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Overview

Professional profile and research vision

I am a mathematical evolutionary biologist. I develop general mathematical theory that treats development and evolution together (evo-devo dynamics). I am building simulation-based inference tools that combine this theory with data to identify the causes of taxon-specific traits, starting with human brain size, and that others can apply to their own study organisms. The theory also predicts the effects of developmental interventions. Two questions drive my research: how development and evolution interact, and why the human brain size evolved.

Core methodological expertise

- **Evolutionary methods:** evolutionary-developmental (evo-devo) dynamics, population genetics, quantitative genetics, adaptive dynamics, and social evolution.
- **Mathematical toolkit:** deterministic and stochastic dynamical systems (including ordinary and partial differential equations and Markov chains), constrained static and dynamic optimization (including optimal control and a gradient-ascent approach to dynamic optimization that I developed), matrix algebra and calculus, mathematical statistics, and sensitivity analysis.
- **Statistical inference:** parameter estimation by grid search; simulation-based inference, approximate Bayesian computation, and Bayesian model selection (in development).
- **Programming languages:** Julia, Mathematica, MATLAB, and R.

Key research contributions

- Evo-devo dynamics: I formulated a general mathematical framework that integrates development and evolution, including sexual reproduction and discrete genotypes, and showed that development shapes the outcome of adaptation and not only its transient trajectory (*Evolution* 2023; *Theoretical Population Biology* 2024; *Genetics*, in second revision).
- Sensitivity of recurrences and dynamic optimization: I derived general analytical sensitivity formulas for recurrence equations, which are analytical versions of backpropagation with wide applicability, and a gradient-ascent method for constrained dynamic optimization that gives Lagrange multipliers (costates) as total derivatives of the objective function. The method allows far more analytical treatment of my brain model than was possible with optimal control, and makes its numerical computation over 1000 times faster (*Theoretical Population Biology* 2024; *Nature Human Behaviour* 2024).
- Human brain evolution: I built a mechanistic model that recovers major patterns of human brain and body size development and evolution, including the timing of childhood, adolescence, and adulthood (*PLoS Computational Biology* 2017; *Nature* 2018). The model recovers the evolution of the brain and body sizes of seven hominin species and, with evo-devo dynamics, shows that

brain expansion could arise as a by-product of selection for reproductive traits (*Nature Human Behaviour* 2024). I also derived a formula that mechanistically relates adult brain size to adult cognitive ability (*PLoS Computational Biology* 2017).

- Social evolution: I showed mathematically how ancestral manipulation can lead to the evolution of voluntary altruism and eusociality (*American Naturalist* 2013; *Evolution* 2014; *Proceedings of the Royal Society B* 2021).
- Applications: I used the sensitivity formulas to predict how health interventions change healthy life expectancy (*Demography*, in second revision) and to quantify mechanistically the contribution of genes, environment, and development to trait differences between individuals (*Evolutionary Human Sciences*, in second revision).

Academic appointments

2025–2028 **Senior Postdoctoral Fellow**
Konrad Lorenz Institute for Evolution and Cognition Research, Klosterneuburg, Austria.
Focus: advancing a mathematical framework integrating development and evolution.

2018–2024 **Research Fellow**
Supervisor: Andy Gardner.
University of St Andrews, UK.
Focus: mathematical modeling of the evolutionary and developmental (evo-devo) dynamics of the human brain size.

2016–2018 **Marie Skłodowska-Curie Individual Fellow**
Supervisor: Andy Gardner.
University of St Andrews, UK.
Focus: mathematical modeling of human brain size evolution under social interactions.

2013–2016 **Postdoctoral researcher**
Supervisor: Laurent Lehmann.
University of Lausanne, Switzerland.
Focus: mathematical modeling of human brain size evolution without social interactions.

2010–2012 **Graduate research associate**
Funded by the National Institute of Mathematical and Biological Synthesis (NIMBioS).
University of Tennessee, Knoxville, USA.
Focus: mathematical modeling of the evolution of eusociality via maternal manipulation.

Education

2007–2013 **PhD in Ecology and Evolutionary Biology**
University of Tennessee, Knoxville, USA.
Thesis: Evolution of acquiescence to manipulation.
Advisor: Sergey Gavrilets.
Postgraduate coursework taken in the Departments of Mathematics and Statistics:

Mathematical ecology I–II, Mathematical evolutionary theory, Stochastic modeling (Markov chains), and Statistical inference I–II.

1999–2006 **BSc in Biology (and the equivalent of a minor in Mathematics)**
University of Antioquia, Medellín, Colombia.
Thesis: Species: a mathematical formalization.
Undergraduate coursework taken in the Mathematics and Physics majors:
Calculus I–III, Linear algebra, Multilinear algebra, Ordinary differential equations, Vectorial geometry, Mathematical logic, Set theory, and Physics I.

Research

Peer-reviewed publications

González-Forero M, Gómez-Robles A. (2025) Why did the human brain size evolve? A way forward. *Philosophical Transactions of the Royal Society B* 380, 20240114. Open access. https://doi.org/10.1098/rstb.2024.0114.

González-Forero M. (2024) Evolutionary-developmental (evo-devo) dynamics of hominin brain size. *Nature Human Behaviour* 8, 1321–1333. Open access. https://doi.org/10.1038/s41562-024-01887-8.

González-Forero M. (2024) A mathematical framework for evo-devo dynamics. *Theoretical Population Biology* 155, 24–50. Open access. https://doi.org/10.1016/j.tpb.2023.11.003.

González-Forero M. (2023) How development affects evolution. *Evolution* 77, 562–579. Open access. https://doi.org/10.1093/evolut/qpac003.

González-Forero M, Peña J. (2021) Eusociality through conflict dissolution. *Proceedings of the Royal Society B* 288, 20210386. Open access. https://doi.org/10.1098/rspb.2021.0386.

González-Forero M, Gardner A. (2018) Inference of ecological and social drivers of human brain-size evolution. *Nature* 557, 554–557. https://doi.org/10.1038/s41586-018-0127-x. Accessible PDF.

González-Forero M, Faulwasser T, Lehmann L. (2017) A model for brain life history evolution. *PLoS Computational Biology* 13, e1005380. Open access. https://doi.org/10.1371/journal.pcbi.1005380.

González-Forero M. (2015) Stable eusociality via maternal manipulation when resistance is costless. *Journal of Evolutionary Biology* 28, 2208–2223. https://doi.org/10.1111/jeb.12744. Accessible PDF.

González-Forero M. (2014) An evolutionary resolution of manipulation conflict. *Evolution* 68, 2038–2051. https://doi.org/10.1111/evo.12420. Accessible PDF.

González-Forero M, Gavrilets S. (2013) Evolution of manipulated behavior. *American Naturalist* 182, 439–451. https://doi.org/10.1086/671932. Accessible PDF.

González-Forero M. (2009) Removing ambiguity from the biological species concept. *Journal of Theoretical Biology* 256, 76–80. https://doi.org/10.1016/j.jtbi.2008.09.016. Accessible PDF.

Preprints

González-Forero M. A mathematical synthesis of genetics, development, and evolution. In second revision at *Genetics*. Preprint: https://doi.org/10.64898/2026.02.25.707927.

González-Forero M, Gómez-Robles A. Mechanistic quantification of the effects of genes, environment, and development on human behaviour. In second revision at *Evolutionary Human Sciences*. Preprint: https://doi.org/10.1101/2025.03.17.643651.

Riffe T, Villavicencio F, **González-Forero M**. Sensitivity and decomposition of multistate healthy life expectancy. In second revision at *Demography*. Preprint: https://dx.doi.org/10.4054/MPIDR-WP-2024-014.

Non-peer-reviewed publications

González-Forero M. (2026) Invited chapters "From nerve cells to comprehension" and "Growing brains." In Roberts A. (Ed.) *Humans: The Evolution of a Species*. Dorling Kindersley (DK), a popular science book that includes an illustrated rendering of a figure from my *Nature Human Behaviour* paper. https://geni.us/Humans-DK.

Edelaar P, Dingemanse NJ, Patrick SC, Réale D, Wilson AJ, Baud A, Bolnick D, Bonte D, Costa Pereira R, Day T, Fogarty L, Frankenhuis W, **González-Forero M**, Kaiser MI, Martin JGA, Matthiopoulos J, Reinhold K, Schielzeth H, Wittmann MJ, Wright J, Dammhahn M. (2026) Towards a better understanding of adaptation: Problem description, partial solutions, and recommendations. Position paper arising from the Volkswagen Foundation scoping workshop. Preprint: https://doi.org/10.32942/X2108Z.

González-Forero M. (2018) Two articles about my *Nature* paper: The human brain from ecology and seemingly culture, a Behind the Paper blog post at *Nature Ecology & Evolution Community*; and Why do humans have such large brains? Our study suggests ecology was the driving force, in *The Conversation*.

Research grants, awards, and honors

2025–2028 **Independent Senior Postdoctoral Fellowship, Konrad Lorenz Institute**
Project title: Advancing a mathematical theory integrating development and evolution.
Independent fellowship without a PI: I manage my own research. Awarded by the Konrad Lorenz Institute for Evolution and Cognition Research, Austria.

2016–2018 **Marie Skłodowska-Curie Individual Fellowship**
Amount: €195,455. Hosted at the University of St Andrews, UK.
Project title: Brain growth under social pressure: mathematical modeling of brain growth when individuals face social challenges.
Awarded by the European Commission.

2010–2012 **Graduate Research Assistantship**
Project title: Evolution of eusociality mediated by maternal induction.
Awarded by the US National Institute for Mathematical and Biological Synthesis, NIMBioS.

2009 **Santa Fe Institute Complex Systems Summer School** (US$550). Awarded by the Santa Fe Institute, Santa Fe, NM, USA.

2006 **Undergraduate thesis award** for the thesis "Species: a mathematical formalization." Awarded by the Faculty of Natural and Exact Sciences, University of Antioquia, Colombia.

2005 **Third place in the National Biology Exam (ECAES)**, taken by all undergraduates in Colombia. Awarded by the Ministry of Education, Colombia.

Consultancy

2023–2025 **Consultancy for Tim Riffe, Ikerbasque and University of the Basque Country**
Paid from his project "Multistate healthy life expectancy decomposition (MultiLED)," funded by the la Caixa Foundation.
Sensitivity of human life expectancy to perturbation: I applied my sensitivity formulas to derive analytical sensitivity and decomposition results, leading to Riffe, Villavicencio & González-Forero (*Demography*, in second revision).

Invited talks

2026 Edinburgh Alliance for Complex Trait Genetics (e-ACTG), Genetics Society special interest group meeting, Edinburgh, UK (scheduled for November 27, 2026).
45th Altenberg Workshop in Theoretical Biology "The Developmental Origins of Evolvability," Konrad Lorenz Institute for Evolution and Cognition Research, Austria. https://www.kli.ac.at/en/events/kli_workshops/view/744

2025 Willem Frankenhuis lab meeting, University of Amsterdam, the Netherlands (online).

2024 Symposium "Connecting Macro and Micro Evolution of Form and Function Relationships," Evolution Conference, Montreal, Canada (online).
Royal Society meeting "Natural Selection Shapes Animal Cognition," Bath, UK, organized by Elli Leadbeater and Alex Thornton.

2023 Institute Seminar, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.
Applied Mathematics Seminar series, School of Mathematics & Statistics, University of St Andrews, UK.

2020 Institute for Advanced Study, Toulouse, France (online).

2016 Centre for Biological Diversity, School of Biology, University of St Andrews, UK.

2015 Department of Theoretical Biology, Max Planck Institute for Evolutionary Biology, Plön, Germany.

Self-initiated talks and lab meetings

2026 Department of Biology, Lund University, Sweden.
Department of Zoology, Stockholm University, Sweden.

2025 Modeller's Seminar, The Francis Crick Institute, London, UK.
Department of Anthropology, University College London, UK.
Nick Barton lab meeting, Institute of Science and Technology Austria (ISTA).

2024 School of Psychology & Neuroscience, University of St Andrews, UK.

2023 Roberto Salguero-Gómez lab meeting, Department of Biology, University of Oxford, UK (online).

2019 Evolutionary Anthropology Research Group, Department of Anthropology, Durham University, UK.
Applied Mathematics Seminar series, School of Mathematics & Statistics, University of St Andrews, UK.

2018 Stochastic Models for the Inference of Life Evolution group, Collège de France, Paris.

2017 Department of Zoology, University of Cambridge, UK.

Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.

Other invitations

2025 Invited to the Volkswagen Foundation Scoping Workshop "Building a framework to integrate diverse routes to adaptation in a changing world," organized by Melanie Dammhahn and colleagues, Hannover, Germany.

2024 Invited paper for the special issue of *Philosophical Transactions of the Royal Society B* "Natural Selection Shapes Animal Cognition", following the Royal Society meeting.

Organized workshops and symposia

2026 Co-organizer, with Tom Van Dooren, of the symposium "Advances in theoretical evo-devo". Conference of the European Society for Evolutionary Developmental Biology (Euro Evo Devo), Glasgow, UK, June 9–12, 2026. I also helped evaluate the best student posters at the conference.

2020 Co-organizer, with Reyes Sanles-Falagan, of a fellowship writing workshop for early-career researchers of the School of Biology, University of St Andrews, UK. Ten speakers from the University presented tips to 26 participants, and a video recording was made available online. The workshop was highlighted on page 55 of the School's Athena SWAN Gold application, which was awarded in 2021, with participant feedback such as "This has been the most useful type of ECR event I have ever been to!"

2019 Co-organizer, with Piret Avila, of the symposium "Life history evolution: bridging theory and data". Congress of the European Society for Evolutionary Biology (ESEB2019), Turku, Finland.

Contributed conference presentations

22 talks and 6 posters.

2026 Talk and poster, Conference of the European Society for Evolutionary Developmental Biology (Euro Evo Devo), Glasgow, UK.

Talk, Mathematical Models in Ecology and Evolution conference, Cork, Ireland.

2025 Talk and poster, European Society for Evolutionary Biology conference, Barcelona, Spain.

Talk, EvolVienna meeting, Vienna, Austria.

2024 Talk, Conference of the Australasian Society for Human Biology (online).

2022 Talk, Mathematical Models in Ecology and Evolution conference, Reading, UK.

Talk, Euro Evo Devo, Naples, Italy.

Talk, Population Genetics Group (online).

2021 Talk, Evolution conference (online).

2019 Talk, Mathematical Models in Ecology and Evolution conference, Lyon, France.

Talk, European Human Behaviour and Evolution Association conference, Toulouse, France.

2018 Talk, Models in Population Dynamics, Ecology, and Evolution conference, Leicester, UK.

2017 Talk, European Human Behaviour and Evolution Association conference, Paris, France.

2016 Talk, Institute of Behavioural and Neural Sciences mini symposium, St Andrews, UK.

Talk, European section of the International Union for the Study of Social Insects conference, Helsinki, Finland.

Talk, Swiss Biology '16 conference, Lausanne, Switzerland.

2015 Two posters, European Society for Evolutionary Biology conference, Lausanne, Switzerland.
Talk, Mathematical Models in Ecology and Evolution conference, Paris, France.
Poster, 3rd Economics and Biology Workshop of the Institute for Advanced Study, Toulouse, France.

2012 Talk, Society for Mathematical Biology conference, Knoxville, TN, USA.
Talk, Evolution conference, Ottawa, Canada.

2011 Talk, Evolution conference, Norman, OK, USA.

2010 Talk, Biocomplexity[XI] conference: The evolution of cooperation, Bloomington, IN, USA.

2007 Talk, South Eastern Population Ecology and Evolutionary Genetics meeting, Tremont, TN, USA.

2005 Poster, European Conference on Mathematical and Theoretical Biology, Dresden, Germany.

Teaching and mentoring

Teaching experience

2027 **Co-instructor** (planned)
Pre-conference workshop on multistate models and decomposition methods, with Tim Riffe and others, 38th REVES Conference, May 18, 2027.
Conference organized by the University of the Basque Country, Bilbao, Spain.

2018–2020, 2023 **Guest lecturer**
Designed and gave 1 lecture on Brain evolution: comparative neuroanatomy and controversies (third-year Evolution course, 2023).
Gave 3 lectures on social evolution (Price equation, kin selection, and group selection; third-year Evolution course, 2019).
Also contributed essay topics, advised on essay writing, and graded essays in Evolutionary biology (second-year; Fall 2018, 2019, 2023) and Evolution (third-year; Fall 2019, 2020).
In Fall 2020, posed an essay question, gave feedback on the first drafts of the 7 students who chose it, and graded their final essays.
University of St Andrews, UK.

2022 **Training in inclusive practice**
Active Bystander Training (90-minute online session with case studies on how to respond to discriminatory behavior in academic settings), December 1, 2022.
Organized by the Biology Equality and Diversity Committee, University of St Andrews, UK.

2013–2016 **Teaching assistant**
Contributed a project to the Experimental design course (2014), graded MSc projects (2015, 2016), and contributed to Population genetics exercise sections (2015, 2016).
University of Lausanne, Switzerland.

2010 **In charge of a full course**
Instructor of record, Spring 2010. Designed the syllabus, lectures, homework, and exams, graded all work, and held office hours for the semester-long course.
Module: Mathematics for life sciences. 17 students completed the evaluation (teaching effectiveness 4.1, amount learned 4.5 out of 5).
University of Tennessee, Knoxville, USA.

2009 **Teaching training**
Graduate seminar on teaching college mathematics (1 credit hour), Fall 2009. University of Tennessee, Knoxville, USA.

2007–2009 **Graduate teaching assistant**
Teaching assistant for laboratory sections of introductory Biology and Genetics (2007–2009) and exercise sections of Mathematics for life sciences (Fall 2009). University of Tennessee, Knoxville, USA.

Mentoring

2018–2020 **Informal mentoring** of PhD students and a postdoc at the School of Biology, University of St Andrews, confirmed in a letter from Andy Gardner: contributed LaTeX code, discussed Mathematica coding, and described mathematical modeling techniques. Acknowledged for comments and discussion in four papers by these group members (2019–2022).

2015–2016 **Informal mentoring** of a postdoc at the University of Lausanne on optimal control theory and the GPOPS software, and feedback on her manuscript at various stages, acknowledged in the resulting paper (*Evolution* 2019).

Service

Administrative experience

2022–2024 Postdoctoral representative of the School of Biology for the Institute of Behavioural and Neural Sciences (IBANS), University of St Andrews. Scored applications for IBANS-funded undergraduate research internships and helped coordinate the website and the student exchange programme with Emory University, including co-hosting a visiting Emory faculty member.

2019–2021 Postdoctoral representative for the Biology Equality and Diversity Committee, School of Biology, University of St Andrews. Provided documentation and organizational support for equity and career-development initiatives that fed into the School's Athena SWAN Gold application, most substantially by co-organizing the fellowship writing workshop described above.

Journals reviewed for

Peer reviewer for 20 journals (some reviews are listed in my ORCID record): *American Naturalist, Biological Reviews, Biological Theory, Bulletin of Mathematical Biology, eLife, Evolution, Evolution Letters, Genetics, iScience, Journal of Evolutionary Biology, Journal of Theoretical Biology, Journal of Zoology, Nature, Nature Communications, Nature Ecology & Evolution, PLOS ONE, PNAS Nexus, Proceedings of the Royal Society B, Science Advances, Theoretical Population Biology*.

Grants reviewed for

Research Foundation – Flanders (FWO), Belgium: postdoctoral fellowship application.

Outreach and training

Selected media coverage

2024 *Helsingin Sanomat* (Finland). "Isot aivomme voivat olla sivutuote – kaiken takana olikin munarakkula" (Our big brains can be a by-product – there was a follicle behind it all). https://www.hs.fi/tiede/art-2000010573820.html.

PNAS journal club. Model of how humans got their big brains stirs interest and controversy. https://www.pnas.org/post/journal-club/model-humans-got-their-big-brains-stirs-interest-and-controversy.

Also covered by Phys.org and ScienceAlert.

2023 IFLScience. We may finally know why humans have such big brains (on the preprint of the *Nature Human Behaviour* paper). https://www.iflscience.com/we-may-finally-know-why-humans-have-such-big-brains-70453.

2021 *Illustreret Videnskab* (Denmark, August). "Vores hjerner nærmer sig abernes igen" (Our brains approach the apes' again), in the feature "4 millioner år lang skilsmisse" (A 4-million-year-long split). Print feature.

2019 *Discover Magazine* (USA). State of Science: Finding Human Ancestors in New Places. https://www.discovermagazine.com/planet-earth/state-of-science-finding-human-ancestors-in-new-places.

2018 *Associated Press* (USA). Study offers new look at why our brains evolved to be so big. https://apnews.com/article/7fe4e81cbb114ee2adf42c6e49f19b45.

LA Times (USA). Can simulating evolution on a computer explain our enormous brains? https://www.latimes.com/science/sciencenow/la-sci-sn-human-brain-evolution-20180523-story.html.

Vox (USA). Why do humans have such huge brains? https://www.vox.com/science-and-health/2018/5/23/17377200/human-brain-size-evolution-nature.

New Scientist (UK). We may have got the evolution of our big brains entirely wrong. https://www.newscientist.com/article/2169862-we-may-have-got-the-evolution-of-our-big-brains-entirely-wrong/.

Dagens Nyheter (Sweden, May 27). "Vår stora hjärna gav oss mat – komplicerade samhällen fick vi på köpet" (Our big brain gave us food – complex societies came as a bonus). Print feature.

The National (Scotland, May 24). Tough times drove brain growth, say biologists. Print feature.

Weekendavisen (Denmark, June 1). "Vores svulmende investering" (Our swelling investment). Print feature.

TBS eFM Radio, This Morning program (Korea). Radio interview. https://cdn.podbbang.com/data1/tbsadm/thism180529002.mp3.

Also interviewed by AFP (France) and *La Vanguardia* (Spain).

2017 *PBS NewsHour* (USA). Why did humans evolve big brains? We don't know, but math can help. Interview. https://www.pbs.org/newshour/science/humans-evolve-big-brains-dont-know-math-can-help.

Also covered by ScienceDaily, EOS Wetenschap, and ANSA.

2013 *Der Standard* (Austria). Manipulation könnte Wurzel für selbstloses Verhalten sein. http://derstandard.at/1376533943228/Manipulation-koennte-Wurzel-fuer-selbstloses-Verhalten-sein.

Attended workshops and summer schools

2017 Two workshops, Mean field games and Numerical methods for optimal control problems, Sapienza University, Rome, Italy.

2015 Workshop, 3rd Economics and Biology Workshop, Institute for Advanced Study, Toulouse, France.

2014 Workshop, Social evolution: merits and limitations of inclusive fitness theory, Arolla, Switzerland.

2010–2012 Working group, Large-scale demographic, network, and behavioral trait analyses of sociality, four meetings at the National Evolutionary Synthesis Center, Durham, NC, USA.

2009 Summer program, Mathematical Biosciences Institute Summer Graduate Program, Columbus, OH, USA.

Summer school, Complex Systems Summer School, Santa Fe Institute, Santa Fe, NM, USA.

2004 Workshop, Bases in Studies of Entomologic Diversity in Ibero-America, Quito and Yasuní National Park (Amazon rainforest), Ecuador.

Additional funding: travel and small grants

2015 €500 from the Institute for Advanced Study, Toulouse, to attend its 3rd Economics and Biology Workshop.

2012 US$1,000 from NIMBioS and US$350 from the Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, to attend the Evolution conference in Ottawa, Canada.

2011 US$500 from NIMBioS, US$200 from the Graduate Researchers in Ecology, Behavior and Evolution of UTK, and US$200 from the Department of Ecology and Evolutionary Biology to attend the Evolution conference in Norman, OK, USA.

2010 US$400 from the workshop committee and US$500 from NIMBioS to attend Biocomplexity[XI]; US$650 from NIMBioS to visit Gro Amdam and James Hunt at Arizona State University.

2009 US$400 of travel support and a US$300 stipend from the Mathematical Biosciences Institute to attend its Summer Graduate Program.

2005 About US$30 from the Research Development Committee (CODI), University of Antioquia, as an undergraduate thesis improvement grant.

2004 US$1,040 from the Society for Mathematical Biology and €950 from the European Society of Mathematical and Theoretical Biology to attend the European Conference on Mathematical and Theoretical Biology and the Society for Mathematical Biology conference in Dresden, Germany.