

# Étienne Fodor

Physics of Active Matter

Associate Professor

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Dept of Physics and Materials Science (DPhyMS)

Univ of Luxembourg

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## Scientific positions and education

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- Since 2025 **Associate Professor**, DPhyMS, Univ of Luxembourg
- 2020–25 **Assistant Professor**, DPhyMS, Univ of Luxembourg
- 2017–20 **Oppenheimer Research Fellow**, DAMTP, Univ of Cambridge
- 2016–17 **Postdoctoral Research Associate**, DAMTP, Univ of Cambridge (Supervisor: ME Cates)
- 2013–16 **PhD in Physics**, Univ Paris Diderot (Supervisors: P Visco, F van Wijland), summa cum laude
- 2012–13 **Masters (2<sup>nd</sup> year) in Physics**, École Normale Supérieure (ENS), Paris
- 2011–12 **Agrégation de Physique**, Training program for teaching in Physics Bachelors, ENS Cachan
- 2009–11 **Bachelors + Masters (1<sup>st</sup> year) in Physics**, ENS Lyon

## Research, supervision, and teaching

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Since 2022 **Masters course in Physics**, DPhyMS, Univ of Luxembourg | 14 weeks/year

Since 2020 **Group supervision**, DPhyMS, Univ of Luxembourg

8 Postdocs | LK Davis (20–22), A Manacorda\* (21–24), T Banerjee<sup>†</sup> (22–26), WD Piñeros\* (22–25), UA Dattani (23–25), F Serafin (24–25), A Soriani (26–27), F Thewes (26–27)

\*Marie-Curie Fellow (Horizon Europe), <sup>†</sup>CORE Junior Fellow (Luxembourg)

6 PhDs | Y Zhang (20–23), BN Radhakrishnan (21–25), L Casagrande (23–26), N Setzkorn (24–27), IJC Miranda (24–27), M Antonioli (24–27)

4 Masters | L Casagrande (22–23), T Desaleux (22–23), N Setzkorn (23–24), A Jagannathan (25–26)

2024 **Masters course in Physics**, Dept of Physics, Univ of Liège | 10 hours, 1 week

2021 **Doctoral course in Physics**, DPhyMS, Univ of Luxembourg | 6 hours, 1 day

2016–20 **Student co-supervision**, DAMTP, Univ of Cambridge (Supervisor: ME Cates)

2 PhDs | ØL Borthne (17–20), T Ekeh (18–21)

3 Masters | D Martin (16–17), T Ekeh (17–18), JW Knight (19–20, best thesis prize)

2015–16 **Research visit**, YITP, Kyoto Univ (Host: H Hayakawa) | 2 months/year

2013–16 **Bachelors tutorials in Physics**, Univ Paris Diderot | 14 weeks/year

2013 **Research internship**, Univ Paris Diderot (Supervisors: P Visco, F van Wijland) | 16 weeks

2012–13 **Bachelors tutorials in Physics**, Lycée Fénelon, Paris | 30 weeks

2011 **Research internship**, Univ of Oxford (Supervisors: AS Wyatt, IA Walmsley) | 12 weeks

2010–11 **Bachelors tutorials in Physics**, Lycée la Martinière Monplaisir, Lyon | 30 weeks

2010 **Research internship**, Univ de Genève (Supervisors: L Bonacina, J-P Wolf) | 8 weeks

## Funding, fellowships, and awards

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2026 **Outstanding Junior Fellowship**, Institute of Advanced Studies, Tel-Aviv University

2026–29 **CORE grant**, Fonds National de la Recherche (FNR), Luxembourg | 800 kEUR

2025–28 **Innovative training network**, Horizon Europe (Program lead: R Blythe) | 1 PhD

2024–27 **CORE grant**, FNR, Luxembourg | 830 kEUR

2021–26 **Doctoral training unit**, FNR (Program lead: M Esposito) | 1 PhD

2020–25 **ATTRACT Fellowship**, FNR | 1.5 MEUR

2017–20 **Oppenheimer + Junior Research Fellowship**, St Catharine's College, Univ of Cambridge

2017 **PhD prize**, Institut Systèmes Complexes, Paris + **Best talk**, SIAM-IMA Conference, Cambridge

2015 **Best talk**, Active Liquids, Lorentz Center, Leiden

2013–16 **Teaching Assistantship**, Univ Paris Diderot + **PhD Scholarship**, ENS Cachan

## Scientific events and committees

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### Invited conference talks

- 2026      **Nonequilibrium Dynamics, from Active Matter to Evolutionary Dynamics**, KITP  
              **Control and Optimisation of Out-of-equilibrium Processes**, Beg Rohu  
              **SigmaPhi2026, Statistical Physics of Complex Systems**, Kolymbari  
              **Frontiers in Statistical Physics and Soft Matter**, Edwards Symposium, Univ of Cambridge
- 2025      **Statistical Physics of Living Systems**, CECAM, Lausanne  
              **International Discussion Meeting on Relaxations in Complex Systems**, Barcelona  
              **Self-Organization Far From Equilibrium**, APS March meeting, Anaheim  
              **Machine Learning for Enhanced Sampling of Atomistic Systems**, Berkeley
- 2024      **The Many Faces of Active Mechanics**, KITP, Santa Barbara  
              **Nonequilibrium Statistical Physics of Complex Systems**, Seoul
- 2023      **Computational Advances in Active Matter**, Lorentz Center, Leiden  
              **Frontiers in Nonequilibrium Physics: Active Matter, Topology and Beyond**, Kyoto  
              **Conference on Statistical Mechanics**, Sitges  
              **Physics of Dense and Active Disordered Materials**, Kyoto  
              **Frontiers in Nonequilibrium Physics**, Institute of Mathematical Sciences, Chennai
- 2022      **Statistical Mechanical Theories of Emergence in Biological Systems**, Edinburgh  
              **Numerical Techniques for Nonequilibrium Steady States**, CECAM, Mainz
- 2020      **Symmetry, Thermodynamics and Topology in Active Matter**, KITP (online)
- 2018      **Why Measure Entropy Production?**, Princeton Univ  
              **Active Matter Session**, Berkeley

### Contributed conference talks

- 2026      **DPG Spring Meeting**, Dresden
- 2025      **Multiscale Modeling of Chemically Active Mixtures**, CECAM, Lausanne  
              **StatPhys29, Out-of-equilibrium Statistical Physics**, Florence  
              **From Flocking Birds to Migrating Cells: Recent Advances in Active Matter**, Leiden
- 2024      **Dissipative Processes in Molecular Systems**, Padova  
              **Workshop on Stochastic Thermodynamics V** (online)  
              **DPG Spring Meeting**, Berlin
- 2023      **StatPhys28, Soft Matter**, Tokyo  
              **Bridge between Non-equilibrium Statistical Physics and Biology**, Cambridge  
              **New Perspectives in Active Systems**, Dresden  
              **From Soft Matter to Biophysics**, Les Houches
- 2021      **Liquid Matter Conference**, Prague (online)  
              **Workshop on Stochastic Thermodynamics II** (online)
- 2020      **Motile Active Matter Conference**, Bonn (online)
- 2019      **StatPhys27, Out-of-equilibrium aspects**, Buenos Aires  
              **International Soft Matter Conference**, Edinburgh  
              **Statistical Physics of Complex Systems**, Nordita, Stockholm
- 2018      **Nonequilibrium Collective Dynamics**, Technische Univ Berlin  
              **Fundamental Problems in Active Matter**, Aspen Center for Physics
- 2017      **SIAM-IMA Annual Conference**, Univ of Cambridge  
              **Edwards Centre Mini Conference**, Univ of Cambridge  
              **Open Statistical Physics**, Milton Keynes
- 2016      **StatPhys26, Biological Physics**, Lyon  
              **Non-Gaussian Workshop**, YITP, Kyoto
- 2015      **Active Liquids**, Lorentz Center, Leiden
- 2014      **Condensed Matter in Paris**, Univ Paris Descartes  
              **ESPCI, Journées de Physique Statistique**, Paris

## Invited seminars and colloquia

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| 2026 | <b>Center for Data Science and Complexity Colloquium</b> , Univ of Münster<br><b>Institut für Theoretische Physik Seminar</b> , Univ of Münster<br><b>Gulliver Lab Seminar</b> , ESPCI, Paris<br><b>Dept of Physics</b> , Univ of Palermo<br><b>Institute of Advanced Studies</b> , Tel-Aviv University  |
| 2025 | <b>Soft Condensed Matter Seminar Series</b> , Harvard University<br><b>Biophysics Seminar Series</b> , Massachusetts Institute of Technology<br><b>Solitons at work</b> , online   |
| 2024 | <b>Dept of Chemistry</b> , Univ of California, Berkeley<br><b>LPTMC</b> , Sorbonne Univ, Paris<br><b>Dept of Physics</b> , Univ of Liège<br><b>Institute of Physics</b> , Univ of Leiden<br><b>Niels Bohr Institute</b> , Univ of Copenhagen   |
| 2023 | <b>Biological, Soft and Complex Materials and Theory Seminar</b> , Univ of Bristol<br><b>EMBL Theory Seminar</b> , Heidelberg  |
| 2022 | <b>Biological Physics and Physical Biology</b> , online<br><b>DAMTP, Soft Matter Seminar</b> , Univ of Cambridge (online)<br><b>Mathematical Physics Seminar</b> , Imperial College London (online)  |
| 2021 | <b>Dept of Physics</b> , Guangdong Technion (online)<br><b>Quantum Science and Technology</b> , Univ of Luxembourg (online)<br><b>Non-equilibrium Statistical Physics</b> , Georg-August-Univ Göttingen (online)<br><b>Centre de Physique Théorique</b> , Aix-Marseille Univ (online)  |
| 2020 | <b>School of Physics and Astronomy</b> , Univ of Edinburgh (online)<br><b>Dept of Physics</b> , Univ of Bath   |
| 2019 | <b>ICTP, Quantitative Life Sciences Group</b> , Trieste<br><b>James Franck Institute, Dept of Chemistry</b> , Univ of Chicago<br><b>Physics of Living Systems</b> , Massachusetts Institute of Technology<br><b>Physics and Materials Science Research Unit</b> , Univ of Luxembourg<br><b>Institute of Physics, Computational Soft Matter</b> , Univ of Amsterdam |
| 2018 | <b>LiPhy Laboratory</b> , Univ Grenoble Alpes<br><b>Charles Coulomb Laboratory</b> , Univ de Montpellier<br><b>ESPCI, Gulliver Laboratory</b> , Paris<br><b>St Catharine's College, Graduate Research Seminars</b> , Cambridge<br><b>Research Colloquium Series</b> , California State Univ, Fullerton   |
| 2017 | <b>DAMTP, Soft Matter Seminar</b> , Univ of Cambridge<br><b>DAMTP, BioLunch Seminar</b> , Univ of Cambridge  |
| 2016 | <b>School of Mathematical Sciences</b> , Queen Mary Univ of London<br><b>DAMTP, Soft Matter Seminar</b> , Univ of Cambridge<br><b>MSC Laboratory Seminar</b> , Univ Paris Diderot<br><b>Yukawa Institute for Theoretical Physics</b> , Kyoto   |
| 2015 | <b>LiPhy Laboratory</b> , Univ Grenoble Alpes<br><b>Physics-Biology Interface Seminar</b> , Univ Paris Sud<br><b>DAMTP, Soft Matter Seminar</b> , Univ of Cambridge<br><b>Yukawa Institute for Theoretical Physics</b> , Kyoto   |
| 2014 | <b>MSC Laboratory, Physique du vivant</b> , Univ Paris Diderot<br><b>MSC Laboratory, Theory Group</b> , Univ Paris Diderot   |

## Organized events

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| 2026 | <b>Nonequilibrium Statistical Mechanics</b> , Univ Paris Cité, Paris   Workshop, 1 day  |
| 2025 | <b>Nonequilibrium Systems Under Control</b> , Lorentz Center, Leiden   Workshop, 1 week   |
| 2024 | <b>Energy, Information and Evolution in Biology</b> , Cargèse   Summer school, 2 weeks<br><b>Physics Meets Mathematics</b> , Univ of Luxembourg   Workshop, 1 day |

- 2018–20 **Statistical Physics and Soft Matter**, DAMTP, Univ of Cambridge | Weekly seminar  
 2019 **Colloids as a Toolbox for Statistical Mechanics**, Univ of Cambridge | Workshop, 1 day  
 2018 **Nonequilibrium Biophysics**, World Congress of Biomechanics, Dublin | Session,  $\frac{1}{2}$  day

### **Outreach activities**

- 2024 **Outreach lecture**, Institut d'Etudes Scientifiques, Cargèse  
**Chercheurs à l'école**, Seminar in high schools, Luxembourg  
 2023 **Inaugural lecture**, Faculty of Science, Technology and Medicine, Univ of Luxembourg  
 2022 **Student fair**, DPhyMS, Univ of Luxembourg  
 2021 **Open day**, DPhyMS, Univ of Luxembourg  
 2021–24 **Internship supervision**, High-school students, Univ of Luxembourg | 1 week/year

### **Review and editorial service**

- Since 2025 **Editorial board member**, Journal of Statistical Mechanics  
 Since 2016 **Reviewer for scientific journals and agencies** | ca 30 reviews/year  
 Journals | Commun Phys, Entropy, EPL, EPJE, J Chem Phys, J Phys A, J Stat Mech,  
 Nat Commun, Nat Phys, New J Phys, Phys Rev (E, Lett, Res, X), PNAS, Science,  
 Science Adv, Soft Matter  
 Agencies | ANR (France), DFG (Germany), DOE (USA), FRS-FNRS (Belgium), ISF (Israel)  
 2026 **Guest editor**, Physical Review E | Special topics: “Controlling stochastic dynamics across scales”  
 2026 **Guest editor**, New Journal of Physics | Special topics: “Statistical mechanics of active matter”

### **PhD committees**

- 2026 DPhyMS, Univ of Luxembourg (Student: A Kabylda, Supervisor: A Tkatchenko)  
 Univ of Barcelona (Student: Y Rouzaire, Supervisor: D Levis)  
 Tata Institute of Fundamental Research (Student: A Bansal, Supervisor: M Rao)  
 2025 DPhyMS, Univ of Luxembourg (Student: SGM Srinivas, Supervisor: M Esposito)  
 Univ of Mons (Student: G Palumbo, Supervisor: P Damman)  
 DPhyMS, Univ of Luxembourg (Student: M Puleva, Supervisor: A Tkatchenko)  
 DPhyMS, Univ of Luxembourg (Student: BN Radhakrishnan, Supervisor: TL Schmidt)  
 2024 Univ Grenoble Alpes (Student: L Guislain, Supervisor: E Bertin)  
 Univ Paris Cité (Student: A Dinelli, Supervisor: J Tailleur)  
 DPhyMS, Univ of Luxembourg (Student: N Carabba, Supervisor: A del Campo)  
 DPhyMS, Univ of Luxembourg (Student: L Dupays, Supervisor: A del Campo)  
 2023 Imperial College, London (Student: Z Zhang, Supervisor: G Pruessner)  
 2022 DPhyMS, Univ of Luxembourg (Student: D Forastiere, Supervisor: M Esposito)  
 DPhyMS, Univ of Luxembourg (Student: E Penocchio, Supervisor: M Esposito)  
 DPhyMS, Univ of Luxembourg (Student: V Vassilev Galindo, Supervisor: A Tkatchenko)  
 2021 Luxembourg Centre for Systems Biomedicine (Student: S Martina, Supervisor: A Skupin)  
 DPhyMS, Univ of Luxembourg (Student: J Ekström, Supervisor: TL Schmidt)

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### **Scientific production**

Main publications: Phys Rev Lett [40][35][34][32][7], Phys Rev X [36][25][18][17][9], Reviews [28][24][13]

[48] **Contraction waves in pulsating active liquids: From pacemaker to aster dynamics**

T Banerjee, T Desaleux, J Ranft, and ÉF, arXiv:2509.19024

[47] **Irreversibility in scalar active turbulence: The role of topological defects**

BN Radhakrishnan,\* F Serafin,\* TL Schmidt, and ÉF, arXiv:2507.06073

[46] **Control of active field theories at minimal dissipation**

A Soriani, E Tjhung, ÉF, and T Markovich, arXiv:2504.19285

[45] **Hydrodynamics of pulsating active liquids**

T Banerjee, T Desaleux, J Ranft, and ÉF, arXiv:2407.19955

- [44] **Entropy production rate in thermodynamically consistent flocks**  
T Agranov, RL Jack, ME Cates, and ÉF, New J Phys **27**, 104602 (2025)
- [43] **Quantifying dissipation in flocking dynamics: When tracking internal states matters**  
K Proesmans, G Falasco, A Tanaji Mohite, M Esposito, and ÉF, Phys Rev E **112**, 024103 (2025)
- [42] **Diffusive oscillators capture the pulsating states of deformable particles**  
A Manacorda and ÉF, Phys Rev E **111**, L053401 (2025)
- [41] **Species interconversion of deformable particles yields transient phase separation**  
Y Zhang, A Manacorda, and ÉF, New J Phys **27**, 043023 (2025)
- [40] **Biased ensembles of pulsating active matter**  
WD Piñeros and ÉF, Phys Rev Lett **134**, 038301 (2025) | Editors' suggestion
- [39] **Nonequilibrium thermodynamics of non-ideal reaction-diffusion systems: Implications for active self-organization**  
F Avanzini, T Aslyamov, ÉF, and M Esposito, J Chem Phys **161**, 174108 (2024)
- [38] **Controlling active matter: The need for thermodynamic consistency**  
ÉF, Europhys News **55**, 20 (2024)
- [37] **Thermodynamically consistent flocking: From discontinuous to continuous transitions**  
T Agranov, RL Jack, ME Cates, and ÉF, New J Phys **26**, 063006 (2024)
- [36] **Active matter under control: Insights from response theory**  
LK Davis, K Proesmans, and ÉF, Phys Rev X **14**, 011012 (2024) | Highlight in Physics 17, 20 (2024)
- [35] **Pulsating active matter**  
Y Zhang and ÉF, Phys Rev Lett **131**, 238302 (2023)
- [34] **Non-ideal reaction-diffusion systems: Multiple routes to instability**  
T Aslyamov, F Avanzini, ÉF, and M Esposito, Phys Rev Lett **131**, 138301 (2023)
- [33] **Towards a liquid-state theory for active matter**  
YI Li, R Garcia-Millan, ME Cates, and ÉF, EPL **142**, 57004 (2023)
- [32] **Thermodynamic control of activity patterns in cytoskeletal networks**  
A Lamtyugina, Y Qiu, ÉF, AR Dinner, and S Vaikuntanathan, Phys Rev Lett **129**, 128002 (2022)
- [31] **From predicting to learning dissipation from pair correlations of active liquids**  
G Rassolov, L Tociu, ÉF, and S Vaikuntanathan, J Chem Phys **157**, 054901 (2022)
- [30] **Mean-field theory for the structure of strongly interacting active liquids**  
L Tociu, G Rassolov, ÉF, and S Vaikuntanathan, J Chem Phys **157**, 014902 (2022)
- [29] **Power fluctuations in sheared amorphous materials: A minimal model**  
T Ekeh, ÉF, SM Fielding, and ME Cates, Phys Rev E **105**, L052601 (2022)
- [28] **Irreversibility and biased ensembles in active matter: Insights from stochastic thermodynamics**  
ÉF, RL Jack, and ME Cates, Annu Rev Condens Matter Phys **13**, 215 (2022)
- [27] **Stochastic hydrodynamics of complex fluids: Discretisation and entropy production**  
ME Cates, ÉF, C Nardini, T Markovich, and E Tjhung, Entropy **24**, 254 (2022) | Editor's choice
- [26] **Optimal power and efficiency of odd engines**  
ÉF and A Souslov, Phys Rev E **104**, L062602 (2021)
- [25] **Thermodynamics of active field theories: Energetic cost of coupling to reservoirs**  
T Markovich, ÉF, E Tjhung, and ME Cates, Phys Rev X **11**, 021057 (2021)
- [24] **Active engines: Thermodynamics moves forward**  
ÉF and ME Cates, EPL **134**, 10003 (2021)
- [23] **Statistical mechanics of active Ornstein-Uhlenbeck particles**  
D Martin, J O'Byrne, ME Cates, ÉF, C Nardini, J Tailleur, and F van Wijland, Phys Rev E **103**, 032607 (2021)

- [22] **Collective motion in large deviations of active particles**  
Y-E Keta, ÉF, F van Wijland, ME Cates, and RL Jack, Phys Rev E **103**, 022603 (2021)
- [21] **Time-reversal symmetry violations and entropy production in field theories of polar active matter**  
ØL Borthne, ÉF, and ME Cates, New J Phys **22**, 123012 (2020)
- [20] **Thermodynamic cycles with active matter**  
T Ekeh, ME Cates, and ÉF, Phys Rev E **102**, 010101(R) (2020)
- [19] **Dissipation controls transport and phase transitions in active fluids: Mobility, diffusion and biased ensembles**  
ÉF, T Nemoto, and S Vaikuntanathan, New J Phys **22**, 013052 (2020)
- [18] **Autonomous engines driven by active matter: Energetics and design principles**  
P Pietzonka, ÉF, C Lohrmann, ME Cates, and U Seifert, Phys Rev X **9**, 041032 (2019)
- [17] **How dissipation constrains fluctuations in nonequilibrium liquids: Diffusion, structure and biased interactions**  
L Tociu, ÉF, T Nemoto, and S Vaikuntanathan, Phys Rev X **9**, 041026 (2019)
- [16] **Driven probe under harmonic confinement in a colloidal bath**  
V Démery and ÉF, J Stat Mech **2019**, 033202 (2019)
- [15] **Optimizing active work: Dynamical phase transitions, collective motion and jamming**  
T Nemoto, ÉF, ME Cates, RL Jack, and J Tailleur, Phys Rev E **99**, 022605 (2019)
- [14] **Non-Gaussian noise without memory in active matter**  
ÉF, H Hayakawa, J Tailleur, and F van Wijland, Phys Rev E **98**, 062610 (2018)
- [13] **The statistical physics of active matter: From self-catalytic colloids to living cells**  
ÉF and MC Marchetti, Physica A **504**, 106 (2018)
- [12] **Extracting maximum power from active colloidal heat engines**  
D Martin, C Nardini, ME Cates, and ÉF, EPL **121**, 60005 (2018) | Editor's choice
- [11] **Active mechanics reveal molecular-scale force kinetics in living oocytes**  
WW Ahmed,\* ÉF,\* M Almonacid,\* M Bussonnier, NS Gov, M-H Verlhac, P Visco, F van Wijland, and T Betz, Biophys J **114**, 1667 (2018)
- [10] **Spatial fluctuations at vertices of epithelial layers: Quantification of regulation by Rho pathway**  
ÉF,\* V Mehandia,\* J Comelles, R Thiagarajan, NS Gov, P Visco, F van Wijland, D Riveline Biophys J **114**, 939 (2018)
- [9] **Entropy production in field theories without time-reversal symmetry: Quantifying the non-equilibrium character of active matter**  
C Nardini, ÉF, E Tjhung, F van Wijland, J Tailleur, and ME Cates, Phys Rev X **7**, 021007 (2017)
- [8] **Nonequilibrium dissipation in living oocytes**  
ÉF,\* WW Ahmed,\* M Almonacid,\* M Bussonnier, NS Gov, M-H Verlhac, T Betz, P Visco, and F van Wijland, EPL **116**, 30008 (2016)
- [7] **How far from equilibrium is active matter?**  
ÉF, C Nardini, ME Cates, J Tailleur, P Visco, and F van Wijland, Phys Rev Lett **117**, 038103 (2016)  
Editor's suggestion | Highlight in Physics 9, s76 (2016)
- [6] **Active cage model of glassy dynamics**  
ÉF, H Hayakawa, P Visco, and F van Wijland, Phys Rev E **94**, 012610 (2016)
- [5] **Modeling the dynamics of a tracer particle in an elastic active gel**  
E Ben Isaac, ÉF, P Visco, F van Wijland, and NS Gov, Phys Rev E **92**, 012716 (2015)
- [4] **Active cell mechanics: Measurement and theory,**  
WW Ahmed, ÉF, and T Betz, Biochimica et Biophysica Acta - Mol Cell Res **1853**, 3083 (2015)

- [3] **Activity-driven fluctuations in living cells**  
ÉF,\* M Guo,\* NS Gov, P Visco, DA Weitz, and F van Wijland, EPL **110**, 48005 (2015)  
Editor's choice | Highlight in Europhysics News 46/5 (2015)
- [2] **Generalized Langevin equation with hydrodynamic backflow: Equilibrium properties**  
ÉF, DS Grebenkov, P Visco, and F van Wijland, Physica A **422**, 107 (2015)
- [1] **Energetics of active fluctuations in living cells**  
ÉF, K Kanazawa, H Hayakawa, P Visco, and F van Wijland, Phys Rev E **90**, 042724 (2014)

\* Equal contribution of these authors to this work