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THINKING LIKE GAIA

The Science of the Probiotic Turn

> I have lived to see state after state extirpate its wolves. I have watched the face of many a newly wolfless mountain, and seen the south-facing slopes wrinkle with a maze of new deer trails. I have seen every edible bush and seedling browsed, first to anaemic desuetude, and then to death. I have seen every edible tree defoliated to the height of a saddlehorn. . . . I now suspect that just as a deer herd lives in mortal fear of its wolves, so does a mountain live in mortal fear of its deer. . . . So also with cows. The cowman who cleans his range of wolves does not realize that he is taking over the wolf's job of trimming the herd to fit the range. He has not learned to think like a mountain. Hence we have dustbowls, and rivers washing the future into the sea.
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> —Aldo Leopold, *Sand Country Almanac*

Aldo Leopold wrote this lament in 1947, toward the end of a long pioneering career as an ecologist and founder of the science of wildlife management in North America. Leopold had grown increasingly dissatisfied with established approaches to game and forest management premised on varmint (predator) extermination and clean (tightly controlled) production. Retreating to a cabin on a small degraded farm in Midwest sand country, he proposed his famous land ethic. He encouraged wildlife managers to "think like a mountain," developing a holistic appreciation of the interdependencies between species and the landscapes they inhabit. He wrote lucidly about what ecologists now describe as a trophic cascade, with top-down regulation performed by predation. He appealed for a model of conservation that could live with species like wolves and coyotes.

In this chapter I explore the ecological science that informs the probiotic turn. I trace how the scientists involved in rewilding and biome restoration conceive the relations and interdependencies within and between the different ecological scales at which they work. Many of these figures may never have encountered Leopold, but all, in their different ways, are informed by the Gaian thinking of James Lovelock and Lynn Margulis, two scientists who might be understood as inheritors of Leopold's commitment to holistic, ecological, and relational science. I call this chapter "Thinking Like Gaia" to capture what I see as a reworking of Leopold's exhortation to think like a mountain. I suggest that those working at the forefront of probiotic ecology expand Leopold's holistic view of dynamic natural systems from the scale of the landscape down to the scale of the microbiome and out to the scale of the planetary. The strands of Gaian thinking that are prominent in ecoimmunology and earth systems science, and the social theory that borrows from them, are centrally concerned with the interrelationships between organisms (taken as individuals, as ecologies, and as aggregate life) and the abiotic environment. For Latour, Haraway, and others, this science thinks like Gaia. Here Gaia is ticklish, intrusive, and unruly; Gaia exists in a metastable, sympoietic world with no necessary beneficent or vengeful commitment to humanity.[1]

Thinking like Gaia involves a commitment to a common ecological ontology, a scientific account of how the world works that comes to shape and ground the ontostories of probiotic social theorists like Haraway, Tsing, and Latour. This chapter maps this ontology, identifying, connecting, and synthesizing concepts that are found in common across the seemingly disparate sciences that support rewilding and biome restoration. As with the previous chapter, my narrative seeks to stay faithful to the accounts of key practitioners. I focus on the five sets of concepts that are most prominent within the scientific literature and from my interviews. I highlight those emblematic of the wider shifts in scientific thinking associated with efforts to diagnose and address the pathologies caused by antibiotic approaches to conceiving (and then managing) life.

I have taken the necessary liberty of uniting the domain specific ideas of rewilders and biome restorers under the conceptual umbrella of the postmodern synthesis, as it is presented in so-called eco-evo-devo (ecological–evolutionary–developmental) biology. Scott Gilbert defines eco-evo-devo as "the scientific programme that incorporates the rules governing the interactions between an organism's genes, development and environment into evolutionary theory."[2] Eco-evo-devo is strongly associated with the work of Margulis and her radical theory of the symbiotic origins and evolutionary dynamics of life, which influenced Lovelock and shaped their joint writings on Gaia.[3] In its attention to context, mutualisms, and planetary precarity, the postmodern synthesis departs from the individualism, reductionism, and anthropocentrism of the modern synthesis. Not all of my participants are involved in eco-evo-devo; many are not even aware of its existence. However, in the final section of this chapter, I show how it offers a useful framework for understanding the intellectual significance of the proliferation of Gaian thinking and for mapping the flows of ecological concepts between the micro and the macro that are central to the probiotic turn.

Symbiosis

The *Oxford English Dictionary* defines symbiosis as "an association between two different organisms which live attached to each other . . . and contribute to each other's support." Symbiotic relationships tended to be treated as rare and unimportant events in the modern synthesis of neo-Darwinian biology, with its preoccupations with competitive relations between individuals. However, this marginalization has been challenged by a series of developments that happened in the different branches of biology and ecology caught up in the probiotic turn. I focus on three here. The first challenge comes from Margulis's radical theory of the symbiotic origins of eukaryotic (or multicellular) life.[4] Margulis argues that life evolved when one bacterium incorporated another, thereby domesticating it to create the mitochondria common to all eukaryotic life-forms.[5] She calls this process symbiogenesis. Subsequent work has confirmed the microbial (bacterial and viral) origins of a significant portion of the genetic diversity of animals. It has also revealed the ability of bacteria to share genetic components laterally, without reproduction.

The diminished cost and increased speed of high-throughput DNA sequencing has helped map the human microbiome—or, better, the multibiome. Most of these microorganisms are commensal or even beneficial mutualists. This work challenges the prevalent pathological associations of microbes (as germs) and implicates them in the successful development and everyday functioning of animal bodies.[6] In this process, these microbes shape animal behavior and mood in ways that are understood to help secure their own futures. The microbiome is presented as an animal organ, akin to the heart or the lungs, and the biological individual is refigured as a porous, symbiotic holobiont, a "eukaryotic organism [host] plus its persistent symbionts."[7] The past primacy of the individual is being displaced by a focus on relations of interdependency.[8]

William Parker, a prominent immunologist working with hookworms, explains, "What we figured out, and what we got ridiculed for at first, but now everybody accepts, is the idea that the immune system is actually supporting the growth of the microbiota and spends most of its time, effort and energy devoted to supporting that symbiotic growth."[9] Certain microbes, like hookworms, are now understood to play vital roles in calibrating the infant immune system as well as enabling metabolism and ensuring the development of the brain. In accounting for the developmental and salutary role of microbes, Graham Rook develops the concept of an "environment of evolutionary adaptedness"; he suggests that for humans, this is the "hunter-gatherer environment."[10] He acknowledges that the hunter-gatherer lifestyle and environment were heterogeneous, but he argues that three types of old-friend microbial organisms would have been abundant in all cases. He terms these the commensals, the pseudo-commensals (found in water and mud, but not reproducing in the human body), and the helminths. He suggests, "Over millions of years a state of Evolved Dependence might have developed, where the induction of appropriate levels of immunoregulation by the 'old friends' has become a physiological necessity. In other words, some genes involved in setting up appropriate levels of immunoregulation are located in microbial rather than mammalian genomes."[11] As Rick Maizels and Ursula Wiedermann, immunologists working with helminths, put it, "We carry the evolutionary imprint of microbes throughout the immune system."[12]

Symbiotic relations have also become a central concern in work on the theory of niche construction—that is, "an evolutionary idea that emphasizes the capacity of organisms to modify their environments and thereby act as codirectors of their own evolution and that of other species."[13] The concept of heredity beyond vertical genetic transmission has a long and contested history in evolutionary biology; indeed, it fell out of fashion with the rise of neo-Darwinian biology.[14] But in the postgenomic present, scientists now talk of an ecological inheritance that is passed down between generations of organisms.[15] This inheritance is partly embedded within the local ecological context within which an organism develops. It involves both abiotic factors (like the hydrological effects of a beaver dam) and biotic relationships with other species (like those between the hookworm and its host). Ecological inheritance configures the evolved dependencies outlined above (e.g., hookworms to train the immune system), and works both inside and outside of animal bodies.

Symbiotic relations have become more prominent through the growing interest in ecology in the role of interaction webs in configuring the structure and function of ecosystems. A shift has been taking place in ecological theory since at least the 1970s, in which an increased importance is afforded top-down regulation over bottom-up supply-side pressures.[16] This theory—which is central to the rise of rewilding—argues that the composition and dynamics of an ecology are shaped not only by physical processes and the productivity of producers and consumers at the bottom of the food chain, but also by the regulatory pressure applied by a select group of strongly interactive keystone species, the most famous example being the wolves of Yellowstone National Park and their ecology of fear.

Microbiologists Heather Filyk and Lisa Osborne note the recent passage of this approach into work on the multibiome, where the focus is on how the interkingdom cross talk between highly interactive organisms influences microbial colonization and ecological structure.[17] For example, helminth researchers have explored how communication between microbes and their hosts influences "local and systemic immune homeostasis, health, and disease."[18] They suggest that "similar to other ecosystems, the intestinal community is dynamic, responsive, and regulated by interactions between distinct biological entities."[19] Margaret McFall-Ngai and colleagues suggest that these symbiotic relationships occur within nested ecosystems that cut across and link the familiar biological scales of the body and its environment.[20] This model of scalar relationships resonates with the influential concept of panarchy from complex systems theory. Philosopher Josef Keulartz explains how panarchy "refers to the dynamic interactions among system scales. A system at a particular scale will usually be comprised of smaller subsystems as well as being nested within larger systems."[21]

Keystone Species

Within this broader interest in symbiotic relations, attention has focused in particular on a relatively small number of strongly interactive keystone species, including a subset termed "ecosystem engineers."[22] A keystone species is an organism that exerts disproportionate influence on an ecology relative to its abundance or body mass. The term originates in studies conducted in the 1960s by marine ecologists (like Robert Paine) of the top-down regulatory influence of predators (starfish, otters) on populations of consumers (mussels, urchins) and subsequently on producers (seaweed) within a food web.[23] Like Leopold, Paine and his colleagues were concerned with the environmental effects of human hunting—in this case of otters—on ecological functioning. Subsequent work on the topology (or spatial arrangement) of species interactions has focused in particular on the role of apex predators, like the wolf, in regulating populations of herbivores, like elk or deer, and shaping the abundance and diversity of plant species. The keystone metaphor has since proliferated to encompass a wider set of ecological relations, with ecologists claiming keystone herbivores, keystone parasites, and keystone mutualists.[24]

The trophic cascade is a central concept in this ecology of asymmetric interactions. It describes "the propagation of impacts by consumers on their prey downward through food webs."[25] The interest here is in the disproportionate ability of some species to shape and modulate the flows of energy within their ecology.[26] Ecologists have described a range of processes through which these cascades occur, including how the "affective atmospheres"[27] associated with species interactions come to shape behavior. For example, attention has focused on the landscape or ecology of fear created by changes in the behavior of prey species in the presence of predators.[28] Work on the wolves introduced to Yellowstone National Park highlights how the vigilance and avoidance behaviors of elk affect their grazing, with landscape-scale consequences for the distribution and abundance of different plant species.[29] The argument, which is still contested, is that it is the place-specific fear of death, rather than absolute increases in mortality rates, which comes to reconfigure ecological interaction networks.

An ecosystem engineer is a specific type of keystone species that is capable of creating, maintaining, or destroying a habitat.[30] All organisms change their habitat to some degree, so this label requires a calculation of the magnitude of impact. Ecosystem engineers are defined as "agents of system state change."[31] Tim Caro explains that ecosystem engineers tend to be divided into two types: "autogenic engineers that change environments via their own physical structures (i.e., their living and dead tissues), and allogenic engineers that change the environment by transforming living or non-living materials from one physical state to another via mechanical or other means."[32] Corals are a classic example of an autogenic engineer and beavers of an allogenic engineer. Darwin notes the ecosystem engineering abilities of earthworms, and subsequent work has identified a great diversity of engineering techniques.[33] These include grazing and browsing (as enacted by the cattle, horses, and deer at the OVP), seed dispersal (by introducing tortoises to oceanic islands or feral horses to Central America), dam making (by beavers), and disturbance regimes (enacted by boars or elephants). The concept of an ecosystem engineer is a vital conceptual precursor to the concept of niche construction.[34]

The concepts of keystone species and ecosystem engineers continue to have traction as they are imported into the science that informs biome restoration, although much less is known about the ecological composition, structure, and dynamics of the human multibiome. Microbiologists have long been interested in beneficial or probiotic bacteria and the roles they play in delivering human health. Specific strains of bacteria have been promoted and used for therapeutic purposes alongside the early efforts by gastroenterological surgeons who pioneered FMT to assist postsurgical patient recovery. The science behind probiotic supplements has an extensive, albeit checkered, history.[35] There has been a new wave of scientific interest in probiotic bacteria with the advent of metagenomics, the development of mouse models of the human microbiome, and the growth in data on normal and pathological gut microbial ecologies.[36] These developments have enabled scientists to model the topology of interspecies ecological interactions in the microbiome and to identify a small number of strongly interactive keystone species that exert a disproportionate influence on gut ecologies.[37] Interest in the ecological structure of the microbiome is especially prominent in research seeking to explain the microbial mechanisms associated with successful FMT. Scientists studying how healthy human stool restores the gut microbiome have identified the bacterial compositions that can provide desired forms of ecological functionality—in this case an ability to establish a stable ecology, and to outcompete and exclude pathogenic flora.[38]

Studies of the gut multibiome have been extremely bacteriocentric, with relatively little attention being paid to ecological roles of microeukaryotes like helminths.[39] Nonetheless, William Parker and colleagues have proposed that hookworms and some other helminths might act as keystone species within gut ecologies. They develop the hypothesis that humans have an evolved dependency on microbes so that a small subset of old-friend microbes might exert a disproportionate influence on the ecology of the human gut and on the human immune system.[40] Scientific interest in helminths as old friends has focused on the role of these organisms in first training and then modulating or exercising the human immune system.[41] Extensive laboratory studies using mouse models have begun to reveal the mechanisms through which worms communicate directly with their host and modify the commensal bacteria of the gut in order to achieve immunosuppression.[42]

Immunologists suggest that helminths communicate with their host and its microbes by releasing a wide range of molecules. Some of these chemicals interact with host immune cells to down-modulate the standard aggressive immune response. Other chemicals encourage the production of mucus on which worms feed. A further set stimulates the host to release antimicrobial and probiotic products that create conditions favorable to a desired subset of commensal bacteria. Helminths enhance this ecosystem engineering through host manipulation by communicating directly with the gut bacteria.[43] They are able to sense the presence of different bacteria to locate and orientate themselves within the gut so that they take up residence in the right location.[44] Worm secretions further encourage the selective growth of desired commensals, which help them feed and assist with masking their presence from the host immune system.[45] A complex three-way network of symbiotic relationships is presented in which hosts, helminths, and some commensal bacteria are mutually dependent. Although immunologists have yet to draw on the concept, some helminths, like hookworms, appear able to engineer gut ecologies toward their own ends.

Tipping Points and Regime Shifts

Rewilding and biome restoration conceive of ecologies as having shifted into an undesirable state as a result of the excesses of antibiotic modes of managing life. They are founded on a common understanding of the dynamics of ecological change that draws on concepts and metaphors from systems biology, especially those concerned with the resilience of socioecological systems. Resilience thinking has become popular across a wide range of policy domains, and it has both passionate advocates and critics. I focus here on a few key concepts as they feature in the science of rewilding and biome restoration.

The first common idea is that an ecology, be it a temperate nature reserve or the human gut, can have multiple stable states. There is no single timeless balance of nature. Many different ecological conditions are possible. As such, there is no necessary linear trajectory along which an ecology will develop or change, and there is no universal final destination. The model of symbiotic ecologies regulated and engineered by keystone species is therefore founded on a nonlinear and nonequilibrium model of ecological change or succession. In the terms of resilience thinkers, the different possible stable states of an ecology are known as strong attractors. These are the conditions toward which an ecology will tend in the presence of common abiotic and biotic influences.

Ecological disturbances have been generally pathologized in the equilibrium model that informed antibiotic modes of immunology, natural resource management, and the traditional approaches to nature conservation that concern rewilders. Infection, pests, floods, and fire all threatened social and ecological productivity. In contrast, a probiotic approach emphasizes the generative importance of disturbances for ensuring the functional integrity and ongoing stability of an ecosystem. Wolves scare deer, cattle open up the forest, and helminths exercise the immune system, and in so doing, each maintains a degree of homeostasis within its ecology. Homeostasis describes the "dynamic processes that return the system to a balanced state after perturbation."[46] In rewilding and biome restoration, ecologies are understood to be metastable—that is, they are stable provided they are subjected to no more than small disturbances.

Yet these ecologies are also characterized by tipping points or thresholds. These are the points at which an ecology shifts from one state to another, pushed out of one basin of attraction with the potential of shifting toward another stable state. This may happen as a result of changes to the topology of the interaction webs within an ecological system—for example, when the loss of a keystone species like a wolf or a hookworm shifts the passage of energy within the trophic cascade. As geographer Steve Hinchliffe and his colleagues suggest in their work developing this thinking in the context of agricultural biosecurity, such topological twists shift the intensities within an ecosystem, potentially triggering complex, nonlinear changes in composition and function.[47] In this reading, ecological change is emergent from or immanent to an ecosystem, rather than something that is visited upon it from the outside. Ecologist Daniel Botkin offers a musical metaphor, suggesting that ecologies are marked by "discordant harmonies"—that is, multiple, interacting trajectories of potential change.[48] Environmental anthropologist Anna Tsing offers a comparable depiction of ecologies as "polyphonic assemblages."[49]

This thinking is evident in the theory of ecological succession advanced by Frans Vera in his wood pasture hypothesis.[50] Vera challenges the Clementsian (after Frederic Clemens) model, in which ecological succession follows a linear trajectory toward a stable archetype: the closed canopy forest in the case of Northern Europe. He instead suggests that the ecosystem engineering of large herbivores leads to a continuous, nonlinear, but nonetheless cyclical rhythm of ecological change. The animals' grazing and browsing maintains open areas within the forest, and the regeneration of trees species like oak is dependent on what have become known as Vera cycles (Figure 11): the growth of saplings within unpalatable or impenetrable scrub. For Vera, the stable high forest climax community—beloved of many Western European conservationists—results from the absence of the large herbivore disturbance regime. It is evidence of an ecology that has crossed a tipping point into a different stable state and is missing its regenerative disturbance regime.

Tipping points and regime shifts are central to the adaptive cycle of socioecological change proposed by resilience theorists. As the philosopher Josef Keulartz explains, in this account, "ecosystems tend to move through cycles of change. These changes are not entirely predictable, but often follow a pattern in which four phases are commonly observed. Generally, they move from a rapid *growth* phase through to a *conservation*

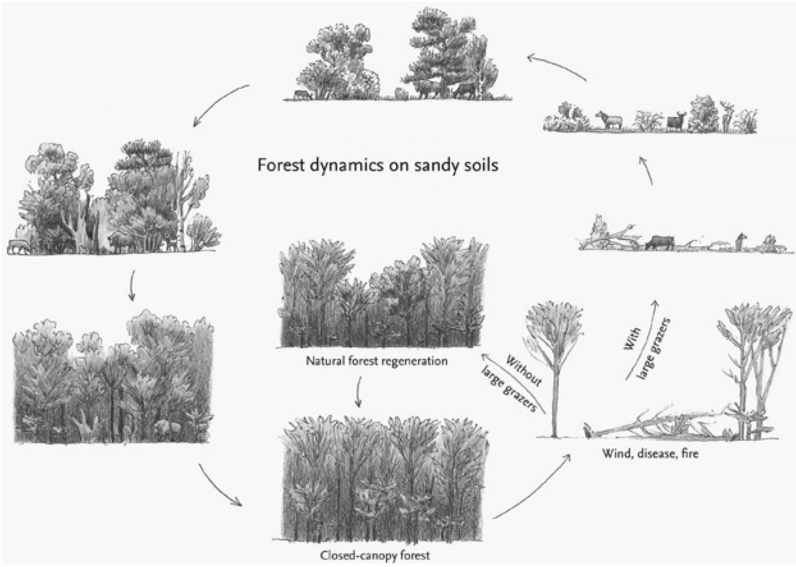


Figure 11. The Vera cycle. Illustration by Jeroen Helmer; reprinted with permission.

phase in which resources are increasingly unavailable, locked up in existing structures, followed by a *release* phase that quickly moves into a phase of *reorganization* and hence into another growth phase."[51] This nonteleological model of ecological change suggests that there are many different ecological combinations that could emerge in any given context. For example, there are lots of normal, functional human multibiome compositions that ensure eubiosis, or "the microbiota in a disease-free host."[52] Similarly, several different but normal, functional ecologies can emerge in any biogeographical region. Those involved in rewilding and biome restoration focus on ecologies subject to such severe disturbance regimes that they have undergone "catastrophic regime shifts,"[53] crossing thresholds and tipping into new conditions with deleterious consequences for valued forms of human and nonhuman life.

In the macrobiome, ecologists have focused on the trophic downgrading that results from the (largely anthropogenic) loss of keystone species. One strand of this work links the prehistoric loss of megaherbivore[54] ecosystem engineers (like elephants, rhinos, or mammoths) to declines in biodiversity, and to regional and global changes in biogeochemistry and climate. The loss of these animals changes the distribution of seeds and nutrients within ecosystems. It alters the distribution of vegetation, leading to changes in carbon dioxide and methane cycles (more vegetation, less farting) as well as shifts in global albedo (more vegetation leads to less light reflection).[55] A second strand has focused on the impacts of the more recent declines in the populations of large carnivores (like wolves, lynx, and lions).[56] Together, this work suggests that in the absence of the trophic cascades performed by these keystone species, "ecosystems convulse through harsh transitions to simpler alternative states."[57]

Similar concerns with catastrophic regime change drive those seeking biome restoration. Here, missing microbes are understood to have triggered contemporary epidemics of absence.[58] The widespread rise of allergic, autoimmune, and inflammatory disease is associated with the loss of the roles played by old-friend microbes in both training the human immune system and regulating the composition of the gut microbiome. Immunologists and microbiologists speak of a generalized condition of dysbiosis that results from the excesses of modern health, hygiene, and lifestyle practices. Meanwhile, Graham Rook and others have expressed concerns that the absence of old-friend microbes might also enable colonization by pathogenic crowd infections, including bacterial strains with drug resistance.[59] However, the mechanisms through which the absence of worms cascades through a gut immune ecology are still poorly understood. Others have even suggested that the coexistence of helminths and crowd infections might actually enhance disease risk, as the ability of worms to suppress the immune system might facilitate infection.[60]

A nascent body of scientific work is beginning to link catastrophic changes in the microbiome with equivalent changes in the macrobiome. This research offers a "biodiversity hypothesis" for the rise in inflammatory disease.[61] It proposes that the loss of wildlife (both inside and outside the human body), coupled with modern lifestyles that reduce human exposure, helps account for the absence of old friends and their immune-regulating functions.[62] This writing, which links immunologists and conservationists, tends to pathologize the disconnections associated with urban life and draws attention to the benefits of exposure to soil and agricultural animals associated with a rural lifestyle.[63]

Those involved with rewilding and biome restoration are especially concerned with the positive feedback loops associated with regime shifts, as well as with the ease with which their focal ecological system might be tipped back into a desired stable state. This ease of transition is known as hysteresis. In the context of biome restoration, William Parker and Jeff Ollerton suggest that "elements of a vicious cycle are in place, since immune hypersensitivity due to loss of helminths enhances the tendency of the immune system to interact adversely to a normal microbiome, and alteration of a normal microbiome by aberrant immune activity is likely to further destabilize the immune system."[64] Others have noted the irreversibility of some of the effects of biome depletion as a result of the influence of missing microbes on the development of the human body—for example by generating type 1 diabetes or autism. Similar concerns are expressed about situations in which the missing keystone species has gone extinct and cannot be replaced with a surrogate, as in the case of saber-toothed tiger or woolly rhinoceros, or where the ecology has shifted to such a degree that a returning keystone species would not be able to survive or would come into immitigable conflict with human land uses, as in the return of wolves, hippos, or elephants to lowland Britain.

Finally, in theorizing what prevents regime change (both catastrophic and recuperative), those involved in rewilding and biome restoration focus on a common set of systemic properties that confer resilience on an ecology. Here resilience is understood as the ability of the system to withstand and recover from shocks. It is linked to biological abundance and diversity, and understood in terms of both species and functions. Importance is afforded functional redundancy (lots of species with an unclear ecological role) in the context of systems understood to adhere to complex, nonlinear dynamics, and in a science marked by high levels of epistemic uncertainty. It is important to note that the resilience of a micro- or macroecology is not necessarily valued as a normative good. Prominent rewilding scientists, like Jens-Christian Svenning, caution that there are plenty of depleted or dysfunctional ecologies that show high levels of resilience to socioecological change.[65] Instead, quoting a much-cited paper by Steve Carpenter, such scientists interrogate the "resilience of what to what" and value resilience only when it is the property of a desired ecology or enables the transition toward a desired future condition.[66]

Dysbiosis and Resurgence

Fully functional ecologies of the kind desired by those involved in rewilding and biome restoration are extremely rare. Much of the scientific thinking associated with the probiotic turn has therefore emerged from studies of ecologies that have undergone catastrophic regime changes. A great deal of attention has thus focused on situations marked by forms of dysbiosis. This term has become common in work on the microbiome. It has been defined in several different ways, with a common reference to "any perturbation of the normal microbiome content that could disrupt the symbiotic relationship between the host and associated microbe and result in diseases."[67] Dysbiosis is tied to changes in ecological composition, especially the loss of keystone taxa or beneficial commensals, and a general loss of biodiversity. Some functional definitions of dysbiosis are now emerging.[68] Dysbiosis is not often used to describe trophically downgraded or otherwise dysfunctional macroecologies, but I borrow this term as a general descriptor to identify common explanations of the character of dysfunctional ecologies.

One common conception of dysbiosis emerges from a shared engagement in rewilding and biome restoration with both paleoecology and evolutionary biology. There is a consistent reference in these fields to the idea of "ecological memory," or how contemporary ecologies are haunted by the absence of keystone species.[69] Ecologists talks of "ghosts from the past"[70] that leave an "extended legacy"[71] or "ecological inheritance"[72] in the present. They worry about ecological anachronisms—that is, ecologies whose current (seemingly dysfunctional) dynamics can only be understood with reference to the now-absent and past presence of a megaherbivore or predator.[73] In an example from his best-selling book on rewilding, George Monbiot suggests that tree species like hawthorn, which make up hedgerows in places like the United Kingdom, evolved their ability to withstand heavy browsing and frequent destruction in the presence of now-extinct elephants. In a mournful passage, he reflects, "We live in a shadowland, a dim, flattened relic of what once was, of what there could be again . . . our ecosystems are the spectral relics of another age, which, on evolution's timescale, is still close."[74] Michael Soulé cautions that there is a time lag to this unraveling in which the "functional extinction of species interactions often occurs well before the species themselves have completely disappeared."[75]

In a similar fashion, William Parker and Graham Rook attribute the rise in allergic and inflammatory disease to an evolutionary mismatch between the human immune system and the modern microbiome to which it is exposed.[76] They offer a "fish-out-of-water model of disease"[77] in which the evolved dependence of the immune system on the hunter-gatherer environment means it goes awry in the absence of the calibrating and symbiotic effects of the old-friend microbes. This idea of the evolutionary mismatch between modern, sedentary urban life and humans' Paleolithic past is a central component of a wider field of medical, psychological, and social theory associated with what has become known as the paleo movement. The mismatch—without or without microbial mediation—has been used to account for a wide range of pathologies, including obesity, stress, depression, addiction, and violence.[78]

Like extinct megaherbivores or absent predators, some helminths have come to figure as ghosts whose absence haunts dysbiotic gut ecologies, although research on the immunomodulatory abilities of helminths and the autoimmunity associated with their absence has drawn attention to the importance of the timing of their going missing. Researchers have suggested that the ecological memory of human-evolved dependence on helminths might be transient, and that the gut microbiome and immune system might be able to adapt. Immunologists speculate about an epigenetic mechanism that might account for this lag.[79] In a similar fashion, rewilding scientists developing an "ecological memory-rewilding framework" to guide interventions suggest that the strength and transience of ecological memory is likely linked to the speed of abiotic and biotic turnover in an ecosystem.[80]

Another common strand of thinking associated with these discussions of dysbiosis relates to the concept of blowback that I introduced in chapter 1. In particular, ecologists working between the macro and the micro scales of ecology have noted how the absence of the top-down, regulatory role of keystone species can lead to what Anna Tsing has called the "proliferation" of a small number of invasive species or pathogens.[81] In this context, microbiologists have developed the concept of the pathobiont: an organism that can switch between a mutualistic and a pathogenic relationship, often as a result of significant ecological disturbance.[82] For example, antibiotics reduce microbial diversity and remove colonization resistance, allowing some otherwise commensal but drug-resistant bacteria—like *Clostridium difficile*—to proliferate in the lower intestine.[83] Likewise, research on the microbial drivers of colon cancer has identified the role played by pathogenic "alpha bugs," a term that describes a small number of commensal bacterial species that come to configure dysbiotic microbial ecologies in patients with low-fiber diets that in turn induce a cancer-causing immune response.[84] In chapter 5, I explore the hookworm as a pathobiont, whose immunological relations are configured by the intensities of its political ecological relations.

While the concept of the pathobiont is not commonly used in the macrobiome, ecologists suggest that otherwise mutualistic species can become invasive as a result of trophic downgrading. Terborgh and Estes describe a "trophic shunt" enacted by "organisms that . . . short-circuit the hierarchical food chain by usurping primary productivity at low trophic levels."[85] For example, as Aldo Leopold observes in the epigraph to this chapter, the loss of apex predators—like wolves—can lead to increases in their herbivore prey—like deer—with deleterious consequences for plant diversity,[86] whereas the absence of apex predators can enable the expansion in populations of smaller (or meso) predators—like coyotes or foxes—that they would previously have controlled. This process of mesopredator release may lead to declines in populations of their prey. One example is the increase in the predation of beavers by coyotes, which had been released from predation by the wolves' near absence in much of North America.[87]

Ecologists also suggest that invasive species proliferate more easily in heavily disturbed ecologies, especially those marked by trophic downgrading. This is the case for many common animal and plant species dubbed pests and weeds. As with microbial pathobionts, these organisms are not inherently deleterious to their host ecology but become so once its structure and dynamics are altered in ways conducive to their proliferation. Many invasive species reproduce quickly and have evolved to make use of newly disturbed conditions. Some of these figure as "transformer species" that can engineer new, stable, and resilient ecologies.[88] Sometimes the new ecologies they create are marked by significantly lower levels of biological diversity than the ecologies they have replaced, though the past tendency to pathologize all nonnative species has been criticized and tempered, in part in response to the challenges of adapting to the novel ecosystems of the Anthropocene.[89] Nonetheless, a common argument is that deleterious changes to ecological function and the emergence of pathogens result from changes to the character and intensity of ecological interactions. As Steve Hinchliffe, Anna Tsing, Rob Wallace, and others have argued, pathogenesis is immanent to intensive and antibiotic modes of ecological management like plantations or factory farms, which become disease hot spots.[90] Disease and dysbiosis are inherent problems, not necessarily the result of an encounter with an exotic, foreign, or otherwise premodern other. Indeed, premodern, antibiotic, and probiotic modes of management all have the potential to create such disease hot spots.

Behind all of this work on dysbiosis is a shared commitment to understanding and facilitating what Tsing terms ecological resurgence, or "the remaking of livable landscapes through the actions of many organisms."[91] Tsing differentiates resurgence from proliferation, equating the former with the convivial premodern human–environment relations of the Holocene and the latter with the intensive and globalized relations of the Anthropocene, exemplified for her in the political ecologies of agricultural plantations. In the context of the probiotic turn, this resurgence is commonly figured as the self-willed outcome of the ecological ability of keystone species to reconfigure dysbiotic ecologies through the return of their regulatory effects.[92] Rewilders describe this as the (often unexpected) emergent properties of a landscape ecology.[93] Wolves redress the trophic cascade caused by their absence, beavers engineer aquatic ecologies, and hookworms exercise the immune system and foster eubiotic microbial ecologies. Here resurgence is the transformative enhancement of ecological structure and functions—like diversity, immunity, and resilience—through interventions that change the antibiotic status quo. This valorization of the self-willed landscaping abilities of transformer and keystone species creates ambivalence and discord among ecologists involved with both rewilding and biome restoration. It raises challenging biopolitical questions as to which forms of life are let or made to live and die to ensure multispecies flourishing.

Anthropocene Humanisms

As responses to the excesses of antibiotic modes of managing life, both of these fields of science acknowledge the profound ecological, even geological, influence of human activities. Ecoimmunology and conservation biology are crisis disciplines. They focus on human–environmental entanglements, which are conceived through a range of ontologies that depart from the modern nature–society and human–nonhuman binaries that have been so central to antibiotic modes of managing life. For example, while they make frequent reference to paleoecology, those developing "science for a wilder Anthropocene"[94] place their interventions within novel ecosystems: ecologies so inflected by human actions that they are not analog to what has come before.[95] They acknowledge the importance of human infrastructure in configuring the contemporary biogeographies of species distribution and movement, and they attend to the legacies—and potential—of antibiotic technologies for managing life, like chemicals, fences, and genetic engineering.

Likewise, the recognition of the microbial origins of human life and of our symbiotic dependence on microbes for core bodily functions, including cognition, has decentered the modern figure of the rational Human as a disembodied mind in a vat. Thinking the human as holobiont flags the porosity and precarity of the body and the risks posed by the unraveling of the human microbiome. It draws attention to the ways in which humans and other life-forms are inadvertently shaped by a host of modern health, hygiene, and lifestyle practices such that no component of the microbiome remains unaffected by human activity. In this way, and to differing degrees, both rewilding and biome restoration have begun to link their science to the concept of the Anthropocene and the wider intellectual zeitgeist that it has named and propelled.[96] Ecologists involved with rewilding draw the hypothesized advent of this new epoch back from the modern (eighteenth to twentieth centuries) origin points that are popular in the geosciences. The significance of coal or nuclear energy is downplayed to give preference to the planetary effects of the extinction of the megaherbivores (100,000 to 10,000 BP), subsequent declines in predators, and widespread trophic downgrading.[97] The discussion of the Anthropocene and its contested periodization are less pronounced in work on the microbiome, although immunologists involved in biome restoration share a comparable interest in identifying the moment of the historical fall to which the origins of dysbiotic relations can be traced.

As such, the science of rewilding and of biome restoration operate ontologically "after nature" in the sense described by Marilyn Strathern.[98]

Like Heather Paxson's probiotic cheese makers, these immunologists and conservation biologists are "at once post-nature, recognizing that there is no pristine natural world outside human cultural activity, and also ever in pursuit of some kind of remade nature as a ground for appropriate human action."[99] There is significant and contested heterogeneity to the types of remade natures that come to ground the probiotic projects that feature in this book. Here I will foreground the most prominent position afforded people in the novel ecologies of rewilding and biome restoration, which I call "enlightened anthropocentrism," following Josef Keulartz.[100]

The diagnosis of the Anthropocene has been taken by many environmentalists as a caution against the hubris of modern dreams of planetary management and a portent of apocalyptic futures with the potential to unravel the hospitable conditions of the Holocene. Those involved in rewilding tend not to share these concerns. Instead, rewilding is promoted as a redemption narrative in which optimistic, beneficent environmentalists turn to face the future and seize the opportunities presented by the event of "the age of Man."[101] Such accounts mobilize the long history of (largely) inadvertent human planetary influence to present humans as potential ecosystem engineers capable of large-scale niche construction. In some prominent accounts, humans figure as enlightened "hyperkeystone species" with the potential for facilitating a functional future of mutualistic coevolution.[102] Popular science writer Ed Yong describes the human hyperkeystone as follows: "We are the influencer of influencers, the keystone species that disproportionately affects other keystone species, the ur-stone that dictates the fate of every arch."[103] In keeping with the tenor of the North American ecomodernist movement, some rewilding manifestoes propose that humans (aggregated in the universal "we") embark on ambitious, continental-scale schemes for environmental management. Such schemes would involve "decoupling" people from nature and setting aside large areas for new wildlands.[104]

This model of enlightened anthropocentrism also characterizes the position afforded people in biome restoration. While the identification of the human as a symbiotic holobiont has been taken by some social theorists to undermine models of the competitive, individual human subject and to challenge the modern "masters of our own destiny" narrative, this is not how the microbiome is commonly conceived by immunologists working with helminths. The theory of biome depletion does recognize the anthropogenic nature of "modern dysbiotic drift"[105] and its associations with a wide range of scientific and technological developments previously heralded as archetypally modern: sanitation, antibiotics, urbanization. But these are not understood to challenge the logics of human exceptionalism. Instead, the prevalence of human impacts on the microbiome is read as evidence of human power and a portent of the promise of more rational and ecological modes of microbiome management.[106] Ecoimmunology after nature operates cognizant of the Anthropocene signature in the microbiome, but in search of a naturalistic ontology on which to ground new projects of anthropocentric world making.

Gaian Thinking in Context

It is well beyond the scope of this book to fully situate these concepts in the history of ecological ideas, or to disentangle the flow of ecological concepts into and between conservation biology, immunology, and microbiology. But it is worth taking the time to place Gaian thinking into an intellectual context. Scientific concerns with ecological changes caused by the anthropogenic loss of species have a long and varied provenance. Since at least the late nineteenth-century writings of Élie Metchnikoff and Sergei Vinogradsky, microbiologists have developed ecological understandings of bacteria, including an interest in the salutary roles of beneficial microbes and concerns that their absence leads to dysbiosis.[107] Ecological research on bacteria and their viruses (or bacteriophages) was especially prominent in the Soviet Union (Russia, Georgia, and Poland) in the early part of the twentieth century, and phages and probiotics were used to treat citizens and Soviet soldiers in World War II.[108] Ecological research remained prominent in the postwar microbiology of figures like Rene Dubos and Joshua Lederberg, but receded (at least in Europe and North America) during what the historian Scott Podolsky has described as "the antibiotic era."[109] Since the production of penicillin in 1942, successive waves of so-called wonder drugs have helped control infectious bacteria and diminished the importance of research on the ecological origins of disease. But the decline in new drugs and the growth of concerns about antibiotic resistance since the

1980s, coupled with the advent of metagenomics and concerns for missing microbes in the 2000s, have all placed microbial ecology firmly back on the agenda.[110]

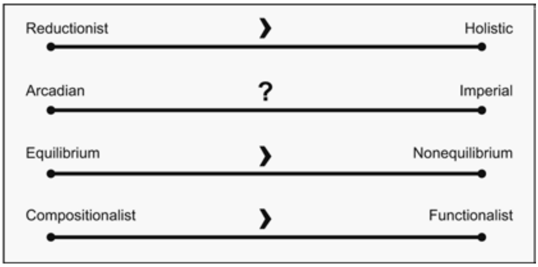
Likewise, as this chapter's epigraph makes clear, scientific concerns about what is now known as trophic downgrading have a longer history, in some cases preceding Leopold's cautionary observations. In North America, opposition to the science-led agriculture and forestry of settler colonialism catalyzed a romantic tradition in ecology that was driven by a combination of elite hunters and naturalists encompassing figures like John Muir, Teddy Roosevelt, and Henry Thoreau.[111] In Europe, an earlier pastoral tradition of poets, writers, and natural historians, including Robert Burns, John Clare, and William Wordsworth, initiated an ecological concern with the loss of species that found scientific expression in the early twentieth-century writings of figures like Charles Elton, Julian Huxley, and Arthur Tansley—figures who were instrumental in founding the institutions of European and international conservation.[112] Meanwhile, ecologists working within and against the institutions of European colonialism in Africa and South Asia frequently commented on how indigenous and colonial hunting, trapping, and pest control led to landscape-scale change for species as diverse as elephants, tigers, and tortoises.[113]

Conservation biology, microbiology, and immunology have all come to embrace ecology in response to different social anxieties about environmental or human health. Scientists have turned to ecology to forge mission-oriented crisis disciplines that aim to name, popularize, and address socioecological problems.[114] As I trace in chapter 4, the compressed temporality of this crisis framing, and the normativity of mission-orientation, shape their epistemic practices. This coproduction of ecological science and social concerns about environmental and then human health has had important consequences for the history of ideas. Historians of science have diagnosed various "ages of ecology" across different disciplines. Donald Worster argues that the first Earth Day in 1970 marked the advent of the age of ecology in environmental management, as the ecological science of figures like Leopold went mainstream and was heralded as providing a blueprint for planetary survival.[115] Others suggest that this age comes later, with the rise of anxieties about climate change.[116] In comparison, the early 2000s have been identified as a golden age for microbial ecology, and historian Alfred Tauber has claimed that an ecological turn is underway with the twenty-first-century rise of ecoimmunology.[117] Tauber links this ecological enthusiasm to the wider influence of "the ether of environmentalism": "the collective experience that the earth is facing an environmental crisis, if not a catastrophe."[118]

The asynchronous timings of these ages of ecology hint at the unequal flow of ecological ideas between micro- and macrobiology. The origins of ecological science lie in thinking with larger plants and animals whose dynamics are slower, are easier to observe, and more readily excite popular sensibilities. While Lovelock and Margulis both shaped Gaian thinking, the subsequent traffic in probiotic concepts has been somewhat unequal, with microbiologists and immunologists borrowing more frequently from their macroecology colleagues. It is only with the twenty-first-century advent of metagenomics that microbiologists could begin to map the types of ecological network interactions that had become familiar to plant and animal biologists in the later decades of the twentieth century. Only very recently have they been able to test the utility of concepts like niche construction, trophic cascades, and keystone species in the microbiome. Indeed, the idea of helminths as ecological engineers has been most comprehensively discussed by wildlife biologists studying the immune systems of wild animal populations, perhaps because they are more acquainted than immunologists with this branch of ecological theory.[119] The ether of environmentalism infused conservation biology well before it intoxicated microbiology and immunology, so the science of plant and animal restoration has served as the primary concept generator for the probiotic turn. Conversations across this scalar divide are only just beginning, and we might expect future conceptual traffic as Gaian thinking takes stronger hold.

In his classic history of ecological ideas, Donald Worster identifies four axes of philosophical difference to help us to begin to specify and contextualize the type of ecology involved in thinking like Gaia: reductionist–holistic, Arcadian–imperial, equilibrium–nonequilibrium, and compositionalist–functionalist (Figure 12).[120] I only sketch these here; they need further research and elaboration. The first is a shift away from the reductionist approaches that characterized much twentieth-century biology, toward more holistic approaches. In microbiology, this is shown by the return to long-standing interests in microbial ecology

Figure 12. Four conceptual axes for specifying the type of ecology that informs probiotic science.



with symbiosis and in the new focus on symbiogenesis, which have culminated in the postmodern synthesis. Margaret McFall-Ngai describes biologists in "future shock" as they struggle to deal with the wealth of data made available by new sequencing technologies, trying to adapt their models to grapple with a much wider range of relevant ecological relations.[121] A holistic turn in immunology is evidenced by the figure of the holobiont, the growing appreciation of coevolved mutualistic relations between microbes and their host, and of the role of the microbiome in both enabling and constraining antibiotic resistance. This holistic understanding challenges reductionist models that link disease to microbial presence, foregrounding the pathological potential of microbial absence and dysbiosis. The holistic character of rewilding is evidenced by its focus on ecological interactions, trophic cascades, and top-down regulation, shifting away from the reductionism of both endangered species conservation and productivist models of single resource management. As I explore in chapter 4, this holism drives an emphasis on specificity, complexity, contingency, and emergent properties over the derivation of general mathematical principles.

We can orientate holistic probiotic science in relation to the differences Worster identifies between the Arcadian and imperial traditions in ecology. For Worster, the Arcadian view "advocated a simple, humble life for man with the aim of restoring him to a peaceful coexistence with other organisms," whereas the imperial tradition aimed "to establish, through the exercise of reason and by hard work, man's dominion over nature."[122] Here there is more ambiguity as to where to position probiotic science, which relates in part to the different forms and degrees of anthropocentrism that we will encounter in the chapters that follow. On the one hand, the prevalent model of enlightened anthropocentrism folds the human as holobiont into a probiotic planetary ecology. Microbiologists and immunologists take issue with neo-Darwinian model of individualistic competition and with imperial metaphors of immunity as all-out Hobbesian warfare. Cold War–esque depictions of the martial and antibiotic defense of the pure human self are being recalibrated toward more historical, dialogic, and communitarian understandings commensurate with the human as a porous and entangled holobiont.[123] Likewise, some rewilders promote themselves as hyperkeystone species, capable of instigating nature-based solutions to anthropogenic planetary dysbiosis. On the other hand, some figure the human as a God species with the potential for rational planetary stewardship. While Lovelock's Gaia has been folded into popular models of Arcadian environmentalism, his science and the emerging model of Gaia 2.0 has the earth as humans' dominion. However, this imperialism is not universal, as I explore in chapter 7 and in the conclusion.

It is easier to place probiotic science on the third of Worster's axes. The ecology of rewilding and biome restoration departs from the equilibrium models that are prominent in the Arcadian tradition. Common interests in sympoiesis, tipping points, and metastability situate probiotic science within the "ecologies of chaos" that Worster argues came to prominence in the second half of the twentieth century with the rise of nonequilibrium systems biology.[124] This enthusiasm for nonequilibrium over equilibrium ecology is evident in rewilding in the examples of the Vera cycles of forest–pasture dynamics and the emphasis this model places on the disturbance regimes enacted by large herbivores. This theory offers a polyphonic ecology marked by discordant harmonies and capable of tending toward several contrasting compositions. This model pushes against the pathologization of anthropogenic disturbance in conservation and presents the conservationist as the conductor of ecological dynamics, one informed by the adaptive cycle of resilience theory. Likewise, a nonequilibrium model of human ontogenesis has become prominent in immunology, with a recognition of the haunting power of missing microbes and the hysteresis of dysbiotic gut microbiomes plagued by drug-resistant bacteria. Beneficial microbes are valued for their ability to disturb gut microbiomes and exercise the immune system.

In keeping with this shift away from equilibrium, the ecology of rewilding and biome restoration is more functionalist than compositionalist.

As J. Baird Callicott explains, compositional ecology focuses on units, especially the distribution and dynamics of species and habitats.[125] Compositionalist approaches were prominent in twentieth-century conservation, especially with the creation of the International Union for Conservation of Nature's Red List of Threatened Species and its focus on rarity and extinction.[126] In contrast, rewilding focuses on ecological functions and processes—grazing, predation, decomposition—as they are enabled by species interactions and biotic–abiotic dynamics. Likewise, those mapping the microbiome and dysbiosis in the interests of biome restoration are less concerned with the work done by specific species. Indeed, a taxonomy of species proves hard to apply to bacteria as a result of their interorganism genetic promiscuity. While they might be concerned with pathogenic strains, ecological microbiologists focus much more on understanding the functional ecological configurations that deliver desired bodily processes. As I explore in chapter 7, this functionalist ecology lends itself to the calculation of ecosystem services, in which the ability of an ecology to deliver immunity and metabolism, or to manage flooding and sequester carbon, matters more than the composition of organisms delivering these services.

Conclusions

This chapter has given an overview of probiotic science and what it means to think like Gaia through an analysis of the science that informs rewilding and biome restoration. To summarize, this work identifies five common sets of concepts that are understood to operate across nested scales. Taken together, this science presents a symbiotic understanding of evolution as well as of ecological function and dynamics. Ecologies are strongly influenced by a small number of keystone species, the absence of which can lead to dramatic regime shifts resulting in situations of ecological dysbiosis and the proliferation of biological miscreants. Aggregated humans are responsible for these shifts, but they also have the knowledge and potential to set them right through proactive practices of enlightened ecosystem engineering to enable resurgence. I identified four axes to specify the type of ecology that informs probiotic science. We should note that this positioning is not universal, nor is it uncontested by other scientists. We should use this figure to highlight the alternative ecological ontologies from which probiotic thinking departs and with which it differs. Indeed, with striking frequency, those involved in developing probiotic science feel obliged to promote their work as shifting paradigms, and in keeping with this model of epistemic change, they often seek to court debate and controversy among their peers.[127] In the chapters that follow, I explore these controversies and the ways in which they encourage wider debates about how ecological science is generated, and how it used, abused, and ignored in its applications to both policy and interdisciplinary research.