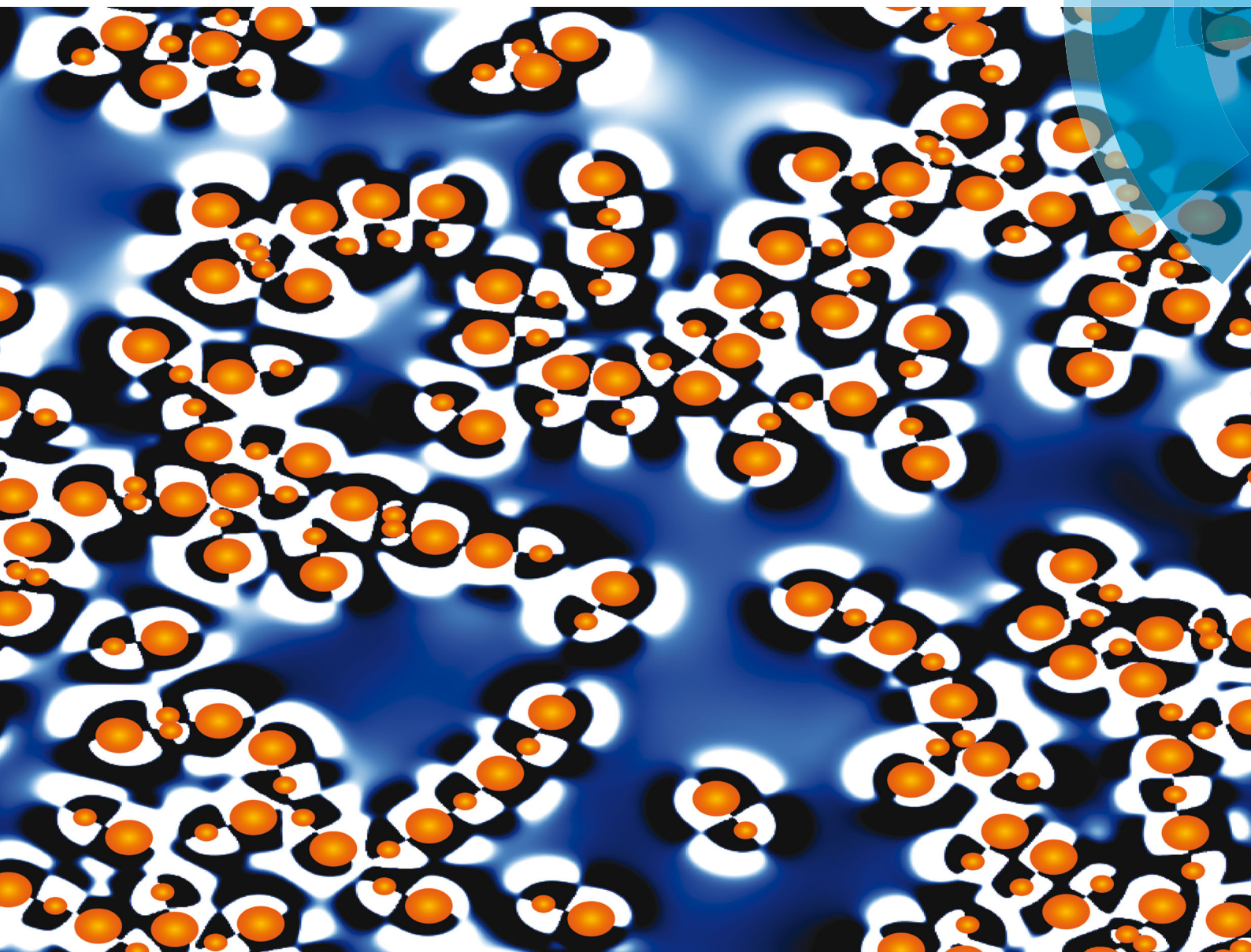


Soft Matter

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PERSPECTIVE

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As above, so below, and also in between: mesoscale active matter in fluids



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Daphne Klotsa 

Living matter, such as biological tissue, can be viewed as a nonequilibrium hierarchical assembly, where at each scale self-driven components come together by consuming energy in order to form increasingly complex structures. The remarkable properties of living or “active-matter” systems, as they are generally known, such as versatility, self-healing, and self-replicating, have prompted the following questions: (1) do we understand the biology and biophysics that give rise to these properties? (2) can we achieve similar functionality with synthetic active materials? In this perspective we specifically focus on why it is important to study active matter in fluids with finite inertia. Finite inertia is relevant for mesoscale organisms that swim or fly covering at least three orders of magnitude in size (≈ 0.5 mm–50 cm) and their collective behavior is generally unknown. As a result, we are limited both in our understanding of the biology of mesoscale swarms and processes but also in our design of self-powered machines and robots at those scales. We expect interesting collective behavior to emerge because with finite inertia, come nonlinearities and the many-body hydrodynamic interactions between the organisms/particles can become quite complex, potentially leading to phenomena, such as novel flocking states and nonequilibrium phase transitions that have not been observed before and which could have great impact in materials applications.

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When fish school, the tiniest jolt from an intruder (a larger fish, a human, a fishing hook) creates a momentary frenzy; the school explodes, propelling its members in all directions, only to reform seconds later. Indeed the school of fish looks like one continuous living “material” with a life and intelligence of its own, grander than the sum of its parts, smarter than the individual organisms. This observation, commonly seen in nature, has led to a breakthrough at the interface of materials, biology and physics of systems we call “living matter” or “active matter”, that consist of groups of self-propelled particles or organisms that interact with one another and exhibit collective behavior (*e.g.* swarms, flocks).^{1–7}

The dynamic properties and versatility of operations of such living materials are in sharp contrast with the static characteristics of traditional materials; the former consist of active components (*e.g.* fish, bacteria, self-propelled nanorods, molecular motors) that locally consume energy to move, exert forces, or perform chemical reactions, thus being inherently out of equilibrium, while the latter are made out of passive building blocks (*e.g.* molecules, nanoparticles) at equilibrium. Even “smart materials” that can change their properties based on external inputs of energy, have limited responsiveness that fade in comparison to cellular living matter. Imagine therefore, designing a new class of metamaterials by combining active components to create active matter. In the

same way that schools of fish respond to predators, swarms of bacteria swim towards nutrients, or skin heals itself when wounded, an artificial active material of self-propelled colloids or buzzing insect drones will respond to stimuli, restore coherence of the flock (self-heal), adapt, store energy and information, assemble and disassemble at will. Understanding the fundamental principles governing these nonequilibrium systems in the various environments and scales they naturally occur, is an essential step towards formulating a theoretical framework and subsequently the design rules to make synthetic active materials a reality.^{2,5–7}

The emergent behavior of active matter has been demonstrated at many length-scales with both biological and artificial active particles in different environments. Examples include bacterial turbulence^{9,10} and self-assembled “living” colloidal crystals in solution,¹¹ fish schooling in the ocean,¹² and robot swarming on a flat surface.¹³ A number of theoretical and computational studies have proposed minimal models (*e.g.*, Vicsek,¹⁴ Run and Tumble,^{3,15,16} Active Brownian Particle^{3,17}) capturing some of the remarkable behavior seen in experiments and nature, while providing theory with new insights and predictions for experiments.^{2,3} However, these (dry) models do not include many-body hydrodynamic interactions and therefore cannot describe systems where hydrodynamics matters,^{18–21} such as certain intracellular processes in the cytoskeleton,²⁰ organ function,²² marine and aerial organisms^{23,24} or robots^{25,26} that swim or fly. To date, studies that include hydrodynamic interactions have focused on

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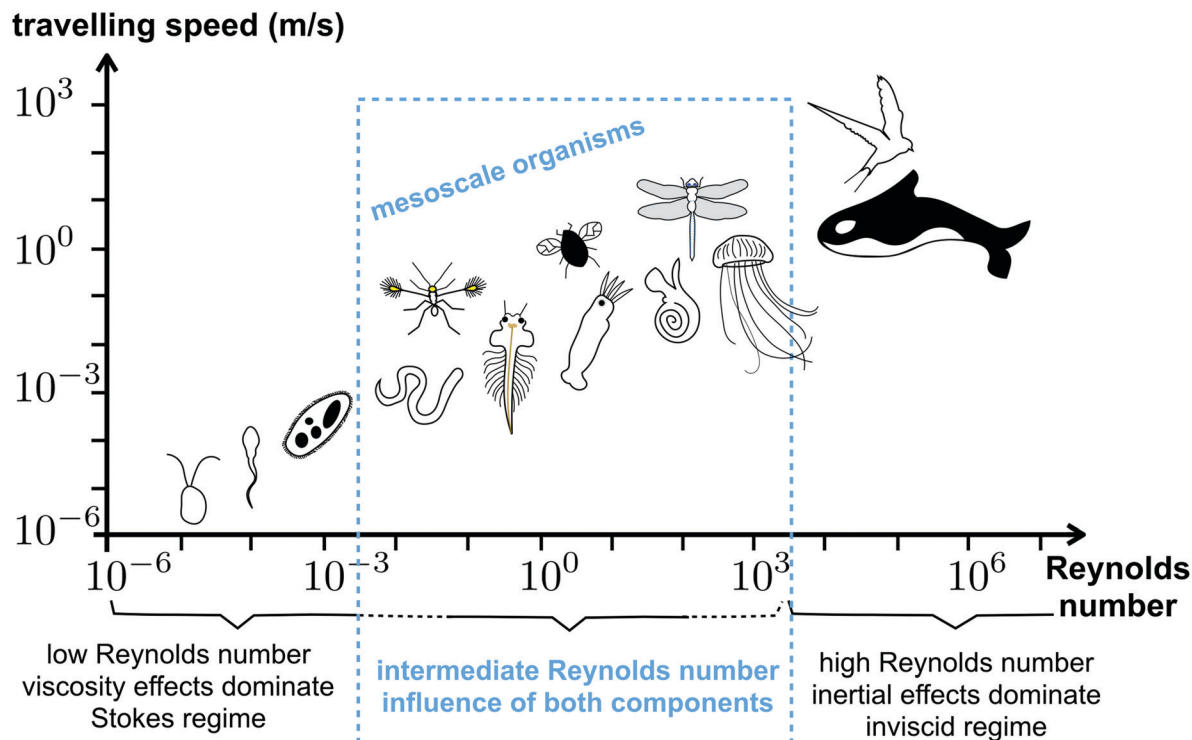


Fig. 1 Reynolds numbers in the animal kingdom, highlighting the intermediate Reynolds range for swimming and flying organisms. The organisms shown schematically from low to high Reynolds numbers are: algae, bacterium, paramecium, nematode, fairyfly, brine shrimp, larval squid, wasp, pteropod, dragonfly, jelly fish, whale, swallow. Layout inspired by Nachtigall.⁸

either microscopic scales *i.e.*, Stokes flows, where the Reynolds number[†] (Re) approaches zero, $Re \ll 1$, viscosity dominates and inertia can be neglected,^{2,20,27–29} or at high Re , $Re \gg 1$, where inertia dominates and viscosity can be neglected.^{30–34} In these two limiting cases, one can make mathematical simplifications to the Navier–Stokes equations that govern the fluid dynamics. In-between resides the intermediate Reynolds regime, $Re_{int} \approx 1–1000$, where both viscosity and inertia matter and these mathematical simplifications cannot be made. Note that specific active matter systems have been studied both in the Stokesian and weakly inertial regime showing the effects of weak inertia on emergent behavior.^{5,35–37}

The collective behavior of mesoscale organisms (operating at intermediate Reynolds numbers) remains largely unexplored even though these organisms cover at least three orders of magnitude in size (≈ 0.5 mm–50 cm), include thousands of different marine and aerial animals that we can study for their biology or as model systems,^{38–41} (*e.g.* ciliates, plankton, brine shrimp, fish larvae, copepods, flies, mosquitoes, bees), as well as autonomous machines (*e.g.* flying insect-drones, marine robots) and self-propelled particles and aggregates at those scales (Fig. 1).

[†] The Reynolds number (Re) is the dimensionless ratio that determines the relative importance of inertial over viscous forces, $Re = \text{inertia forces}/\text{viscous forces} = \rho u L / \mu$, where, in the context of motility, ρ is the density of the surrounding fluid, u is the velocity of the organism, L is a characteristic length scale, usually the organism's size, and μ is the dynamic viscosity of the surrounding fluid.

The viewpoint of this perspective article is that mesoscale active matter, comprised of mesoscopic self-propelled particles, can be regarded as a material, an active inertial suspension. Currently, there is a striking gap both in our theoretical understanding of active matter at those scales, as well as in our experimental exploration. We are thus missing out on a plethora of interesting phenomena, relating both to biological and synthetic active systems. Below, we outline the scientific and technological motivation for studying mesoscale active matter in fluids:

Mesoscale organisms

While the collective behavior of mesoscale swimming or flying organisms is largely unknown, closely related systems indicate that it can be quite interesting. For example, (i) in Stokes flows, it has been established that hydrodynamic interactions between swimmers drive the emergence of various collective phenomena and swarms at the microscale ($Re \ll 1$).^{2,18,29,42–44} (ii) At intermediate Re , it has been shown that externally driven granular systems self-organize into dynamic patterns, induced by nonlinear hydrodynamic interactions.^{45–47} Thus, we expect the additional complexity of finite inertia (in (i)) and of self-propulsion (in (ii)) to lead to novel phase behavior, different types of swarming, dynamics and transitions. Moreover, (iii) studies looking at the flows around swarms of mesoscopic swimmers, such as zooplankton and brine shrimp, found that their collective swimming induces nonlinear flows that contribute to the transport and large-scale mixing of nutrients in the oceans, known as

biogenic mixing.^{48–51} It is remarkable to think that such small organisms (size $\sim$ cm) could have such a large-scale effect, and the reason is that there are many of them and their hydrodynamic flows have finite inertia.

Mathematically, the complexity already arises when studying the interactions of just two swimmers, *e.g.* the inertial squirmers.^{52,53} Unlike for Stokes flows, where the velocities of the two swimmers are only functions of the viscous force or stress acting on them and their relative separation vector, the pair dynamics in the intermediate regime is also a function of Re and time. Considering a swarm, particles will interact through many-body nonlinear hydrodynamic forces, which we expect to strongly influence collective behavior, generating different swarming phases, with various levels of stability, and unexplored transition mechanisms between phases. Chatterjee *et al.* recently showed that inertia drives a flocking transition in extensile active suspensions.³⁷ We present simulation results of the collective behavior of a mesoscopic model swimmer⁵⁴ in Fig. 3. Already a small number of these swimmers show distinct collective behavior at two different Reynolds numbers (an active stationary “network” at $Re \approx 5$ versus swimming triplets at $Re \approx 100$) both within the intermediate Reynolds number range (Fig. 3). The result highlights another important point: even within the intermediate Reynolds range the behavior of a system is likely to change at different values of Re , *i.e.* we expect different behavior at $Re = 1, 10, 100, 1000$ and none of this has been investigated in the context of active matter.

Swarms of microscopic organisms

The boundaries between the low and intermediate Reynolds regimes are not always clear (Fig. 1). Even if the individual swimmer is approximately microscopic, when a swarm or aggregate of swimmers is considered, the relevant length scale (used to calculate Re) may be that of the collective rather than the individual swimmer (Fig. 2). Thus, the validity of the Stokes flow assumption needs to be tested for microscopic active-matter systems too and it is essential to establish conditions under which the assumption breaks down. This directly impacts current efforts in theory and experiments of microscopic active

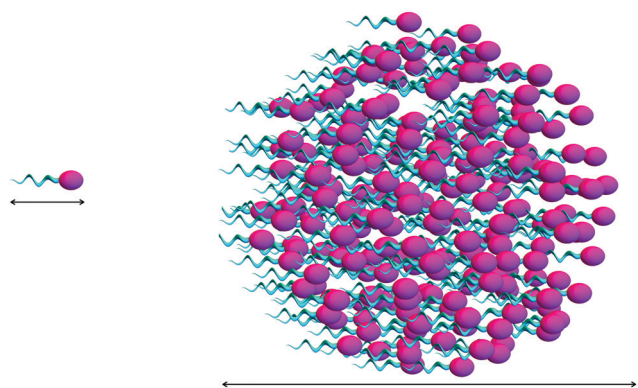


Fig. 2 Arrows indicate different characteristic sizes for a single swimmer versus a swarm, possibly affecting the relevant Reynolds number.

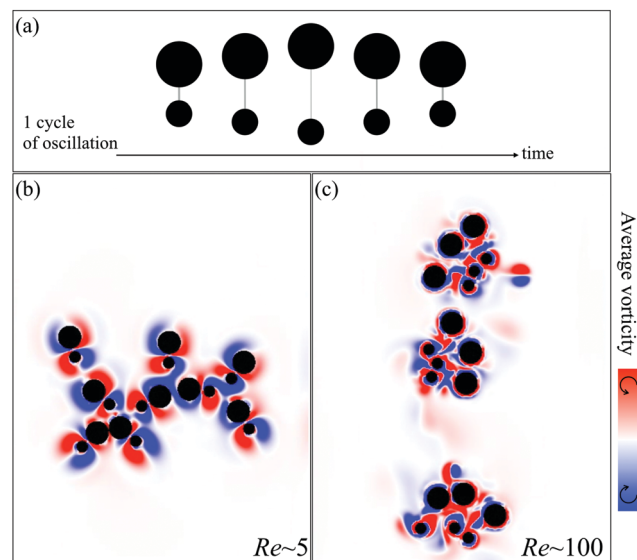


Fig. 3 A simple reciprocal model swimmer, made of two spheres that oscillate in anti-phase⁵⁴ (a). Nine swimmers with the same initial conditions showing emergent collective behavior and different dynamic patterns at different intermediate Reynolds numbers, forming an active stationary “network” at $Re \approx 5$ in (b) versus swimming triplets where swimmers were arranged side by side at $Re \approx 100$ in (c). Blue and red colors indicate clockwise and counterclockwise fluid vorticity, respectively. Figure courtesy of Thomas Dombrowski.

matter. Take the example of *B. Subtilis*: this microscopic bacterium (size $\approx 5 \mu\text{m}$) has been shown to generate “bacterial turbulence” when in swarms on the order of thousands.^{10,55} The single organism has $Re \approx 10^{-5}$ (speed on the order of $10 \mu\text{m/s}$). If we now consider 100 000 bacteria, with reported velocities up to $100 \mu\text{m/s}$, the effective Reynolds number for the swarm can shift up to $Re_{\text{swarm}} \approx 10$. The idea of an effective dimensionless ratio that would explain this apparent turbulence at $Re \ll 1$ has already been proposed without the inclusion of inertia.⁴³ Inertia probably does not play a role in *B. Subtilis* but our calculation provides a warning certainly relevant for swarming systems that operate near the boundary of low-to-intermediate Re , that Stokes flow should not hastily be assumed on the basis of a single swimmer.

Transitions

Identifying thresholds for the onset of inertia for swarms and active suspensions will open up the possibility to control switching between finite-inertial and inertia-free regimes. Low and intermediate Reynolds regimes have markedly different physics; highly dissipative, linear, time-reversible flows at low Re versus inertial, nonlinear, with memory at intermediate Re . For example, Chisholm *et al.* have shown that the same squirmer swimmer behaves differently at low and intermediate Reynolds numbers.⁵⁶ We have shown that as Re increases from 5 to 50 there is a switch in the swimming direction of a simple model swimmer induced by inertia.⁵⁴ Generally, for an active particle with a reciprocal stroke, *e.g.* Purcell’s scallop⁵⁷ or the

spherobot,^{47,54} the onset of inertia means a transition from “rest” (meaning no net motion) to swimming (net motion). In other words, in Stokes flows, a reciprocal swimmer will not swim, according to Purcell’s scallop theorem,⁵⁷ it will perform its stroke (beating at some frequency) but end up going back and forth with no net motion after a cycle. As inertia increases, however, the reciprocal swimmer will start to swim, *i.e.* have net motion. Consider the possibilities if we have suspensions of swimmers either beating in place with no net motion or already swimming and swarming at low *Re*, as in Wensink *et al.*,¹⁰ whose behavior we can then control by increasing the swimmers’ beating frequency, or amplitude thus pushing the system to have finite inertia. Nonlinear interactions will come into play and the global behavior, patterns, steady states *etc.* will drastically change. We could thus design active suspensions that switch between a beating stationary swarm and a moving dynamic one.

Hierarchy in active matter

In the example of the school of fish in the introduction, the swarm is a nonequilibrium assembly of self-propelled components, in this case a living organism (the fish). Each organism is made of biological tissue, which itself is a nonequilibrium assembly of cells. Cells consist of many nonequilibrium components that move in a directed way, such as molecular motors and enzymes. So, at each of these scales, the system of interest (*i.e.* the swarm, the organism, the tissue, the cells) can each be viewed as an active material that itself is made of active subunits. Hierarchy is an important characteristic of living systems. In their review,⁶ Needleman and Dogic gave Leibniz’ description of a living organism:⁵⁸ “an organism is a machine in which each part is a machine” thus capturing the complexity, hierarchy and nonequilibrium nature seen in living systems at many scales. One of the goals of materials science is to make synthetic materials that match the functionality of biology. In order to do that we need to design hierarchical active matter, where active units come together to form larger units and so on, *i.e.* machines made out of machines. As microscopic units come together and form larger ones, and those come together and form yet larger ones, at some point the active assemblage will be affected by inertia. Thus, understanding how mesoscopic units interact with one another in solution, and accounting for the interplay of forces as we scale up in size will be crucial for materials applications.

Conclusions

Nature has perfected obtaining robust collective behavior and global order from simple local interactions. A great challenge for the broad soft-matter community is to engineer similar systems at all scales that are composed of many agents, ranging from self-propelled nanoparticles to swarming drones, and to be able to control their emergent collective properties, their emergent “intelligence”. While we have witnessed remarkable advances in the field of active matter, mesoscale active matter in fluids remains largely unexplored. In this perspective article,

we presented the scientific and technological motivation for studying mesoscale active matter. We believe and hope that it will inspire and open the door to lots of new theoretical and experimental research with applications both in biology and novel synthetic materials.

Conflicts of interest

There are no conflicts to declare.

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