SOFT ROBOTICS
Volume 1, Number 2, 2014
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DOI: 10.1089/soro.2014.0014

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Soft Robotics

INVITED REVIEW

Growing Fine-Grained Multicellular Robots

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Abstract

Engineers are torn between an attitude of strong design and dreams of autonomous devices. They want full mastery of their artifacts while wishing these were much more adaptive or ''intelligent.'' Today, while we must still spoon-feed (program, repair, upgrade) our most sophisticated computer and robotic systems, insatiable demand for novelty has created an escalation in system size and complexity. In this context, the tradition of rigid top-down planning and implementation in every detail has become unsustainable. Natural complex systems, large sets of elements interacting locally and producing nontrivial collective behaviors, offer a powerful alternative and source of innovative ideas. Going beyond metaheuristic disciplines based on ''neurons'' (machine learning), ''genes'' (genetic algorithms), or ''ants'' (ant colony optimization), this article highlights a new avenue of bioinspired engineering that simulates the growth of fine-grained multicellular organisms. It presents a brief overview of morphogenetic engineering and one of its instances, embryomorphic engineering, which are two fields that explore the decentralized self-organization of artificial complex morphologies and behaviors. MapDevo3D, an embryomorphic engineering model of developmental animats in a 3D virtual physics world, is described in more detail. Bodies are composed of several hundreds of cells, giving them a quasi-continuous texture close to the tenets of ''soft robotics.'' Motion results from local muscle twitching without a central nervous system. Altogether, the challenge is not to build a system directly but find the rules that its components must follow to build it for us.

Introduction

Morphogenetic engineering (ME), the topic of a recent book,[1] concerns the design—or rather ''metadesign''—of the self-organizing abilities of the elements of complex systems toward functional architectures. In general, natural phenomena of spontaneous pattern formation (PF) are random and repetitive,[2] whereas, on the opposite end of the spectrum, artifacts and elaborate devices are the deterministic product of human design. Yet, multicellular biological organisms (and, to a certain extent, collective insect constructions) are striking examples of complex systems that are both entirely self-organized and strongly architectural. Accordingly, the goal of ME is to establish a new field of research to explore the intersection between these traditionally disconnected domains, that is, the modeling and implementation of ''self-architecting'' systems.[3] It places particular emphasis on the computational abilities and programmability of self-organization—properties that are often underappreciated in complex systems science—while, conversely, the benefits of self-organization are often underappreciated in engineering methodologies.

In this context, the present article proposes an overview of embryomorphic engineering (EE),[4–6] a particular instance of ME, which takes its inspiration directly from biological development to create new hardware, software, or network architectures—or literally let them ''grow''—through the decentralized aggregation and self-assembly (SA) of a myriad of small agents, or ''cells.'' At its core, EE combines three key principles of multicellular embryogenesis: (1) chemical gradient diffusion, providing positional information to the cells; (2) gene regulatory networks (GRNs), triggering the differentiation of cells into types, thus creating patterns; and (3) cell division, imposing structural constraints, thus creating new shapes. We illustrate the applicative potential of EE to collective/reconfigurable robotics via an abstract 3D model of artificial multicellular organisms called MapDevo3D (modular architecture by programmable development; Fig. 1). It involves virtual robotic superstructures, or ''animats,''[7] developing and behaving in a virtual physics

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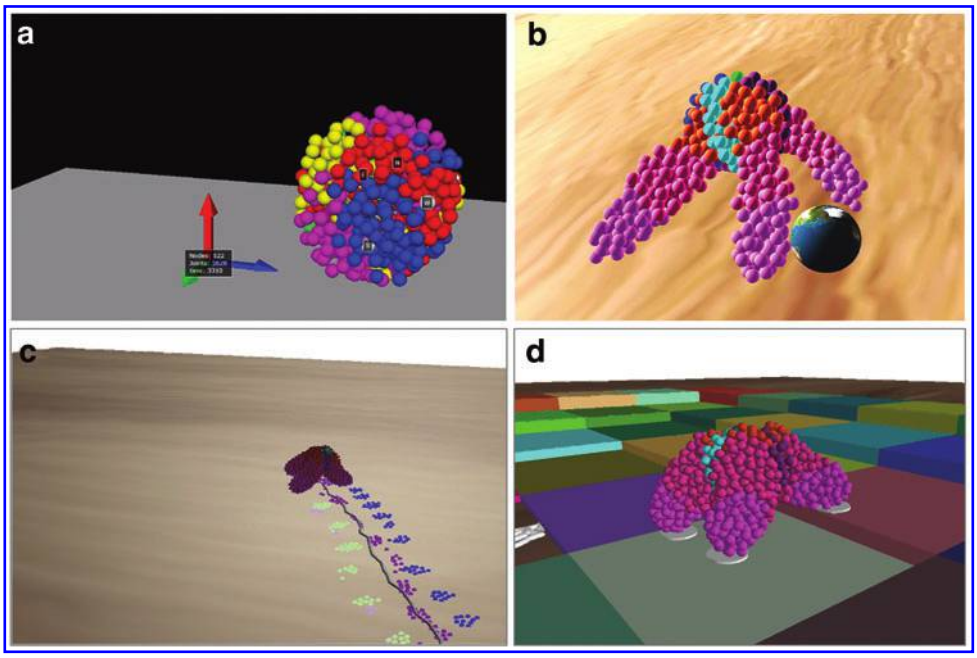

FIG. 1. Preview of embryomorphic creatures and scenarios: the underlying model and experiments are summarized in this article. **(a)** Development of a multicellular creature's body, before growth of the appendages, displaying regions of differentiated cells (see section Modular Architecture by Programmable Development in 3D). **(b)** Mature organism with four long, thin legs (one of which hidden by the perspective) walking on a floor and kicking a ball (see section Behaving Morphologies in a Physical Environment). **(c)** Footprints and center-of-mass trajectory of another walking creature with thicker legs. **(d)** Evolutionary scenario involving a stair-climbing challenge (see section Function from Structure from Development). Color images available online at www.liebertpub.com/soro

world. Their bodies consist of a fine-grained texture arising from a large number of cells, which can represent tiny robotic modules or self-propelled robots. This quasi-continuous aspect brings MapDevo3D close to the ideals of ''soft robotics.''[8] In all cases, the specific genotype that cells share makes the phenotype's complex architecture and function modular, programmable, and reproducible.

The Challenge of Evolutionary Development

Unlike traditional engineering disciplines, the metadesign of the agent rules professed by ME must not exclusively rely on human inventiveness, but should also involve an important automated and self-adaptive part, fundamentally relying on an evolutionary search and optimization process. In that sense, by combining not only self-organization and architecture but also evolution, ME shares the views of *evolutionary development*, a recent and rapidly expanding field of biology nicknamed ''evo-devo.''[9–13] This section points out the challenges raised by evo-devo research in biology, and the potential benefits of transferring them to the artificial life (Alife) versant toward bio-inspired engineering endeavors. The next section offers a brief review of current attempts and issues in ME.

Evo-devo in biology

In the variation/selection couple of evolutionary biology, ''selection'' has received most of the honors while ''variation'' remained the neglected child. Darwin discovered the evolution of species, based on random mutations and nonrandom natural selection, and established it as a central fact of biology. During the same period, Mendel brought to light the laws of inheritance of traits. In the twentieth century, his work was rediscovered and became the foundation of the science of genetics, which culminated with the revelation of DNA's role in heredity by Avery, and its double-helix structure by Watson and Crick. Integrating evolution and genetics, the ''modern synthesis'' of biology has successfully demonstrated the existence of a fundamental correlation between genotype and phenotype and between their respective changes: mutation in the first is causally related to variation in the second. Yet, 150 years after Darwin's and Mendel's era, the nature of the link from genes to organismal forms, that is, the actual molecular and cellular basis of the mechanisms of development, is still unclear. How does a one-dimensional genome lead to or influence the construction of a three-dimensional plant or animal?[10] How does a static, linear DNA ''unfold'' in time (regulation dynamics) and space (cellular SA)? What is the part played by epigenetics—in both its molecular and environmental senses? These questions constitute the missing link of the modern synthesis and the main challenge of evo-devo.

While the attention was focused on selection, it is only during the past decade that analyzing and understanding variation as the core engine of phenotypic novelty by comparing the developmental processes of different species (at both the embryonic and the genomic levels) became a major concern of biology. Researchers realized that the genotype–phenotype pairing could not forever remain an abstraction if they wanted a deeper understanding of the unique power of evolution to produce countless innovative structures—and, concerning Alife and bio-inspired engineering, ultimately

transfer this knowledge to self-organized technological systems. Kirschner and Gerhart[13] stress the fine granularity of the scale, that is, the individual cell, on which variation is at work:

> When Charles Darwin proposed his theory of evolution by variation and selection, explaining selection was his great achievement. He could not explain variation. That was Darwin's dilemma.…To understand novelty in evolution, we need to understand organisms down to their individual building blocks, down to their deepest components, for these are what undergo change. (p.ix)

Evo-devo casts a new light on the question still seldom addressed by today's predominant gene-centric view of biology: To what extent are organisms also the product of complex physicochemical developmental processes not necessarily or always controlled by complex underlying genetics? Before and during the advent of genetics, the study of developmental structures had been pioneered by the ''structuralist'' school of theoretical biology, which can be traced back to Goethe, D'Arcy Thompson, and Waddington. Later, it was most actively pursued by Kauffman[12] and Goodwin[11] under the banner of *self-organization*, argued to be an even greater ''force'' than natural selection in the production of viable diversity.

Recent dramatic advances in the genetics and evolution of biological development have paved the way toward explaining morphological self-organization and sketching an encompassing ''generativist'' theory of embryogenesis. For example, animal early development can be reconstructed computationally at the single-cell level using image processing methods[14] followed by agent-based modeling and simulation.[15] The objective is to unify organisms beyond their seemingly ''endless forms most beautiful,'' in the words of Darwin,[9] by unraveling the generic mechanisms that make them variations around a common theme. The variations are the particular genetic and epigenetic information; the theme is the core developmental dynamics that this information steers. It comprises the elementary laws by which the genome produces the very proteins that can further interpret it, controlling cell division, differentiation, adhesion, and death, and producing an anatomy. On this keyboard, evolution is the ultimate player.

Evo-devo in artificial life

Looking at the full evolutionary and developmental picture should also be a primary concern of systems engineering and computer science when venturing into the new arena of autonomous, distributed architectures. Evolutionary computation (EC) techniques such as genetic algorithms or genetic programming, which were inspired by evolutionary biology in its traditional modern-synthesis form, have just like their natural model principally focused on selection through virtual ''genomic operators,'' ''fitness functions,'' and ''reproduction rates.'' As a consequence, the great majority of these approaches rely on more or less direct and abstract mappings from artificial genomes to artificial individuals, while including only little or no morphogenesis.

Therefore, one important goal of a new field of ''Alife evo-devo'' would be to provide the computational foundation for a virtual re-engineering of the ''strongly morphogenetic'' complex systems spontaneously produced by nature, such as biological development. To this aim, one must design a programmable and reproducible two-way indirect mapping between the local rules of SA followed by the elementary cells at the microscopic level (the genotype G), and the collective structure and function of the system at the macroscopic level (the phenotype Φ). Calculating the transformation from G to Φ corresponds to developing an organism—while solving the inverse problem of finding an appropriate G given a desired Φ (or family of similar Φ's) would be the challenge of an evolutionary search, whether goal-oriented, open-ended, or a mix of the two. Of course, in biology, development and evolution occur at significantly different time scales, and the inverse problem of unraveling entire gene networks ''responsible'' for an organ (via the complex physicochemical machinery) is essentially unsolvable—although progress can be made in establishing certain G-Φ correlations, such as the pathways underlying regenerative growth via ''morphological formalisms.''[16] Unlike artificial evo-devo, where certain target shapes and functions can be set, there is no teleology in natural evo-devo; survival is the only criterion.

Still, mirroring the evo-devo paradigm in biological systems, new EC avenues need to stress the importance of fundamental laws of developmental variations as a prerequisite to selection on the evolutionary time scale of artificial systems.[17,18] From the EC viewpoint, it means an implicit or *indirect* mapping from genotype to phenotype. Fine-grained, hyperdistributed architectures similar to multicellular organisms (i.e., many lightweight agents, as opposed to a few heavyweight agents) might be in a unique position to provide the ''solution-rich'' space needed for successful selection and spontaneous innovation through developmental modularity and composition.

From embryogenesis to embryomorphic engineering

This article presents an overview of the latest advances in EE[4–6,19,20] to explore the causal and programmable link from genotype to phenotype needed in many emerging computational disciplines and put it to innovative uses. Its endeavors as a bioinspired computing technology follow those of biological evo-devo, and for this reason it could be equivalently referred to as ''evo-devo engineering.'' EE works on two levels in parallel. It consists of simultaneous genetic engineering (G) and functional shape engineering (Φ), based on a common playground made of a multitude of small cells capable of self-assembling into a particular organism. These cells are guided by the genetic instructions they carry, which parameterize and modulate the fundamental laws of biomechanical-like assembly and biochemical-like signaling that they obey, creating appropriate context-sensitive rules.

After a review of the recent literature in the section Current Attempts and Issues, the remainder of the text illustrates the potential of EE in the SA and autonomous function of 3D physical swarms (whether interpreted as societies of robot parts, mobile robots, synthetic bacteria, or nanocomponents). The section Modular Architecture by Programmable Development in 3D shows *how structure can emerge from development*. It introduces and explains the MapDevo3D model, an extension of the original 2D EE model[5] of fine-grained embryonic development based on SA, PF, and genetic regulation. Next, the section Behaving Morphologies in a Physical Environment suggests *how function can emerge from structure*; it examines how the above 3D morphologies

become functional by endogenous animation and exogenous immersion in a virtual physical environment, where they can interact with objects, exhibit various types of behavior, and execute tasks. Finally, taken together, these two steps pave the way toward a systematic evolutionary exploration of a genomic space of development, that is, an ''artificial evo-devo'' agenda, which is discussed in the section Function from Structure from Development.

Current Attempts and Issues

In ME, especially robotic applications, four classes of metadesign methods are identified[3] (Fig. 2): morphologies that can be achieved (I) by ''constructing,'' where a few agents build a precise, relatively sparse structure; (II) by ''coalescing,'' where larger flocks or swarms of agents create certain patterns or adopt global shapes; (III) by ''developing,'' where agents are recursively added by aggregation (pseudo-division) to an initial cell or seed group; and (IV) by ''generating,'' where subsets of the system are transformed or replaced by others based on grammar rules. Naturally, these classes overlap to some extent.

Constructing

Modular robotics and collective robotics, two instances of the same fundamental idea that robotic systems can be made of a number of distributed components, have traditionally fallen in the first category above. Modular or ''self-reconfigurable'' robotics is interested in how autonomous but interdependent parts can rearrange themselves to change the overall structure and morphology of a robot. For example, the M-TRAN system[21] is able to perform a snakelike locomotion or quadruped walk, avoid obstacles, and self-transform dynamically from one shape to another. Other modular systems, such as Molecubes[22] (Fig. 2Ia), in which half-cube segments swivel on top of each other, demonstrate self-reproduction and self-repair of simple morphologies, as well as (simulated) evolution toward novel forms. Collective, or ''swarm,'' robotics focuses primarily on individual mobile robots that can get together and form a larger system by attaching to each other, via clamps or magnets. Typically, ''s-bots''[23] (Fig. 2Ib) have the capacity to assemble into appropriate morphologies and operate as a single entity when physically connected together. A low-level logic controls the inter-robot connections at certain angles, while a higher-level logic manages the sequence of connections toward desired morphologies and appropriate collective response to a task. Distributed morphogenesis control schemes for the symbiotic SA of 3D ''robotic organisms'' were also the (partially fulfilled) goal of the Symbrion project.[24] In a way similar to slime mold, initially scattered robots would start aggregating into a 2D planar structure, and then the flat organism had to lift itself to a 3D morphology and move and function as a whole.

While the boundary between modular and collective robotics is becoming blurred, these two domains are still facing the challenge of engineering reliable and functional self-organized robotic collectives. Often, considerable effort is spent on the design of sophisticated hardware, especially actuators capable of precise docking, to the detriment of system size and higher-level morphogenetic principles. There is a tendency to manufacture a small number (dozen) of heavyweight, expensive units, as opposed to mass-producing a great number (hundreds) of simple and cheap, even disposable ones. As a consequence, physical realizations have permitted so far only sparse structures made of units arranged in exact formations, such as chains and T-junctions.

Coalescing

Systems from the second ME category contain a much greater number of mobile agents, which form a dense mass or network. Without attaching, they flock or huddle by staying near each other, and try to maintain peer-to-peer

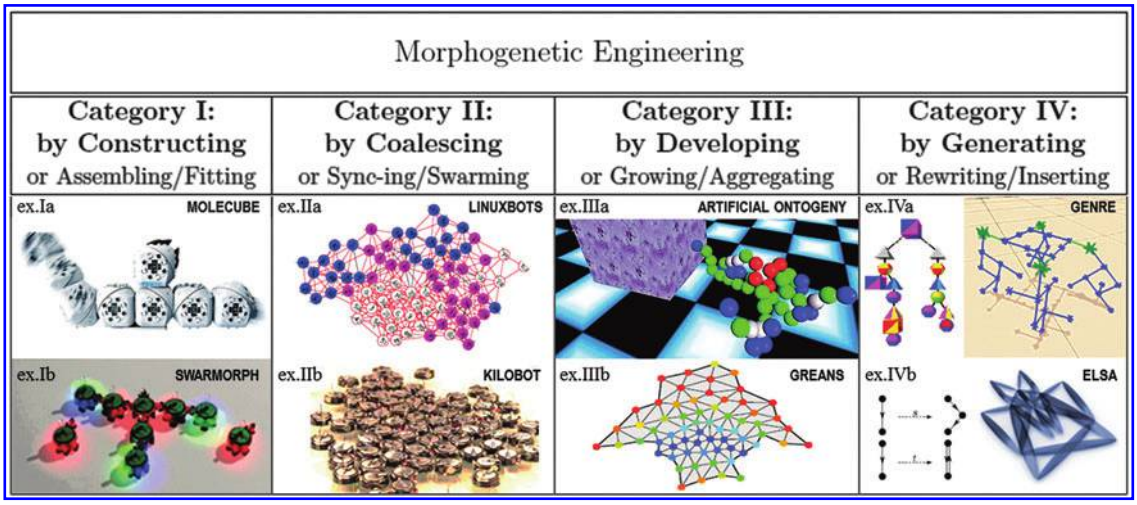

FIG. 2. The four categories of morphogenetic engineering,[1,3] each one illustrated with two examples of robotic systems, physically realized or simulated. **(I)** ''Constructing'': a few agents build a precise, relatively sparse structure, whether in modular robotics (ex. Ia: Molecubes[22]) or collective robotics (ex. Ib: Swarmorph[23]); **(II)** ''Coalescing'': larger flocks or swarms of agents create certain patterns or adopt global shapes (ex. IIa: Linuxbots[25]; ex. IIb: Kilobot[26]); **(III)** ''Developing'': agents are recursively added by aggregation (pseudo-division) to an initial cell or seed group (ex. IIIa: Artificial Ontogeny[27]; ex. IIIb: GReaNs[7]); and **(IV)** ''Generating'': subsets of the system are transformed or replaced by others based on a grammar (ex. IVa: GENRE[34]; ex. IVb: ELSA[35]). Color images available online at www.liebertpub.com/soro

communication. Here, motion dynamics is typically inspired by chemical concepts such as ''pheromones'' (as in ant colonies) or ''morphogens'' (as in cell tissues) and their concentration gradients, which are the basis for ''chemotactic'' self-guidance. Decentralized control algorithms, implemented, for example, on e-pucks or Linuxbots, have been proposed to link local wireless connectivity to low-level robot motion and create global ''coherence,'' based on clustering and uninterrupted connectivity[25] (Fig. 2IIa). In another notable achievement, the Kilobot project[26] (Fig. 2IIb), hundreds of robot units made of cheap parts that are quick to assemble were designed specifically to provide a large-size swarming platform on which to test decentralized control algorithms.

Yet, despite a potentially higher number of participants, the morphogenetic abilities of these robotic assemblies are still very limited. In contrast to the ''constructing'' systems above, neither the local connections nor the macroscopic structure are precise or reliable enough. While they may collectively achieve some functional goal, such as displaying simple patterns or moving around without breaking up, coalescing systems are either too fluid (flock-types undergoing continual spatial rearrangement) or too static (herd-types placed by hand or randomly, and hardly moving, if at all). In the case of Kilobot, the coin-sized hardware units—with three vibrating needles by way of propellers and no sense of bearing—are in fact too simplified for morphogenetic purposes.

Developing

The work presented here, EE, belongs to the third ME category—which, we argue, offers the best of both worlds. It combines the precise SA abilities of ''constructing'' systems with the high redundancy and robustness of ''coalescing'' systems. The aim is to make a large swarm of agents come together to form reproducible macroscopic anatomies. While we want to preserve the essential property of programmability (the focus of ME and EE), it is also important to introduce variability and redundancy in the system—although at a much smaller scale. In biological development, the position and number of individual cells is imprecise, while the tissues and organs they form are reliably shaped and positioned. Similarly, multiscale artificial development can afford to be irregular at the microscopic level of individual agents while retaining an orderly arrangement at the higher meso- and macro-levels of groups of agents.

Quite naturally, the inspiration for this category is close to the cell-based dynamics of biological morphogenesis, and most of its models could be qualified as (virtual) ''soft robotics.''[8] Systems start from a single agent or a few agents, and grow to a large size by repeated, yet differential, division or aggregation. Growth mechanisms involve biological features such as molecular signaling and chemotactic gradients. More importantly, they are also controlled by a ''genotype'' that endows the units with the necessary amount of information to make context-dependent decisions from a rich repertoire of possible behaviors. This genotype can be modeled by a GRN of kinetic reactions and/or by a cell behavior ontology (CBO) based on discrete cell types and a lookup table of sensing/actuating rules and parameters.[15]

In particular, ''artificial ontogeny,''[27] (Fig. 2IIIa) or ''artificial embryogeny,''[18,28,29] systems have ushered in a new paradigm in EC (although an old one in natural evolution!) relying on indirect mappings from genotype to phenotype via more or less complex developmental stages, similar to multicellularity. Instead of coding directly for macrofeatures of the phenotype (the system), genetic parameters code for microfeatures of the cells (the agents), that is, their ability to communicate, propensity for motion, and affinity for assembly with other cells. Imitating cell division, differentiation, and self-positioning, a cell spawns new cells, follows its own execution path within the common genetic program (depending on its position), and creates specific links with neighboring cells according to its fate. Again, the major challenge of this approach is the highly ''nonlinear'' inverse problem of finding an appropriate G for a desired Φ (discussed in the section Evo-Devo in Artificial Life). At such a fine degree of component granularity, how should the low-level encoding and rule parameters be modified to make the complex morphogenetic machinery produce a new robot feature or capability?

Beyond the body plan and overall shape, however, what ultimately matters is how the developed creature is going to function in a physical environment (real or simulated). Like artificial ontogeny, GReaNs[7] (Fig. 2IIIb) is a model of parallel, or ''body–brain,'' coevolution of development and motion control in 2D multicellular, soft-bodied animats. Development is guided by an artificial GRN, and embryos are converted to ''animat'' structures by connecting neighboring cells with elastic springs. Then, outer cells, which form the external envelope, are subjected to drag forces in a fluidlike environment. Both the developmental program and locomotion controller are encoded by a single genomic sequence, which consists of regulatory regions and genes expressed into transcription factors and morphogens. A genetic algorithm is applied to evolve individuals able to swim in the simulated fluid, where the fitness depends on distance traveled during the evaluation phase. Similar work in 2D has been realized with wormlike, spring-mass animats.[30] The present article demonstrates another combination of development, behavior, and evolution in much larger 3D organisms.

Generating

In this last ME category, very similar to development but schematically more inspired by plants than animals, a system is generated by successive transformations of components in 2D or 3D space. This process is controlled by ''grammar'' rules, designed by hand or evolved, which have the effect of ''rewriting'' (that is, inserting and deleting) components. The most popular family of geometric generative models, L-systems,[31] originated from a formal description of plant growth at the cellular level. They use a hierarchical representation based on symbolic strings and embedded bracketed groups. It is a powerful formalism frequently used for the modeling and simulation of botanical growth in theoretical ecology[32] and computer graphics. Accordingly, L-systems quite literally produce treelike, branching structures, which also make them suited to the vascular and respiratory systems of animal models. To diversify the morphogenetic abilities of Lsystems beyond self-similar fractal topologies, rewrite rules can also be made context-dependent, that is, reintroduce some of the dynamical, simultaneous peer-to-peer interactions among components that are characteristic of development but generally absent from generative systems.

The combination of morphogenetic grammar systems with evolution was probably best exemplified by Framsticks[33] (of the *devel* flavor) and GENRE[34] (Fig. 2IVa), two frameworks for the automated design of walking robots or static structures. Since then, the usefulness of evolutionary generative systems has also been demonstrated in behavior-finding animats[35] (Fig. 2IVb) and large tensegrity structures.[36] A recent popular methodology, where body plans are evolved offline and then executed in a generative fashion based on global real-valued functions of space, is called ''compositional pattern-producing networks.''[37] There, cells are replaced with a fixed lattice of pixels or voxels, and shapes can be obtained in the end by removing domains where values of the pattern function lie below a threshold. This was applied, for example, to 3D walking creatures cut out of foam.[38]

Like GRNs and CBOs in development, generative representations are indirect and must express themselves through elaborate genotype–phenotype transformations—although less dynamical and more preplanned ones. The difference is that a ''generated'' organism is essentially the product of a scheduled scenario (even if it may be multiscale and contain probabilistic elements), while a ''developed'' organism emerges from a complex system of agents forming a recurrent network of interactions. Taken together, however, both generative and developmental systems[17] support the notion that indirect representations are worth the added complexity and computational cost, as they allow long-term evolvability via accumulated elaborations and the spontaneous appearance of new features, hence leading to open-ended and scalable genotypes. By contrast, direct representations are not capable of open-ended innovation because they restrict phenotype space to predefined features. All the works mentioned above aim to achieve better fitness and/or robustness by reusing successful elements from the design space and allowing large-scale, yet viable, mutations in the phenotype. On the other hand, their main challenge is the absence of directly invertible encoding, hence the necessity of extensive evolutionary explorations, especially ones that attempt to preserve or encourage diversity.[38]

Modular Architecture by Programmable Development in 3D

This part offers a brief overview of MapDevo3D, a spatial computational model and simulation of morphogenesis that combines mechanical SA and chemical PF. These two main processes are parameterized by a genotype G stored inside each cell of a 3D swarm. The differential properties of cells (orientation, division, adhesion, motion) are determined by the regions of gene expression to which they belong, while at the same time these regions further expand and segment into subregions because of the SA of the differentiating cells (Fig. 3). Following the artistic metaphors employed by plant biologist Enrico Coen to describe embryonic development,[10] one could say that PF is akin to a ''self-painting canvas'' and SA to ''self-shaping putty''—their mutual integration creating a self-made colored sculpture.

In the following summary of the model, divisions and movements inside a homogeneous swarm of cells (pure SA), then signal diffusion and cell differentiation across a fixed swarm (pure PF), are introduced separately. Next, these two sides are united to form reproducible growing patterns (SA + PF). Finally, this combination is repeated in modules ($SA^k + PF^k$) inside a larger, heterogeneous system to create full-fledged complex morphologies by recursive refinement of details. Additional technical aspects of the model (in 2D and 3D) can be found in previous publications.[4–6,19,20]

Growth and deployment of a homogeneous swarm (SA)

The model consists of a 3D swarm of small spherical cells that incorporate two major laws of cellular biomechanics: cell adhesion, in the form of elastic rearrangement, and cell division (Fig. 3a). Cell domains are shaped by mutual adhesion affinities, implemented via a local interaction potential V among pairs of neighbors, based on three parts: (i) infinite repulsion (solid core) for $r < r_c$, (ii) quadratic (elastic) attraction around r_e, and (iii) flat potential for $r > r_0$. Neighborhood relationships are calculated by a 3D Delaunay triangulation from which long links are removed above a cutoff distance d. Starting from a small clump, cells divide with probabilities p in the direction of local vectors $\overrightarrow{S}$ (normal to the cleavage plans) and with an initial distance δ. Subjected to virtual spring forces $\overrightarrow{F} = -\overrightarrow{\nabla} V$, which are an abstraction of membrane contacts, they continually rearrange themselves into a quasi-regular mesh near equilibrium. In this part, each cell possesses fixed ''genetic'' SA parameters $G_{SA} = \{d, r_c, r_e, r_0, p, \delta\}$.

Propagation of positional information (PF-I)

Pieces of a jigsaw puzzle are also defined by the image they carry. In the self-forming swarm, this role is played by state variables that determine the PF activity inside each cell. The model distinguishes between two types of PF-specific state variables: gradient variables (PF-I) and expression variables (PF-II). First, gradient values propagate and establish positional information[39] across the swarm (Fig. 3b). For example, a source cell W contains a ''hop counter'' $g_W = 0$, passing 1 to its neighbors, which in turn instruct their neighbors to set g_W to 2, and so on. The result is a roughly circular wave of g_W values centered on W, encoding, for example, a decreasing concentration of diffusing ligand, $c_W \sim \exp(-\lambda g_W)$. At W's antipode, a source cell E creates the same type of gradient in the opposite direction. Together with two other pairs of gradient sources, (N, S) and (F, B), they form a 3D coordinate system based on equatorial planes (set of cells where opposite counters are equal ± 1). Source cells are not placed by hand, but also hop away from each other by maximizing their internal counters. Using gradients, cell proliferation in SA can also be regulated with a threshold parameter $g_{\max}$. When one of their gradient counters g_W, g_E,..., g_B reaches $g_{\max}$, border cells stop dividing and send a stop signal to their neighbors, so that the entire region eventually settles on a fixed size by quorum sensing.

Programmed differentiation (PF-II)

Next, pattern values are calculated on top of the gradients through differentiated types (Fig. 3c). This process marks the emergence of heterogeneity, that is, the segmentation of the swarm into ''identity regions.''[14] To this aim, each cell contains a GRN, denoted by G_{PF}, whose weights $\{w_{mn}\}$ represent the genetic parameters of the PF process. The GRN

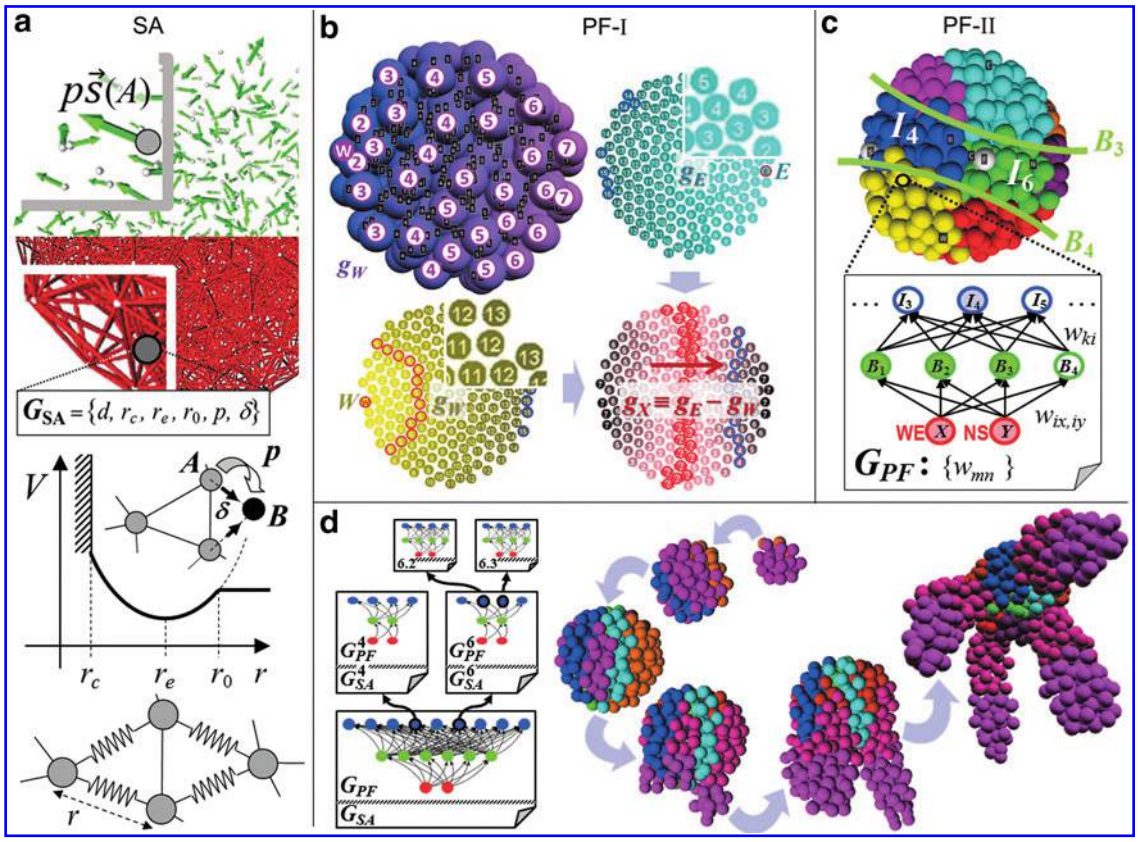

FIG. 3. Overview of the essential mechanisms of MapDevo3D. **(a)** Self-assembly (SA). *Bottom*: plot of the adhesion potential V between neighboring cells, equivalent to elastic springs. At every time step, a cell A may also divide with probability p. *Top, lower half*: view of the 3D mesh of neighborhood interactions in a swarm of 600 cells (with zoom inset), each containing a set of genetic parameters G_{SA}. *Top, upper half*: same simulated swarm showing the field of division vectors $\vec{S}$. **(b)** Pattern formation by spread of positional information (PF-I). Circular gradients of ''hop counters'' g originating from source cells W and E and colored by shading. *Left*: g_W gradients in a 3D and 2D swarm (with zoom inset). *Right*: opposite, g_E gradient in a 2D swarm and equatorial line $|g_E - g_W| \leq 1$ (red rings). **(c)** Pattern formation by programmed differentiation (PF-II): the colored regions represent virtual *in situ* hybridization revealing the ''hidden geography'' of the embryo. Each region contains cells of one type I_k, whose expression level is an output of the underlying gene regulatory network G_{PF}, which takes the gradient counters in input. **(d)** Modular growth and patterning ($SA^k + PF^k$): an idealized view of a typical three-tier modular genotype giving rise to an artificial organism by simultaneous limblike growth process and patterning of these limbs. Color images available online at www.liebertpub.com/soro

used here is a feed-forward, three-layer caricature of regulation dynamics, as it does not contain recurrent links. Yet, it is also very similar to the initial five-tier cascade in *Drosophila* based on ''gap'' and ''pair-rule'' gene groups. Each identity region ultimately reflects the high level of expression of one particular identity gene: I_1, I_2,….These output genes are a function of the six input ''maternal'' gradients g_W, g_E,…, g_B, via the expression of intermediate ''segmentation'' genes B_i that each divide the embryo into two unequal halves.

Simultaneous growth and patterning (SA + PF)

The self-assembly of a nonpatterned swarm, SA, and the patterning of a given swarm, PF, are combined to create growing patterns. Agents continually adjust their positions according to the elastic SA constraints, at the same time that they continually exchange gradient values and PF signals over these dynamic links. The dual SA + PF dynamics is guided by a combined genotype $G = G_{SA} \cup G_{PF}$. During cell division, any cell B spawned by a cell A inherits all of A's attributes, including G and its internal state variables. It immediately starts contributing to SA forces and the traffic of PF gradients that maintain the pattern's consistency at all times in the swarm.

Modular, recursive patterning (PF^k) and anisotropic growth (SA^k)

Embryos do not develop in one shot but in numerous incremental stages. To pursue the example of *Drosophila*, regions first acquire leg, wing, or antenna identity (''imaginal discs'') via global diffusion, and then develop local coordinate systems of morphogen gradients to form the planned limb or organ. To reflect this, the gene network G_{PF} is extended to include a hierarchy of network modules that can generate patterns in a recursive fashion (Fig. 3d, left). First, the base network G_{PF} establishes main identity regions as before, and then a few subnetworks G^k_{PF} triggered by nodes I_k in G_{PF} further partition these regions into smaller identity compartments at a finer scale. Modularity, a principle that biological evolution ''discovered'' naturally, is also desirable in robotic or software architectures. Moreover, to obtain true

deformation dynamics and confer nontrivial shapes to the system beyond blobs, cells must be able to diversify their SA characteristics depending on their PF type and spatial position, thus closing the feedback loop between SA and PF. In particular, they have to exhibit inhomogeneous, anisotropic cell division (varying p) and differential adhesion (varying V). For example, the growth of limblike structures (Fig. 3d, right) can be achieved by a coarse imitation of plant offshoots. In this process, only the tip or ''apical meristem'' of the limb (highest gradient values) is actively dividing at any time. Moreover, V's parameters can be programmed in such a way that they are attractive only among homotypic cells (within the limb) and repelling between heterotypic cells. Like inhomogeneous division, differential adhesion is an essential condition of complex shape formation.

Finally, putting everything together, full morphologies can develop and self-organize from a few cells. These morphologies have a complex architecture because they can be made of any number of various modules and parts that are not necessarily repeated in periodic or regular ways. They are programmable phenotypes emerging from the same genotype carried by every cell of the swarm. They are also reproducible, as their morphological structures are not left to chance but controlled by the genotype. The exact cell positions at the microscopic level are still random, but not the mesoscopic and macroscopic regions that they form. The modularity of the phenotype is a direct reflection of the modularity of the genotype: the hierarchical SA + PF dynamics recursively unfolds inside the different regions and subregions that it creates. Each $SA^k + PF^k$ block can have different internal genetic SA and PF parameters, potentially giving each region a different morphodynamic behavior and different activity landscape. The integration between SA and PF happens at the identity nodes I_k. Just as these nodes turn on gene expression activity in subordinate G^k_{PF} modules to create new segmentation patterns locally, they simultaneously turn on behavioral changes in subordinate G^k_{SA} modules to create new morphodynamical behaviors at the same scale.

Behaving Morphologies in a Physical Environment

While the task of ''metadesigning'' laws of artificial development inspired from biology is already challenging in itself, it only constitutes the first part of the EE effort. What sensing/actuating and behavioral capabilities can a grown robotic organism support? What do its ''cells'' (agents) and ''organs'' (regions) actually represent and achieve in practice? This section describes preliminary work transitioning from morphological to functional goals through animated MapDevo3D organisms immersed in a virtual environment.[6] After a creature has fully developed (was ''born'') through the processes described in the section Modular Architecture by Programmable Development in 3D, it must interact with a simple external world, made of a rigid floor and possible obstacles in a gravitational field (simulated here with the ODE physics engine). To exhibit movement, locomotion, and primitive behavior, organisms contract adhesion links between ''muscle'' cells, while other cells differentiate into ''bones'' and ''joints'' to support and articulate the body's structure (Fig. 4). Finally, a parametric exploration and evolutionary search introduced in the section Function from Structure from Development should complete this original demonstration of an evo-devo Alife system, in which self-organization is not only programmable but also functional and evolvable.

In the embryomorphic paradigm, the genotype-guided development of an organism not only provides a reproducible overall shape, but can also equip this shape with built-in

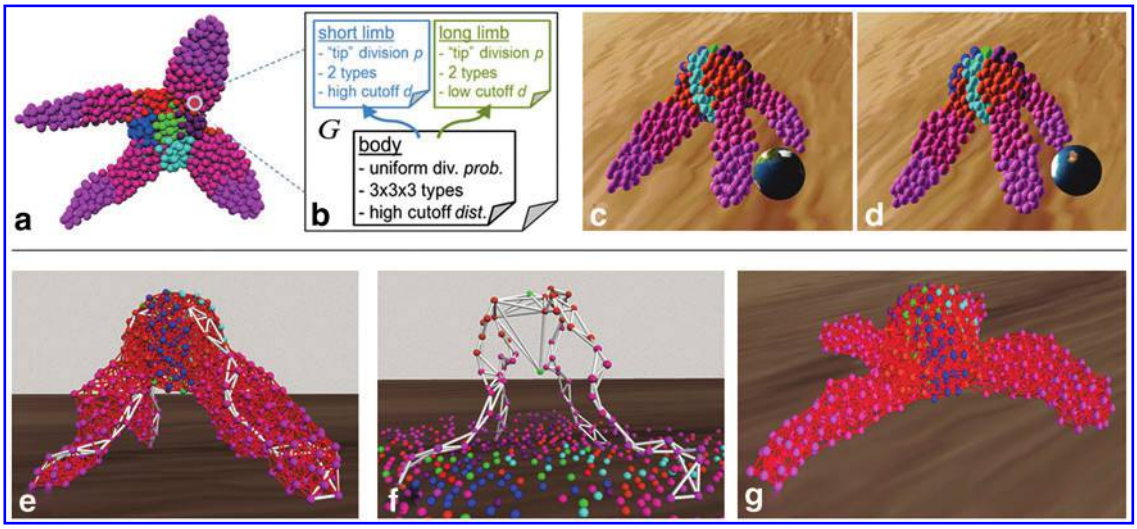

FIG. 4. Structural differentiation and dynamics. **(a)** Fully grown creature. **(b)** Genetic program G executed by all cells during development, comprising three modules: a body module (uniform field of division probability, 27 cell types), a short-limb module (tip-area division field, 2 subtypes), and a long-limb module. Each limb module is triggered in two different regions of the body, creating a total of four legs. **(c** and **d)** Locomotion and ball-kicking behavior, achieved by stimulating and contracting the ''muscle'' regions (*pink* trunks of the limbs) in specific subregions at specific time intervals—a coordination and control program that would be typically the task of a central nervous system. **(e)** The grown organism also contains a skeleton made of differentiated ''bone'' cells and rigid links connecting them (displayed in *white*). **(f)** Experiment where all other links (the ''flesh'' in *red*) have been dissolved, showing the stability of the naked bone structure under gravitational pull. **(g)** Opposite experiment where bone differentiation was turned off: the organism spreads on the floor like a starfish. Color images available online at www.liebertpub.com/soro

structural features that confer it specific mechanical properties. In Figure 4, for example, a few cells at the base of the limbs have differentiated into ''muscles,'' while others have become ''bones'' inside the limbs and ''joints'' at the junction between the limbs and the body. Computationally, this amounts to adding various Boolean fields—functions of the local gradients, like the division and type fields—to each genetic module (Fig. 4b). Here, the muscle field corresponds to the base cylindrical section of a limb, for example, where $g_S \leq 5$ (trunks, distinct from the tips), while the bone field is 1 only along some thin south–north path on each limb and inside a small cluster at the center of the body. Link types are then simply deduced by connecting neighboring cells of identical types; for example, the bone links are formed exclusively between bone cells (white edges). In this case, for a link to turn into ''bone'' means becoming rigid, that is, acquiring a virtually infinite spring coefficient, so that it maintains a fixed spatial relationship between its two extremities. The net effect is that a connected bone structure forms a ''skeleton'' that can support the whole organism and keep it standing on the floor under gravitational pull (Fig. 4e–g).

Finally and most importantly, once the mechanical features of cells and links have been established by development, the organism is immersed in a physical environment where it can exhibit locomotion and other types of behavior. In Figure 4c and d, it is shown walking on the floor and kicking a ball. For now, and without going into details, this is essentially achieved by letting specific muscle regions (pink bases of the limbs) contract periodically and nonuniformly according to a predetermined schedule—a coordination and control program that should be typically the task of a future central nervous system, itself the result of a combined and integrated ''brain-body co-evo-devo''.

Function from Structure from Development: A Twice-Indirect Evolutionary Process

In sum, MapDevo3D proposes principles for the metadesign of self-made robot organisms capable of creating precise morphologies in a purely endogenous manner. It establishes generic rules for the emergence of nonrandom (except for possible redundancies at the microscopic level), programmable structures that are neither repetitive nor imposed by external conditions. Beyond the engineering of stereotypical genotype–phenotype mappings, however, growth must also be *adaptive*. It is critical to be able to rely on dynamic structures that can co-develop with a rapidly changing situation by remaining open to influences and modifications coming from the environment in which they are expected to function (Fig. 5). This could occur on multiple taxonomic levels—on the long time scale through speciation reflecting new genotypes (Fig. 5d), on the shorter time scale through polymorphism of a single species (Fig. 5c), or even on one individual's time scale through developmental polyphenism (Fig. 5b).

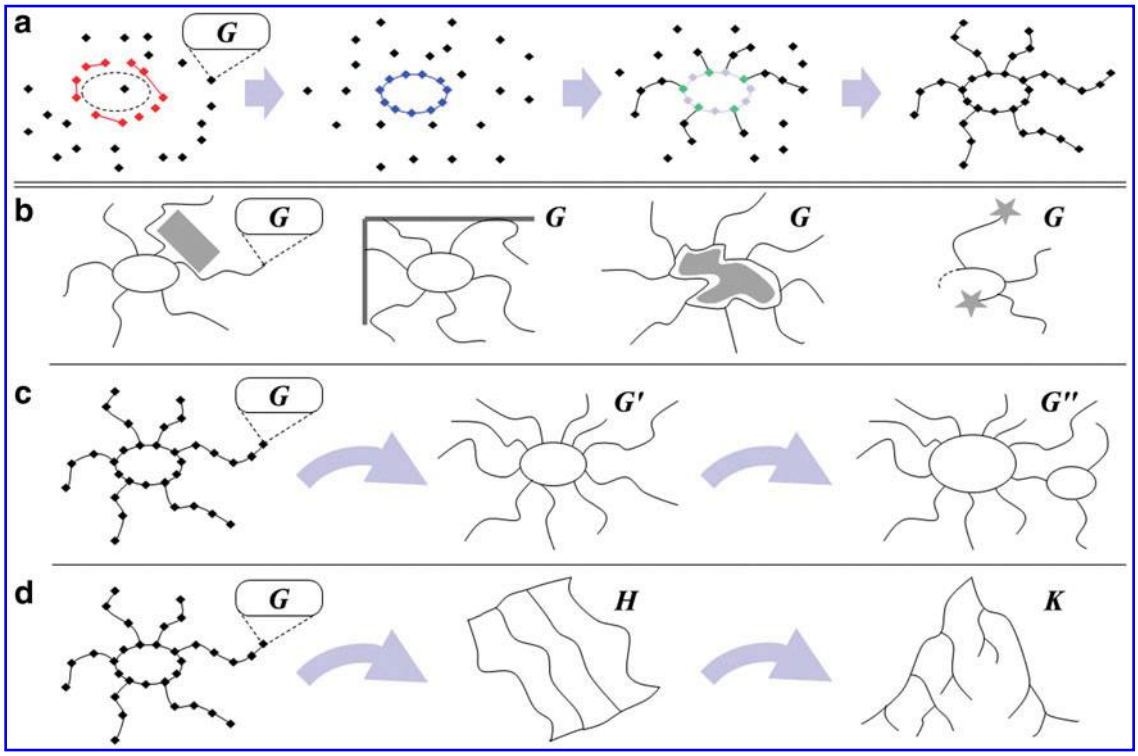

FIG. 5. Illustration of various types of phenotypic adaptation in a programmable growth model. **(a)** Stereotyped development: a certain genotype *G* gives nodes a strong bias toward self-assembling into a certain shape; here a schematic spiderlike formation made of one ring and six legs. **(b)** Developmental ''polyphenism'': similar to a plant, the same *G* gives rise to variants of the above shape modified by external conditions from the environment, such as obstacles or attractors. **(c)** ''Polymorphism'': slight parametric variants of *G*, denoted by *G'* and *G''*, produce other structural variants, such as size of ring, number of legs, or ring location. **(d)** ''Speciation'': drastically different genomes, denoted by *H* and *K*, create drastically different structures—although there is no real qualitative difference with the previous case, as it is only a matter of degree and time scale of evolution. Color images available online at www.liebertpub.com/soro

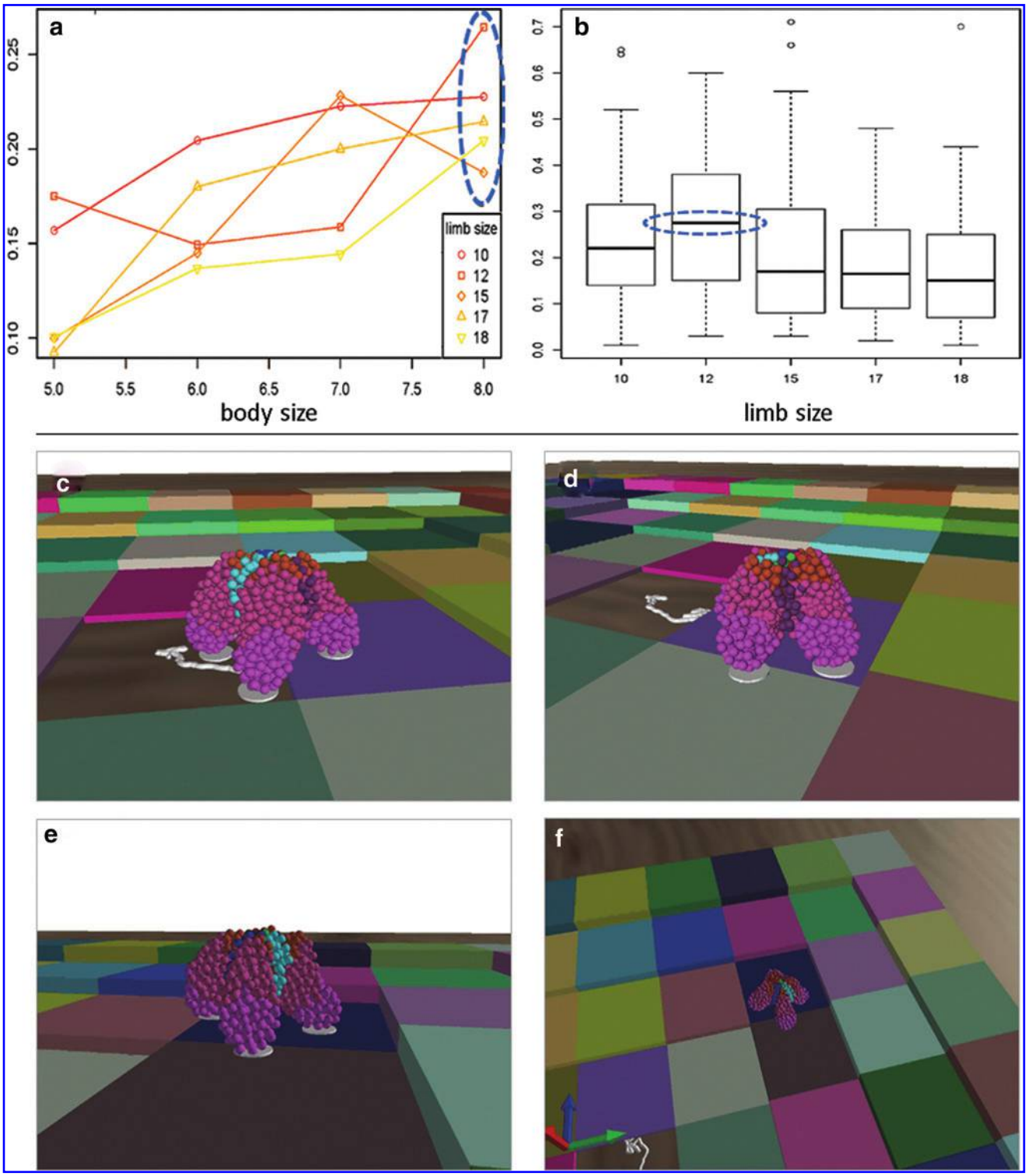

FIG. 6. Simple parametric exploration of a MapDevo3D creature in a stair-climbing challenge. The fitness function measures the straightness of the walk (flight distance divided by path length, which is always less than 1). The basic wild-type genome G is a four-legged creature, of which two parameters are varied: ''body size,'' represented by a maximum gradient value $g^b_{\max}$ stopping cell division in the body, and ''limb size,'' represented by a similar parameter $g^l_{\max}$. **(a)** Increasing body size under various limb sizes: average fitness values calculated over 16 individuals per couple of sizes seem to indicate that bigger creatures perform better. **(b)** Increasing limb size under various body sizes: the same values show an optimal limb setting at $g^l_{\max} = 12$ (plots by Taras Kowaliw; simulation data by C. Sánchez). **(c–f)** Four snapshots of the best stair-climbing creature during its walk. In *white*: track left by the center of mass on the ground floor. To prevent the creature from swaying too much and tramping around the same spot, because of the asperities on its feet, it was also endowed with ''hooves'' (hardened cell springs) and fitted with ''horseshoes'' (saucers). Color images available online at www.liebertpub.com/soro

Evolutionary polymorphism: varying the genotype

A genotype may provide internal parameters controlling different ''traits'' of the final structure. Slight variants of the former produce slight variants of the latter (Fig. 5c). This is similar to the classical laws of population genetics within the same species, schematically corresponding to the concepts of ''alleles'' or single-nucleotide polymorphisms in DNA. Varying and combining genotypic parameters gives rise to a family of different ''breeds''—like Mendel's peas or Darwin's pigeons. However, the distinction between polymorphism and speciation (Fig. 5d) is not clearcut; it is only a matter of degree and time, as the same evolutionary mechanisms are at work in both cases.

Developmental polyphenism: varying the phenotype

Under an invariant genotype, however, development can also be modified by environmental conditions (Fig. 5b). External cues surrounding one individual during its growth can also play an important role in its final structure. This is the level of the phenotype, for which natural analogies can be found more readily in the plant kingdom, by contrast with animals. Plants and trees can be pruned, bent, arranged, or sculpted, whether by human intervention (bonsais, espaliers, topiaries, etc.) or by natural conditions (wind, rocks, soil, light, etc.).

The preliminary study shown here is a simple parametric exploration of MapDevo3D structures in the sense of ''polymorphism'' above, where slight variants of a given genome *G* (the ''wild type'') produce slight structural variants of the phenotype. In this case, variations are even more modest than the ones pictured in Figure 5c, as they are only ''quantitative'' and concern the size of the body and the length of the limbs in a four-legged creature—everything else in the genotype remaining the same. What is evaluated, however, is not the morphology but the behavioral success in a stair-climbing challenge. The fitness measures the straightness of the path by calculating the ratio of total distance traveled over actual path length. Results are shown in Figure 6; they seem to indicate that bigger bodies perform better, while there might exist an optimum for limb size. Obviously, beyond these proof-of-concept trials, a wider evolutionary search allowing drastic modifications of the body plan is needed. Further work must be conducted on how an embryomorphic system can spontaneously evolve, that is, how it can be randomly varied and nonrandomly selected based on its success in performing certain tasks.

Conclusions

EE is inherently interdisciplinary, as it closely follows biological principles at an abstract level but does not attempt to model detailed data from real genomes or organisms. Thus, it sits at crossroads between different domains, from developmental and systems biology to artificial life, in particular amorphous/spatial computing,[40,41] evolutionary programming, and swarm robotics. Following the tenets of ME, it constitutes an original attempt to ''endow a physical system with information'' or, from the opposite viewpoint, ''embed an informational system in physics.''[3] It does so by combining (1) mechanical SA and (2) computational PF, under (3) the control of a genomic program (*G*). In MapDevo3D, these principles are modeled by dynamical processes, respectively: (1) cell adhesion (through elastic forces), (2) morphogen diffusion (through integer hop counters), and (3) gene expression (through a schematic GRN).

Recent models of gene-controlled animats based on ''body–brain coevolution'' (and codevelopment) have also shown a promising path toward a fully integrated artificial evo-devo approach.[7,27,30] Ultimately, abstracting farther away from biological development, an important goal of EE is to contribute to the design of new self-organizing systems able to replace omniscient architects with large-scale decentralized collectivities of agents.[42] Many research works have investigated the possibility of obtaining self-formation properties from a variety of complex computing components: nano-units, bacteria, software agents, robot parts, mini-robots, and so on.[1,3] Since functionality is distributed over a great number of components, it would be an insurmountable task to assemble and instruct each of them individually. Rather, in a way similar to biological cells, these components should be easily mass-produced, initially as identical copies of each other, and only acquire their specialized positions and functions by themselves within the system once mixed together.

Acknowledgments

The authors wish to thank Barry Trimmer, *Soft Robotics* Editor-in-Chief, for his insightful comments on the article; Taras Kowaliw (ISC-PIF) for analyzing the data and producing the plots (two of which are shown in Fig. 6); Jose David Fernández (Research Group in Biomimetics; GEB) for his advice; and Francisco J. Vico, head of GEB, for his support. C.S. received funding from Junta de Andalucia through project GENEX (P09-TIC-5123).

Author Disclosure Statement

No competing financial interests exist.

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