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Biotic analogies for self-organising cities

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Introduction

Nature has inspired urban designers since they first attempted to understand the complex functional order of cities. Cities have been seen as organisms (Mumford, 1938; 1961) or ecosystems (Girard, 2014; Marshall, 2009); comprising components analogous with cells, tissues, organs, flesh, blood, tentacles and skeletons (Le Corbusier, 1947; Mumford, 1938; Soria y Mata, 1998); and subject to urban growth, morphogenesis, metabolism, adaptation and evolution (Geddes, 1915; Marshall, 2009; Rogers, 1998). Mining of other disciplines for inspiration and describing phenomena using analogies, metaphors and similes has advanced understanding of urban problems and investigation of possible solutions, as seen in the proliferation of biomimicry solutions for designing more sustainable cities (Benyus, 2009), evacuation routes (Dias et al., 2013), and new building materials (Vogel, 1998).

However, amid the profusion of biological comparisons it remains unclear whether or not usage is consistent or biologically robust. In these circumstances, biological analogies risk being dismissed as unscientific, or merely figures of speech, so opportunities for their advancement of understanding and application may be missed. As 'nature-based solutions' and scientific approaches to urbanism (Batty, 2012; Marshall, 2012) gain increasing attention, drawing inspiration from appropriate models (Batty, 2007; Moroni, 2015), analogies (Steadman, 2008), and metaphors (Chettiparamb, 2006; Tippett, 2010), it is an opportune time to revisit the nature of biological analogies in a systematic way.

This overall mission would imply an extensive research agenda, potentially tracking relationships between biological and urban phenomena on multiple fronts, including several processes such as self-organisation, metabolism, adaptation and evolution. As a first step, this paper addresses self-organisation.

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5 Self-organisation refers to a bottom-up process where pattern emerges from numerous
6 interactions among the components of an initially unpatterned system. Self-organisation does
7 not require sentience of the self-organising units or an external agent. Rather, pattern
8 emerges through local interactions between the system's components using positive and
9 negative feedback.
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19 Self-organisation research occurs across the natural and physical sciences, and urban
20 researchers have drawn upon these to inspire bottom-up approaches to generating urban order
21 (Batty, 1998; Portugali, 1997). It is an inherently cross-disciplinary domain, routinely
22 recognised as having both biological and non-biological manifestations, with direct
23 operational equivalences that go beyond the figurative. Consequently, our treatment of self-
24 organisation provides a lens through which to study phenomena spanning the biological and
25 the urban, offering a model for future application to other areas where biology has influenced
26 urban design including development, adaptation, and evolution.
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40 Here, our aims are to (i) identify a set of analogies, metaphors and similes based on self-
41 organisation that are used in urban design; (ii) for analogies, establish a method for assessing
42 their clarity, depth, and application to urban design; (iii) assess the validity of analogies
43 according to contemporary biology; (iv) explore how these analogies link up or relate to each
44 other in a more systematic way; and hence (v) establish a framework which contains and
45 expresses the observed urban/biological relationships, and may also be used to generate new
46 ones. We believe that this is a potentially pioneering agenda, generating a method that could
47 find further application in other contexts, and wherein the scrutiny from contemporary
48 biology is itself novel, yielding insights that are correspondingly original.
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5 First, we briefly introduce the history of self-organisation and its current use in urban design
6 and biology. Secondly, we undertake a systematic analysis of analogy between urban and
7 biological disciplines, quantifying the use of analogy, and their biological validity. Finally,
8 we suggest a new biotic framework through which to interpret the analogical space, locating
9 existing analogies in relation to each other and helping to stimulate new analogies for urban
10 application.
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21 **Self-Organisation**

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23 Whilst the idea that order can emerge by itself dates back to Democritus and Lucretius, it was
24 Emmanual Kant who first coined the term 'self-organisation' arguing that organised beings
25 can be distinguished from non-living entities because they have a self-organising 'formative
26 power' which propagates itself that required a new type of science to explain it, because
27 neither physics nor chemistry could (Karsenti, 2008; Keller, 2008).
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38 A major challenge was that biology is largely based on chemical and biochemical reactions
39 which don't self-organise (Tabony, 2006). Lotka (1909; 1925) submitted that chemical
40 reactions might self-organise into oscillating chemical systems, akin to predator-prey
41 population size dynamics, later confirmed experimentally by Belousov (1951) and
42 Zhabotinsky (1964) and mathematically by Turing (1952). Interest proliferated across fields,
43 leading to new understanding of the thermodynamic properties of dissipative systems
44 (Prigogine and Nicolis, 1967), cybernetics and feedback (Ashby, 1960; Wiener, 1948),
45 synergetics (Haken, 1977), fractals (Mandelbrot, 1982) etc. Such studies ushered in a new
46 era in self-organisation research where both the animate and inanimate were products of self-
47 organisation in nonlinear, far-from-equilibrium, open systems, and their results have been
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3 applied across the social, computational, economic, physical and biological sciences (Keller,
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5 2009).
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10 In biology, Goldbeter and Lefever (1972) used Belousov-like equations to describe glycolytic
11 oscillations, and Turing's work has been applied to pattern formation in mammals' coats
12 (Murray, 1988), and embryogenesis (Glover et al., 2017). Today, self-organisation research
13 spans all levels of biological complexity, from micro: formation of the first polymers (Freire,
14 2015) and cell division (Karsenti, 2008); to macro: schooling fish (Camazine et al., 2001),
15 species distributions (Alados et al., 2007), ecosystems (Lenton et al., 2018).
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26 Urbanists also adopted self-organisation from the physical sciences. Prigogine's theory of
27 dissipative systems was applied to the appearance of central places (Allen et al., 1985).
28 Portugali (Haken and Portugali, 1996; Portugali, 1997) introduced synergetics, Batty and Xie
29 (1997) pioneered cellular automata techniques, and both applied fractal and synergetic
30 approaches to chaos theory (Batty and Longley, 1994; Portugali, 1997). Today, self-
31 organisation is routinely considered a central process in urban development (Yamu and
32 Frankhauser, 2015) yielding important insights for urban planners considering topics
33 including: urban intensification (Janssen-Jansen, 2013), urban codes (Moroni, 2015) and self-
34 governance (Rauws and de Roo, 2016); for a recent mapping of research see de Bruijn and
35 Gerrits (2018).
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51 As biology has drawn from the physical sciences, urban designers are applying biological
52 self-organisation to urban environments. Indeed, the richest potential for understanding
53 urban self-organisation would appear to lie in learning from biology, which exhibits the
54 fullest range of self-organising phenomena, from inanimate biomolecules through the
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3 animate world of sentient beings to ecosystems and Gaia. As such, a key challenge is to
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5 clarify how the biological component of self-organisation is being related to urban processes
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7 and where further insights might be found.
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10 11 12 **Methods**

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14 To examine how biological inspiration is being used within studies of urban self-organisation
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16 we identified all articles referencing self-organisation between 2000-2016 in five urban
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18 design and five biology journals, resulting in 69 urban design and 205 biological articles. We
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20 listed 25 biological terms (Fig.1) and recorded their frequency per paper. Biology-inspired
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22 similes, metaphors and analogies were identified in the urban literature, and analogies were
23
24 assessed for clarity, depth, biological soundness, and applicability using a 1 to 5 scale
25
26 (1=low, 5=high). We used mapping analyses and boxplots to compare term usage between
27
28 disciplines, and Sankey diagrams and 3D-scatterplots to assess how analogies were
29
30 employed. For a fuller version of the methods and results see SM1.
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38 **Results**

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40 The number of urban articles referring to self-organisation increased overall between 2000-
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42 2016 (SM2), and covered a wide range of urban design topics (SM3) including mechanistic
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44 models, unplanned local initiatives, and the planning process.
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49 *Biological Terms*

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51 All urban papers contained at least one of our biological terms other than self-organisation.
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53 Mapping of terms revealed inconsistencies in connections between the two disciplines (Fig.1)
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55 highlighting differences in the way the terms are used (SM4).
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3 [Fig.1]
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8 In both disciplines the closest links were between ‘self-organisation’ and ‘evolution’.
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10 ‘Adaptation’ and ‘ecology’ are also closely connected, after which, the two disciplines
11
12 diverge. The biological mapping stressing the importance of ‘gene’, ‘mutation’, ‘natural
13
14 selection’, ‘organism’, and ‘morphology’, the urban mapping highlighting ‘morphology’,
15
16 ‘feedback’, ‘multilevel’, and ‘organism’ (Fig.1).
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21 Herein lies a key difference between the biological and urban realms. The biological
22
23 mapping points to biology’s central theorem: that an organism’s adaptive traits are the
24
25 product of evolution through natural selection and mutation is one mechanism of introducing
26
27 genetic variation. Direct analogues of biological evolution are largely absent in urban
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29 planning (Mehmood, 2010), because those that do so face significant challenges including:
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31 defining urban genes and fitness, characterising urban gene to phenotype translation,
32
33 identifying the units of survival and reproduction.
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40 *Biological Comparisons*

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42 Through further review of the urban articles 66 biological terms were identified, which were
43
44 used 2371 times. Biological terms were most often used *without* consciously invoking a
45
46 biological comparison; despite this, 31.88% of urban articles contained a biological
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48 comparison: 15.94% analogy, 23.18% metaphor, 7.25% similes (The sum is more than
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50 31.88% as some papers contained more than one kind of biological comparison. SM3)
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56 Thirteen analogies were identified, in eleven papers. 69.23% of which were made between
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58 different hierarchical levels e.g. city–organism is cross-level analogy, person–organism is a
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3 direct-level analogy (Fig.2). 38.46% of the analogies related directly to self-organisation.
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5 Analogies were often found to be either unclear (mean=2, s.d.=1), and/or, of limited depth
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7 (mean=2.15, s.d.=1.07); whilst depth of analogy showed no connection with urban
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9 applicability we found a positive association between the depth, and to a lesser extent the
10
11 clarity, of an analogy and its biological soundness (SM5). Applicability was found to be
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13 higher when an analogue was both clearly conveyed and the biological content was accurate
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15 (SM5).
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21 [Fig.2]
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26 **Nature-Inspired Urbanism?**

27 *Depth, Clarity, Biological Soundness*

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29 Overall, the analogies lacked depth and clarity. Lack of depth had nominal effect on the
30
31 applicability of an analogy to the urban realm. Rather, the more reliable the biological basis,
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33 and the more clearly the information was applied, the better the fit of the biological analogue.
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35 As depth and clarity increased, the biological information was found to be more dependable,
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37 a not wholly surprising result as clarity and depth are both qualities required to adequately
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39 assess biological content.
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47 That an analogy was not required to be deep to be successful is more interesting. An analogy
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49 may be so commonly employed that in-depth interrogation is not required to impart meaning
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51 e.g. city is organism. The purpose of the analogy may not call for an in-depth analysis of
52
53 biological theory. Or, the biological connection may not be particularly important to the
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55 author, who instead could opt for deeper analogies with other disciplines, which may
56
57 themselves be analogous, and produce similar insights (Helbing et al., 2001).
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6 Concerningly a lack of depth and/or clarity can make it difficult to distinguish the type of
7
8 biological comparison being used, leaving readers to infer meaning according to their own
9
10 biases. For example, depending on the author, and reader, city as organism may be purely
11
12 symbolic (Nientied, 2016), or an analogy from which logical arguments can be extended and
13
14 planning decisions made (Golubiewski, 2012). Combine this with terms having multiple
15
16 definitions or context sensitivity and it is easy to see how confusion may occur.
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21 All of these are common problems facing writers who use comparative language to express
22
23 ideas (Chettiparamb, 2006). However, with over half of the world's population inhabiting
24
25 cities and increasing disconnection from the natural environment (Cox et al., 2017), urban
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27 authors face a more fundamental problem when using biological comparisons: that of using
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29 the unfamiliar to describe the familiar.
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35 Urban DNA is a particularly interesting example (Boelens, 2014; Nientied, 2016; Wu and
36
37 Silva, 2011). Whilst DNA is a part of us, it is not a part we see or feel, or identified the role
38
39 of until Avery et al. (1944). Thanks to the efficacy of language, art, and the fundamental
40
41 desire to understand the nature of being, DNA has become relatable. Its structure, the
42
43 information it inscribes and 'mystical powers' have been described as a twisted ladder, a
44
45 blueprint, an immortal spiral (Rovira, 2008).
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51 The particular comparisons employed can markedly alter our understanding, and the
52
53 implications, of a concept. Informational and essentialist DNA metaphors have shaped our
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55 laws (Silvestro, 2016), and metaphors regarding DNA's components have shaped research
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57 trajectories (Avisé, 2001). New findings may invalidate descriptors, eliciting calls for their
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3 alteration or discontinuation e.g. 'DNA is a blueprint' lost favour because it implies a direct
4 mapping of genetic information to phenotype, when in actuality, the same genetic code can
5 produce remarkably different phenotypes e.g. queen and worker honeybees. Perhaps 'genetic
6 code' remains in good standing because 'code' does not suggest decryption method, allowing
7 many final forms and the capacity to integrate new research findings. As such, the analogy
8 of urban DNA might better be conceptualised as a set of generative codes, or framework
9 rules, resulting in a self-organised urban order, as opposed to urban order generated by a
10 blueprint.
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24 Ultimately, research requires the clear communication of ideas, so they can be assessed and
25 discussed. Where confusion occurs advancement is hampered (Steadman, 2008). Defining
26 terms and the limits of one's analogies can help reduce confusion, clarify thinking, and
27 elucidate when a field where inspiration is being drawn from is itself using the same term in
28 different ways. For example, in biology, terms such as metabolism are regularly used across
29 disciplines and hierarchical levels but refer to different processes (Golubiewski, 2012). Thus,
30 referring to the city as ecosystem and as organism, particularly in the same paper, can have
31 very different implications, muddling the narrative.
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45 *Description, Inspiration, and Mechanism*

46 Analogies were used to either describe, inspire or suggest mechanism. In description, the
47 opportunity for an extended metaphor to be confused for analogy was highest. For example,
48 is Frenkel's (2004) description of cities as '*multistructural organisms as reflected in the*
49 *spectrum of their functions*' and use of taxonomic methods to '*classify cities according to*
50 *their characteristics*' a metaphor, or an obvious extension to the commonly expressed
51 analogy?
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6 Inspirational analogies encouraged new ways of thinking about the urban environment.

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8 Salingaros (2010) used the earliest bio-molecules to inspire urbanists to look beyond an urban
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10 element's primary function to consider secondary and potential catalytic effects. Finally,
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12 mechanistic analogies such as Barker (2012) and Adamatzky et al. (2017) who employed
13
14 different slime mould species to reveal how simple, local, bottom-up interactions lead to
15
16 urban formation and efficient transport networks, respectively.
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21 Three of the five analogies that proposed mechanism were directly related to self-
22
23 organisation. Of course, as self-organisation is a mechanism this correlation is unsurprising.
24
25 More interesting is that two of these three studies drew comparisons of urban systems from
26
27 the behaviour of slime moulds, which, over recent years, have helped overturn notions of the
28
29 minimum level of intelligence needed to solve complex problems, leading to the development
30
31 of simpler algorithms to solve modern day human problems.
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38 Difficulties arise in that: models have mostly been deductive rather than predictive, limiting
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40 their current value to urban planning (Adamatzky et al., 2017); the focus on economic
41
42 'rationality' can favour highly productive regions rather than the growth of underdeveloped
43
44 regions (Vanoutrive et al., 2016); the spatial scale and morphology of slime mould
45
46 experiments may dramatically change the solutions arrived at and might not always be
47
48 optimal (Reid et al., 2012), as slime moulds can make irrational decisions, similar to humans
49
50 (Latty and Beekman, 2010).
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56 Examining a variety of organisms may be more informative to urban planners, providing a
57
58 variety of solutions to choose from. For example, Argentine ant (*Linepithema humile*)
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3 networks prioritise cost and efficiency over robustness (Cabanès et al., 2014), the fungus
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5 *Phanerochaete velutina*'s networks maximise robustness and efficiency (Bebber et al., 2007),
6
7 whilst the networks of wild polydomous ant colonies, which can stretch thousands of
8
9 kilometres, have more connections than those found in lab populations, suggesting robustness
10
11 may be a more important factor in ecologically valid situations (Cook et al., 2014).
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16 17 *Analogies Across Levels of Scale*

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19 Both biological and urban systems are characterised by nested levels of increasing
20
21 complexity, where each level is primarily composed of the level below but possesses
22
23 emergent properties not present in that level. Mechanisms leading to the spatial organisation
24
25 of lower level entities forming higher hierarchical levels include self-organisation,
26
27 environmental constraint, and cooperation (Maynard-Smith and Szathmáry, 1995; Takeuchi
28
29 and Hogeweg, 2009)
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36 Biological levels extend from molecules to Gaia, although authors generally define a
37
38 narrower, question-appropriate range. The delineation between biological hierarchies is not
39
40 as neat as it might initially appear. Single celled organisms, for example, inhabit both the cell
41
42 and organismal levels, and an organism is a community, called the holobiont, when
43
44 microbiome, virome and parasites are accounted for.
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50 The urban realm can include human concepts of geographical/economical/political areas but,
51
52 for most urban researchers their questions will fall between the people and regions levels, and
53
54 like biological levels of organisation, delineation between urban levels and elements at
55
56 different scales is not always clear cut (Alexander et al., 1977; Kropf, 2014). Actually, the
57
58 urban hierarchy is nested within the biological hierarchy. People are organisms so are found
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3 on the biological hierarchy at the level of organism. The urban environment is a type of
4 ecosystem; however, it can also be considered at lower hierarchical levels (e.g. community),
5
6 depending on the question being asked.
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12 Most of the analogies we identified crossed hierarchical levels (Fig.2), analogising city to
13 organism, land uses to genes, and pedestrian paths to capillaries. Analogies existing at
14 equivalent hierarchical levels included city as ecosystem and models derived from slime
15 moulds because, whilst a slime mould and transport network (for example) may not
16 immediately appear to be at the same hierarchical level, the rules for their formation are both
17 generated at the organismal level, for modern human transport networks are often founded
18 atop the informal, emergent trails of our ancestors.
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31 Logically, all analogies that operate below the level of the organism must be cross-level
32 analogies. However, an interesting anomaly may occur with plan/blueprint/design as urban
33 ‘genotype’. A plan/design is neither nested within nor essential for the construction or
34 functioning of higher-level entities. Indeed, it may merely be a representation of a completed
35 form, rather than its generator. What is nested within and essential to the construction and
36 functioning of urban form is the urban population, each with genomes, and so, one could
37 postulate that *people* are the urban genotype.
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50 Employing evolutionary analogy Silva (2016) states that tactical urbanism (a self-organised
51 approach that transform the urban environment through self-built interventions) provides the
52 ‘energy’ for urban evolution, implying ‘energy’ translates to mutation. However, tactical
53 urbanism can be more clearly and instructively described in terms of niche construction
54 where, rather than city as organism it is analogous to a hive, burrow etc.
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6 Niche construction theory is a broadening of Dawkins' (1982) extended phenotype hypothesis
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8 such that any manipulation of the environment by the organisms inhabiting it, and the effects
9
10 of those manipulations on adaptive fitness of the organism, its progeny and other organisms
11
12 in the environment, are now included (Odling-Smee et al., 2003).
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17 Niche construction theory recognises that by altering their environments organisms alter the
18
19 selection pressures acting upon them, such that the organism adapts to the environment *and*
20
21 the environment adapts to the organism. Thus, the organism produces an ecological
22
23 inheritance (Odling-Smee et al., 2003) which, if fitness enhancing, will promote co-evolution
24
25 of trait and constructed niche. In social groups, cultural inheritance can also drive niche
26
27 construction (Ellis, 2015; Kendal et al., 2011).
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33 Theoretical examinations integrating ecological and cultural inheritances have found that
34
35 niche construction is capable of overriding, reversing or accelerating natural selection, and of
36
37 generating unusual population dynamics (Laland and Brown, 2006; Laland et al., 2001).
38
39 Further, gene-culture-co-evolution has been proposed as the dominant mechanism of
40
41 adaptation in humans (Ellis, 2015; Laland et al., 2010). Therefore, the creation of the human
42
43 built environment is not only part of urban evolution, it is a part of human evolution, past and
44
45 present. In other words, '*we co-evolve with the environment we create*' (Kropf, 2017).
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51 It is often self-organisation, operating amongst individuals or across environmental
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53 components, that shapes constructed niches. Social insects build nests, orders of magnitude
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55 larger than an individual through self-organised collective action, following cues derived
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57 internally, from nestmates, or environmentally (Green et al., 2017). Architecture has
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3 produced buildings inspired by social insect nests but none has captured the adaptive quality
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5 of nest architecture, where structure and function have become one, and mechanism is
6
7 derived through a desire to maintain a stable internal environment that can be cognitively and
8
9 physiologically produced (Penn and Turner, 2018; Turner and Soar, 2010).
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15 Returning to the example of tactical urbanism: as in niche construction theory, tactical
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17 urbanism denotes a self-organised, bottom-up approach, that transforms the urban
18
19 environment, through self-built interventions (Silva, 2016), rather than being a mutation in an
20
21 organism. Tactical urbanism initiatives include ‘Guerrilla Gardening’, ‘Intersection Repair’,
22
23 ‘Pop-up Cafes’. Their role seems often to beautify and connect, and these homeostatic
24
25 desires could be routed in a physiologically evolved need to reduce stress. When possible,
26
27 portions of the urban population may be intuitively transforming their environments,
28
29 removing or reducing aspects that negatively impact fitness. In doing so, they not only
30
31 enhance their own fitness but that of their neighbours, increasing the probability of accruing
32
33 benefits through reciprocal altruism or kin selected benefits. The fitness enhancement may,
34
35 today, be small, but for the urban planner, the lessons may be of use. Firstly, such initiatives
36
37 are likely excellent venues of inspiration for positive design ideas that can be extended more
38
39 widely. Thus, allowing space for citizen-led, self-organised, bottom-up approaches to exist is
40
41 of great import. Secondly, urban planners could co-opt this mechanism by identifying ways
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43 to translate innate homeostatic preferences into urban design, enabling the urban population
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45 to alter their environments for public good by building environmental feedback mechanisms
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47 into architecture (Pasquero and Zaroukas, 2016).
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56 **Analogical Space to Biotic Framework**

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3 Our analysis revealed a preponderance of cross-level comparisons over equivalences (direct-
4 level analogies). Indeed, even when a level of equivalence was being evoked it was often
5 masked. Barker (2012), for instance, modelled how land-use decisions generate cities, where
6 the model and decision rules were inspired by self-organised slime mould agglomerations.
7
8 That the land-use decisions are made by humans and the model is using slime mould
9
10 behaviour to propose simple rules underpinning human behaviour, is not explicitly stated.
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12 Operating so, the urban literature risks overlooking key areas of instructive insights that fall
13
14 at the level of equivalence.
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24 In biology, evidence accrues through analogous research across taxa, where different
25 evolutionary and life histories lead to different predictions drawn from the same theory. In
26 feeding into these bodies of literature direct-level analogies (equivalences) could provide a
27
28 more substantial contribution to urban researchers than the purely figurative. For, after all,
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30 humans are organisms too.
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38 To demonstrate our thinking we propose the biotic framework (Fig.3) – so named because it
39 emphasises that both organisms and their constructed environments are biotic - relating to or
40 resulting from living organisms. In a very literal sense, our cities, indeed all human
41
42 environmental modifications, are biotic. Our emphasis on the biotic is in contradistinction to
43
44 traditional emphases on human versus nature, or organic versus inorganic – though both of
45
46 these form part of the framework.
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54 [Fig.3]
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3 The framework provides a rationale for locating and identifying analogies, particularly those
4 where the processes operating are most likely to be comparable to urban processes, and
5 encourages awareness of the entire system. We present two versions of the biotic framework
6 (a) presenting the framework and its dimensions, (b) showing a subset of the biological
7 comparisons identified in the reviewed literature (green solid lines), some well-known
8 comparisons that not present in the reviewed literature (orange dashed lines), and some
9 connections that we suggest could provide new inspiration for urban designers (grey dashed
10 lines) (Fig.3).
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24 Protruding into the foreground are the lower hierarchical levels. At the front are
25 biomolecules and compounds which form the basis of life, composing every living organism,
26 prompting ‘the continuity thesis’ which suggests that there is no break between
27 physiochemical and biological systems (Freire, 2015). The coalescence of molecules forms
28 the constituent parts of cells, which come together to form tissues, organs, and organism.
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38 Biological comparisons between urban elements and levels below that of organism have
39 proved popular, inspiring new conceptions of urban environments and processes.
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42 Comparisons made between molecules (Salingaros, 2010), or parts of an organism (Furtado
43 et al., 2012; Mehaffy et al., 2010; Salingaros, 2010), and the urban environment are, by
44 definition, cross-level analogies. Whilst there is no denying the merits of such comparisons,
45 we propose that, where an analogy relates to process, inspiration will more readily be found
46 and likely better fit the example, when it is drawn at the level of equivalence.
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55 The level of the organism is the first hierarchical level where drawing upon equivalence is
56 possible. Here, the living entity, be it human, slime mould, ant, or bower bird, is the focus.
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3 Its cognition, behaviour, and decision making, are of primary importance because such rules
4 determine how organisms use, move around and understand the environment, and population
5 distributions. At this level, natural and cultural selection play dominant roles in shaping the
6 behavioural rules and physiological requirements of the organism.
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14 Moving into the diagram from the position of the organism, two planes run parallel, the lower
15 signifying increasingly large clusterings of the same organism (group, population, species),
16 the upper signifying the organism's constructed environment. We adopt the definition from
17 niche construction theory to characterise a constructed environment - any modification of the
18 environment by an organism which alters the selective pressures acting upon it and other
19 organisms inhabiting that environment. As such, constructed niches vary dramatically
20 between organisms including leaf litterfall (Bigelow and Canham, 2015), birdsong repertoire
21 size (Creanza et al., 2015), and termite mega-structures (Turner, 2004). The two planes run
22 parallel because to differing extents the constructed niche will impact the selective pressures
23 acting on those groupings.
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40 To represent hierarchical relationships between elements within the human built environment
41 we build upon a representation proposed by (Kropf, 2014), adding neighbourhood, city and
42 conurbation as familiar reference points, although these do not imply an exact structural
43 continuation of the lower levels.
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51 Humans, like all organisms, don't inhabit the world alone or immune from the effects of the
52 environment. When organisms interact they form communities; the combination of
53 communities and physical processes are ecosystems, which in turn combine to biomes and
54 eventually Gaia. At these levels, natural selection plays a muted role. Rather, system
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3 evolution and adaptation may be guided by self-organised mechanisms (Lenton et al., 2018).

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5 The urban environment is an ecosystem and so, analogies drawn between mechanisms of
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7 natural ecosystem functioning, resilience, evolution, adaptation etc., with urban processes are
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9 examples of equivalences.
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14 As each hierarchical level is an emergent property from coalescence of the level below,
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16 disturbance at one level can trigger changes upwards and downwards. The biotic framework
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18 draws attention to the interconnected and hierarchical nature of the whole system and can be
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20 used to interrogate the implications of transformations across hierarchical levels. Analogy
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22 does not have to include multiple hierarchical levels to be of use. However, by considering
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24 the implications of an analogy across multiple hierarchical levels, and defining the limits of
25
26 the analogy, not only are the clarity and biological soundness likely to be improved (a key
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28 indicator of the fit of an analogy to the urban realm) but the potential to identify novel
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30 insights is markedly increased.
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38 Indeed, the framework motivated us to propose, for demonstrative purposes, three new
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40 comparisons, that might serve to inspire urban design and the rules that formulate urban
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42 environments (Fig 3). Firstly, we refer back to transport networks and the observation, from
43
44 lab and field experiments with ants and slime moulds, that outcomes of self-organisation are
45
46 highly dependent on environmental variables, and that looking at a variety of organisms how
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48 they respond to environmental variability will be most instructive to urban planners when
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50 determining similar situations and trade-offs. Secondly, as initiatives work to bring food
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52 production into our urban environments (Whittinghill and Rowe, 2011) using natural
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54 communities to inspire our understanding of the needs of urban communities will become
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56 ever more crucial. A classic example of farming in animal societies is that of fungus farming
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ants; this turns out to be a multi-species mutualism (Barke et al., 2010) highlighting the need to consider community dynamics even within complex constructed niches, and the role of the constructed niche in shaping those communities and dynamics. Thirdly, we propose that epigenetic mechanisms for pattern formation (non-genetic influences on gene expression that affect traits such as coat pattern, caste differentiation, and that allow organisms to rapidly respond to changing environments) could inspire a new (or newly recognised) layer of ‘epigenetic’ directions within urban design/planning. Such an epigenetic layer would guide where and when different codes or framework rules are deployed, and could include ‘rules for the production of rules for the activation of processes’ (Moroni, 2015), integrated with ‘location-specific development regulations, traditionally expressed in the land-use plan, with generic regulations’ (Rauws and de Roo, 2016). In other words, identifying and deploying the urban equivalent of epigenetic mechanisms could help guide self-organising urbanism in a third way that offers a balance between more purely bottom-up or top down processes.

Conclusion

Our research has found a rich diversity of biological analogies associated with urban phenomena relating to self-organisation but these are currently applied with limited depth and relation to each other. Still, they could be applied more deeply and systematically, and we show how via the biotic framework, which has also stimulated new analogies. We believe this analysis breaks new ground – perhaps most significantly bringing fresh biological insight and scrutiny into this territory since the time of Patrick Geddes – and can pave the way for further research agendas, including application to other analogical processes (e.g. urban adaptation, evolution) and other disciplinary domains.

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3 In our analysis we found that analogies between biological and urban realms were drawn
4 from molecule to ecosystem and human to city. They mostly crossed hierarchical levels and
5 the potential for confusion from the complexity of these different relationships led us to
6 generate the biotic framework (Fig.3). This framework was initially created to articulate the
7 analogical space that has been the focus of this paper, but in doing so provides a structure for
8 conceptualising and interpreting relationships between key domains of the biotic sphere.
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19 Our analysis suggests that attention could be usefully directed to the more direct analogies or
20 equivalences because: (i) cities are actually ecosystems; (ii) our built environments are
21 actually constructed niches; (iii) our built environments have a material effect on our species'
22 actual ongoing evolution. Furthermore, these three statements are linked and can be made
23 more visually explicit via the biotic perspective. In addressing equivalence, insights from
24 reading across human and natural realms may be particularly pertinent because they access
25 overarching theories, built on evidence from a wide array of organisms, to explain and
26 describe the evolution and mechanistic underpinnings of the phenomena.
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40 For the urban environment, comparisons operating at the level of the organism and providing
41 feedback between organism and environment will be particularly pertinent. Niche
42 construction theory has already been applied to human evolution (Laland and Brown, 2006;
43 Laland et al., 2001; 2010) and combining biological theory e.g. optimal foraging or cultural
44 niche construction, with insights from past trends, could help identify planning perspectives
45 that are adaptive, resilient, commensurate with our inherent desires for physiological comfort,
46 and advance theory.
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3 At higher ecological levels, the environmental effect of humans is ever more tangible. Calls
4 to circularise our systems (Williams, 2019), or mimic the services provided by natural
5 ecosystems (Benyus, 2009) do not benefit from the view of city as organism; rather, the view
6 of cities as ecosystems, and drawing inspiration from natural ecosystem functioning, failures
7 and resilience, provides a stronger basis from which to construct solutions to the ultimate
8 problems facing future urban environments. As such, choosing the right analogy is not
9 purely a choice of literary expression but, as with the example of DNA, can make a material
10 difference to our perception of a problem and hence appropriate solutions.
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24 Interestingly, the biotic framework can be seen as a freshly explicit expression of Geddes's
25 understanding of the equivalence of the human and natural realms, that has more often
26 remained implicit (Geddes, 1915). His assertions regarding the interaction between human
27 evolution and environment invoke modern niche construction theory, his concept that
28 cooperation overrides conflict is supported by multilevel selection theory. As biology
29 furthers its understanding of evolutionary processes, self-organisation is emerging as a
30 principal force, shaping form through the self-organised behaviours of organisms, and
31 ecosystems through self-organising mechanisms far removed from the reach of the genes.
32 This could provide an area for future application linking *urban* self-organisation and
33 evolution, wherein generative codes or framework rules could play a fitting part in future
34 urbanism. Overall, analogies at the level of equivalence could become of increasing interest,
35 even to those wary of organicist metaphors, not despite their biological roots but because
36 through them comparison can go beyond the purely figurative.
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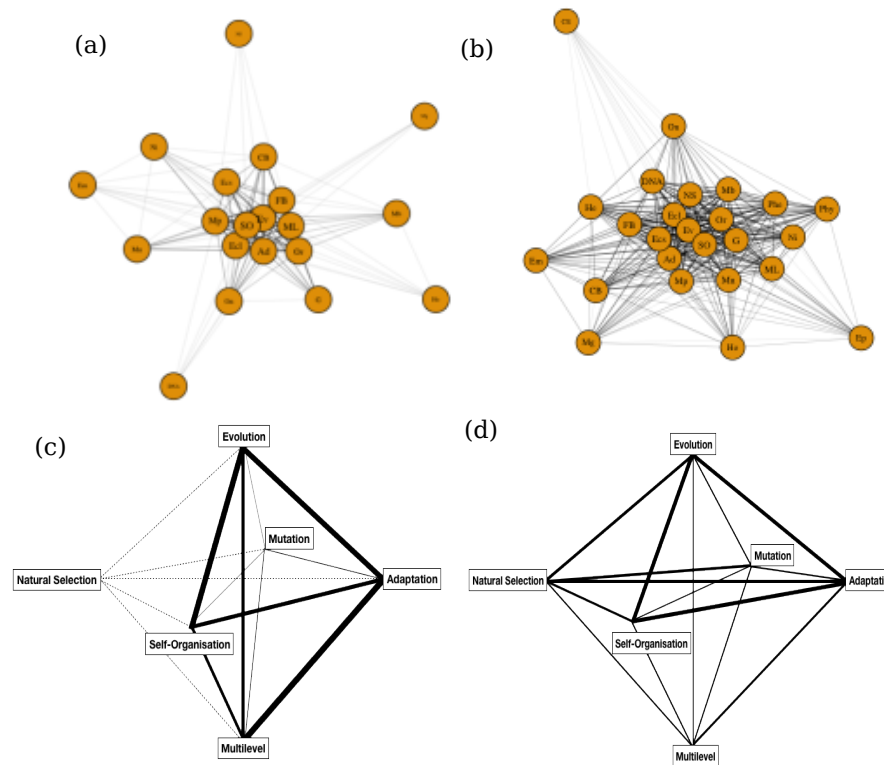


Figure 1. Word-map and key term linkage comparisons, showing the use of biological terms in studies examining self-organisation in (a) & (c) the urban design literature, (b) & (d) the biological literature. In (a) and (b) the letters refer to the terms: Ad=adaptation, CB=collective behaviour, CE=cultural evolution, DNA=DNA, Ecl=ecology, Ecs=ecosystem, Em=embryo, Ep=epigenetic, Ev=evolution, FB=feedback, G=gene, He=heritable, Ho=homology, Mb=metabolism, Mg=morphogenesis, Mp=morphology, ML=multilevel, Mu=mutation, NS=natural selection, Ni=niche, On=ontology, Or=organism, Pt=phenotype, Phy=phylogeny, SO=self-organisation. The size of the letters indicates the frequency of use and the darkness of the connecting lines indicates the frequency of the terms being used in the same papers. In (c) and (d) the width of the line represents the proportion of times terms are mentioned in the same paper. Dashed lines signify that the terms did not appear in the same paper. Terms not mentioned in any of the papers are not shown on the word maps.

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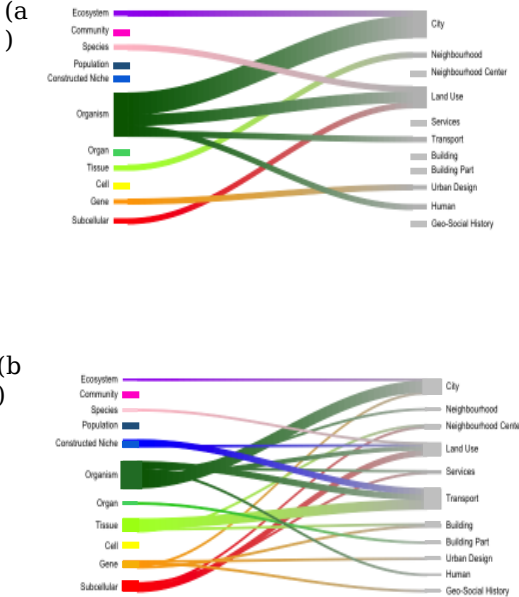


Figure 2. Mapping of the propensity for biological levels to be used as (a) analogies, and (b) analogies, metaphors and similes, for phenomena operating at urban levels. The thickness of the lines indicates the number of times the comparison was made.

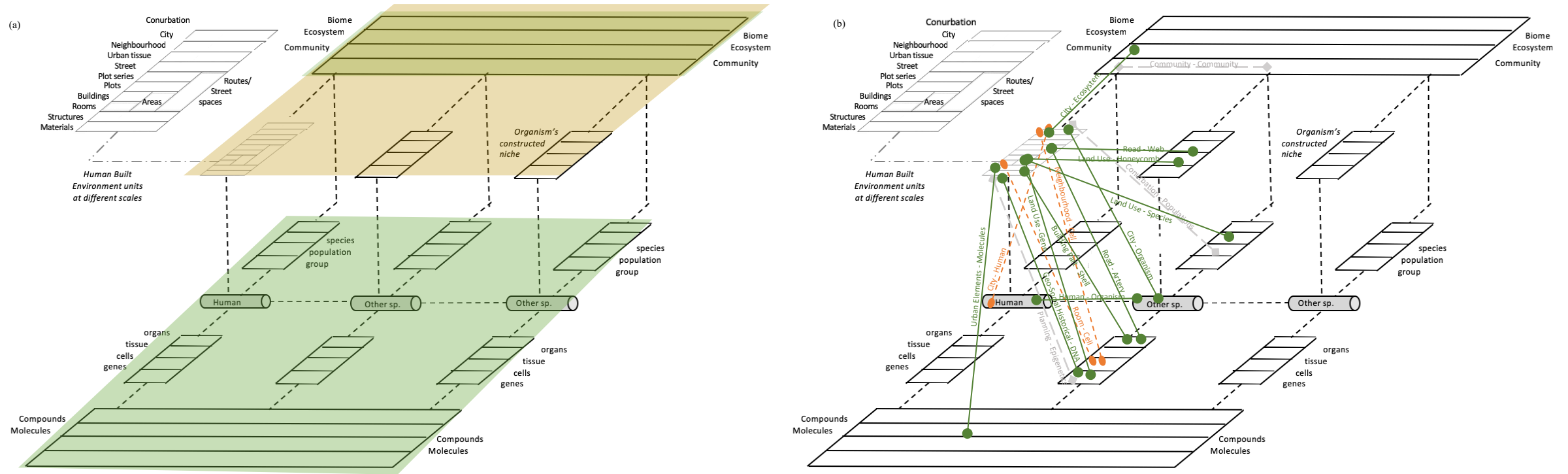


Figure 3. The Biotic Framework. (a) The left most section denotes the human realm, whilst the central and right most sections denote the natural world, focused on other organisms. The central nodes are the organism with lower hierarchical levels in the foreground and hierarchical levels containing the organism in the background. In the plane above that of the organism is its constructed niche and runs parallel to increasing organism number, signifying that, to varying extents, niche constructions affect all members of a species. The green represents organisms, their constituent parts etc., but excluding their constructions; the brown area represents the organisms' constructions and the brown/green zone represents where the part of the hierarchical levels where both organism and construction define the levels. (b) Analogical space where solid green coloured lines represent some of the biological comparisons identified during the literature review. Dashed orange lines represent 'classic' comparisons that we previously identified but did not fall within our literature sample (Sharpe and Wallock, 1987; Alexander, 1977; Bennett et al., 2003). Grey dashed lines represent potential analogies that we have identified using the biotic framework.

The (human) built environment structure (top left inset) is derived from (Kropf, 2014) and to which we have added 'neighbourhood', 'city' and 'conurbation'.

Methods

Identification of Journal Articles

To investigate the use of biological inspiration in the urban self-organisation literature we identified five urban design related journals (Built Environment, Environment and Planning B: Planning and Design, Journal of Urban Design, Urban Design and Planning, Urban Design International) and five biology journals (Biology Letters, BMC Cell, Ecological Modelling, Ecology Letters, Theory in Biosciences), and extracted all articles mentioning self-organisation between 2000-2016 (Urban Design and Planning started in 2008 so its literature search spanned 2008-2016).

Articles were searched for using the advanced search tools in Google Scholar and Web of Knowledge. To account for differences in the spelling of self-organisation we searched for “self-organisation”, “self-organization” for each of the 5 journals, limiting the results to since 2000. In Web of Knowledge we used “self-org*”, the asterisk allows any combination of letters to follow the initial string. Once duplicates were removed 92 urban planning articles and 388 biological articles were downloaded.

For an article to be included in the study it had to mention self-organisation at least once in the body of the text, be a research or review article, thus eliminating articles such as editors’ summaries of special issues and book reviews, and have been published between 2000 and 2016, articles published online in 2016 were included. In total 69 urban planning articles and 205 biological articles were found to meet the criteria and were examined further.

Data Collection

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3 25 biological terms were selected because they either embodied fundamental or emerging
4 concepts in biology e.g. evolution and epigenetics, were known to have been used previously
5 by urban researchers e.g. metabolism, were relevant to self-organisation e.g. collective
6 behaviour, or particularly relevant to the study of humans e.g. cultural evolution (a complete
7 list is given in Figure 1). The frequency of each of these terms was recorded for each
8 biological and urban paper. For a term to be counted it had to appear in the abstract or body
9 of the article. Terms appearing in the title and sub-headings, figure captions, reference
10 section, appendices etc were not counted.
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24 All urban papers were read to identify how biological terms were used. The basic list of 25
25 terms was extended as the papers were read to ensure that biological comparisons that did not
26 use one of our 25 terms were captured. Biological terms were classified by the mode of use:
27 analogy, metaphor, simile, other. We employed definitions from the Oxford Dictionary of
28 English (2017) to interpret these terms. As such, simile is defined as:
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38 *‘a figure of speech involving the comparison of one thing with another thing of a different*
39 *kind, used to make a description more emphatic or vivid’*,
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44 metaphor as:
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49 *‘a figure of speech in which a word or phrase is applied to an object or action to which it is*
50 *not literally applicable’*,
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55 and analogy as:
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3 All statistical analyses and data visualisations were produced in RStudio using R version
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5 3.4.0. In total, there were seven biological terms (including self-organisation) that appeared
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7 in one third or more of the urban planning papers (23 or more papers). The seven terms were
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9 ‘adaptation’, ‘ecology’, ‘evolution’, ‘feedback’, ‘morphology’, ‘multi-level’, and ‘self-
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11 organisation’. The distribution of each term’s usage was mapped using boxplots. As the data
12
13 were non-parametric, two-tailed Wilcoxon-Mann-Whitney tests were used to examine
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15 differences in the likelihood that a particular term was used, between the two disciplines.
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21 Mapping analyses were employed to compare differences and similarities in the handling of
22
23 the 25 biological terms between the disciplines. Because the terms: ‘cultural evolution’,
24
25 ‘epigenetics’, ‘heredity’, ‘phenotype’, and ‘phylogeny’ did not appear in the urban literature
26
27 they were omitted from the mapping analysis. The Fructerman-Reingold layout was
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29 employed to distribute terms across the page, sending the least connected nodes furthest,
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31 whilst darkness of the lines between nodes was used to indicate the frequency with which the
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33 terms are used in the same paper.
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40 The R library ‘riverplot’ was used to produce Sankey diagrams that graphically represent the
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42 frequency with which particular biological comparisons were employed in the urban
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44 literature.
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49 To visualise the relationship between the clarity, depth, biological soundness and application
50
51 of analogies, 3D scatterplots were employed as per Ligges et al. (2003). The points are
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53 anchored to a grid on the xy-axis to make clear their location. A linear model was calculated
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55 and plotted, resulting in a regression plane, from which the +ve (red lines) and -ve (blue
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3 dotted lines) residuals are drawn. The fourth dimension is shown using different symbol
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5 types.
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10 **Results**

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12 The number of urban articles mentioning self-organisation remained relatively constant
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14 between 2000-2011, rising between 2011-2016, a trend consistent with the findings of (de
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16 Bruijn and Gerrits, 2018; SM2). The number of biological papers mentioning self-
17
18 organisation decreased after 2011, resulting in more urban papers being identified that
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20 contained self-organisation in 2016 than biological papers (SM2).
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26 Self-organisation was referenced across a wide range of urban design topics (SM3).

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28 Discussion of self-organisation took many forms from models elucidating the mechanisms of
29
30 urban self-organisation (Daffertshofer, 2001), the use of techniques to look for indicators of
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32 self-organisation (Chen and Zhou, 2006; Porta et al., 2006), unplanned, local initiatives such
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34 as guerilla gardening groups (Ache and Ferowitz, 2012; Silva, 2016), techniques for
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36 incorporating self-organisation into the planning process (Rauws and de Roo, 2016), to a
37
38 cursory mention of self-organisation at some point in the article, for example as a potential
39
40 area of interest for future research (Janssen-Jansen, 2013), or an intrinsic aspect of urban
41
42 complex systems (Vancheri et al., 2008).
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49 Kant and self-organisation's biological foundations were rarely mentioned; instead discussion
50
51 of the history of self-organisation focused on the 20th century (Partanen, 2015) when major
52
53 developments in the modern study of self-organisation occurred in the physical sciences.
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Biological Terms

All urban papers contained at least one of our biological terms other than self-organisation. Self-organisation was the only term to appear in all 69 articles; however it was not the most used, appearing 474 times compared to the most popular biological term, evolution, found 497 times in 55 of the articles.

The frequency of use of 'self-organisation' was found to be consistent between the biological and urban literature ($W=6355.5$, $p=0.1944$). The same was true for adaptation ($W=6656$, $p=0.4371$) and feedback ($W=7072.5$, $p=1$). 'Ecology' was found to be employed significantly less in the urban literature ($W=10852$, $p<0.001$), whilst, 'evolution', 'morphology' and 'multi-level' were significantly more common in the urban than biological literature ($W=5733$, $p<0.05$; $W=5595$, $p<0.001$; $W=5318.5$, $p<0.001$, respectively, SM4).

Mapping of the terms revealed further inconsistencies in connections between the two disciplines (Fig.1). Whilst all 25 of our biological terms appeared in the biological literature, 'cultural evolution', 'epigenetics', 'heredity', 'phenotype', and 'phylogeny' did not appear in the urban literature. Of these, in the biological word map, 'heredity', 'phenotype', and 'phylogeny' are found on the outside edge of the central cluster, whilst 'cultural evolution' and 'epigenetics' were more distantly connected (Fig.1).

In both disciplines the strongest link is between 'self-organisation' and 'evolution', and both are linked to 'adaptation' (Fig.1). In the urban papers 'self-organisation' is also tightly bound to 'ecology', to which it is slightly less closely connected in the biological literature. From here, the two disciplines differ notably. Whilst, the biological mapping stresses the

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3 importance of 'gene', 'mutation', 'natural selection', 'organism', and 'morphology', the
4 urban mapping highlights 'morphology', 'feedback', 'multilevel', and 'organism' (Fig.1).
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10 This disparity and the discrepancy in central mapping of terms emphasises a key difference
11 between the biological and urban realms. In biology, evolution is often defined in terms of
12 changing allele frequencies in a population over time. New alleles enter a population in
13 several ways e.g. mutation and immigration, whilst change is driven by gene flow, genetic
14 drift and natural selection. Natural selection is the only mechanism that actively promotes
15 organisms better adapted to their environment. Natural selection requires variation in the
16 phenotypic expression of traits, that the expression of these traits is heritable between
17 generations, and that these traits result in improved reproductive success. If so, individuals
18 with beneficial traits reproduce more than individuals without beneficial traits, passing on
19 those traits to their offspring, increasing trait occurrence in the population and so, the allele
20 frequencies that underpin it. As such, the terms at the centre of the biological mapping all
21 relate to biology's central theorem, that adaptive traits are the product of evolution through
22 natural selection.
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42 Direct analogues of biological evolution have been largely absent in urban planning
43 (Mehmood, 2010). Those that do so face a multitude of challenges including: defining urban
44 genes, characterising urban genes to phenotype translation, identifying the units of survival
45 and reproduction, and defining urban fitness.
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52 *Biological Comparisons*

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54 In depth review of the urban articles resulted in the identification of 66 biological terms,
55 which were used 2371 times. Biological comparisons were found in 31.88% of the urban
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3 articles. 15.94% of urban papers analogised the urban realm to the biological realm, 23.18%
4 used metaphor, 7.25% similes (SM3). The total is more than 31.88% because some papers
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6 contained more than one type of biological comparison.
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12 However, biological terms were more commonly used in a way *not* consciously invoking a
13 biological comparison, e.g. “Cities are physical objects that display extreme variety of size
14 and morphology” (Benguigui et al., 2001). Indeed, of the 2371 biological terms identified
15 only 5.44%, 6.28%, and 2.91% were used as analogy, metaphor, or simile, respectively.
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24 Of the 13 analogies identified, in 11 papers, 69.23% were made between entities at different
25 hierarchical levels e.g. city–organism is cross-level analogy whilst person–organism is a
26 direct level analogy (Fig.2). 38.46% of the analogies related directly to self-organisation.
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28 Where analogies were identified they were often found to be either unclear (mean=2, s.d.=1),
29 and/or, of limited depth (mean=2.15, s.d.=1.07).; whilst, depth of analogy showed no
30 connection with urban applicability of the analogy to the urban situation we found a positive
31 association between the depth, and to a lesser extent the clarity, of an analogy and its
32 biological soundness (SM5). The applicability of the biological analogue to the urban realm
33 was found to be higher when it was both clearly conveyed and the biological content was
34 accurate (SM5).
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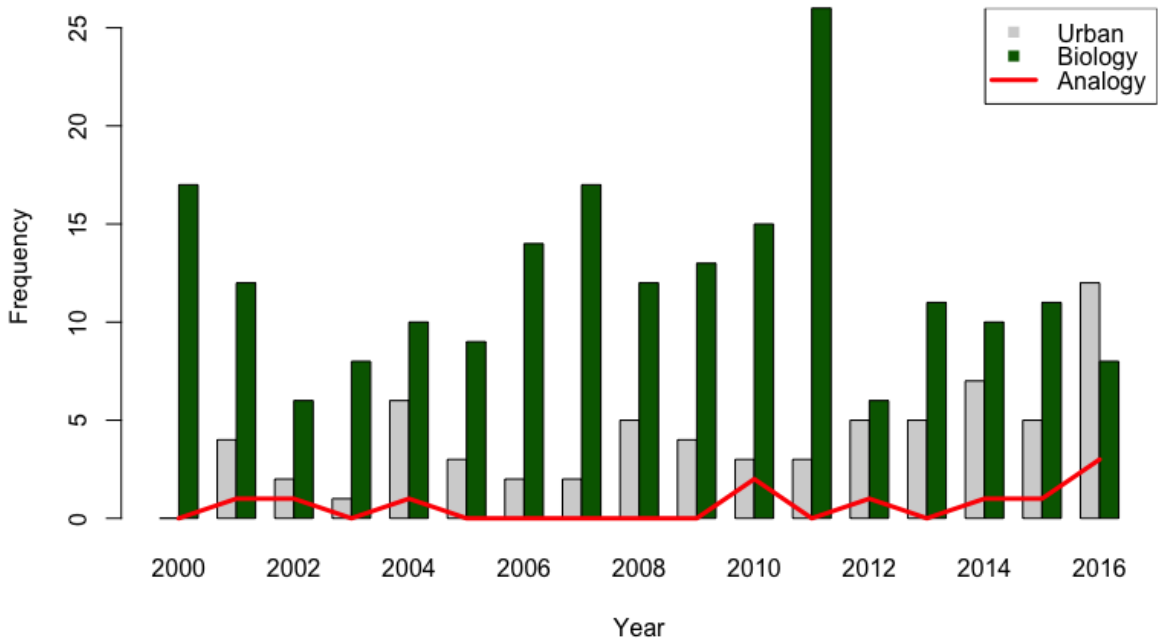
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Supplementary Material 2. Frequency plot of the number of articles using the term self-organisation found in the biological (green) and urban (grey) literature, and the frequency of urban articles containing a biological analogy, by year.

Topic	No. S-O Papers	No. Papers with Analogy	Analogy
Urban Design/Planning	12	4	City is an organism or tree (Ganis et al., 2016)*. City is an organism and tactical urbanism the energy for its evolution (Silva, 2016). Metabolism is urban economy with city as organism (Girard, 2014). Metabolism is urban economy with city as ecosystem (Girard, 2014). Assembly of molecules to form life akin to assembly of elements to form cities, including translational mechanisms e.g. genetic blueprints (Salingaros, 2010). City as living organism where rules govern structural and functional complexity and the breakdown of these rules leads to pathologies (Salingaros, 2010).
Methods	20	2	Parts of the city are species in an ecosystem (Partanen, 2015). City is a multistructural organism (Frenkel, 2004).
Transport	7	2	Slime mould formation of transport networks (Adamatzky et al., 2017)**. Collective behaviour of people like that of bird swarms (Helbing et al., 2001).
Urban Growth	4	2	Slime mould growth and urban growth (Barker, 2012). Fitness of land uses is relative to the fitness of other land uses on the fitness landscape, least fit land uses are removed, most fit are added (Andersson et al., 2002).
Urban Morphology	8	1	Systems of internal body flow akin to human movement (Mehaffy et al., 2010).
Land Use	9	0	
Demographics	3	0	
Architecture	1	0	
Environmental	1	0	
Governance	1	0	
Housing	1	0	
Philosophy	1	0	
Policy	1	0	

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3 Supplementary Material 3. Articles included in the literature review by topic of article. Analogies are described where present. The table is
4 sorted by (i) number of papers with analogies, (ii) number of self-organisation papers. * signifies where the analogy was used during a critique
5 of analogy and was not presented as the authors' own. ** signifies that the article was published online in 2016.
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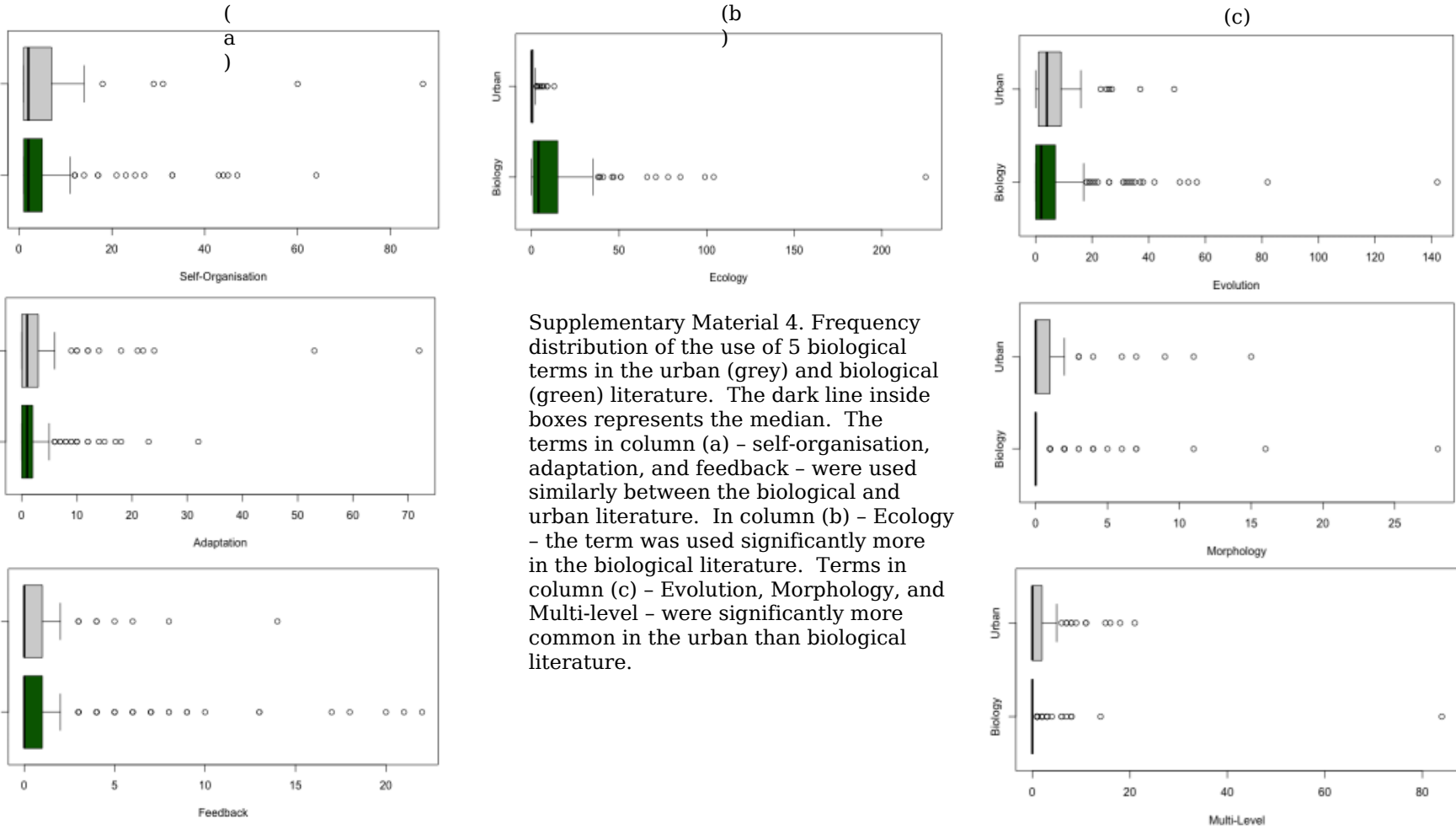
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11 Partanen J. (2015) Indicators for self-organization potential in urban context. *Environment and Planning B*. **42**:951–971
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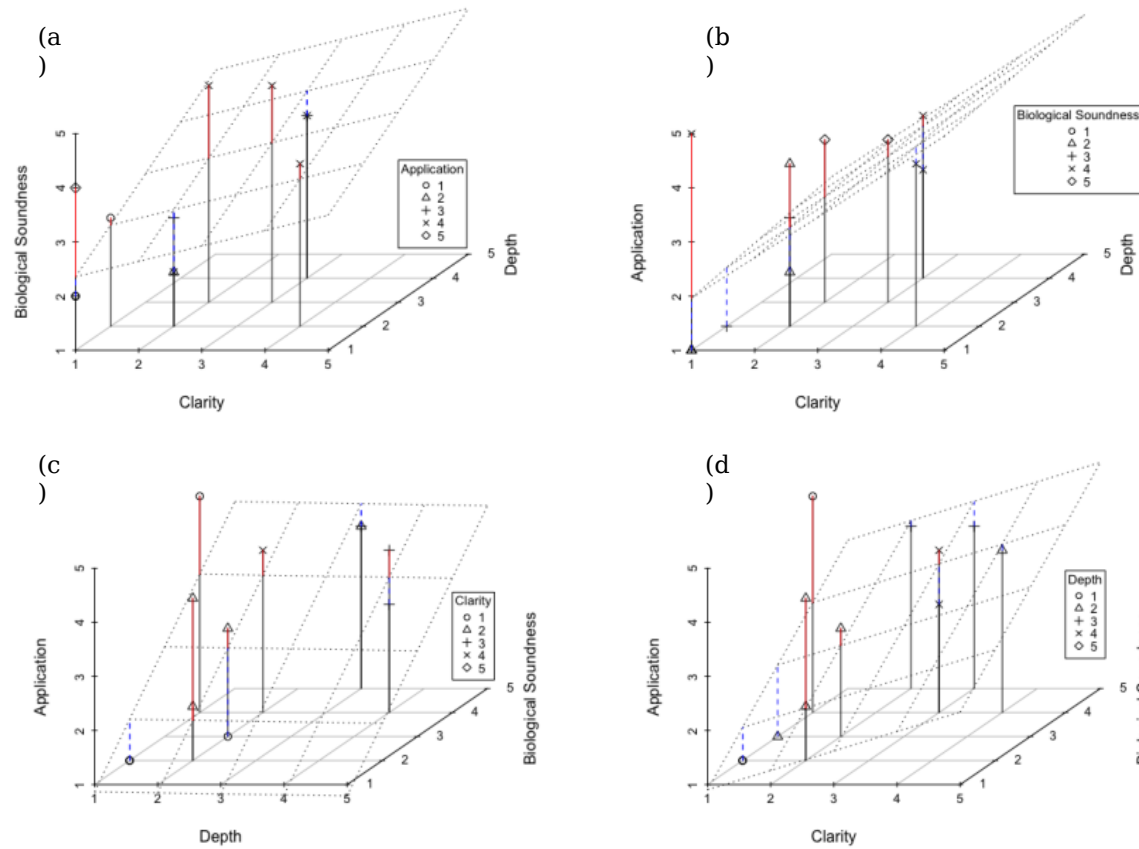
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Supplementary Material 4. Frequency distribution of the use of 5 biological terms in the urban (grey) and biological (green) literature. The dark line inside boxes represents the median. The terms in column (a) - self-organisation, adaptation, and feedback - were used similarly between the biological and urban literature. In column (b) - Ecology - the term was used significantly more in the biological literature. Terms in column (c) - Evolution, Morphology, and Multi-level - were significantly more common in the urban than biological literature.



Supplementary Material 5. Scatterplots showing the relationship between the clarity, depth, biological soundness and application of analogies in the urban planning literature. The point symbols show the fourth dimension. The black lines indicate the points position on the xy-axis. The red lines are the positive residuals, and blue-dashed lines the negative residuals, from the regression plane, drawn using a linear model.

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Introduction

Nature has inspired urban designers since they first attempted to understand the complex functional order of cities. Cities have been seen as organisms (Mumford, 1938; 1961) or ecosystems (Girard, 2014; Marshall, 2009); comprising components analogous with cells, tissues, organs, flesh, blood, tentacles and skeletons (Le Corbusier, 1947; Mumford, 1938; Soria y Mata, 1998); and subject to urban growth, morphogenesis, metabolism, adaptation and evolution (Geddes, 1915; Marshall, 2009; Rogers, 1998). Mining of other disciplines for inspiration and describing phenomena using analogies, metaphors and similes has advanced understanding of urban problems and investigation of possible solutions, as seen in the proliferation of biomimicry solutions for designing more sustainable cities (Benyus, 2009), evacuation routes (Dias et al., 2013), and new building materials (Vogel, 1998).

However, amid the profusion of biological comparisons it remains unclear whether or not usage is consistent or biologically robust. In these circumstances, biological analogies risk being dismissed as unscientific, or merely figures of speech, so opportunities for their advancement of understanding and application may be missed. As ‘nature-based solutions’ and scientific approaches to urbanism (Batty, 2012; Marshall, 2012) gain increasing attention, drawing inspiration from appropriate models (Batty, 2007; Moroni, 2015), analogies (Steadman, 2008), and metaphors (Chettiparamb, 2006; Tippett, 2010), it is an opportune time to revisit the nature of biological analogies in a systematic way.

Overall this mission would imply an extensive research agenda, potentially tracking relationships between biological and urban phenomena on multiple fronts, including processes such as self-organisation, metabolism, adaptation and evolution. As a first step, this paper addresses self-organisation.

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6 Self-organisation refers to a bottom-up process where pattern emerges from numerous
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8 interactions among the components of an initially unpatterned system. Self-organisation does
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10 not require sentience of the self-organising units or an external agent. Rather, pattern
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12 emerges through local interactions between the system's components using positive and
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14 negative feedback.
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19 Self-organisation research occurs across the natural and physical sciences, and urban
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21 researchers have drawn upon these to inspire bottom-up approaches to generating urban order
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23 (Batty, 1998; Portugali, 1997). It is an inherently cross-disciplinary domain, routinely
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25 recognised as having both biological and non-biological manifestations, with direct
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27 operational equivalences that go beyond the figurative. Consequently, our treatment of self-
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29 organisation provides a lens through which to study phenomena spanning the biological and
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31 the urban, offering a model for future application to other areas where biology has influenced
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33 urban design including development, adaptation, and evolution.
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40 Here, our aims are to (i) identify a set of analogies, metaphors and similes based on self-
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42 organisation that are used in urban design; (ii) for analogies, establish a method for assessing
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44 their clarity, depth, and application to urban design; (iii) assess the validity of analogies
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46 according to contemporary biology; (iv) explore how these analogies link up or relate to each
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48 other in a more systematic way; and hence (v) establish a framework which contains and
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50 expresses the observed urban/biological relationships, and may also be used to generate new
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52 ones. We believe that this is a potentially pioneering agenda, generating a method that could
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54 find further application in other contexts, and wherein the scrutiny from contemporary
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56 biology is itself novel, yielding insights that are correspondingly original.
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5 First, we briefly introduce the history of self-organisation and its current use in urban design
6 and biology. Secondly, we undertake a systematic analysis of analogy between urban and
7 biological disciplines, quantifying the use of analogy, and their biological validity. Finally,
8 we suggest a new biotic framework through which to interpret the analogical space, locating
9 existing analogies in relation to each other and helping to stimulate new analogies for urban
10 application.
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21 **Self-Organisation**

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23 Whilst the idea that order can emerge by itself dates back to Democritus and Lucretius, it was
24 Emmanual Kant who first coined the term 'self-organisation' arguing that organised beings
25 can be distinguished from non-living entities because they have a self-organising 'formative
26 power' which propagates itself that required a new type of science to explain it, because
27 neither physics nor chemistry could (Karsenti, 2008; Keller, 2008).
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38 Kant's 'new science' emerged much later, after his ideas received a series of rejections and
39 revocations (Keller, 2008). A major challenge was that biology is largely based on chemical
40 and biochemical reactions which don't self-organise (Tabony, 2006). Lotka (1909; 1925)
41 submitted that chemical reactions might self-organise into oscillating chemical systems, akin
42 to predator-prey population size dynamics, later confirmed experimentally by Belousov
43 (1951) and Zhabotinsky (1964) and mathematically by Turing (1952). Interest proliferated
44 across fields, leading to new understanding of the thermodynamic properties of dissipative
45 systems (Prigogine and Nicolis, 1967), cybernetics and feedback (Ashby, 1960; Wiener,
46 1948), synergetics (Haken, 1977), fractals (Mandelbrot, 1982) etc. Such studies ushered in a
47 new era in self-organisation research where both the animate and inanimate were products of
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3 self-organisation in nonlinear, far-from-equilibrium, open systems, and their results have
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5 been applied across the social, computational, economic, physical and biological sciences
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8 (Keller, 2009).
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12 In biology, Goldbeter and Lefever (1972) used Belousov-like equations to describe glycolytic
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14 oscillations, and Turing's work has been applied to pattern formation in mammals' coats
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16 (Murray, 1988), and embryogenesis (Glover et al., 2017). Today, self-organisation research
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18 spans all levels of biological complexity, from micro: formation of the first polymers (Freire,
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20 2015) and cell division (Karsenti, 2008); to macro: schooling fish (Camazine et al., 2001),
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22 species distributions (Alados et al., 2007), ecosystems (Lenton et al., 2018).
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29 Urbanists also adopted self-organisation from the physical sciences. Prigogine's theory of
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31 dissipative systems was applied to the appearance of central places (Allen et al., 1985).
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33 Portugali (Haken and Portugali, 1996; Portugali, 1997) introduced synergetics, Batty and Xie
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35 (1997) pioneered cellular automata techniques, and both men applied fractal and synergetic
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37 approaches to chaos theory (Batty and Longley, 1994; Portugali, 1997). Today, self-
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39 organisation is routinely considered a central process in urban development (Yamu and
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41 Frankhauser, 2015) yielding important insights for urban planners considering topics
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43 including: urban intensification (Janssen-Jansen, 2013), urban codes (Moroni, 2015) and self-
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45 governance (Rauws and de Roo, 2016); for a recent mapping of research see de Bruijn and
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47 Gerrits (2018).
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54 As biology has drawn from the physical sciences, urban designers are applying biological
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56 self-organisation to urban environments. Indeed, the richest potential for understanding
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58 urban self-organisation would appear to lie in learning from biology, which exhibits the
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3 fullest range of self-organising phenomena, from inanimate biomolecules through the
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5 animate world of sentient beings to ecosystems and Gaia. As such, a key challenge is to
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7 clarify how the biological component of self-organisation is being related to urban processes
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9 and where further insights might be found.
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14 **Methods**

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17 To ~~address this challenge~~ examine how biological inspiration is being used within studies of
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19 urban self-organisation we identified all articles referencing self-organisation between 2000-
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21 2016 in five urban design and five biology journals, resulting in 69 urban design and 205
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23 biological articles. We listed 25 biological terms (Fig.1) and recorded their frequency per
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25 paper. Biology-inspired similes, metaphors and analogies were identified in the urban
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27 literature, and analogies were assessed for clarity, depth, biological soundness, and
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29 applicability using a 1 to 5 scale (1=low, 5=high). We used mapping analyses and boxplots
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31 to compare term usage between disciplines, and Sankey diagrams and 3D-scatterplots to
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33 assess how analogies were employed. For a fuller version of the methods and results see
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35 SM1.
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43 **Results**

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45 The number of urban articles referring to self-organisation increased overall between 2000-
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47 2016 (SM2), and covered a wide range of urban design topics (SM3) including mechanistic
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49 models, unplanned-local initiatives, and the planning process.
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53 *Biological Terms*

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55 All urban papers contained at least one of our biological terms other than self-organisation.
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3 Mapping of terms revealed inconsistencies in connections between the two disciplines (Fig.1)
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5 highlighting differences in the way the terms are used (SM4).
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10 [Fig.1]
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15 In both disciplines the closest links were between 'self-organisation' and 'evolution'.
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17 'Adaptation' and 'ecology' are also closely connected, after which, the two disciplines
18
19 diverge. The biological mapping stressing the importance of 'gene', 'mutation', 'natural
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21 selection', 'organism', and 'morphology', the urban mapping highlighting 'morphology',
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23 'feedback', 'multilevel', and 'organism' (Fig.1).
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29 Herein lies a key difference between the biological and urban realms. The biological
30
31 mapping points to biology's central theorem: that an organism's adaptive traits are the
32
33 product of evolution through natural selection and mutation is one mechanism of introducing
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35 genetic variation. Direct analogues of biological evolution are largely absent in urban
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37 planning (Mehmood, 2010), because those that do so face significant challenges including:
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39 defining urban genes and fitness, characterising urban gene to phenotype translation,
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41 identifying the units of survival and reproduction.
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47 *Biological Comparisons*

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49 Through further review of the urban articles 66 biological terms were identified, which were
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51 used 2371 times. Biological terms were most often used *without* consciously invoking a
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53 biological comparison; despite this, 31.88% of urban articles contained a biological
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55 comparison: 15.94% analogy, 23.18% metaphor, 7.25% similes (The sum is more than
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57 31.88% as some papers contained more than one kind of biological comparison. SM3)
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6 Thirteen analogies were identified, in eleven papers. 69.23% of which were made between
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8 different hierarchical levels e.g. city–organism is cross-level analogy, person–organism is a
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10 direct-level analogy (Fig.2). 38.46% of the analogies related directly to self-organisation.
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12 Analogies were often found to be either unclear (mean=2, s.d.=1), and/or, of limited depth
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14 (mean=2.15, s.d.=1.07); whilst depth of analogy showed no connection with urban
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16 applicability we found a positive association between the depth, and to a lesser extent the
17
18 clarity, of an analogy and its biological soundness (SM5). Applicability was found to be
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20 higher when an analogue was both clearly conveyed and the biological content was accurate
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22 (SM5).
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[Fig.2]

32 33 **Nature-Inspired Urbanism?**

34 35 *Depth, Clarity, Biological Soundness*

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37 Overall, the analogies lacked depth and clarity. Lack of depth had nominal effect on the
38
39 applicability of an analogy to the urban realm. Rather, the more reliable the biological basis,
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41 and the more clearly the information was applied, the better the fit of the biological analogue.
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43 As depth and clarity increased, the biological information was found to be more dependable,
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45 a not wholly surprising result as clarity and depth are both qualities required to adequately
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47 assess biological content.
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54 That an analogy was not required to be deep to be successful is more interesting. An analogy
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56 may be so commonly employed that in-depth interrogation is not required to impart meaning
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58 e.g. city is organism. The purpose of the analogy may not call for an in-depth analysis of
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3 biological theory. Or, the biological connection may not be particularly important to the
4 author, who instead could opt for deeper analogies with other disciplines, which may
5 themselves be analogous, and produce similar insights (Helbing et al., 2001).
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12 Concerningly a lack of depth and/or clarity can make it difficult to distinguish the type of
13 biological comparison being used, leaving readers to infer meaning according to their own
14 biases. For example, depending on the author, and reader, city as organism may be purely
15 symbolic (Nientied, 2016), or an analogy from which logical arguments can be extended and
16 planning decisions made (Golubiewski, 2012). Combine this with terms having multiple
17 definitions or context sensitivity and it is easy to see how confusion may occur.
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28 All of these are common problems facing writers who use comparative language to express
29 ideas (Chettiparamb, 2006). However, with over half of the world's population inhabiting
30 cities and increasing disconnection from the natural environment (Cox et al., 2017), urban
31 authors face a more fundamental problem when using biological comparisons: that of using
32 the unfamiliar to describe the familiar.
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42 Urban DNA is a particularly interesting example (Boelens, 2014; Nientied, 2016; Wu and
43 Silva, 2011). Whilst DNA is a part of us, it is not a part we see or feel, or identified the role
44 of until Avery et al. (1944). Thanks to the efficacy of language, art, and the fundamental
45 desire to understand the nature of being, DNA has become relatable. Its structure, the
46 information it inscribes and 'mystical powers' have been described as a twisted ladder, a
47 blueprint, an immortal spiral (Rovira, 2008).
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3 The particular comparisons employed can markedly alter our understanding, and the
4
5 implications, of a concept. Informational and essentialist DNA metaphors have shaped our
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7 laws (Silvestro, 2016), and metaphors regarding DNA's components have shaped research
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9 trajectories (Avisé, 2001). New findings may invalidate descriptors, eliciting calls for their
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11 alteration or discontinuation e.g. 'DNA is a blueprint' lost favour because it implies a direct
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13 mapping of genetic information to phenotype, when in actuality, the same genetic code can
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15 produce remarkably different phenotypes e.g. queen and worker honeybees. Perhaps 'genetic
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17 code' remains in good standing because 'code' does not suggest decryption method, allowing
18
19 many final forms and the capacity to integrate new research findings. As such, the analogy
20
21 of urban DNA might better be conceptualised as a set of generative codes, or framework
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23 rules, resulting in a self-organised urban order, as opposed to urban order generated by a
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25 blueprint.
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33 Ultimately, research requires the clear communication of ideas, so they can be assessed and
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35 discussed. Where confusion occurs advancement is hampered (Steadman, 2008). Defining
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37 terms and the limits of one's analogies can help reduce confusion, clarify thinking, and
38
39 elucidate when a field where inspiration is being drawn from is itself using the same term in
40
41 different ways. For example, in biology, terms such as metabolism are regularly used across
42
43 disciplines and hierarchical levels but refer to different processes (Golubiewski, 2012). Thus,
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45 referring to the city as ecosystem and as organism, particularly in the same paper, can have
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47 very different implications, muddling the narrative.
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54 *Description, Inspiration, and Mechanism*

55 Analogies were used to either describe, inspire or suggest mechanism. In description, the
56
57 opportunity for an extended metaphor to be confused for analogy was highest. For example,
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3 is Frenkel's (2004) description of cities as '*multistructural organisms as reflected in the*
4 *spectrum of their functions*' and use of taxonomic methods to '*classify cities according to*
5 *their characteristics*' a metaphor, or an obvious extension to the commonly expressed
6 analogy?
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15 Inspirational analogies encouraged new ways of thinking about the urban environment.

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17 Salingaros (2010) used the earliest bio-molecules to inspire urbanists to look beyond an urban
18 element's primary function to consider secondary and potential catalytic effects. Finally,
19 mechanistic analogies such as Barker (2012) and Adamatzky et al. (2017) who employed
20 different slime mould species to reveal how simple, local, bottom-up interactions lead to
21 urban formation and efficient transport networks, respectively.
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31 Three of the five analogies that proposed mechanism were directly related to self-
32 organisation. Of course, as self-organisation is a mechanism this correlation is unsurprising.
33 More interesting is that two of these three studies drew comparisons of urban systems from
34 the behaviour of slime moulds, which, over recent years, have helped overturn notions of the
35 minimum level of intelligence needed to solve complex problems, leading to the development
36 of simpler algorithms to solve modern day human problems.
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47 Difficulties arise in that: models have mostly been deductive rather than predictive, limiting
48 their current value to urban planning (Adamatzky et al., 2017); the focus on economic
49 'rationality' can favour highly productive regions rather than the growth of underdeveloped
50 regions (Vanoutrive et al., 2016); the spatial scale and morphology of slime mould
51 experiments may dramatically change the solutions arrived at and might not always be
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3 optimal (Reid et al., 2012), as slime moulds can make irrational decisions, similar to humans
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5 (Latty and Beekman, 2010).
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10 Examining a variety of organisms may be more informative to urban planners, providing a
11 variety of solutions to choose from. For example, Argentine ant (*Linepithema humile*)
12 networks prioritise cost and efficiency over robustness (Cabanès et al., 2014), the fungus
13 *Phanerochaete velutina*'s networks maximise robustness and efficiency (Bebber et al., 2007),
14 whilst the networks of wild polydomous ant colonies, which can stretch thousands of
15 kilometres, have more connections than those found in lab populations, suggesting robustness
16 may be a more important factor in ecologically valid situations (Cook et al., 2014).
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29 *Analogies Across Levels of Scale*

30 Both biological and urban systems are characterised by nested levels of increasing
31 complexity, where each level is primarily composed of the level below but possesses
32 emergent properties not present in that level. Mechanisms leading to the spatial organisation
33 of lower level entities forming higher hierarchical levels include self-organisation,
34 environmental constraint, and cooperation {MaynardSmith:1995wr, Takeuchi:2009el},
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45 Biological levels extend from molecules to Gaia, although authors generally define a
46 narrower, question-appropriate range. The delineation between biological hierarchies is not
47 as neat as it might initially appear. Single celled organisms, for example, inhabit both the cell
48 and organismal levels, and an organism is a community, called the holobiont, when
49 microbiome, virome and parasites are accounted for.
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3 The urban realm can include human concepts of geographical/economical/political areas but,
4 for most urban researchers their questions will fall between the people and regions levels, and
5 like biological levels of organisation, delineation between urban levels and elements at
6 different scales is not always clear cut (Alexander et al., 1977; Kropf, 2014). Actually, the
7 urban hierarchy is nested within the biological hierarchy. People are organisms so are found
8 on the biological hierarchy at the level of organism. The urban environment is a type of
9 ecosystem; however, it can also be considered at lower hierarchical levels (e.g. community),
10 depending on the question being asked.
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24 Most of the analogies we identified crossed hierarchical levels (Fig.2), analogising city to
25 organism, land uses to genes, and pedestrian paths to capillaries. Analogies existing at
26 equivalent hierarchical levels included city as ecosystem and models derived from slime
27 moulds because, whilst a slime mould and transport network (for example) may not
28 immediately appear to be at the same hierarchical level, the rules for their formation are both
29 generated at the organismal level, for modern human transport networks are often founded
30 atop the informal, emergent trails of our ancestors.
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43 Logically, all analogies that operate below the level of the organism must be cross-level
44 analogies. However, an interesting anomaly may occur with plan/blueprint/design as urban
45 ‘genotype’. A plan/design is neither nested within nor essential for the construction or
46 functioning of higher-level entities. Indeed, it may merely be a representation of a completed
47 form, rather than its generator. What is nested within and essential to the construction and
48 functioning of urban form is the urban population, each with genomes, and so, one could
49 postulate that *people* are the urban genotype.
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3 Employing evolutionary analogy Silva (2016) states that tactical urbanism (a self-organised
4 approach that transform the urban environment through self-built interventions) provides the
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8 'energy' for urban evolution, implying 'energy' translates to mutation. However, tactical
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10 urbanism can be more clearly and instructively described in terms of niche construction
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12 where, rather than city as organism it is analogous to a hive, burrow etc.
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17 Niche construction theory is a broadening of Dawkins' (1982) extended phenotype hypothesis
18
19 such that any manipulation of the environment by the organisms inhabiting it, and the effects
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21 of those manipulations on adaptive fitness of the organism, its progeny and other organisms
22
23 in the environment, are now included (Odling-Smee et al., 2003).
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28 Niche construction theory recognises that by altering their environments organisms alter the
29
30 selection pressures acting upon them, such that the organism adapts to the environment *and*
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32 the environment adapts to the organism. Thus, the organism produces an ecological
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34 inheritance (Odling-Smee et al., 2003) which, if fitness enhancing, will promote co-evolution
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36 of trait and constructed niche. In social groups, cultural inheritance can also drive niche
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38 construction (Ellis, 2015; Kendal et al., 2011).
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44 Theoretical examinations integrating ecological and cultural inheritances have found that
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46 niche construction is capable of overriding, reversing or accelerating natural selection, and of
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48 generating unusual population dynamics (Laland and Brown, 2006; Laland et al., 2001).
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51 Further, gene-culture-co-evolution has been proposed as the dominant mechanism of
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53 adaptation in humans (Ellis, 2015; Laland et al., 2010). Therefore, the creation of the human
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55 built environment is not only part of urban evolution, it is a part of human evolution, past and
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57 present. In other words, '*we co-evolve with the environment we create*' (Kropf, 2017).
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6 It is often self-organisation, operating amongst individuals or across environmental
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8 components, that shapes constructed niches. Social insects build nests, orders of magnitude
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10 larger than an individual through self-organised collective action, following cues derived
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12 internally, from nestmates, or environmentally (Green et al., 2017). Architecture has
13
14 produced buildings inspired by social insect nests but none has captured the adaptive quality
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16 of nest architecture, where structure and function have become one, and mechanism is
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18 derived through a homeostatic desire to maintain a stable internal environment that can be
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20 cognitively and physiologically produced (Penn and Turner, 2018; Turner and Soar, 2010).
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26 Returning to the example of tactical urbanism: as in niche construction theory, tactical
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28 urbanism denotes a self-organised, bottom-up approach, that transforms the urban
29
30 environment, through self-built interventions (Silva, 2016), rather than being a mutation in an
31
32 organism. Tactical urbanism initiatives include ‘Guerrilla Gardening’, ‘Intersection Repair’,
33
34 ‘Pop-up Cafes’. Their role seems often to beautify and connect, and these homeostatic
35
36 desires could be routed in a physiologically evolved need to reduce stress. When possible,
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38 portions of the urban population may be intuitively transforming their environments,
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40 removing or reducing aspects that negatively impact fitness. In doing so, they not only
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42 enhance their own fitness but that of their neighbours, increasing the probability of accruing
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44 benefits through reciprocal altruism or kin selected benefits. The fitness enhancement may,
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46 today, be small, but for the urban planner, the lessons may be of use. Firstly, such initiatives
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48 are likely excellent venues of inspiration for positive design ideas that can be extended more
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50 widely. Thus, allowing space for citizen-led, self-organised, bottom-up approaches to exist is
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52 of great import. Secondly, urban planners could co-opt this mechanism by identifying ways
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54 to translate innate homeostatic preferences into urban design, enabling the urban population
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3 to alter their environments for public good by building environmental feedback mechanisms
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5 into architecture (Pasquero and Zaroukas, 2016).
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10 **Analogical Space to Biotic Framework**

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12 Our analysis revealed a preponderance of cross-level comparisons over equivalences (direct-
13
14 level analogies). Indeed, even when a level of equivalence was being evoked it was often
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16 masked. Barker (2012), for instance, modelled how land-use decisions generate cities, where
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18 the model and decision rules were inspired by self-organised slime mould
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20 agglomerationslime-mould agglomeration behaviour. That the land-use decisions are made
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22 by humans and the model is using slime mould behaviour to propose simple rules
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24 underpinning human behaviour, is not explicitly stated. Operating so, the urban literature
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26 risks overlooking key areas of instructive insights that fall at the level of equivalence.
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33 In biology, evidence accrues through analogous research across taxa, where different
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35 evolutionary and life histories lead to different predictions drawn from the same theory. In
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37 feeding into these bodies of literature direct-level analogies (equivalences) could provide a
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39 more substantial contribution to urban researchers than the purely figurative. For, after all,
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41 humans are organisms too.
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47 To demonstrate our thinking we propose the biotic framework (Fig.3) – so named because it
48
49 emphasises that both organisms and their constructed environments are biotic - relating to or
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51 resulting from living organisms. In a very literal sense, our cities, indeed all human
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53 environmental modifications, are biotic. Our emphasis on the biotic is in contradistinction to
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55 traditional emphases on human versus nature, or organic versus inorganic – though both of
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57 these form part of the framework.
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10 The framework provides a rationale for locating and identifying analogies, particularly those
11 where the processes operating are most likely to be comparable to urban processes, and
12 encourages awareness of the entire system. We present two versions of the biotic framework
13 (a) presenting the framework and its dimensions, (b) showing a subset of the biological
14 comparisons identified in the reviewed literature (green solid lines), some well-known
15 comparisons that not present in the reviewed literature (orange dashed lines), and some
16 connections that we suggest could provide new inspiration for urban designers (grey dashed
17 lines) (Fig.3).
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31 Protruding into the foreground are the lower hierarchical levels. At the front are
32 biomolecules and compounds which form the basis of life, composing every living organism,
33 prompting ‘the continuity thesis’ which suggests that there is no break between
34 physiochemical and biological systems (Freire, 2015). The coalescence of molecules forms
35 the constituent parts of cells, which come together to form tissues, organs, and organism.
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45 Biological comparisons between urban elements and levels below that of organism have
46 proved popular, inspiring new conceptions of urban environments and processes.
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49 Comparisons made between molecules (Salingaros, 2010), or parts of an organism (Furtado
50 et al., 2012; Mehaffy et al., 2010; Salingaros, 2010), and the urban environment are, by
51 definition, cross-level analogies. Whilst there is no denying the merits of such comparisons,
52 we propose that, where an analogy relates to process, inspiration will more readily be found
53 and likely better fit the example, when it is drawn at the level of equivalence.
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5 The level of the organism is the first hierarchical level where drawing upon equivalence is
6 possible. Here, the living entity, be it human, slime mould, ant, or bower bird, is the focus.
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8 Its cognition, behaviour, and decision making, are of primary importance because such rules
9
10 determine how organisms use, move around and understand the environment, and population
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12 distributions. At this level, natural and cultural selection play dominant roles in shaping the
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14 behavioural rules and physiological requirements of the organism.
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21 Moving into the diagram from the position of the organism, two planes run parallel, the lower
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23 signifying increasingly large clusterings of the same organism (group, population, species),
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25 the upper signifying the organism's constructed environment. We adopt the definition from
26
27 niche construction theory to characterise a constructed environment - any modification of the
28
29 environment by an organism which alters the selective pressures acting upon it and other
30
31 organisms inhabiting that environment. As such, constructed niches vary dramatically
32
33 between organisms including leaf litterfall (Bigelow and Canham, 2015), birdsong repertoire
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35 size (Creanza et al., 2015), and termite mega-structures (Turner, 2004). The two planes run
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37 parallel because to differing extents the constructed niche will impact the selective pressures
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39 acting on those groupings.
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47 To represent hierarchical relationships between elements within the human built environment
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49 we build upon a representation proposed by (Kropf, 2014), adding neighbourhood, city and
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51 conurbation as familiar reference points, although these do not imply an exact structural
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53 continuation of the lower levels.
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3 Humans, like all organisms, don't inhabit the world alone or immune from the effects of the
4 environment. When organisms interact they form communities; the combination of
5
6 environment. When organisms interact they form communities; the combination of
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8 communities and physical processes are ecosystems, which in turn combine to biomes and
9
10 eventually Gaia. At these levels, natural selection plays a muted role. Rather, system
11
12 evolution and adaptation may be guided by self-organised mechanisms (Lenton et al., 2018).
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14 The urban environment is an ecosystem and so, analogies drawn between mechanisms of
15
16 natural ecosystem functioning, resilience, evolution, adaptation etc., with urban processes are
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18 examples of equivalences.
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24 As each hierarchical level is an emergent property from coalescence of the level below,
25
26 disturbance at one level can trigger changes upwards and downwards. The biotic framework
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28 draws attention to the interconnected and hierarchical nature of the whole system and can be
29
30 used to interrogate the implications of transformations across hierarchical levels. Analogy
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32 does not have to include multiple hierarchical levels to be of use. However, by considering
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34 the implications of an analogy across multiple hierarchical levels, and defining the limits of
35
36 the analogy, not only are the clarity and biological soundness likely to be improved (a key
37
38 indicator of the fit of an analogy to the urban realm) but the potential to identify novel
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40 insights is markedly increased.
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47 Indeed, the framework motivated us to propose, for demonstrative purposes, three new
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49 comparisons, that might serve to inspire urban design and the rules that formulate urban
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51 environments. Firstly, Secondly, we refer back to transport networks and our assertion that
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53 examining networks of polydomous ant colonies may be instructive for urban planners,
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55 particularly as field studies show that networks of nests, analogous to a conurbation or
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57 network of cities, favour different network characteristics than lab colonies (Cook et al.,
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3 2014). Secondly, as initiatives work to bring food production into our urban environments
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6 (Whittinghill and Rowe, 2011) using natural communities to inspire our understanding of the
7
8 needs of urban communities will become ever more crucial. A classic example of farming in
9
10 animal societies is that of fungus farming ants; this turns out to be a multi-species mutualism
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12 (Barke et al., 2010) highlighting the need to consider community dynamics even within
13
14 complex constructed niches, and the role of the constructed niche in shaping those
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16 communities and dynamics.- Secondly, we refer back to transport networks and our assertion
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18 that examining networks of polydomous ant colonies may be instructive for urban planners,
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20 particularly as field studies show that networks of nests, analogous to a conurbation or
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22 network of cities, favour different network characteristics than lab colonies (Cook et al.,
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24 2014). Thirdly, we propose that epigenetic mechanisms for pattern formation (non-genetic
25
26 influences on gene expression that affect traits such as coat pattern, caste differentiation, and
27
28 that allow organisms to rapidly respond to changing environments) could be used for
29
30 inspiring a new type of responsive planning inspire a new (or newly recognised) layer of
31
32 'epigenetic' directions within urban design/planning. Such an epigenetic layer would guide
33
34 where and when different codes or framework rules are deployed, perhaps in conjunction
35
36 with outline planning or strategic zoning (combined with, or as an alternative to, urban plans,
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38 codes or framework rules), making our cities more adaptive and resilient to future challenges,
39
40 formalising Moroni's (2015) suggestion of 'rules for the production of rules for the activation
41
42 of processes' and/or integration of 'location-specific development regulations, traditionally
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44 expressed in the land-use plan, with generic regulations' {Rauws:2016hl}. In other words,
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46 the urban equivalent of epigenetic mechanisms could be used to help guide self-organising
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48 urbanism in a third way that offers a balance between more purely bottom-up or top down
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50 processes.-
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Conclusion

Our research has found a rich diversity of biological analogies associated with urban phenomena relating to self-organisation but these are currently applied with limited depth and relation to each other. Still, they could be applied more deeply and systematically, and we show how via the biotic framework, which has also stimulated new analogies. We believe this analysis, including assessing the biological soundness of analogies, is original in a way unprecedented since the time of Patrick Geddes, and can pave the way for further research agendas, including application to other analogical processes (e.g. urban adaptation, evolution) and other disciplinary domains.

In our analysis we found that analogies between biological and urban realms were drawn from molecule to ecosystem and human to city. They mostly crossed hierarchical levels and the potential for confusion from the complexity of these different relationships led us to generate the biotic framework (Fig.3). This framework was initially created to articulate the analogical space that has been the focus of this paper, but in doing so provides a structure for conceptualising and interpreting relationships between key domains of the biotic sphere.

Our analysis suggests that attention could be usefully directed to the more direct analogies or equivalences because: cities are actually ecosystems; our built environments are actually constructed niches; our built environments have a material effect on our ongoing evolution. Furthermore, these three statements are linked and can be made more visually explicit via the biotic perspective. In addressing equivalence, insights from reading across human and natural realms may be particularly pertinent because they access overarching theories, built on evidence from a wide array of organisms, to explain and describe the evolution and mechanistic underpinnings of the phenomena.

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5 For the urban environment, comparisons operating at the level of the organism and providing
6 feedback between organism and environment will be particularly pertinent. Niche
7
8 construction theory has already been applied to human evolution (Laland and Brown, 2006;
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10 Laland et al., 2001; 2010) and combining biological theory e.g. optimal foraging or cultural
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12 niche construction, with insights from past trends, could help identify planning perspectives
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14 that are adaptive, resilient, and commensurate with our homeostatic-inherent desires for
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16 physiological comfort, and advance theory.
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24 At higher ecological levels, the environmental effect of humans is ever more tangible. Calls
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26 to circularise our systems (Williams, 2019), or mimic the services provided by natural
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28 ecosystems (Benyus, 2009) do not benefit from the view of city as organism; rather, the view
29
30 of cities as ecosystems, and drawing inspiration from natural ecosystem functioning, failures
31
32 and resilience, provides a stronger basis from which to construct solutions to the ultimate
33
34 problems facing future urban environments. As such, choosing the right analogy is not
35
36 purely a choice of literary expression but, as with the example of DNA, can make a material
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38 difference to our perception of a problem and as such appropriate solutions.
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45 Interestingly, the biotic framework can be seen as a freshly explicit expression of Geddes's
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47 understanding of the equivalence of the human and natural realms, that has more often
48
49 remained implicit (Geddes, 1915). His assertions regarding the interaction between human
50
51 evolution and environment invoke modern niche construction theory, his concept that
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53 cooperation overrides conflict is supported by multilevel selection theory. As biology
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55 furthers its understanding of evolutionary processes, self-organisation is emerging as a
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57 principal force, shaping form through the self-organised behaviours of organisms, and
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3 ecosystems through self-organising mechanisms far removed from the reach of the genes.
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5 This could provide an area for future application linking urban self-organisation and
6
7 evolution. Overall, analogies at the level of equivalence could become of increasing interest,
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9 even to those wary of organicist metaphors, not despite their biological roots but because
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11 through them comparison can go beyond the purely figurative.
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