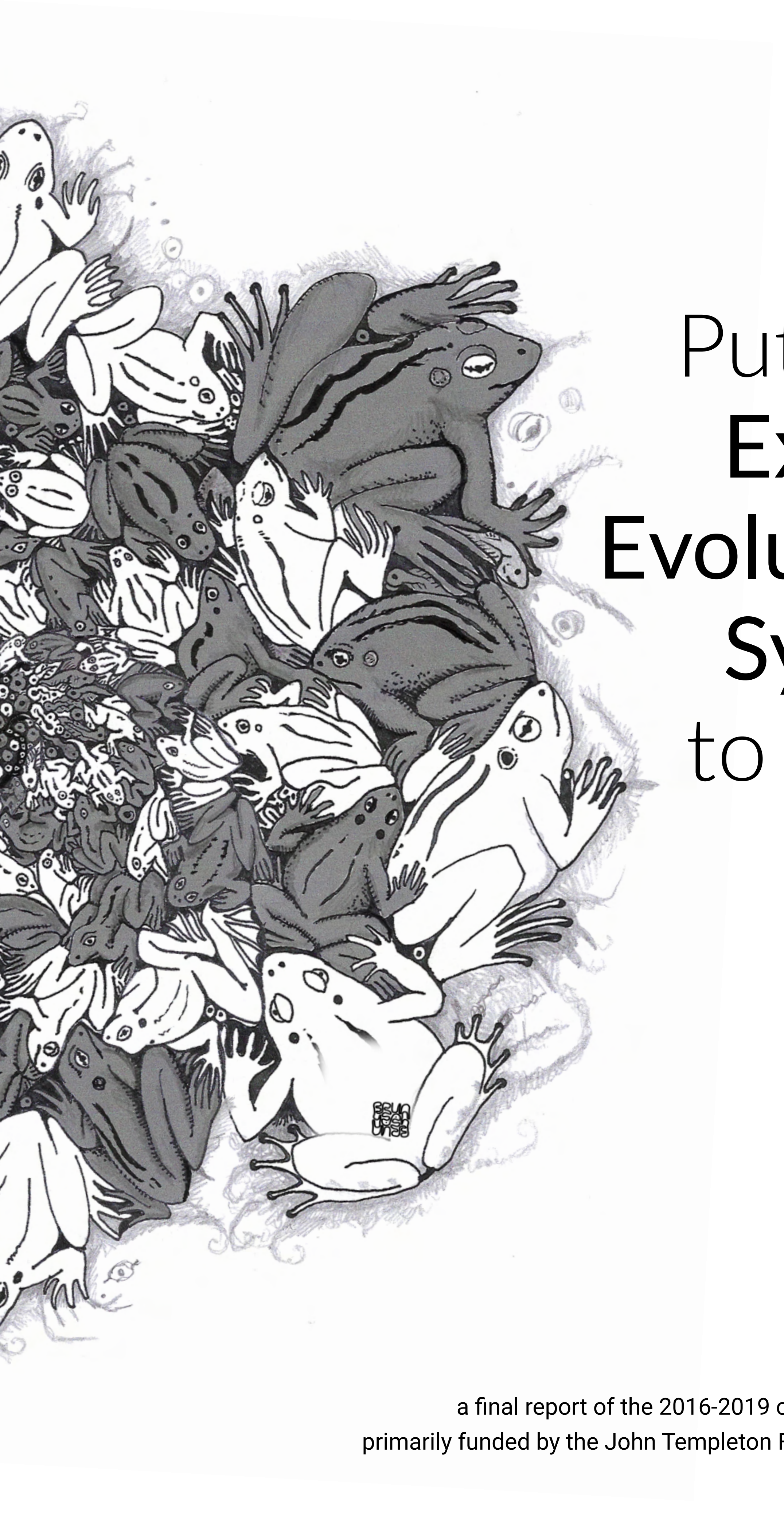

# Putting the **Extended Evolutionary Synthesis** to the Test

a final report of the 2016-2019 consortium
primarily funded by the John Templeton Foundation

Extended Evolutionary Synthesis

Between September 2016 and May 2019, a consortium of 92 researchers, led by 29 experts at 8 top academic institutions, put a novel evolutionary perspective called the Extended Evolutionary Synthesis (EES) to the test through a coordinated program of empirical and theoretical work.

The EES represents a new way of thinking about evolution, with its own assumptions, structure and predictions. This document is a summary of the main hypotheses, results and activities of the project, and of the team that participated.

## Project leaders

**Kevin Laland**

University of St. Andrews

**Tobias Uller**

Lund University

2021. Report by Lynn Chiu,
Text by Kevin Laland

Extended Evolutionary Synthesis

John Templeton Foundation

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Clark University
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Stanford University

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# Overview

# EES at a glance

The extended evolutionary synthesis is a new way to think about and understand evolutionary phenomena. It differs from the conception that has dominated evolutionary thinking since the 1930s (i.e., the modern synthesis) by focusing on the evolutionary significance of developmental causes.

*constructed development*

*reciprocal causation*

Two central, unifying concepts lie at the heart of the EES perspective: constructed development and reciprocal causation. The EES recognizes that development is a process of active self-organization, with organisms interacting reciprocally with their internal and external environments.

Our research program tested twelve key hypotheses, each of which made a novel prediction about evolutionary processes and outcomes.

12 **hypotheses put to the test**

These predictions were tested in 22 separate research projects, organized into four main areas of inquiry: historical and philosophical foundations (2 projects), evolutionary innovation (6 projects), inclusive inheritance (5 projects), and evolutionary diversification (9 projects).

4 **areas of inquiry**

Conceptual foundations
Evolutionary innovation
Inclusive inheritance
Evolutionary diversification

The 22 projects explored the evolutionary significance of niche construction, developmental bias, developmental plasticity, and multiple channels of inheritance.

# 2016-2019

A total of 92 researchers conducted foundational research into evolutionary biology, combining conceptual analyses, empirical and theoretical approaches.

92 **29 investigators**
**43 students and staff**
**20 affiliated researchers** in 8 institutes

**1** conference
**3** workshops
**260+** talks

We organized a major international conference "Evolution Evolving" and three workshops (on *Causes and Processes in Evolution, Inclusive Inheritance, and Developmental Bias*). The team put together an edited book (*Evolutionary Causation*, MIT Press) and a special issue in the journal *Evolution and Development*.

More than 200 papers have been published under the project, and more than 260 talks were given by consortium members, over a three-year period.

**1** edited book
**1** special issue
**200+** publications

2 **social media platforms**
+ 2 **resource websites**

Extensive outreach and engagement activities include prominent public lectures (e.g. Royal Institution), popular science articles (e.g. Scientific American) and podcasts, 80+ online articles (blogs), and two major new resource websites that capture developments in the EES and niche construction theory, communicated through an active social media presence.

EES website: extendedevolutionarysynthesis.com
Niche construction website: nicheconstruction.com
Twitter: @EES_Update Facebook: EES Update

# EES predictions

The project put to the test 12 novel predictions about evolution, contrasting each with a more traditional expectation. These predictions have been simplified below. For a more precise description of EES predictions, see Laland KN, Uller T, Feldman MW, Sterelny K, Müller GB, et al. 2015. Proc. R. Soc. B. 282(1813):20151019 .

| | Traditional expectation | EES prediction |
|---|---|---|
| **What comes first?** | | |
| i | Genetic change causes, and logically precedes, phenotypic change in adaptive evolution | Phenotypic change can precede, rather than follow, genetic change, in adaptive evolution |
| **Generation of variation** | | |
| ii | Genetic mutations, and hence novel phenotypes, will be random in direction and typically neutral or slightly disadvantageous | Novel phenotypic variants will frequently be directional and functional |
| iii | Mutations generating novel phenotypes will occur in a single individual | Novel phenotypic variants will frequently be environmentally induced in multiple individuals |
| **Evolutionary novelty** | | |
| iv | Adaptive evolution typically proceeds through selection of mutations with small effects | Strikingly different novel phenotypes can occur through mutation of a major regulatory control gene expressed in a tissue-specific manner, or through facilitated variation |
| **Repeated evolution** | | |
| v | Convergent selection is the main cause of repeated evolution in isolated populations | Developmental bias and convergent selection together cause repeated evolution in isolated populations |
| **Propagation of adaptive variants** | | |
| vi | Adaptive variants are propagated through selection | Adaptive variants are also propagated through repeated environmental induction, non-genetic inheritance, learning and cultural transmission |

# 4 areas of inquiry

Conceptual foundations
Evolutionary innovation
Inclusive inheritance
Evolutionary diversification

# 12 hypotheses put to the test

**Rapid phenotypic evolution**

| | | |
|---|---|---|
| vii | Rapid phenotypic evolution requires strong selection on abundant genetic variation | Rapid phenotypic evolution can also result from the simultaneous induction and selection of functional variants |

**What evolutionary causes explain taxonomic diversity?**

| | | |
|---|---|---|
| viii | Taxonomic diversity is explained by diversity in the selective environments | Taxonomic diversity will sometimes be better explained by features of developmental systems (evolvability, plasticity) than features of environments |

**Is heritable variation biased?**

| | | |
|---|---|---|
| ix | Heritable variation is unbiased | Heritable variation will be systematically biased, often towards variants that are adaptive and well-integrated |

**Are constructed environments special?**

| | | |
|---|---|---|
| x | Environments modified by organisms are not systematically different from other environments | Niche construction will systematically create environment factors well-suited to the constructor’s, or its descendants’ phenotype, and that enhance fitness |

**Niche construction explanations of parallel evolution**

| | | |
|---|---|---|
| xi | Parallel evolution is explained by similarity in environmental conditions | Parallel evolution may also be due to niche construction |

**The causes of ecosystem properties**

| | | |
|---|---|---|
| xii | Ecosystem stability, productivity and dynamics explained by competition and trophic interactions | Ecosystem stability, productivity and dynamics also dependent on niche construction and ecological inheritance |

# Putting the EES to the test

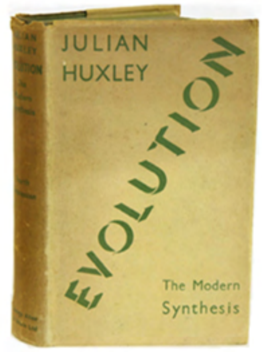
The twelve EES predictions, together with some key historical and philosophical issues, were investigated through 22 projects. Twenty of the projects were divided into three main empirical areas: **evolutionary innovations**, **inclusive inheritance**, and **evolutionary diversification**.

| *predictions* | Evolutionary innovations | Inclusive inheritance | Evolutionary diversification |
|---|---|---|---|
| *i* | 3, 4, 5, 7, 8 | 12 | 14, 15, 16, 17 |
| *ii* | 3, 4, 5, 8 | 12 | 14, 15 |
| *iii* | 3, 4, 5, 7, 8 | 12 | 14, 15, 16, 17 |
| *iv* | 4, 5, 8 | | 14, 16 |
| *v* | 4, 5, 7 | | 14, 15, 16 |
| *vi* | 3 | 9, 10, 12, 13 | |
| *vii* | 3 | 12 | 14, 15 |
| *viii* | | | 14, 15, 16, 17, 18, 19, 20, 21 |
| *ix* | 3, 4 | 9, 10, 12 | |
| *x* | | 13 | 18 |
| *xi* | | | 18 |
| *xii* | | | 20, 21, 22 |

# Projects

# A. Conceptual Issues

the EES in historical and philosophical focus




If the EES is to be tested, it is essential to understand how it relates to earlier approaches to evolution, and the nature of the conceptual change that it represents.

The question of whether evolutionary theory needs an extension turns on how scientists have characterized the field, and the sufficiency of traditional approaches.

As for all fields, theories and practices in evolutionary biology can constrain and direct research and the types of explanations offered. Philosophers and historians of biology were brought together with biologists to explore how the conceptual structures of evolutionary theory affected research.

## Research projects

| # | Project title | Principal investigators | link |
|---|---|---|---|
| ***1*** | EES in **historical** focus | *Lewens, Halina, Hopwood & Birch* | |
| ***2*** | EES in **philosophical** focus | *Lewens, Halina, Hopwood, Birch, Lachmann, Bateson, Clarke, Noble, Odling-Smee, Endler, Müller, Jablonka, Sterelny, Laland & Uller* | |

**How do the conceptual structures of evolutionary theory affect the way researchers ask and answer evolutionary questions?**

# Key findings

Our analyses revealed difficulties in giving any simplistic characterizations of "the Modern Synthesis (MS)," and demonstrated ways in which the MS has become a moving target[1]. There are multiple conceptual issues at stake in the EES debate, including different interpretations of scientific data, readings of history, and approaches to science[1-4] and scientific explanations[5], as well as alternative assumptions regarding the causal structure of evolution[3, 6].

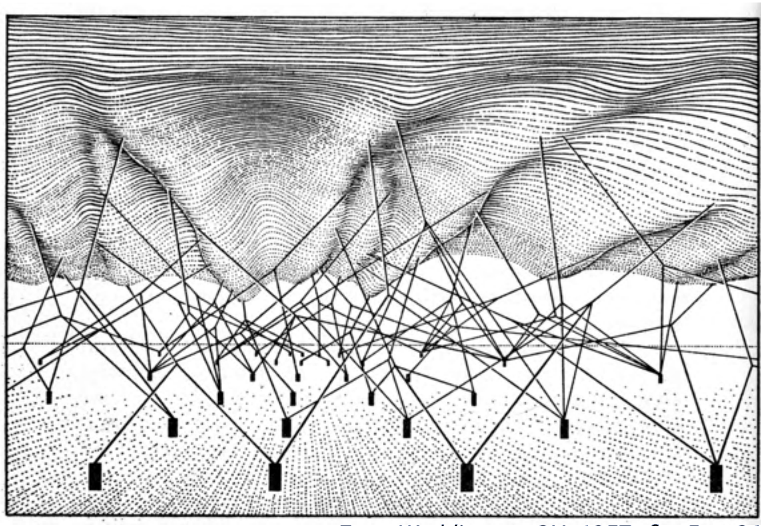
These differences explain why the debates have been hard to resolve[1]. We developed constructive suggestions for ways forward, especially with respect to niche construction and adaptation, and reciprocal causation.

## What is the modern synthesis?

## Why is the EES contentious?

## Why are the debates so hard to resolve?

## How can researchers move forward?



*From Waddington, CH. 1957, fig. 5, p. 36*


**References:**

**1.** Lewens. 2019. *Biol J Linn Soc*, 127:4, pp.707-721
**2.** Buskell. 2020. *Studies C*, 80:101244
**3.** Evolutionary Causation, eds Uller and Kaland. 2019. *MIT Press*
**4.** Philosophy of Science for Biologists, eds Kampourakis and Uller. 2020. *CUP*
**5.** Uller et al. 2020. *Evol Dev*, 22:1-2, pp. 47-55
**6.** Uller & Helanterä. 2019. *Brit J Philos Sci*. 70:351-375

# B. Evolutionary Innovations

How can proximate causes generate evolutionary innovations?

How does development contribute to evolutionary innovations? To answer this question, eight theoretical and experimental research projects investigated the evolutionary roles of **developmental plasticity** and **developmental bias**, as well as **major transitions** in evolutionary organization.

## Research projects

| # | Project title | Principal investigators | Predictions tested | link |
|---|---|---|---|---|
| **3** | How evolution learns from experience | *Watson, Wagner & Uller* | i, ii, iii, vi, vii, ix | 🔗 |
| **4** | Developmental bias and the origin of adaptive variation | *Uller, Cornwallis & Lundberg* | i, ii, iii, iv, v, ix | 🔗 |
| **5** | The role of developmental plasticity in innovation and diversification of Onthophagus beetles | *Moczek & Snell-Rood* | i, ii, iii, iv, v | 🔗 |
| **6** | Evolution and ontogeny of complex group adaptation | *Gardner* | | 🔗 |
| **7** | The origins of organismal complexity | *Cornwallis & Lundberg* | i, ii, iii | 🔗 |
| **8** | Plasticity and house building in social insects | *Ruxton* | i, ii, iii, iv | 🔗 |

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# Key findings

## Extensive evidence for plasticity-led evolution.

### What is plasticity-led evolution?

*Novel complex traits can arise through environmental induction, which initiates and directs adaptive genetic divergence along particular trajectories.*

## comparative analyses

Two major analyses of published findings found support for 'plasticity-led evolution,' showing that adaptive divergence commonly mirrors ancestral plasticity in natural populations of plants and animals[1,2]. The analyses imply that evolution will commonly, but not always[3], proceed through genetic changes that stabilize what are initially plastic responses.

## experimental studies

Experimental investigations in dung beetles found that their horns evolved from wing serial homologs[4], identified that the underlying mechanisms of nutrition-responsive development[5], and highlighted the role of genetic fixation of initially plastic responses in the evolution of morphology and behavior[6].

## computational modeling

Computational models were developed to explore how plasticity and developmental organization influence evolution and allow it to learn from experience. One study showed that evolution with these extensions is different from evolution without them (e.g., it can generate pre-adaptation to novel environments)[7]. A highly counterintuitive new finding is that adaptive plasticity can evolve when selected against[8]!


**References:**

**1.** Noble et al. 2019. *PNAS*, 116:27, pp. 13452-13461; **2.** Radersma et al. 2020. *Evol Lett*, 4:4, pp. 360-370; **3.** Feiner et al. 2020. *eLife*, 9:e57468; **4.** Hu et al. 2019. *Science*, 366:6468, pp. 1004-1007; **5.** Casasa et al. 2020. *Nat Ecol Evol*, 970–978; **6.** Linz et al. 2019. *Proc R Soc Lond B*, 286:1896, pp. 20182427; **7.** Kouvaris et al. 2017. *PLOS Comput Biol*, 13:4, pp. E1005358; **8.**Rago et al. 2019. *PLOS Comput Biol*, 15:3, pp. E1006260

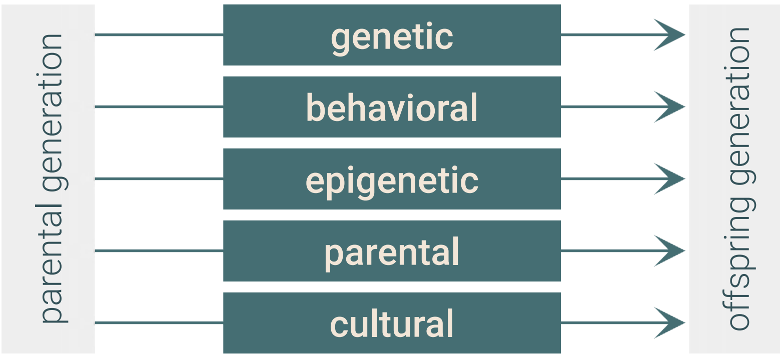

Beetle photo by Alex Wild.

# C. Inclusive Inheritance

What are the implications of extra-genetic inheritance?

In contrast to traditional perspectives, the EES stresses that diverse inheritance mechanisms play important evolutionary roles.

This includes genetic, behavioral, epigenetic, parental, and cultural pathways of transmission.




## Research projects

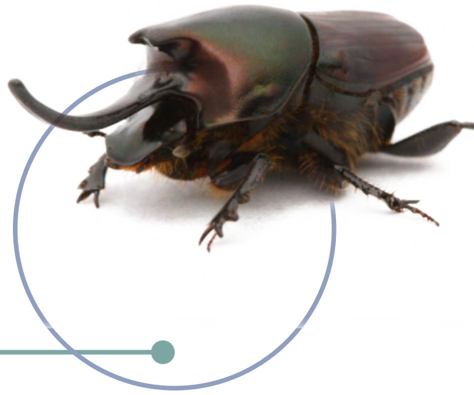
| # | Project title | Principal investigators | Predictions tested | link |
|---|---|---|---|---|
| **9** | The evolution of inclusive heredity through the genomic interactions of symbionts | *Wade & Moczek* | *vi, ix* | |
| **10** | Adaptation through genes without change to the genome: host adaptation via change in its microbiome composition | *Feldman* | *vi, ix* | |
| **11** | Evolution of extra-genetic inheritance: a life-cycle perspective | *Johnstone & Kuijper* | | |
| **12** | Extra-genetic inheritance and adaptation to novel environments | *Uller* | *i, ii, iii, vi, vii, ix* | |
| **13** | Adaptation through niche construction and microbiome function in *Onthophagus* beetles | *Moczek* | *vi, x* | |


Image: Christiaan Conradie and Caroline Schuppli

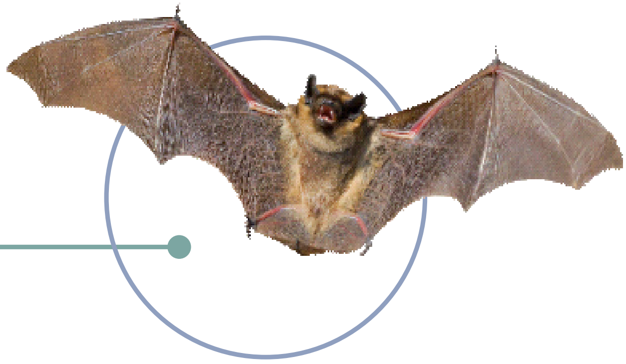

Image: Robert Pitman

# Key findings

## Experimental studies showed that the microbiome, a key feature of development partly inherited from the mother, is important in evolution.



Investigations of dung beetles showed that the inherited microbiome is critical for beetle growth, digestion and sexual dimorphism, and that host species diverge in their reliance on microbiota, suggesting host-microbiome co-diversification[1-3].



An analysis of the fruit bat microbiome found, strikingly, that the meaningful ecological unit in the bat microbiome is at the colony-level, with coordinated microbial change across groups[4].

## Learned and culturally transmitted behaviors also affect biological evolution.

Other studies investigated how learned and culturally transmitted behavior affects biological evolution. Some collated growing evidence that animal culture can affect evolutionary processes, including by triggering speciation, shaping population structure and gene flow, and driving coevolution[5-6], whilst others deployed mathematical models to explore how culture affects human evolutionary dynamics[7-9].


**References:**

**1.** Ledon-Rettig et al. 2018. *PNAS*, 115:42, pp. 10696-10701; **2.** Schwab et al. 2016. *Am Nat*, 188:6, pp. 679-692; **3.** Schwab et al. 2017. *Ecol Lett*, 20:11, pp. 1353-1363; **4**. Kolodny et al. 2019. *Nat Ecol Evol*, 3, pp. 116–124; **5.** Whitehead 2019. *Nat Commun*, 10, 2405; **6.** Whiten et al. 2017. *PNAS,* 114:30, pp. 7775-7781; **7.** Creanza et al. 2017. *PNAS*, 114:30 pp. 7782-7789; **8.** Kolodny et al. 2016. *PLOS Comput. Biol*, 12:12, pp. e1005302; **9.** Ram et al. 2018. *PNAS*, 115:6, pp. E1174-E1183


Beetle photo by Alex Wild.

# D. Evolutionary Diversification

Does development influence macroevolutionary patterns?

Can proximate causes— physiological, developmental, and behavioral causes at the level of individual organisms—explain patterns of divergence between species and at a macro-evolutionary level? Several projects addressed this question by investigating a wide range of biological systems, including three-spined sticklebacks, Anolis lizards, insects such as butterflies, beetles, and dragonflies, corals, nest-building birds and fishes, web spiders, bacteria, and through the use of theoretical models.

## Research projects

| # | Project title | Principal investigators | Predictions tested | link |
|---|---|---|---|---|
| **14** | An experimental test of plasticity-led evolution | *Foster, Baker, Gibbons, Cresko, Laland, Merilä & Wund* | *i, ii, iii, iv, v, vii* | |
| **15** | Plasticity and adaptive radiation in Anolis lizards | *Uller & Feiner* | *i, ii, iii, v, vii* | |
| **16** | Phenotypic plasticity, developmental bias and evolutionary diversification in butterflies | *Brakefield* | *i, iii, iv, v* | |
| **17** | Plasticity as a bridge between micro- and macroevolution | *Svensson, Cornwallis & Uller* | *i, iii* | |
| **18** | Adaptive trends and parallel evolution generated by niche construction | *Laland, Odling-Smee, Japyassu, Street & Healy* | *viii, x, xi* | |
| **19** | Niche construction, plasticity and the diversity of coral reef fauna | *Dornelas, Madin, Hoogenboom & Williams* | *viii* | |
| **20** | Niche construction and evolutionary diversity in experimental marine microbial communities | *Paterson, Holden & Lundberg* | *viii, xii* | |
| **21** | Macro-evolutionary dynamics of niche construction | *Erwin, Krakauer & Flack* | *viii, xii* | |
| **22** | Ecosystem networks and system-level functions | *Watson, Odling-Smee, Wade & Gardner* | *xii* | |

# Key findings

## Evolutionary consequences of niche construction

Several projects explored whether developmental processes can guide evolution, either by shaping the phenotypic variation subject to natural selection, or through niche construction (e.g. modifying selective environments). A meta-analysis of published selection gradients shows that organism-constructed and non-constructed environmental components have different properties, and elicit distinctive evolutionary responses[1].

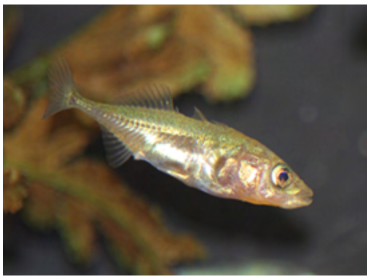
## Evidence for developmental bias in evolution

Experiments show that developmental bias limits the independent evolution of butterfly eyespots, but that some groups can escape to evolve more diverse wing patterns[2].

Members of the project collaborated to write a comprehensive review of the evidence for developmental processes biasing evolution[3], and produced a special issue of the journal *Evolution & Development* on this topic[4].

## Niche construction and phenotypic plasticity

A key theoretical analysis established that without niche construction and phenotypic plasticity, major transitions in evolution (e.g., from single cells to multicellular organisms) cannot happen[5].




**References:**
**1.** Clark et al. 2020. *Am Nat*, 195:1, pp. 16-30
**2.** Brattström et al. 2020. *PNAS*, 117:44, pp. 27474-27480
**3.** Uller et al. 2018. *Genetics*, 209:4, pp. 949-966
**4.** Moczek (ed) Developmental Bias in Evolution. *Evol & Dev*. 22:1-2
**5.** Watson & Thies, 2019. *MIT Press*, pp. 197-226

# Activities

# Conference & workshops

**Workshop 1**
**May 2017**
*Cause & process in evolution*

**Workshop 2**
**February 2018**
*Integrating development and inheritance*

**Workshop 3**
**November 2018**
*Directional biases in evolution*

**Conference**
**April 2019**
*Evolution evolving*

Conference

## Evolution evolving: process, mechanism, and theory


**Organizers: Paul Brakefield, Kevin Laland, Tobias Uller, Katrina Falkenberg & Andrew Buskell**

“Evolution Evolving” was an international conference on the evolving mechanisms and theoretical framework of evolutionary biology. Topics included the evolutionary causes and consequences of developmental bias, plasticity, niche construction and extra-genetic inheritance – all of which contribute to evolvability.

https://evolutionevolving.org/

**Invited Speakers**
Alexander Badyaev (Arizona)
Renee Duckworth (Arizona)
Laurel Fogarty (Max Planck)
Jukka Jernvall (Helsinki)
Alan C. Love (Minnesota)
Joanna Masel (Arizona)
Armin Moczek (Indiana)
Angela Potochnik (Cincinnati)
Sean Rice (Texas Tech)
Jessica Riskin (Stanford)

Workshop 1

## Cause and process in evolution

May 11-14, 2017
Konrad Lorenz Institute for Evolution and Cognition Research

**Organizers: Tobias Uller & Kevin Laland**

This workshop brought together philosophers of science and biologists to reflect on the nature of causation in biological evolution. The EES has a different perspective on causation in evolution, and ascribes a greater range of processes evolutionary significance than traditional perspectives. The workshop scrutinized these claims, with both philosophers (acting as independent arbiters) and non-project members (including non-sympathizers) present to ensure good debate.

https://kli.ac.at/en/events/event_calendar/view/373

Workshop 2

## Integrating development and inheritance

Feb 13-15, 2018
Santa Fe Institute

**Organizers: Kevin Laland, Tobias Uller, Marcus Feldman & Michael Lachmann**

This workshop discussed the historical origins of the separation of development and inheritance, their description in genetic terms, and how this shaped the development of research programmes within biology. It also explored emerging alternative conceptualizations, and the re-integration of this relationship, that are emerging through recent advances in the biological sciences, and are emphasized by the EES.

https://www.santafe.edu/events/integrating-development-and-inheritance

Workshop 3

## Directional bias in evolution

Nov 14-16, 2018
Santa Fe Institute

**Organizers: Kevin Laland, Tobias Uller, Marcus Feldman & Michael Lachmann**

The aim of this workshop was to reflect anew on the processes that give phenotypic evolution directionality. Traditionally, only natural selection was granted a creative role in evolution. However, changing concepts of development, and of the interaction between organism and environment, are increasingly leading researchers to consider a broader range of processes as potentially imposing directionality and adaptation. Key foci included developmental bias, niche construction, and the role of plasticity in generating these biases.

https://www.santafe.edu/events/directional-biases-evolution

# Edited book

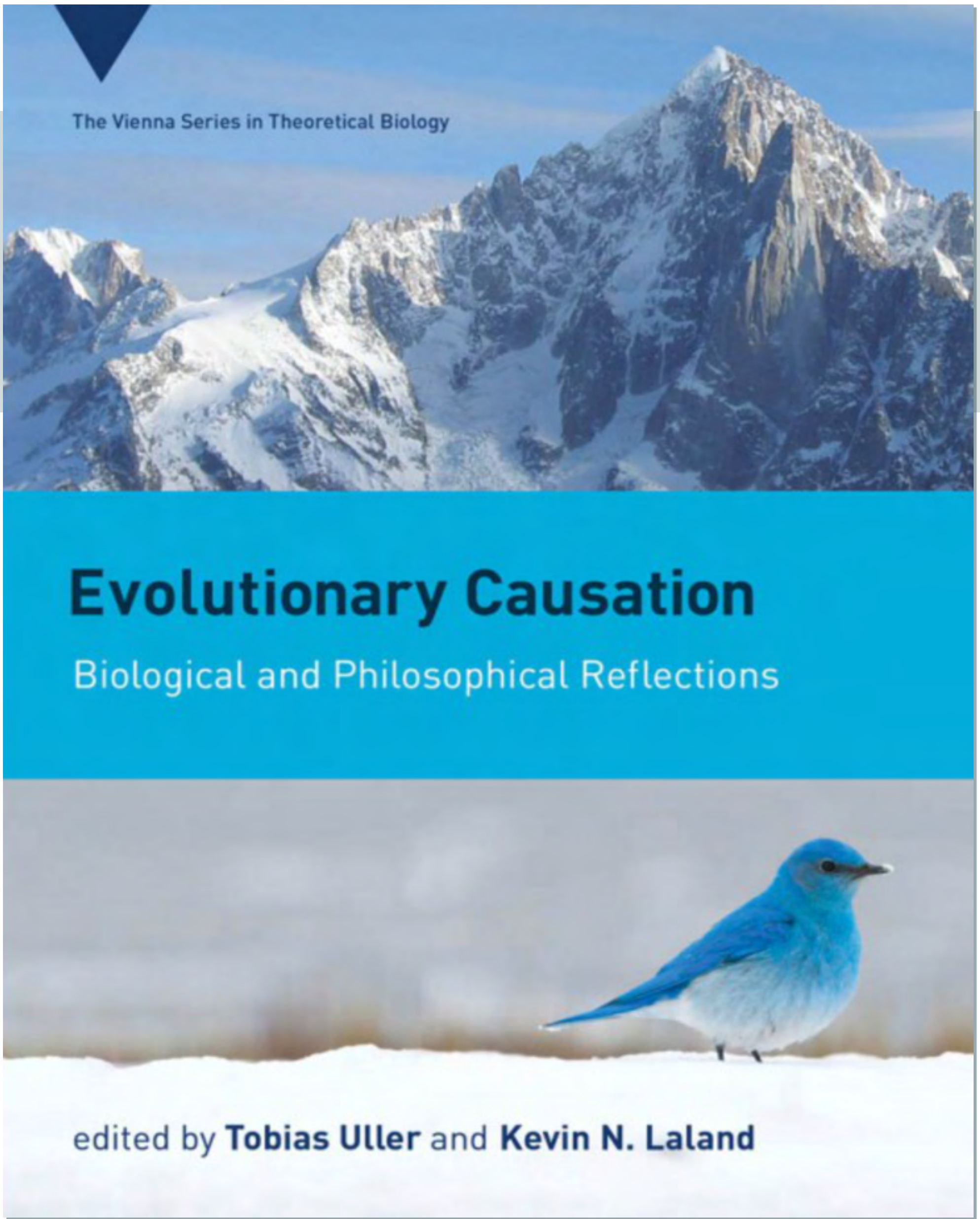
Leaders of the project edited a book on evolutionary causation in the MIT Press.

## Evolutionary Causation (2019)

Biological and Philosophical Reflections

**Edited by Tobias Uller and Kevin N. Laland**

### Table of Contents




Publisher website

***A comprehensive treatment of the concept of causation in evolutionary biology that makes clear its central role in both historical and contemporary debates.***

# Special issue

Leaders of the project edited a special issue in the journal *Evolution and Development* on developmental bias.

## Developmental Bias in Evolution (2020)

Special issue in *Evolution & Development*

**Edited by Armin P. Moczek**

Publisher website

### Table of Contents


**This special issue covers a wide range of approaches toward the study of developmental bias. These include investigations of how developmental systems produce phenotypic variation, the impact of developmental bias on evolutionary dynamics, and the methods that exist to assess the nature and consequences of this impact.**

- **A Striking Example of Developmental Bias in an Evolutionary Process: The "Domestication Syndrome"**
  by Adam Wilkins
- **Developmental Symbiosis Facilitates the Multiple Origins of Herbivory**
  by Scott Gilbert
- **Developmental Bias In Horned Dung Beetles and its Contributions to Innovation, Adaptation, and Resilience**
  by Yonggang Hu, David M. Linz, Erik S. Parker, Daniel B. Schwab, Sofia Casasa, Anna L. M. Macagno, Armin P. Moczek
- **Relative Developmental Duration Organizes, Scales and Adapts the Mammalian Retina and Cortex, with a Note on Dunnarts, Mole Rats and Bats**
  by Barbara Finlay and Kexin Huang
- **Developmental Plasticity Associated with Early Structural Integration and Evolutionary Patterns: Examples of Developmental Bias and Developmental Facilitation in the Skeletal System**
  by Kathryn Kavanagh
- **Parthenogenesis and Developmental Constraint**
  by Frietson Galis and Jacques van Alphen

# Selected publications

## 2021

Evolution of the locomotor skeleton in *Anolis* lizards reflects the interplay between ecological opportunity and phylogenetic inertia. Feiner N, Jackson ISC, Stanley EL, Uller T. Nat Commun. 12(1525)

## 2020

Nutrition-responsive gene expression and the developmental evolution of insect polyphenism. Casasa S, Zattara EE, Moczek AP. Nat Ecol Evol. 4: 970-978

A release from developmental bias accelerates morphological diversification in butterfly eyespots. Brattström O, Aduse-Poku K, van Bergen E, French V, Brakefield PM. PNAS. 117(44):27474-27480

Philosophy of Science for Biologists. Kampourakis K, Uller T. (eds). Cambridge University Press

Plasticity and evolutionary convergence in the locomotor skeleton of Greater Antillean *Anolis* lizards. Feiner N, Jackson ISC, Munch KL, Radersma R, Uller T. eLife. 9:e57468

Synthesising arguments and the extended evolutionary synthesis. Buskell A. Stud Hist Philos Sci C. 80:101244

Young birds switch but old birds lead: How barnacle geese adjust migratory habits to environmental change. Oudman T, Laland KN, Ruxton G, Tombre I, Shimmings P, Proup J. Front Ecol Evol. 7

Plasticity leaves a phenotypic signature during local adaptation. Radersma R, Noble DAW, Uller T. Evol Lett. 4:360-370

Different perspectives on non-genetic inheritance in evolutionary biology illustrate the versatile utility of the Price Equation. Helanterä H, Uller T. Phil Trans R Soc Lond B. 375: 20190366

## 2019

The Extended Evolutionary Synthesis: what is the debate about, and what might success for the extenders look like? Lewens, T. Biol J Linn Soc. 127(4):707-721

Beetle horns evolved from wing serial homologs. Hu Y, Linz DM, Moczek AP. Science 366(6468):1004–1007.

Niche construction affects the variability and strength of natural selection. Clark AD, Deffner D, Laland KN, Odling-Smee J, Endler J. Am Nat. 195(1):16-30

Evolutionary lability in Hox cluster structure and gene expression in Anolis lizards. Feiner N. Evol Lett. 3(5):474-484

Plastic responses to novel environments are biased towards phenotype dimensions with high additive genetic variation. Noble DWA, Radersma R, Uller T. PNAS 116(27):13452-13461

How adaptive plasticity evolves when selected against. Rago A, Kouvaris K, Uller T, Watson RA. PLoS Comput Biol. 15(3):e1006260

The origins of novelty from within the confines of homology: the developmental evolution of the digging tibia of dung beetles. Linz DM, Hu Y, Moczek AP. Proc R Soc B. 286(1896):20182427

Niche construction and conceptual change in evolutionary biology. Uller T, Helanterä H. Brit J Philos Sci. 70:351-375

Replicated evolutionary inhibition of a complex ancestral behaviour in an adaptive radiation. Foster SA, O'Neil S, King RW, Baker JA. Biol Lett. 15(1):20180647

On the reciprocally causal and constructive nature of developmental plasticity and robustness. Schwab DB, Casasa S, Moczek AP. Front Genet. 9

Social learning strategies regulate the wisdom and madness of interactive crowds.Toyokawa W, Whalen A, Laland KN. Nat Hum Behav. 3:183–193

Vertical and oblique cultural transmission fluctuating in time and in space. Ram Y, Liberman U, Feldman MW. 2019. Theor Popul Biol. 125: 1-19

## 2018

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# Resource websites

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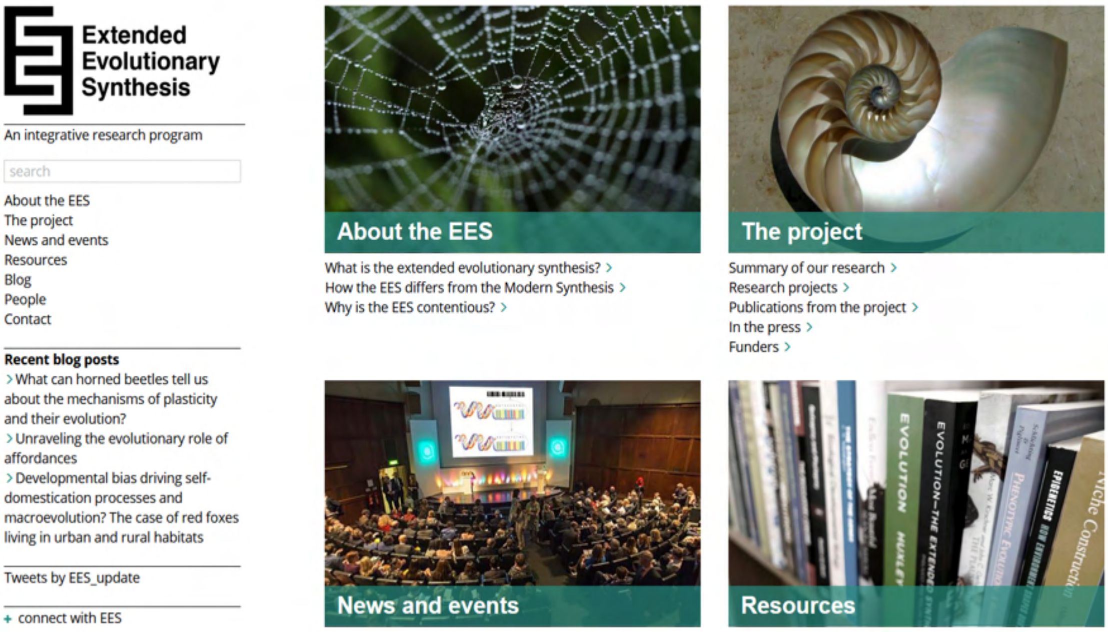


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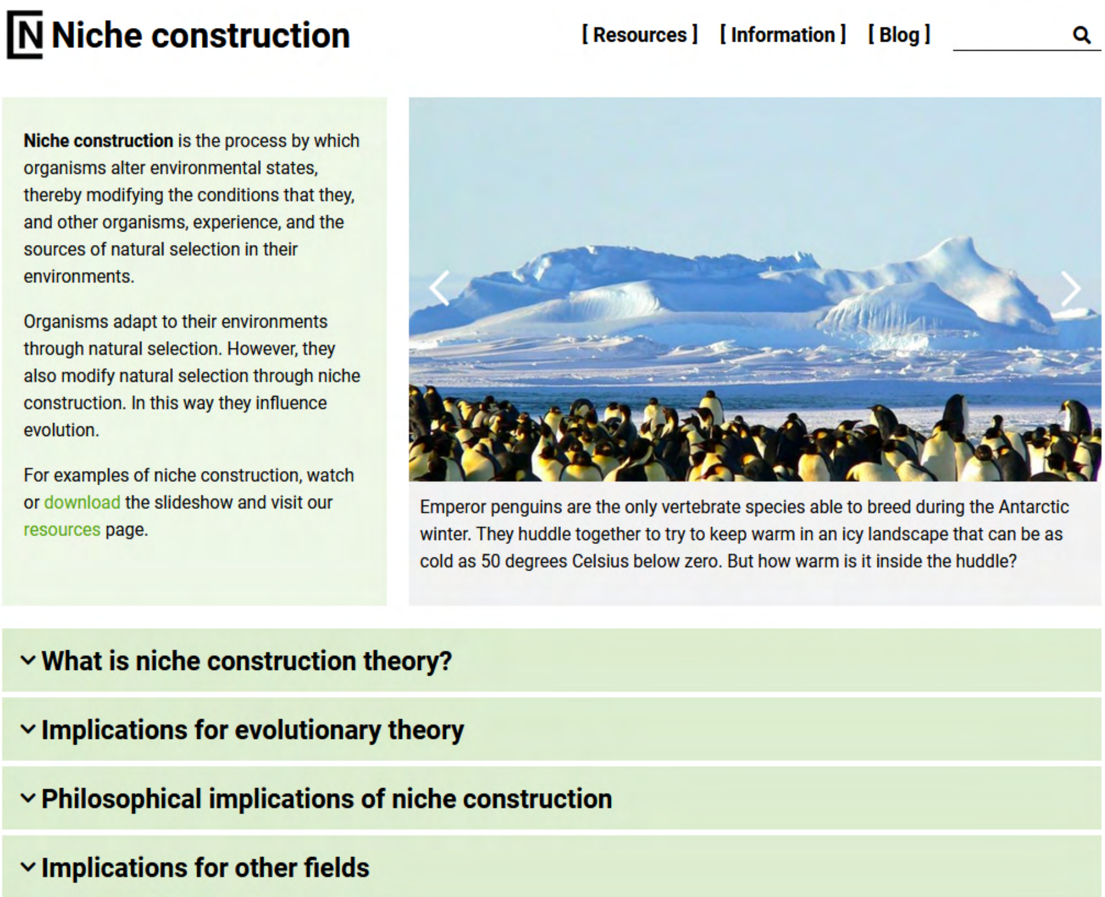


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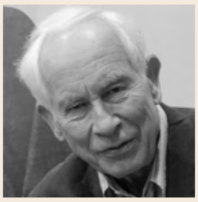
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Full bios and further information can be found on our website: https://extendedevolutionarysynthesis.com/people/

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Katrina Falkenberg, Lynn Chiu

# ANURA (or a drawing about evolving amphibians)

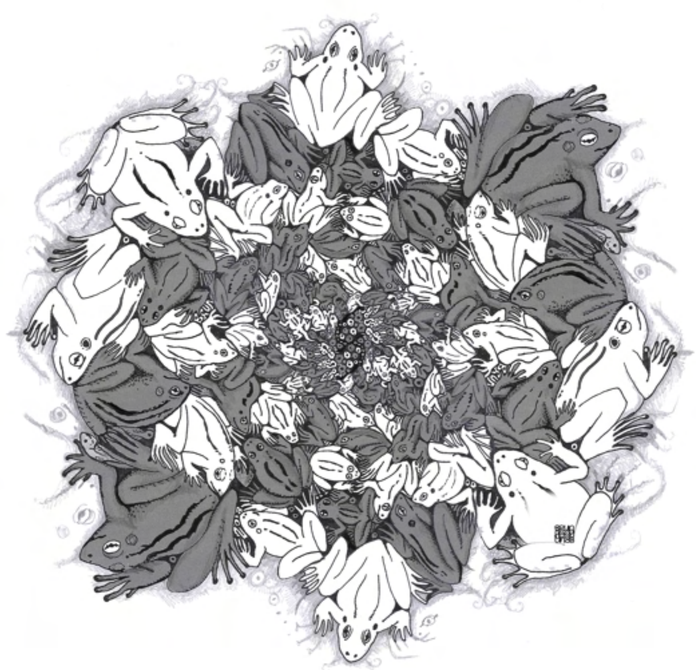
*Fine-liner and pencil on paper / digital collage*

**Artist: Dr. Miguel Brun-Usan**
**University of Southampton (UK) / Lund University (SE)**

The cover illustration is strongly inspired by the art of M.C. Escher, a Dutch artist who explored the relationship between art and mathematics. His most known pieces are the so-called "tessellations" (surfaces tiled with repeated geometric elements or tiles). Escher realized that, from mathematical considerations, there exists a limited number of symmetry groups amenable for creating visually appealing tessellations, from which he had to choose (Escher, 1971). Had he made different choices, he would have had to cope with geometrical frustration, which would have broken the balanced symmetry of the composition. The charm of tessellations can only arise in the transition zone that exists between the unleashed artistic imagination and the hard mathematical regularity; a narrow path that Escher walked majestically.

This tension makes tessellations a very suitable metaphor to illustrate different phenomena occurring at the boundary between creativity and regularity. One of these processes, which I have tried to capture in the drawing, is the evolution and development of organic forms. In a purely genetic view of evolution (which reduces it to change in gene frequencies), evolving organisms navigate a vast ocean of almost infinite possible sequences, propelled by the winds of natural selection. As is for the unconstrained artist, no route is forbidden in that open sea.

However, evolving organisms are more than naked DNA sequences. Since they are all made of soft physical matter, organisms will exhibit some sensitivity to the surrounding environment, which will inescapably become a causal agent in their development. Furthermore, organisms must obey the biophysical rules that govern the transformation of such soft materials by environmental and genetic factors (Thompson, 1942). Employing different sub-sets of rules would lead to different forms of variation (developmental biases).



By analogy, employing a different geometrical matrix in the drawing would have changed the kind of frog-like shapes that can be fit in each tile and, ultimately, the general style of the composition.

Understanding this interplay between explorative processes (natural selection) and the different forms of biases arising from development is one of the main challenges of current biology, and one of the main promises of the Extended Evolutionary Synthesis (EES). By disentangling these universal rules of change, adaptive and variational explanations can be unified into a deeper explanatory framework that I believe, ultimately, will provide a richer understanding of how nature works.

- Miguel Brun-Usan

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