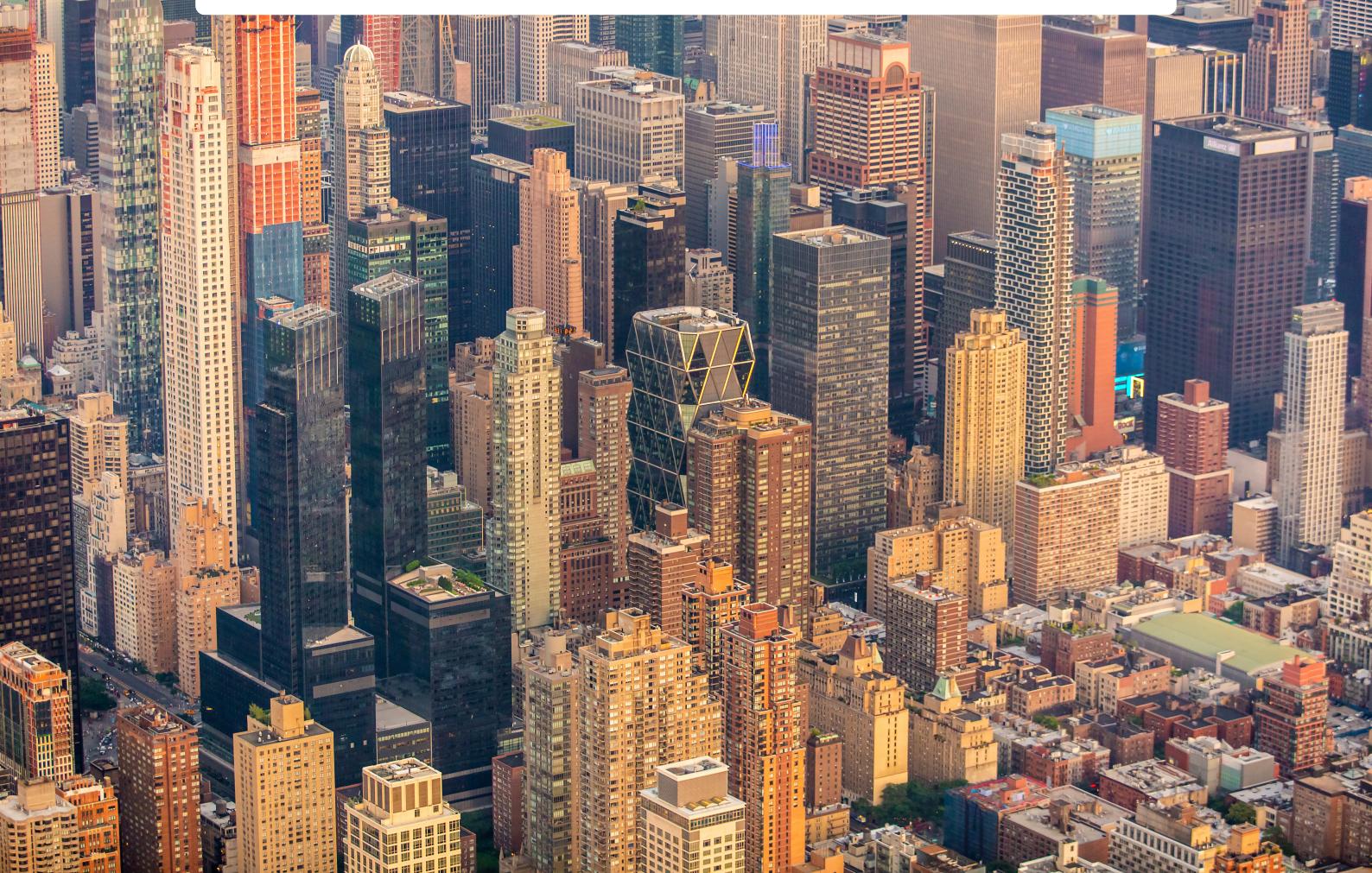


Forward and inverse modelling of eco-evolutionary dynamics

in biological and economic systems

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

„ Nature loves to hide.

— Heraclitus (c.6th-5th century BCE)

1.1 Context

1.1.1 Biological and economic systems as complex adaptive systems

What are the similarities between the dynamics of biological and economic systems? Think of a biological system as community of interacting biological organisms ([chapin2002principles](#)), and think of an economic system as a community of interacting economic agents (Dopfer and Potts, 2007). *A priori*, the processes underlying the dynamics of an economic system strongly differ from that of biological systems, because the behavior of economic agents is motivated by rationality ([XXX](#)), where economic agents maximize utility. Nonetheless, economic agents are faced with uncertainty ([Foster2012](#)) and their rationality is bounded ([HerbertSimon](#)). As a result, economic agents adopt a variety of behavioral rules (e.g. technological, organizational, institutional, [Foster2012](#)) through trial-and-errors, which are subject to natural selection through competition processes ([Schumpeter](#)). In this perspective, both biological and economic systems are complex adaptive systems (CAS) (Levin, 2002), composed of heterogeneous entities that interact in nonlinear ways and experience evolutionary processes. Interestingly, the stochasticity of the processes involved, and their couplings, do not necessarily lead to unpredictable structures and dynamics ([Olff2009](#)), but rather induce organised structural properties and invariant patterns ([Olff2009](#); [mitchell2009complexity](#)). In biological systems, invariant patterns include patterns of species richness, where for instance montane regions are often associated with a disproportionately high number of species (Rahbek et al., 2019b). In economic systems, invariant patterns include the bimodal shape of the distribution of international income, where some countries have systematically developed much more rapidly than others ([ace moglu2001colonial](#)). The processes of interaction and evolution involved take many different forms and operate at different organizational level ([Levin1998](#)), from genes to ecosystems, and from



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

organizational routines to economies (see Fig. 1.1). A common direction on the research agenda to understand the dynamics of biological and economic systems is to identify the fundamental dynamical processes involved, and the associated mechanisms (Fig. 1.1,Nordbotten et al., 2018). In biological systems, the fundamental processes resulting in patterns of species richness are identified (Hagen; Rahbek et al., 2019a; Rangel et al., 2018), and the current challenge is to underpin the mechanisms resulting from their couplings (Fig. 1.2). In economic systems, we still do not exactly understand the fundamental processes at stake.

1.1.2 Ecological and evolutionary processes drive the dynamics of biological systems

In biological systems, interaction processes are more commonly designated as ecological processes, and encompass the processes of interaction between organisms (biotic interactions) and between organisms and their environment (abiotic interactions), as well as dispersal processes (movement of individual across space) (Vellend, 2010). 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 acknowl-

edged since the very birth of the theory of evolution. During his voyage on the Beagle, Darwin documented 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](#)). 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 interact with evolutionary processes, and together shape the long term dynamics of biological systems ([Hagen](#); Rahbek et al., 2019a; Rangel et al., 2018). Empirical studies have now demonstrated that evolution can be rapid and occur on similar time scales as ecology ([Hairston2005](#); Pelletier et al., 2009) and have quantifiable effects on ecological dynamics ([Ezard2009](#)), leading to feedbacks between ecological and evolutionary processes, so-called eco-evolutionary feedbacks ([Schoener2011](#); [Govaert2019](#); Pelletier et al., 2009). Eco-evolutionary feedbacks involve situations where an ecological process (e.g., replication, competition, dispersal) influences an evolutionary process (e.g. phenotypic change), which then feeds back to an ecological process, or vice versa ([Govaert2019a](#)). Examples are feedbacks between population dynamics (replication and competition) and trait evolution (phenotypic change), which can lead to evolutionary branching through the effect of competition ([Doebeli1999](#)). In spatially structured populations, an other classical example of eco-evolutionary feedbacks is the mechanism of local adaptation (Savolainen et al., 2007), where feedbacks between population dynamics, dispersal and trait evolution can facilitate or prevent populations to adapt to local environmental conditions (Meszéna et al., 1997; Doebeli and Dieckmann, 2003). Importantly, the eco-evolutionary feedbacks involved in adaptation mechanisms are expected to affect the dynamics of the biosphere in the coming decades (Norberg et al., 2012; Urban et al., 2016), because of rapid changes in local environmental conditions experienced in ecosystems, through the effects of anthropogenic pressure and climate change (Ellis, 2011; Midgley and Hannah, 2019). Nevertheless, our understanding of their effect and modality under realistic biological scenarios is limited ([Lion2022](#)). Eco-evolutionary feedbacks may greatly influence the dynamics of ecosystems (Norberg et al., 2012; Urban et al., 2016), calling for a better understanding of their effect in realistic biological scenarios ([Lion2022](#)).

1.1.3 Drivers of economic change

The processes that determine economic change is controversial in economics ([Nelson2014](#)). To explain economic development, mainstream economic theory (Lawson, 2013) 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 (Hodgson, 2019). For instance, firms or economic activities may interact positively or negatively (Pistorius2007Ozman2009; Wernerfelt, 1989; Saavedra et al., 2009; Cohendet et al., 2018; Menon, 2015), spread across space (Rogers, 2003; Zahra et al., 2000), and adapt (Cordes, 2006) or transform into new economic institutions (Freeman, 2002; Hodgson and Knudsen, 2004; Aldrich et al., 2008), 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 (Tacchella et al., 2018; Saavedra et al., 2009; Scholl et al., 2021; Zhang et al., 2018; Modis, 1997; Saavedra et al., 2014; Farmer and Lo, 1999; Michalakelis et al., 2011; Marasco et al., 2016; Gatabazi et al., 2019; Cauwels and Sornette, 2012; Applegate and Lampert, 2021; Suweis et al., 2015). For instance, (Saavedra et al., 2009) has successfully used a model of mutualistic interaction to explain structural patterns in industrial cooperation. Also, (Scholl et al., 2021) 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.

1.2 Modeling eco-evolutionary dynamics

1.2.1 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; Pontarp et al., 2019). As such, a deductive approach, relying on forward modelling, has traditionally been put forward to advance our understanding of the mechanisms underlying (Brummitt et al., 2020). 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 simplifying 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](#); Lion, 2016). The recent development of mathematical techniques, such moment closure approximations ([law1999moment](#); [Gandhi2000](#); Nordbotten et al., 2020; Lion, 2016), adaptive dynamics theory ([Metz1995](#)), and probability theory (Champagnat et al., 2006), 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 (Lion, 2016).

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 (Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2003). An other example is the work of ([Debarre2013a](#); Meszéna et al., 1997; Mirrahimi and Gandon, 2020), that has provided new insights on the effect of habitat heterogeneity on population dynamics. However, our current

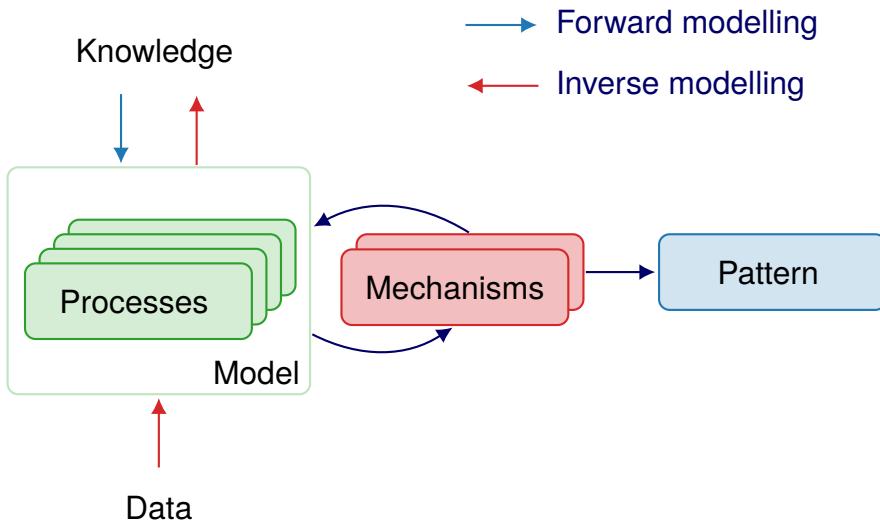


Fig. 1.2: Forward and inverse modelling approaches for the understanding of CAS.
A forward modelling approach starts with assuming a set of processes, that are embedded in a model, and seeks to understand how their interplay transforms in mechanisms that are associated with a macroscopic pattern (macroscopic invariance). An inverse modelling approach integrates empirical observation to constrain the model output, generating knowledge by inferring the probability and the strength of the processes investigated, given the empirical observations. Similarly to forward modelling, mechanisms may be deduced from the processes inferred, leading to the undersanding of invariances (pattern).

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 understandning, but raises challenging methodological issues. In particular, complex models may hinder the fundamant 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.

1.2.2 Inverse modelling

While in forward modelling, observation data is uniquely considered at the end of the modelling cycle - when comparing predicted and empirical patterns to refine

prior knowledge on the system investigated -, inverse modelling integrates empirical data right at the start the modelling cycle to characterise the processes involved (XXX)(Fig. 1.2). Inverse modelling can take the form of parameter estimation (Schartau et al., 2017) or model selection (Johnson and Omland, 2004), both involving the use of inference methods to estimate, respectively, the most probable model parameter value, or the most probable model among candidates, given empirical data. In parameter estimation, provided that they are inferred together with uncertainties, parameters can be interpreted to better understand the strengths and effects of the associated processes (Pontarp et al., 2019). For instance, (Higgins et al., 2010; Curtsdotter et al., 2019) infer and analyse the parameters of population dynamic models to understand the processes involved in ecosystem functions. In model selection, the candidate models embed competing hypotheses about processes and mechanisms, and the relative support of each model given the data is used to discriminate (Johnson and Omland, 2004). For instance, (**Skeels2022**) shows that temperature-dependent evolutionary speed is the most likely mechanism to explain variations in biodiversity patterns, using inverse modelling to discriminate different evolutionary hypotheses embedded in alternative eco-evolutionary models. Inverse modelling strongly relies on inference methods, used to calculate the parameter and model probabilities given the data. Inference methods proceed by characterising the global, or minimum, distance between the model simulation and the observation data (XXX), which relates to the probability of the data given the model and the parameter values (Schartau et al., 2017). Inference methods are limited by the difficulty to compute the global or minimum distance between a model and the empirical data. This problem is tightly related to the model complexity (**Csillery2010**), where the number of model parameters, the computational cost associated to the model integration, and the model nonlinearity prevent to correctly approximate the distance. As such, inverse modelling methods have mostly been used with simple evolutionary models (**Csillery2010**). In contrast, eco-evolutionary models are characterised by a high computational cost (Fisher et al., 2018), are dependent on a large number of parameters (Boyd, 2012), and are strongly nonlinear (Hastings et al., 1993; Huisman and Weissing, 1999; Benincà et al., 2008), challenging the use of inverse modelling to uncover eco-evolutionary processes. Advances in the field of artificial intelligence could circumvent these issues, allowin to confront eco-evolutionary models with empirical systems (XXX).

1.2.3 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 (LeCun et al., 2015). 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 (Barnosky et al., 2012; Urban et al., 2016). Nevertheless, their traditional applications and associated methods have been successfully derived in other scientific fields for this purpose (Rolnick2023; Kashinath et al., 2021; Schneider et al., 2017; Yazdani et al., 2020).

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) (Sirignano and Spiliopoulos, 2018), 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 (Rackauckas et al., 2020a), 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).

1.2.4 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 (Rackauckas et al., 2020a). 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). 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.

1.3 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 (Pelletier et al., 2009; Urban et al., 2016), 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 (Hodgson, 2019), a quantification of their effect is missing. Under increasing anthropogenic pressure, these research directions become essential (Urban et al., 2016), 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.

Discussion

”

*To be but one with all living things, to return, by
a radiant self-forgetfulness, to the All of Nature.*

— Friedrich Hölderlin (1770-1843)

2.1 Contributions

Understanding biological and economic systems involves the underpinning of the elemental processes underlying the systems' macroscopic features, and establishing the associated mechanisms (Levin, 2002, Fig. 1.2). Following this approach, my work aimed at advancing our 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 ??,
- (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 Advancing our fundamental understanding of eco-evolutionary processes in biological and economic systems

Linking eco-evolutionary processes to patterns of differentiation

Spatial patterns of biodiversity result from the processes of selection, mutation and dispersal, that act upon individual organisms ([hamilton2021population](#)). In finite size populations, mutations result in "drift" ([Slatkin1987a](#)), causing stochastic

variations in the allelic proportions and phenotypes of biological populations. In geographically structured population, drift results in patterns of neutral differentiation (**Slatkin1987a**), where isolated populations are characterised by differentiated allelic proportions and phenotypes. Dispersal tends to reduce neutral differentiation (**Slatkin1987a**), and this effect is modulated by landscape connectivity (Wright, 1943; McRae, 2006; McRae and Beier, 2007) through the mechanism of "isolation by limited dispersal" (Orsini et al., 2013). By increasing the dispersal ability of organisms, landscape connectivity decreases neutral differentiation (Lande, 1991). When landscapes present heterogeneous habitats, natural selection can supplement the effect of genetic drift and increase the sole effect of stochasticity on differentiation (**fisher1958genetical**). Under this scenario, local environment conditions select individuals with traits that provide them higher fitness (**Gaither2018**). At the population level, this results in populations adapting to their local environment, a mechanism coined "local adaptation" (Kawecki and Ebert, 2004) 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 (Meszéna et al., 1997; Débarre et al., 2013; Mirrahimi and Gandon, 2020). 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 (Billiard et al., 2015; Lepers et al., 2021). 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 process of intra-specific 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 how the mechanism of local adaptation 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.

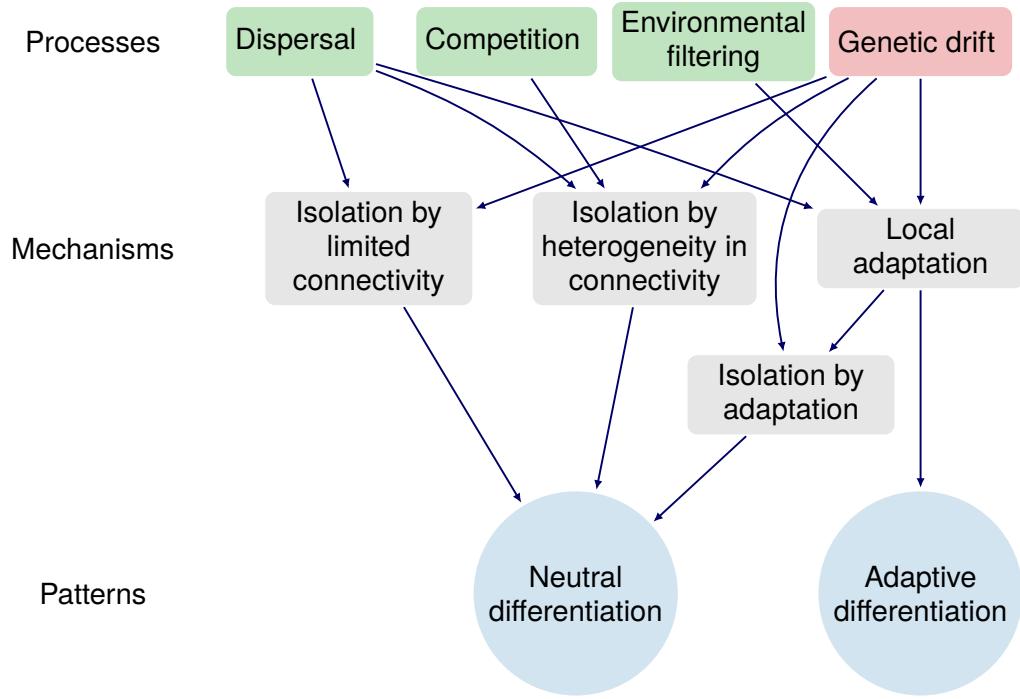


Fig. 2.1: Summary of the causal pathways involved in neutral and adaptive differentiation, disentangled in ?? . Ecological processes are displayed in green boxes, evolutionary processes are displayed in red boxes.

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 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 an extensive map of 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. 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 (Boschma and Frenken, 2005). 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 (Metcalfe2006; Hodgson, 2019). In opposition to this approach, complexity economics (Hidalgo, 2021) seeks to predict variations in national income by using fine-grained data of economic activity outputs and dimensionality reduction techniques (Mitchell, n.d.), without making 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. Our 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 temporal variations and couplings that can be conveniently modelled by biologically inspired population dynamic models, which use are additionally justified by deep analogies between economic activities and biological populations. Analogously to biological populations that are characterised by genes, economic activities are characterised by organizational routines (NelsonWinter), which experience evolutionary processes and define how they engage in ecological processes (NelsonWinter). As a result, and similarly to the size of biological populations, the capital growth of economic activites is determined by the ensemble of organizational routines that characterise them (Boschma and Frenken, 2005). Similarly to approaches used in ecology and evolution (Skeels), inverse modelling approaches can then be used to disentangle, from their signatures (Skeels) left on the dynamics of economic activities, the role of the eco-evolutionary processes acting upon them.

Specifically, ?? explores the effect of eco-evolutionary processes, proposed in the evolutionary economics and geography economics literature, on the dynamics of economic activities at the national scale. In particular, ?? seeks to test whether the dynamics of economic activities can be explained by different types of interdependencies, including positive (XXX) and negative interactions (XXX), spatial transfers (XXX), and economic transformations (XXX). Using population dynamic models capturing the different interdependencies, ?? 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 (Ozman, 2009; Saavedra et al., 2009) and knowledge spillovers (Menon, 2015). Its support implies that diversity promotes economic development (**Hidalgo2018**), as economic activities promote each other. The support for spatial transfers implies that, besides international patent laws (**XXX**), transfers of knowledge and organisational routines have a considerable effect on economic activities. Nevertheless, 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 across countries (**XXX**). 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 Leveraging forward and inverse modelling with ML

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 population structures and phenotypic distributions. Evolutionary dynamics have been traditionally studied in the context of regular population structures (Lieberman et al., 2005). For instance, Slatkin, 1973; Slatkin, 1978; Kirkpatrick and Barton, 1997; Polechová and Barton, 2015; Polechová, 2018; AndradeRestrepo et al., 2019; Doebeli and Dieckmann, 2003; Meszéna et al., 1997; Yeaman and Otto, 2011; Débarre et al., 2013; Mirrahimi and Gandon, 2020 consider regular spatial structures to investigate differentiation in biological populations, missing the effect of spatial complexity on the underlying mechanisms. Biological habitats differ in their connectivity (**XXX**), and economic entities are structured through complex networks (**XXX**). Lieberman et al., 2005 and subsequent studies of "evolutionary dynamics on graphs" (**XXX**) show that this complexity affects the interplay between selection and drift. However, evolutionary dynamics on graphs does not consider eco-evolutionary feedbacks (**Govaert2019a**). Thus far, models that include frequency dependence together with realistic, complex population structures were missing.

While a vast majority of the work on eco-evolutionary feedbacks has focused on the evolution of scalar phenotypes (**Doebeli2011**), in most organisms, many phenotypic properties combine in complicated ways to determine ecological processes (**Doebeli2014**). For instance, **Doebeli2011** shows that the consideration of multiple traits is likely to generate more diversity than expected with one dimensional models. Trade-offs in traits is also an essential feature shaping the evolutionary dynamics

of biological populations, with consequences on the dynamics of e.g. cancer cell evolution (XXX) and plankton dynamics (XXX). While there is overall a genuine need to better understand evolutionary dynamics in high dimensional spaces, the simulation of high dimensional models is tremendously difficult, since the numerical cost of traditional methods grows exponentially in the number of dimensions of the phenotypic space.

?? develops a generic modelling framework to capture the effect of eco-evolutionary processes on biological populations structured in complex landscapes, and ?? provides tools to efficiently simulate the resulting high-dimensional models. The IBM presented in ?? involves the combination of graphs and highly dimensional phenotypic spaces, together with eco-evolutionary feedbacks, to model population structures. The modelling framework presented can readily be generalised, and the code associated to the numerical experiments in ?? include a Julia library, **Evoid.jl**, that implements a more general version of the model. As such, the modelling framework presented in ?? may be used to investigate other questions involving complex population structures and the co-evolution of characterisits. Reproducing the discrete and stochastic nature of ecological and evolutionary processes (Champagnat et al., 2006), simulations of the IBM may not provide a general understanding of system investigated (XXX), and cannot be scaled to simulate large systems involving millions of individuals (XXX). Nevertheless, the IBM proposed in ?? is mathematically tractable under simplifying assumptions, and can be efficiently simulated with a deterministic PDE approximation. Tractability allows to obtain analytical insights on how structural properties affect macroscopic population under simplifying assumptions (??). The PDE approximation, combined with the numerical methods presented in ??, further allow efficient simulations. I have implemented the numerical methods for simulating high dimensional models in the Julia library **HighDimPDE.jl** (**HighDimPDE**), a registered Julia package belonging to the SciML organisation (XXX). The user interface respects standards from the SciML organisation, meaning that Julia users can easily adopt it. The package aims at hosting many more solver algorithms that break down the curse of dimensionality, and is currently receiving contributions from developers to implement the DeepBSDE scheme (Han et al., 2018).

The combination of analytical insights and numerical simulations can help to elucidate the links between microscopic processes and macroscopic properties (Levin). ???? provide novel analytical and numerical tools to better understand how complex spatio-evolutionary structures affect the interplay between eco-evolutionary processes and generate macroscopic patterns.

Advances in inference methods for the investigation of eco-evolutionary processes

???? develop and test a novel inverse modelling method that allows to infer highly nonlinear dynamical processes from observation data, opening up new venues to advance our understanding and prediction of the dynamics of biological and economic systems. The most developed inference methods in current use for inverse modelling are Bayesian inference methods with Markov Chain Monte Carlo (XXX) and variational methods (XXX). Bayesian inference methods require a large number of forward model integrations (Schneider et al., 2017), and are highly affected by the number of model parameters (Csillary2010). Variational methods require the model sensitivity to its parameters (XXX) and are prone to converge to local minima, especially with complex models (XXX). Those central issues likely explain the very poor number of studies that have used inverse modelling to further our knowledge on eco-evolutionary dynamics (XXX).

?? presents a novel inference framework that can efficiently recover the most probable parameter values of eco-evolutionary models, given temporal data. The framework is based on a variational method, but resolves its main shortcomings by including key ingredients in the recipe, including automatic differentiation (Rackauckas et al., 2020b), state-of-the-art optimizers (Kingma and Ba, 2014), and a learning strategy based on a mini-batch method. The use of automatic differentiation simply eliminates the effort required to obtain the model sensitivity to its parameters, and the state-of-the-art optimizers, together with the mini-batch method, ensure the efficiency and reliability of the method in handling highly nonlinear models. ?? is part of an ongoing effort to blend ML and traditional models to gain scientific understanding and extrapolability (XXX). In physical systems such as ocean and atmospheric systems (XXX), invariant laws are known, and ML is mostly used to improve model forecast skill. In contrast, models of biological and economic systems are yet to be formulated, methods such as the the ML framework presented in ?? can greatly contribute to gain scientific knowledge. By contrasting competing hypotheses embedded in alternative models, ???? provide concrete examples, both with synthetic and empirical data, that the ML framework can successfully elucidate eco-evolutionary mechanistic pathways. The proposed method is also relevant for improving the forecast of predictive eco-evolutionary model Urban et al., 2016, and integrates the practical constraints of datasets including short time series with partial, noisy, shallow and independent observations (Dornelas et al., 2018).

The ML framework is implemented in the multi-purpose Julia package **MiniBatchInference.jl** (**MiniBatchInference**), readily available to the scientific community. **MiniBatchInference.jl** is built around the celebrated differential equation solver

`DifferentialEquations.jl` and the deep learning library `Flux.jl`. As such, the use of `MiniBatchInference.jl` requires very limited efforts to any user familiar with those libraries.

Overall, the method proposed in ?? successfully blends ML methods with mechanistic ecosystem models to improve our gain scientific knowledge from observation data. Concrete case examples in ???? show that it enables the testing of eco-evolutionary theories against data, advancing our understanding and the improvement of current mechanistic models, with the potential to provide better forecasts of ecosystems states (Urban et al., 2016).

2.2 Limitations

2.2.1 Forward modelling

Alternatives to the methods presented in ???? may be more appropriate for the forward modelling of eco-evolutionary dynamics. While IBMs are interesting tools to investigate stochastic drift in finite size populations, the Gillespie algorithm (Gillespie, 1976) used to simulate the IBM in ?? is computationally intensive, and requires to compute the fitness of all individuals at each time step, which depends on the characteristics of all the other individuals. The resulting computational complexity grows polynomially with the number of individuals ($\mathcal{O}(N^2)$). While it is an interesting tool to investigate stochastic drift in finite size populations, it cannot be used to model large populations. On the other hand, PDEs can provide deterministic approximations of IBMs (Champagnat et al., 2006), while demanding less computational power. The methods presented in ?? can approximate PDEs in high dimensions (up to 10 traits, which seems more than enough in practice (XXX)), but still suffer from a number of issues that may prevent their practical use. In particular, the MLP method can only provide the population density for one single trait value, and as such, cannot characterise the total population density with a reasonable computational complexity. On the other hand, the ML based approximation method can provide the full population density, but involves the training of many neural networks, one at each time step. This is worrying, since the training of a neural network is numerically costly, and that long simulation times may be required by practitioners. An other problem with the numerical methods proposed in ?? is that they involve the tuning of meta parameters, including the choice of a kernel for the integration of the nonlocal term. This choice is critical for the success of the approximation, but how to determine it is not clear. Together, the methods proposed in ?? may require further development to be used in practice by practitioners. Yet irrespective of the numerical method used, solving PDEs inevitably

requires a considerable computational effort, because PDEs track the evolution of the full phenotypic density of populations. Nevertheless, only the first three moments of the population density are usually of interest to investigate eco-evolutionary dynamics (population size, trait mean and trait variance, see **XXX**). Instead of seeking to numerically approximate the full phenotypic density, moment closure approximation methods (**Wickman2021; Lion2022**; Nordbotten et al., 2020) may be, so far, more appropriate tools. Those approaches consist in approximating the population density with a gaussian distribution. This, in turn, allows to transform the PDE problem into a system of coupled differential equations involving the time evolution of the population size (1 variable for a single species population), the mean trait value in each dimension of the trait space (d variables), and the variance-covariance matrix of the trait density (d^2 variables). As such, the computational cost of this method scales only polynomially with the number of dimension ($\mathcal{O}(d^2)$), while providing the exact information required to investigate eco-evolutionary dynamics in high dimensional spaces. It is worth noting that instead of neural networks, gaussian functions could easily be used with the ML-based approximation method to simulate PDEs. Equivalent to the assumption taken in the moment closure methods presented in **Wickman2021; Lion2022**; Nordbotten et al., 2020, we expect that this approach would greatly improve the computational efficiency of the ML-based approximation method in simulating eco-evolutionary models, while solving the problem of the choice of a kernel for the integration of the nonlocal term. Using Gaussian functions may considerably lower the number of iterations required in the training process, while reducing the computational cost, as they involve less parameters ($d(d + 1) + 1$) than neural networks (*xx* in ??).

2.2.2 Inverse modelling

The inverse modelling framework proposed in ?? and used in ?? also present shortcomings, which may favor the use of other methods to infer eco-evolutionary processes from data. First, the mini-batching learning strategy requires the choice of a minibatch size to ensure the convergence to the maximum likelihood estimate. This choice is arbitrary, but may affect the model selection process. Reducing the batch size implies that the model is fitted on the short term dynamics of the data, but because the model is likely to only characterise some of the features of the data, the resulting support could differ, were the model rather fitted to long term dynamics. Theoretical developments will be required to better understand the assumptions behind the choice of the mini-batch size, which may provide guidance to the choice of this meta parameter. Second, the proposed method may fail to find the maximum likelihood estimate of complex models, since the associated likelihood landscape is

harder to navigate than simpler ones. This may lead to a bias in the model selection process towards simpler models. Third, the information criterion-based model selection procedure used in **????** is uniquely based on a trade-off between goodness-of-fit and number of parameters of the model, which may not be satisfactory to characterise the complexity of dynamical models. For instance, **XXX** shows that the logistic map, which consists of only two parameters, can be fitted to any pattern. Other criterion, involving the complexity of the dynamical behavior of the model (such as, e.g., its Lyapunov exponent), could as such be developed. Fourth, the ML framework developed in **??** requires a differentiable model, a strong prerequisite that may not be met by stochastic models (**XXX**). Fifth, the ML framework provides a single point estimate of the posterior distribution, which is subsequently used for model selection. Yet the models' posterior distributions may be multimodal, where the alternative modes carry valuable information to consider in the model selection process (**Daniels2015**). In this case, fully Bayesian method may be required to characterise the full posterior distribution. Alternatively, **Skeels2022** employs a more flexible approach for model selection, which does not require differentiability. The method consists in aggregating model simulation outputs into summary statistics, which are used to train classifier algorithms in recognizing the generating model. The classifier algorithms, such as random forests and neural networks, are further used on summary statistics obtained from the empirical data, recovering the most likely models and associated hypotheses. This approach is similar to Approximation Bayesian Computation methods **Csillary2010**, and requires summary statistics that can correctly discriminate between models. This is a strong requirement to grant the success of the model selection procedure, but it has the major advantage of clarifying why the model is more likely.

Overall, the methods presented in **????** solve major problems arising in the forward and inverse modelling of eco-evolutionary dynamics, but suffer from shortcomings. These limitations may direct practitioners to alternative methods, but also invite to further developments.

2.3 Perspectives

Opportunities for inverse modelling

The mini-batch method presented in **??** and the ML-based approximation method developed in **??** offer unique opportunities to leverage inverse modelling.

The mini-batch method is relevant beyond the ML framework presented in **??**, and could be used within a fully bayesian framework (**XXX**), where the full posterior distribution of the model is estimated. While Bayesian inference with MCMC

chains methods may not be appropriate for eco-evolutionary models (because they require a large number of forward model integration, which, additionally, grows considerably with the number of model parameters, while eco-evolutionary models are computationally intensive and are characterised by a high number of parameters), Automatic Differentiation Variational Inference (ADVI, (XXX)) offers an appealing alternative. With ADVI, the posterior distribution is approximated by a gaussian distribution (XXX), which significantly reduces the number of model integration (Gosh et al., 2021). As such, ADVI could account for potential multimodality in the model posteriors (by approximating the a multimodal distribution with a gaussian distribution with large variance). The consideration of multimodality could, in turn, improve the model selection procedure, and provide uncertainites measures to the value of the parameters inferred. An other possible extension of the ML framework to provide uncertainty estimates would be to use Bayesian Learning via Stochastic Gradient Langevin Dynamics (Welling2011BayesianLV). This method builds upon recent advances in Bayesian Deep Learning (Wilson2020) and interprets the iterative gradient-based optimization procedure as a Markov chain with an equilibrium distribution over the posterior distribution of the model parameters. It therefore comes with the scalability of variational methods and the interpretability of Bayesian methods, and can provide good estimates of uncertainty errors for complex models.

The ML-based approximation method for high dimensional PDEs, presented in ??, could also be easily extended for inverse modelling. While throughought ??, the parameters of the PDE model are assumed fixed, they could be set as free parameters, analogously to the parameters of the neural networks. The loss function in ?? would then take the PDE model parameters as additional arguments, and an additional term, involving the distance between the PDE model solution and the data, would be added, similarly to ?? in ???. The extension of the ML-based approximation method for inverse modelling would readily provide an efficient tool to perform inverse modelling with high-dimensional eco-evolutionary models. Because Julia is language with pervasive AD, this development would require little effort with the Julia library **HighDimPDE.jl**.

Together, the ML methods developed in ???? offer unique development opportunities to bring more robustness to inverse modelling, and extend it to high dimensional models.

Eco-evolutionary model on spatial graphs to advance our understanding and forecast of the dynamics of life on Earth

The eco-evolutionary model on spatial graphs presented in chap:diff-in-graphs, together with its predictions, and inverse modelling methods, could be used to advance our understanding of the processes shaping the distribution of life on Earth, and contribute to a formalization of the theory, to provide forecasts

Econobiology, a new venue to understand economic systems, and design more appropriate governance

2.4 Concluding remarks

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