

1 **Complexity Biomechanics:**

2 A Case Study of Dragonfly Wing Design from Constituting Composite Material to Higher
3 Structural Levels

4

5 Arman Toofani^{1,2*}, Sepehr H. Eraghi^{1,3*}, Ali Basti², and Hamed Rajabi^{1,3}

6

7 ¹Mechanical Intelligence (MI) Research Group, South Bank Applied BioEngineering Research
8 (SABER), School of Engineering, London South Bank University, London, UK

9 ²Faculty of Mechanical Engineering, University of Guilan, Rasht, Iran

10 ³Division of Mechanical Engineering and Design, School of Engineering, London South Bank
11 University, London, UK

12

13 *These authors contributed equally to this work

14

15

16

17

18

19

20

21

22

23

24

25

26

27

28

1 **Abstract**

2 Presenting a novel framework for sustainable and regenerative design and development is a
3 fundamental future need. Here we argue that a new framework, referred to as Complexity
4 Biomechanics, that can be used for holistic analysis and understanding of natural mechanical systems
5 is key to fulfilling this need. We also present a roadmap for the design and development of intelligent
6 and complex engineering materials, mechanisms, structures, systems, and processes capable of
7 automatic adaptation and self-organization in response to ever-changing environments. We apply
8 Complexity Biomechanics to elucidate how the different structural components of a complex
9 biological system as dragonfly wings, from ultrastructure of the cuticle, the constituting bio-
10 composite material of the wing, to higher structural levels, collaboratively contribute to the
11 functionality of the entire wing system. This framework not only proposes a paradigm shift in
12 understanding and drawing inspiration from natural systems but also holds potential applications in
13 various domains, including materials science and engineering, biomechanics, biomimetics, bionics,
14 and engineering biology.

15

16

17 **Keywords:** Complexity theory, biological composites, cuticle, collective intelligence, holistic
18 biomimetics.

19

20

21

22

23

24

25

26

27

1

2 **Introduction**

3 Nature hosts a diverse array of creatures. Each resilient survivor in nature is a potential source of
4 data, which can be the raw material for our information, knowledge, understanding, and wisdom [1].
5 As we observe the natural world, draw inspiration from it, and derive solutions in order to gain
6 deeper insights into our planet, address industrial challenges, and confront global issues, the first
7 conspicuous feature is complexity [2]. According to the Cambridge dictionary, '*complexity*' is the
8 state of having many parts and being difficult to understand or find an answer to. This precisely
9 characterizes what we encounter in numerous natural systems across various scales and levels of
10 organization.

11 To unravel the intricate nature of complex systems, scientists have increasingly turned to a
12 reductionist approach. This approach involves breaking down natural systems into comprehensible
13 physical components and phenomena. While the reductionist approach has successfully answered
14 numerous scientific questions, it falls short in scenarios, such as chaotic systems, insect swarms, bird
15 flocks in flight, insect combat behaviors, ant social networks, human brain neural networks, and
16 various other cases. In these instances, the reductionist approach proves inefficient due to the
17 inherent unpredictability, interdependencies, and interconnectedness of the examples mentioned
18 [3]. In these cases, complexity theory is the key to explain how such systems work [4]. Complexity
19 theory helps us understand how the collective behaviors and properties of complex systems emerge
20 from the interactions of seemingly independent elements. These elements collaborate to form,
21 grow, learn, adapt, and evolve the entire system [4-8]. Consequently, complexity theory can
22 facilitate our understanding of the social and collective behaviors exhibited by complex natural
23 creatures.

24 When we approach nature from an engineering perspective and focus on the mechanical design
25 of natural systems, we uncover collective mechanical behaviors and emergent mechanical properties
26 resulting from their specialized design. For example, observations of snake locomotion systems [9-
27 11], fish body armors [12-14], gecko adhesive pads [15-18], insect flight systems [19-24], beetles
28 fighting mechanisms [25,26], and many more indicate that natural mechanical systems consist of
29 complicated material composition, nano- and micro-architecture, and structural elements. This
30 complicatedness can arise from two underlying design principles: (1) a network of simple design

1 elements that collectively form a complex system, and/or (2) a collection of complicated subsystems
2 that together constitute the entire system. Here, the 'simple design element' denotes the most
3 elementary building block within a mechanical system, while a 'complicated subsystem' refers to a
4 more intricate design element characterized by numerous design details. These design principles
5 give rise to 'complex mechanical systems,' which, in turn, yield complex mechanical functions,
6 collective mechanical behaviors, and emergent mechanical properties.

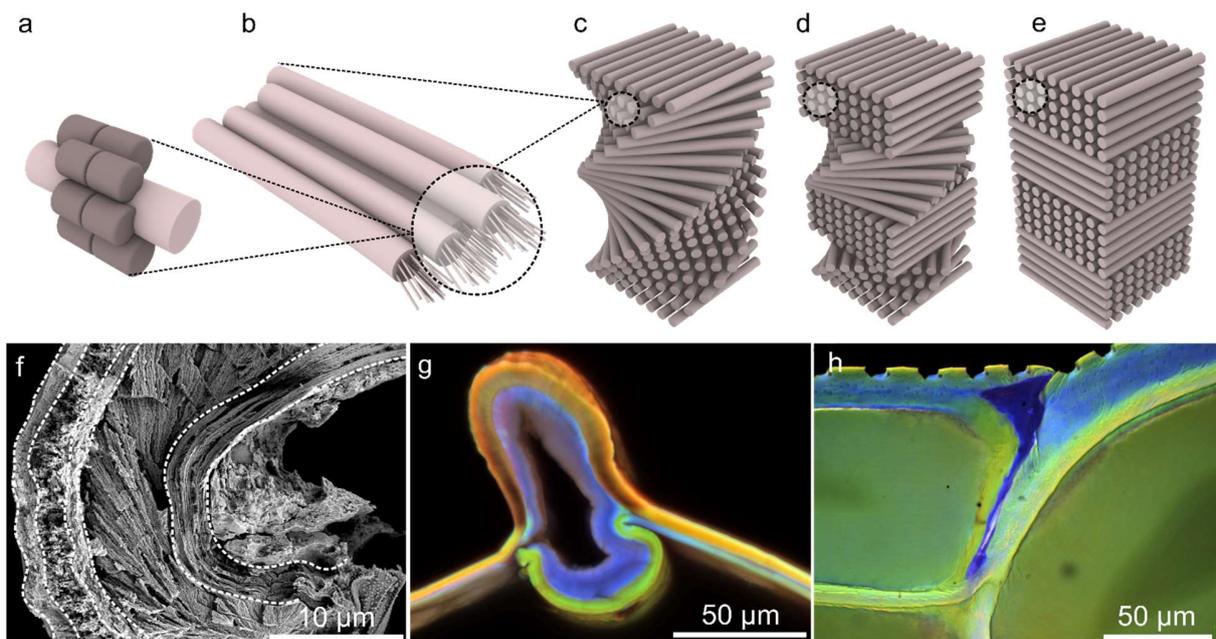
7 A striking example of such complex mechanical systems can be found in wings of dragonflies. The
8 wings comprise numerous simple design elements and complicated subsystems, ranging from the
9 material composition and ultrastructure to larger structural components, all collaborating as part of
10 a complex network system. Thanks to their specialized wing design, dragonflies have become one of
11 the most proficient flyers with ~97% hunting success rate [27]. These agile insects can spontaneously
12 change their directions in flight [28,29], and further display an array of flight behaviors and long-
13 distance flights across oceans with minimal energy consumption [30-32]. However, a puzzling
14 question remains: how do dragonfly wings enable such sophisticated flight capabilities, especially
15 considering they lack any musculature within their wings?

16 One of the key reasons behind the flight ability of dragonflies is the automatic deformability and
17 the flapping modes of their wings, which results in a variety of flight modes (i.e., flapping, hovering,
18 gliding, etc.) and high maneuverability. The principal function of the wings is to generate
19 aerodynamic forces. That is when emergent mechanical properties and collective mechanical
20 behaviors arise from interactions between wing material and structural elements. To understand the
21 complexities, emergent mechanical properties and collective mechanical behaviors of natural
22 mechanical systems, including the automatic deformability of dragonfly wings, we introduce a novel
23 framework, called "Complexity Biomechanics." This framework is rooted in complexity theory and is
24 applied to dragonfly wings as a prime example. In doing so, we present a roadmap for the future of
25 engineering design, utilizing the Complexity Biomechanics framework, which is essential as it enables
26 us to push the boundaries of engineering design to align more closely with the designs found in
27 nature, taking a holistic approach.

28 **Complexity Biomechanics in dragonfly wings**

29 In this section, we first elucidate the concept of the Complexity Biomechanics framework and
30 how it enables us to better understand and interpret how the dragonfly wings work. According to

1 Complexity Biomechanics, simple and/or complicated design elements of a natural mechanical
 2 system come together to form an interconnected and interdependent complex network system. This
 3 network system exhibits collective mechanical effects that surpass the combined impacts of
 4 individual elements. These emergent properties result from several characteristics of the system: (1)
 5 synergistic relations between the design elements, including material and structural elements, (2)
 6 sensitivity of mechanical behavior to boundary conditions and loading scenarios, (3) non-linearity in
 7 geometry, material, and contact, along with non-linearity in boundary conditions and loading
 8 scenarios, (4) sensitivity of mechanical behavior to initial design parameters, (5) continuous
 9 adaptation in response to unpredictable loading scenarios in volatile and ever-changing
 10 environments, which leads to (6) self-organization of the whole system without a necessity for a
 11 central control system. In the following, we will explore the specific design elements present in
 12 dragonfly wings and illustrate how their interactions give rise to collective mechanical behaviors and
 13 emergent mechanical properties.



14

15 **Figure 1.** Micro-architectural design of the dragonfly wings' cuticle. (a) Chitin nanofibrils wrapped
 16 with proteins. (b) Chitin-protein fibers in protein matrix. (c-e) Different arrangement of chitin-protein
 17 planes. (f) Micro-architecture of the wing veins cuticle consisting of six distinguishable cuticle layers.
 18 (g) Confocal Laser Scanning Microscopy (CLSM) image of the cross-section of the veins showing
 19 different levels of sclerotization: Red, green, and blue colors are indicators of sclerotized cuticle, less-

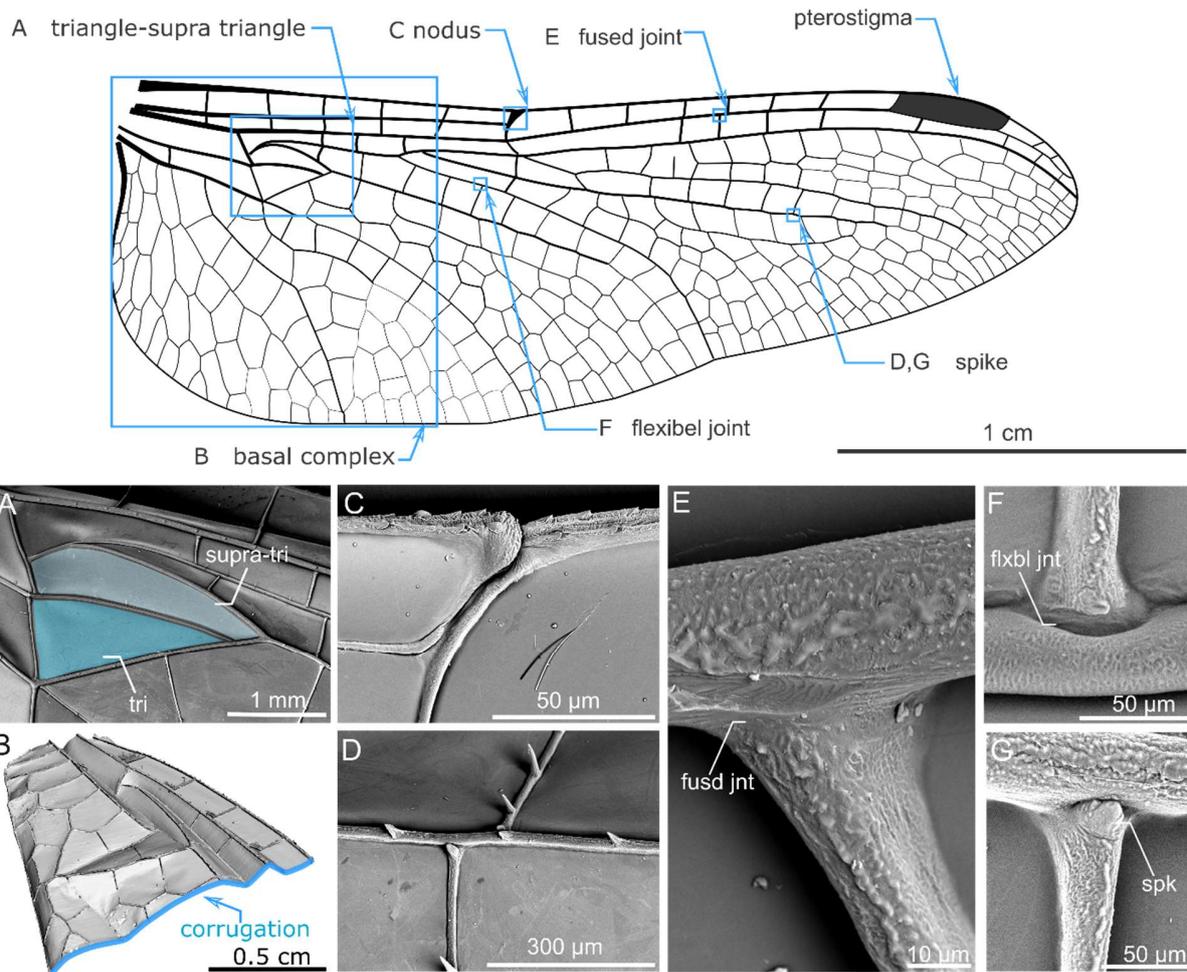
1 sclerotized cuticle, and soft cuticle, respectively. (h) CLSM image showing the presence of soft
2 cuticle, i.e., resilin, in nodus. The panels a and b are inspired by [61]; The panel f is reproduced from
3 [35]; The panel g is reproduced from [47]; And, the panel h is reproduced from [42].

4 Dragonfly wings exhibit complicated mechanical design, ranging from the smallest elements of
5 their constituting composite material, i.e., cuticle, to the entire wing structure. These wings must
6 strike a balance between stiffness to prevent detrimental deformations and flexibility to generate
7 flight forces. These mutually exclusive properties of the wings are made possible through several
8 design strategies.

9 The primary material of dragonfly wings is cuticle, a biological composite material primarily
10 composed of chitin nano- and microfibrils embedded within a protein matrix (**Fig. 1 a,b**). Chitin
11 microfibrils, in their pure form, have a stiffness of approximately 150 GPa [33]. The arrangement of
12 these microfibrils varies depending on the specific cuticle layer (**Fig. 1 c-f**).

13 Dragonfly wings have a complex layered architecture. Veins, for example, consist of up to six
14 cuticle layers, which vary in their ultrastructure (**Fig. 1 f**) [34]. These layers may or may not be present
15 in other veins, depending on their location in the wing [34, 35]. The number of layers is also different
16 in the wing membrane, which usually consists of three cuticle layers only [34, 36]. The mechanical
17 properties of the wing cuticle are influenced by the arrangements of the microfibrils and other
18 factors, such as chemical composition, sclerotization, hydration level, and porosity, resulting in a
19 wide range of properties, from high stiffness to extreme flexibility in this biological composite (**Fig. 1**
20 **g, h**) [33].

21 In a structural level, wings feature a corrugated structure, supported by a complex network of
22 veins. Cross veins are linked to robust, span-wise longitudinal veins by vein micro joints. This design
23 provides the wings with notable rigidity against span-wise forces while allowing flexibility in the
24 chord-wise direction. Additionally, other design elements, such as resilin-rich flexible joints, fused
25 joints, spikes, spike-containing joints, nodus, basal complex, pterostigma, and flexion lines together
26 create a complex network, enabling the wing to achieve the necessary camber and twisting for
27 aerodynamic force generation during flight (**Fig. 2**) [37-41]. These elements not only establish
28 synergistic relations, operating as a mutually dependent and interconnected wing structure, but also
29 exhibit mechanical responsiveness influenced by their initial design factors.



1
 2 **Figure 2.** Dragonfly's wing and its design elements. Triangle (tri) and supra-triangle (supra-tri) (A), basal
 3 complex and corrugation from the fore wing (B), nodus (C), spikes (D), fused joint (fused jnt) (E), flexible joint
 4 (fixbl jnt) (F), spike-containing joint (spk) (G). The panel A is reproduced from [43]. The panel B image is
 5 reproduced from [41]. The panels C and D images are reproduced from [47]. The panels E, F, and G images are
 6 reproduced from [37].

7 The variation of these design parameters in dragonfly wings leads to distinct mechanical
 8 adaptations to the forces encountered during insect flapping flights. In typical or challenging
 9 scenarios, such as flying in windy and rainy conditions for hunting, dragonflies' wings experience
 10 continuous changes in boundary conditions and loading scenarios. These variations depend on
 11 factors like flight direction and flapping modes. To successfully hunt other insects, the dragonfly
 12 must continually adjust its flapping wings to unpredictable external and internal loading scenarios.
 13 The simple and complicated elements of dragonfly wings collaborate passively, forming a self-

1 organizing system that emerges from the wings' continuous adaptability. Despite generating flight
2 forces through active muscles at the flapping wings' base, the wings' deformability primarily occurs
3 mostly in an automatic way without centralized control systems dictating their shape. This wing
4 response, which includes automatic shape changes, is the emergent complex mechanical behavior of
5 the wings [42-44].

6 The emergent complex mechanical behavior of the wings is the result of non-linear interactions
7 between all elements of the wing network, which originates from the different sources of non-
8 linearity, i.e., geometric non-linearity (e.g., symmetric or asymmetric corrugations, and the pre-
9 cambered cross-section of the wing), material non-linearity (e.g., in different arrangement of chitin
10 microfibrils, and in resilin patches as a hyper-elastic material), and contact non-linearity (especially in
11 spike-containing joints, and nodus). The mechanical interactions between the network of design
12 elements as well as the associated non-linearities can be viewed as a network of distributed
13 information processing, a process called mechanical computing [45]. This form of mechanical
14 computation or information processing can not only be regarded as a material property [45] but also
15 as an intelligent structural property of the entire wing system.

16 Dragonfly wings often encounter collisions with objects in their environment, which can lead to
17 flight instability and wing damage [46, 47]. To overcome these issues, some emergent mechanical
18 properties and collective mechanical behaviors of the wings come into play. The damping property
19 of the wings enables the dragonflies to maintain their flight stability, which is the result of the
20 interplay between the complex network of resilin-rich flexible joints and hinges with other parts of
21 the wing [46]. Damage resistance of the wing is an outstanding example of emergent mechanical
22 properties of the wing, protecting the wings during accidental collisions, which results from the
23 flexibility of the material of wings caused by some specific areas of elasticity, i.e., resilin-rich areas
24 [48]. Although wings are damage resistant, in some extreme cases they may still undergo damage,
25 leading to wing area loss. Surprisingly, when damage occurs, another damage-mitigating property
26 emerges, which is the by-product of the presence of cross veins. Cross veins function as barriers
27 against crack propagation and, therefore, mitigate damage progression [49-51]. Another
28 extraordinary emergent property within the dragonfly's flight mechanism arises in the aftermath of
29 wing damage – it compensates for the loss of wing area by increasing flapping frequency and/or
30 amplitude [46,47]. This adaptive change in the flapping frequency and/or amplitude underscores the
31 complex nature of the entire flapping system, demonstrating its ability to dynamically respond to

1 new and unpredictable scenarios. It is crucial to note that the adjustment in flapping frequency can
2 be understood as an active response involving neuronal cellular sensing, neural circuit steering, and
3 direct flight musculature engagement.

4 Taken together, the narrative reveals the emergence of “collective intelligence” within dragonfly
5 flapping system, spanning multiple levels of organization, from a material level and small-scale
6 architecture to large scale structural design elements. This collective intelligence empowers the
7 insect to continually adapt to novel and unforeseen loading scenarios, serving as a remarkable
8 example of mechanical intelligence (MI) in nature [52], where a biological system, here the insect
9 flapping system, responds to environmental stimuli mostly in a passive-automatic way, though some
10 active responses are also involved.

11 **A roadmap to holistic biomimetics**

12 Complexity Biomechanics offers a holistic perspective for synthesizing the information acquired
13 through a reductionist approach. This enhances our interpretation and understanding of the physical
14 working principles, complex mechanical behaviors, functions, and emergent properties of the
15 system under investigation, in this case the insect wings. This understanding extends beyond the
16 wings alone, encompassing the insect's behavior and its dynamic interaction with the environment.
17 Yet, a question remains: How does Complexity Biomechanics contribute to the development of a
18 holistic biomimetic framework?

19 The answer lies in recognizing the system under study as an integral part of an organism engaged in
20 continuous interaction with its ever-changing environment (**Fig. 3**). This paradigm shift allows us to
21 transcend the confines of reductionism, opening avenues for a more integrative and holistic
22 approach to biomimetics, where the intricate interplay between biological systems and their
23 surroundings is considered in the design and development process.

24 To achieve a holistic biomimetic framework, there is a need to revolutionize the current
25 biomimetic framework. This transformation can be achieved by aligning engineering designs as
26 closely as possible with the successful design solutions found in nature, which inherently possess the
27 capability for continuous adaptation. To tackle this goal, a reductionist approach to clarify design
28 principles (**Box. 1**), a holistic view of natural mechanical systems, holistic design imitations, and
29 holistic manufacturing systems are needed (**Fig. 3**). The first step involves understanding the natural
30 system at various hierarchical levels, from material level to higher structural level and the entire

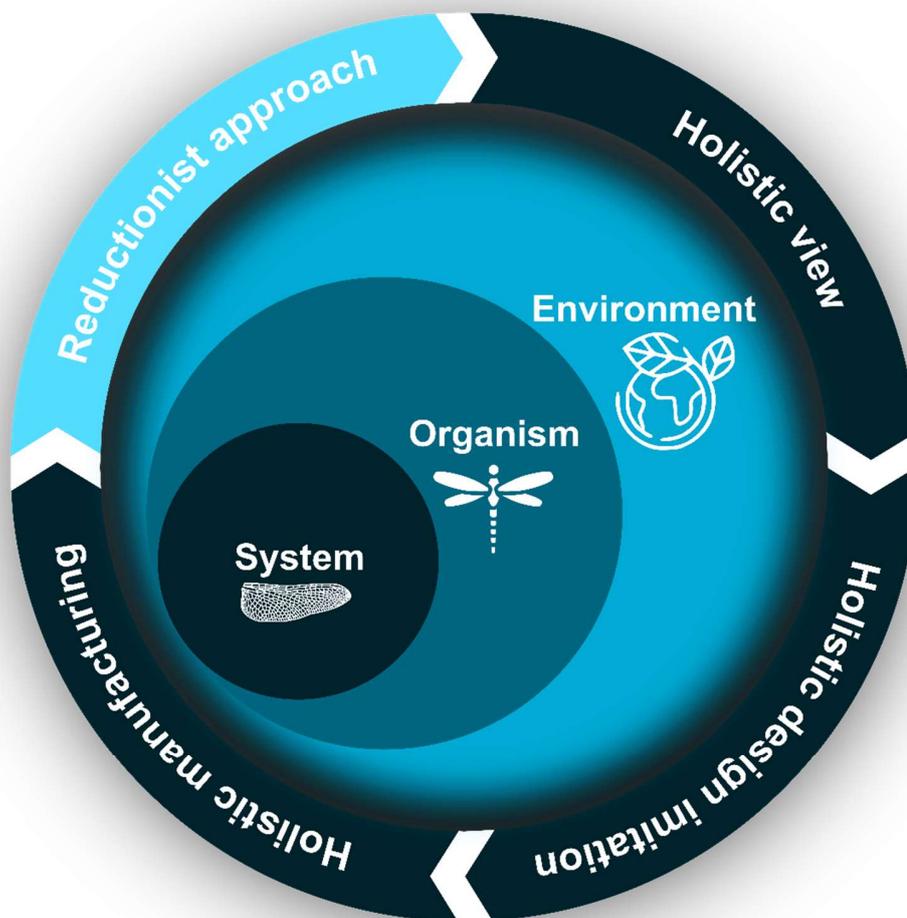
1 network system, and how it interacts with the environment. Then, the results of the exploration can
2 be used to provide insights into how the systems contribute to essential functions and behaviors of
3 an organism, and its dependence on environmental interactions for survival (see **Fig. 3**). To achieve
4 this, new mathematical methods including the Bayesian mechanics [53] are needed that can model,
5 quantify, and predict the interdependencies, interconnectedness, and complex interactions between
6 the design elements of the systems.

7 With this data, it becomes possible to adopt a holistic view to interpret and comprehend the
8 complexities of natural mechanical systems. Complexity Biomechanics, along with its principles, may
9 serve as the linchpin to achieve this holistic perspective, ultimately enabling the creation of
10 engineering designs that truly mimic natural systems and their interactions with the environment.
11 This entails the incorporation of all initial design parameters, boundary conditions, loading scenarios,
12 and nonlinearities derived from the interactions of the system with the environment. For example, in
13 the case of flapping wing systems, holistic understanding not only reveals collective intelligence,
14 emergent properties, and behaviors of the system but also encompasses crucial aspects such as
15 material and structural design, control systems design, and overall functionality of the whole
16 flapping wing.

17 To this end, it is necessary to develop and utilize a more advanced infrastructure for a holistic
18 manufacturing system, i.e., software, hardware, and manufacturing tools. This includes but is not
19 limited to, generative design, generative artificial intelligence (AI), brain-inspired computing [54],
20 image processing, augmented reality (AR), virtual reality (VR), digital twin, advanced central
21 processing units (CPU), graphics processing units (GPU), hard drives, and random-access memories
22 (RAM) as well as Nvidia Omniverse platform.

23 For example, to achieve a comprehensive understanding of the design and manufacturing of
24 flapping wing systems, Complexity Biomechanics suggests a multidisciplinary approach, utilizing
25 state-of-the-art technologies mentioned earlier to develop a virtual environment in the immersive
26 Nvidia Omniverse platform. In this virtual platform, generative AI is employed to simulate and
27 generate wing interactions, providing valuable insights into emergent properties and behavioral
28 patterns. Virtual reality and augmented reality technologies are utilized to create immersive
29 environments, enabling the visualization and analysis of the complex dynamics of flapping wings
30 within diverse surroundings. Image processing techniques enhance our ability to extract detailed
31 engineering data, facilitating a deeper understanding of collective intelligence, control systems,

1 material design, and structural complexities. Additionally, virtual environment development serves
2 as a tool for acquiring real-time engineering data to study the dynamic interplay between flapping
3 wings and their environment in a controlled and replicable setting. Advanced 3D and 4D printing
4 technologies, capable of material and structural gradient printing with high precision on a small scale
5 using biodegradable materials, are employed not only to ensure the creation of requisite material
6 properties but also to facilitate easy decomposition in the environment after use.



7

8 **Figure 3.** From complexity biomechanics to holistic biomimetics.

9 **Why Complexity Biomechanics?**

1 As stated by Gregory Bateson: “*The major problems of the world are the result of the difference*
2 *between the way nature works, and the way people think*”. For instance, our current engineering
3 frameworks, which predominantly employ reductionist approaches, have contributed to
4 environmental damage, global issues, and other unintended consequences. Therefore, embracing a
5 holistic approach to design and manufacturing becomes imperative to alleviate these negative
6 impacts by harmonizing engineering designs more closely with natural systems.

7 Complexity Biomechanics is the key to tackle these issues presenting a paradigm shift in our
8 understanding of mechanical systems, especially natural mechanical systems as they show complex
9 mechanical behaviors, complex functions, and emergent mechanical properties. It adopts a holistic
10 approach along with the conventional reductionist approach by incorporating the principles of
11 complexity theory to investigate, analyze, and understand the complexity and emergent properties
12 of mechanical systems found in nature. In addition, Complexity Biomechanics can facilitate the
13 establishment of a holistic engineering design framework through which the underlying design
14 principles of natural systems can be transferred to design and develop bio-inspired complex
15 mechanical systems. These complex mechanical systems can show collective intelligence and,
16 thereby, interact and adapt to their immediate environment, for real-life applications. A few practical
17 applications of Complexity Biomechanics in the design of intelligent systems, matters [55], materials,
18 structures, and processes can be miniaturized flapping robots, autonomous robots, soft robots,
19 intelligent composite materials, and adaptive structures with the ability of automatic shape control.

20 Albeit here we only demonstrated the application of Complexity Biomechanics in the analysis of
21 the biomechanics of dragonfly wings, the extent of its applicability in biomechanics, biomimetics,
22 biomimicry, bionics, and bio-inspired design can be well-beyond the presented case study. Other
23 areas of science and engineering can take advantage of this novel paradigm to develop a new
24 engineering design framework since the design principles of Complexity Biomechanics are in line
25 with those of sustainable and regenerative design and developments [56]. This can lead to a
26 quantum leap forward in a variety of mechanical and engineering sciences to build a sustainable and
27 even regenerative future for the next industrial revolution.

Box.1**Bio-inspired applications of complex natural systems: reductionism or holism?**

“It’s not what you look at that matters, it is what you see.”

Henry David Thorea

To address industrial challenges, the utilization of biomimetic engineering applications based on complex natural systems has been significantly growing. This surge is attributed to the rich biological diversity of natural creatures, which serves as a valuable source of inspiration for engineering designs. Despite the intricate functions of many of these creatures, some offer simple yet effective design solutions, making them potential case studies for engineering innovation. An exemplary example of this nature-to-engineering approach is the study of dragonfly wings. In recent years, various design elements from dragonfly wings have been incorporated to create durable bio-inspired kites [57], splints that combine mobility and support [58], dual stiffness origami grippers and impact resistant quadcopters [59], and triple stiffness airplane wings that resist typical flight forces but elastically buckle in collisions [60]. In these applications (**Fig. 4**) researchers have used a reductionist approach for the analysis and modeling of engineering systems. Reductionism, as one of the main principles of engineering disciplines, has been shown to be a highly practical approach. However, in the design of intricate systems aimed at sustainability and regenerative development, comprising numerous diverse, interdependent, and interconnected networks of elements, relying solely on the reductionist approach becomes impractical. This is where Complexity Biomechanics, as an alternative holistic perspective, comes into play. We propose that Complexity Biomechanics represents the future direction for science and engineering disciplines.

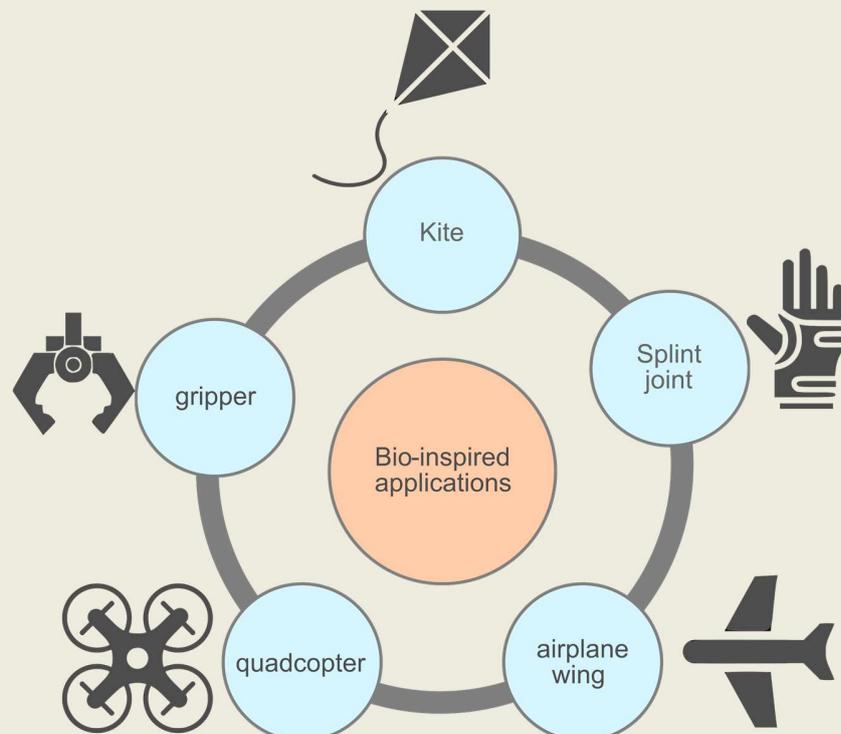


Figure 4. Engineering applications inspired by the structural and material design elements of dragonfly wings, namely bio-inspired kite, splint joint, airplane wing, dual-stiffness origami, and gripper.

1 **Acknowledgments**

2 We would like to thank Dr. Soheil Jafari for his support and valuable comments on writing the first
3 draft. The kite icon is made by [Stockio](#), the splint icon is made by [Surang](#), drone, airplane, and
4 Environment icons are made by [Freepik](#), dragonfly icons created by cah nggunung from
5 www.flaticon.com.

6 This work was supported by the LSBU Early Career Researcher (ECR) Springboard Funding (to HR).

7 **Author contribution**

8 Conceptualization: A.T., S.H.E., H.R.; investigation of concept: A.T., S.H.E.; project administration:
9 A.T., S.H.E.; data resources: H.R.; supervision: A.B., H.R.; visualization: A.T., S.H.E; writing-original
10 draft preparation: A.T., S.H.E.; writing-review & editing: S.H.E., A.B., H.R.

11 **References**

12 [1] Ackoff, R. L. (1989). From data to wisdom. *Journal of applied systems analysis*, 16(1), 3-9.

13 [2] Weaver, W. (1948). Science and complexity. *American Scientist*, 36(4), 536-544.

14 [3] Weber, M., & Schmid, B. (1995). Reductionism, holism, and integrated approaches in biodiversity
15 research. *Interdisciplinary Science Reviews*, 20(1), 49-60.

16 [4] Sammut-Bonnici, T. (2015). Complexity Theory. In *Wiley Encyclopedia of Management* (pp. 1-2),
17 Wiley.

18 [5] Manson, S. M. (2001). Simplifying complexity: a review of complexity theory. *Geoforum*, 32(3),
19 405-414.

20 [6] Pippenger, N. (1978). Complexity theory. *Scientific American*, 238(6), 114-125B.

21 [7] Sammut-Bonnici, T. (2015). Complex Adaptive Systems. In *Wiley Encyclopedia of Management*
22 (pp. 1-3), Wiley.

23 [8] Gell-Mann, M. (2002). What is complexity? In *Complexity and industrial clusters* (pp. 13-24).
24 Physica-Verlag HD.

25 [9] Rieser, J. M., Li, T. D., Tingle, J. L., Goldman, D. I., & Mendelson III, J. R. (2021). Functional
26 consequences of convergently evolved microscopic skin features on snake locomotion. *Proceedings*
27 *of the National Academy of Sciences*, 118(6), e2018264118.

28 [10] Filippov, A. E., & Gorb, S. N. (2016). Modelling of the frictional behaviour of the snake skin
29 covered by anisotropic surface nanostructures. *Scientific reports*, 6(1), 1-6.

30 [11] Tramsen, H. T., Gorb, S. N., Zhang, H., Manoonpong, P., Dai, Z., & Heepe, L. (2018). Inversion of
31 friction anisotropy in a bio-inspired asymmetrically structured surface. *Journal of The Royal Society*
32 *Interface*, 15(138), 20170629.

- 1 [12] Ghosh, R., Ebrahimi, H., & Vaziri, A. (2014). Contact kinematics of biomimetic scales. Applied
2 Physics Letters, 105(23), 233701.
- 3 [13] Yang, W., Chen, I. H., Gludovatz, B., Zimmermann, E. A., Ritchie, R. O., & Meyers, M. A. (2013).
4 Natural flexible dermal armor. Advanced Materials, 25(1), 31-48.
- 5 [14] Spinner, M., Schaber, C. F., Chen, S. M., Geiger, M., Gorb, S. N., & Rajabi, H. (2019). Mechanical
6 behavior of ctenoid scales: joint-like structures control the deformability of the scales in the flatfish
7 *Solea solea* (Pleuronectiformes). Acta Biomaterialia, 92, 305-314.
- 8 [15] Heepe, L., Kovalev, A. E., Varenberg, M., Tuma, J. G. S. N., & Gorb, S. N. (2012). First mushroom-
9 shaped adhesive microstructure: a review. Theoretical and Applied Mechanics Letters, 2(1), 014008.
- 10 [16] Heepe, L., Höft, S., Michels, J., & Gorb, S. N. (2018). Material gradients in fibrillar insect
11 attachment systems: the role of joint-like elements. Soft Matter, 14(34), 7026-7033.
- 12 [17] Borijindakul, P., Ji, A., Dai, Z., Gorb, S. N., & Manoonpong, P. (2021). Mini review: Comparison of
13 bio-inspired adhesive feet of climbing robots on smooth vertical surfaces. Frontiers in Bioengineering
14 and Biotechnology, 9.
- 15 [18] Labonte, D., Clemente, C. J., Dittrich, A., Kuo, C. Y., Crosby, A. J., Irschick, D. J., & Federle, W.
16 (2016). Extreme positive allometry of animal adhesive pads and the size limits of adhesion-based
17 climbing. Proceedings of the National Academy of Sciences, 113(5), 1297-1302.
- 18 [19] Taylor, G., Bomphrey, R., & 't Hoen, J. (2006, January). Insect flight dynamics and control. In 44th
19 AIAA Aerospace Sciences Meeting and Exhibit (p. 32).
- 20 [20] Dickinson, M. (2001). Solving the mystery of insect flight. Scientific American, 284(6), 48-57.
- 21 [21] Ellington, C. P. (1985). Power and efficiency of insect flight muscle. Journal of Experimental
22 Biology, 115(1), 293-304.
- 23 [22] Toofani, A., Eraghi, S. H., Khorsandi, M., Khareshi, A., Darvizeh, A., Gorb, S., & Rajabi, H. (2020).
24 Biomechanical strategies underlying the durability of a wing-to-wing coupling mechanism. Acta
25 Biomaterialia, 110, 188-195.
- 26 [23] Eraghi, S. H., Toofani, A., Khareshi, A., Khorsandi, M., Darvizeh, A., Gorb, S., & Rajabi, H. (2021).
27 Wing coupling in bees and wasps: From the underlying science to bioinspired engineering. Advanced
28 Science, 8(16), 2004383.
- 29 [24] Rajabi, H., Eraghi, S. H., Khareshi, A., Toofani, A., Hunt, C., & Wootton, R. J. (2022). An insect-
30 inspired asymmetric hinge in a double-layer membrane. Proceedings of the National Academy of
31 Sciences, 119(45), e2211861119.
- 32 [25] Emlen, D. J. (2008). The evolution of animal weapons. Annual Review of Ecology, Evolution, and
33 Systematics, 387-413.
- 34 [26] Emlen, D. J. (2014). Animal weapons: the evolution of battle. Henry Holt and Company.
- 35 [27] Olberg, R. M., Worthington, A. H., & Venator, K. R. (2000). Prey pursuit and interception in
36 dragonflies. Journal of Comparative Physiology A, 186(2), 155-162.

- 1 [28] Newman, D. J. S., & Wootton, R. J. (1986). An approach to the mechanics of pleating in
2 dragonfly wings. *Journal of Experimental Biology*, 125(1), 361-372.
- 3 [29] Wootton, R. J., Kukalová-Peck, J., Newman, D. J. S., & Muzón, J. (1998). Smart engineering in the
4 mid-carboniferous: how well could palaeozoic dragonflies fly? *Science*, 282(5389), 749-751.
- 5 [30] Junior, R. S. L., & Peixoto, P. E. C. (2013). Males of the dragonfly *Diastatops obscura* fight
6 according to predictions from game theory models. *Animal Behaviour*, 85(3), 663-669.
- 7 [31] MAY, M. L. (1991). Dragonfly flight: power requirements at high speed and acceleration. *Journal*
8 *of Experimental Biology*, 158(1), 325-342.
- 9 [32] Wikelski, M., Moskowicz, D., Adelman, J. S., Cochran, J., Wilcove, D. S., & May, M. L. (2006).
10 Simple rules guide dragonfly migration. *Biology letters*, 2(3), 325-329.
- 11 [33] Vincent, J. F., & Wegst, U. G. (2004). Design and mechanical properties of insect
12 cuticle. *Arthropod Structure & Development*, 33(3), 187-199.
- 13 [34] Appel, E., Heepe, L., Lin, C. P., & Gorb, S. N. (2015). Ultrastructure of dragonfly wing veins:
14 composite structure of fibrous material supplemented by resilin. *Journal of Anatomy*, 227(4), 561-
15 582.
- 16 [35] Rajabi, H., Shafiei, A., Darvizeh, A., Dirks, J. H., Appel, E., & Gorb, S. N. (2016). Effect of
17 microstructure on the mechanical and damping behaviour of dragonfly wing veins. *Royal Society*
18 *Open Science*, 3(2), 160006.
- 19 [36] Song, F., Xiao, K. W., Bai, K., & Bai, Y. L. (2007). Microstructure and nanomechanical properties
20 of the wing membrane of dragonfly. *Materials Science and Engineering: A*, 457(1-2), 254-260.
- 21 [37] Rajabi, H., Ghoroubi, N., Darvizeh, A., Dirks, J. H., Appel, E., & Gorb, S. N. (2015). A comparative
22 study of the effects of vein-joints on the mechanical behaviour of insect wings: I. Single
23 joints. *Bioinspiration & Biomimetics*, 10(5), 056003.
- 24 [38] Rajabi, H., Ghoroubi, N., Darvizeh, A., Appel, E., & Gorb, S. N. (2016). Effects of multiple vein
25 microjoints on the mechanical behaviour of dragonfly wings: numerical modelling. *Royal Society*
26 *Open Science*, 3(3), 150610.
- 27 [39] Rajabi, H., Shafiei, A., Darvizeh, A., & Gorb, S. N. (2016). Resilin microjoints: a smart design
28 strategy to avoid failure in dragonfly wings. *Scientific Reports*, 6(1), 1-5.
- 29 [40] Rajabi, H., Ghoroubi, N., Malaki, M., Darvizeh, A., & Gorb, S. N. (2016). Basal complex and basal
30 venation of Odonata wings: structural diversity and potential role in the wing deformation. *PloS*
31 *One*, 11(8), e0160610.
- 32 [41] Eraghi, S. H., Toofani, A., Guilani, R. J., Ramezanpour, S., Bijma, N. N., Sedaghat, A., ... & Rajabi, H.
33 (2023). Basal complex: a smart wing component for automatic shape morphing. *Communications*
34 *Biology*, 6(1), 853.
- 35 [42] Rajabi, H., Ghoroubi, N., Stamm, K., Appel, E., & Gorb, S. N. (2017). Dragonfly wing nodus: a one-
36 way hinge contributing to the asymmetric wing deformation. *Acta Biomaterialia*, 60, 330-338.

- 1 [43] Rajabi, H., & Gorb, S. N. (2020). How do dragonfly wings work? A brief guide to functional roles
2 of wing structural components. *International Journal of Odonatology*, 23(1), 23-30.
- 3 [44] Wootton, R. J. (2009). Springy shells, pliant plates and minimal motors: abstracting the insect
4 thorax to drive a micro-air vehicle. In *Flying insects and robots* (pp. 207-217). Springer, Berlin,
5 Heidelberg.
- 6 [45] Yasuda, H., Buskohl, P. R., Gillman, A., Murphey, T. D., Stepney, S., Vaia, R. A., & Raney, J. R.
7 (2021). Mechanical computing. *Nature*, 598(7879), 39-48.
- 8 [46] Lietz, C., Schaber, C. F., Gorb, S. N., & Rajabi, H. (2021). The damping and structural properties of
9 dragonfly and damselfly wings during dynamic movement. *Communications Biology*, 4(1), 1-14.
- 10 [47] Rajabi, H., Dirks, J. H., & Gorb, S. N. (2020). Insect wing damage: causes, consequences and
11 compensatory mechanisms. *Journal of Experimental Biology*, 223(9), jeb215194.
- 12 [48] Mountcastle, A. M., & Combes, S. A. (2014). Biomechanical strategies for mitigating collision
13 damage in insect wings: structural design versus embedded elastic materials. *Journal of*
14 *Experimental Biology*, 217(7), 1108-1115.
- 15 [49] Rajabi, H., Darvizeh, A., Shafiei, A., Taylor, D., & Dirks, J. H. (2015). Numerical investigation of
16 insect wing fracture behaviour. *Journal of Biomechanics*, 48(1), 89-94.
- 17 [50] Rudolf, J., Wang, L. Y., Gorb, S. N., & Rajabi, H. (2019). On the fracture resistance of dragonfly
18 wings. *Journal of the Mechanical Behavior of Biomedical Materials*, 99, 127-133.
- 19 [51] Dirks, J. H., & Taylor, D. (2012). Veins Improve Fracture Toughness of Insect Wings. *PLoS ONE*,
20 7(8), e43411.
- 21 [52] Khareshi, A., & Rajabi, H. (2022). Mechanical Intelligence (MI): A Bioinspired Concept for
22 Transforming Engineering Design. *Advanced Science*, 2203783.
- 23 [53] Ramstead, M. J., Sakthivadivel, D. A., Heins, C., Koudahl, M., Millidge, B., Da Costa, L., ... &
24 Friston, K. J. (2023). On Bayesian mechanics: a physics of and by beliefs. *Interface Focus*, 13(3),
25 20220029.
- 26 [54] Mehonic, A., & Kenyon, A. J. (2022). Brain-inspired computing needs a master
27 plan. *Nature*, 604(7905), 255-260.
- 28 [55] Kaspar, C., Ravoo, B. J., van der Wiel, W. G., Wegner, S. V., & Pernice, W. H. P. (2021). The rise of
29 intelligent matter. *Nature*, 594(7863), 345-355.
- 30 [56] Mang, P., & Haggard, B. (2016). *Regenerative development and design: a framework for*
31 *evolving sustainability*. Wiley.
- 32 [57] Khareshi, A., Tramsen, H. T., Gorb, S. N., & Rajabi, H. (2021). Against the wind: A load-bearing, yet
33 durable, kite inspired by insect wings. *Materials & Design*, 198, 109354.
- 34 [58] Khareshi, A., Gorb, S. N., & Rajabi, H. (2021). Spiky-joint: a bioinspired solution to combine
35 mobility and support. *Applied Physics A*, 127(3), 1-7.

- 1 [59] Mintchev, S., Shintake, J., & Floreano, D. (2018). Bioinspired dual-stiffness origami. *Science*
- 2 *Robotics*, 3(20), eaau0275.
- 3 [60] Khaheshi, A., Gorb, S., & Rajabi, H. (2021). Triple Stiffness: A Bioinspired Strategy to Combine
- 4 Load-Bearing, Durability, and Impact-Resistance. *Advanced Science*, 8(11), 2004338.
- 5 [61] Nikolov, S., Petrov, M., Lymperakis, L., Friák, M., Sachs, C., Fabritius, H. O., ... & Neugebauer, J.
- 6 (2010). Revealing the design principles of high-performance biological composites using ab initio and
- 7 multiscale simulations: the example of lobster cuticle. *Advanced materials*, 22(4), 519.