An Ecological Perspective to Master the Complexities of the Digital Economy

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Article

Keywords:

Posted Date: February 9th, 2024

DOI: https://doi.org/10.21203/rs.3.rs-3552451/v1

Additional Declarations: There is **NO** Competing Interest. The authors declare no competing interests

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Abstract

Economic and social interactions are shifting to the digital space, facilitated by digital platforms. Successful platforms grow into vast ecosystems combining multiple offerings, where diverse users derive value from interactions while ecosystem orchestrators harvest massive revenue. The success of the ecosystem business model stems from their ability to swiftly adapt to fast-changing environments, including new technologies and volatile demands. Adaptation happens through dynamic innovation in a decentralised decision-making setting, which renders digital platform ecosystems complex adaptive systems (CAS). Utilizing extensive knowledge on natural ecosystems as prime examples of a CAS, the paper proposes a systematic framework for understanding and describing digital platform ecosystems, rooted in evolution and ecology. The 5M Framework organizes the complexity of the digital economy into a hierarchy of interconnected elements and processes. As platforms face heightened scrutiny about their socio-economic power and societal value, the framework can facilitate the development of sustainable governance of the digital economy.

Introduction

Rapid digitalisation of recent decades has propelled a new type of economic phenomenon: the digital platform (DP), which provides a digital infrastructure to facilitate economic, social, cultural, educational, and other forms of interactions. A DP can grow a vast ecosystem of multiple member groups who have incentives to create, exchange, and consume value generated from facilitated interactions. The remarkable success of the digital platform ecosystem (DPE) business model is evident with their rapid dominance across many economic activities. For example, at the time of writing this paper, five of the top ten companies by market capitalisation globally were DPEs including Apple, Microsoft, and Alphabet (the parent company of Google) [1].

Regulators and even business leaders themselves often struggle to find appropriate frameworks to describe, understand, and debate the economics of DPEs and their broader impact on our socio-environmental systems. Vividly illustrating the scale of this challenge is the frequently cited statement associated with Jack Ma, the founder of Alibaba Group, a prominent DPE in China, where he described himself as "*a blind man riding on a blind tiger*" [2]. During the last decades, observations on the apparent parallels between natural ecosystems (NEs) and networked businesses have inspired business leaders to draw insights from ecology to explain the dynamics of DPEs. As a major milestone, Moore extended ecological metaphors to explain the changes in interactions between competing businesses over time[3]. Another important contribution came from Iansiti and Levien who adapted the notion of 'keystone species' to the role of platform orchestrators in the value creation of business ecosystems[4]. Recently, Lianos and Carballa-Smichowski explored network-based indicators such as centrality, motivated by their relevance in ecology, to measure market power[5]. Such research has contributed insightful terminology and helped to explain some aspects of the complex dynamics underlying DPEs.

However, applications of ecological concepts to DPEs have, thus far, been reduced to casual exploitations of selected metaphors lacking a systematic, guided approach and hence yielding useful, yet limited insights. Conceivably, a deeper and more coherent understanding of the workings of DPEs could be achieved through a comprehensive transfer of concepts from NEs, combining knowledge on evolutionary and ecological dynamics. Such transfers require scientific analogical reasoning founded on systematic links that are due to the shared structures of source (nature) and recipient (digital economy) domains [6].

NEs have long been recognized as complex adaptive system (CAS) [7]. The CAS theory stylizes systems as populations of multiple (semi-)autonomous agents engaging in interactions and adapting to the changing environment and behaviour of other agents. Agents in a CAS can pursue different strategies to maximize individual success. Individual organisms in NEs, for example, maximize their fitness, that is their survival, growth, and reproduction rates. Adaptation incorporates the processes of trial-and-error, as well as copying and passing on information – mutation, replication and inheritance in NEs [8]. Furthermore, feedback loops, path-dependence, and synergism, non-linearity, self-organisation, and emergent patterns are important properties of CASs, emerging from complex, dynamic, and strategic interactions among their members.

The paper maintains that DPEs possess similar characteristics and thus can be viewed as CASs. Indeed, DPEs build on idiosyncratic interactions among multiple heterogeneous members and member groups. There may be various channels for these interactions, including flows of finances, knowledge or user data. Interactions often form feedback loops among DPE members and the orchestrator, and their complexity distinguishes DPEs from the conventional, linear supply chains. As the DPE business model relies on the already available, often underutilized assets or resources, it can rapidly reorient and expand into new markets, and thus exhibits a high degree of adaptability to dynamic surroundings. A DPE's path dependence comes from their high reliance on technology and innovation whereby readily available technologies determine the direction of future developments. Last, but not least on this list of characteristics of DPEs is the synergistic creation of value as a collective good by DPE members [9,10].

Viewing DPEs as CASs provides a scientific basis for systematic linking of their attributes with those of NEs. Recognizing that DPEs are embedded in the context of the digital economy while NEs are an inherent part of nature, this research relies on a well-established hierarchy of biological organization to construct a corresponding hierarchical framework for the digital economy which hosts DPEs. The resultant framework organizes key elements and processes within, and surrounding the DPEs based on parallels across the two domains. The framework allows for the flexible yet consistent transfer of ideas, concepts, and methods from ecology and evolutionary biology to the context of the digital economy beyond the scope of metaphors toward theoretically grounded scientific analogies. This will foster a comprehensive 'eco-logical' understanding for the digital economy which is also capable of informing the design of efficient regulations to govern DPEs.

Framework to organize ecological thinking for the digital economy and digital platform ecosystems

The dynamics of nature emerges from physical, biological, and biogeochemical processes and phenomena, such as primary production, growth, competition, and nutrient cycles. They together ensure that NEs persist, provide ecosystem services, and a living environment for inhabitants.

NEs and in fact the entire biosphere have been recognized as complex adaptive systems (CASs), wherein higher-level units and patterns emerge from interactions and dynamics occurring at lower levels [7]. The living hierarchy of NEs includes cells, tissues, organs, organisms, populations, species, communities, and ecosystems themselves. Cells can live as independent organisms or integrate into clusters such as tissues and organs, organisms form populations of species, which themselves cluster into communities as the living components of ecosystems. The foundation of this living hierarchy lies at the genetic level accommodating genes, the fundamental units of heredity that encode the "instructions" for building and regulating living organisms and play a pivotal role in defining their unique traits and characteristics. On the top of the hierarchy are biomes hosting multiple ecosystems in a particular area and being defined by a set of physical characteristics of the environment such as humidity or intensity of sunlight.

By identifying DPEs as CASs, the paper transfers the principles of biological organization into the domain of the digital economy. The paper focuses on genes (Micro), species (Meso), ecosystems (Macro), and biomes (Mega) as basic levels of nature's hierarchy, which are the most relevant for building systematic parallels between nature and the digital economy, and propose that processes and entities of the digital economy be structured similarly. For example, products (goods and services) and other entities that are involved in the co-creation of value by the DPE, can be compared to the communities of various species, who, likewise, participate in co-creation of ecosystem services by NEs. Consequently, their co-opetative (cooperative and competitive) interactions form DPEs comparable to ecosystems in nature. Equivalent to genes, technological know-how and business strategy emerge as underlying fundamentals of the DPE's specific value-creation model. Finally, ecosystems are embedded in the society including economic and other relevant contexts, just like NEs are embedded into their respective biomes. The four levels considered here provide a broad structure through which objects from the digital economy can be related to their counterparts from nature.

As both NEs and DPEs are CASs, interactions between agents at each level and across levels play a crucial role in determining their dynamics and characteristics. Recognizing the importance and universal nature of interaction types, the paper introduces a Meta level, which is comprised of interactions between components at each level, in the digital domain and in the domain of nature, respectively. Together, Micro, Meso, Macro, Mega, and Meta levels allow for the study of digital economies through the lens of their ecological analogies. The resultant approach is referred to as an *Eco-evolutionary rooted framework for the digital economy*, or the *5M Framework* derived from the initials of the major levels throughout which DPEs are compared to NEs in this paper (see Fig. 1).

1. At the Micro Level: Comparing the fundamentals of digital businesses to genes

The survival and thriving of individual agents in a CAS depend on their ability to adapt to a dynamic environment through innovation. In nature, innovations arise from changes in the genetic makeup of individuals of species. Key phenomena which determine evolutionary changes at the species level are variation (arising from processes including mutation and recombination), selection, and inheritance. Innovations in economic or technological systems have already been analogized to the evolutionary processes [11], and the Micro level of the framework seeks to formally organize such comparisons in the context of the digital economy. Genetic elements, whose combined information determines a living organism, can be compared to the underlying fundamentals of the DPE offerings. These fundamentals can include elements of technology, knowledge (including knowledge related to user behaviour), and business strategy. For example, digital streaming services such as Spotify and Netflix emerged from various innovations in smartphone capabilities, high-volume data transfer, digital payments, and the introduction of machine learning to determine user preferences, among other elements.

In nature, each genetic innovation creates a new selection pressure which may prompt further innovations in response, a perpetual contest termed the Red Queen Mechanism [12]. For example, organisms continuously develop new defence mechanisms against pathogens or new foraging strategies against competitors, prompting counteractive innovations in response. This regularly escalates into an “evolutionary arms race" which draws resources from both sides. Similarly, successful innovations in competitive economic systems provide strategic advantages, which pressures other agents toward further innovation, often via costly R&D [13]. Digitalization and platformization, however, have altered the course of the evolutionary arms race. On the one hand, an open innovation model adopted by many DPEs facilitates innovation within their ecosystems [14], whilst on the other hand, dominating DPEs can suppress nascent innovations through mergers, acquisitions, or extensive competition.

A constant emergence of rich genetic diversity is a pre-requisite for species adaptation. In changing environments, even originally neutral or disadvantageous mutations may become advantageous (the phenomenon of ‘preadaptation’ [15]. Myopic ecosystem management may harm the inherent diversity of NEs and thus prove counterproductive for the sustainable provision of ecosystem services in the long run. Monoculture is a well-known example: despite providing greater yield in the short run, genetically homogenous crops do not allow for the replenishment of key soil nutrients and increases susceptibility to pests, diseases, or climate shocks. To maintain yield, farmers apply costly pesticides and fertilisers, which in the long run further degrades the ecosystem [16]. Likewise, technological or economic innovations are not always beneficial or profitable at their onset, yet maintained diversity of business fundamentals can indeed serve as the driver of economic growth [17]. This is especially true for the digital economy where innovations are constantly being produced, restored, and replaced [18].

Modern management puts emphasis on protecting genetic diversity to ensure ecosystem resilience and sustainable provision of services in the long run; a similar objective should apply to the digital economy. Currently, innovation diversity is not sufficiently emphasized in regulation, and often contrasts directly with the self-vested objectives of DPE orchestrators [19]. Thus, ecological reasoning can be useful for understanding the processes and necessities of innovation in, and for, innovation-favourable regulation of the digital economy.

2. At the Meso Level: Comparing products to species

Species are fundamental units for understanding ecological phenomena. Each species is characterized by a unique combination of traits which allows it to occupy a certain ecological niche, i.e., a set of resources and range of environmental parameters that the species relies on. In digital markets, products can be conceived as analogous to ecological species. In economic systems, products (goods and services) occupy ‘niches’ [17], which are shaped by the product’s position in the value creation network, as well as its reliance on finances, non-financial resources, and customers. The Meso level of the 5M Framework therefore hosts species in nature and products in the digital economy.

Species and products can have flexible definitions. For example, narrower classifications such as subspecies or ecotypes help differentiate groups of individuals of the same species that exhibit some variations, often due to geographical or ecological factors. Conversely, when species boundaries are blurred, broader groupings like genera (which includes sister species) or functional guilds (comprising species with similar functions) may be used. Likewise, boundaries of products and services can be sometimes ambiguous when the focus of analysis requires finer-or coarser-grained categories. For example, the focus can be one online payment service, or a whole portfolio management of financial services. Flexibility of the product definition in the digital realm is a pre-requisite to explain the economics of DPEs. Certain activities such as, for example, facilitation of interactions by the ecosystem orchestrator, provision of attention [20], or supplying data by the user are novel forms of products produced and exchanged within the DPE.

Survival and proliferation are the integral objectives of all species and driven by a dynamic feedback loop between species traits emerging from genetic innovation and environmental niches. These dynamics shape three existential processes for species: i) foraging for food, ii) reproduction, and iii) avoiding fatal situations such as premature death or injury arising from unfavorable environmental conditions, predatorial threats, or competitive pressure. In the digital economy, such feedback loops are equally present. For instance, foraging can be seen akin to seeking resources necessary for growth such as finances, users’ attention, and data of users and their interactions. Reproduction of species can be likened to businesses releasing new versions of their products. In both nature and economy, reproduction provides an opportunity to establish innovation. Life-threatening pressures call for adaptation of species to avoid extinction; similarly digital products must continuously adapt to survive market fluctuations or restrictive regulation.

Theories of life history evolution explain how species optimize their traits to balance across existential processes. For example, the r/K selection theory stylizes the observation that species face a trade-off in the number of offspring they produce and the parental investments they may expend. Likewise, the orchestrator of an open DPE faces a tradeoff between the number and quality of complementors and products hosted on the platform. Just as mature, well-functioning ecosystems include both r-type (high number of offspring, low parental investment) and K-type species (low number of offspring, high parental investment) [21] diversity of complementors in terms of their product quality and the pace of development is an important factor for the DPE success. The concept of r- and K-strategy is yet an unexplored approach that can facilitate a better understanding of the product dynamics in digital economies.

Optimal foraging theory (OFT) may be another useful source of analogies and models. OFT explains how species adjust their strategies to optimize effort spent on acquiring food of different value and availability [21]. Similarly, one may expect that the platform's strategies of 'foraging' new domains of resources can be explained by optimizing metrics describing the required 'effort'. For example, Uber often refrains from extending its operations into rural areas where the density of the 'resource', i.e., potential clients, is low. This is akin to animals spending less time in resource-poor than in resource-rich patches, despite similar travelling time between patches. Policies can affect the optimized metric through monetary or non-monetary instruments and thus the government can opt to steer platform's foraging for resources in the direction of higher societal welfare.

3. At the Macro Level: Comparing natural ecosystems to digital platform ecosystems

The Macro level of the 5M Framework focuses on ecosystems. Both NEs and DPEs emerge from the dynamic interactions of their building blocks - communities of individuals from several species in NEs, and arrays of products (goods and services) in DPEs. For example, species are involved in feeding interactions, such as the predator-prey dynamics, or symbiosis, for example between the gut microbiome and the host. Complementors, the orchestrator, and other DPE members supply specific goods and provide specific services to members of an ecosystem which allows for the production of a collective output. Facilitating this are webs of financial flows, data flows, and influence relationships, among other relevant types of interactions. Figure 2 illustrates such interconnections for a stylized online travel agency.

The interactions within ecosystems are powered by boundary inputs. In NEs, they can take the form of solar energy inputs to the ecosystem's primary producers such as plants. Growth of DPEs is facilitated by financial investments and other inputs such as R&D and data. Tracking boundary inputs throughout the ecosystem allows for the assessment of efficiency with which energy or material are processed within the ecosystem. In NEs, boundary inputs are passed on from primary producers to their consumers and further up to top predators. This organises species into trophic levels, which measures the remoteness of species from the primary source of input. Considering financial or data inputs in a DPE, its members can also be assigned into 'trophic levels' according to their distance from the initial boundary inputs. As interconnections among the ecosystem parts can be complex, the trophic structure can help reveal the complexity and assist in understanding of the dependence of complementors and users on critical inputs into a DPE.

The degree of network complexity is determined by the number and types of interactions in an ecosystem. It has long been recognized that the networked structure is indispensable for the functioning of the system itself [22]. This also speaks true for DPEs [23]. Furthermore, complexity has been demonstrated to both promote and hinder stability in NEs (a so-called stability-complexity debate) [24]. For instance, high species diversity may lower stability of some sub-systems while it may increase stability of the wider ecosystem [25]. Similarly, some DPE network complexities provide for higher resilience while others hinder it, hence one objective of regulators may be to manage the complexity of the interaction structure of socially critical DPEs to increase their resilience.

Resilience is indeed an important characteristic of CASs and also increasingly an objective for DPE managers. Internal or external perturbations can result in a collapse or reorganisation of an ecosystem if stretched beyond its limit of adaptability. Flexible responses to perturbations are key in this phase to prevent a common 'rigidity trap' [26] characterized by low diversity and high connectivity of agents that begets lower resilience and may trigger collapse of the ecosystem. If collapse is avoided, a reorganization and subsequent new growth phase can reutilize the released material and elements [27]. Regulation that recognizes, and is tailored to, different stages of ecosystem dynamics from growth to development and re-organisation, will be more effective than one that ignores the resilience cycle (for details, see Table 2).

4. At the Mega Level: Comparing biomes to societies

NEs are nested within even larger units, known as biomes, which combine the physical and biogeochemical environment and the totality of the biota therein. Likewise, DPEs are one form of an economy embedded into a wider society, which provides the political, economic, social, technological, environmental, legal, and other relevant contexts. Thus, the Mega level focuses on comparing biomes with the wider society.

Natural biomes are categorised mainly by their temperatures, precipitation patterns, and nutrient levels. Evidence shows that biota and ecosystems, even if separated geographically, display patterns of convergent evolution if they reside in the same biome type [28]. For example, the succulent biome provides an arena for the evolution of different drought-adapted plant species across various continents. Likewise, convergence patterns may be observed in the formation and features of DPEs, which emerge from similarities of their societal contexts. For example, in the absence of good digital infrastructure, m-Pesa, a digital banking platform (DBP) providing PIN-secured SMS services for basic banking activities was launched in Kenya. Similar DBP models were launched across Latin America, another region with high mobile usage but poor digital infrastructures.

Furthermore, the abundance and variety of fundamental resources in NEs are major drivers of the evolution of the biome and its biota. For example, biomes such as tropical rainforests with abundant sunlight and precipitation provide suitable habitat for diverse biota with high biomass production whereas only drought-resistant biota with low production of biomass can survive the harsher conditions of succulent biomes. Like NEs, societies which provide abundant flow of resources such as finances and data are likely to generate a richer diversity of large DPEs and extensive innovations, compared to restricted or resource poor regions [29].

Therefore, biomes act as a theatre of evolution directing the evolutionary trajectories and the emerging functionalities of species and of ecosystems [30]. Although there are several pragmatic studies ranking national economies on their digital developments based on various parameters of digital competitiveness, e.g., the IMD World Digital Competitiveness Index [29] or the Ease of Doing Digital Business [31], focused research is needed to analyze in greater detail the impact of digital and analog factors including resources, infrastructure, etc. on the DPE development and convergence patterns within their societal settings.

5. At the Meta Level: Comparing interactions in nature to interactions in the digital economy

Components at each level described above do not function or evolve in isolation. In the NEs, genes may influence the expression of other genes within an organism (Micro level); species feed on and compete for prey and engage in mutually beneficial relationships with other species within an ecosystem (Meso level); ecosystems can influence neighbouring ecosystems through exchanging resources (Macro level); and ultimately a biome can also influence other biomes (Mega level). Likewise, in the digital economy, technology, knowledge, and business strategy components often interact with each other (Micro level); products usually interact with other products (Meso level); DPEs may interact with other DPEs (Macro level); and finally, societies can influence other societies (Mega level). In both natural and digital contexts, at each level, interactions with other components complement the dynamically changing environment in forming pressures on or providing benefits to all participating components. The impact of interactions between components may ripple into the adjacent levels or even beyond. Their universal nature, a unified terminology, and existing tools for their analysis in ecological systems posit interactions between components as a separate level in the framework (Meta level).

Broadly, ecological interactions at all levels can have either a positive, neutral, or negative effect on the participating components, which results in five types of outcomes of pairwise interactions (a mutually neutral interaction is equivalent of no interaction, and called neutralism; see Fig. 3). Importantly, with time, interactions may transform. For example, a mutually beneficial interaction may gradually become parasitic if no controls or sanctions are placed to prevent exploiting the partner, and conversely, parasitism has often evolved into neutral or even beneficial interactions in nature.

Interactions creating positive effect on both involved components at all levels from Micro to Mega, are key enablers of life (see Table 1 for details). For example, bacteria cooperate by synthesizing various compounds to create a community matrix using molecular-based signalling systems. This cooperation enables the growth and maintenance of a biofilm that protects the members from external perturbations. Such interactions are extremely successful, such that biofilms cover almost all surfaces from rocks to human teeth. Likewise, in the digital economy, mutually beneficial cooperation plays a profound role. This is represented by the emergence of the term ‘complementors’ to refer to multiple decentralized firms that can co-create value on a massive scale. Such value co-creation became possible due to efficient coordination enabled through digitalization of firm interactions and transactions as well as artificial intelligence which allows efficient use of big data (see Table 1 for details).

However, it is often challenging to understand how mutualism and cooperation can exist as such interactions are prone to exploitation or free riding. Evolutionary game theory has deepened our understanding of the mechanisms and dynamics underlying the evolution and maintenance of cooperative behaviour in various ecological contexts from the gene- to species- levels and beyond [32,33]. For example, only few species engage in the cooperative act of synthesizing costly compounds of biofilm while the benefit of the protective habitat it provides is enjoyed by the whole community. Defectors, i.e., individuals or even entire species that do not contribute to this process, can free ride on the production of others. Evidence indicates that a certain amount of free riding can be tolerated up to a threshold before the growth and even the survival of the whole community is jeopardized. Similar dynamics can be observed in the digital arena. For example, Wikipedia benefits the public, and is produced and edited by a comparatively very small number of volunteers. The quality of the content is maintained by the cooperative act of supervising, editing, and cleansing. If the amount of false or misleading contributions exceeds a certain limit, the popularity of this online platform is likely to drop with declining reliability of the information it offers.

Table 1
Positive interactions (+/+) in each M-level of NEs and their corresponding examples in DPEs

M-Level	Nature	Digital economy
Micro	Via synergistic interactions between genetic elements, called epistasis, the effect of one genetic element is enhanced by another genetic element. Example: lung tumour growth is prominent if three mutations occur together, whereas the solitary mutations alone cause insignificant tumour growth.	Different components of knowledge, technology or business strategy can reinforce each other. Example: Uber's service is enabled by the combination of smartphones, mobile internet, and search-and-match algorithms which create a multiplicative effect.
Meso	Species can benefit from the presence of other species. Example: corals and their symbiotic algae which benefit from the coral habitat and in turn provide nutrients.	Products can create a facilitating effect on each other. Example: Collaboration between content producers on YouTube facilitates a synergistic growth through transfers of audiences across complementary contents.
Macro	Ecosystems can positively re-enforce each other. Example: a freshwater lake ecosystem receives nutrients from the neighbouring forest ecosystem, while predators inhabiting the forests can visit the lake to feed on the fish.	Ecosystems can positively re-enforce each other. Example: platforms such as Spotify, E-bay rely on the mobile operating system (MOS) infrastructures of Google and Apple to be downloaded on smart devices while the MOS need such apps for their value proposition.
Mega	Biomes can have positive effects on each other. Example: global nutrient cycles or global circulation systems, such as the Gulf Stream or the El Niño connect distinct ecosystems from different biomes influencing the local niche conditions. Such currents can lead to milder temperatures during the winter or affect rainfall in some regions leading to higher or lower productivity of biota.	National economies can synergize each other. Example: Governance of multinational DPEs benefits from cooperation of national policy agencies including informational exchange and uniting approaches.

On the other end of the spectrum are mutually negative interactions. In ecology, they stem from competing for limited resources, such as building blocks (amino acids) or energy (ATP) for protein synthesis during gene expression at the Micro level; food, mating partner, and territory at the Meso level; and habitat and nutritional resources at the Macro and Mega levels. Mutually negative interactions decrease expression of genes, fitness of species, and productivity of an ecosystem or biome in the short run, while in the long run such processes are crucial in promoting resilience and ensuring survival of the fittest. Numerous models have been developed in ecology to study the effects of competition [34]. For example, the competitive Lotka–Volterra model demonstrates how one species competitively excludes another if both compete for a common resource, i.e., habitat or food. Similarly, digitalization amplifies the tendency of markets to tip in favour of one incumbent rather than allowing for co-existence of several competitors. Specific ecological models and insights regarding competition may be useful for a better understanding and regulation of DPEs; one novel analogy might be between intraguild predation, i.e., the killing and sometimes eating a potential competitor, and mergers and acquisitions (M&A) in certain, complex settings.

Other types of interactions include amensalism, a type of interaction, in which a component is inhibited or destroyed as a by-product of another organisms' life cycle, while the opposite, positive effect as a by-product is called commensalism; in these two types of interactions another interacting component is not affected. Finally, under parasitism and predation one component is harmed by another that benefits from this interaction. Interactions in which at least one party suffers a negative effect, such as competition, predation, parasitism, and amensalism, are often referred to as antagonisms.

Discussion

This paper approaches the DPE business model as a type of CAS embedded in the environment of the digital economy. Relying on the CAS theory and analogical reasoning, it presents an Eco-evolutionary rooted framework for the digital economy, which allows for the transfer of concepts, insights, and methodologies from ecology and evolutionary biology to master the complexities of the digital economy. Further examples of transfers are demonstrated at each of the five considered levels, including concepts such as innovation at the Micro level, survival strategies at the Meso level, complexity-versus-stability at the Macro level, ecosystem-enabling conditions at the Mega level, and major types of interactions at the Meta level. This paper aims to provide a wide-ranging overview, and therefore listed only selected examples although scientific analogies can be drawn for many more, including those, which have already been presented in the literature, albeit in a fragmented manner. Table 2 provides a summary of transfers which demonstrate the capability of the Eco-evolutionary rooted framework for the digital economy.

The hierarchical view on the digital economy and DPEs, operationalized through the 5M Framework in this paper, seems to resonate with how the major DPEs understand themselves and the environment in which they operate. For instance, in their responses to the CMA's recent mobile ecosystems market study, both Apple and Google attempt to explain their respective ecosystems as interconnections of technology and products at multiple levels and rebut the agency's vision of products as standalone objects [35].

There are two major limitations of this paper and the framework that open opportunities for future research. Firstly, this paper simplifies the concepts of evolution and systems ecology by omitting many details and nuances. This is done for illustrative purposes, to improve the accessibility of this research for a wider range of disciplines, and to demonstrate the broader insights useful for informing management, competition law, and policy. The framework, as any transfer of analogical reasoning between domains, is subject to trade-off between engaging with nuances or simplifying for dissemination of the main ideas. Secondly, the individual concepts highlighted in this paper were discussed very briefly despite each having the capacity for a research project of its own; moreover, the concepts featured here are merely a few examples in a plethora of further research contributions this research hopes to inspire.

The major novelty and utility of the 5M Framework is that it provides a comprehensive consciousness for the complex phenomenon of the DPE, which, on the one hand, incorporates its constituencies down to the level of individual components of business fundamentals, and, on the other hand, embeds DPEs into a wider context of the digital economy. By incorporating all these levels into one internally consistent structure based on the hierarchies observed in nature, the framework allows for a deep understanding of the phenomenon of DPEs and for anticipating its evolution through major stages under internal and external forces at different focus levels. The five levels included in the 5M Framework are, arguably, the most fundamental and relevant levels for describing and analyzing DPEs, however, depending on the specific application, other levels can be added above, below and in between the five levels to nuance a given analysis.

The 5M Framework presented in this paper aspires to contribute to the development of business and economic disciplines in multiple ways. First, it may help researchers and decision makers to organise existing ecological analogies from the literature and support future expansion of ecological analogies for a better understanding of DPEs, therefore reducing the risk of flaws in application. Second, it may improve efficiency of scientific analyses and policy design by benefiting from the use of the already existing, well-developed, and understood models and approaches in ecology. Third, the proposed framework can guide the formulation and installation of proper regulation of DPEs. A fundamental challenge is often a lack of a commonly accepted language to describe the DPE rationales and pathways of impacts. The framework can provide a basis for a consistent language. Fourth, a holistic, comprehensive view enabled by the 5M Framework can help to reduce the need to constantly develop new policies or regulations in response to arising concerns. Rather, the framework should drive the development of policies and approaches to regulation which can anticipate all stages and major concerns related to them, thus reducing the chance for unforeseen events and increasing the effectiveness of policymaking and gains for society.

Table 2
Examples of concepts and insights in the natural and in the digital context.

Ecological concept	Concept description	Analogy in the digital economy context
Micro Level		
Evolutionary arms race (Red Queen Mechanism)	Genetic innovation of organisms continuously creates new selection pressures on other organisms with which they interact. For example, an organism develops new defence mechanisms against pathogens or new foraging strategies against competitors. This perpetual evolutionary arms race is costly to both sides, but eventually promotes the success of the fittest [12].	Platforms, complementors, and even regulators, are under continuous pressure to innovate new products or actions to compete with the new innovations of their rival counterparts and vice versa [36]. Platformisation modifies the space for innovation, fostering it in some cases, and suppressing in others.
Monoculture/ Monocropping	Farming of unvaried crops such as wheat and oil palm creates unsustainable environments, reduces biodiversity, and exposes the ecosystem to disease pressure, land degradation, and nutrient scarcity [16].	Concentration of the digital markets can be likened to “innovation monoculture” which supposedly leaves the digital economy prone to monopolization, stagnation, asymmetric acquisitions, and skewed value capture [37]. Regulators must encourage diversity to increase resilience and sustainability of the digital economy.
Pre-adaptation (exaptation)	An existing trait or feature of an agent is co-opted for a renewed purpose and improves survival. For example, birds' feathers, originally developed for heat insulation, were gradually co-opted for flight [15].	A technology or strategic decision may overtime become useful for a platform under dynamic market conditions. For example, Global Positioning System (GPS), developed for weapons guidance, was co-opted for commercial navigation use. GPS is now used in training self-driving vehicles.
Meso Level		

Ecological concept	Concept description	Analogy in the digital economy context
Micro Level		
r/K Selection Theory	Species reproduction and parenting strategies and lifecycles can be stylized into: r-strategy: i) short gestation periods, ii) low parenting efforts, iii) early maturation, iv) short lifespan, v) high mortality rate, vi) many offspring. K-strategy: i) long gestation periods, ii) high parenting efforts, iii) slow ageing, iv) late maturation, v) low mortality rate, vi) few offspring[21]. In ecological succession of an empty or disturbed habitat, r-strategists initiate the transformation of the sterile land as the primary colonizers. K-strategists occupy crowded niches and are strong competitors for limited resources. In an established climax community, both r- and K-strategists are present, and their dominance is determined by the rate of disturbance.	Firms in a platformised economy may adopt approaches analogous to r- or K-strategies: r-strategists (*generalists*) offer (several) products without investing too many resources into each; K-strategists (*specialists*) provide (few) products for which they use sizable investment. Most open-DPEs require both r- and K-strategist products to survive. Over-reliance on r-type products may reduce consumer retention. Over-reliance on K-type products only would slow the rate of innovation. Trade-off between product quantity and quality are crucial for regulators to understand. E.g., MOS such as Google Play host several apps with low investments e.g., simple games, as well as high investment apps such complex open-world games.
Optimal Foraging Theory (OFT)	Organisms, given environmental and physiological constraints, optimise the diet and the time spent on searching for food depending on the quality of the resource patch [12]. For example, the Beehive model explains how bees choose parameters of their nectar collection activity (distance to travel, amount of nectar to bring) to optimise long-run hive productivity and survival [38].	Agents in digital markets can be conceived as foraging for consumer attention, data, or venture capital. It is plausible that they optimize their resources to decide between offering new products or entering new markets and continuing to maintain existing activities. Consumers can also be conceived as foragers optimizing the search for products given their budgetary, time, or attention constraints. OFT can inform the development of theories to complement the established utility theory in economics [39].
Keystones	A species which plays an important role in defining the characteristics and functioning of an ecosystem. Without them the ecosystem would be less diverse or less resilient [40]. The ecological niche of a keystone species often cannot be filled by another species. For example, predators are keystones who control the population of prey.	Keystone nodes or agents in DPEs provide the crucial digital infrastructures or interactions which ensure the survival and value creation of an ecosystem. E.g., platform orchestrators are typically the keystones of their ecosystem. Keystones can capture significant value from the ecosystem [4].

Ecological concept	Concept description	Analogy in the digital economy context
Micro Level		
Macro Level		
Ecosystem	A community of species which interact with each other and their environment to create, exchange, and capture 'value', e.g. biomass or ecosystem services. For instance, primary consumers feed on producers (plants) while being hunted by predators. Decomposers and degraders transform dead material for re-use.	A collection of agents and organizations collectively producing, exchanging, and capturing 'value', e.g., revenue or data [3].
Ecosystem Boundaries	Ecosystem boundaries, neither static nor well-defined, exhibit gradients of change in environmental conditions and a related shift in their compositions. They are defined based on the purposes of the observer e.g., for a freshwater lake, the boundary can consist of the lake only, or the surrounding terrain, depending on the subject of analysis.	Like NEs, DPEs do not have rigid boundaries. Digital regulators must adapt to the non-static and context-dependent boundaries of DPEs. Overall, knowing the dynamic nature of DPE boundaries is crucial in managing vast platforms which operate across industries and/or regions.
Boundary Inputs	Flow of resources into an NE that enable its species to survive and thrive. For example, sunlight to primary producers, migrations into ecosystem.	Flow of resources into a DPE that enable its functioning. For example, financial investment, recruitment of new platform users.

Ecological concept	Concept description	Analogy in the digital economy context
Micro Level		
Adaptive Cycles	An adaptive cycle in nature consists of four stages: i) Growth: energy inputs across the system boundary are invested into biomass accumulation and structure. ii) Conservation: internal restructuring improves the efficiency of energy flows between species and builds resilience through redundant pathways and recycling. iii) Collapse: may be triggered from within the ecosystem, e.g., by exponential population growth or environmental perturbations such as extended droughts, or pollution which affect populations and their interactions. iv) Reorganization: species regrow by utilizing resources freed during the collapse, e.g., a forest may regrow and re-assemble biodiversity after a fire. However, the newly formed ecosystem may be less diverse and could also feature fewer mutualistic or symbiotic interactions [26].	Similar to NEs, an adaptive cycle in the digital economies would consist of four stages: i) Growth: DPE grows from high concentration of investment, and acquisitions. ii) Conservation: financial, data and attention related interactions are enhanced and strengthened. Many agents become interconnected. Dependence on initial investment decreases as platform revenues grow. iii) Collapse: may result from internal mismanagement, e.g., overexploitation of resources, market share loss, or external shocks. The Hungarian social platform IWIW collapsed within 12 years due to competition (external perturbation) with Facebook; and since the platform failed to adapt to new strategies of including complementors and app services (internal perturbation) [41]. iv) Reorganization: an ecosystem can re-appear on the market in a transformed design, e.g., the ecosystem of content creators and consumers of short-videos survived the shut-down of Vine and Musical.ly as users moved onto TikTok and YouTube [42]. A DPE that collapses may incur high social cost in the form of information loss, network loss, or loss of income. If a DPE reaches the status of critical infrastructure, regulatory preventative interventions are pertinent [43] for finance, competition, or data handling to minimize social cost.
Stability	Ecosystem stability is the ability of an ecosystem to persist and continue to provide ecosystem services after an internal or external perturbation, e.g., an extreme weather event. There is a strong focus in ecology in working out robust indicators of stability [44].	Analogously to ecosystem stability, DPE stability can be introduced as the ability to withstand perturbations such as regulatory changes or the emergence of a competing DPE. Ecology could inform the development of stability indicators for DPEs.

Ecological concept	Concept description	Analogy in the digital economy context
Micro Level		
Food Web	Food web is a networked model of an ecosystem where nodes are species (or groups of species) and directed edges are flows of energy or matter among them. Networked view on ecosystems allows to study the role of network structure and complexity in ecosystem functioning [40].	A networked view on DPEs could be useful for their better understanding and regulation. In the network model, nodes are firms, complementors, or groups of agents and edges are flows of finances or information.
Trophic Levels (TL)	TL of a species defines the distance (in terms of intermediate species) between the focal species and primary boundary input into a food web. Primary producers are at the first TL, consumers of primary producers are at the second TL, secondary consumers are at the third TL, etc. Apex predators occupy the highest TL of the ecosystem. The number of TLs in the food web is one important indicator of its complexity.	Analogously to NEs, a DPE's trophic structure could be defined which would depend on the entry point of the boundary input. For instance, financial investment can be directed to different parts of a DPE thus defining the trophic levels of other parts of the DPE and its overall complexity. For example, investing into the DPE orchestrator or subsidizing complementor activity changes the trophic structure of the ecosystem. Optimal design of DPEs should include considerations of their overall complexity.
Mega Level		
Biomes	Biome types are defined by conditions of the physical environment (e.g., temperature and precipitation), which to some degree defines biota therein which are best suited for these conditions. For example, *Tundra*: low temperature, low rainfall. *Desert*: high temperature, low rainfall. *Rainforest*: high temperature, high rainfall.	Similar to biomes are types of socio-economic conditions under which DPEs operate. For example, China and USA have the greatest levels of DPE emergence and growth despite China and US having vastly different economic, political, and cultural conditions. Understanding the determinants can help to understand why these countries are so successful in nurturing domestic DPEs. On the other hand, there are significant differences. E.g., the success of financial DPEs and e-wallet platforms has been much more pronounced in China than in the U.S. Institutions and regulatory restrictions are tougher in the U.S., which probably has so far reduced the emergence of DPEs in financial markets for the U.S.
Meta Level		

Ecological concept	Concept description	Analogy in the digital economy context
Micro Level		
Symbiosis	Species that live in a certain proximity can exchange nutrients or services (such as protection, transport), e.g., plants and nitrogen-fixing bacteria. *Endosymbiosis* is a mutually beneficial physical integration of partners, in which none could live without the other, e.g., a bacterial partner living inside a host, such as animals carrying endosymbiont bacteria which produces essential amino acids for the host, in return for a protecting and nurturing environment within the host.	The largest of DPEs have become intertwined. Data has become a commodity transferred between DPEs for mutual benefit. Such symbiosis may be unintentional, but it reinforces market power of such DPEs [45]. Such symbiosis may, although not always, be not in the interest of consumers.
Free-Riders	Gaining from unilateral non-cooperation when others perform a cooperative action that is costly in terms of time and resources. The spread of free riders, such as non-enzyme producing microbes may be detrimental to the entire ecosystem if their population outcompetes producers in natural ecosystems.	Online marketplaces, e.g., Amazon, are open for almost any individual or business. Within sellers, there are those which contribute to the ecosystem through, e.g., the provision of quality products, and those who 'free-ride' on the consumer data selling cheaper, lower-quality products and expending less effort in doing so. Free riding in DPEs specific to data collection and usage is a major concern for which regulators can collect insights from NEs.

Methods

1. General approach

The research presented in this paper focuses on understanding Digital Platform Ecosystems (DPEs) through the lens of natural ecosystems (NEs). This paper proposes that DPEs can be seen as Complex Adaptive Systems (CASs) (see Methods Section 2), which justifies the parallels between them and other CASs. The paper focuses on NEs, the most extensively studied real-life examples of CASs. Such parallels allow for ideas, concepts, and methodologies established in ecology to be transferred and adapted for studying the DPEs operating in the environment of the digital economy.

The presented research designs a framework which links the domain of the digital economy, and DPEs as its fundamental components, to the biosphere and its NEs. To do this, the research first organizes the intricate hierarchies and interactions between DPE components and their surroundings analogously to the counterpart hierarchies and interactions found in NEs and the natural environment (see Methods

Section 3). It then presents a sample of theories and tools, established for NEs, which show a high applicability potential for understanding DPEs (see Methods Section 4).

The existing literature [3,46,47] has thus far been using ecological concepts as illustrative metaphors for DPEs. The approach of this paper goes beyond this and instead utilizes sound analogical reasoning [48] enabled by the CAS theory. Analogical reasoning is based on relational structure, which is independent from object descriptions that engage in the relations. The power of an analogy in "licensing" scientific analysis relies on the systematic structural match between the source and target domains [49]. The rigor ensured by analogy serves as a basis for analogical inference.

2. CAS: An interdisciplinary bridge

The paper proposes that the CAS theory can explain important features and inherent dynamics of DPEs [50]. CASs are abstract systems inhabited by a diversity of (semi-)autonomous agents, embedded in a dynamic interaction network. Agents continuously adapt to the changes in their environment, including the states or behaviors of other agents, by adjusting their attributes with an aim to increase fitness. The dynamics of CAS are often non-linear, non-equilibrium, and path dependent as a result of the perpetual collective co-adaptation of agents leading to the emergence of complex patterns and self-organization that cannot be extrapolated from the isolated behavior of a 'representative' agent.

NEs embedded in the global biosphere are a prime example of CASs in nature [7]. Multiple species co-existing in a particular geographical area interact with each other via feeding and other kinds of relationships and collectively alter their shared habitat. Individuals and whole species may adapt to the dynamic surroundings via (i) short run learning or adjusting of phenotypes enabled by phenotypic or behavioral plasticity, and (ii) undergoing an evolutionary change of traits and species-wide natural selection in the long run. For the latter, multiplication, mutation, heredity, and variability are crucial as they underpin natural selection [51]. The combination of phenotypic and behavioral plasticity and evolutionary change increases the quantifiable success, such as growth rates, survival rates, or reproduction rates, and is vital for species survival and persistence. For example, individual trees can expand their crowns to compete for sunlight with the neighboring trees making use of their phenotypic plasticity. Furthermore, evolutionary change in the leaf size and shape replicating across generations helps the trees to optimize the amount of sunlight captured by the individual leaves.

Evolutionary adaptation integrates new information and develops a strategy by which a locally optimal desired outcome can be attained. Replication is central to this process. Genes are duplicated alongside with their information, however, this duplication may be imprecise. Mutations and recombination of genes occurring at random may lead to genetic variations which eventually manifest into phenotypic diversity which is a precondition for evolution. Fitness-enhancing variants of phenotypes proliferate in the population and result in the spread of information encoded within them, while other variants are less successful and may diminish [51].

The replicator equation is the mathematical formulation of the fundamental thesis of evolutionary dynamics which predicts the proliferation of fitness-enhancing traits and the recession of disadvantageous traits [34]. Evolutionary game theory has been developed to model such population dynamics based on the replicator equation and individuals represented as strategies that encapsulate their properties (genotypes or phenotypes), behavioral decisions, or other attributes which characterize their reactions and interactions with other agents. An important aspect is that the fitness of an individual with a certain strategy depends on the composition of the population, i.e., on the distribution of strategies in the population. Therefore, replicator dynamics includes both the frequencies of different strategies in the population, and how interacting with a particular type contributes to the fitness of the individual.

The dynamics of a capitalist economic system was first compared to an evolutionary process by Joseph Schumpeter [52]. Later, evolutionary economics has been developed as an approach to understand innovation and economic growth with the central idea being that new technologies emerge through random changes in and recombination of existing technologies, and that alternative technologies compete for market success similar to natural selection in ecology [17,53,54].

The business model of DPEs strongly relies on innovation in technology, and, very importantly, in business strategy [18,46]. DPE orchestrators continuously explore opportunities provided by every interaction or perturbation to adjust their technological solution or business strategy accordingly. Advantageous changes are readopted and replicated whereas detrimental changes diminish which could be represented through a replicator equation similarly to the evolutionary dynamics in nature. Through this process DPEs adapt to technological change and compete with their rivals. Complementary to evolutionary innovation is DPE's flexibility in situational adjusting to the volatile market and other external conditions which creates the DPEs' capacity to adapt in the short run. Two kinds of adaptation explain how DPEs are "adaptive" systems. They are also "complex" systems as they consist of multiple members who are semi-autonomous in the sense that they make their own decisions (no centralized decision making) under certain constraints (e.g., provided by law) engaged in localized dynamic interactions among themselves (e.g., they provide data to each other) and the external environment, in which a DPE operates. To summarize, DPEs can be understood as CASs due to their structure of interacting agents, members engaging in decentralized decision making and the fundamental reliance on (technological and strategic) innovation and flexibility.

3. Constructing a hierarchical framework

The analogy established between NEs and DPEs through the CAS theory (see Section 2 here) allows for analogical inference. The 5M Framework is designed to comparatively structure key agents and processes in the digital economy to their analogues in nature. The goal is to enable transfer of concepts and tools from the domain of ecology and evolutionary biology to the domain of the digital economy.

To start, a suitable hierarchical framework was identified from ecology that is used to organize nested agents and processes underlying life on Earth. While ecology offers several such frameworks of different complexity, four-level hierarchy was selected, with Micro, Meso, Macro, and Mega levels representing genes, species, ecosystems, and biomes, respectively. This broad four-level framework is well-positioned to facilitate a structured analogizing between elements (agents) and processes from nature and those from the digital economy for audiences of all disciplines including ecology, law, and economics, among others. As interactions of elements at each level share fundamental characteristics, terminology, and tools for analysis, a fifth level is introduced, Meta, to encapsulate interactions within M1-M4 in one – virtual – level (see Fig. 1).

Next, the paper identifies the most fundamental elements found in the digital economy and maps them with their counterparts in the domain of ecology based on their main attributes, roles, interconnections with other elements, and impact on the wider ecosystem. Altogether, this delivers the 5M Framework.

4. Ecology as a source of concepts and methodologies for the digital economy

The 5M Framework, designed through analogical inference, will also facilitate further application of this approach to transfer specific concepts and tools from the domain of ecology to that of the digital economy. As the digital economy is still a relatively new phenomenon, the existing approaches for both understanding its complexities and effective governance are in their infancy. The paper proposes that the development of such approaches can benefit from the wealth of knowledge and experience accumulated in ecology and evolutionary biology for understanding and managing NEs. This paper provides a handful of candidate concepts, theories, and models which demonstrate immediate relevance and potential applicability to the challenges of the digital economy. It should be acknowledged that many more approaches from ecology and evolutionary biology might be worth exploring to address the most pressing knowledge or regulatory gaps.

The Micro level compares the fundamentals of digital businesses such as elements of technology or business strategy to genes and adapts concepts including evolutionary arms race, monoculture, and pre-adaptation, to the context of the digital economy. These concepts provide relevant insights into the dynamics of genetic innovation in NEs and offer analogies that can effectively address topical issues related to innovation in the digital economies. The theory of the evolutionary arms race explains how continuous competition is costly to individual agents but ensures survival of the fittest. Monoculture meanwhile shows how a race for efficiency in managed ecosystems can exacerbate diversity and hinder innovation, leaving the entire ecosystem vulnerable to collapse. Pre-adaptation highlights the role of neutral mutations which may become beneficial in a changed environment ensuring survival. Overall, these examples underscore the importance of ensuring favorable conditions for innovation and shed light on the complex interplay between competition, diversity, innovation, and resilience of ecosystems.

The Meso level compares species and products. Products refer to conventional commercial products, that is goods and services, offered by a DPE as well as other entities that are exchanged such as user attention or data. The service of interaction facilitation provided by the ecosystem orchestrator can also be included in this level. concepts including theories of life history evolution such as the r/K selection theory and the Optimal Foraging Theory (OFT) are adapted to explain how products concur markets in the digital economy. Theories of life history analyze how natural selection shapes investments made by individuals of a species into their growth. For example, the r/K selection theory highlights the tradeoff between quantity and quality of the next generation of organisms and explains how this tradeoff is affected by the conditions of the environment. OFT studies the resource-seeking behavior of organisms under the constraints of time and resources. Through the analogy between products and species, and by drawing from the understanding of the variety of survival and expansion strategies employed by species in NEs, a more comprehensive and realistic perspective on the business strategies adopted by platforms can be obtained.

The Macro level compares DPEs to NEs, which allows us to apply concepts of boundary inputs, network structures, and resilience from ecology to the context of the digital economy. These concepts focus on providing an understanding of how agents form enduring groupings and how these agent groupings persist and produce collective output. As DPEs have become the crux of the digital economy with some generating services, which are essential to modern societies including e-commerce and social networking, their stable functioning becomes the matter of public concern and hence requires attention of policy. Concepts and methods from ecology can help in understanding the vulnerabilities which may threaten the provision of vital services and plan contingency measures for potential shocks to critical ecosystem infrastructures.

The Macro level primarily derives from the concept of biome as a host of NEs, is applied to the digital economy. Crucially, DPEs must be understood not as a static standalone but a dynamic structure, which frequently repercuss into the national economy and vice versa. Considering the political, economic, social, technological, environmental, and legal and other relevant context in which a particular DPE operates, is crucial both for better understanding of their dynamics and for designing effective regulation.

The overarching Meta level integrates major general categories of pairwise interactions established in ecology to describe relations between agents (components) of the digital economy. Interactions and feedback loops are crucial in the digital economy, and yet one of the least understood aspects in economics[55]. Neoclassical economics focused on idealized competition whereby nonmarket interactions were seen as a deterrence to attaining a social optimum[56]. Later integration of game theory into mainstream economics led to an increased understanding of (long-run) cooperation between economic agents, however, was limited in terms of getting a grasp of other forms of interactions. Deciphering such complex interactions is important for understanding the critical processes behind DPEs such as innovation, value distribution, and data policy which are at the core of the concerns of regulators today.

4. Relation to the existing literature and positioning of the paper

This paper formally establishes the logical links between the domain of ecology and that of the digital economy, based on shared CAS foundations, and utilizes this to transfer established concepts and tools from ecology with the aim to facilitate research and regulatory insights for the digital economy. Historical evidence demonstrates that natural sciences have significantly enriched the development of economics from its inception by providing diverse metaphors, which help to explain phenomena observed in social systems based on well-understood systems from nature[47,57,58]. As a prominent example, biological evolution has been applied to explain both the cause for, and consequences of, economic growth[59]. The idea of 'evolutionary economics', first coined by Thorstein Veblen, was the most significant transfer of ideas between biology and economics with contributions from Alchain, Boulding, Friedman, among many others[58]. Detailed application of insights coming from biological evolution to the economic domain was further substantiated in the Evolutionary Theory of Economic Change[60] which implicits the role of replicator dynamics in the adoption of the most successful strategies employed in business [60]. Ecological metaphors were used to illustrate business ecosystems, and, recently, their application evolved to explaining system interconnectedness and interactions specific to the digital economy, which was not considered in mainstream economics [3,47,55].

On the other hand, the use of concepts and metaphors from ecology has been criticized for their lack of specificity and utility for continued application. For instance, Thomas and Autio argue that Moore's use of the term 'ecosystem' [3] was insufficiently defined[61]. His 'ecological' approach was so vague that the biological metaphors which have since appeared in various business and organizational literatures are not operationally useful while the term 'ecosystem' itself has been applied to systems of vastly different sizes with varying number of actors, and ill-defined boundaries [62]. These conjectures fall into the broader criticism on the use of ecological metaphors or transfers of concepts and tools from ecology to economic and business literature. For example, Parisot et al. point that as some key features from nature such as mortality or reproduction do not find equivalents in business systems, the applicability of the evolutionary view on the organizational dynamics is of limited relevance[63]. However, the fundamentality of CAS as a bridge between the domain of ecology and that of the digital economy allows us to utilize sound analogical reasoning, which is built on a logical, relational structure shared between two domains rather than the equivalence of all parameters. This provides an opportunity to go beyond the scope of illustrative metaphors and perform justified adaptation of concepts and tools that apply to the objects involved in these relational structures. For example, genetic mutation, recombination, and replication enable the long-term adaptation of species to dynamic surroundings, just as perpetual innovation bolsters the agility of the product evolution in a volatile market - while the firm that produces it may change ownership or structure[57].

The presented research complements previous studies which have applied CAS theories to domains in economics adjacent to DPEs. For example, Reeves et al. propose that companies are CASs nested within a business ecosystem just as species population are CASs nested within a natural ecosystem[64]. Using various ecological analogies, the authors put forward several considerations parallel to research shown here, including the importance of maintaining diversity and reducing centrality (or increasing modularity) in business ecosystems. Russell and Smorodinskaya provide observations and policy guidance on patterns found in innovation ecosystems using the CAS theory[65]. More broadly, application of CAS is wide-ranging in organization literature [66–68], various fields of law [69,70], and in social sciences [71].

This paper contributes to the emerging body of literature that identifies new typology inspired from disciplines studying nature to benefit the understanding of specific digital business ecosystem challenges. Such studies focused so far on providing ecological insights for context-specific settings. For example, Moore used anecdotal insights from NEs to support his conceptual model on cooperation and competition in business ecosystems at various stages of their growth[3]; Iansiti and Levien illustrated the 'keystone' role of orchestrators in a particular business environment[4]. This contribution intends to provide a universal framework relevant across multiple contexts. In this vein, it addresses the major curse of regulators regulating digital business. Due to the high agility of these businesses even relatively new concepts and tools developed for the context of yesterday may lose their relevance already today. As a result, regulators often find themselves lagging behind the development of DPEs. The framework covers the dynamical view of the DPE functioning and thus has the potential to support anticipation of new challenges and phenomena in addition to reaction to those which have already manifested themselves. This paper can be seen as a theoretical synthesis and theoretical adaptation[72] in that it aims to unite fragmented transfers between NEs and DPEs by introducing CAS as a new lens for understanding DPEs.

Finally, it is important to briefly discuss other existing examples of hierarchical frameworks which have been used to study economic systems. Wang presents the most comprehensive transfer, focusing on understanding sociotechnical and digital innovation ecosystems as well as mapping the sub-disciplines found within ecology which could serve as domains for insights on these ecosystems[62]. The 5M Framework makes a similar conceptual contribution as Wang, focusing on the digital economy and DPEs therein. The two types of systems overlap, however remain distinctly different. Moreover, the approach of relying on the CAS theory justifies the constructions while Wang's model was not based on an established theoretical foundation[62]. Petit and Schrepel introduced a multilevel analysis for competitive market systems, whereby an industry pertains to the macro-level, market pertains to the meso-level, and firm pertains to the micro-level[56]. This paper advocates for the use of complexity science in neoclassical antitrust, and thereby, introduces a multi-level analysis to assess the interconnectedness between each level and to study competition beyond just product-rivalry. This hierarchical framework, however, is limited in its application due to its exclusive focus on competition systems. In comparison, the competition analysis may be incorporated into the 5M Framework through the Meta level which would cover competition between alternative individual business fundamentals, products, ecosystems and entire digital economies. Reeves et al. also present a hierarchical framework to decipher the various nested components of business ecosystems and derive scientific analogies from NEs to explain market phenomena on the basis of the CAS theory[64]. The article does not serve to expand the use of concepts, tools, and methods from natural sciences to develop understanding for the business environment, rather, it delivers insight on the broader trends shaping the more complex business environment. Nonetheless, this research substantiates the need for a CAS-based approach to understanding economic phenomena, in this case, the digital economy, and strengthens the basis of deriving this approach from the well-founded field of natural sciences.

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Figures

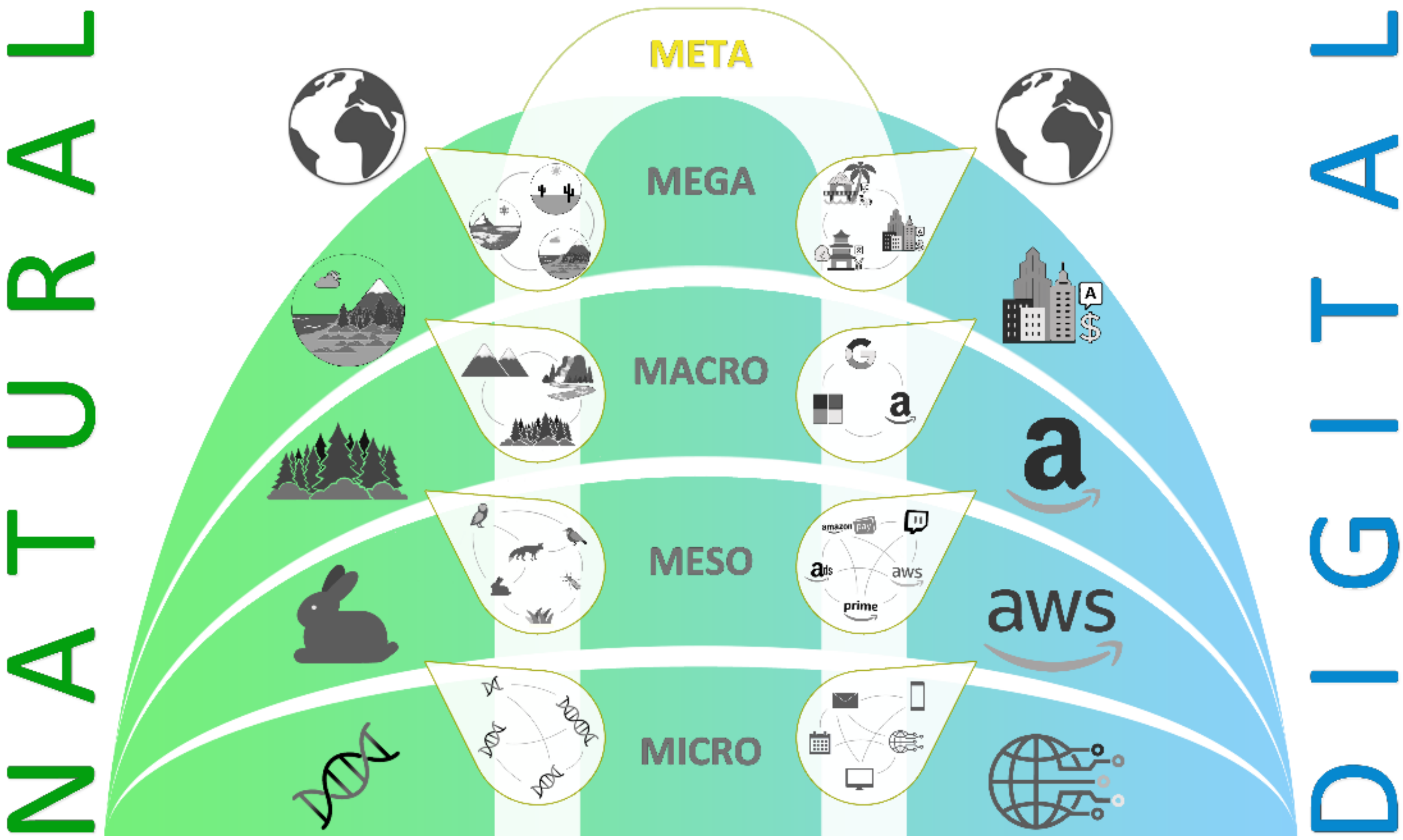

Figure 1

The schematic structure of the 5M Framework.

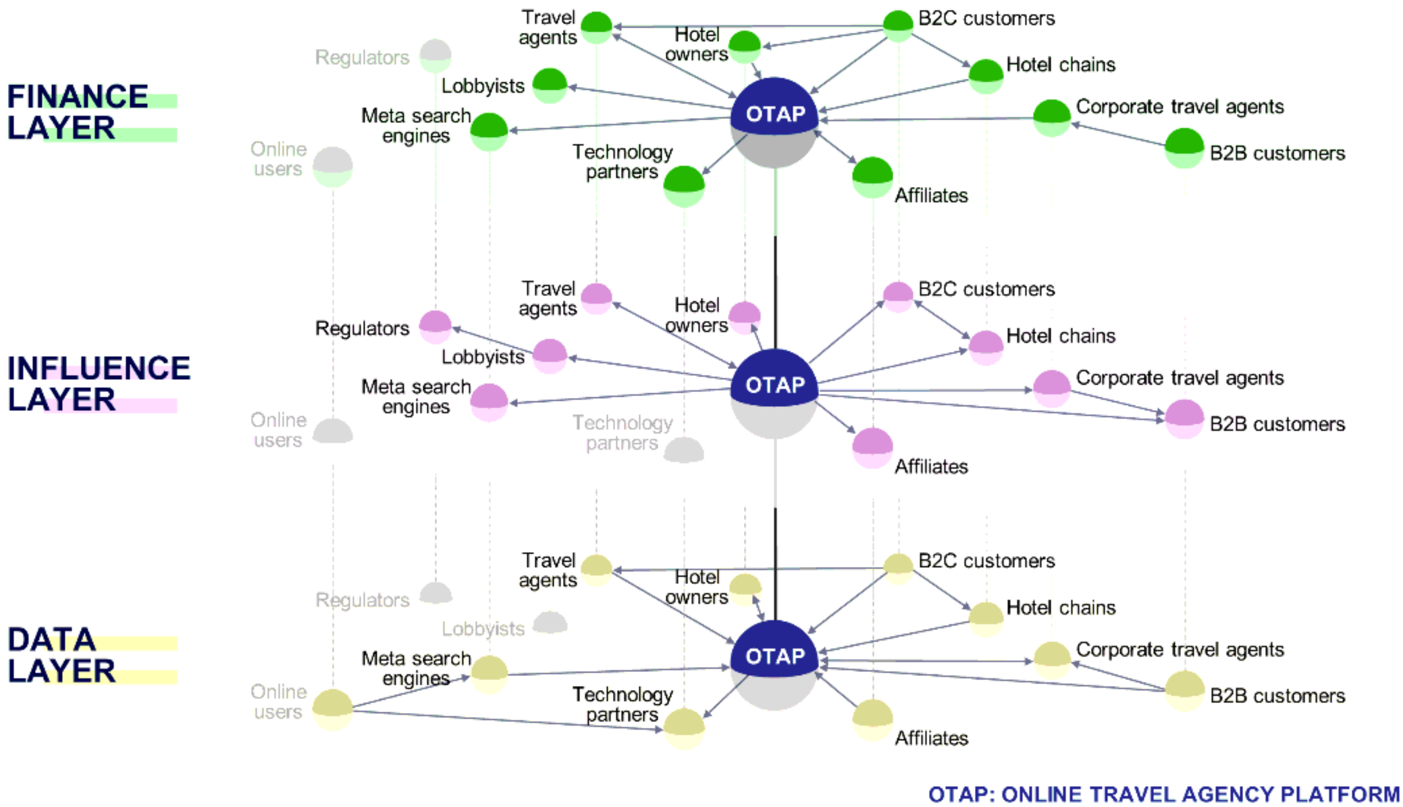

Figure 2

Illustration of the network structures of financial, data, and influence flows for a stylized online travel agency platform.

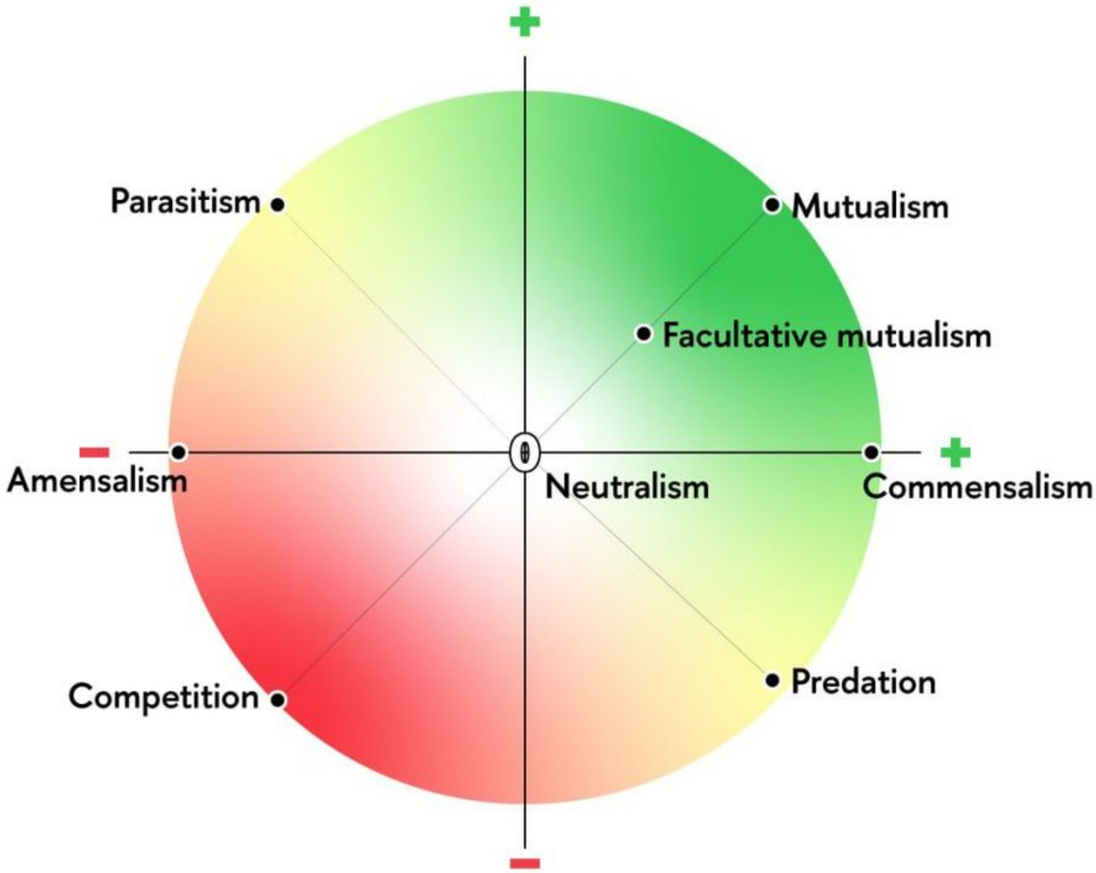

Figure 3

A schematic illustration of the major types of pairwise interactions between species in ecology. The distance from the origin symbolically depicts the interaction strength.