Final report
Project UNICOP

selected within the sDiv-FRB-CESAB 2019 joint call

I. Project identification

Project title: Unification of modern Coexistence theory and Price equation

Acronym: UNICOP

Funded by: sDiv and FRB-Cesab

Co-funding organization (if relevant):

Principal Investigators (names and affiliations): Brad Duthie (University of Stirling), Sébastien Lion (Centre d'Écologie Fonctionnelle et Évolutive)

Name email address of the person writing the report (if not one of the PI): Brad Duthie

Starting date of the project: 2020
Finishing date of the project: 2025

Scientific summary of project (maximum of 300 words)
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UNICOP is an ambitious project towards conceptual synthesis in eco-evolutionary theory, rederiving foundational equations of ecology and evolution from shared first principles and building formal links between eco-evolutionary theory and modern coexistence theory. To achieve these aims, the project brought together an interdisciplinary team of six researchers from five countries with expertise across different areas fundamental to eco-evolutionary theory. In evolutionary biology, the Price equation is fundamental and a unifying framework for understanding evolution in any system. In ecology, modern coexistence theory provides a unifying framework for understanding mechanisms of species coexistence. The UNICOP project has identified a fundamental equation for eco-evolutionary change from which both the Price equation and a universal model of population change can be derived, thereby formally linking the foundations of ecological and evolutionary change through a shared framework. We have also introduced a new method (near persistence) for determining species coexistence in eco-evolutionary models and demonstrated the effect that unequal intraspecific trait variances has on competitor coexistence. Overall, the UNICOP project has made significant advances in eco-evolutionary theory and established a foundation for future modelling.

Key words (5): Eco-evolutionary theory, conceptual unification, Price equation, mathematical modelling, community coexistence

Context and objectives (around 1,500 characters including spaces)
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Many models exist to link evolutionary and ecological phenomena, but the foundational assumptions and equations of eco-evolutionary theory remain mostly separate, conceptually, and more work is needed to understand species coexistence in the context of evolution. The original objectives of UNICOP, established in our project proposal, were as follows:

1. Derive fundamental equations underlying modern coexistence theory and evolution from a minimal sets of axioms of biological processes (e.g., birth, death, reproduction).

2. From the minimal set of axioms underlying modern coexistence theory and evolution, derive an equation(s) that encompasses all ecological and evolutionary change, from which fundamental equations of population and phenotypic change can be re-derived by removing uniquely evolutionary or ecological assumptions, respectively.

3. Investigate the (conceptual, theoretical, and empirical) consequences of a unifying equation of ecology and evolution for modern coexistence theory, and attempt to formally prove one or more general relationships between (co)evolution and species coexistence.

4. Apply new equation(s) and proof(s) to suggest new approaches for modelling eco-evolutionary systems.

We have made significant progress across all objectives and established a strong foundation for future research. In particular, we have uncovered an equation underlying any eco-evolutionary change from a minimal set of axioms. We have also outlined new approaches for modelling eco-evolutionary systems.

II. Project participants

List and attendance of project participants

Please indicate if any project participants were unable to attend a meeting, but were active remotely by using an asterisk (*).

	Name	Affiliation	Country	WS1	WS2	WS 3	WS 4
PI 1	Brad Duthie	University of Stirling	Scotland	Yes	Yes	Yes	Yes
PI 2	Sébastien Lion	Centre d'Écologie Fonctionnelle et Évolutive	France	Yes*	Yes	Yes	Yes
3	Swati Patel	Oregon State University	USA	Yes*	Yes	Yes*	Yes*
4	Victor J Luque	University of Valencia	Spain	Yes	Yes	Yes	Yes
5	Lynn Govaert	Leibniz Institute of Freshwater Ecology and Inland Fisheries	Germany	Yes	Yes	Yes	Yes
6	Kelsey Lyberger	Arizona State University	USA	Yes	Yes	Yes	Yes*

Please list any additional invitees similarly, and identify their category: i.e. students, postdocs or visiting experts

1						
2						
3						
4						

Comment :

III. Activity report

III.1 [For scientific readers] Description of the work conducted and scientific results obtained

The UNICOP project sought to identify fundamental axioms of ecological and evolutionary change, rederiving fundamental equations of ecology and evolution from first principles and establishing new fundamental equations as a foundation from which to build new eco-evolutionary theory. It also sought to integrate eco-evolutionary models more clearly into modern coexistence theory, which is a unifying theoretical framework for understanding coexistence in community ecology. Early on in the project, we recognised that it was necessary to address these two aims separately. Below, we first describe the work on foundations of ecological and evolutionary change, then we describe the work on eco-evolutionary modelling and synthesis with modern coexistence theory.

Foundations of ecological and evolutionary change

Both ecological and evolutionary change are realised through the same biological mechanisms of birth and death. Despite a clear conceptual link between evolutionary fitness, trait change, and population size change, the formal relationship among these phenomena has never truly been established from first principles. Hence, eco-evolutionary models are often a synthesis of separate ecological and evolutionary assumptions and dynamics (Figure 1).

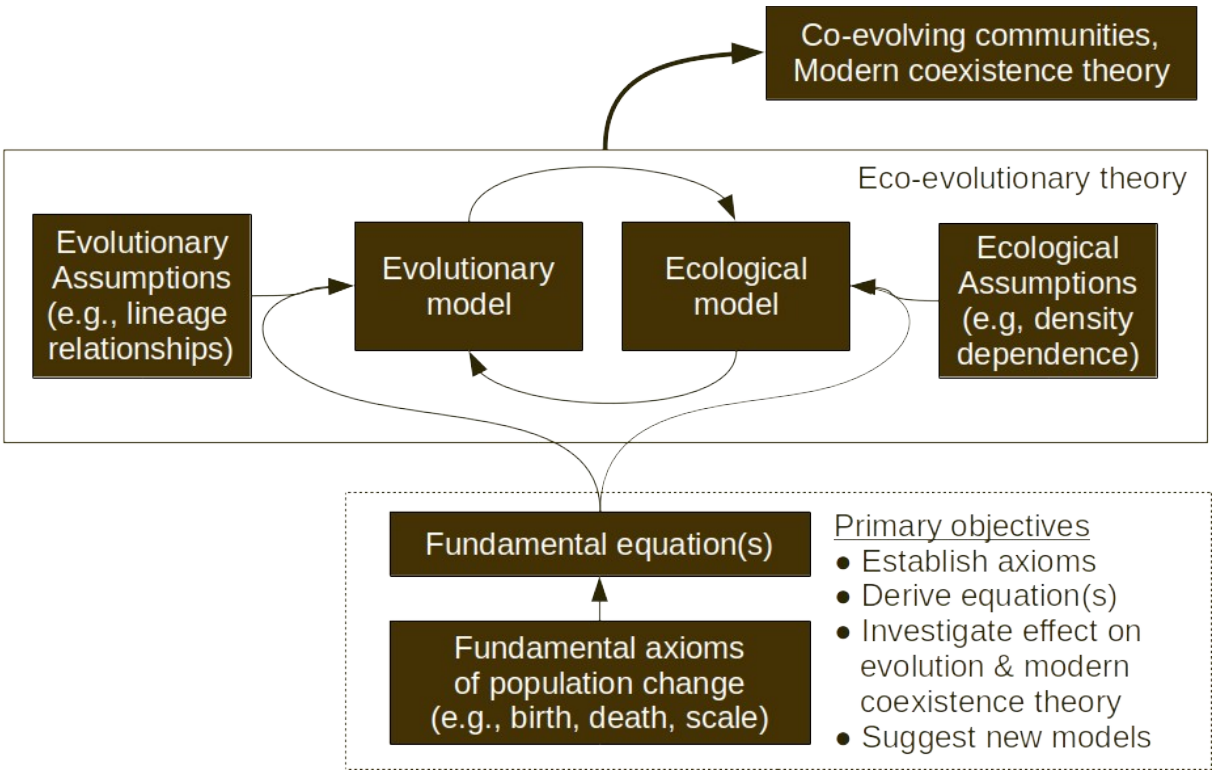

Figure 1: Outline of UNICOP project.

A high risk, high reward component of UNICOP was to attempt to uncover a foundational equation or set of equations that encompass both evolutionary change and population size change. Although the Price equation is widely recognised to be fundamental in describing evolution in any system (e.g.,

Gardner 2008; Luque 2017; Queller 2017), its links to population change remain unclear (e.g., Mayne 2025). The UNICOP project established a formal link between the Price equation and the fundamental model of population size change for any closed population ($N_{t+1} = N_t$ + Births - Deaths). In doing so, we established a new equation from which the fundamental equations of ecology and evolution can be derived,

$$\Omega = \sum_{i=1}^{N} (\beta_i - \delta_i + 1)(z_i + \Delta z_i).$$

The above equation defines eco-evolutionary change in a population of size *N* across an arbitrary length of time. Over this length of time, β_i is the total count of direct descendents of individual *i*, δ_i, is the count of deaths across *i* and any of its descendents, and z_i is any characteristic of *i*. The value Ω is the summed character values in the population, which under some conditions can be a metric of the population's contribution to ecosystem function.

Duthie and Luque (2025) demonstrate how to derive the Price equation and birth-death model from the above equation, and how our fundamental eco-evolutionary equation can also be applied to linking ecology and evolution to ecosystem function. We outline links to density-dependent population growth, multi-level selection, and future modelling syntheses. Our work shows that eco-evolutionary change is, fundamentally, a statistical interaction between fitness and individual characteristics, and it formalises Needham's (1904) description of natural history as "the study of the phenomena of fitness".

Persistence and near persistence via trait evolution

Modern coexistence theory is a unifying framework for understanding the mechanisms that promote species coexistence (Chesson 2000; 2018). Despite its success as a theoretical framework in community ecology, much work remains to understand species coexistence when species interactions are determined by evolving traits. In such cases, the magnitude or even nature of species interactions (e.g., competition) might change over time. Traditionally, modern coexistence theory has relied on invasion analysis, testing whether or not each species can invade a stable community successfully and therefore recover from low population density. When integrating evolving traits into this framework, a key question is how to account for different potential trait distributions?

We developed a modified definition of coexistence, which we term 'near persistence', following on a model from Pastore et al. (2021) and persistence theory (Garay, 1989; Schreiber et al., 2011; Patel & Schreiber, 2018). While persistence theory evaluates species persistence (and therefore coexistence) for all species in a community given any range of species trait means that are possible for a species in isolation, *near persistence* focuses on trait means, and therefore invasion conditions, that are biologically realistic within a community. We demonstrate our approach using a two-species model of competitor coexistence and focus on consequences of inequal trait variances between competing species. We find 15 distinct possibilities for species coexistence that can be categorised into five different ecological scenarios: (1) persistence, (2) near persistence, (3) competitive exclusion, (4) near competitive exclusion, and (5) priority effects (Figure 2; Table 1). Our model shows that in the biologically realistic scenario in which trait variances differ between species, persistence or competitive exclusion is predicted in contrast to to near persistence or priority effects (when trait variances are identical).

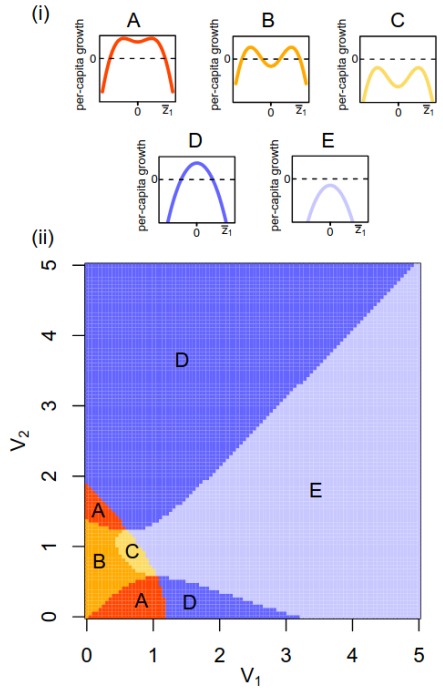

Figure 2: Consequences of ecological invasion given different trait variances in an invader (V1) and resident (V2). (i) Per capita growth rate across different mean trait values (z_1) of an invader against a resident at its equilibrium.

		Species 1				
		A	B	C	D	E
Species 2	A	(I) P	(I) P	(I) CE	(II) P	(II) CE
	B		(I) NP	(I) NCE	(II) NP	(II) NCE
	C			(I) PE	(II) CE	(II) PE
	D				(III) P	(III) CE
	E					(III) PE

Table 1: Predictions of qualitative behaviors from an eco-evolutionary model of competitor coexistence. Letters A-E refer to the per-capita growth rate functions of species 1 and 2 as invading species as shown in Figure 2. Number in parentheses (i.e., I-III) indicates the boundary dynamic cases. Legend: P = Persistent, NP = Nearly Persistent, CE = Competitive Exclusion, NCE = Near Competitive Exclusion, PE = Priority Effect.

Overall, we find that (1) initial trait distributions of species are important when evaluating whether or not mutual invasion criteria are satisfied in eco-evolutionary systems, (2) trait variances need to be evaluated to determine the consequences of species dynamics for coexistence, and (3) limitations that are inherent to modern coexistence theory can be overcome using persistence theory and our criteria of near persistence. We therefore find that a more nuanced treatment of invasion is required in eco-evolutionary systems to predict coexistence of species.

Chesson, P. L. (2000). Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics. 31: 343–366

Chesson, P. (2018). Updates on mechanisms of maintenance of species diversity. Journal of Ecology. 106: 1773–1794. issn: 00220477.

Duthie, A. B., & Luque, V. J. (2024). Foundations of ecological and evolutionary change. arXiv preprint arXiv:2409.10766.

Garay, B. M. (1989). Uniform persistence and chain recurrence. Journal of mathematical analysis and applications. 139(2): 372–381.

Gardner, A. 2008. The Price equation. Current Biology 18:198–202.

Luque, V. J. 2017. One equation to rule them all: a philosophical analysis of the Price equation. Biology and Philosophy 32:1–29.

Mayne, Z. 2025. "Finding the Fundamental Equation of Evolutionary Dynamics: Problems and Prospects". International Society for the History, Philosophy, and Social Studies of Biology (ISHPSSB) Conference. Porto, Portugal.

Pastore, A. I., G. Barabás, M. D. Bimler, M. M. Mayfield & T. E. Miller (2021). The evolution of niche overlap and competitive differences. Nature Ecology and Evolution. 5: 330–337.

Patel, S. & S. J. Schreiber (2018). Robust permanence for ecological equations with internal and584 external feedbacks. Journal of Mathematical Biology. 77: 79–105.

Queller, D. C. 2017. Fundamental theorems of evolution. American Naturalist 189:345–353.

Schreiber, S. J., M. Benaïm & K. A. S. Atchadé (May 2011). Persistence in fluctuating environments. Journal of Mathematical Biology. 62: 655–683. issn: 1432-1416.

III.2 [For large audience] Introduction (around 300 characters including spaces)

How species population sizes and traits change over time are major areas of study in ecology and evolutionary biology, respectively. But how these changes relate at the most foundational level of eco-evolutionary theory is unresolved. UNICOP uncovers what is most fundamental to eco-evolutionary change.

III.3 [For large audience] Methods and approaches used for your project (around 700 characters including spaces)

The UNICOP project applied a deductive approach to uncover a fundamental equation of eco-evolutionary change, mathematically deriving the fundamental equations of population change and evolution (the Price equation) separately from our joint eco-evolutionary equation. To predict species coexistence in light of eco-evolutionary dynamics, we applied mathematical modelling and persistence theory to determine whether or not species coexistence is possible when species have differences in key traits affecting competitiveness in their environment (i.e., trait means and variances). Eco-evolutionary dynamics were simulated for different species invasion scenarios.

III.4 Access to data (if relevant)

No empirical data were used in the UNICOP project. All code used for modelling is available in two GitHub repositories:

- https://github.com/bradduthie/eco_evo_unification
- https://github.com/klyberger/Two-species-eco-evo

For questions concerning these repositories, please contact Brad Duthie or Kelsey Lyberger.

III.5 Scientific outcomes of the project

Publications:

- Baravalle, L., Jonathan Roffé, A., **Luque, V. J.**, & Ginnobili, S. (2025). The value of Price. *Biological Theory*, *20*(1), 12-24.
- **Duthie, A. B., & Luque, V. J.** (2024). Foundations of ecological and evolutionary change. *arXiv preprint arXiv:2409.10766*. (in revision at *Ecology and Evolution*)
- **Patel, S., L. Govaert, K Lyberger, V. J. Luque, A. B. Duthie, and S. Lion.** Persistence and near persistence via trait evolution: pathways to coexistence. biorXiv preprint 10.1101/2025.09.23.676445 (submitted to Journal of Theoretical Biology)

- *Planned*: (1) Oligomorphic dynamics and modern coexistence theory, (2) Variance dynamics under Gaussian assumptions, (3) Connecting the Price equation to processes of community ecology and evolutionary biology, and (4) Price, statistics, and populations (all planned and in various stages of preparation for next 1-2 years).

Talks:

- Duthie, AB, and VJ Luque. "Darwin's Dream: Unifying Ecological and Evolutionary Change (Foundations of ecological and evolutionary change)," 2025 conference of the International Society for the History, Philosophy, and Social Studies of Biology (ISHPSSB), Porto, 25 JUL 2025.
- Luque, VJ. A universal view of evolution. XI Congreso de la Sociedad de Lógica, Metodología y Filosofía de la Ciencia en España. Oviedo 16-19 JUL 2025.
- Duthie, AB, and VJ Luque. 2024. Foundations of ecological and evolutionary change. Institut Universitari Cavanilles de Biodiversitat i Biologia Evolutiva, University of Valéncia, Valéncia, Spain. 22 OCT 2024.
- Luque, VJ. A universal view of evolution. Workshop "Life, Evolution, Sentience: A Philosophical Colloquium", organized by UNED, Madrid on 8-9 FEB 2024.
- Luque, VJ. Endless histories: un recorrido histórico de la(s) teoría(s) evolutiva(s) (invited speaker). Workshop "¿[Revolución? Debates en torno a la síntesis extendida" organized by ICBIBE (Cavanilles Institute for Biodiversity and Evolutionary Biology of the University of Valencia), Valencia on 4 MAY 2023.
- Luque, VJ. The Price equation and the laws of evolution (invited speaker). Workshop "The Price Equation and its Applications" organized by the Institute of Philosophy, Leibniz Universität Hannover on 16-17 MAR 2023 (with Lorenzo Baraballe).
- Luque, VJ. The mirror of physics: on how the Price equation can unify evolutionary biology. XII Encuentro Iberoamericano sobre Metateoría Estructuralista "Homenaje a Joseph D. Sneed: Cinco Décadas de The Logical Structure of Mathematical Physics" (celebrado por video-conferencia desde las sedes de Buenos Aires y Santiago de Compostela, 15-17, diciembre 2021) (with Lorenzo Baravalle).
- Luque, VJ. On how the Price equation can unify Evolutionary Biology. The Valencia Colloquium in Philosophy. 8 OCT 2021.
- Luque, VJ. On how the Price equation can unify Evolutionary Biology (invited speaker and keynote speaker). VII Annual Meeting of the PhD Program of Biodiversity and Evolutionary Biology (University of Valencia) on the 19 JUL 2021.

Grants:

- Mechanism-based approaches to causation in evolutionary biology: prospects, limitations, and applications (**MECAEVOBI**). Conselleria de Educación, Universidades y Empleo, Generalitat Valenciana, Valencia, Spain. Subvenciones a grupos de investigación emergentes– GE 2024 reference CIGE/2023/16. Awarded to Víctor J Luque (Lynn Govaert involved and Brad Duthie giving a workshop talk). **Successful bid 1 JAN 2024 – 31 DEC 2025.**
- New approaches to evidence: theoretical and practical developments (**NATE**). Proyectos de Generación de Conocimiento 2024, Ministerio de Ciencia, Innovación y Universidades, Spain. PID2024-155508NA-I00 awarded to Saúl Pérez González and Víctor J Luque (Duthie involved). **Successful bid 2025.**
- Foundational approaches to ecology and evolutionary theory. Pushing the frontiers of environmental research (NERC) by Duthie and Luque. **Planned 2026**.

IV. Principal conclusions (publishable)

The UNICOP project uncovered a fundamental eco-evolutionary equation from which well-established fundamental equations of evolution and ecology can be derived (Figure 3). It thereby defines the scope of eco-evolutionary change and provides a foundation for future work integrating ecological & evolutionary theory by demonstrating the nature of eco-evolutionary change as an interaction between fitness and individual characteristics. It further clarifies the relationship between evolutionary fitness, population change, and ecosystem function.

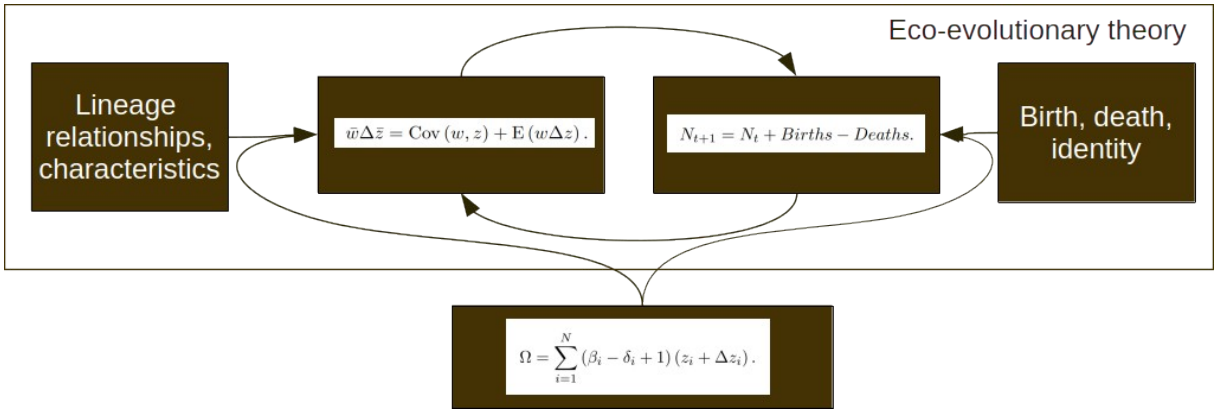

Figure 3: Foundational theory of eco-evolutionary change.

The UNICOP project developed links between eco-evolutionary and modern coexistence theory to better understand how the evolution of traits affects species coexistence. Modelling demonstrated the importance of initial trait distributions and species trait variances for predicting coexistence. This work established new criteria for predicting coexistence given evolving species traits. Given simultaneous ecology and evolution, a careful and nuanced treatment of population dynamics is required to predict species coexistence.

V. Result's impact

Anticipated (or actual) impact of theses results for science, society, public and private decision making (around 1500 characters including spaces): for large audience

Results from the UNICOP project provide a foundation for future theory and modelling of eco-evolutionary change. We anticipate that the general framework linking ecology, evolution, and ecosystem function willl improve conceptual clarity during model development and help resolve theoretical confusion in these areas. Immediate areas of interest for future development include a synthesis of social evolution and density-dependent population growth, and a multi-species expansion of the Price equation to partition different processes of ecological change within and among species (e.g., species interactions, demographic processes) and evolutionary change within species (e.g., selection, genetic drift).

Our eco-evolutionary modelling links to modern coexistence theory will provide insights for future predictions of population change, including models of managed populations to predict the consequences of species invasions and species recovery. In particular, we demonstrate the importance of within-species trait variation for predicting species coexistence versus local extinction. In any real-world population, species will have different trait variances, and our model predicts the outcomes for species coexistence given different species trait means and variances. We expect that our model can be further extended to include the consequences of evolving trait variances, which will further improve prediction in managed populations where interacting species are evolving.

VI. Outreach and dissemination activities (if relevant)

There are no outreach or dissemination activities that directly pertain to the UNICOP project.

VII Next steps – the legacy of the project

Are there any actions planned as a result of the sDiv-CESAB project? Have you submitted proposals resulting from the work conducted during the course of the project for further work? If yes, have you been successful? What is the current status of the post-doctoral researcher affiliated with the project?

The UNICOP project is a foundation for much further work. The MECAEVOBI (2024-2025) and NATE (2025-2026) projects have both been successfully funded, and both of these relied on progress made during UNICOP. A UK NERC project is in the initial planning stages.

In addition to the one published and two submitted manuscripts, there are short-term (i.e., before end of 2026) plans for completing four additional manuscripts, each of which is a direct consequence of discussions and modelling work conducted within UNICOP. Two of these manuscripts are most related to the foundations of ecological and evolutionary change, and will be led by Govaert, Luque, and Duthie. The other two manuscripts are most related to the eco-evolutionary modelling, and will likely be led by Patel, Lyberger, and Lion. While the UNICOP project found two natural strands of inquiry, we have enjoyed working with each other as a group, and it is likely that we will continue to work together on future projects as our research aims continue to overlap. The diverse interdisciplinary expertise has been beneficial.

During this project, **four out of five team members have secured academic posts**, making the transition from PhD or postdoctoral researcher to a permanent academic post:

- **Duthie** started as a Leverhulme Early Career Postdoctoral Fellow; he is now a Senior Lecturer at the University of Stirling.
- **Luque** started as a postdoctoral researcher at UNED (Madrid), and he is now an associate professor (Profesor permanente laboral) at the University of Valencia.
- **Govaert** started as a postdoctoral researcher at the University of Zurich and Eawag, and she is now a Group Leader at the Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB).
- **Patel** started as a postdoctoral researcher at Tulane University; she is now an Assistant Professor at the University of Oregon.
- **Lyberger** started as a PhD student at the University of California Davis, and she is now an Assistant Professor at Arizona State University.

This project has been very valuable in creating a new network of early, and now established, researchers. The legacy work from this project is expected to continue for several years.

VIII Comments on the execution of the project

Please comment on any practical aspects (organization, accommodation etc), difficulties encountered, particular issues related to the management of data, etc.

We are very grateful for the sDiv-CESAB support throughout all practical aspects of the project. We had no major issues in this area, and we appreciate the accomodations made for COVID-19 and the need for some members to join remotely during project meetings.

This was a high risk, high reward project that required considerable time for interdisciplinary discussion and focused thinking, especially in the early stages, in pursuit of uncertain outcomes. We believe that these efforts have paid off, and that we finish the project with the intellectual foundation for a lot of exciting future work and an interdisciplinary team of now-established researchers who are motivated to pursue it. We will continue to acknowledge sDiv-CESAB and the UNICOP project for all relevant future outputs.