

COMMENTARY

Swimming in circles can lead to exotic hyperuniform states of active living matter

Salvatore Torquato^{a,b,c,d,1}

The study of hyperuniform states of matter is an emerging multidisciplinary field, influencing and linking developments across the physical sciences, mathematics, and biology (1, 2). A hyperuniform many-particle system in d -dimensional Euclidean space is characterized by an anomalous suppression of large-scale density fluctuations relative to those in typical disordered systems, such as liquids and amorphous solids. As such, the hyperuniformity concept generalizes the traditional notion of long-range order to include not only all perfect crystals and quasicrystals but also exotic disordered states of matter. Disordered hyperuniform states have attracted great attention across many fields over the last two decades because they can have the character of crystals on large length scales but are isotropic like liquids (2). This hybrid crystal–liquid attribute endows them with unique or nearly optimal, direction-independent physical properties and robustness against defects (3–14). Adding to this flurry of research activity is the finding by Huang et al. (15) that circularly swimming marine algae can robustly self-organize into disordered hyperuniform states through long-range hydrodynamic interactions at air–liquid interfaces.

How is hyperuniformity quantified? Such systems have a structure factor $S(\mathbf{k})$, which can be measured from scattering experiments, that tends to zero as the wave-number $|\mathbf{k}|$ tends to zero (1), where \mathbf{k} is the wavevector. Another way to ascertain hyperuniformity is to randomly place many large spherical sampling windows of radius R in the system and count the number of particles within the window. The number of particles registered within the window will fluctuate, enabling one to find the corresponding local number variance $\sigma^2(R)$, as shown in Fig. 1. Garden-variety disordered systems, such as typical gases and liquids, are characterized by a variance $\sigma^2(R)$ that grows for large R like the volume of the window, that is, R^d , where d is the space dimension. A hyperuniform configuration has a variance that grows more slowly than R^d (1, 2). For example, all perfect crystals have a variance that grows like the surface area of the

window, that is, R^{d-1} . Remarkably, there are disordered systems that have the same growth rate as crystals (Fig. 1) and hence are hyperuniform.

Systems in which $\sigma^2(R)$ grows like R^{d-1} have the strongest form of hyperuniformity, which is called class I (2). States of matter that belong to class I include all perfect crystals (1, 16), many perfect quasicrystals (16, 17), “randomly” perturbed crystal structures (18), and classical disordered ground states of matter (19), as well as systems out of equilibrium (20, 21). Fig. 1 contrasts a typical disordered nonhyperuniform configuration with two different class I hyperuniform configurations in two dimensions, one of which is disordered and the other ordered. Class II systems are an intermediate form of hyperuniformity in which $\sigma^2(R)$ scales like $R^{d-1} \ln(R)$. Examples of class II include some quasicrystals (17), the positions of the prime numbers (22), and many disordered classical nonequilibrium systems (20, 23, 24) and quantum (25, 26) states of matter. The weakest form of hyperuniformity is class III, in which $\sigma^2(R)$ scales like R^β , where $d-1 < \beta < d$. Examples of class III systems include classical disordered ground states (27), nonequilibrium random organization systems (28, 29), and perfect glasses (20).

The majority of studies on disordered hyperuniform systems have been carried out for nonbiological models or systems. Much less is known about hyperuniformity that arises in biology. It has recently been discovered that disordered hyperuniformity can confer to biological systems optimal or nearly optimal functionality, including photoreceptor mosaics in the avian retina (30) and the immune system (31). Is it possible to find disordered hyperuniform states in active matter? Recent investigations, including the present study by Huang et al. (15), have shown that the answer is in the affirmative.

Active matter systems comprise individual entities that consume energy in order to move or exert mechanical forces. The interactions between such entities result in collective motion across certain length and time scales. Active matter systems are intrinsically nonequilibrium states and hence, unlike

^aDepartment of Chemistry, Princeton University, Princeton, NJ 08544; ^bDepartment of Physics, Princeton University, Princeton, NJ 08544;

^cPrinceton Institute for the Science and Technology of Materials, Princeton University, Princeton, NJ 08544; and ^dProgram in Applied and Computational Mathematics, Princeton University, Princeton, NJ 08544

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¹Email: torquato@princeton.edu.

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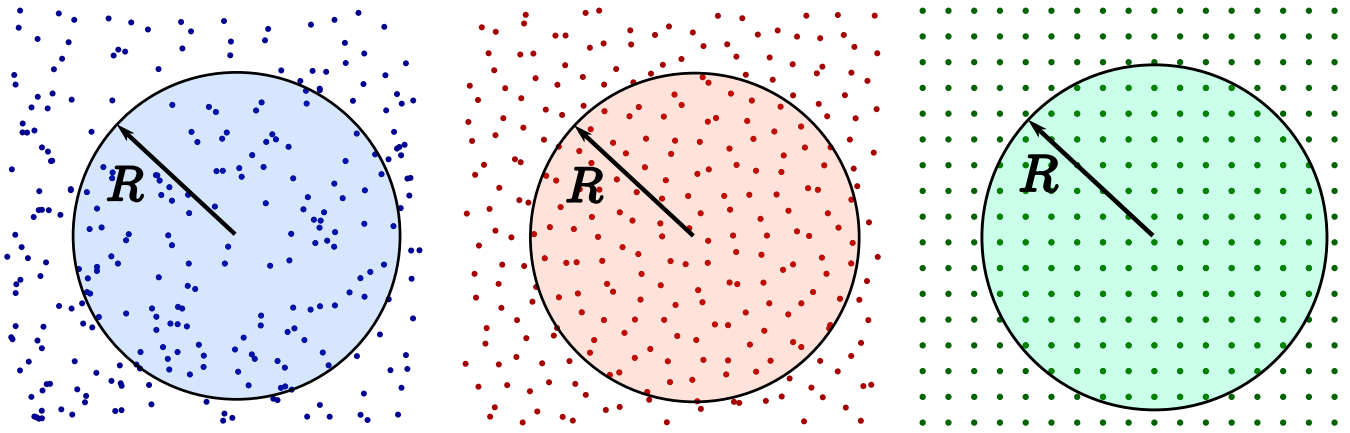


Fig. 1. Schematics indicating circular sampling windows in two dimensions for three different particle systems: garden-variety disordered nonhyperuniform (Left), disordered hyperuniform (Middle), and crystal (Right) configurations, as adapted from ref. 2. In each of these examples, the number of particles within a window will fluctuate as the window position varies, which specifies the local number variance $\sigma^2(R)$. In the case of a garden-variety disordered nonhyperuniform configuration, the variance $\sigma^2(R)$ grows like R^2 (area of the window). By contrast, the disordered hyperuniform system, shown in the Middle, has a variance $\sigma^2(R)$ that grows like R (circumference of the window), which has the same growth rate as the crystal configuration and hence is of class I.

equilibrium systems, break time-reversal symmetry, since the individual entities are continually dissipating energy (32–34). Examples of active living matter abound, including bird flocks (35), bacterial colonies (36), and insect swarms (37), to mention only a few. Exploiting the interactions found in active living matter systems by mimicking them in the laboratory can lead to the design of synthetic materials with unique properties, such as self-motility and self-healing.

The preponderance of current research on active matter focuses primarily on linearly swimming particles that have a symmetric body and self-propel along one of the symmetry axes. However, such perfect alignment between the propulsion direction and body axis is rarely found in reality. It is intuitively clear that deviations from such a perfect alignment would lead to microswimmer trajectories that are curved. Circular motility due to chiral microswimmers has been predicted by theoretical and numerical investigations (see ref. 38 and references therein) but had not been heretofore experimentally verified.

Now enter Huang et al. (15) with their study of the collective dynamics of marine algae *Effrenium voratum*. Such cells are approximately elliptical in shape and possess both longitudinal and transverse flagella for motility. The authors observe the cells at the air-liquid interface on an upright microscope. It turns out that, away from interfaces, that is, in the bulk of the suspension, the cells swim in helical trajectories, which are typical for motile algae. Importantly, when cells get close to an air-liquid interface, they adhere to the interface and start to move in circles. In fact, the authors observe that the cells move in a counterclockwise direction when viewed from the air side of the air-liquid interface. They then go on to measure the typical cell circling radius (order of 10 μm) as well as the angular speed (about 16 $\mu\text{m/s}$) and translational speed (about 180 $\mu\text{m/s}$).

Subsequently, the authors (15) investigate the collective states of many interacting cells at the air-liquid interface. During the first few minutes of the experiments, cells in the bulk suspension swam to the interface such that in the initial configuration the cells were randomly distributed (uncorrelated). Afterward, the cells at the interface slowly self-organized and eventually (after several thousand seconds) achieved a steady-state distribution, which the authors structurally characterize. While these steady-state cell configurations exhibited a type of correlated disorder, they showed no obvious

long-range order and appeared to be quite uniform at large length scales, suggesting that the spatial distribution of the cells is hyperuniform. Indeed, this was verified by conducting the sampling-window procedure qualitatively illustrated in Fig. 1 for two dimensions. The authors found that the local number variance scales like $\sigma^2(R) \approx R^{1.4}$ for large R , which places such systems in class III hyperuniformity. (The authors actually measure the local density variance, which is trivially related to the number variance by $\sigma^2(R)/R^4 \approx R^{-2.6}$.) It is remarkable that the swimmers spatially distribute themselves so that their large-scale density fluctuations are greatly suppressed, especially compared to other active matter systems that are known to have huge density fluctuations at large length scales (39, 40). The latter have more recently been called “antihyperuniform” systems (2) because they are diametrically opposite to hyperuniform ones (since the structure factor $S(\mathbf{k})$ diverges to infinity in the limit $|\mathbf{k}| \rightarrow 0$) with a number variance $\sigma^2(R)$ that grows faster than R^d or the sampling-window volume.

What is the mechanism that leads circular microswimmers to robustly self-organize into exotic disordered hyperuniform states? The authors (15) go on to demonstrate that cell swimming at the interface generates fluid flow that leads to effective repulsions between cells in the far field. It is the long-range nature of such repulsive interactions that suppresses large-scale density fluctuations and generates disordered hyperuniform states under a wide range of density conditions, as validated by the authors’ hydrodynamic numerical simulations of the two-dimensional suspensions. The authors find good agreement between the predictions of the simulations and experiments. It is well known that long-range interactions are required to have an equilibrium disordered state of matter that is hyperuniform at positive temperature, but long-range interactions are not required for nonequilibrium systems to be hyperuniform (2). Collections of circular swimming *E. voratum* cells at steady states are systems out of equilibrium, and the long-range hydrodynamic interactions lead to hyperuniform distributions of cells. The use of long-range hydrodynamic interactions may provide a promising avenue to synthesize novel hyperuniform materials with active matter.

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- 1 S. Torquato, F. H. Stillinger, Local density fluctuations, hyperuniformity, and order metrics. *Phys. Rev. E* **68**, 041113 (2003).
- 2 S. Torquato, Hyperuniform states of matter. *Phys. Rep. Rev. Sec. Phys. Lett.* **745**, 1–95 (2018).
- 3 M. Florescu, S. Torquato, P. J. Steinhardt, Designer disordered materials with large complete photonic band gaps. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 20658–20663 (2009).
- 4 W. Man et al, Isotropic band gaps and freeform waveguides observed in hyperuniform disordered photonic solids. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 15886–15891 (2013).
- 5 O. Leseur, R. Pierrat, R. Carminati, High-density hyperuniform materials can be transparent. *Optica* **3**, 763–767 (2016).
- 6 T. Ma et al, 3D printed hollow-core terahertz optical waveguides with hyperuniform disordered dielectric reflectors. *Adv. Opt. Mater.* **4**, 2085–2094 (2016).
- 7 G. Zhang, F. H. Stillinger, S. Torquato, Transport, geometrical and topological properties of stealthy disordered hyperuniform two-phase systems. *J. Chem. Phys.* **145**, 244109 (2016).
- 8 G. Gkantounis, T. Amoah, M. Florescu, Hyperuniform disordered phononic structures. *Phys. Rev. B* **95**, 094120 (2017).
- 9 L. S. Froufe-Pérez, M. Engel, J. José Sáenz, F. Scheffold, Transport phase diagram and Anderson localization in hyperuniform disordered photonic materials. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 9570–9574 (2017).
- 10 D. Chen, S. Torquato, Designing disordered hyperuniform two-phase materials with novel physical properties. *Acta Mater.* **142**, 152–161 (2018).
- 11 H. Zhang, H. Chu, H. Giddens, W. Wu, Y. Hao, Experimental demonstration of Luneburg lens based on hyperuniform disordered media. *Appl. Phys. Lett.* **114**, 053507 (2019).
- 12 S. Gorsky et al, Engineered hyperuniformity for directional light extraction. *APL Photon.* **4**, 110801 (2019).
- 13 J. Kim, S. Torquato, Multifunctional composites for elastic and electromagnetic wave propagation. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 8764–8774 (2020).
- 14 S. Yu, C. W. Oiu, Y. Chong, S. Torquato, N. Park, Engineered disorder in photonics. *Nat. Rev. Mater.* **6**, 226–243 (2021).
- 15 M. Huang, W. Hu, S. Yang, Q-X. Liu, H. P. Zhang, Circular swimming motility and disordered hyperuniform state in an algae system. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2100493118 (2021).
- 16 C. E. Zachary, S. Torquato, Hyperuniformity in point patterns and two-phase heterogeneous media. *J. Stat. Mech. Theor. Exp.* **2009**, P12015 (2009).
- 17 E. C. Oğuz, J. E. S. Socolar, P. J. Steinhardt, S. Torquato, Hyperuniformity of quasicrystals. *Phys. Rev. B* **95**, 054119 (2017).
- 18 M. A. Klatt, J. Kim, S. Torquato, Cloaking the underlying long-range order of randomly perturbed lattices. *Phys. Rev. E* **101**, 032118 (2020).
- 19 S. Torquato, G. Zhang, F. H. Stillinger, Ensemble theory for stealthy hyperuniform disordered ground states. *Phys. Rev. X* **5**, 021020 (2015).
- 20 G. Zhang, F. H. Stillinger, S. Torquato, The perfect glass paradigm: Disordered hyperuniform glasses down to absolute zero. *Sci. Rep.* **6**, 36963 (2016).
- 21 Q.-L. Lei, R. Ni, Hydrodynamics of random-organizing hyperuniform fluids. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 22983–22989 (2019).
- 22 S. Torquato, G. Zhang, M. de Courcy-Ireland, Hidden multiscale order in the primes. *J. Phys. A Math Theor.* **52**, 135002 (2019).
- 23 A. Donev, F. H. Stillinger, S. Torquato, Unexpected density fluctuations in jammed disordered sphere packings. *Phys. Rev. Lett.* **95**, 090604 (2005).
- 24 C. E. Zachary, Y. Jiao, S. Torquato, Hyperuniform long-range correlations are a signature of disordered jammed hard-particle packings. *Phys. Rev. Lett.* **106**, 178001 (2011).
- 25 L. Reatto, G. V. Chester, Phonons and the properties of a Bose system. *Phys. Rev.* **155**, 88–100 (1967).
- 26 S. Torquato, A. Scardicchio, C. E. Zachary, Point processes in arbitrary dimension from Fermionic gases, random matrix theory, and number theory. *J. Stat. Mech. Theor. Exp.* **2008**, P11019 (2008).
- 27 C. E. Zachary, S. Torquato, Anomalous local coordination, density fluctuations, and void statistics in disordered hyperuniform many-particle ground states. *Phys. Rev. E* **83**, 051133 (2011).
- 28 D. Hexner, D. Levine, Hyperuniformity of critical absorbing states. *Phys. Rev. Lett.* **114**, 110602 (2015).
- 29 J. H. Weijs, R. Jeanneret, R. Dreyfus, D. Bartolo, Emergent hyperuniformity in periodically driven emulsions. *Phys. Rev. Lett.* **115**, 108301 (2015).
- 30 Y. Jiao et al, Avian photoreceptor patterns represent a disordered hyperuniform solution to a multiscale packing problem. *Phys. Rev. E* **89**, 022721 (2014).
- 31 A. Mayer, V. Balasubramanian, T. Mora, A. M. Walczak, How a well-adapted immune system is organized. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 5950–5955 (2015).
- 32 M. C. Marchetti et al, Hydrodynamics of soft active matter. *Rev. Mod. Phys.* **85**, 1143–1189 (2013).
- 33 M. E. Cates, J. Tailleur, Motility-induced phase separation. *Ann. Rev. Cond. Matter Phys.* **6**, 219–244 (2015).
- 34 F. Ginot et al, Nonequilibrium equation of state in suspensions of active colloids. *Phys. Rev. X* **5**, 011004 (2015).
- 35 A. Cavagna, I. Giardina, Bird flocks as condensed matter. *Annu. Rev. Condens. Matter Phys.* **5**, 183–207 (2014).
- 36 H. P. Zhang, A. Be'er, E. L. Florin, H. L. Swinney, Collective motion and density fluctuations in bacterial colonies. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 13626–13630 (2010).
- 37 J. Buhl et al, From disorder to order in marching locusts. *Science* **312**, 1402–1406 (2006).
- 38 Q.-L. Lei, M. P. Ciamarra, R. Ni, Nonequilibrium strongly hyperuniform fluids of circle active particles with large local density fluctuations. *Sci. Adv.* **5**, eaau7423 (2019).
- 39 J. Deseigne, O. Dauchot, H. Chaté, Collective motion of vibrated polar disks. *Phys. Rev. Lett.* **105**, 098001 (2010).
- 40 J. Palacci, S. Sacanna, A. P. Steinberg, D. J. Pine, P. M. Chaikin, Living crystals of light-activated colloidal surfers. *Science* **339**, 936–940 (2013).