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An ecological perspective to master the complexities of the digital economy

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Economic and social interactions are shifting to digital platforms which grow into vast ecosystems where user engagement creates value for members while ecosystem orchestrators harvest massive revenue. The digital ecosystem business model succeeds by adeptly navigating fast-changing environments, including new technologies and volatile demands, through dynamic innovation in a decentralized decision-making setting. This renders digital platform ecosystems complex adaptive systems. Recognizing that natural ecosystems are a prime example of complex adaptive systems, we propose a systematic hierarchical framework for describing and understanding digital ecosystems, rooted in ecology and evolution. Our framework compares digital ecosystems hosted by societies to natural ecosystems embedded in biomes, products to species, and technologies and elements of business strategy to the genetic makeup of a species. As digital platforms face heightened scrutiny about their socio-economic power and societal value, our approach contributes to the development of deeper understanding and sustainable governance of the digital economy.

Rapid digitalisation of recent decades has propelled a new type of economic phenomenon: the digital platform, which provides a digital infrastructure for a wide range of economic, social, and other interactions such as e-commerce, mobility, and social organization. Such platforms can grow into vast ecosystems of multiple member groups who create, exchange, and consume value generated from the facilitated interactions. The remarkable success of the digital platform ecosystem business model is evident with their rapidly gained dominance across many economic activities. For example, as of early 2024, five of the top ten companies by market capitalisation globally were digital platform ecosystems including Microsoft, Apple, Alphabet (the parent company of Google), Amazon, and Meta[1]. The unprecedented accumulation of economic power by major ecosystems, evading the scrutiny of competition authorities, has raised significant concerns of policymakers, experts, and the public.

Business leaders, social actors, and regulators often struggle to find appropriate frameworks to describe, understand, and debate the economics of digital platform ecosystems and the impact the economic dominance of a few ecosystems has on our socio-environmental systems. Vividly illustrating the scale of this challenge is the frequently cited statement associated with Jack Ma, the founder of China's prominent Alibaba ecosystem, where he described himself as '*a blind man riding on a blind tiger*'[2]. Clearances of major deals, such as Facebook's acquisition of WhatsApp and Google's acquisition of an online advertising company DoubleClick, which only furnished the incumbency of these tech giants, illustrate the challenges faced by the competition authorities worldwide in identifying effective measures to limit the accumulation of economic power by major ecosystems.

During the last decades, observations on the apparent parallels between natural ecosystems and networked businesses, including digital platform ecosystems, have inspired a handful of transfers of insights from ecology to explain their dynamics, pioneered by Moore coining the term 'business ecosystems' and discussing a 'new ecology of competition'[3]. To discuss economic power of platform orchestrators stemming from their critical position in the network of interactions within their ecosystem, Iansiti and Levien[4] adapted the notion of 'keystone species', i.e., those species with a disproportionate effect on the network in relation to their abundance[5]. Or, Lianos and Carballa-Smichowski[6] recently explored network-based indicators such as centrality to measure market power, a concept also applied extensively to identify key components critical for various types of interactions within natural ecosystems[7].

While such research has contributed vivid metaphors and insightful terminology to help explain selected aspects of the complexity underlying digital platform ecosystems, past applications of ecological concepts to such ecosystems have been fragmented and yield limited insight. Thus, a deeper and more coherent understanding of the workings of digital platform ecosystems

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could be achieved through a comprehensive and guided transfer of concepts from the domain of natural ecosystems. We aim to achieve such transfers through analogical reasoning founded on systematic links that are due to the shared structures and dynamics of the two domains, nature and the digital economy[8–10]. Their principal structure and dynamics, together with the resulting patterns of their behaviour allow us to adopt the view of digital platform ecosystems as complex adaptive systems[11]. This provides a solid conceptual basis for a systematic linking of their attributes with those of natural ecosystems, which represent a prime and thoroughly studied example of complex adaptive systems.

Within the conceptualization of digital platform ecosystems as complex adaptive systems, we recognize that these ecosystems are embedded within their respective context, the digital economy—just like natural ecosystems are an inherent part of nature. We rely on a well-established understanding of the hierarchical organization of natural ecosystems to construct a corresponding hierarchical framework for the digital economy hosting platform ecosystems. The resultant framework organizes key elements and processes within and surrounding the digital platform ecosystems based on parallels between the two domains. Therefore, this organization allows for a structured transfer of 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.

We demonstrate the potential of this approach to describe and explain critical phenomena and concerns in the domain of the digital economy by presenting several concepts providing easy-to-understand yet powerful new analogies from the realm of nature. We surmise that our framework will foster a comprehensive 'eco-logical' understanding for the digital economy, guide the design of effective policies and inform the implementation of appropriate enforcement to effectively govern digital platform ecosystems.

Digital platform ecosystems as complex adaptive systems

Natural ecosystems have long been recognized as complex adaptive systems[11]. In fact, the development of complex adaptive system theory was spurred by observations of the emergent complexity in natural ecosystems and the growing recognition of the intricate linkage between this complexity and both the ecosystem structure and the dynamics of its components. Complex adaptive system theory stylizes real-world systems as populations of entities, called agents, driven by the pursuit of survival and thriving. Agents are often heterogenous, characterized by unique attributes defined by the information 'encoded' within them. Agents take actions, interact with each other, and adapt to their surroundings, including other agents, which is enabled by the evolution of their attributes. Successful agents proliferate in the population while other less successful variants may diminish. The multitude of dynamic interactions among agents, collective co-adaptation, and the evolutionary processes shaping their attributes contribute to the systems' complexity and lead to emergent phenomena such as self-organization, synergism, and non-linear dynamics.

The comparison of capitalist economy to an evolutionary process was coined by Joseph Schumpeter[12], which subsequently developed into evolutionary economics, with the central idea 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[13–15]. The digital platform ecosystem business model strongly relies on rapid and dynamic innovation in technology, and importantly, in business strategy[16,17]. Ecosystem orchestrators continuously explore opportunities to adapt in response to new market developments. As with nature's evolutionary dynamics, advantageous changes are readopted and replicated in the digital economy whereas detrimental changes usually diminish over time.

Like natural ecosystems, digital platform ecosystems build on idiosyncratic interactions of multiple heterogeneous entities—products—that occur through strategic partnership and integration aligning key actors and underpinned by flows of finances and user behaviour data[18]. Numerous elements of technology and business strategy behind a product define its 'niche' in the market[14]. Digital platform ecosystems generate value through the harnessing of synergies across members[19,20], enabled by continuous innovation of technology and business strategy that drive the competitiveness of the ecosystems' products. Strong reliance on innovation, along with the complexity and synergism of interaction among members, distinguish digital platform ecosystems from conventional linear modes of production[21] and make the complex adaptive system model a particularly well-suited framework for their analysis and understanding.

Hierarchical framework for the digital economy

The observation that digital platform ecosystems, as complex adaptive systems, share structural and functional characteristics with natural ecosystems, leads us to propose a hierarchical *eco-evolutionary rooted framework for the digital economy*, through which we draw parallels between hierarchies observed in nature and those found in digital economies. The framework includes five major levels—Micro, Meso, Macro, Mega, and Meta, which gives rise to a concise name, the *5 M Framework*.

Biological prototypes for Micro, Meso, Macro, and Mega levels are, respectively, genes, species, ecosystems, and biomes[22] as four fundamental nested levels encompassing major biological, ecological, and evolutionary processes and phenomena. At each level, entities act and adapt, and the fittest survive and thrive, while their interactions lead to the emergence of higher-level entities. Namely, genes that encode information for defining traits collectively shape individuals of a species, while species linked together by interactions and exchange of resources collectively form an ecosystem that is hosted by a biome[23]. Interactions within and between these four levels lead to ecological and evolutionary dynamics, which we capture within an interaction-dedicated Meta level—a fifth level in our 5 M Framework.

Correspondingly, we systematically identify analogies between processes and phenomena in the domain of the digital economy to those in nature, at each of the five levels, which will serve as a basis for transferring concepts and tools from evolutionary biology and ecology to the realm of digital platform ecosystems. Thus, we consider fundamentals of digital business such as elements of technology, knowledge, and business strategy (including user behaviour data) at the Micro level of our 5 M Framework—analogous to genes; products at the Meso level—analogous to species; digital platform ecosystems themselves at the Macro level—analogous to natural ecosystems; wider societies hosting platform ecosystems at the Mega level—analogous to biomes, and interactions within and between these four levels at the Meta level (see Fig. 1).

Transferring concepts and tools from ecology to digital economy

The digital economy has emerged only recently, hence the existing approaches for describing and understanding its complexities as well as designing and implementing effective governance are in their early stages of development. We propose 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 natural ecosystems. The 5 M Framework, designed through analogical inference, facilitates the application of such inference to foster the transfer of specific concepts and tools between the natural and digital domains. Here we briefly discuss some *candidate concepts and methodologies*, which demonstrate the potential of our 5 M Framework to facilitate the identification of a variety of useful analogies. The criteria for their selection were their 1) accessibility for non-specialists in biology and ecology, 2) relevance to challenges of the digital economy, and 3) diversity and coverage of all 5 M levels. The actual application of each of candidate concepts, theories, and models would naturally require a separate, thorough process, which is beyond the scope of this paper. Facilitated by our proposed 5 M Framework, future research may explore many more approaches from ecology and evolutionary biology to address the most pressing knowledge or regulatory gaps.

At the micro level: understanding technological and economic innovation through evolutionary dynamics

The Micro level of the 5 M Framework enables the comparison of innovation to evolution for the context of the digital economy. Genetic elements,

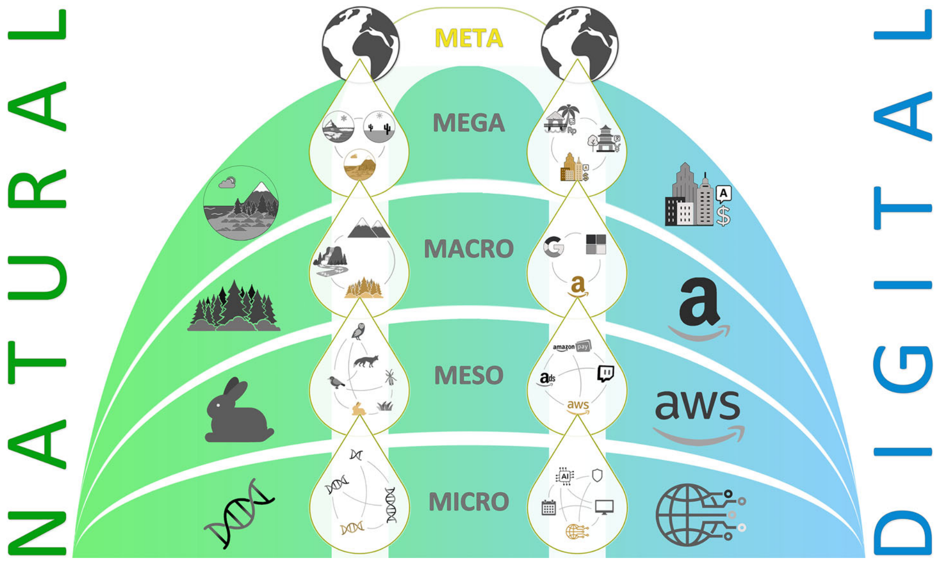

Fig. 1 | The schematic structure of the 5 M Framework. The figure illustrates the hierarchy of the five levels of the 5 M Framework and the corresponding parallels between the domain of nature and the domain of the digital economy. In each level, the droplet depicts (in a stylized fashion) a collection of entities, which form a structural foundation for an individual component at the level above. On the left-hand side, in green, the realm of natural ecosystems is represented. The figure illustrates that genetic information at the Micro level (a collection of genes) forms an organism hosted at the Meso level. Likewise, several organisms of the same and different species collectively form an ecosystem at the Macro level. Several ecosystems may co-exist in a biome, which is hosted at the Mega level. On the right-hand side is the digital economy depicted, in blue. Analogously to the genes found in nature, individual knowledge and technological components are located at the Micro level. A collection of such components forms the basis of a product at the Meso level. An ecosystem is formed at the Macro level, where several, often complementary components combine to co-create value. Digital platform ecosystems may co-exist with each other within a wider society. In both domains, individual components at the Mega level, i.e., biomes or wider societies form the total existence of these domains. Lastly, the white stripes in the figure illustrate the totality of interactions that operate within and in between each of the remaining levels, placed in the Meta level, which is key to understanding the complexities inherent to each domain. The logos and pictograms in this figure are used for illustrative purposes.

whose combined information determines a living organism, are compared to the underlying fundamentals of products offered by a digital platform ecosystem. These fundamentals can include elements of technology, knowledge, and business strategy (including user behaviour data). For example, digital streaming services such as Spotify and Netflix emerged from a combination of various innovations in smartphone capabilities, high-volume data transfer, digital payments, and the introduction of machine learning to determine user preferences, among other elements.

Boosting innovation remains a significant challenge for governments around the world, with competition seen as a pivotal catalyst for fostering innovation. The *evolutionary arms race* theory underscores that continuous competition is costly to individual agents but, through survival of the fittest, ensures the continuation of species. 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[24]. For example, organisms continuously develop new defence mechanisms against pathogens, e.g., growth-inhibiting antibiotic compounds, prompting counteractive innovations, such as developing enzymes that neutralize such compounds in response.

Similarly, successful innovations in competitive economic systems provide strategic advantages, which pressures other agents toward further innovation, often via costly R&D investments[13]. Digitalization and platformization, however, have altered the course of the evolutionary arms race. Open innovation models adopted by many digital platform ecosystems facilitate innovation within their ecosystems[25], however, large established companies gravitate toward proven technological and business solutions, which reduces space for innovation. Furthermore, dominating players can suppress nascent innovations through mergers, acquisitions, or various forms of anticompetitive behaviour. Similarly, operating under tight fiscal constraints, governments are often tempted to support selected areas of innovation based on anticipations of their promise. However, such a skewed approach may not be optimal in settings characterized by significant uncertainty around the direction of technological and economic progress.

In contrast, innovation in nature is driven by random mutations generating rich genetic diversity essential for species adaptation in volatile environments. In such environments, originally neutral or even disadvantageous mutations may become advantageous to thriving and survival – the phenomenon of *preadaptation*[26]. 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[14]. This is especially true for the digital economy, where innovations are constantly being produced, restored, and replaced[17]. For example, Global Positioning System (GPS), originally developed for weapons guidance, was co-opted for commercial navigation use and is now a core technology for self-driving vehicles.

Myopic ecosystem management may harm their genetic diversity hindering 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 certain key soil nutrients and increase 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[27]. Adverse experiences with monoculture demonstrate how a race for efficiency in managed ecosystems can exacerbate diversity loss and hinder innovation, making them vulnerable to collapse. These observations have prompted modern ecosystem management to prioritize genetic diversity for resilience and sustainability—an approach that could also be applied to the digital economy. However, innovation diversity often directly clashes with the self-serving objectives of ecosystem orchestrators, and current regulations do not adequately emphasize or protect it[28]. Overall, ecological reasoning underscores the importance of ensuring favourable conditions for innovation and sheds light on the complex interplay between competition, diversity, innovation, and resilience of ecosystems.

At the meso level: understanding product dynamics through species survival and proliferation strategies

The Meso level of the 5 M Framework focuses on products and species. Products, whether goods or services, are foundational elements of economic activity, offering utility to consumers and driving market dynamics. Products have also been the prime object of consideration and scrutiny by authorities. For example, traditionally, competition authorities assess a company's monopoly power based on its product share in relevant markets. Products evolve through innovation and act as agents in a complex adaptive system model of the digital economy.

Products can be compared to species, which constitute fundamental units for understanding phenomena in nature. A species is defined by a unique combination of traits that enable it to occupy a certain ecological niche, providing the necessary resources and environmental conditions for its survival and thriving.

Similarly to nature, products also occupy 'niches'[14], defined by their position within the value creation network and their reliance on both financial as well as non-financial resources, including access to technology and a customer base. Companies' strategies to bring out established and new products to consumers can be diverse and multifaceted, tailored to meet evolving market conditions and consumer preferences. A grasp of these strategies is crucial for elucidating the workings of the digital economy and safeguarding consumer and broader societal welfare, which stands as the ultimate goal of regulators.

Both species and products enjoy flexible definitions. For example, narrower classifications such as subspecies or ecotypes can help differentiate groups of individuals of the same species exhibiting some variations, often due to geographical or ecological factors. Conversely, when species boundaries are blurred, broader groupings like genera (which include sister species) or functional guilds (comprising species with similar functions) may be used, depending on the analysis context. Likewise, boundaries of products, especially in the digital economy, can be ambiguous, in which case analysis may require finer- or coarser-grained categories. For example, LinkedIn can either be considered as one product within a vast ecosystem of Microsoft or it can be seen as several interconnected products such as online job board, social media for professional networking, and digital advertising, among others. Flexibility of the product definition in the digital realm is a pre-requisite to explain the economics of digital platform ecosystems. Certain activities such as facilitation of interactions by the ecosystem orchestrator, 'renting' user attention[29], or supplying data by the user, are novel forms of products produced and exchanged within the digital economy. The Meso level accommodates such novel product forms alongside the more traditional goods and services.

How products concur and hold markets is akin to how species survive and thrive in nature. For instance, species' foraging for food compares to seeking resources necessary for business growth such as finances, users' attention, and data of users and their interactions. *Optimal foraging theory* explains how species adjust their strategies to optimize the effort spent on acquiring food of different values and availability[30]. How products concur and hold markets is akin to how species survive and thrive in nature. For instance, species' foraging for food compares to digital platform ecosystems seeking new resources such as consumer attention, data, or venture capital while optimizing between launching new products, entering new markets, or maintaining existing activities. 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 influence the metric optimized by a digital platform ecosystem through monetary or non-monetary instruments, steering the platforms' foraging patterns toward greater consumer or societal welfare. Similarly, understanding the foraging strategies of complementors working within the ecosystems can better inform law enforcers and regulators about an intra-platform competition. On the other hand, consumers can also be conceived as foragers optimizing the search for products given their budgetary, time, or attention constraints. Given these diverse parallels, optimal foraging theory can inform the development of theories to complement the established utility theory in economics[31].

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 on them individually. Likewise, a digital platform ecosystem orchestrator 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)[32], diversity of complementors in terms of their product quality and the pace of development is an important factor for ecosystem success. Over-reliance on r-type products may reduce consumer retention. Over-reliance on K-type products only would slow the rate of innovation. The trade-off between product quantity and quality is crucial for regulators to understand. For example, app stores such as Google Play may host several gaming apps with low investments e.g., simple games, as well as few high-investment complex gaming apps. such complex open-world games. The concept of r- and K-strategy is yet an unexplored approach that may facilitate a better understanding of the product dynamics in digital economies as a simplified yet meaningful analogy.

Thus, the analogy between products and species allows us to draw on extensive biological insights into the variety of survival and expansion strategies of species. Optimal foraging theory and theories of life history strategies are two examples that illustrate how these insights can inspire a more comprehensive and realistic understanding of the business strategies adopted by platforms.

At the macro level: understanding ecosystem complexity and dynamics

The Macro level compares digital platform ecosystems to natural ecosystems. The focus at this level is on the ecosystem as a whole, which we treat as an enduring grouping of agents collectively producing, exchanging, and capturing 'value', such as revenue or data[3,20]. Many large and established digital platform ecosystems are entrenched into the economy and society generating essential services, including e-commerce and social networking. The recent case of Microsoft outage demonstrates how disruptions of stable service provision can lead to significant losses[33]. Ensuring stable operation of essential ecosystems becomes therefore a matter of public concern and requires policy attention. Concepts and methodologies from ecology can help identify ecosystem vulnerabilities that may threaten vital services and guide the planning of effective contingency measures.

In the digital economy, the orchestrator, complementors, and other ecosystem members bring their products to the market, while harnessing advantageous synergies. This is enabled by exchanges of resources and influence relationships, which include strategic partnerships and integration aligning the key actors. Data constitutes an essential resource in digital platform ecosystems, and data exchange is crucial for synergistic value creation in the digital economy[34]. Just as energy and nutrient flows connect species into a stable food web, data—along with financial flows and influence relationships—binds an ecosystem together (see Fig. 2).

Ecosystems and their entire existence are powered by *boundary inputs*, that is subsidy flows from outside the system, while *ecosystem boundaries* are often flexible and depend on the scale, perspective, or specific ecological or management goals being considered. Like natural ecosystems, digital platform ecosystems do not have rigid boundaries as they simultaneously operate in several industries. Regulators must adapt to the non-static, context-dependent boundaries of ecosystems to effectively manage their cross-industry and cross-regional operations.

In natural ecosystems, primary producers are the main recipients of boundary inputs. The way these inputs trickle down to other species organises the ecosystem into *trophic levels*, which measure the remoteness of any one species from the primary source. Financial investments and other inputs such as R&D and data facilitate growth of digital platform ecosystems

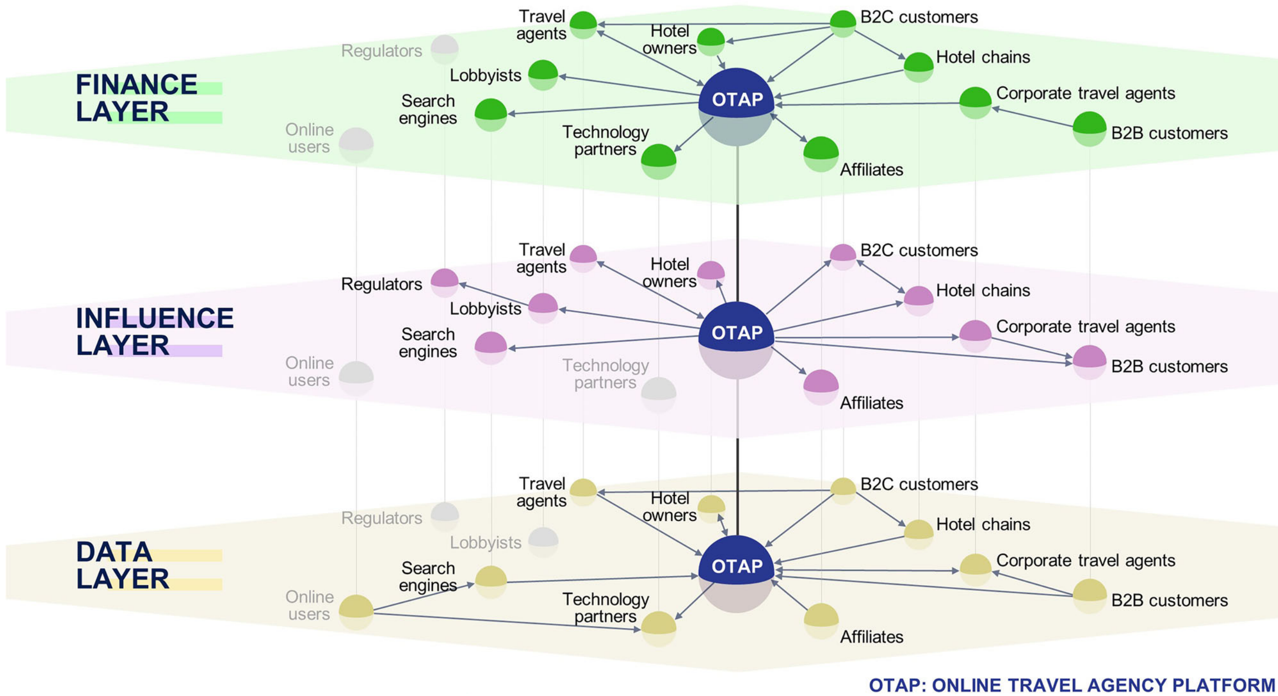

Fig. 2 | Illustration of the network structures of financial, data, and influence flows for a stylized online travel agency platform. This figure illustrates a network of actors, represented by spherical labelled nodes, which collectively facilitate the products provided by a hypothetical online travel agency platform, represented by the large blue sphere. Each layer represents a resource, which is created and/or exchanged between the actor nodes active (shown by colour) at that layer. For example, the online travel agency platform receives finances from hotel owners in the finance layer in green but also exchanges data at the bottom layer with the same actor(s). The nodes represent three types of actors: i) consumers, ii) product providers e.g., hotel owners, and iii) product facilitators e.g., search engines. The financial and data exchanges and the exertion of influence between the actors support the value creation and consumption process within the online travel agency platform ecosystem. This hypothetical case represents the utility of multiplex network diagrams when analyzing the value creation and exchange processes within networks of complex adaptive systems. Separating each resource into a layer for the same network of actors allows us to analyze the flow and exchange of each resource within the network and identify differences in the flows for each resource. Multiplex network diagrams may also be used to illustrate the flow of resources between separated layers.

and can enter the ecosystem through different channels. For example, primary recipients of money issued in an economy, including banks or venture and investment funds, inject finances to start-ups and other companies, which then pass on to their customers and further to other members of the economic system. Governments may offer additional resources, in various formats, directly to the orchestrator, particularly when a digital platform ecosystem fulfils a socially essential function[35–37].

Analogously to natural ecosystems, considering the architecture of financial or data flows within a digital platform ecosystem, its members can 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 an ecosystem.

The *network complexity*, defined by the number and the architecture of interactions in an ecosystem, has been demonstrated to both promote and hinder *stability* of natural ecosystems with respect to perturbations, fuelling a so-called stability-complexity debate[38]. For instance, high species diversity may lower stability of some sub-systems while it may increase stability of the wider ecosystem[39]. Similarly, network complexities may provide for higher stability of a digital platform ecosystem in response to perturbations such as regulatory changes or the emergence of a competing ecosystem, while others might hinder it. Hence one objective of regulators could be to manage the complexity of the interaction structure of socially critical ecosystems to increase their resilience while ecology could inform the development of stability indicators for digital platform ecosystems.

Resilience is indeed an important characteristic of complex adaptive systems and increasingly an objective for digital platform ecosystem 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'[40] 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[41]. 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.

At the mega level: understanding the wider societal context, in which ecosystems operate

The Mega level of the 5 M Framework compares the wider societal systems, in which digital platform ecosystems are embedded, to biomes hosting natural ecosystems. This analogy reflects the fact that digital platform ecosystems are not standalone entities, but dynamic structures that frequently repercuss into the national economy and vice versa. The Mega level accommodates considerations of ecosystems from the perspective of societal benefit, which is the most relevant for regulators as well as all participants of the wider economy.

Natural ecosystems are shaped by their surroundings, defined by factors such as prevailing nutrient conditions and interactions with adjacent ecosystems. For instance, a forest and a lake influence each other's nutrient cycles, altering the physical environment where they mutually encroach upon one another. Several natural ecosystems can interact and compete for resources collectively shaping their biome, while the biome, in turn, modulates the conditions that enable their survival and flourishing.

Likewise, several digital platform ecosystems can interact and compete for resources and markets within a society, while simultaneously influencing its economic, social, or cultural norms through, for example, the adaptation of technologies or regulations. For example, China and USA have the greatest levels of emergence and growth for digital products and wider ecosystems, despite having vastly different economic, political, and cultural conditions. Understanding the factors behind this success can shed light on why these nations excel at fostering domestic digital platform ecosystems and how their unique developmental trajectories unfold. On the other hand, the success of digital financial ecosystems and e-wallet platforms has been much more pronounced in China than in the USA, where the latter's stricter institutions and regulatory restrictions have likely hindered their emergence in financial markets.

Biomes act as a theatre of evolution, directing the evolutionary trajectories and the emerging functionalities of species and of ecosystems[42]. Evidence shows that biota and ecosystems, even if separated geographically, display patterns of *convergent evolution* if they reside in the same biome type[43]. For example, different types of drought-adapted plant species evolved in the succulent biomes across various continents. Furthermore, the abundance and variety of fundamental resources in biomes are major drivers of the evolution and diversity of its biota. For example, tropical rainforests with abundant sunlight and precipitation host diverse biota with high biomass production, whereas only drought-resistant biota with low production of biomass can survive the harsher conditions of succulent biomes. Similarly, each society acts as the arena, wherein legal, political, social, technological, and other factors shape the development of their digital economy and the digital platform ecosystems within. For example, societies that provide abundant resources like finances and data are more likely to generate a greater diversity of successful ecosystems compared to restricted or resource-poor regions[44].

Pragmatic studies such as the IMD World Digital Competitiveness Index[44] or the Ease of Doing Digital Business[45] provide rankings of digital developments of countries by assessing their key economic, legal, institutional, and infrastructural dimensions. Moreover, similar convergence patterns in innovation and digital platform ecosystem development often emerge from comparable societal contexts. For instance, mobile money transfer platforms such as Kenya's m-Pesa services took advantage of high mobile phone usage in countries with weaker online infrastructures by offering PIN-secured SMS banking services without requiring internet access. m-Pesa and similar mobile money transfer platforms were quickly adopted across countries such as Senegal and Bangladesh. Yet despite resembling the conditions of Kenya's digital infrastructures, the launch of m-Pesa was less successful in countries such as India and South Africa due to harsher regulatory structures, illustrating that convergences depend on the alignment of several condition factors.

Considering the overall political, economic, social, technological, environmental, legal, and other relevant contexts, In which a particular ecosystem operates, is crucial both for better understanding of their dynamics and for designing and enforcing regulation effectively. As digital platform ecosystems expand their operations across borders, often spanning multiple jurisdictions simultaneously, regulators must strive for more multifaceted regulatory approaches that are attuned to other settings beyond their own framework. Effectively addressing this global dimension of digital platform ecosystem operations requires a systematic understanding of the parameters of various national and international circumstances, underscoring the importance of the Mega level in our 5 M Framework.

At the meta level: understanding ecosystems as a whole

Entities at the Micro, Meso, Macro, and Mega levels do not function or evolve in isolation. In the digital economy, technology, knowledge, and business strategy components often integrate and influence the adoption of each other; products and digital platform ecosystems can complement or compete with other products and digital platform ecosystems; and finally, societies can influence other societies. In nature, likewise, genes may influence the expression of other genes within an organism; species feed on and compete for prey and engage in mutually beneficial relationships with other species within an ecosystem; ecosystems and even biomes can influence neighbouring ecosystems and biomes through exchanging resources.

Additionally, numerous interactions connect entities across levels into a coherent system. For example, in nature, major changes at the biome level, such as climate change, can affect the feeding habits of several species. Or heavy fishing can alter the development and maturation patterns of fish through changes at the genetic level. Similarly, in the digital economy, social habits, such as dining out versus cooking at home, influence the direction of innovation in the food delivery sector. Or, as another example of cross-level interaction, data protection regulations influence business strategies behind targeted advertising, which many platforms rely on to monetize their user base.

Since interactions are fundamental to the cohesion of the entire digital economy, we introduce a fifth level, Meta, to capture interactions both within and between the first four levels into a unified virtual level. In this paper, we primarily focus on interactions within the same level, as these phenomena have been more thoroughly studied leading to a unified terminology and an extensive toolkit for analysis. While cross-level interactions are more diverse and context-specific, and analogies between such interactions in nature and the digital economy are likely, exploring these in depth is beyond the scope of this paper.

Broadly, ecological interactions at each level 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).

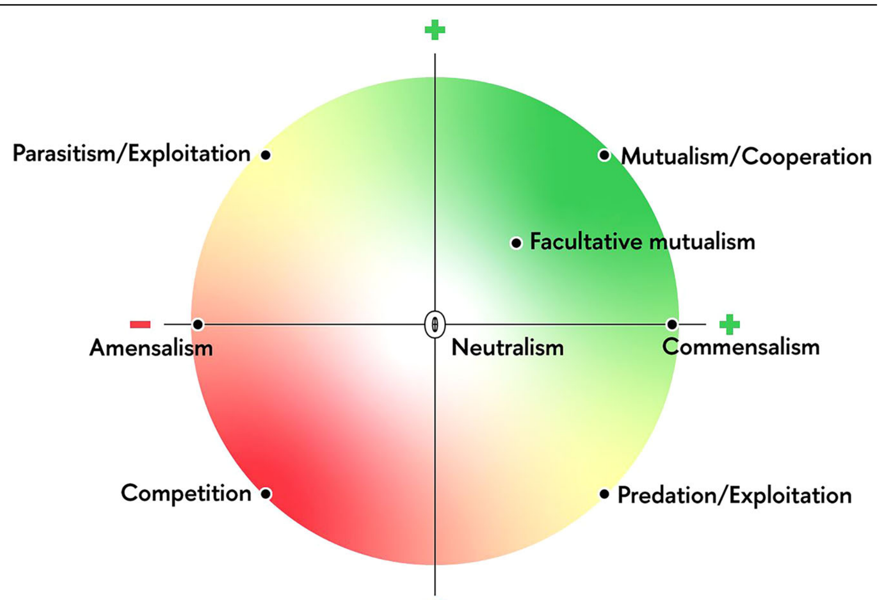

Fig. 3 | A schematic illustration of the general types of pairwise interactions. Each interaction can have a positive, negative, or neutral impact on the subject entity. Each axis represents an interacting entity of a pairwise interaction. The terms used for impact combinations in this figure correspond to established interaction types among or within species, serving as a prominent example of biological interactions. The distance from the origin symbolically depicts the interaction strength.

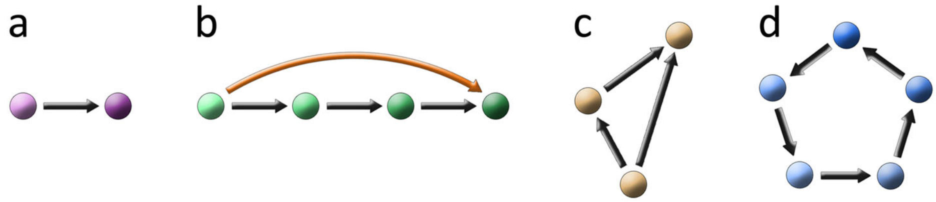

Fig. 4 | Schematic illustration of direct and indirect interaction examples. Nodes represent abstract entities that, within the 5 M framework, can model genes, species, whole ecosystems, or even entire biomes in natural systems, or elements of technology or business strategy, products, digital platform ecosystems, or socio-economic systems in the context of the digital economy. Examples include a pairwise direct predatory interaction (**a**), an indirect effect through a chain of pairwise predatory interactions (**b**), an indirect effect of an intraguild predation (**c**), and a series of pairwise predatory interactions forming a feedback loop (**d**).

Table 1 | Examples of mutually positive interactions in natural and in digital platform ecosystems

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 tumor growth is prominent if three mutations occur together, whereas the solitary mutations alone cause insignificant tumor 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 reinnforce 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 reinnforce each other. Example: platforms such as Spotify or E-bay rely on the mobile operating system infrastructures of Google and Apple to be downloaded on smart devices while the mobile operating system 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 digital platform ecosystems benefits from cooperation of national policy agencies including informational exchange and uniting approaches.

Pairwise interactions occurring between adjacent entities may form indirect effects and feedback loops (see Fig. 4). 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.

Pairwise interactions creating a positive effect on both involved components at all levels from Micro to Mega are key enablers of life (such interactions are referred to as cooperation when occurring between members of the same species and mutualism when occurring between different species). For example, some apex predators such as lions hunt together to increase their chances for success, plants may form a mutually beneficial association with pollinators, such as bees, whose interactions are essential for fertilizing the flowers of plants.

Likewise, mutually beneficial cooperation is crucial for the co-creation of value by digital platform ecosystems. This is represented, for example, by the emergence of the term 'complementors' to refer to multiple decentralized entities that 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. For example, a ride-hailing service and a bike rental service both generate journey data, which can help optimize the offerings of each service within the same ecosystem. Another example is the Apple ecosystem, where iOS developers contribute to the variety of iOS-compatible apps thus increasing the consumer value of the Apple ecosystem and the revenue of its orchestrators.

Table 1 provides examples of mutually positive interactions at the Micro, Meso, Macro, and Mega levels. Importantly—as in nature—the benefits of cooperation or mutualism can be asymmetric for the parties involved, depending on the circumstances. For example, if an ecosystem orchestrator imposes high fees on complementors, it can shift the distribution of added value toward the orchestrator, disadvantaging the complementors.

Despite its profound role in maintaining natural ecosystems, it is often challenging to understand how mutualism and cooperation can exist as it is prone to exploitation or free riding. For example, only few microorganism 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 the synthesising 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[46].

Similar dynamics can be observed in the digital realm as well. For example, Wikipedia serves the public by providing free access to a vast and democratic repository of knowledge, while being created and maintained by a relatively small group of volunteers who ensure the content quality by the cooperative act of open editing and cross-checking. False or misleading contributions would undermine Wikipedia's reliability, eroding the widespread trust it currently enjoys. Similarly, online marketplaces like Amazon are open to almost any individual or business. High-quality sellers attract consumers, while low-quality sellers often 'free-ride' by offering cheaper, lower-quality products, which can diminish the consumer experience while requiring less effort on their part.

Free riding in digital platform ecosystems, particularly with regard to data collection and usage is a major concern for which regulators can collect insights from natural ecosystems. Evolutionary game theory has deepened our understanding of the mechanisms and dynamics underlying the evolution and maintenance of cooperative and mutualistic behaviour in various ecological contexts, from the gene- to species- levels and beyond[47,48]. In the digital economy, this approach could be useful for modelling product strategies that leverage the benefits of an ecosystem business model, leading to co-creation of value by ecosystem members.

On the other end of the spectrum of pairwise interactions are mutually negative interactions—*competition*[49]. 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 reduce expression of genes, fitness of species, and ecosystem/biome productivity in the short run, while in the long run of *competition*[49] is crucial for promoting resilience and driving evolution. Numerous models have been developed in ecology to study the effects. For example, the competitive Lotka–Volterra model[50] 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. Fierce competition may drive a competitor to sacrifice some of its products to regain overall competitiveness, like, for example, Meta discontinued its Workplace tool after failing to compete with Microsoft Teams and Zoom. However, the competition winners may suffer from fewer incentives to innovate.

Specific ecological models and insights into competition may be useful for better understanding and regulation of digital platform ecosystems. So-called 'killer' acquisitions[51] can be analogized to *intraguild predation*, where a top predator kills (and sometimes eats) a potential competitor for a common prey (see Fig. 4c). Such acquisitions aim to eliminate a potential or existing competitor threat, thus stifling competition, reducing innovation, and consolidating market power. For example, after acquiring the GIF search engine Giphy, Meta discontinued Giphy's advertising product, eliminating a potential competitor. A concern over killer acquisitions was among the reasons the UK Competition and Markets Authority eventually blocked the Meta/Giphy merger[52].

Other types of pairwise 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, the other interacting component is unaffected. Finally, under parasitism and predation, one component is harmed by another that benefits from this interaction. In a predator-prey interaction usually the prey dies and is fully consumed by the (usually) larger predator, while in a parasitic interaction, the parasite is much smaller than the host it attacks, does not always kill the host, and often the host can recover from the harms of such an encounter. Interactions in which at least one party suffers a negative effect, such as competition, predation, parasitism, and amensalism, are often referred to as antagonisms.

In nature, several types of interactions may take effect simultaneously. Notably, competition and cooperation sometimes occur between the same entities, depending on the context. For example, pack hunters (e.g., lions) cooperate during hunts to increase their chances for success, later competing for a larger share of the captured prey[53], for mates, or territories. Likewise, digital platform ecosystems can enter into mutual product partnerships while at the same time competing for overall market shares. For example, Apple was reported to make use of Google's data centres to train its AI models while at the same time, Apple and Google are competing in the wider AI technology market[54]. Models developed to understand such *competitive cooperation* in nature could be useful to unravel the phenomenon of co-opetition[55], emphasized by experts attempting to explain similar phenomenon in the digital economy.

Intraguild predation exemplifies how multiple pairwise interactions within an ecosystem can produce indirect effects, where one member influences another even without direct interaction (see Fig. 4). Indirect effects result from a propagation of impacts along a series of pairwise interactions, for instance through cascading effects of changing population dynamics (see Fig. 4b). Indirect effects play a critical role in natural ecosystems, as demonstrated by their prevalence[56] and in assessments of climate change impacts on living systems[57].

Additionally, indirect effects, when arranged in loops (see Fig. 4d), may amplify a direct interaction through positive feedback, or dampen an effect through negative feedback[58]. Positive feedback loop may result in 'runaway' scenarios, e.g., a population explosion of a particular species to the detriment of other species, or bioengineering by a particular species that makes the habitat more conducive for itself, with the same negative result on other species. Negative feedback in ecosystems can balance population sizes or resource use helping to maintain species populations at equilibrium. Understanding the power and interplay between negative and positive feedback loops in an ecosystem can assist in developing adequate management policies.

Indirect effects and feedback loops can also be crucial for innovations in the digital economy. For instance, AI technologies rely on cloud computing infrastructures to operate and commercialize its services. Currently, cloud computing infrastructure is a concentrated market mainly dominated by Amazon, Microsoft, and Google[59]. Accelerated adoption of AI tools drives the demand for cloud computing that is likely to further consolidate their power, an example of indirect effects. Positive feedback loop arises, as these companies already established themselves in the AI sector through investments and partnerships with AI firms, which may influence AI development to steer users back into their ecosystems. Encouraging competition in cloud computing could be one option to reduce the strength of this feedback loops which can also help combat the dominance of Big Tech in AI.

Ecology has developed tools to reveal and measure the strengths and impact of both direct and indirect effects[60]. The Meta level of the 5 M framework facilitates transferring of these methods and beyond that, through a systematic and unified treatment of different interaction types within and in between levels, fosters a reframing of our conception of a healthy economy. This shift would move away from a focus on competition towards a more comprehensive recognition of the entirety of various interactions.

Discussion

This paper approaches digital platform ecosystems as a complex adaptive system embedded in the environment of the digital economy. Relying on complex adaptive system theory and analogical reasoning, it presents an eco-evolutionary rooted framework for the digital economy, the 5 M Framework. The five Ms, i.e., the nested focus levels of the framework, allow for a comprehensive accommodation of processes necessary to grasp the complexity of the digital economy going beyond the traditional focus on products.

In the 5 M framework, products are complex adaptive system agents operating at the Meso level. Technological and business strategy innovation occurring at the Micro level helps to explain the emergence and dynamics of products. The Macro level hosts entire ecosystems enabling analysis of a product within the web of other products, constituting the digital platform ecosystem, to understand its value creation. The Mega level, meanwhile, facilitates considerations of the wider societal systems, in which the ecosystems are embedded. Crucially, the cross-cutting Meta level accommodates interactions—a central phenomenon of complex adaptive systems responsible for its emergent complexity. These five levels of the 5 M Framework provide the backbone for describing and analyzing digital platform ecosystems. Depending on the specific application, other levels may be added for nuance.

The existing literature has thus far been using ecological concepts as illustrative metaphors for business and platform ecosystems[3,16,61]. The approach of this paper goes beyond this, utilizing analogical reasoning[9] enabled by complex adaptive system theory. Analogical reasoning is based on relational structures, independent from the descriptions of object involved in those relations, with the power of an analogy in 'licensing' scientific analysis coming from the systematic structural match between the source and target domains[10].

We underscore that analogical reasoning does not imply the existence of a 1:1 mapping of all phenomena between the source and target domains. The natural world and the digital economy are distinct systems with many unique features which do not find immediate analogies in another system type. For example, we did not identify an obvious analogy in the digital economy for sexual reproduction or intra-species competition. However, the abstraction of complex adaptive systems enables a wealth of analogies, which reflect the fundamental features of digital platform ecosystems—including the emergence of products from innovation in technology and business strategy alongside value co-creation by combining several products.

The 5 M Framework allows for flexible application. For example, users may enter a digital platform ecosystem at various levels as user data are essential for match-making algorithms at the level of know-how, technological solutions, and business strategy components, while user preferences shape the dynamics of products success and the success of entire ecosystems, which makes them part of the level of enabling conditions.

There are two main limitations of this paper. First, like any product of analogical reasoning, both the 5 M Framework and the transferred concepts we suggested, must balance nuances with simplification for effective communication. Thus, we omitted many details from evolution and systems ecology to improve the accessibility of our research and to demonstrate its usefulness for informing management, competition law, and policy. Secondly, the individual concepts highlighted in this paper were discussed very briefly despite each having the capacity for a standalone research project; moreover, the concepts featured here are merely a few examples in a plethora of further research contributions this research hopes to inspire.

Complex adaptive system theory has facilitated a hierarchical view on the digital economy and digital platform ecosystems therein, which we have operationalized through the 5 M Framework. Such a perspective seems to resonate with the presentations of major digital platform ecosystems on themselves and their environment. For instance, in their responses to the UK Competition and Markets Authority'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[62]. For example, Apple argues that its AppStore and devices businesses create a 'mutually reinforcing consumer proposition' and thus should be assessed in combination[63], while Google warned that regulatory interventions could have 'asymmetric effects on different stakeholders across the ecosystem'[64].

Competition authorities worldwide have started to acknowledge the implications of 'ecosystems' in the digital economy. This is recognized in the emergence of 'ecosystem theories of harm', which attempt to explain how the economy of scope, data aggregation, network effects, and other platform strategies exploiting interconnections between their products can impact competition dynamics, consumer welfare, and other socio-economic parameters. These arguments are increasingly being made as part of merger reviews, such as Meta's acquisition of Giphy[52] or Google's acquisition of the fitness tracker company Fitbit[65], as well as in market studies, such as the UK Mobile Ecosystems study[62]. However, the lack of a common framework consolidating regulatory actions continues to allow ecosystem orchestrators to challenge scrutiny which further complicates the challenges of the competition authorities.

To summarize, the 5 M Framework presented in this paper aspires, first, to facilitate better understanding of digital platform ecosystems by organising existing ecological metaphors, supporting the expansion of analogies, and reducing the risk of flaws in this process. Second, it may improve efficiency of scientific analyses of the digital economy by leveraging readily available models and approaches in evolution and ecology. Lastly, it can guide the crafting of efficient policy and regulation measures by providing a basis for a consistent language and a guidance for a comprehensive approach to ensure that digital platform ecosystems continue to deliver services sustainably and serve toward a resilient, competitive, and innovative society.

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Author contributions
E.R. and A.I. developed the overall approach; G.B. initiated the concept of the 5 M Framework, G.B., U.S., and E.R. contributed insights from ecology and evolutionary biology; A.I., E.R., D.K., and S.H. contributed insights from the domain of digital economy; G.B., E.R., and S.H. provided reviews of relevant literature; E.R. led the preparation of the manuscript with all other co-authors contributing to writing; G.B. and S.H. led the development of the figures.

Competing interests
The authors declare no competing interests.

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