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Reticulate evolution underlies synergistic trait formation in human communities

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Abstract

This paper investigates how reticulate evolution contributes to a better understanding of human sociocultural evolution in general, and community formation in particular. Reticulate evolution is evolution as it occurs by means of symbiosis, symbiogenesis, lateral gene transfer, infective heredity, and hybridization. From these mechanisms and processes, we mainly zoom in on symbiosis and we investigate how it underlies the rise of (1) human, plant, animal, and machine interactions typical of agriculture, animal husbandry, farming, and industrialization; (2) diet-microbiome relationships; and (3) host-virome and other pathogen interactions that underlie human health and disease. We demonstrate that reticulate evolution necessitates an understanding of behavioral and cultural evolution at a community level, where reticulate causal processes underlie the rise of synergistic organizational traits.

KEYWORDS

agriculture, communities, diet-microbiome relationships, host-pathogen interactions, ontological hierarchies, reticulate causation, reticulate evolution, symbiosis

1 | INTRODUCTION

Reticulate or network-like evolution is evolution as it occurs by means of symbiosis, symbiogenesis, lateral gene transfer, infective heredity, and hybridization.[1] In all cases, reticulate evolution involves the crossing or intersecting of distinct evolutionary lineages. Bacterial genes or plasmids can become transferred laterally; multicellular organisms exchange bacteria or viruses horizontally; and through hybridization, distinct lineages can merge into new evolutionary descent lines.

Reticulate evolution differs from the vertical evolution studied by the Neodarwinian paradigm. In the latter paradigm, the focus lies on how evolutionary descent lines ramify and diversify into distinct lineages by means of natural selection or drift. The branching out of lineages brings forth tree of life typologies and these are classically understood to depict the gradual descent with modification that Darwin hypothesized to underlie the origin and evolution of species over time. Reticulate evolution instead requires network typologies and web of life metaphors that depict how organisms belonging to different species interact in space.[2–4] Combining tree and network analyses gives a more complete outlook of how evolution occurs.[5]

The growing recognition of the widespread occurrence of reticulate interactions within and between organisms and species belonging to different evolutionary lineages has demanded a reconceptualization of the scope and the limitations of the classic Neo-Darwinian paradigm.[6–11] The Neodarwinian Synthesis is mostly focused on explaining evolution at a microgenetic, or meso-evolutionary organismal level, while reticulate evolution investigates the interactions occurring between organisms belonging to different species and even to different kingdoms or domains of life, and such requires an above-organismal level of analysis.

The advances made within evolutionary biology toward a better understanding of the nature and wide occurrence of reticulate evolution have incited a rising interest in how reticulate evolution possibly impacts human cognitive-behavioral, sociocultural, and linguistic evolution. Here, we examine the prominent role played by symbiosis in bringing forth human, animal, plant, and machine interactions typical of agriculture, animal husbandry, farming, and

BOX 1. Mechanisms and processes underlying reticulate evolution

Hybridization: The sexual reproduction of organisms belonging to different species.
Symbiosis: The phenomenon whereby organisms belonging to different species maintain ecological interactions, possibly lasting over generations through time.
Symbiogenesis: Evolution induced by symbiosis, also known as hereditary symbiosis.
Lateral gene transfer: The horizontal transmission of DNA fragments between genomes or gene-carrying agents.
Infective heredity: Evolution through contagion.

industrialization; diet-*microbiome* interactions; and host-*virome* and other pathogen interactions underlying human health and disease. We will demonstrate that these symbiotic interactions occur at a community level, where reticulate causation underlies the rise of synergistic organizational traits. We conclude that communities, more so than demes, groups, or populations, need to be recognized as ontological levels of evolution, and it is here that synergistic traits evolve. We take off by providing a short overview of the different types of reticulate evolution.

2 | TYPES OF RETICULATE EVOLUTION

Reticulate evolution is evolution as it occurs by means of symbiosis, symbiogenesis, lateral gene transfer, infective heredity, and hybridization (Box 1). Of these, only hybridization comes about by sexual reproduction. All other types of reticulate evolution occur asexually. These asexual forms of reticulate evolution take place within the life course of an organism, and this then impacts the further course of evolution.

2.1 | Hybridization

Hybridization happens when organisms belonging to different species reproduce sexually.[12] This can sometimes lead to offspring sterility. Mules, for example, that are a cross between a female horse and a male donkey, cannot produce offspring. But there exist many other cases in nature where reproduction is possible either amongst the hybrid offspring or amongst the hybrids and members of the parental species (which then enables backcrossing). The chromosomes of hybrid species often also remain compatible with those of closely related species which facilitates successful reproduction amongst multiple species. From an evolutionary perspective, hybridization enables the introgression of foreign DNA into the species genome, and this is a means to increase variation, to reduce genetic fatigue, to expand toward new ecologies, or to avoid (the total) extinction of a species.[13]

Hybridization has played a far-reaching role in human and hominin evolution.[14–17] Genetic research demonstrates that Neanderthals and humans, Neanderthals and Denisovans, and Denisovans and humans crossed a sufficient number of times to leave genetic traces thereof within the human genome, and there is evidence of hybridization having occurred with all of these species and as of yet unidentified other hominin species. Vernot and Akey[18] estimate that around 20% of Neanderthal DNA endures within the human genome. Danneman and Kelso[19] demonstrated that among that 20% are skin traits enabling adaptation to colder climates. Early humans migrating out of Africa must have received these traits during admixture with European Neanderthals.

2.2 | Lateral gene transfer

Bacteria and *Archaea* are *prokaryotic* organisms. During their life history, they form colonies, biofilms, and other communities where they exchange genes laterally (Box 2).[2] As the name implies, lateral gene transfer involves the horizontal transmission of genes. In prokaryotes, well-known processes whereby lateral gene transfer occurs include conjugation, transformation, and transduction. During conjugation, bacteria touch and exchange *plasmids*. In a process called transformation, bacteria can simply take up genetic material from the surroundings, even from dead bacteria. During transduction, bacteria acquire genes from other bacteria via *bacteriophages* that serve as transmission vectors.

Lateral gene transfer can moreover take place within *eukaryotes*, between the cell nucleus and cell organelles[20]; and between eukaryotes.[21,22] Lateral gene transfer thus takes place between all three domains of life, although it comes about more easily amongst prokaryotes.[23]

2.3 | Symbiosis

Symbiosis is an ecological phenomenon first defined in 1879 by Anton de Bary as the living together of unlike-named organisms.[24] Symbiotic associations are either facultative or obligate, and they can occur haphazardly or repeat over generations through time in which case they can become necessary and hereditary.[25]

Symbiotic interactions can be neutral, beneficial, or harmful for one or all of the participants in the symbiosis (Table 1). Parasitism refers to a symbiotic association harmful to the host but beneficial for the parasitic symbiont; commensalism is beneficial for one of the interacting organisms while it leaves the other unaffected by the symbiosis; and mutualism is a symbiotic association where both host and symbiont benefit from the association. Parasitism, commensalism, and mutualism are the three main types of symbiosis. These were first distinguished by Pierre Joseph van Beneden in 1875 in the context of research on the “social” interactions that exist between

BOX 2 Glossary of italicized terms (ordered alphabetically)

Archaea: The oldest domain of life, comprising prokaryotes living mostly in extreme or oxygen-low environments, known for maintaining mutual and commensal symbioses with eukaryotes.

Bacteria: The second-oldest domain of life, also comprising prokaryotes, some of which are parasitic upon eukaryotes.

Bacteriophages: Viruses that infect bacteria.

Biofilm: A stable structure formed from previously free-floating microorganisms commencing holobiont formation.

Colony: A group of (micro)organisms all deriving from the same progenitor.

Community traits: Synergistic/organizational traits characterizing a community. Community traits result from the cumulative, transgenerational, and constructed niches in turn acquired through biological, ecological, and socio-cultural, extra-genetic inheritance.

Community: Interacting populations of which the individual members can belong to the same as well as to different species. Communities include the biotic and abiotic environmental niche inhabited and constructed by the community.

Eukaryotes: The third domain of life containing unicellular organisms belonging to the protist kingdom as well as multicellular organisms belonging to the plant, animal, or fungi kingdoms. Eukaryotic cells contain a nucleus where the DNA is packaged into different chromosomes, and they often also contain small cell bodies called organelles, several of which have a symbiogenetic origin.

Holobiont: A biological individual made up of multiple organisms together defining a new habitable zone of life (Figure 1).

Host: The larger individual amongst a group of organisms maintaining symbiotic interactions.

Microbe: Infectious agents, broadly defined, as including bacteria, archaea, fungi, algae, protozoa, and (bacterial or other) viruses.

Microbiome: The sum of all microbes living in or onside organisms.

Plasmids: Small circular DNA molecules.

Prokaryotes: Single-celled microorganisms comprising Archaea and Bacteria whose cells lack nuclei.

Symbiont: The smaller individual/s amongst a group of organisms maintaining symbiotic interactions.

Synergy: Cooperation or interaction leading to a collective.

Virome: The sum of all viruses infecting organisms.

TABLE 1 Main types of symbiosis

Type	Effect on host	Effects on symbionts
Commensalism	Neutral	Beneficial
Mutualism	Beneficial	Beneficial
Parasitism	Harmful	Beneficial

different organisms. Van Beneden thus already emphasized that symbiosis requires social or community living.[24]

2.4 | Symbiogenesis

Symbiosis can lead to symbiogenesis which is evolution induced by symbiosis. While lateral gene transfer involves the transmission of genes only, symbiogenesis occurs through cell transfer and cell fusion.[26] Symbiogenesis has played a momentous role in the origin of the eukaryotic cell and several of its organelles. Mitochondria, for example, which are organelles present in the cells of protists, fungi, plants and animals, evolved from bacteria related to alpha-proteobacteria. Chloroplasts, which are organelles found in the cytoplasm of plant cells, evolved from cyanobacteria. These symbiogenetic events occurred some two billion years ago, when several of the first eukaryotic organisms engulfed bacterial cells, and the eukaryotic host and the bacterial symbionts commenced a symbiosis. They started living together and this symbiosis became permanent and hereditary, a process which resulted in these bacteria losing their individuality and evolving into the organelles they are today. Symbiogenesis is thus a form of hereditary symbiosis that induces evolutionary change.[25]

2.5 | Infective heredity

Another form whereby reticulate evolution can occur is by means of infective heredity.[27] Infective heredity occurs through microbial transfer. Microbes are contagious agents such as viruses, bacteria, archaea, or other pathogens such as protozoa or worms. Over the course of their lifetime, members of all three domains of life, Archaea, Bacteria, and Eukaryota, are prone to acquiring infections induced by numerous contagious agents encountered within their communities. Human viral infections such as the flu (*Influenza IAV*, *IBV*, *ICV*) or bacterial infections underlying diseases such as tuberculosis (*Mycobacterium tuberculosis*) or pneumonia (*Streptococcus pneumoniae*), for example, always involve the horizontal transfer of pathogens. On a macroscale, these pathogens are "carried" by the population, and many are also shared with other species. Infections can furthermore become repeated over generations, and under specific circumstances, viral and also bacterial DNA can even permanently introgress into the host genome.[11,28]

2.6 | Reticulate evolution by what is transferred

Reticulate evolution occurs through horizontal interactions during which individuals transfer either genes, cells, sex cells, contagious agents, or more general matter and energy (Table 2). Reticulate evolution extends nuclear inheritance by occurring through cytoplasmic inheritance, or by altogether occurring through interactions that extend genetic interactions. In all cases, reticulate evolution concerns life-history events that impact the future course of evolution.

2.7 | Reticulate evolution and current evolutionary theory

Reticulate evolution goes beyond the tenets of the Modern Synthesis because it sheds new light on the far-going interrelation that exists between ecology, evolution, and development, as well as the role herein played by epigenetic processes.

The Modern Synthesis made a strict distinction between ontogeny, phylogeny, and ecology. Eco-evo-devo research[29,30] originated out of the need to reevaluate this relationship. Studies in embryology,[31] together with the discovery that regulatory gene complexes such as the homeobox complex underlie the formation of anatomical form, made scholars realize that the study of evolution cannot be separated from development. It furthermore made scholars recognize the important role played by the internal as well as the external environment in bringing about evolutionary change.[32,33] Today, eco-evo-devo research joins ecology, evolution, and development into an Extended Evolutionary Synthesis.[34,35] This program recognizes the importance of phenomena such as phenotypic plasticity,[36–38] niche construction,[33] and ecological inheritance,[39] and it makes way for the concept of inclusive inheritance[40] as well as a general understanding of evolution as occurring along genetic, epigenetic, behavioral, and symbolic dimensions.[41]

Reticulate evolution studies further broaden the scope of this gene-organism-environmental axis by investigating gene function not only within single organismal genomes, species genomes, or monophyletic taxa, but within multispecies communities composed of genes, organisms, and species belonging to different kingdoms and domains of life. Phenomena such as gene mobility further broaden the reach of epigenetic and epigenomic phenomena on the one hand, and on the other, multicellular and multispecies agglomerations such as bacterial colonies, biofilms, or eukaryotic organisms redefine community ecologies and the nature of biological individuality. Their study requires the Third Way of Evolution.[42,43]

Scholars active in both the Extended Evolutionary Synthesis and the Third Way of Evolution agree that beyond natural selection, evolution can occur through a multitude of mechanisms and processes. A more pluralistic account of evolution is needed,[44] and reticulate evolution has an important role to play in this ongoing debate.[3,6,45–49]

3 | CASE STUDIES OF RETICULATE EVOLUTION IN HUMAN EVOLUTION

Network-like evolution not only characterizes biological evolution, it also occurs abundantly within sociocultural evolution. Phenomena such as cargo cults, cultural contact, pidgin and creole formation, word borrowing and language mixing, multiculturalism, and globalization significantly rely on reticulation. These network-like interactions occur either directly between members belonging to distinct linguistic and cultural groups and traditions, or they occur within and between the cognitive constructs and material artifacts produced by different groups.[50,51] Also ideas of transhumanism or cyborg and android formation within the technosciences, and the idea of personalized medicine in the biomedical sciences depend upon a notion of reticulate evolution.

Sociocultural evolution literature, however, predominantly works from within the Neodarwinian framework and it continues to follow the population genetic approach[52] where microevolution is thought to bring forth macroevolution.[53] In this regard, sociocultural evolution has been defined by analogy with biological evolution, and such has implied a search for analogs to genes such as culturgens,[54] memes,[55] and linguemes[56] or other cultural and linguistic replicators.[57] Scholars then investigate how these replicators spread within populations of gene, meme, or lingueme pools. These ideas imply that the unit[58] of selection resides at a microlevel and that the level[53] where selection occurs either resides at a meso or a macrolevel, which means that it is the gene, the organism, or the group that is selected by the environment. Above and between species phenomena have hereby been ignored.[3,59]

In linguistics, Croft,[56] however, already noted that linguistic evolution often takes on a "plantish approach" because of the many hybridizations occurring between languages. In sociocultural evolution studies, Gontier[60] has introduced the symbiont as a unit of reticulate cultural evolution. Just as symbiosis is a neutral term, so too the symbiont is a neutral term that can refer to either the host and its symbiotic partner in biology, or to the material, cognitive, cultural, or technological artifacts that form the basis of reticulate cognitive or sociocultural interaction. These ideas reach back to the works of Alfred Kroeber,[61] who, as one of the founders of

TABLE 2 Types of reticulate evolution by what is transferred

Lateral gene transfer	Symbiosis	Symbiogenesis	Hybridization	Infective heredity
Gene transfer	Matter and energy transfer	Cell transfer	Sex cell transfer	Microbe transfer

American, cultural anthropology, already in the early 1920s emphasized the reticulate nature of what he called cultural and linguistic diffusion or blending. Unaware of the work done outside of the Neodarwinian paradigm, Kroeber ended up arguing that cultural evolution differs in its entirety from biological evolution.

We are just now coming to terms with the remarkable resemblances there are between reticulate biological and sociocultural evolution, and here, the transition from tree to network thinking, or from intrapopulation to between-population thinking itself forms part of a broader scientific revolution.[3] In this part, we focus our attention on three critical cases in sociocultural research where reticulate evolution has been overlooked: human-animal, plant, and machine interactions; diet-*microbiome* interactions; and host-*virome* and other pathogen interactions.

3.1 | Human, animal, plant, and machine interactions

Humans maintain lifestyles ranging from nomadic dwelling or hunter-gathering to domesticated living in pastoral, agrarian, agricultural, or technological societies.[62] Behaviors such as fishing, hunting, herding, dairying, fermenting, farming, crop cultivation, livestock maintenance, and breeding, all depend, first and foremost, upon fundamental acts of symbiosis that human communities maintain with other living organisms such as bacteria, archaea, plants, animals, and fungi, as well as with machines and other technological devices.

Biological and artificial symbiotic interactions give opportunity to human hosts to start the community-wide domestication and artificial selection or artificial breeding of nonhuman organisms. Artificial and selective breeding includes the application of artificial hybridization. The American corn industry,[63] for example, and Asian rice cultivation have significantly increased productivity by applying artificial hybridization and four cross-fertilization techniques. In these cases, the offspring demonstrate hybrid vigor, a process already described by Darwin,[64] that is typified by stronger and larger crops.[65] Hybrid vigor is also demonstrated by the mule, for example, which because of its strength is often used as a transport and carrier animal.

Similarly, farmers are known to turn grasses and crop foliage of maize, potato, or oats into silage. The grasses and foliage are bundled into airtight heaps that start fermenting. *Lactobacillus* bacteria turn carbon sugar molecules into lactic acid, which results in the preservation of the symbiotic product and this silage then becomes a provender for livestock. Silage made from maize has become the main provender for dairy cows, and research by Khan et al.[66] suggests that the maturity of maize silages significantly impacts milk yield and protein content.

Omomowo and Babalola[67] in this regard point toward microbial and fungal inoculation of soils and crops to increase eco-friendly and sustainable food production worldwide. Microbial and fungal endophytic, epiphytic, and rhizospheric microorganisms function as biofertilizers because they promote plant growth, increase stress tolerance, suppress plant pathogens and pests, and contribute to overall plant immunity. A fungal endophytic strain called *Beauveria bassiana*, for example, increases spike production in bread and durum wheat plants, which increases the mortality of cotton leafworms that feed on the plants.[68] Inoculations increase plant sustainability and therefore present alternatives to synthetic agrochemicals that are known to be harmful to humans for their role in promoting pathogens, for harboring carcinogens, and for causing immune-defense reactions such as allergies.

Animal and plant interactions can encompass the full spectrum of symbiotic associations. Hunting or farming, for example, often results in the parasitic (over)exploitation of animals and plants, and in this regard, humans often disrupt existing ecosystems.[69] But by taking our predatory place in the ecological food web, humans can also contribute to maintaining and facilitating the populations of other animal and plant species.[70] History demonstrates that domesticated animals and plants have a longer species life span than their wild counterparts.[24] The auroch (*Bos primigenius*), for example, which is ancestral to modern domesticated bovines, has long died out, but its descendants live on through the symbiotic associations maintained with humans. Such can be understood in mutualist terms because both symbiotic partners keep one another alive.

Domesticated livestock or cultivated crops, both of which are characterized by artificial selection and artificial breeding, underlie the formation of new "biological realities."[71] That means that through animal and plant symbioses, humans can integrate existing life forms into their expanding ecological,[33,39,72] and cultural[73,74] niches. The symbiotic associations maintained by humans with other organisms also result in the modification of those species. Consequently, many of the initial facultative symbioses have become permanent and obligate for both the symbionts as well as their human hosts.

Due to their size, artificially selected cattle, for example, often require human veterinary help for insemination, birthing, or infant rearing. Plant and animal cultivars and hybrids tend to differ significantly from their "wild" counterparts, and they do so anatomically, genetically, and behaviorally. This can even underlie species recognition problems and as such bring forth reproductive barriers. Long-term symbioses with domesticated livestockhas furthermore resulted in a reduction in size and a selection for more docile behavior.

Symbiotic interactions also impact our cognitive niches.[75] This is because the newly developing biological reality induced by the myriad of symbiotic associations humans have come to maintain with other species brings forth a need for more specialized cognitive-behavioral and sociocultural repertoires. At a linguistic level, the domestication of different plant and animal species, as well as the processes involved in farming and herding or breeding and fermentation go hand in hand with the introduction of new sociocultural rituals and practices as well as with new cognitive problem-solving activities. This must have associated with the invention of entirely new vocabulary and linguistic jargon.

Within these newly created habitable zones of life, the line between "natural" and "artificial" organisms is only a thin one and one that is also easily crossed by artificial symbiotic "organisms" such as machines[76] or human-made artifacts and technologies. These items are materialized symbionts resulting from the merger of different tools and technological devices. A bow and arrow, for example, is just that, a reticulate or symbiotic combination of a bow and an arrow that through its composition brings forth a weapon ideal for hunting. An ax used to timber tree organisms is a technologically advanced tool that becomes attached to a wooden stick via a binding device that not only brings forth a compositional tool that can be understood as symbiotic, it also requires complex compositional thought that in the past has been identified as conceptual blending.[77] Compositional tools furthermore are recognized to materialize and to extend the mind,[78] and this too leads to new and hybrid forms of being.

With the introduction of agriculture and animal breeding, humans have thus commenced what the philosopher Hannah Arendt long ago characterized as the human ability to demonstrate "action into nature."[79] This ability underlies the industrial and the technological revolution as well as what we here characterize as the biomedical revolution. It relies on nothing more or less than artificial lateral gene transfer, artificial symbiosis, and artificially induced infections. These techniques underlie any and all forms of genetic tinkering,[11] gene editing (by e.g., making use of the CRISPR technique),[80] vaccine development,[81] or personalized medicine.[82]

To summarize, the symbiotic, interactional, and reticulate aspects of human, animal, plant, and machine interactions have been ignored in favor of their selectionist, competitive, and Neodarwinian aspects. Nonetheless, humans have gained many mutual and commensal benefits from living in close association with other organisms.

3.2 | Diet-*microbiome* relationships

Human and hominin diets form part and parcel of (paleo)anthropological and archaeological research.[83] Diets are often linked, on the one hand, to the evolution of anatomical form, and on the other, to the evolution of sociocultural rites and practices. Regarding the former, a classic example is the influential work initiated by Aiello and Wheeler[84] and continued by Dunbar[85] where the hominin diet is linked to brain and gut size. Regarding the latter, another classic example is the important research initiated by Holden and Mace[86] that links the rise of lactose tolerance in human societies to those societies' sociocultural dairying practices. Results of both types of research exemplify the importance of epigenetic processes in human evolution, and this in turn demonstrates the role played in evolution by extragenetic, sociocultural inheritance.[41,87,88]

These studies now need to be complemented with the incoming results of *microbiome* studies. The microbiome refers to the sum of all microbes living symbiotically, in and onside our body. Microbial communities impact human health and disease. The gut microbiome, for example, provides us with nutrients and vitamins,[89] and it enables us to digest specific foods our body is unable to digest by itself. A significant part of the human microbiome is acquired, altered, or maintained through diet. The numerous symbiotic associations that we maintain with food sources such as seeds, flowers, plants, legumes, tubers, insects, animals, birds, fish, mollusks, or crustaceans determine our diet, and such in turn underlies the composition of our microbiome, for as Doolittle has argued, "you are what you eat."[90]

We can here add to this catchy phrase by noting that on a sociocultural level, diets are a means to differentiate amongst groups because "individuals that eat together group together." While there is a genetic component to the types of microbiota that species attract, members of the same group or organisms belonging to different taxa, but sharing the same ecological habitat, often maintain a similar diet and a similar microbiome composition.

When the microbiome of humans is compared intraspecifically and interspecifically with those of other primates, it appears that humans lost much of their ancestral microbiome diversity. Hunter-gatherers have a more varied microbiome than urban and industrialized humans, and apes in general have a more varied microbiome than humans.[91] The Neanderthal microbiome also leans closer to that of apes.[92]

Another study demonstrates that humans with nonindustrial subsistence patterns such as the Bantu and the BaAka have a gut microbiome relating more closely to that of baboons with whom they share their environment than to that of genetically more closely related chimpanzees on the one hand, and on the other to that of industrialized humans which in the case study were North-Americans.[93] Research by Schnorr et al.[94] has even linked a gender-based division of labor in the Hazda hunter-gatherers to differences in gut microbiome composition. An earlier study conducted by Li et al.[95] also demonstrated the flexibility and plasticity of the microbiome. The composition of the saliva microbiome of humans and chimpanzees, for example, although different from one another, is not species-specific, and the composition is dependent upon ecological settings. When these change, the microbiome changes.

Within the human population, Adler et al.[96] demonstrated that the increased consumption of domesticated wheat and barley during the Neolithic revolution, and the innovative ways of processing, preserving, and packaging foods during the industrial revolution, have significantly altered the microbiome composition of agricultural and industrialized humans. In both cases, the new lifestyles led to significant alterations in the composition of the mouth microbiome. A reduction in the diversity of the mouth microbiome correlated to the onset of new types of periodontal disease in the Neolithic, and in more recent times to caries, the effects of which might have impacted also the gut microbiome composition (for a discussion see Weyrich[97]).

Numerous studies are today demonstrating the impact that our microbiome has on health as well as disease. Illnesses associated with the microbiome include obesity[98] and neurodegenerative diseases.[99] Research is in addition implicating the microbiome in personality traits and disorders.[100] Beyond anatomical form, the microbiome thus affects the brain and cognition.[101] Also the vaginal microbiome influences infant microbiome composition and this in turn impacts infant health, disease, and behavior.[102]

Symbiosis has even been implicated in social communication because the microbiome affects body odor[103] and as such it forms barriers to social group identification, sexual attraction, and mate choice.[24] Much of this remains virgin territory awaiting further exploration, but it is already safe to say that microbiome studies can complement the classic theories that understand the rise of language in hominin society as a form of vocal grooming[85] enabling speakers to address larger crowds.

Microbiome composition is flexible and for a large part dependent upon food intake. Specific foods can induce or inhibit the growth of specific bacterial groups that form part of our gut microbiome and this can increase or decrease health. Sweet potato fiber[104] and pomegranate,[105] for example, increase concentrations of *Bifidobacteria* and *Lactobacilli* that are known probiotics, and they induce a significant decrease of pathogens including *Enterobacilli* (associated with gastroenteritis), *Clostridium perfringens* (responsible for food poisoning), and *Bacteroides* (associated with appendicitis). It is important to note that raw fruit and vegetables are also one of the main sources of pathogen acquisition including *Listeria monocytogenes*, *Salmonella*, *Escherichia coli*, all of which form health hazards.[106] A study by Rincón and Neelam[107] found that tomato, lettuce, spinach, maize, pepper, mustard, soybean, artichoke, and pumpkin mostly come with good bacteria. Broccoli, cauliflower, cabbage, carrot, celery, chili, cucumber, parsley, pepper, and radish often harbor pathogenic bacteria.

Vice versa, as organisms, our food sources also have their own microbiomes, many of which have become altered through the dietary symbiotic interactions we maintain with them. Selective breeding practices, for example, alter both the genetic makeup of the cultivated crops and farm animals, as well as the composition of the microbiome composition of these organisms.

Apples serve as an example. As fruits, apples form an important raw food resource that fuels the human gut microbiome. Wasserman et al.[108] estimate that with the consumption of one whole apple, humans acquire about 100 million bacterial cells. The stem, peel, pulp, seeds, and calyx of apples are inhabited by different bacterial communities, the composition, and diversity of which correlate significantly with human farming and storage conditions. Research demonstrates that the seeds of organically-farmed apples have more bacterial diversity. How apples are farmed therefore impacts both human as well as apple microbiome diversity, and this is important to know given that seeds are indicative of vertical microbiome transmission.

These and other results demonstrate the need to go beyond the study of organisms to the study of physiological systems as well as the community-wide, symbiotic interactions that are maintained with the organisms underlying our diet as well as our ecological niche. Reticulate evolution in general and symbiosis, in particular, is demonstrating how erroneous it is to understand human evolution by *only* studying the past and how, as some authors have claimed,[109] humans adapted long ago to a Pleistocene environment. Instead, evolution occurs incessantly, even today, during individual life history. This underlies rapid evolutionary change.

FIGURE 1 Schematic of holobiont formation

Until now, however, sociocultural evolution studies have focused on attributing evolutionary success to individuals or to their organismal traits, and such has mostly gone at the expense of recognizing the decisive co-evolutionary role played by the microbiome in bringing forth healthy human individuals readily able to function in larger communities of like and unlike-named organisms. Symbiosis research is demonstrating that there are no individuals in evolution,[110] and scientific advance will therefore depend upon how able we are in reformulating our research questions and in reorienting our attention to the important role played by the microbiome and also the virome.

Of use thereby is the recognition that no organism lives or dies alone. Rather prokaryotic organisms form colonies of unicellular individuals and multicellular organisms are communities of different living organisms or bionts.[11] Together, these different bionts form a *holobiont* (Figure 1)[111,112] that simultaneously functions as a new and heterogeneous individual as well as a new habitable zone of life for these microorganisms.[60] Holobionts carry with them a *hologenome* that comprises the host genome together with the virome and microbiome genomes.[113] The concept provides an elaborate alternative to inclusive fitness theories[114,115] that merely take genetically-similar individuals into account. Instead, the hologenome concept demands fitness calculations to include the genes of all symbionts that make up the holobiont. This is one of the reasons why we need to move away from an organismal-focused research outlook and incorporate a community-level approach in how we formulate the questions.[3,116]

Humans are no different in this regard. Rather than understanding humans as individuals, we foresee a future where in the term human will be reserved for communities made up of multiple bionts. From an anthropological viewpoint, such is a bold statement to make, and it requires the replacement of the introspective "I" with an extrospective "we." This idea finds convergence with rising theories within symbiology that try and replace classic species concepts with symbiogenetic species[112] and speciation concepts[117] that take the numerous symbiotic interactions underlying holobiont formation into account.

3.3 | Host–pathogen interactions

Haldane, one of the founders of the Modern Synthesis, and by studying sickle cell anemia and other ailments, already investigated the role of disease on human evolution.[118] This study too needs to expand toward the research performed on symbiosis and infective heredity.[27] Symbiotic interactions not only impact diet-microbiome interactions, they also expose the human host to the more pathogenic members of the virome and microbiome accompanying the organisms with which we maintain holobiont or more general symbiotic associations. The *virome*[119] refers to the different viruses that can infect us, and note that only a small part of the human virome actually causes disease.

Here, however, we focus on that small part of the human virome and microbiome that is pathogenic and parasitic. Living in close association with livestock and consuming cultivated crops has exposed humans to numerous new viral and organism-induced diseases. Live-stock affecting diseases such as anthrax, which is caused by bacteria called *Bacillus anthracis*, and Brucellosis, caused by *Brucella spp*., for example, are contagious and can cause severe illness in humans.

Our past is characterized by an evolutionary arms race[120] where host and pathogen incessantly coevolved to keep up with one another. While the selectionist nature of such interactions has long been recognized,[121] again the symbiotic aspect has often been ignored. Species often come with species-specific microbial and viral pathogens, and these pathogens have evolved the keys to unlock the door to their host and to block or suppress its immune responses, while the host has often evolved pathogen-specific detection mechanisms allowing an early response to infection. Some organisms are even known to make their own antibiotics, and human blood, saliva, or stomach acid, for example, have evolved in such a way that they eliminate many microbes. An individual's health or disease status is therefore a result of cooperation.

Viruses and species tend to group together, but viruses can also make the jump from one species to another and such cross-species transmission is a widespread phenomenon. Zoonotic diseases, for example, are diseases humans contract from animals, and anthroponotic diseases are diseases animals contract from humans. Examples of anthroponotic diseases are the Ebola viruses of the *Filoviridae* group, some of which underlie Ebola Virus Disease. Originating in bats, the virus somehow made its way to humans, and from there it now also infects other primates. Examples of zoonotic diseases are avian (HPA1) and swine influenza viruses (SIV or S-OIV strains). Their name indicates their origin. Other examples are the two main HIV viruses that stem from SIV (Simian Immunodeficiency Virus) viruses found in chimpanzees (SIVcpz) and sooty mangabeys (SIVsmm) and that cause AIDS in humans. These viruses have long coevolved with their host where they underlie harmless infections. These viruses have somehow been able to make the jump to humans where they then cause severe infections that can lead to death.

Another example of a zoonotic disease is the COVID-19 virus currently causing the worldwide pandemic. This virus is maintained by the human population where it spreads horizontally due to the incessant social contact humans maintain with one another. But the virus likely finds its origin in bats and their SARS-like coronaviruses (SL-CoVs).[122] Some of these bat viruses are presumed to have made their way to humans via intermediate species. The SARS-CoV responsible for SARS (Severe Acute Respiratory Syndrome), for example, presumably spread via masked palm civets, and MERS-Cov2 responsible for MERS (Middle East Respiratory Syndrome) was transmitted by camels.[123] The COVID-19 (SARS-Cov-2) virus presumably originated in Wuhan in November 2020, and it was able to spread across the globe in as little as 3 months' time by infecting our species. Maintained by the human population, we are living proof of how fast a virus can spread geographically and how quickly it can cause for more than 6 million deaths. Phenomena like these are demonstrating the swiftness with which pathogens can wipe out entire groups of individuals. Ryan[28] has argued that our past is plagued by multiple such pandemics that must have introduced evolutionary bottlenecks if not the extinction of certain hominin species.

On a more positive note, children have now been born with antibodies against the virus that they acquired from their mothers, some of whom recuperated, others who were vaccinated against the virus. Such phenomena are exactly what Lederberg[27] intended to refer to when he introduced the concept of hereditary symbiosis. The COVID-19 virus, moreover, is demonstrating the human agility and the global response brought forth by our species, through the implementation of international laws and embargos, as well as support and sensibilization campaigns, vaccine development (of course based upon artificial symbiosis, and lateral gene transfer), and quarantining techniques. Such is a relief and an example of positive globalization, one that stands in sharp contrast to our human past, where pathogen-induced diseases in humans such as leprosy (*Mycobacterium leprae*) or the plague (*Yersinia pestis*) are known to have introduced social stigmas and to have served as social and reproductive barriers with noninfected societal members.

4 | COMMUNITY LEVEL EVOLUTION WITH RETICULATE CAUSATION

Reticulate evolution extends individual organisms because it occurs above the organismal level, at a community level, where synergistic, behavioral and sociocultural, organizational traits evolve.[116] The *synergy* concept goes back to Peter Corning's work[8] and his notion of synergistic selection. Synergy refers to cooperation or interaction existing between more than one individual that brings forth a collective. Such a collective underlies community formation and communities represent an as-of-yet underappreciated level of evolution where these *synergistic traits* evolve.

To make our argument, we need to turn to theoretical biology and evolutionary epistemology,[3] and investigate how the Neodarwinian synthesis defines units and levels of selection (Figure 2). The Neodarwinian Synthesis is founded upon the idea that the unit of evolution is the organism that evolves at the level of the environment by means of the mechanism of natural selection. Natural selection is thought to operate either on organisms or on the genes bringing forth

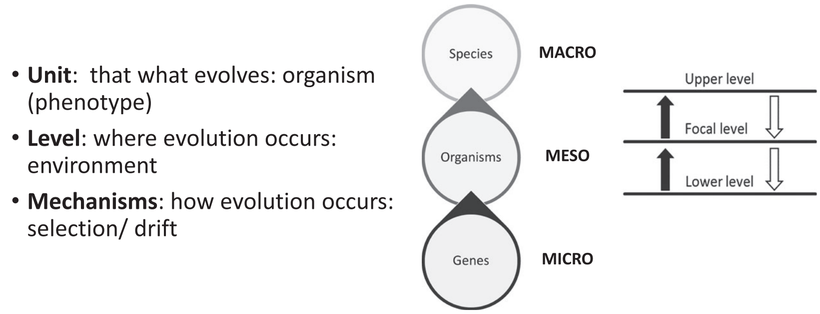

FIGURE 2 How units, levels, and mechanisms of selection are defined by the Neodarwinian synthesis (left), hierarchically (middle), and causally (right). Black arrows depict upward causation, white arrows downward causation.

the organism or on both, resulting in differential survival and reproduction in turn leading to shifts in populations of organisms over time. As such, natural selection brings forth a pattern of descent with modification.

When understood from within hierarchy theory,[59,124–128] that means that genes residing on a microlevel are thought to bring forth organisms on a mesolevel (where environmental selection occurs) and such brings forth species on a macrolevel. When understood from within causality theory,[3] the lower level of a hierarchy (genes) is thought to bring forth the focal level (organisms) and the focal level is thought to bring forth the upper level (species). In technical terms, this defines upward causation and upward causation is often associated with reductionist schools of thought because there is a tendency to reduce causality to the lower level of an evolutionary hierarchy. But upward causation theories in particular study evolutionary affordances and thus how genes enable the evolution of organisms and how organisms enable the evolution of species.

Epigenetic research and eco-evo-devo schools in contrast investigate downward causal processes[129] and such implies a study of evolutionary constraints.[125] Eco-evo-devo, for example, examines how species impact how organisms evolve, and how organisms constrain how genes evolve. Eco-evo-devo thus investigates how development and ecology, or life history events, can alter the future course of phylogeny. Gene-culture coevolutionary theories or sociocultural and linguistic evolution theories are in this regard investigating how cultural practices such as dairying can impact evolution.

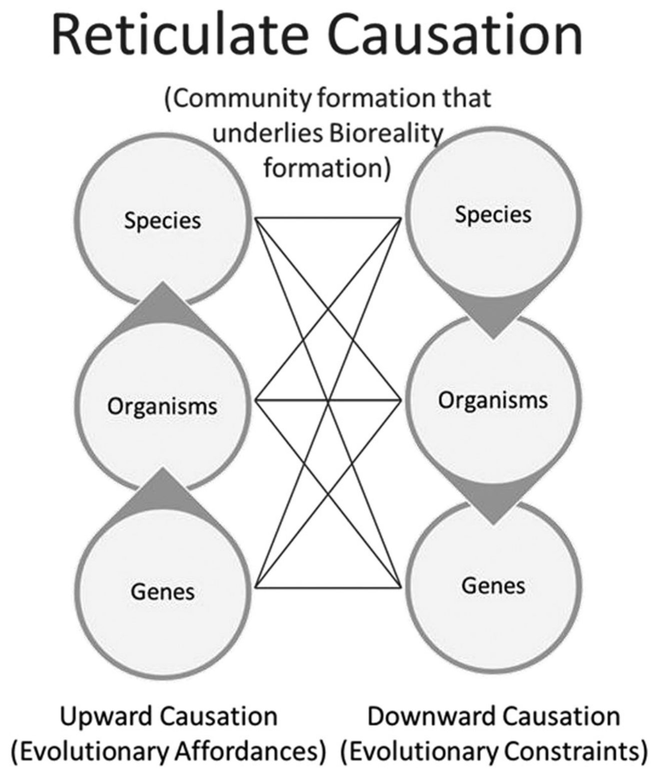

FIGURE 3 Reticulate causation underlies community formation and community formation underlies bioreality formation.

Gontier[3] has demonstrated that reticulate evolution studies in addition necessitate the recognition of reticulate causation studies (Figure 3). Such studies investigate how bacteria, for example, can infect multicellular organisms; or, how genes from one organism can infect the genome of another organism and thereby impact the future course of evolution; or, how organisms of one species can engage in horizontal interaction with organisms of other species in such a way that the evolution of both is differential. This kind of reticulate causation underlies the formation of communities.

Communities are levels of evolution. We define a community as "an agglomeration of interacting populations of which the individual members can belong to the same as well as to different species. Communities include the biotic and abiotic niche inhabited and constructed by the community."[116] We recognize synergistic community traits as units evolving at this community level, and we define these traits as resulting from "the cumulative, transgenerational, and constructed niches resulting in turn from biological, ecological, and sociocultural, extra-genetic inheritance."

Communities complement the more classic concepts of populations,[52] demes,[130] groups,[88,131] or species.[53,132] These latter concepts were introduced with the purpose to study group formation amongst members belonging to the same species. The communities that we distinguish as levels of evolution surpass group-specific organisms and include interacting organisms belonging to different species.

Holobionts are such communities of individuals, as are human societies. Humans, for example, of course, all belong to the same species. However, the symbiotic interactions maintained by human groups with organisms belonging to different species vary through the sociocultural processes of agriculture, herding, animal breeding, diet, and so forth. This makes the human species diversify into gene, organism, and species-extending, larger communities.

That also implies that the concepts of inclusive fitness[114,115] or parental investment[130] require a rethink because both have so far been formulated by focusing on how genes of the same species bring forth inclusivity. Instead, a shift needs to occur from inclusive fitness to the hologenome fitness of holobionts and how this extends toward communities.

5 | CONCLUDING REMARKS AND FUTURE PROSPECTS

In conclusion, we need to recognize the plural nature of evolution. Lateral gene transfer, symbiosis, symbiogenesis, infective heredity, and hybridization underlie reticulate evolution in living organisms, and these processes also directly impact how human individual and group behavior as well as sociocultural phenomena evolve. Reticulate evolution complements natural selection theory which demonstrates how evolution can occur vertically. And drift theory, although not discussed in this study, demonstrates how evolution can sometimes occur randomly or stochastically.[133–138]

The insight that all evolutionary paradigms provide valid scientific theories whereby we can understand biological as well as sociocultural evolution requires us to recognize the plural nature of evolution. It demands a more selection-neutral definition of evolution as the universal process that occurs when units evolve at levels of ontological hierarchies by mechanisms and processes.[3]

In addition, also the old units and levels of selection debate, and multilevel selection theory, need to expand toward other units and levels, not of selection per se, but of evolution in general. Evolution occurs through numerous units, levels, mechanisms and processes, and such brings forth the need to recognize ontological pluralism.

Ontological pluralism in turn requires the development of multidirectional causality theories. Beyond up-and-downward causation, we can include reticulate causation in the list of causal processes.

It is reticulate causation that goes above and beyond organismal, group, and species levels, and that brings forth the need to distinguish communities as levels of evolution where synergistic, organizational traits delineate the units that evolve at such levels.

These insights carry imperative consequences for the anthropological sciences where the adoption of a community-level analysis sheds new light on human evolution.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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