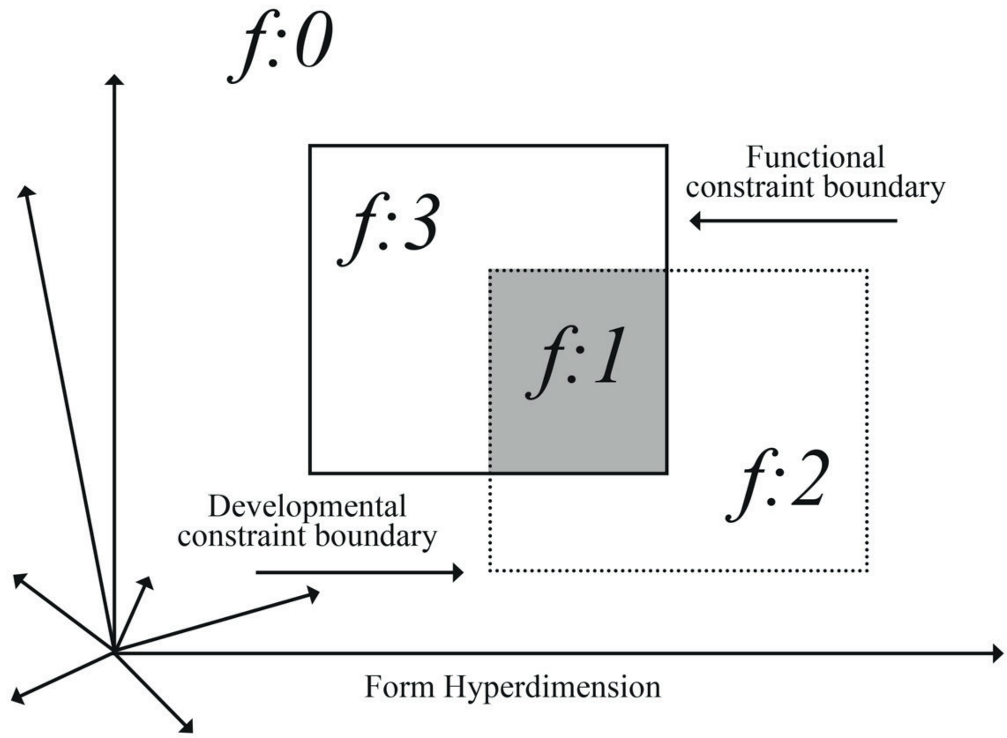

Figure 3: McGhee's (2011, p. 249) proposed theoretical morphospace of organic life.

In a consideration of the convergence of morphological traits, McGhee (2011) extended the concepts of functional and developmental constraints by visualising them in a theoretical morphospace (Fig. 3). This is a framework consisting of a hyperdimensional space where each dimension represents a measurable morphological trait of any organism. Each coordinate in the morphospace therefore describes one possible biological form, and the set containing all coordinates includes every possible biological form. With this view, convergence can be interpreted as two or more organic forms moving through the morphospace via evolutionary mechanisms from distinct to overlapping regions. McGhee envisions constraints in this space as the boundaries of sets: functional constraints encompass the set containing every form that is functionally viable (f:3), and likewise, developmental constraints encompass the set containing every form that is developmentally viable (f:2). Naturally, every species that has adapted to its niche is both developmentally and functionally viable, so they are contained within the intersection of these sets (f:1).[1]

Conceptualising the two constraints as the boundaries of spatial sets allows for a more structured inquiry into the nature of, and limitations to, morphological possibility and how this relates to the phenomenon of convergence. Perhaps more importantly however, the morphospace concept has also seen practical use through the construction of analytical morphospaces from real-life fossil records, which have helped provide empirical evidence of limitations to evolution. Before discussing this though, it is first important to explain space syntax's conjectural explanation for urban convergence and how this aligns with McGhee's framework of developmental and functional constraints.

3.2. How cities converge

A number of articles produced in the later stages of Hillier's career were dedicated to explaining the phenomenon of urban convergence. He hypothesised that the emergent form of any growing city is largely the product of two factors universal to human settlements (Hillier, 1999a; 2002). These factors are both related to the property of integration and are conjectured to interact to produce convergent urban morphologies.

The first factor that Hillier proposes is shared across all cases of city development is a set of spatial laws. These laws are autonomous, meaning their effects are "independent of human will or intention", and govern the way in which local spatial moves impact the configurational properties of the global system (Hillier, 2002, p. 154). Hillier (1999a; 2002; 2012) demonstrates these laws formally by analysing the effect that placing an obstructive object has on a theoretical spatial system's global integration (the total integration of every element in the system).[2] In doing this, he shows multiple ways in which the object's placement has a predictable effect on the system as

[1] It is worth noting that McGhee's theoretical work on convergent evolution was criticised in a review by Powell and Mariscal (2014). However, their critiques, which concern McGhee's views on the philosophical implications of the phenomenon, are largely tangential to his framework of limitations to a morphospace discussed here.

[2] The measure Hillier initially used to demonstrate the configurational effects of object placement was global depth. However, integration is a fine proxy to use here, as it is also calculated from depth values and was later used by Hillier (2012; Fig. 5) as the measure to formally demonstrate these laws.

a whole. One of these, the law of centrality, is illustrated in Fig. 4 in the context of placing an obstruction directly between two other objects. What is shown is that placing the obstruction in the centre of the system reduces its global integration more than placing it at the periphery. This can be intuitively understood by considering that a peripheral obstruction will block potential movement through the system less because more possible trips through the space are direct and "do not require deviations around the blocking object" (Hillier, 2012, p. 16). Thus, equidistant placement of the obstruction reduces system-wide integration more dramatically.

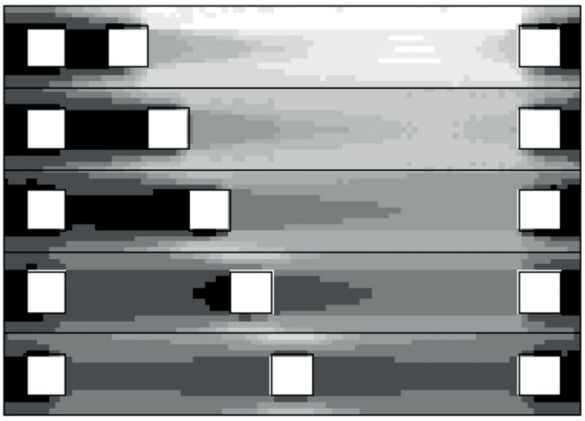

Figure 4: A demonstration of the law of centrality (Hillier 2012, p. 18). Spatial regions with greater integration are shaded lighter.

How might this abstract law manifest in urban systems? As established, the development of a deformed grid settlement can be conceptualised as the largely uncoordinated placement of buildings by multiple distributed human agents. We can consider a scenario where an agent must place a building that will necessarily block one of two differently sized axial lines in the network. A corollary of the law of centrality is that choosing to obstruct the longer line would cause the system's global integration to diminish to a greater extent. Therefore, an agent whose strategy is to preserve integration in the system would choose to block the shorter line, whereas an agent looking to minimise it would do the opposite (Hillier, 2002; Weissenborn, 2022). One can imagine how a hypothetical settlement whose inhabitants are united by one of these strategies might develop. An integration-preservation society would preferentially block shorter axial lines, retaining their longest and most integrated ones and producing a street network characterised by "a few long lines and a greater number of short lines" (Weissenborn, 2022, p. 638). Conversely, an integration-minimisation society would consistently block their longest axial lines, creating a labyrinthine system of streets of equal length with considerably lower global integration. These contrary processes were illustrated by Hillier (2002) through modifications to the rules restricting a simplified model of settlement formation, the outcomes of which can be seen in Fig. 5. Both show the aggregative product of randomly placing cells (representing buildings), restricted on the left side by the rule to “conserve longer [axial] lines”, and on the right side by the inverse (Hillier, 2012, p. 21). As anticipated, the global integration of the former is greater.

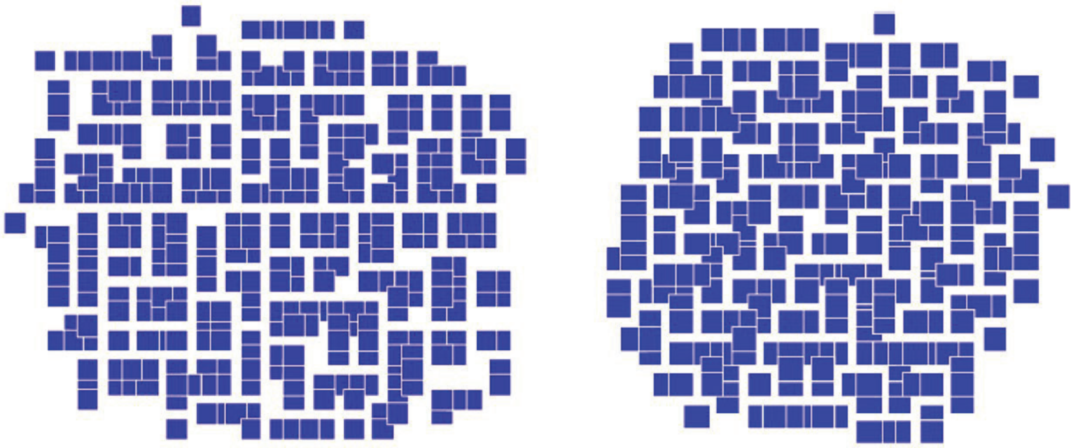

Figure 5: Products of a restricted-random process of cell aggregation modelling two strategies for settlement formation. The left side represents an integration-preservation strategy that conserves the system’s longest lines, and the right side the inverse (Hillier 2012, p.21).

Of the two cell aggregates, only the one produced by the integration-preservation process bears a resemblance to the urban invariants discussed earlier. By avoiding the obstruction of the network’s longest axial lines, some streets are able to stretch from the centre to the periphery of the system in a manner reminiscent of the deformed wheel structure. Furthermore, the obstruction of all but the longest lines produces a street network that most closely approaches the near-logarithmic distribution of line length observed in real cities (Hillier, 2002). Therefore, as human settlements grow, their form usually tends towards one that is indicative of the preservation of global integration. To understand why this is, the relationship that integration has to the dynamics of urban activity must be outlined.

The first aspect of integration to note is that it is essentially a measure of accessibility. It represents how easy it is to reach one axial line from every other in the system in terms of the number of intermediary steps (Hillier, 2012). It is thus appreciable that a settlement with greater global integration would feel more habitable to a citizen because it is easier to move through. Secondly, when considering differential integration *within* a system, it is reasonable to expect that the degree of integration of an axial line in some capacity determines the potential movement along it; given a choice of two destinations, a pedestrian would generally choose the more accessible option. This is the theoretical basis underlying one of space syntax’s key discoveries, that of any variable for measuring the spatial qualities of a street network, independent of other factors such as land use, integration is empirically the best predictor for pedestrian movement

(Hillier et al., 1987; 1993). Simply put, greater foot traffic is more likely to occur in real cities' more integrated areas, other things being equal.

There is also evidence that more integrated areas are better associated with microeconomic processes. Shops and markets are more likely to be found along more integrated axial lines, while religious and civic buildings are "more variably located" (Hillier, 2002, p. 162). The well-integrated spokes of the deformed wheel are generally long high streets linking the surrounding city to a concentrated hub of retail activity, with low-integrated residential areas lying in the interstices (Hillier, 2002). Hillier's (2012, p. 26) explanation for this correlation is that, because integration influences movement patterns, it "also over time shapes land use patterns, in that movement-seeking land uses, such as retail, migrate to locations which the network has made movement-rich, while others, such as residence, tend to stay at movement-poor locations". In summary, more integrated spaces have better accessibility, and therefore higher levels of pedestrian movement, in turn attracting and subsequently benefitting microeconomic activity (Hillier, 1996).

It is from a consideration of the above that Hillier (2002; 2014) posits the second factor that generates urban convergence. He argues that microeconomic activity is a universal social force invariantly driving settlement growth towards a structure which maximises grid-induced movement. Integrating this with the autonomous spatial laws already discussed, we come to Hillier's ultimate hypothesis regarding urban convergence. In his view, all developing urban systems are provided by their shared intrinsic spatial laws with a range of possibilities for structuring space. These possibilities are the emergent global products of placing buildings according to different strategies, independently applied by distributed human agents. Collectively driven by the microeconomic social force universal to cities, these agents employ the law of centrality to preserve the growing street network's global and local integration, optimising system-wide accessibility and inducing movement towards certain areas that will become occupied by retail land uses. Resultantly, cities most often tend towards a spatial form indicative of an integration-preservation strategy of urban growth. This is manifested in the invariant distribution of line lengths, as the strategy necessitates the conservation of longer axial lines at the expense of shorter ones, producing the global emergent structure observed universally in cities: the deformed wheel.

3.3. Urban convergence as the product of constraints

Parallels become apparent when comparing how space syntax and evolutionary biology approach the phenomenon of convergence. As their objects of study develop, pervasive similarities are observed to emerge independently and autopoietically. In explaining this phenomenon, both fields propose that there are universal influences directing cities' and species' respective processes of self-organisation towards a limited number of forms. Elaborating on the nature of these influences, McGhee and Hillier independently strike upon the notion that they can be divided into two kinds. For McGhee, convergent traits between species are the result of the intersecting constraints of functionality and developability. Likewise, Hillier describes how invariant urban morphologies are the product of an interplay between a shared microeconomic social force and autonomous spatial laws intrinsic to human settlement construction. From these analogous perspectives, a strong connection between the two fields can finally be made.

Hillier consistently evokes the language of constraints when discussing the causes of urban convergence. Perhaps most explicitly, in Space is the Machine (1999a), he writes the following:

> If we think of cities as aggregates of cellular elements – buildings – linked by space, then … spatial laws are the 'first *filter*' between the boundless *morphological possibility* for such aggregates and the properties of the vanishingly small *subset* we call cities. Social and economic processes are then the second *filter*, guiding the basic paths of evolution this way or that to give rise to recognisable types.
>
> (Hillier 1999a, p. 265, emphasis added)

This quotation displays a powerful resemblance to McGhee's idea of evolutionary constraints in a theoretical morphospace. The autonomous spatial laws and the microeconomic social force are here described as independent "filters" limiting a vast range of hypothetical urban morphologies towards the narrow subset seen in reality, in the same way that functional and developmental constraints are said to restrict the process of evolution towards similar forms. It is therefore reasonable to assert that, for both cities and species, convergence is purported to be the product of morphological restrictions imposed by universal constraints.

In the quotation, Hillier envisions that the constraints imposed by the spatial laws precede those imposed by social processes, reframing his conjecture that potential microeconomic activity is maximised in urban systems by constructing highly integrated aggregates whose forms are ultimately dictated by the law of centrality. This highlights a parallel with McGhee's binary framework of constraints, where evolution is understood to be limited first by what is possible for the species to develop and secondly by whether those possibilities are functional in its environmental context. This provides a preliminary indication that spatial laws behave as developmental constraints, and the social force as a functional constraint.

There is yet further justification for these groupings. Hillier's spatial laws are hypothesised to autonomously constrain the potential aggregate forms of a settlement by dictating the emergent consequences that strategies for local building placement have on the global configuration of space. This is similar to a form of developmental constraint exemplified earlier: principles of organisation inherent to the elemental building blocks of life, which define the possible forms that larger structures can take. Both of these cases describe how a system's properties are determined by fundamental rules that govern the arrangement of its constituent parts. In this way, autonomous spatial laws and principles of organisation are constraints internal to their respective systems, restricting morphology to what is developmentally possible. Turning to the other grouping, the microeconomic social force constrains urban morphology by driving settlement aggregation towards a form which maximises integration. In turn, the system becomes more accessible, and highly integrated regions form retail hubs due to their influence on pedestrian movement. Altogether, the social force generates urban convergence not by way of deterministic laws, but by directing cities to morphologies that optimise microeconomic activity. In other words, the constraint imposed by the social force restricts settlements to forms that are, in terms of accessibility and thus economics, functional.

The correspondence between the perspectives on convergence from space syntax and evolutionary biology is now fully appreciable. For both biological evolution and urban development, convergence has been conceptualised as the product of constraints limiting the potential morphologies that can be realised. In biology, McGhee conceives of a binary typology which distinguishes constraints caused by external, functional factors from those imposed by internal laws of the adapting system. This dichotomy remarkably aligns with the two factors hypothesised by Hillier to generate convergence in cities. Specifically, the universal social force can be understood to operate as a functional constraint by limiting urban systems to morphologies that maximise microeconomic activity and the autonomous spatial laws as developmental constraints defining what is possible to construct from the system's component parts. Having established this connection, it is now possible to explore the possible ways that approaches to convergent evolution might inform our understanding of urban convergence.

4. ANALYSING CONVERGENCE

The analogous explanations for urban and biological convergence laid out thus far are based upon inductive reasoning – for both, the presence of constraining factors was inferred from the prevalence of independently developed similarities. This alone is not enough to assert that these theories are unequivocally valid; Hillier (2002, p. 173) explains that his hypotheses regarding the genesis of urban invariants are currently conjectural, and require "a whole research program to test them". However, in the biological literature, there are several instances where the existence of evolutionary constraints has been empirically demonstrated with deductive models, often involving the analysis of a morphospace built from actual fossil data (Thomas and Reif, 1993). Unlike McGhee's *theoretical* morphospace, these morphospaces are more specific, focusing on particular traits that have converged within limited taxa. With these models, more substantial (albeit less universal) claims can be made about the constraints imposed on evolution.

4.1. Empirical morphospaces

Raup's investigation of the geometric properties of ammonoid shells was the first implementation of the morphospace as an analytical tool in biology (Raup, 1967; Budd, 2021). From three metric variables, a set of two-dimensional morphospaces were constructed and compared against the fossil record to ascertain which form variants had evolved in reality. This revealed that the forms that had evolved were "restricted to one part of the geometric spectrum", with a large portion of the morphospace left unoccupied (Raup, 1967, p. 64). This is illustrated in Fig. 6, where computer-generated shell forms with equivalents in the fossil record are only found in the lower-left region of the space, as demarcated by the heavy line. McGhee (2015) cites this as one of several morphospace models that empirically demonstrate the existence of constraints upon evolution. Experimental evidence suggests that as shell forms deviate outside of this region, their swimming efficiency decreases (Chamberlain, 1981, cited in McGhee, 2015). As such, it is hypothesised that this form restriction is a result of natural selection towards higher swimming efficiency, or, in McGheeian terms, a functional constraint imposed by hydrodynamics (McGhee, 2015).

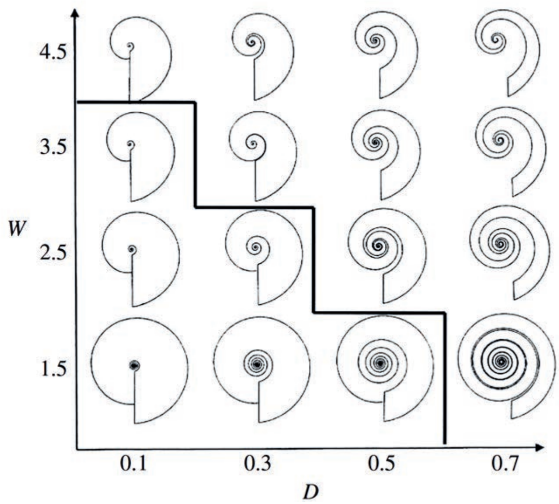

Figure 6: A morphospace of ammonoid shell geometry. Forms observed in reality are found to the left of the heavy line. Originally by Raup (1967), modified by McGhee (2015, p. 2).

McGhee utilised a second morphospace, one of brachiopod shell forms, to illustrate the impact of developmental constraints. More precisely, this model shows how the possible forms that a group can evolutionarily exploit lie at the intersection of viability as delimited by the two constraint types. Brachiopod shells are constructed from two valves, a ventral and a dorsal, whose respective whorl expansion rates increase along the x- and y-axes of Fig. 7. Like the previous example, the region of actualised shell forms is encompassed by a heavy line. However, the occupied region of this morphospace has both upper and lower bounds, reflecting two separate restrictions on shell morphology. The upper limit is again a result of functional constraint. The ideal brachiopod shell form is the sphere because it maximises internal volume for filter-feeding efficiency whilst minimising the surface area of the shell and thus its metabolic cost of production. Higher whorl expansion rates are therefore less prevalent because this results in less spherical shell forms that are selected against (McGhee, 2015; 2018). Developmental constraint, conversely, manifests as a minimum threshold value for whorl expansion rate, below which the dorsal and ventral valves begin to overlap. Shell forms with this overlap, distinguished by a white fill colour in the figure, would see their whorls interpenetrate each other, a geometric impossibility imposed by the nature of brachiopod shell structure. This is a developmental constraint because, even though these forms are functionally viable, they cannot be produced due to structural limitations inherent to brachiopod biology (McGhee, 2015).

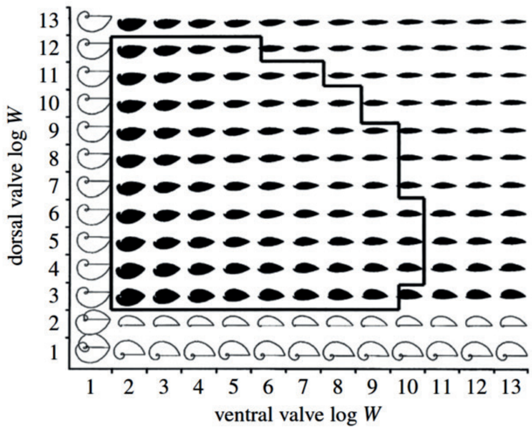

Figure 7: A morphospace of brachiopod shell geometry (McGhee, 2015, p. 2). Forms observed in reality are contained within the heavy black line.

4.2. An urban morphospace?

Since its inception, the concept of the morphospace has seen a number of interdisciplinary applications, including in the analysis of man-made artefacts. Most relevantly, Steadman (2014, p. 202) generated several morphospaces visualising the distribution of schools' floor plans according to measures such as their compactness and the percentage area devoted to corridors. Similarly, McGhee (2018) proposed that morphospaces could be used in archaeology to understand whether functional and developmental constraints impacted the designs of prehistoric stone tools. However, from our research, a morphospace that analyses the development of undesigned autopoietic artefacts has not yet been created. This is likely due to the relative obscurity of both the morphospace technique and the idea that such objects can exhibit convergence. It is in this context that we propose a possible avenue for future research in the study of cities: a morphospace of urban street networks. This would require a large number of axial maps to be gathered and measured for a number of morphological properties. From this, an array of scattergrams could be produced to understand the extent to which the field of urban morphological possibility is occupied by real-life cities.

A number of these graphs would ideally exhibit an area of clustering delimited by boundaries past which no cities are plotted. This would leave empty regions of morphospace, which would be evidence in support of there being constraints on the development of urban form. It is possible to hypothesise a property wherein one of these boundaries might manifest. In cities, functional constraint is imposed by the microeconomic social force. One would therefore expect to see almost all cities clustered in a region of high integration, as well as a lower integration threshold that no city drops below. Conversely, it is harder to predict how developmental constraint might be demonstrated due to the difficulty of envisioning the morphology of a city unrestrained by spatial laws. A morphospace of urban form nonetheless has strong potential as a tool for visualising the extent of morphological convergence in cities and identifying the degree to which the various properties of street networks are limited. This, in turn, may corroborate the existence of functional and developmental constraints on urban development, supporting Hillier's hypothesis that urban invariants are the result of a shared microeconomic social force and autonomous spatial laws.

5. REFRAMING THE SPATIAL GENOTYPE

Earlier, it was highlighted that the term 'genotype', as it is used in space syntax, can be problematic when discussing urban convergence. We now return to this issue through a discussion of an empirical morphospace that uses nominal rather than quantitative variables, a change in approach that will be shown to have consequences for the way that convergent features are conceptualised. This unique perspective will be applied to the study of urban invariants, finally allowing the concept which underlies the spatial genotype to be reframed.

5.1. The skeleton space

In spite of their utility, the empirical morphospaces examined thus far have been fairly limited in their scope, focusing on quantitative variations on a single body type. A more comprehensive morphospace would account for a larger diversity of forms across a wider range of taxa. This was the motivation behind Thomas and Reif's (1993) construction of a morphospace containing every skeletal structure in the animal kingdom. The key divergence from the approaches outlined prior is that nominal variables, rather than quantitative ones, formed the dimensions of their skeleton space, meaning that a greater variety of morphologies could be described, thus producing a more universal model.

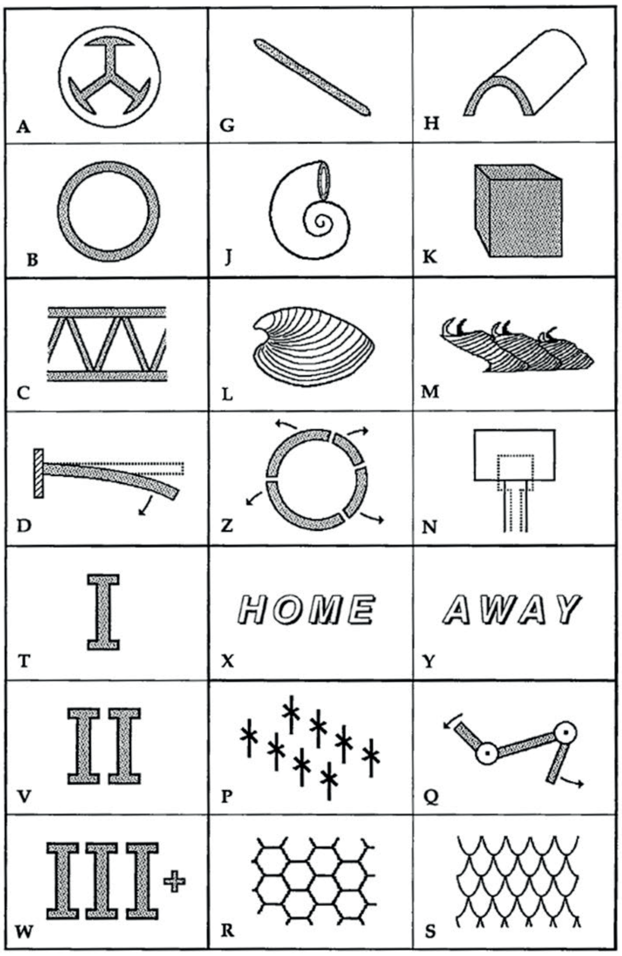

Figure 8: The states constituting the seven dimensions of the skeleton space (Thomas and Reif, 1993, p. 345).

Thomas and Reif's skeleton space is built from seven dimensions, each composed of several states defining different rules for skeletal geometry or construction (Fig. 8). For example, the rigidity dimension has two states: skeletal parts can either be unbending (C) or flexible (D). As intradimensional states are mutually exclusive, every possible skeletal form can be represented by a seven-letter code denoting for each dimension which state they fall into. Thomas and Reif (1993, p. 344) emphasise that these codes are structural paradigms, schematic models formed from idealised categories that only generally represent the “less sharply defined” properties of “real skeletons”. Nevertheless, a wide range of animal skeletons across multiple phyla were categorised under this framework, allowing broad patterns, produced by evolution’s exploitation of possible skeletal structures, to be identified.

The skeleton space was analysed by assessing the frequency that pairs of states appeared together in actual skeletons. This revealed that 172 out of 178 possible pairwise state combinations have evolved at least once (Fig. 9). In other words, an overwhelming majority of the skeleton space is occupied, a stark contrast from the quantitative morphospaces examined earlier. Each phylum was shown to exploit the skeleton space to a “large extent” with significant overlap, demonstrating “extensive convergence” of skeletal structure across different evolutionary pathways (Thomas and Reif, 1993, p. 349).

		Internal	External	Rigid	Flexible	One element	Two elements	> Two elements	Rods	Plates	Cones	Solids	Accretionary	Unit/serial	Replace/molt	Remodeling	In place	Prefabrication	No contact	Imbricate	Jointed	Fused, sutured
1.	Internal	-	-																			
	External	-	-																			
2.	Rigid	3	3	-	-																	
	Flexible	3	3	-	-																	
3.	One element	1	3	3	2	-	-	-														
	Two elements	1	3	3	1	-	-	-														
	> Two elements	3	3	3	2	-	-	-														
4.	Rods	3	3	3	1	1		3	-	-	-	-										
	Plates	3	2	3	2	1	2	3	-	-	-	-										
	Cones	1	3	3	1	3	3	1	-	-	-	-										
	Solids	2	2	3	1	1	1	3	-	-	-	-										
5.	Accretionary	3	3	3	1	3	3	3	3	3	3	2	-	-	-	-						
	Unit/serial	3	3	3	2	F		3	3	3	2	2	-	-	-	-						
	Replace/molt	F	3	3	3	1	1	3	3	3	2	3	-	-	-	-						
	Remodeling	3	2	3	2	1	1	3	2	2	2	1	-	-	-	-						
6.	In place	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	-	-				
	Prefabrication	1	2	3	1	1	1	3	1		1	3	1	2	2	F	-	-				
7.	No contact	2	1	2	1	3	1	2	1	1	1	1	3	2		1	2	2	-	-	-	-
	Imbricate	1	3	3	1	F	1	3	1	3	F	F	2	2	2		3		-	-	-	-
	Jointed	3	3	3	3	F	3	3	3	3	3	1	3	3	3	3	3	1	-	-	-	-
	Fused, sutured	2	1	3	1	F	1	3	2	3	1	1	3	3	2	2	3	1	-	-	-	-

Figure 9: A matrix displaying the relative frequency of pairs of character states across all vertebrates analysed. ‘F’ denotes “impossible or unviable” combinations (Thomas and Reif, 1993, p. 348).

To explain the recurrent evolution of state configurations across phyla, Thomas and Reif (1993, p. 350) frame convergence in the language of systems theory. They re-characterise the structural paradigms that make up the skeleton space as a set of topological attractors, defined as "simple, generalised forms that real organic structures approach but rarely match exactly" due to the stochasticity of their external adaptive contexts. The attractors are "stable configurations" that emerge from the constraints imposed on the evolutionary process: functionally, the necessity for an organism to be adapted to its external environment, and developmentally, the principles of organisation which govern the "organisation of … complex structures". Convergent evolution can therefore be conceptualised as independent evolutionary lines that are directed to the same stable topological attractor due to the influence of shared constraints.

Thomas and Reif's research furthers our understanding of convergence on two fronts. Practically, it proposes a variant of the morphospace through its use of nominal variables. This has significant implications, as it allows the convergence of qualitative traits to be identified, a form of convergence not accounted for by the quantitative morphospaces examined previously. However, perhaps even more valuable are the researchers' theoretical contributions. By reframing the skeleton space's structural paradigms as attractors, they invoke the idea that there are certain universal forms in biology that "evolution cannot avoid" (Thomas and Reif, 1993, p. 354). Convergence is therefore not only a symptom of the constraints on evolution, but also a product of evolution's tendency towards topological stability.

5.2. The deformed wheel as a topological attractor

Thomas and Reif's nominal morphospace would likely be less suitable than its quantitative variants as a tool for empirically analysing urban convergence. Nominal variables allow a wider variety of forms to be accounted for, which is useful for the analysis of animal skeletons due to their highly differentiated morphologies, but less appropriate for subjects with less structural variation, such as shells or cities. Despite this, there are a number of urban structural forms that space syntax defines qualitatively, which would resultantly not be captured in a morphospace constructed from quantitative properties alone. These are commonly referred to as 'genotypes', structures shared across cities with a configurational likeness but with individual 'phenotypic' differences. As established, this term is problematic as it implies urban invariants are the result of shared heredity, rather than convergent. However, the core underlying concept is clearly useful, as indicated by the word's continued use within space syntax. Further interdisciplinary research into the relationship between urban convergence and convergent evolution would therefore benefit from a term which invokes this idea but without its associated conceptual baggage.

A promising alternative to space syntax's genotype is Thomas and Reif's concept of the topological attractor. To illustrate this, we will now transpose its definition to a quintessential example of an urban genotype, the deformed wheel. Like topological attractors, the deformed wheel is a category of spatial organisation, a structural paradigm which is expressed varyingly in reality. It derives from constraints, both functional and developmental, that direct the autopoietic development of cities towards predictable morphologies. The recurring skeletal forms that comprise topological attractors are likewise the product of these two constraints. The deformed wheel is additionally an explicitly topological structure, manifesting in the configuration of cities, as evidenced by its identification under the non-metric technique of integration analysis. These parallels indicate that the deformed wheel can be described as a topological attractor for cities, a configurational form that developing urban systems tend towards.

In comparing 'topological attractor' to 'genotype', it is clear that the former is more appropriate for referring to the deformed wheel, at least in the context of interdisciplinary communication between space syntax and biology. Both terms evoke the idea of an archetypal form with variable manifestations, but where the latter presents problems for examining the parallels between urban and evolutionary convergence, the former evocatively suggests that the deformed wheel is so prevalent because it is the most stable configuration that a street network can assume. In short, describing urban invariants as 'topological attractors' preserves the notion that they can arise independently and are thus convergent. For this reason, we propose that future interdisciplinary research of this nature opts to use the term as a less troublesome stand-in for 'genotype', and that space syntax research explores its theoretical potential as a more permanent alternative.

6. CONCLUSIONS

In space syntax and evolutionary biology, convergence implies the presence of constraints upon the autopoietic development of their objects of study which restrict a large range of hypothetical forms to the more limited set observed in reality. This paper synthesised these viewpoints by characterising Bill Hillier's conjectural explanation for urban convergence through George McGhee's binary framework of evolutionary constraints. More precisely, the autonomous spatial laws and microeconomic social force that are hypothesised to produce urban convergence were shown to be understood in biological terms as, respectively, developmental and functional constraints. This interdisciplinary connection justified an exploration into the utility that approaches to convergent evolution may have for understanding invariance in urban morphologies. Through morphospace analysis, biological research has empirically demonstrated the existence of functional and developmental constraints. We therefore propose that analysing a morphospace of urban street networks has potential as a future research direction for space syntax, as it may provide evidence in support of Hillier's conjectured dual causes of urban convergence.

Additionally, a possible communicative problem between biology and space syntax was highlighted. Space syntax research regularly uses the biological term 'genotype' to evoke the idea of a generalised abstract structure with varied particular manifestations in urban morphology. However, we found this word implies that the invariants are a result of something akin to shared ancestry, and therefore not convergent. For this reason, we suggest that future space syntax research critically assess its use of this term and perhaps explore 'topological attractor' as an alternative. This term, coined by Thomas and Reif, refers to a paradigmatic stable configuration of biological elements with varied manifestations in reality. When applied to urban systems, the term broadly refers to the same concept as 'genotype', but supports rather than contradicts urban convergence as a phenomenon, suggesting that invariant structures are stable configurations of street network morphology.

It should be emphasised that the analytical and theoretical approaches to urban convergence outlined in this paper are at this stage solely suggestions for future research. As such, though we have illustrated the potential of convergent evolution as an interdisciplinary concept for generating new knowledge in urban analysis, the actual value of these approaches is yet to be confirmed. Our research can thus most accurately be described as the preliminary stages of an interdisciplinary dialogue on convergence between space syntax and evolutionary biology, which we hope will prove itself to be fertile ground for future research innovations in either field.

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