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Repaying Darwin's Debt to Agriculture

THIS BOOK EXPLORES new approaches to improving agriculture, inspired by nature and informed by evolutionary biology. Biologists are nearly unanimous in accepting the multiple lines of evidence that life on earth has evolved and is evolving,[1–3] so applying evolutionary biology to agriculture should be no more controversial than applying chemistry and microbiology to soil science. Yet some implications of past and ongoing evolution for agriculture have often been neglected.

Nature, Agriculture, and Evolutionary Tradeoffs

In particular, I will argue that two popular approaches to improving agriculture have tended to ignore *evolutionary tradeoffs*—that is, cases where an evolutionary change that is positive in one context is negative in another. Biotechnology advocates have often overlooked tradeoffs that arise when we genetically modify processes like photosynthesis, which have already been improved over millions of years of evolution.[4] On the other hand, people looking to nature for ideas to improve agriculture have sometimes ignored tradeoffs between the collective performance of plant and animal communities and the individual competitiveness of plants and animals. When such tradeoffs exist, evolutionary processes tend to improve individual competitiveness rather than restructure communities.[5] Therefore, the overall organization of natural communities may not be optimal, particularly as a model for agriculture. Once we drop the assumption of perfection, however, we can learn much from studying natural communities. Whether we focus on genetic improvement of crops or better management of agricultural ecosystems, identifying (and sometimes accepting) tradeoffs that constrained past evolution can often lead to new solutions to agricultural problems.

Both agricultural biotechnologists and people looking for agricultural inspiration in nature have valuable expertise and good ideas; they simply need to pay more attention to evolutionary tradeoffs. I hope this book will be read by members of both groups who want to increase their chances of success. Similarly, I hope that readers whose background is mainly in evolution or mainly in agriculture will find something here to interest them in the intersection of these fields.

I assume that readers will start—and end!—with different views on many issues, from organic farming to biotechnology (see glossary). Readers will also presumably vary in their overall familiarity with agriculture and with biology. Therefore, I include an introductory chapter on agriculture's challenges and one on evolutionary biology, emphasizing aspects key to my arguments. Many terms are defined at their first appearance in the text; I have also included an extensive glossary following the text that you can use for reference. Those who want more information, or who wonder how I have simplified a particular issue, are encouraged to read the relevant source materials listed in the references section; these are noted throughout the text using superscript numbers.

Agricultural Challenges . . . and Two Incomplete Solutions

"Store grain everywhere," advised Chairman Mao, to ensure food security in the event of war or natural disaster. Thousands of years earlier, Egypt reportedly found a seven-year supply to be adequate.[6] More recently, in 2006, total public and private grain reserves worldwide fell to a two-month supply, as population growth outpaced increases in grain production.[7] Population growth and other trends discussed in the next chapter are predicted to increase global demand for grain (which directly and indirectly supplies most of our protein and food energy) by 40 to 60 percent over the next 30 years.[8] Although different assumptions would lead to somewhat different numbers, some increase in grain production will almost certainly be needed.

But at what environmental cost? For hundreds of years, we have increased food production by using more land and water for agriculture. Agriculture has expanded to use more water and land than any other human activity, accounting for up to 80 percent of our water use and 35 percent of the world's ice-free land surface.[9,10] Much of the remaining land is too steep, dry, wet, or cold for farming, or is set aside for parks and nature preserves. Do we really want to divert more water from rivers for irrigation, perhaps endangering fish or other wildlife? Do we really want to clear more forests or drain more wetlands to expand farmland?

I don't think so. Instead, we need to use the resources already allocated to agriculture more efficiently. For example, we need to increase the ratio of food produced to water used. This is one definition of *water-use efficiency (WUE)*. The ratio of food produced to land area used could be called *land-use efficiency*, but I will use the traditional term, *yield*. Farms account for only 3 to 5 percent of energy use in industrialized countries,[11] but rising fuel prices will make energy-use efficiency increasingly important to farmers.

Resource-use efficiency and food security (including quality, affordability, year-to-year reliability, and long-term sustainability) are not the only challenges facing agriculture, but they are the main focus of this book. Our goals for agriculture are considered in more detail in the next chapter.

When there are tradeoffs among multiple goals, which should have priority? Because agriculture uses a larger fraction of our water and land than it uses of fossil fuels, maybe water-use efficiency and yield should be higher priorities than energy-use efficiency. On the other hand, water and land can be reused, if we don't degrade them. Fossil fuels, once burned, are gone forever. The information in this book should help you draw your own conclusions, which may differ from mine. But even if we disagree on some answers, perhaps can we at least agree on this central question:

> How can agriculture reliably meet our needs for high-quality food and other farm products (like cotton or wool) over the long term, without environmental damage?

Two approaches that have often been proposed—rarely by the same people!—are biotechnology (such as adding genes from unrelated species to our crops, making them transgenic; see glossary)[12,13] or, alternatively, agriculture that attempts to mimic nature.[14,15] The theme of this book is that although each of these approaches has potential, both of them would benefit from greater attention to evolution, both past and ongoing.

Well-intentioned biotechnology experts may underestimate some risks of their approach. These include accidental consumption of crops grown to produce pharmaceuticals. Some less-direct risks discussed in later chapters may be even more important. Modern industrial agriculture is largely based on *monoculture*, that is, growing only one crop at a time in each field. Regionally and globally, we practice *oligoculture*, relying mainly on only a few crops, particularly corn (maize), wheat, and rice. Our major crops have been represented by many different varieties, reducing the risk that disease will destroy the crop over large enough areas to cause food shortages. Because developing each transgenic crop is so expensive, however, there are typically far fewer transgenic varieties than there are varieties developed by traditional plant breeding. If most farmers choose from only a few transgenic options, reducing overall crop diversity, are we putting too many eggs in too few baskets?

Industrial agriculture uses various methods to reduce losses to disease-causing pathogens, insect pests, and weeds, but use of toxic sprayed pesticides (see glossary) is common. The relationship between biotechnology and pesticide use is complex. The two most-common transgenic crops arguably reduce use of some pesticides, but their overall environmental impact is less clear. Widespread use of transgenic crops resistant to the weed-killing *herbicide* glyphosate presumably increases the use of that herbicide, while reducing the use of other, more-dangerous herbicides, at least until weeds evolve resistance to glyphosate. Transgenic crops with bacterial genes that make an insect-killing *insecticide* may reduce the use of insecticide sprays. But does this insect resistance in transgenic crops lead to complacency regarding other methods of pest control, such as growing different crops in sequential rotation (see glossary), increasing the risk of eventual outbreaks that would trigger greater pesticide use?

In rich countries, a large fraction of corn grain is fed to animals raised for food. Critics note the inefficiency of animal agriculture, where only a fraction of the protein and food energy (calories) in grain eaten by animals ends up in meat, milk, or eggs.[16] They suggest that we would need less grain if we ate the grain ourselves, moving "lower on the food chain." This concern predates biotechnology, but criticism of biotechnology and of other aspects of industrial agriculture may sometimes share common philosophical roots.

My own concerns about biotechnology are different. I will have more to say about the possible risks of biotechnology, but here is one of the main points I want to make in this book: *the likely near-term benefits of biotechnology have been exaggerated*. I will argue that biotechnology is unlikely to deliver soon on some key promises, such as crops that yield more grain while using much less water.

Starving research on ecologically inspired ways to improve agriculture to provide massive funding to biotechnology and its allied scientific disciplines may be fueling a biotechnology bubble. What will happen when the bubble bursts, when we finally realize that much of the money spent on biotechnology has been wasted? I hope we will then redirect some of that money to agricultural ecology and its cousins evolutionary biology, plant breeding, whole-plant physiology, soil microbiology, agronomy, and so on. But by then we may have squandered years pursuing an approach that will provide, at most, an incomplete solution to increasingly pressing agricultural problems. Population growth, depletion of natural resources, and other ongoing trends may not give us a second chance to rebalance our research priorities.

Where Does Nature's Wisdom Lie?

Agricultural innovations inspired by nature seem more promising than many of the approaches currently being pursued by biotechnology. But we need to choose carefully which ideas from wild species and natural landscapes we apply to agriculture. How should we choose among nature's innovations?

The title of this section asks where nature's wisdom is to be found, but also whether superficial observations of nature can lead to misleading conclusions.

"Lies" are indeed common in nature. A bird may pretend to have a broken wing, to lead us away from her young. Bolas spiders eat male moths, which they lure to their deaths by mimicking the scent of a female moth.[17] But these are not the kinds of lies that worry me. We may even want to copy some of the deceptive strategies of wild plants, to mislead insect pests on our farms. Instead, I am concerned that we may sometimes mislead ourselves, if we expect to find perfection in nature. Yes, evolution has been improving nature for many millions of years. But evolution's criteria for improvement may not always coincide with our own goals for agriculture.

Leaf-cutter ants illustrate this point. I remember long lines of these ants, carrying leaf fragments back to their nest, through our rented house in Costa Rica. Our family was there because my father, later known for his pioneering research on the lichen and fern communities that cover the tops of old-growth trees,[18] took us along on a summer field trip for his students at Swarthmore College.

The ants don't eat the leaves; they use them to grow fungi and then eat the fungi. Ants have been cultivating fungi for fifty million years.[19] So if we're looking for ancient wisdom, this might seem like a good place to start. "Local food" advocates[20] might be impressed that the ants not only grow all their own food, but also rely entirely on inputs available within walking distance.

Yet the fungus farms of ants share many of the features that, in industrial agriculture, have been criticized as unsustainable. Leaf-cutter ants practice an extreme version of monoculture; each ant colony grows only one strain of one species of fungus for food.[21] Like crop monocultures grown by humans, fungal monocultures grown by ants often become infested with agricultural pests. The most harmful of these pests is another fungus, which attacks and consumes the ants' fungal crop.[22]

Like many human farmers, ants physically remove fungal "weeds" from their gardens, but they also use toxic chemicals to control the pest fungus.[23] Although these pesticides are produced by symbiotic bacteria, I will argue in chapter 11 that evolutionary aspects of this practice resemble pesticide use by human farmers more than they resemble biological control of pests by beneficial predatory insects.

Fungi are more closely related to animals than they are to plants. In other words, fungi and animals are descended from a common ancestor more recent than the one shared with plants.[24] Like animals, fungi are unable to use sunlight as an energy source, so they rely on plants for food.

The fungi cultivated by leaf-cutter ants are kept underground their entire lives, consuming leaves brought to them by the ants, much as cattle in feedlots consume grain or hay brought to them by human farmers.

Like feedlots (see glossary), ant fungus farms are inefficient in some ways. Just as meat and milk contain only a fraction of the food energy in the grain eaten by the cattle, the ants' fungal crop contains only a fraction of the food energy originally present in the leaves consumed by the fungi. If only the ants themselves could digest leaves, they might reduce their impact on the environment by harvesting fewer leaves and consuming them directly, thereby eating "lower on the food chain."

To summarize, leaf-cutter ants practice monoculture, use pesticides, and manage inefficient fungi as if the fungi were cows in crowded feedlots rather than in pleasant pastures. Ants have been following these practices for fifty million years.

As we look to nature as a source of ideas for agriculture, how should we react to this information? We have at least three options.

First, we could continue to insist that nature is perfect, but deny those aspects of nature that are inconsistent with our ideals. This is a very popular approach, but not one I advocate.

Second, if we believe that agriculture should copy nature whenever possible, we could endorse monoculture, pesticides, and feedlots, without any reservations. For example, one biotechnology advocate has argued that it is acceptable for us to use toxic pesticides, because many plants use toxic chemicals to defend themselves from insect pests.[25] But I don't like this mindless-mimicry-of-nature option much either.

Or, third, we could choose carefully *which* ideas from nature we apply to agriculture. If some of the "wisdom" of the leaf-cutter ants turns out to be "lies," how can we avoid being misled in other cases, where the risks of mimicking nature are less obvious? How can we be sure we are copying only nature's best ideas?

In 2009, we celebrated the 200th anniversary of Charles Darwin's birth and the 150th anniversary of his best-known book, *The Origin of Species*. Darwin saw agriculture as a rich source of information for understanding nature, an approach that, he complained, was often "neglected by naturalists."[26] His best argument for the power of natural selection—the central idea in his book—was the success of plant and animal breeders, greatly improving crops and livestock simply by selecting which individual plants and animals get to reproduce. In borrowing this key idea from agriculture, Darwin incurred an intellectual debt, acknowledged by him and inherited by today's evolutionary biologists. Can evolutionary biology repay Darwin's debt to agriculture in the same currency of ideas, identifying evolutionary innovations in the natural world that we can adapt to agriculture? If so, where in the natural world will we find these innovations?

To answer this question, we need to determine which aspects of nature have been improved most by evolutionary processes. I will argue that evolution has improved trees much more consistently than it has improved forests. In other words, nature's wisdom is to be found more in the adaptations of individual plants and animals than in the overall organization of the natural communities and ecosystems (see glossary) where they live. Often, individual adaptations that have been tested by millions of years of evolution will be more sophisticated than anything biotechnologists can imagine and implement. For example, evolution is unlikely to have missed simple, tradeoff-free opportunities to improve biochemical processes like photosynthesis.[4]

But tradeoffs that constrained past evolution need not always limit us today. Tradeoffs between adaptation to past versus present conditions suggest various options for crop improvement through traditional breeding methods or biotechnology.[27] Tradeoffs between individual competitiveness and the collective performance of plant and animal communities may be even more important.[28] For example, although cooperation between species is already common in nature, an evolutionary perspective suggests considerable room for improvement.[29]

When evolution has already been working on a problem for millions of years (improving drought resistance, for example), keeping or copying nature's innovations will often be our best option. But when past evolution has not been fully consistent with our goals, we may be able to improve on nature. Often, this will involve accepting tradeoffs previously rejected by evolution.

Overview of This Book

Here is a brief overview of this book. The next two chapters introduce agriculture and evolution, respectively, but even those familiar with these areas may find new information or ideas to consider. Chapter 2 will discuss some of the challenges that agriculture is facing now or will face soon. Chapter 3 will review some definitions and concepts from those aspects of evolutionary biology that are central to subsequent arguments.

Chapter 4 proposes three core principles that will be developed throughout the rest of the book. First, natural selection is fast enough, and has been improving plants and animals for long enough, that it has left few simple, tradeoff-free opportunities for further improvement. Therefore, implicit or explicit acceptance of tradeoffs has been and will be key to crop genetic improvement, through biotechnology or traditional breeding methods. Some tradeoffs, such as adaptation to conditions that no longer exist, will be easier to accept than others. Second, nature's testing of natural ecosystems merely by endurance is weaker than the repeated competitive testing of individual adaptations by natural selection. Testing by endurance shows sustainability—some natural ecosystems have persisted for millennia—but there may still be considerable room for improvement. We can use what we learn about natural ecosystems to design better agricultural ecosystems, but simply copying the organization of natural ecosystems is unlikely to improve the performance of our farms, by most criteria. Last, I advocate a greater diversity of crops—not necessarily in mixtures—and a greater diversity of research approaches, to hedge our bets against future uncertainty.

Chapter 5 builds on chapters 3 and 4 to argue that some of biotechnology's stated goals, such as more efficient use of water by crops, are unlikely to be achieved without tradeoffs. Possible benefits and risks from biotechnology are discussed. Chapter 6 explores natural selection's limitations: it has bequeathed many sophisticated adaptations to individual plants and animals, but it has not consistently improved the overall organization of the natural communities where they live. The available evidence suggests that no other natural process has optimized natural communities either. Building on these conclusions, chapter 7 evaluates some of the more-popular proposals for how agriculture might attempt to mimic nature. In each case, I suggest some reasons for caution.

Beginning in chapter 8, I turn from criticizing popular but problematic approaches and take a more optimistic view, describing past successes and future opportunities. Many past agricultural improvements have involved accepting tradeoffs previously rejected by evolution, reversing some negative effects of past natural selection. For example, humans have selected for greater cooperation among plants, improving the collective performance of crop-plant communities by sacrificing some individual-plant competitiveness. Selection for more-cooperative plants has not usually been deliberate, but it can be. Chapter 9 focuses on cooperation between two species. Such cooperation is already widespread, but there is plenty of room for improvement. Understanding tradeoffs between the interests of symbiotic partners is key to unlocking this potential.

These first nine chapters mainly emphasize implications of past evolution. Chapter 10 considers ongoing evolution, particularly as it relates to control of agricultural pests. Chapter 11 discusses fungus-growing ants in more detail and extends our search for nature's wisdom to interactions among more species. I argue that natural landscapes need not have optimal structure to be valuable sources of ideas. Last, chapter 12 summarizes key conclusions and cautions against exclusive reliance on any single approach, even those proposed in this book. I argue that although processes similar to competitive natural selection may help us choose the best ideas, we should also hedge our bets by maintaining a diversity of approaches.