



# Forward and inverse modelling of eco-evolutionary dynamics



in biological and economic systems

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September 12, 2022

Cover picture: Top: forest in Sorapiss, Dolomites, Italy. Bottom: New York City, USA. @ Luca  
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# Introduction

” Concepts without precepts are empty, and precepts without concepts are blind.

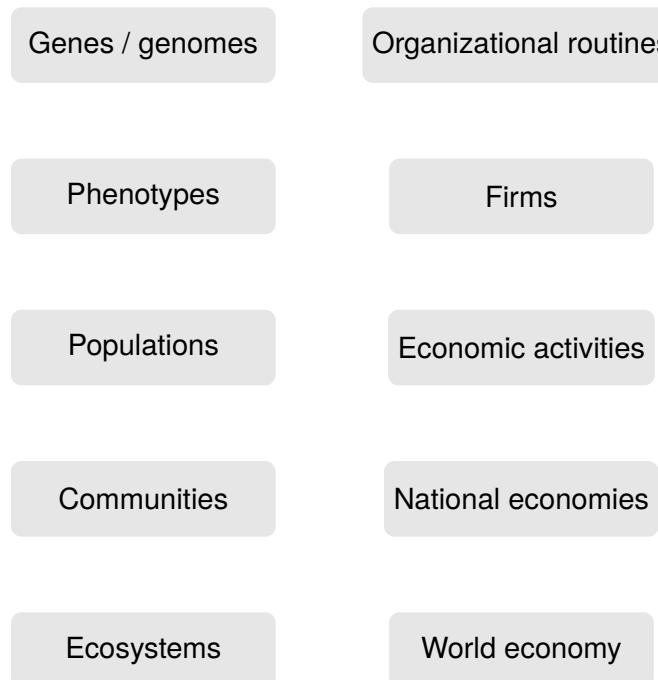
— Immanuel Kant  
Critique of Pure Reason

## Biological and economic systems as complex adaptive systems

What are the similarities between biological and economic systems? Both are complex adaptive systems (CAS) [1], which are composed of heterogeneous entities structured at different levels of organizations, that interact in nonlinear ways and experience evolutionary processes. Interaction and evolutionary processes take many different forms and operate at different organizational level [Levin1998] (see Fig. 1.1). Interestingly, the variety of processes involved and their couplings do not necessarily lead to unpredictable, chaotic, or erratic structures and dynamics [Olff2009], but rather induce organised structural properties and behavior [mitchell2009complexity]. In biological systems, those include patterns of species richness, where for instance montane regions are often associated with a disproportionately high number of species [2]. In economic systems, those include the distribution of international income, where some countries have systematically developed much more rapidly than others [acemoglu2001colonial]. A common direction on the research agenda in Biology and Economics is to comprehend the set of interaction and evolutionary processes that determine these emergent properties [3], and how do they do so. In biological systems, the nature of the processes of interaction and evolution is identified, and the current challenge is to comprehend the mechanisms resulting from their couplings. In economic systems, we still do not exactly understand the nature of those processes, and how are they involved.

## Ecological and evolutionary processes drive the dynamics of biological systems

In biological systems, interaction processes are generally designated as ecological processes, and involve fluxes of energy and matter across space and time, encompassing the processes of interaction between organisms (biotic interactions) and between



**Fig. 1.1:** Schematic diagram of proposed organisational levels in biological and economic systems. A is inspired from [Hendry+2016]

organisms and their environment (abiotic interactions), and dispersal processes (movement of individual across space) [4]. Evolutionary processes designate those processes responsible for the change of heritable characteristics (DNA, genes, phenotypes) over successive generations [Hall2013]. The coupling between ecological and evolutionary processes is acknowledged since the very birth of the theory of Evolution, when Darwin realised a link between the different ecological opportunities across the Galápagos islands and the different beak shapes in the finches he found in each island [darwin2004origin], during his voyage on the Beagle. He reasoned that the variations in ecological opportunities lead to a differential in survival for certain phenotypes, which over time resulted in the evolution of different beak shapes. Since then, we know that ecological processes directly affect evolutionary response [Ezard2009]. In the recent years, the idea that not only ecological processes can affect evolutionary response, but also that evolutionary processes could affect ecological processes, has developed [XXX]. Empirical studies have demonstrated that evolution can be rapid and occur on similar time scales as ecology [Hairston2005, 5] and have quantifiable effects on ecological dynamics [Ezard2009], leading to feedbacks between ecological and evolutionary processes, so-called eco-evolutionary feedbacks [Schoener2011, 5]. Eco-evolutionary feedbacks involve situations where an ecological property influences evolutionary change, which then feeds back to

an ecological property, or vice versa [Govaert2019a]. Examples are feedbacks between population density (ecological property) and trait evolution (evolutionary change), which can lead to evolutionary branching through the effect of competition [Doebeli1999]. Eco-evolutionary feedbacks are also involved in adaptation mechanisms [Doebeli1999], where species disperse and phenotypic variations allow to adapt to local environments [XXX]. Those feedbacks may greatly influence the mechanisms driving the dynamics of ecosystems [6], but our understanding of their nature and effect is limited [Lion2022]. In particular, eco-evolutionary feedbacks are expected to play a critical role in the evolution of the biosphere in the coming decades [7], as ecosystems are being rapidly affected by anthropogenic pressure and with climate change [8, 9]. In order to mitigate the consequences of human development, it is of utmost urgency to better understand eco-evolutionary feedbacks [7], and develop mechanistic models embedding this knowledge [6]. This will in turn provide more reliable forecasts of ecosystem states [Clark2001], to help designing adequate management of ecosystem services [6].

## Drivers of economic change

The processes that determine economic change is controversial in economics [Nelson2014]. To explain economic development, mainstream economic theory [10.1093/cje/bet027] assumes that economic systems are in equilibrium, in the sense that the demand and supply of goods and services are balanced on all relevant markets. Firms are rational in maximizing profits by adapting to demand and supply, and the observed economic change is driven by exogenous forces, such as technological change [Romer1986]. Evolutionary economics, promoted by the seminal work of Ref. [Nelson2014], criticizes this view and seeks to explain economic change by focusing on endogenous forces. Evolutionary economics suggests that interactions between firms and economic activities, and evolutionary processes acting upon them, are major processes contributing to economic change [Hodgson2019]. For instance, firms or economic activities may interact positively or negatively [Wernerfelt1989, Pistorius2007Ozman2009, Saavedra2009a, Cohendet2018, Menon2015], spread across space [RogersEverettM2003DoI, Zahra2000], and adapt [Cordes2006] or transform into new economic institutions [Freeman2002, Hodgson2004, Aldrich2008], affecting economic development at the regional and national scale. Because these processes are analogous to eco-evolutionary processes driving the dynamics of biological systems, a number of modelling approaches have borrowed concepts and methods from biology in the last decades, aiming at better understanding the processes underlying emergent properties in economic systems [Tacchella2018, Saavedra2009a, Scholl2020, Zhang2018, Modis1997,

[Saavedra2014](#), [Farmer1999](#), [Michalakelis2011](#), [Marasco2016](#), [Gatabazi2019](#), [Cauwels56](#), [Applegate2021](#), [Suweis2015](#)]. For instance, [[Saavedra2009a](#)] has successfully used a model of mutualistic interaction to explain structural patterns in industrial cooperation. Also, [[Scholl2020](#)] uses the concepts of foodwebs and density dependence to explain market malfunctions and excess volatility in financial markets. However, those studies did not seek to understand how these processes may affect economic development. Recent modelling approaches developed in evolutionary biology may help to disentangle whether eco-evolutionary processes could explain differences in economic development across countries.

### **Forward modelling of eco-evolutionary processes**

The complex interplay between ecological and evolutionary processes, acting at different scales of time and space and organization, can hardly be studied with experimental approaches [[Hagen2022](#), 10]. As such, a deductive approach, relying on forward modelling, has traditionally been put forward to advance our understanding of the mechanisms underlying [[Brummitt2020](#)]. Along this approach, hypotheses about causal processes are embedded in a model, which forward integration generates emergent properties. Such emergent behavior may be seen as predictions from the consideration of the causal processes [[May2004](#)]. The role of the modeller is to point at the mechanisms by which the properties emerge, disentangling the underlying interplay between the processes. In the early 1930s to 1940s, by formulating tractable mathematical models implementing the processes of reproduction, dispersal and mutations, the work of Fisher, Wright and Haldane has greatly contributed to the modern synthesis of evolutionary biology [[huxley1942evolution](#)], generally accepted as the basis of our current understanding of evolutionary dynamics. The mechanistic models commonly take the form of differential equations (DE), and express how the processes under investigation affect the rate of change of the population characteristics, such as the proportion of a given allele. However, the requirement of tractable mathematical models (DEs that yield analytical solutions) has involved strong assumptions on the processes investigated, that are poorly representative of the complexity of eco-evolutionary feedbacks in nature [[Govaert2019a](#)]. In particular, ecological scenarios have been strongly simplified, and did not take into account how evolution could affect population dynamics [[Lion2022](#)]. As such, traditional mathematical models have omitted eco-evolutionary feedbacks and density dependence.

With the increase in computational capacity, novel modelling approaches relying on individual based models (IBMs) have appeared [[deangelis2005individual](#)]. IBMs allow to capture processes acting at the individual level, requiring less simplification.

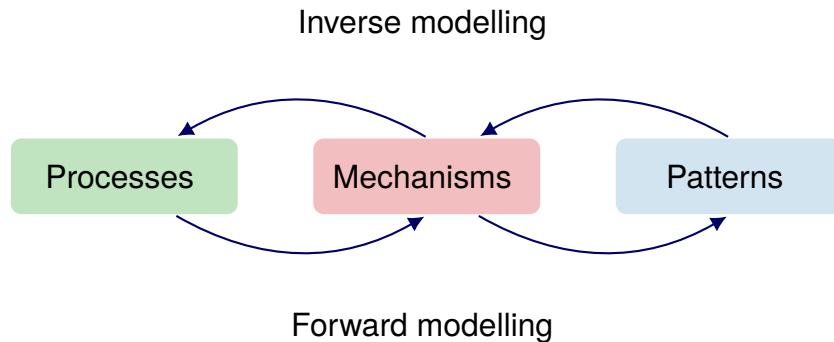
ing assumptions than traditional mathematical models [deangelis2005individual]. Capturing more realistic scenarios by allowing the forward integration of complex hypothesis, the lack of analytical tractability of IBMs may nonetheless occult the mechanisms underlying emergent properties [May2004, 11]. The recent development of mathematical techniques, such moment closure approximations [law1999moment, Gandhi2000, 12, 11], adaptive dynamics theory [Metz1995], and probability theory [13], are generating novel pathways by filling the gap between IBMs and mathematical models. Analogous to renormalisation group analysis developed in quantum and statistical physics [Sayama], they form a toolbox to rigorously derive how emergent properties are influenced by processes operating at different organizational levels. As such, they allow an analytical underpinning to IBM simulations, and can generate a general understanding of the key mechanisms at stake [11].

The combination of numerical simulations and, e.g., adaptive dynamics theory, has successfully shed new lights on the emergence of evolutionary branching under frequency-dependent selection [14, 15]. An other example is the work of [Debarre2013a, 16, 17], that has provided new insights on the effect of habitat heterogeneity on population dynamics. However, our current understanding of eco-evolutionary feedbacks omits potentially significant factors, such as the structuration of populations over complex spatial structures [XX] and highly dimensional phenotypic space [XXX].

The consideration of such details is important to advance our understanding, but raises challenging methodological issues. In particular, complex models may hinder the fundamental mechanisms underlying the emergence of a pattern. Also, the consideration of multiple traits leads to an increase in the dimensionality of the associated DE problem, which in turn leads to an exponential increase in computational cost [XXX]. In order to better understand eco-evolutionary feedbacks, we need to investigate more realistic scenarios, which will, in turn, require the development of novel numerical methods that can cope with the extra computational cost.

## Inverse modelling

Diametrically opposed to forward modelling, inverse modelling consists in using observation data to infer causal processes [18]. Inverse modelling has recently seen an increased attention, thanks to the increased computational power and availability of datasets [Csillary2010]. It involves the use of inference methods to estimate model parameters, such as bayesian or maximum likelihood inference methods [19]. Those methods proceed by defining a distance between the model simulation and



**Fig. 1.2:** Forward and inverse modelling approaches for the understanding of CAS. A forward modelling approach starts with assuming a set of processes, and seeks to understand how their interplay transforms in mechanisms that are associated with macroscopic patterns. An inverse modelling approach starts from empirical patterns (or observations) to deduce the underlying mechanisms and associated processes.

the observation data, which relates to the probability of the parameters given the model and the data [19]. The most likely parameters are associated with the minimum distance, obtained using ad-hoc algorithms. Provided that they are inferred together with uncertainties, parameters can be interpreted to better understand the strengths and effects of the embedded processes [10]. For instance, [20, 21] infers and analyse the parameters of population dynamic models to understand processes involved in ecosystem functions. Because the parameter estimation problem is equivalent to finding the maximum probability of the model given the observation data, inference methods can also be used to discriminate between candidate mechanisms embedded in alternative models [22, 23]. For instance, [Skeels2022] shows that temperature-dependent evolutionary speed is the most likely mechanism to explain variations in biodiversity patterns, using inference methods to discriminate between alternative dynamic models embedding different hypotheses. Nonetheless, the use of inverse modelling in evolutionary biology has been limited because of a number of issues, some of which specifically relating to eco-evolutionary models. Central to these issues are the high computational cost of the forward integration of eco-evolutionary models [24], the large number of parameters involved [25], and their strong nonlinearities[26, 27, 28]. Advances in the field of artificial intelligence could circumvent these issues.

### Machine learning to leverage forward and inverse modelling

In the recent years, the field of artificial intelligence (AI) has made enormous progresses in computer vision [XXX] and natural language processing [XXX]. At

the backbone of this success are key computational techniques that could leverage the forward and inverse modelling of CAS. Computer vision and natural language processing rely on deep learning methods, that allow neural networks to learn abstract representation of mechanisms from large datasets [29]. These abstractions are hardly interpretable by humans [XXX], and their prediction ability is limited by the information contained in the training datasets. As such, neural networks cannot be used *per se* to gain scientific insights and extrapolate beyond observed trends [30, 6]. Nevertheless, their traditional applications and associated methods have been successfully derived in other scientific fields for this purpose [Rolnick2023, 31, 32, 33].

Neural networks have been used in forward modelling, to reduce the cost of the forward integration of climate models, by learning more efficient representations of physical mechanisms [XXX]. They have also been used to approximate the solution of partial differential equations (PDEs) [34], with the major advantage of approximating high dimensional problems at a lower computational cost than traditional methods. Underlying the training of neural network is the technique of backpropagation [XXX]. This technique can be generalised to any scientific model against data [35], with the potential to leverage inverse modelling techniques. As such, the derivation of AI techniques to investigate causal processes in CAS offers unique opportunities [Frank2022].

## Programming languages

Combining ML techniques with scientific models requires computational environments that allow to easily develop scientific models, ensure simulation performance, and provide composability between ML and other scientific libraries [35]. Unfortunately, performance and composability are features that are poorly represented in mainstream programming languages used by the scientific community, such as Python, Matlab or R. Those languages are naturally attractive because they are dynamically typed [XX], allowing convenient development iterations. Nonetheless, prototypes written in Python, Matlab or R need to be rewritten in low level, compiled languages such as C, C++ or Fortran for speed and predictable mapping to hardware [Perkel2019, Bezanson2017]. This conversion requires significant involvement, leading to a problem commonly designated as the "two language problem" [Bezanson2017]. In order to circumvent issues of performance, most libraries in Python, Matlab or R rely on bindings with low level languages. For instance, the most used deep learning libraries in Python, TensorFlow and PyTorch, are internally written in C. However, bindings with low level languages come with major negative externalities, such as restricting the understandability of their internals

to computer scientists – prohibiting potential development contributions from the scientific community –, and preventing the composability of libraries [XXX].

Julia is a programming language that was launched in 2012 to address the issue of the two-language problem [Bezanson2017, Bezanson2018]. Julia was built over a type-specializing, just-in-time compiler, which makes it easy to generate highly performant programs, while preserving the essential features of Python, Matlab or R, such as dynamic typing and automatic memory management. Importantly, it relies on multiple dispatch, which allows to generate highly generic code with good performance. This permits to write libraries in pure Julia, guaranteeing productivity and composability. As such, the internals of any Julia library can be understood by non computer-scientists, who can further use his expertise to participate to its development. Many Julia libraries benefit from a high number of contributions of independent users (see, e.g., [github.com/DifferentialEquations.jl](https://github.com/DifferentialEquations.jl)). Multiple dispatch also allows to automatically generate the gradient of any Julia program without any modification [**ForwardDiff.jl**, **Zygote.jl**]. This means that any scientific library in Julia, such as differential equation solvers, can be combined with deep learning tools, with unique opportunities for forward and inverse modelling problems [Frank2022]. As such, Julia allows to prototype a program which is readily generic and can directly be shared to the research community. Further, by granting the composability of libraries, it allows to blend ML techniques with scientific models. This makes Julia a promising computational environment to accelerate research in CAS.

## Thesis outline

In summary, while it is increasingly acknowledged that feedbacks between ecological and evolutionary processes play an important role in the dynamics of biological systems [5, 6], our understanding of the mechanisms in which they are involved has been limited to simplified scenarios. Further, while analogous processes have been suggested to influence the dynamics of economic systems [Hodgson2019], a quantification of their effect is missing. Under increasing anthropogenic pressure, these research directions become essential [6], but raise challenging methodological issues. Here, I present novel forward and inverse modelling approaches to advance our understanding of eco-evolutionary dynamics in biological and economic systems, and utilise them to shed light on the underlying processes and resulting mechanisms.

In ??, I investigate how eco-evolutionary processes, in combination with complex habitat spatial structures, influence the trait distribution of biological populations. I proceed using a forward modelling approach, building a stochastic eco-evolutionary IBM where individuals are structured over a spatial graph, and experience the fundamental processes of reproduction, competition, mutation and migration. I

seek to understand how those microscopic forces result in trait differentiation at the population level. I derive DE approximations of the IBM that, together with extensive numerical simulations, provide analytical insights into how the graph properties affect the population size and trait differentiation. In particular, I show that three main graph properties, measuring landscape connectivity, heterogeneity in connectivity, and habitat spatial auto-correlation, shape the trait differentiation of the biological population. These results establish mechanistic links between landscape features and the eco-evolutionary dynamics of biological populations.

In ??, I develop an inverse modelling method to estimate the parameters of highly nonlinear population dynamic models. The method is based on a machine learning framework and involves AI techniques together with a novel learning strategy. This learning strategy consists in training the model against mini-batches of data with short time horizon, which I analytically show to regularize the learning problem. I implement the ML framework in the Julia library **MiniBatchInference.jl**, and demonstrate through numerical experiments that it can efficiently estimate model parameters and provide statistical evidences for causal processes from noisy, incomplete and independent time series. Altogether, the proposed ML framework is a workhorse for inverse modelling and can elucidate mechanistic pathways in biological and economic systems.

In ??, I quantify the effect of eco-evolutionary processes on the dynamics of economic systems. I employ the ML framework developed in ?? to investigate how alternative eco-evolutionary population dynamic models can explain the dynamics of economic activities in the richest 100 countries, relying on 59 year of economic data. The models embed the processes of ecological interactions between economic activities, spatial transfers, and economic activity transformations, which support is compared to a simple logistic growth model, taken as a null model. I find strong statistical evidence for positive interactions between national economic activities, and spatial transfers across countries. To my knowledge, this is the first study that provides quantitative evidences that similar processes may influence the dynamics of biological and economic systems.

In ??, I extend two recent methods to solve high dimensional PDEs, in order to handle non-local nonlinear terms. The first method relies on Picard iterations, while the second is based on machine learning and involves neural networks to approximate PDE solutions. The numerical difficulties arising due to the non-local term are avoided by using a plain vanilla Monte Carlo integration. I implement the methods in the Julia library **HighDimPDE.jl**, and evaluate their performance on high dimensional PDE models arising in physics and biology, including population dynamic eco-evolutionary models. For all models, the methods yield good results

with short run times, offering the possibility to include more realism in future eco-evolutionary models.

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# Discussion

„ Les données pertinentes détiennent les réponses.

— French anagram

## 2.1 Contributions

Understanding biological and economic systems involves the understanding of the necessary and sufficient elemental processes, and their couplings, that result in mechanisms constraining their dynamics [1]. Along this line, my work aimed at advancing our quantitative understanding of how ecological and evolutionary processes, and their interplay, shape the dynamics of biological and economic systems. In particular, this thesis contributed to

- (i) a fundamental understanding of the role of eco-evolutionary processes in shaping the dynamics of biological populations structured in complex landscapes [chap1],
- (ii) the quantification of the effect of mechanisms associated with eco-evolutionary processes in economic systems ??,
- (iii) methodological advances in the forward and inverse modelling of eco-evolutionary dynamics ??????.

In the following, I discuss the chapters of my thesis collectively within the broader context of our current understanding of the dynamics of biological and economic systems, and the accompanying modelling paradigm.

### 2.1.1 Advances in the fundamental understanding of biological and economic systems

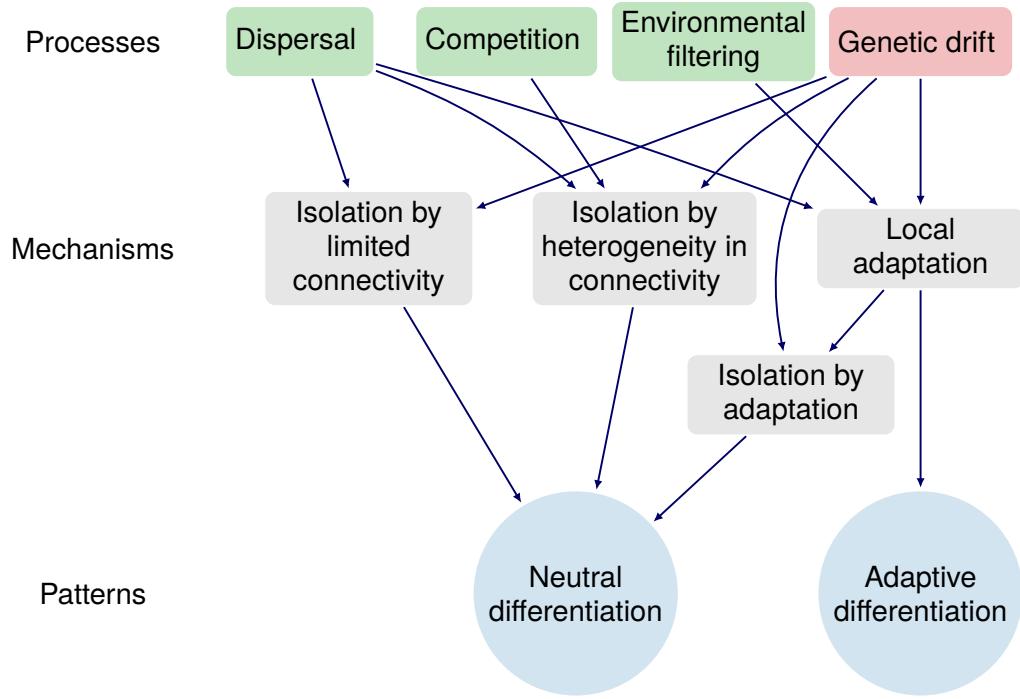
#### Linking eco-evolutionary processes to patterns of differentiation

Spatial patterns of biodiversity result from microscopic processes acting upon individual organisms [2], which include reproduction, competition, mutation and dispersal. Mutations result in genetic drift, which promotes stochastic variations in the allelic proportions and phenotypes of biological populations [XXX]. In spatially structured

populations, this results in turn to "neutral differentiation", where spatially isolated populations are characterised by differentiated alleles and traits [XXX]. Dispersal tends to reduce neutral differentiation, and this effect is modulated by landscape connectivity [3, 4, 5] through the mechanism of "isolation by limited dispersal" [6]. By increasing the dispersal ability of organisms, landscape connectivity decreases neutral differentiation. When landscapes present heterogeneous habitats, natural selection can supplement the effect of genetic drift and increase the sole effect of stochasticity on differentiation. Under this scenario, local environment conditions select individuals with traits that provide them higher fitness [XXX]. At the population level, this results in populations adapting to their local environment, a mechanism coined "local adaptation" [7] and resulting in patterns of "adaptive differentiation". Adaptive differentiation is hindered by dispersal, which prevents local adaptation by bringing maladapted individuals, that destabilise the evolution of traits towards the optimal. While adaptive differentiation concerns traits under selection, it indirectly affects the differentiation of neutral traits, that are co-evolving with traits under selection through linkages [XXX]. This results in turn to the mechanism of "isolation by adaptation", where habitat heterogeneity, rather than landscape connectivity, increases neutral differentiation [nosil2008]. Simple mechanisms resulting in neutral and adaptive differentiation are identified, but how they are modulated by eco-evolutionary feedbacks and landscape complexity is unclear.

In ??, I demonstrate a novel mechanism, involving the ecological process of competition, that considerably affects neutral differentiation. Through the creation of unbalanced migration fluxes which increases the intensity of competition in highly connected populations, heterogeneity in connectivity reduces gene flow and reinforces neutral differentiation. I also investigate the mechanism of local adaptation and how it results in adaptive differentiation in complex landscapes, where habitats are arranged in a realistic fashion. I show that the complexity of habitat spatial distribution can be reduced to a measure of habitat spatial auto-correlation, coined the "habitat assortativity". Landscapes characterised by a high habitat assortativity systematically support populations that are locally better adapted than in landscape with low assortativity, resulting in higher adaptive differentiation. Specifically, I provide an analytical condition for local adaptation that sheds light on how it relates to dispersal intensity, selection strength, habitat heterogeneity, and habitat assortativity.

Because habitat assortativity affects local adaptation, it must also affect neutral differentiation through the mechanism of isolation by adaptation. Closing the loop, I demonstrate that habitat assortativity affects population differentiation through two antagonistic effects. By favoring local adaptation, it promotes isolation by adaptation, therefore increasing neutral differentiation. In parallel, it also favors gene flow within clusters of similar environmental conditions, decreasing isolation by limited



**Fig. 2.1:** Summary of the causal pathways involved in neutral and adaptive differentiation, disentangled in ???. Ecological processes are displayed in green boxes, evolutionary processes are displayed in red boxes.

dispersal. This results in habitat assortativity decreasing neutral differentiation for low dispersal intensity, and increasing neutral differentiation for high dispersal intensity. This complex feedback is essential to understand population differentiation in complex landscapes.

I provide a summary of the processes and resulting mechanisms shaping neutral and adaptive differentiation in Fig. 2.1. Overall, ??links processes to patterns, establishing a map of the causal pathways involved in the phenotypic differentiation of populations.

### Linking economic patterns to eco-evolutionary processes

??provides a novel understanding of the role of eco-evolutionary processes in economic systems by assessing their effect on the dynamics of economic activities from data. Neoclassical economics and evolutionary economics seek to explain economic change with formal modelling, focusing on the relationships between economic variables such as output, employment and productivity [Boschma2005a]. In particular, evolutionary economics is concerned with explaining economic change by endogenous forces, such as interactions between firms and economic activities, and evolutionary processes acting upon them [Hodgson2019, Metcalfe2006]. In oppo-

sition to this approach, complexity economics seeks to predict variations in national income by using fine-grained data of economic activity outputs and dimensionality reduction techniques, without assumptions on the underlying processes [Hidalgo]. While a current concern in evolutionary economics is to obtain an agreement between the mechanisms proposed and empirical observations [XXX], complexity economics seeks to understand the causal processes underlying the success of the dimensionality reduction technique [XXX].

By being agnostic to economic variables yet providing a causal link with the most probable processes underlying economic development, ??bridges evolutionary economics and economic complexity. The approach relies on the simple observation that the dynamics of economic activities contains signatures from the many complex processes that underpin them. These signatures consist in peculiar effects that can be conveniently modelled by biologically inspired population dynamic models. Economic activities are characterised by organizational routines, which experience evolutionary processes and define how they engage in ecological processes. As a result, economic outputs behave similarly to the size of biological populations [Boschma2005a]. Inverse modelling approaches to infer the eco-evolutionary processes involved in patterns in biological systems can then be used to disentangle the role of the processes investigated.

Using population dynamic models embedding capturing the effect of fundamental processes proposed in the evolutionary economics literature [XXX], ??provides empirical evidence that economic activities engage in positive interactions, and benefit from spatial transfers of knowledge and routines. Positive interactions may arise from a variety of processes proposed in the evolutionary economic literature, such as supply chains [Ozman2009, Saavedra2009a] and knowledge spillovers [Menon2015]. Its support implies that diversity promotes economic development [Hidalgo2018], as economic activities promote each other. Discrepancies in the strength of evidence obtained for spatial transfers across countries highlight that some countries are overall more akin to spatial transfers than others, which may be explained by differences in cognitive, organizational, social, institutional or geographic proximities. I provide a summary of the mechanisms evidenced in economic systems in ?. Overall, ??bridges approaches in economics and biology to understand the mechanisms shaping the endogenous dynamics of economic systems.

## 2.1.2 Methodological advances in forward and inverse modelling

### Advances in the modelling of realistic spatial and phenotypic structures

???? provide new tools to better understand mechanisms resulting from ecological and evolutionary processes, and their interplay, in the context of realistic spatial and phenotypic structures.

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