The Canadian Field-Naturalist

Book Reviews

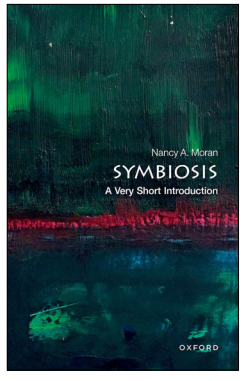
Book Review Editor's Note: The Canadian Field-Naturalist is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those on any species (native or non-native) that inhabits Canada, as well as books covering topics of global relevance, including climate change, biodiversity, species extinction, habitat loss, evolution, and field research experiences.

Currency Codes: CAD Canadian Dollars, USD United States Dollars, EUR Euros, AUD Australian Dollars, GBP British Pounds.

Biology

Symbiosis: a Very Short Introduction

By Nancy A. Moran. 2025. Oxford University Press. 144 pages, 13.50 CAD, Paper, 6.99 CAD, E-book.



Evolutionary biologist Nancy Moran begins with a basic definition: "Symbiosis is the intimate and sustained association of individuals of different species, often for mutual benefit" (p. 1). The caveat ("often") is significant because the relationship doesn't always benefit both or all participants, and determining the degree of reciprocity can require close study.

The author reveals she had never heard of symbiosis in any biology course, even by the late 1970s (although the subject had been studied at least by the late 1800s). Due to a lack of supporting DNA breakthroughs, Moran writes that symbiosis was being "ignored as a factor in evolution or development" (p. 5). However, I distinctly remember being introduced to the three primary flavours of symbiosis in my high school environmental biology class in 1971: mutualism (both/all benefit), parasitism (one benefits, the other is harmed), and commensalism (one benefits, the other is unaffected). Although this delineation is not directly dealt with in *Symbiosis*, Moran does point out that while mutuality is not a prerequisite in symbiotic relationships, biological diversity means "opportunities for trading favors" can be frequent (p. 38).

Paul Buchner, an early advocate of symbiosis, published a detailed book of observations in 1921, relying on his microbial microscopy work, about the requirements of animals to acquire nutrients they could not produce themselves. He speculated that symbionts are more frequently found within animals with restricted diets, but he couldn't prove his thesis (pp. 7–8). Researchers would later discover through DNA sequencing that a bacterium genus, *Buchnera*, found in aphids (Moran's own research focus) produces a required amino acid lacking in the plant sap the insects feeds on (p. 15). Because animals lack the ability to self-produce amino acids, they must acquire them by eating other organisms (p. 22).

Symbiosis, says Moran, is widespread across a range of species. It is "central in the expansion and diversification of life on Earth" and is better understood now because of advances in molecular biology (p. 2). Whereas speciation produces distinct species, two (or more) organisms can fuse and provide resources and survival advantages for one another. Symbiosis can fast-track evolutionary change caused by mutation, fitness advantage, and geographic isolation.

Participating species in a co-relationship tend to be quite different from one another. This makes sense, Moran argues, because they don't compete for the same resources and can provide different complementary capabilities (p. 18). Or, conversely, other symbionts might alter the reproductive state of their male and female hosts so that they are unable to breed successfully (pp. 16–17). And there are "cheating" free riders and "selfish" mutant symbionts that provide little if any gains and even degrade the survivability of their hosts (pp. 61–64). They may be "punished" through natural selection for doing so (pp. 61–70).

The 'intimacy' in Moran's definition of symbiosis refers to the degree of integration of partnering species, be it the generally larger host or an attached or encased symbiont. While now easier to determine where the actors physically reside with modern microscopes, it isn't so simple to discern what each is doing. Few will argue with Moran when she disqualifies from symbiosis the relationship between (for example) a hummingbird and a plant it is pollinating, even though both species benefit. This is because the association is neither intimate nor sustained. "Hummingbirds flit from flower to flower, and often roam quite freely" (p. 37). In contrast, the Acacia Ant (*Pseudomyrmex ferruginea*)–acacia plant (*Vachellia*) relationship may qualify because the plant provides housing and food, and the ant protects the plant by attacking predators: "Ants cannot make sugar, and plants cannot sting" (pp. 37–38).

Lichens

Swiss botanist Simon Schwendener was ridiculed when he suggested in 1867 that lichens were alliances of two species, a proposition that decades later would be seen as the prescient beginnings of an important biological concept (pp. 5–6). Lichens are a ubiquitous hybrid partnership that cover 8% of the earth's landmass, including inhospitable zones (p. 112). They provide half of the nitrogen input in Douglas Fir (*Pseudotsuga menziesii*) forests, supply homes for many invertebrates, and are a key food source for Reindeer in winter (p. 113). They are a relationship primarily between a fungus (which supplies inorganic nutrients and a protective structure) and a phototroph, either an alga or a photosynthetic bacterium supplying energy for growth (p. 24). We can now also add a diversity of other microbial partners, including basidiomycete yeasts and additional bacteria that play "a variety of roles" (p. 113; Grube and Gabriel. 2009; Bates *et al.* 2011). And, as Moran points out, while some fungi have become "lichenized", others have "reverted to life on their own" (p. 113).

Symbionts, Holobionts, and Evolution

The book describes many other examples of symbionts, including the marine segmented worm *Olavius algarvensis*, the marine flatworm *Paracatenula galateia*, and the giant tubeworm *Riftia pachyptila*, all of which live in inhospitable environments and rely on chemosynthetic partners for nutrition (pp. 25–26). Symbionts that offer a degree of protection to hosts (and thereby benefit soils) include the bacteria housed and transported on *Mortierella* fungi that produces toxins offensive to fungi-consuming nematode worms (p. 33). Microbes have been relying on each other for billions of years. In Australia, studies reveal a community of bacteria and archaea that have existed together since life began (p. 35). The extensively studied human microbiome—which establishes itself during birth from mother to offspring and subsequently through dietary choices—significantly impacts human health. Some research suggests that missing bacteria in processed foods, together with the introduction of antibiotics, are among the root causes of a modern epidemic of chronic diseases in industrial societies (p. 122). However, as Moran cautions, "probiotic" products do not effectively recolonize our guts, despite the advertised hype (pp. 120–123).

Other examples offered in *Symbiosis* include Hawaiian Bobtail Squid (*Euprymna scolopes*), which house the bioluminescent bacterium *Vibrio fischeri* (a 40-million-year-old relationship; p. 33); some stink bugs (the family Pentatomidae), which use a gut valve to selectively filter desirable microbes (p. 54); tortoise beetles whose allies produce enzymes enabling the digestion of leaves (p. 43); and termites and their wood-digesting tenants—termites produce 4% of global methane (p. 117)! Digger wasps rely on bacteria they carry in their antennae to protect their offspring from other harmful bacteria (p. 43).

Symbionts acquire access to one another through different transmission methods: vertical, from parent to offspring via egg, embryo, or plant seed; horizontal, from non-parents or the external environment; or a combination of the two (pp. 44–45). "Not all symbionts are a gift from mom", Moran writes, referring to the large number of plants and animals that acquire symbiotic partners from discrete organisms (p. 52). Gut bacteria are almost universally present in animals and are rarely acquired from parents, and both cows and humans contain elaborate communities of them. Some symbionts are 'non-obligates' or unrequired, either because the relationship they provide is temporary and ephemeral, or replaceable by other symbionts.

Because both host and symbiont acquire survival advantages from their relationship, their co-evolutionary alignment can enhance mutual fitness success, and their ancestry trees can diversify in tandem (p. 93). On the other hand, Moran points out, in the longer term there can be a diminution of survival status. Co-dependence can develop, and also what is called the "symbiosis rabbit hole" (pp. 134–138). In these cases, "hosts become addicted to their symbionts" and may even "blur the distinction between symbiont and organelle" (Bennett and Moran 2015). This can be an adaptation limitation and creates the potential risk for future extinction. Here the external (horizontal, non-familial) acquisition of symbionts is an advantage by spurring hosts to incorporate new genes (p. 57). Benevolent symbionts may be welcomed, but

cheaters and harmful (non-symbiont) pathogens are deterred (p. 64). This shows how competing natural selection mechanisms can remain in play.

Evolutionary biologist Lynn Margulis famously proposed that cell organelles such as mitochondria and chloroplasts originated from bacteria that came to be engulfed by a host cell, a relationship known as endosymbiosis (pp. 126–128). "Many squabbles ensued" over this theoretical shift, but most now agree with Margulis (p. 74).

DNA and fossil evidence show symbioses spanning vast periods of time, and that a significant event occurred 1.2 to 2.5 billion years ago when exclusively prokaryotic unicellular life was eclipsed (pp. 95–98). The search continues for "the original cell that swallowed a bacterial symbiont", the shared matriarch affectionately known as LUCA or the last universal common ancestor (p. 83). Moran spends several fascinating pages on the origins and development of complex organisms. Groundbreaking new understanding has led to an updated tree (or network) of life that reveals eukaryotes (organisms including plants, animals, and fungi that have cells with a membrane-bound nucleus and other organelles) are an offshoot of an archaea to bacteria symbiotic transition (pp. 76–80; 103–107).

Controversially, Lynn Margulis proposed that symbiosis is the primary driver of evolutionary change (p. 126; The Economist 2023; also see a harsh critique by Coyne 2011). She also popularized the term 'holobiont' to conflate the collectivity of organisms involved in a symbiosis. Others invented 'hologenome' to describe a single gene pool of those organisms. This contested framing implied that evolutionary selection acts on the collective, and therefore "symbionts should evolve to maximize the fitness of their hosts and vice versa" (p. 127). It challenged mainstream evolutionary theory's focus on the survivability of individuals within species, not relationships between organisms. Moran includes a full chapter exploring reciprocity and "the appearance of altruistic harmony" between species, and also parasitic and injurious interactions (p. 59). She concludes, however, that while a holistic level of selection can apply, relationships (mammals with grasses, for example) are not a singular unit of natural selection and "referring to their pooled genomes as a hologenome is not helpful" (p. 128).

Climate Change

Current climate warming pressures reveal how symbiosis helps survivability because of the relatively rapid evolution of microbes in microbiomes. Symbionts can be manipulated to provide protection through drought resistance, enhanced reforestation, or coral recolonization (pp. 140–143; The Economist 2023). For over 160 million years, coral reefs have generated carbon dioxide that is fed to their algal symbionts (collectively known as zooxanthellae), which in turn convert it into carbon compounds rich in energy used by the coral. The coral feeds the algae limited nitrogen for their own survival (p. 24). The reefs that corals construct provide homes for a quarter of all ocean species (p. 98; NOAA 2024). This remarkable contribution is now under threat from coral bleaching caused by human-driven rising ocean temperatures, pollution, and nutrient concentration shifts (pp. 115–116). Absent the right balance of symbionts, corals deteriorate into white calcium carbonate skeletons.

Moran's *Symbiosis* is a compact introductory guide to the symbiosis story with plenty of examples of the relationship in action. The book usefully outlines several of the ongoing and settled debates. The text is enhanced by more than 20 clear illustrations.

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