EVOLUTION, CONSTRAINT, COOPERATION, AND COMMUNITY STRUCTURE IN SIMPLE MODELS

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Abstract

This dissertation studies models for evolutionary change in ecological communities, particularly the Lotka-Volterra equations and the adaptive dynamics tradition of evolutionary modeling. A recurring theme is the role of constraints on evolution, and how they shape the direction evolution takes, particularly with regard to cooperation. In several different modeling settings, an argument is constructed that cooperation can take many forms, and is not always undermined by temptation to behave selfishly.

The first chapter is a nontechnical introduction, which talks in general terms about the role of scientific models in larger social discourses. Chapters 2 and 3 review the published literature on Lotka-Volterra equations and adaptive dynamics. Chapter 3 introduces new techniques for studying the effects of constraints on evolutionary motion.

Chapter 4 studies evolution in Lotka-Volterra models when interactions are derived from simple characteristics of single populations; chapter 5 removes that assumption and allows the interactions to evolve directly. This choice produces a kind of diversification that is not seen in previously known adaptive dynamics models, and illuminates how phenotypes can constrain the evolution of cooperation. Chapter 6 applies the techniques of chapter 5 to a variety of models.

Chapter 7 shifts to a game theory model, exploring ways out of the "prisoner's dilemma", and chapters 8 and 9 look at cooperation in the form of large-scale ecological regulation. In these chapters as well, the tension between constraints and cooperation is central. Also in chapter 9, I describe a process with some similarity to animal learning that may contribute to the regulation of planetary processes and the Gaia hypothesis.

The concluding chapter explores the themes of constraint and cooperation that recur throughout, and discusses the learning hypothesis of chapter 9 and problems of degeneracy that occur when models are oversimplified.

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Contents

Abstract **iii**

Acknowledgements **v**

1 Introduction **1**

1.1 Modeling in context . . . 3
1.2 Models and metaphors . . . 8
1.3 Trees and rhizomes . . . 14
1.4 Natural selection as rhizome . . . 17
1.5 A web of models . . . 19
1.6 Ecology and other rhizomes . . . 21
1.7 Ecologists beyond biology . . . 25
1.8 Introduction to the dissertation . . . 29

2 Lotka-Volterra Dynamics **33**

2.0 Notation . . . 34
2.1 The Lotka-Volterra equations . . . 36
2.2 Analysis of Lotka-Volterra dynamics . . . 37
2.3 One dimension . . . 38
2.4 Two dimensions . . . 39
2.5 More than two dimensions . . . 44
2.6 The time average . . . 44
2.7 The time average and the invasion function . . . 45
2.8 Competitive systems . . . 47

2.9 Noncompetitive systems . . . 51
2.10 Invasion and extinction . . . 53
2.11 Boundedness . . . 54

3 Adaptive Dynamics 57
3.1 Adaptive dynamics . . . 58
3.2 Stable points and branching points . . . 63
3.3 Adaptive dynamics of one strain in one dimension . . . 65
3.4 Adaptive dynamics of one strain in multiple dimensions . . . 66
3.5 Adaptive dynamics of coexisting strains . . . 68
3.6 Constraints on phenotypes . . . 70
3.7 Example . . . 73
3.8 Attraction and branching on a constraint curve . . . 75
3.9 Discussion . . . 77

4 Evolution of Phenotypes and Interactions 79
4.1 Adaptive dynamics in Lotka-Volterra systems . . . 80
4.1.1 Phenotypes and interactions . . . 80
4.1.2 Lotka-Volterra adaptive dynamics formulas . . . 85
4.1.3 Classification of singular strategies . . . 86
4.1.4 Evolution of phenotypes and interactions . . . 89
4.2 A multi-dimensional evolutionary system . . . 91
4.2.1 Deriving interactions from a vector of traits . . . 91
4.2.2 Two dimensions . . . 92
4.2.3 More than two dimensions . . . 98
4.2.4 Nonlinear variant model . . . 100

5 Evolution Of Interactions Without Phenotypes 105
5.1 The basic model . . . 107
5.2 Behavior of the basic model . . . 109
5.3 Are *a* values like phenotypes? . . . 113
5.3.1 How *a* values are constrained by phenotypes . . . 113

5.3.2 When *a* values are not constrained . . . 117
5.4 A different kind of branching . . . 123
5.5 A closer look at invasion and replacement . . . 125
5.6 Diagonal terms and levels of selection . . . 131
5.7 How to model this system . . . 134
5.8 Discussion . . . 135
5.8.1 Comparison to related models . . . 135
5.8.2 Conversion to mutualism in biology . . . 138
5.8.3 Mutualism, unboundedness and the Lotka-Volterra equations . . . 139
5.8.4 The replacement and coexistence theorems . . . 140

6 Variant Models Without Phenotypes 141
6.1 Replicator dynamics . . . 142
6.2 Space limitation . . . 145
6.3 Competition . . . 153
6.4 Food webs . . . 159

7 Evolution Of Mutualism As An Alternative To Reciprocal Altruism 167
7.1 The evolution of cooperation . . . 169
7.2 The prisoner's dilemma . . . 170
7.3 Game theory dynamics . . . 173
7.4 Evolution of behaviors and their interactions . . . 174
7.5 Conversion of defection to cooperation . . . 175
7.6 Discussion . . . 181

8 Biological Control of Seawater Composition 187
8.1 Introduction . . . 188
8.2 Resource-consumer model . . . 189
8.3 Collision model . . . 190
8.4 Waiting time model . . . 191
8.5 Generalized results . . . 193
8.5.1 Unspecified number of species and resources . . . 193

8.5.2 General functional form . . . 195
8.6 Discussion . . . 195

9 Nutrient Cycles and Global Homeostasis 197
9.1 Global self-regulation and the Gaia hypothesis . . . 198
9.2 Introduction of basic model . . . 200
9.3 Continuous and discontinuous evolution . . . 202
9.4 Equilibrium solutions . . . 204
9.5 Ecological results . . . 205
9.6 Evolution results . . . 206
9.7 Chemistry . . . 208
9.8 Temperature regulation . . . 210
9.9 Conclusions . . . 216

10 Discussion 219
10.1 Constraints and cooperation . . . 221
10.2 Dilemmas and non-dilemmas . . . 225
10.3 Cooperation in ecosystems . . . 227
10.4 Continuous phenotypes and branching . . . 228
10.5 The learning model . . . 229
10.6 When is a simple model too simple? . . . 231
10.7 Other questions about models . . . 232

Bibliography 252

Chapter 1

Introduction

Most of this introductory chapter is a stand-alone essay about the ways in which ecological and evolutionary modeling are a part of a more extensive scientific discourse, which is inseparable from global issues about how society works and how to live in the world amidst environmental and social crises. I explore how mathematical and verbal models can support or challenge existing power structures, with examples, and then introduce the subjects of the rest of the dissertation in the terms of the framework I have set up.

science walks in beauty:

nets are many knots
skin is border-guard, a pelt is borrowed warmth;
a bow is the flex of a limb in the wind
a giant downtown building
  is a creekbed stood on end.

detritus pathways. “delayed and complex ways
to pass the food through webs.”

maturity. stop and think. draw on the mind’s
stored richness. memory, dream, half-digested
image of your life. “detritus pathways”—feed
the many tiny things that feed an owl.
send heart boldly travelling,
on the heat of the dead & down.

– Gary Snyder

Look at mathematics: it’s not a science, it’s a monster slang, it’s nomadic.

– Deleuze & Guattari

1.1 Modeling in context

Ecology has always occupied at least a dual role in our society. On the one hand, ecology is what ecologists do: the study of patterns and processes of biological coexistence. Ecologists try to explain observed patterns of species diversity, what makes some assemblages of species more resistant to invasion or disturbance than others, what changes are likely to result from extinctions and climate change and we can do about them, and other such questions.

At the same time, ecology is commonly perceived as a set of moral imperatives. Ecology is often used as a synonym for environmentalism; the message is that environmental degradation and species extinction are problems that we must solve, and people must be made aware of these issues so that they will take action. "Ecology now!" was a common slogan among 1960s activists advocating for conservation, controls on pollution, and a return to simpler living, and the word "ecologist" is still used in parts of Europe to refer to environmental activists.

While it is certainly possible to study the patterns of ecology without advocating for conservation or social change, or to act as an environmentalist without studying ecology, these pursuits are clearly linked. The most straightforward connection between ecological science and advocacy is that scientists sometimes expose tangible facts that responsible people wish to change, as when Rachel Carson documented the declines in bird populations and other consequences of pesticide use in the early 1960s (Carson 1962), which sparked a movement to control pesticides and other forms of pollution. Also, since conservation, public health, and sustainability have become major political issues, ecological theories and models, and ecologists themselves, are often called upon to set policy.

Possibly as important, though, are the less tangible ramifications of ecologists' work. Revelations of human-caused environmental problems challenge the widespread characterization of science and technology as bringing unambiguously beneficial advances in human

power and quality of life. More abstractly, ecology is seen as delivering the message that all organisms are interconnected, that humans are not separate from nature but are part of it, that what we do to nature will affect us as well and in order to survive we must live in harmony with the rest of nature. Many see this message as a direct challenge to many aspects of the way we live and work in Western society, claiming that many of our institutions and habits reflect assumptions that humans exist on a separate plane from nature, that we can manipulate "the environment" in whatever way we choose without fearing the consequences, that any problems we might encounter with our food supply, health, or climate can be solved by technological innovations, and other such ideas. Consequently, the work of ecologists is frequently invoked, not only in support of environmentalist reforms, but also to recommend a deep and massive "paradigm shift" reaching to the heart of our civilization and hopefully leading to a new era of peace and well-being.

Does it matter to scientists and mathematicians what conclusions other people will draw from our theories? Should we worry about such things, or should we put them aside in order to examine nature without bias?

The caricature of the scientist interested in nothing but pure, disembodied knowledge is surely only fiction. Everybody cares about the world in some way, and most of us have complex motivations and hopes for our work, whether it is to cure diseases or save species, or to bring more reason and understanding to the world. Since we do care what our work does to the world, it is only sensible to examine how that process works, in order to understand what we are doing and how to be effective.

Of course, the idea of examining nature without bias is by now thoroughly discredited. Philosophers of science, sociologists and psychologists have made it clear that all observations of the world are partially determined by theory, and that theories are deeply intertwined with values (Jasanoff et al. 1995; Lewontin 1993; Nader 1996). Donna Haraway has famously documented how the unseen biases of male primatologists influenced

their analysis of primates' social structures, and the changes that followed the entry of female scientists into the field (Haraway 1989). A look into the history of scientific racism or the study of sexual dimorphisms, for instance, is enough to make anyone wonder what mistakes we might still be making today.

The assumptions and values that practitioners bring to science do not only affect the quality of their descriptions of the world; they also have an impact on the world. Scientific racism, to choose an obvious and extreme example, played an indispensable role in legitimizing the widespread slaughter of American Indians, discriminatory U.S. immigration policies and anti-miscegenation laws, and the genocidal projects of the Nazi regime and the colonial powers of the 19th and early 20th centuries.

For a more relevant example to contemporary studies of ecology and evolution, consider the famous Tragedy of the Commons model. In Garrett Hardin's original presentation of the scenario (Hardin 1968), a number of herders must each decide whether to increase their grazing on a common pasture, which is a way to benefit at the expense of the community; but if too many herders increase grazing, the common pasture will be degraded and nobody will benefit. The conclusion suggested by this model is that commonly held resources are inevitably destroyed by overexploitation; Hardin argues from this conclusion that either heavy-handed control measures must be imposed to protect commonly held resources, such as pastures, fisheries, water reserves, and the atmosphere, or else they must be privatized to prevent environmental degradation.

Since the appearance of Hardin's paper, this logic has been applied to actual cattle herders around the world. Attributing environmental degradation and desertification to overgrazing and comparable failures of social coordination, policy makers introduced massive and radical programs of privatization and centralization of ownership and power. These interventions, including the conditions of World Bank loans, U. S. aid packages and International Monetary Fund structural adjustment policies, have had far-reaching effects on the societies targeted, including forcing farmers and nomads out of subsistence economies and

into wage labor, taking political and economic power away from women, and disrupting the social structures responsible for maintaining traditional, local ecological knowledge, and, in many cases, have failed to protect the natural resources in question from further devastation (Taylor 1998; International Forum on Globalization 2002).

With further research, it has become clear that natural resources can, in fact, be held in common and still protected from overexploitation by a great variety of means (Taylor 1998; Berkes et al. 1989; Ostrom 2001). Herders and other participants in many traditional economies have developed complex, sensitive ethnosciences of resource management (McCabe and Ellis 1987; Horowitz and Little 1987; Ostrom 2001). In a number of cases, ongoing successful management of communal resources has been disrupted by centralization of management or an influx of non-natives, either of which can create a tragedy of the commons–like scenario leading to overexploitation (Berkes et al. 1989).

It's not that the tragedy of the commons model is wrong. It describes a pattern of causation that corresponds pretty well with a number of situations in the real world, when the circumstances correspond reasonably well to the assumptions of the model: for instance, that at least a significant number of economic actors act as individuals, without communication and coordination with others in the system, and are in fact motivated by economic benefit, conceived in terms of personal material wealth, rather than social well-being, sustainability, or a web of mutual obligations with the rest of the natural world (as is the norm in many indigenous societies). When the appropriate conditions apply, the model can provide valuable insight into what is likely to happen and what to do about it; when they do not, applying the model anyway is unhelpful and possibly dangerous.

Ecologist and philosopher of science Peter Taylor has presented a critique of the tragedy of the commons model (Taylor 1998) that highlights these features of the model as well as others that make it often inappropriate, and some of the effects of its use. Application of the tragedy of the commons model to a real-world situation asserts not only that the humans involved act like individualistic, self-interested economic actors, but also that they

are more or less undifferentiated in terms of power and choices, that the choices are fixed, and that everything outside of the system composed of the commonly-held resource and the humans who use it can be considered extraneous. When the model's assumptions are called into question, a number of alternative approaches are exposed (this list is reproduced from Taylor 1998):

(i) Instead of viewing the system as composed of individuals the nature of whose interactions are given at the outset, the system's dynamics are allowed to be mutable.

(ii) By thinking about the networks of social support in which 'individuals' are raised and in which they then operate as adults, 'sociality', not individuality, is made primary. There can be no atomized individuals in the form Hardin presented. Networks of social support make communication—even through people's silence—unavoidable. The networks give power to sanctions, in the form of withdrawal of social links, and thus also strengthen the threat of such sanctions.

(iii) Any boundaries defining a system are seen as permeable.

(iv) Inequality among individuals within the system colours the paths that they can pursue, including their responses to developments 'outside' the system.

In the real world, inequality is always present, and is often a central cause of resource exploitation. Obscuring the presence of economic inequality also obscures the fact that privatization usually reinforces existing inequities, and can make it much easier for those with money and power to consolidate and amplify their power, which often accelerates exploitation and degradation of humans and natural resources. In Taylor's words, "negotiations and contestations among groups with different interests, wealth and power—the messy stuff of most politics—are kept out of the picture. The 'tragedy' thus naturalizes

the liberalized economics of structural adjustment and obscures the politics through which structural adjustment is imposed and implemented in poor, indebted countries."

The use of a model based on economic self-interest, and the claim that the model is a necessary simplification whose shortcomings can be addressed by progressively readmitting complications, that is, that the fundamental assumptions of the model need not be removed in order to construct a sufficiently accurate description of the real situation, reinforce the belief that humans do in fact behave selfishly. This obscures the importance of social embeddedness and cultural differences in behavior and values, and contributes to belief in the inevitability of the spread of Western social and economic structures to the rest of the world.

Taylor proposes that since heterogeneity, social embeddedness, and intersecting processes of social and ecological change on a range of spatial and temporal scales are central to most real-world resource management crises, they are better served by approaches that "view embeddedness as primary" and "examine diverse intersecting processes". To take these basic assumptions as a "null model", rather than the assumptions of the tragedy of the commons model, can help to expose the limitations of models and policies that violate them. Viewed with a critical eye, those models and policies can continue to be employed where appropriate.

1.2 Models and metaphors

Scientific theories and models assert not only their stated conclusions, but also a whole vocabulary of background assumptions about the nature of the world, and even about epistemology itself. Many models, the tragedy of the commons, for example, and other assertions of scientists, and their unstated implications, can take on a life of their own and enter the larger culture's repertoire of stories, finding themselves applied as metaphors in all kinds of situations where they do not apply literally.

According to exciting research by cognitive linguist George Lakoff and others (see Lakoff and Johnson 1980 and their subsequent work), human cognition does not operate like a disembodied process of reasoning based on logical categories and deduction. Instead, according to their analysis of linguistic evidence, even some of the most basic concepts we use, such as set membership and logical implication, are fundamentally metaphorical, and we use metaphorical reasoning to apply familiar mental frameworks to new situations.

Since science and the new technologies it spawns are perhaps the most important source of new metaphors in the modern world, the role science plays in shaping our basic mental frameworks for thinking about the world may be at least as important as its role in constructing literal explanations of how the world works and making new technological inventions possible.

Many people have written about the connections between the scientific tradition and the worldviews that characterize society since the Industrial Revolution. Some of the most important work has come from feminist scholarship. Susan Griffin's *Woman and Nature* (1978) and Carolyn Merchant's *The Death of Nature* (1989) trace historical and metaphorical connections between the development of scientific practices and descriptions of the natural world and patterns of oppressive treatment and characterization of women.

The metaphorical connection between science, nature, and women is notoriously visible in the writings of Francis Bacon, one of the most important founders of the scientific method and the modern research institute, who frequently referred to the natural world as a woman, calling her a "common harlot" and similar terms. Drawing inspiration from the inquisition of witches, which was ongoing at the time—Bacon himself served as attorney general for King James I, who imposed the death penalty for all practitioners of witchcraft, where previously it had been invoked only for killing by witchcraft—he advised pursuing the same techniques of violence, violation and torture to discover nature's secrets:

> For you have but to follow and as it were hound nature in her wanderings, and you will be able when you like to lead and drive her afterward to the same

> place again. Neither am I of opinion in this history of marvels that superstitious narratives of sorceries, witchcrafts, charms, dreams, divinations, and the like, where there is an assurance and clear evidence of the fact, should be altogether excluded. . . . howsoever the use and practice of such arts is to be condemned, yet from the speculation and consideration of them . . . a useful light may be gained, not only for a true judgment of the offenses of persons charged with such practices, but likewise for the further disclosing of the secrets of nature. Neither ought a man to make scruple of entering and penetrating into these holes and corners, when the inquisition of truth is his whole object—as your Majesty has shown in your own example.
>
> There is therefore much ground for hoping that there are still laid up in the womb of nature many secrets of excellent use having no affinity or parallelism with anything that is now known . . . only by the method which we are now treating can they be speedily and suddenly and simultaneously presented and anticipated.

Investigators should not think that the "inquisition of nature is in any part interdicted or forbidden": they are to "bind her to your service and make her your slave"; in this way, "nature betrays her secrets more fully . . . than when in enjoyment of her natural liberty" and thus "the human race can recover that right over nature which belongs to it by divine bequest". (Merchant 1989)

The rhetorical identification of nature and women is visible throughout the history of the Age of Exploration and into the twentieth century. It is by means of this formula, for instance, that Sir Walter Raleigh, European explorer of Guyana, could write of "a countrey that hath yet her mayden head, never sakt, turned, nor wrought" (Griffin 1978).

On closer examination, this metaphor is anything but an incidental poetic flourish. As Susan Griffin exposes more fully in a more recent work (Griffin 1995), it is part of a larger

system of dichotomies: man and woman, man and nature, white and black, nobility and commoners, God and man, heaven and earth, spirit and matter, mind and body, reason and emotion, the sacred and the profane. In each of these dichotomies not only a difference is implied, but also a hierarchy of value. When they are metaphorically linked together, as they often are, it is understood which poles of each pair are to be identified with each other, and it is understood which side of each is more highly valued. Men, white people, and rational thought are identified with God and enlightenment, while women, people of color, animals, and emotion are identified with imperfection, impurity, and danger.

While it is no longer supposed to be acceptable to express racist, sexist, and other bigoted ideas, this epistemology of separation and hierarchical dichotomies is very much alive in our culture, and encoded in our social structures. Physical labor is valued less than intellectual labor, and domestic labor performed by married women is not paid or counted in the Gross Domestic Product or other economic measures. People of color are portrayed in entertainment and news reports as physical, even violent, and women are portrayed as emotional rather than intellectual, or as collections of body parts whose subjectivity is not acknowledged, while white men are represented as intelligent, authoritative, and capable of acting on the world. When humans come into conflict with the natural world, the needs, desires or rights of plants and animals are rarely taken into consideration, and essentially never given equal weight.

When a man assigns to himself the realms of reason, action, and the public life, and consigns the realms of emotion, nurturance and basic sustenance of the physical body to women or hired workers, he can achieve for himself a kind of luxury, or a feeling of cleanliness, of being insulated from the grimy, repetitive details of daily life. That comfortable life comes too often at the expense of others who are denied the power to pursue intellectual and public lives, having instead to do domestic work for both themselves and others. But the man himself also loses something, in Griffin's words "an understanding that can only develop from an emotional confrontation with the requirements of survival", from "a daily

immersion in a world of need and dependency, reciprocity, and natural exigencies". He can become cut off from his own inner life, unable to experience the intimacy of physical and emotional interdependence, perhaps even unable to participate in relationships based on affection rather than power.

In a similar way, when a society, like ours, seeks to achieve as nearly as possible the ideals of cleanliness, order, rationality, and freedom from need, while distancing ourselves from the people who do the messy, physical work that sustains our society, and the animals, plants, and ecological communities that ultimately provide our sustenance, our feelings of success come at a cost. Not only are millions of people around the world trapped in lives of deprivation, forced to work hard and do without to provide luxury and comfort for others far away, but that luxury and comfort come to take on a hollow feeling, as people feel no sense of meaning in their lives, no feeling of connection or community, and depression and violence are endemic. At the same time, the consequences of our inattention to our impact on the natural world threaten to undermine that comfort and perhaps even our survival. And in our attempts to understand how to address these crises, just as in our intimate relationships, to the extent that we look at the world through the lenses of separation, hierarchy, and domination, we can fail to perceive the very patterns that we need to expose and transform.

In George Lakoff's recent study of the U.S. political landscape (Lakoff 1996), the resonance between family and society is of central importance. Lakoff outlines two dominant conceptual systems of morality that Americans use to talk about politics. Of course there is a great deal of variation, and nobody fits either description perfectly, but the claim is that these are the centers of two major clusters of variation, which include most of the mainstream discussion of American politics. Both of these conceptual systems are metaphorical models based on images of the family. The "Strict Father" model places the father at the head of the family, responsible for supporting and protecting the family and setting family policy. The world is a dangerous, difficult place, and the father must teach the children self-discipline by exercising authority and enforcing discipline through punishment.

Competition among family members is not only necessary but good, because it teaches self-discipline and self-reliance.

The "Nurturant Parent" model, on the other hand, centers on mutual caring and being cared for. Parents help children develop by supporting, protecting, providing for and caring for them. Open, respectful two-way communication is crucial. As children mature, they enter into a balanced, mutually supportive and respectful relationship with their parents. They learn to care for themselves and others responsibly. According to Lakoff, these family images, standing metaphorically for the country and the world, provide the organizational structure for the belief systems of, naturally, conservatives and liberals, respectively.

I include Lakoff's model not to argue that ecology is politically liberal (I would rather not use such a simplistic binary opposition!), but to illustrate how a number of different metaphorical habits can cluster together to form a regular worldview: dichotomy and hierarchy often tend to bring control, domination, individualism, and a pessimistic, competitive view of interactions along with them, in various combinations. Here is an example from the early literature of sociobiology:

> The evolution of society fits the Darwinian paradigm in its most individualistic form. Nothing in it cries out to be otherwise explained. The economy of nature is competitive from beginning to end. Understand that economy, and how it works, and the underlying reasons for social phenomena are manifest. They are the means by which one organism gains some advantage to the detriment of another. No hint of genuine charity ameliorates our vision of society, once sentimentalism has been laid aside. What passes for cooperation turns out to be a mixture of opportunism and exploitation. (Ghiselin 1974) (from Hull 1988)

Lakoff's model also points to an alternative world view in which interconnection, equality, mutual aid, and respect for diversity are central, and suggests that these ideas may also tend to arise together in regular ways.

Any number of cultural critics connect the history of technological domination, environmental crisis, alienation, and oppression with “the scientific worldview”, “linear thinking”, “the Cartesian paradigm”, “the dominator paradigm”; consistently, ecology is explicitly named as the source of an alternative worldview, since it challenges the separation between actor and acted-upon, declaring that acts of domination will rebound upon the dominator, and that “we are all interconnected”. In a way, this is a very strange proposal, that the undoing of science and technology should come from within science. Of course, these ideas are nothing new; they are central to most indigenous cultures, to some Eastern religions, and, by some accounts, held especially often by women even within our own culture; but when they come from science, they carry more authority for many people.

1.3 Trees and rhizomes

According to the massively influential historian Michel Foucault, the late twentieth century has been marked by an “insurrection of subjugated knowledges”. In Foucault’s trademark style, this refers to at least two things at once: to “the historical contents that have been buried and disguised in a functionalist coherence or formal systemization”, but also to “a whole set of knowledges . . . located low down on the hierarchy, beneath the required level of cognition or scientificity.” “It is through the re-appearance of this knowledge,” he writes, “of these local popular knowledges, these disqualified knowledges, that criticism performs its work.” Both the hierarchy of knowledge, in which expertise belongs to experts and not to workers, colonized people, mental patients, and the other participants in this insurrection, and the systems of expert knowledge themselves, many of which are themselves hierarchical, such as the Freudian theory of id, ego, and superego, or the racist theories of colonialism, are being subverted by the emergence of other systems of knowledge which undermine the separation between observer and observed, between theorist and system. These forms of knowledge come at the “global, totalitarian theories” from a multiplicity of

directions, calling into question even the existence of a single, unitary system of knowledge that can explain all aspects of the world in the same terms. (Foucault 1980)

In the same passage, speaking of "a period characterized by what one might term the efficacy of dispersed and discontinuous offensives", Foucault names as an example the work of philosopher Gilles Deleuze and psychoanalyst Félix Guattari. Deleuze and Guattari's *A Thousand Plateaus* (1987) takes on this subject by highlighting the image of the rooted tree, which is the image behind all hierarchies: Linnaeus's scheme of classification, the evolutionary tree of descent, Chomsky's generative grammar, and hierarchical social structures from the patriarchal family to the Church, the military, the presidency, and business administration. The tree always converges on a single center point: the taproot, the point of origin or center of command. As an alternative image through which to approach the world, Deleuze and Guattari recommend the *rhizome*, which is an underground network with no center, which sprouts upward in many places and spreads outward into new territories. The rhizome is characterized by "principles of connection and heterogeneity", by multiplicities, parallelisms and alternatives. "There are no points or positions in a rhizome . . . there are only lines . . . "

The rhizome is one of a family of metaphorical structures and processes with no central point of control or origin. The unifying metaphor is the network. Structures like neural networks, computer networks and social networks all provide rich vocabularies of associated concepts and patterns of behavior. A particularly interesting network, similar in many ways to the plant rhizome, is the underground mat of fungal hyphae, the densely interwoven threads that produce mushrooms and toadstools springing up out of the ground in many places at once when the conditions are right, that cooperate with plants to gather nourishment from the soil, air and sunlight, and that may form a connected network delivering nutrients and even information of some kind across the distances between plants and trees (Offwell Woodland and Wildlife Trust 2001). While plant rhizomes do not connect up with themselves in loops, many of these other structures do, forming intricate feedback loops

and higher-level aggregate structures.

In many ways it seems that these conceptual shifts described by Foucault and Deleuze and Guattari are in fact underway in our culture, and have been happening for some time, though in fragmented and ambiguous ways. Images of networks are becoming a great deal more prominent throughout the sciences, driven partly by the availability of the Internet as a fresh metaphor, to take the place of older images such as clockwork machines, factories and so on, and partly by the availability of powerful computers capable of doing the computational work necessary to study complex network-structured models. All up and down the partly nesting levels of organization, network structures can be seen as fundamental, from the recursive cycles of interaction through which elementary particles define each other, to the intricate patterns of genomics that make cell biology impossible to reduce to genetics, to, of course, ecological interconnections, to the snarled socioeconomic webs of human communities and the global economy (Capra 2002). Even the evolutionary tree of life looks less and less like a tree and more and more like a tangled web, as it becomes clear how much different species exchange genetic material, especially among single-celled organisms (Doolittle 1999).

Corporations are going through a major shift (this was big news in the 1980s, and is by now practically taken for granted), trying to learn how to reorganize as complex networks, with diversity, flexibility, and local knowledge, while still somehow maintaining control, dominating their markets, and collecting the profits. However, the decentralization of corporate power is paradoxically coinciding with possibly the greatest concentration of power in history, as a very small and shrinking number of corporations and individuals control a massive and growing proportion of the world's wealth, and increasingly have the power to force even entire nations to do their bidding. "Swarm intelligence" is helping the U.S. military to "project its presence" across the globe, cementing its position as the sole dominant superpower. The rise of genomics has not stopped biologists from scrambling to create new genetically engineered organisms that contribute to transferring power from

small farmers and traditional communities to a very small number of very large agricultural and pharmaceutical corporations, and bringing the design and production of nature itself under the centralized, self-interested control of these huge businesses. Undermining conceptual hierarchies does not always mean undermining the hierarchies of power.

1.4 Natural selection as rhizome

Darwin's development of the theory of evolution by means of natural selection was inspired not only by Malthus, as is commonly known, but also by Adam Smith's theory of the invisible hand of economic optimization, and the metaphorical resonance between evolution in the natural world and sources of order, complexity, and change in other spheres has never been absent (Schweber 1977; Lewontin 1993). In the century and a half since its introduction, Darwin's new mode of explanation has proven well adapted to migrate to other fields including the social sciences, chemistry and physics. Evolution by means of selection has been invoked as a literal cause of progressive change in prebiotic chemical ecosystems (Schuster 1986; Kauffman 1993), mammalian immune systems (Hull, Langman, and Glenn 2001), animal learning (Glenn 1991; Glenn, Ellis, and Greenspoon 1992; Hull, Langman, and Glenn 2001; Rand, Wilson, and McGlade 1994), cultural patterns of behavior (Dawkins 1976; Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985), human thought (Bateson 1972; Gabora 1998), human languages (Nowak and Krakauer 1999; Nowak, Plotkin, and Jansen 2000), patterns of economic exchange (Anderson, Arrow, and Pines 1988; Dercole 2002), lineages of scientific theories (Hull 1978[1], Hull 1988), technological innovation (Ziman 2000), and even the creation of multiple universes by descent with modification (Smolin 1997).

Even within biology, selection has gradually come detached from its original role as

[1]Featuring the lovely line, "Certain aspects of co-operative behaviour among scientists may be as explicable in terms of reciprocal altruism as is mutual regurgitation among African dogs."

a force operating only on variation among individual organisms, and it is now widely accepted by biologists that selection can operate directly on groups of organisms and on species within a clade, as well as on separate genes. Currently, evolutionists are engaged in a lively debate, not over whether selection acts on levels other than the organismic, but over whether gene selection encompasses all other levels of selection (Williams 1966; Dawkins 1976), or whether selection must be considered on a whole hierarchy of levels at once (Lewontin 1970; Gould 2002). Selection may act very differently on different levels, as for instance, adaptation caused by Darwinian natural selection on organisms produces directional changes in the character of a species, which can be passed on directly to daughter species, producing a form of Lamarckian inheritance on the species level (Gould 2002).

Traditional Darwinian natural selection itself operates differently on different kinds of organisms; on one view, clonal and asexual organisms have no recombination and no need for reproductive isolation to delineate the boundaries of species (and so do not undergo species selection in the sense that sexual organisms do; rather, clone selection is the corresponding process (Gould and Eldredge 1977)—this process will come into play in chapter 5, below), while at the same time, according to recent evidence (Doolittle 1999), many single-celled organisms exchange genetic material with unrelated organisms at such a high rate that the traditional concept of a branching tree of descent may not be appropriate at all, a difference which must certainly have a serious impact on the patterns of evolutionary change that predominate among such organisms. (In addition to being capable of directed variation, cultural evolution is thick with lateral transfer and probably has more in common with unicellular evolution than with systems in which lineages remain distinct.)

Many multicellular organisms, ourselves included, are in fact associations of a number of different kinds of organisms, and natural selection has been shown in lab experiments to be capable of operating on entire ecosystems at once (Goodnight and Stevens 1997; Swenson, Arendt, and Wilson 2000; Swenson, Wilson, and Elias 2000), a phenomenon which may conceivably operate in nature as well; this suggests another form of selection

which may be operating on the organisms that make up such a superorganismal assemblage, as well as any other organisms participating in a community that reproduces and perishes as a unit often enough to be subject to selection as an individual. In species that engage in social behavior and cultural transmission as well, many different kinds of selection may be operating at the same time in the same place, on different kinds of individuals, some of which are parts or collections of others.

In addition to the many different forms of selection that appear to be in operation in the natural world, evolution by means of natural selection is now being used by scientists and engineers to create optimized solutions to various technological problems, in techniques such as genetic algorithms (Holland 1975) and evolutionary programming (Koza 1994).

Referring to biological selection, many evolutionists have come to speak of a "hierarchical" view of evolution, including processes from gene-level to clade-level selection. However, conceptual and other selection processes do not fit so neatly into this nesting pattern. The overlaps, similarities and differences are surely complex and diverse. Considering selection as a large class of related but not identical processes driving the creation and development of multiple kinds of reproducing individuals, we face the possibility of not one but many theories of evolution, accounting for both the differences between the different kinds of evolutionary processes that exist and the common patterns that connect them, using our developing understanding of each particular evolutionary process to inform the others.

1.5 A web of models

Stories of scientific advance that depict a progressive lineage of new theories refining or supplanting older ones in each discipline do not do justice to the process of creating and developing models. Like most real processes, it is a lot more messy and disdainful of boundaries. Mathematical models do not simply offer maps of real processes, they actually

construct fictional alternate worlds and propose that the processes observed there operate in the real world as well. Mathematical biologist Richard Levins, some time ago, introduced the idea of a *robust proposition*, which is one that is supported by a range of models with different presuppositions, suggesting that it may hold in a range of real situations as well (Levins 1966). A number of different breeds of models, equally useful in different ways, make different tradeoffs between "generality, realism, and precision", so that some attempt to describe particular specific systems accurately, while others attempt to isolate simple, theoretically useful patterns by idealizing the systems being modeled, and others, idealized to make them more mathematically tractable, are used for exploration in search of understanding and new hypotheses.

In this picture, different models apply, to varying degrees, to different ranges of real systems. Where models agree, there may be a robust pattern. Where they disagree, there is a tension over which models best describe which real systems. Add to this picture the perception that some models have relevance to multiple systems of different kinds—biological, technological, and conceptual adaptation, for instance—and the world of models comes to look like an interconnected, heterogeneous patchwork of different modeling projects, conversing and negotiating with each other where their ranges overlap.

Levins' picture presents an alternative to the reductionist "unity of science program": system- and network-oriented modeling, like Deleuze and Guattari's analysis, can go after patterns that recur in systems made up of different kinds of things. Instead of chemistry "reducing" to physics, biology to chemistry, and so forth, biologists can be as informed by anthropology, literary theory, or psychoanalysis as by physics and chemistry. In this way we can develop an understanding of patterns that cut across the reductionist hierarchy of sciences, just as bacterial gene swapping and retroviruses cut across the tree of life. Physics is not "more basic" than anything else, science is not a hierarchy but a conversation that goes all directions at once, spilling over into other disciplines, with no clear distinction between science, art, and humanities, and certainly no dominance relationship.

1.6 Ecology and other rhizomes

In the same way that we can come to see Darwinian natural selection as one of a class of selective processes which provide opportunities for theoretical cross-fertilization, we can also consider selection in relation to other classes of processes that produce adaptive change, and look for opportunities to contrast and connect these different processes. For instance, students of the evolution of multicellular organisms have concluded that in order to persist, these groupings of cells are forced to evolve regulatory mechanisms to enforce 'altruism' by preventing individual cells from doing 'selfish' things that endanger the collectivity (Buss 1987). The same conflict is identified in social insect colonies, where cooperation is believed to be maintained by kin selection, a very different process than the germline segregation and Darwinian selection that maintains 'order' in organisms. In what way do these findings relate to the question of how human social institutions maintain their own integrity, whether by policing their members or through other means? Is there a sense in which these processes are not merely analogous, and are in fact literally instances of the same causal process, as different kinds of selection are? Is this possible even if the ontogeny of social institutions occurs by a process other than selection? What are the connections and distinctions between selection-driven evolution and other processes of adaptive change, such as self-organization, institutional learning, individual learning, the coalescence of cosmological structure, and so on?

Sociologist Hilary Rose (2000) presents an elegant defense of social explanations for individual behavior that cannot be reduced to qualities of individuals, and so cannot be explained by the action of selection on individual humans. In response to the claims of evolutionary psychologists John Tooby and Leda Cosmides (1992), who propose to "unify" the sciences under biological reductionism, she writes, focusing on the classic sociological work of Emile Durkheim (1897),

> Of a piece with the new experimental biology, defending its autonomy and

> irreducibility to chemistry and physics, Durkheim defended the autonomy of the social as a legitimate level of analysis irreducible to individual psychology. This argument is most elegantly shown in his classic study *Suicide*. He takes this phenomenon, which seems above all to be about private agony and individual psychology, to demonstrate the autonomy of the social. Using pioneering statistical techniques . . . he showed that personal agony and suicidal outcome were causally linked to religious values which bind or fail to bind the individual to the group and thence to life. Durkheim's theory thus explains both why Protestants kill themselves and why Catholics in the selfsame agony do not.

Some applications of evolutionary theory to outside domains such as philosophy of science and free market economics seem convincing and useful. This does not imply, however, that selection is the sole cause of adaptive change in these systems. For instance, progress in scientific knowledge does not come only from variation and selection among published ideas, it is also dependent on individual scientists developing a deep understanding of their study systems. While this process may ultimately be reducible to a form of selection among hypotheses within the mind, I see no reason to assume so. The process of observing a system's behavior and constructing a mental model of its function may be basically different from the trial and error process of reproduction with variation described by selection models.

Non-selective adaptive change is important both in biology and out, and is a rich source of analogy among non-selective processes as well as between selective and non-selective processes. Consider Hegel's classic depiction of conceptual development as a growing plant:

> The bud disappears in the bursting-forth of the blossom, and one might say that the former is refuted by the latter; similarly, when the fruit appears, the blossom is shown up in its turn as a false manifestation of the plant, and the fruit now

> emerges as the truth of it instead. These forms are not just distinguished from one another, they also supplant one another as mutually incompatible. Yet at the same time their fluid nature makes them moments of an organic unity in which they not only do not conflict, but in which each is as necessary as the other; and this mutual necessity alone constitutes the life of the whole. (Hegel 1931) (from Bookchin 1982)

An important question raised by the discussion of fruitful analogies between processes of change is whether the flow of ideas from biology to the study of other systems can be reversed. For instance, philosopher of biology David Hull has proposed to his colleagues that they should make in-depth use of the work of evolutionary biologists, not only as a study system, but as a source of theory for understanding the evolution of lineages of scientific theories. He has also put this proposal into action, producing intriguing and fruitful theories about the constraints and forces operating within scientific communities, derived from the careful application of evolutionary theory to those systems (for instance, Hull 1988; see also Ruse 1989). Meanwhile, many other philosophers, historians, and sociologists of science are at work producing very different accounts of how science works, drawing from long and rich traditions, not derived from biology, of analysis of the tensions between individual and community needs, constraint and creativity, creation and destruction, and so on. Hegel's famous comparison, of course, fits into a much larger tradition of analysis of historical processes and conceptual unfolding. If social and cultural adaptive systems are in some ways like biological systems, in what ways are biological systems like social and cultural systems? What understanding might we gain by attempting to understand natural systems in the ways that others understand human systems? If processes of adaptation caused by the action of selection on heritable variation sometimes produce the same results as other processes of adaptation, what can we learn about selection from these other processes?

Social phenomena, as well, are in some cases available to explanation by selection acting on groups or on some other scale of associations of humans, but they must often have

other explanations, such as selection among social structures independent of the life and death of humans, natural self-organization processes, influence by cultural change of the kind described by Hegel and many since, or simply being the only viable option available to humans in a particular time and place. As sociality is apparently common among animals, bacteria, algae, and perhaps even trees (Baldwin and Schultz 1983), it makes sense to entertain the possibility that many of these social structures may have non-selective explanations, and where appropriate, to look to sociology and anthropology for sources of possible explanation of these phenomena.

Evolution due to selection happens in many different kinds of systems. Devised to explain patterns of variation among plants and animals, it has escaped from its domain of origin and become a rhizome that cuts across the hierarchy of knowledge. The work of ecologists, also, may have the potential to flourish in environments other than biology.

Models from mathematical ecology, including the Lotka-Volterra equations, have been carried over to economics (Saviotti and Mani 1995; Solomon 1997; Farmer 1998), and epidemiology has always been closely allied with ecological modeling. Ideas from ecology have dispersed more widely: computer scientists speak of “information ecologies”; Gregory Bateson’s central work on cybernetic epistemology, though it deals mostly with evolutionary ideas, is nonetheless titled *Steps to an Ecology of Mind* (1972). The very title of Vandana Shiva’s *Monocultures of the Mind* (1993) is an eloquent argument against the globalization of Western culture and technological practices.

Since scientists do not work in isolation, passively observing nature and dispassionately summarizing their observations, but rather “mobilize heterogeneous resources”, including nature, technological artifacts, existing theories, workers and students, other scientists, journals and so forth, to construct, strengthen, and champion their theories, sociologists of science are now trying to look at the processes of science in terms of networks and “clusters of processes, subjects, objects, meanings and commitments” including all of the above, that produce and inform “situated knowledges” (Haraway 1998; Taylor 1997), and speaking of

"ecologies of knowledge" (Rosenberg 1988; Star 1995). Given the mileage Hull has been able to cover developing a theory of conceptual inclusive fitness, cladistics, and such things for the evolutionary development of scientific theories, what can we say about the ecology of science? Do scientists need to occupy different niches? Do research programs? Do they compete for resources? If so, do they also modify their social environment in a way that changes the outcome of the competition? Does diversity strengthen science? What about systems of knowledge other than science?

Ecologists, of course, are the experts on ecology, and should be more qualified than most to speak about these things. Ecologists also, whether by choice or not, are central to these projects that are happening outside of biology: ecologists create the images that people use to make these things happen.

1.7 Ecologists beyond biology

Darwinism arose contemporaneously with the free-market economics of industrial capitalism, and the two theories have a great deal in common, especially in their popular forms. Darwin's theory focuses on the effects of differences in individuals' fitnesses in a given environment, and minimizes the effects of individuals on their environment and on each others' fitnesses; Adam Smith's theory does essentially the identical thing, considering individuals' "utility" in an economic environment. Individuals are considered separately, and what happens in the system is deduced from the behavior and fate of all the separate individuals. Organisms, and economic actors, adapt to their environment; they do not adapt the environment to themselves, or destroy their own enterprises by ruining the earth and going extinct. Nor do they get together and work out how to avoid ruining their environment. (Lewontin 1993)

Ideas of competition, and struggle, and fierce battle, commute freely between these domains, and in both settings fit easily into a by now well-known story about survival in

the world. The prevailing conditions are given, and everyone must adapt as best they can—"you can't fight city hall" (Lewontin 1993). Everyone is out for themselves; get what you can while you can. In economic discourses, we end up not only viewing the world as made up of interchangeable utility-seeking individuals, but also making the world conform to the model by replacing traditions and informal institutions with business interactions; we are led directly to Prime Minister Margaret Thatcher declaring that "there is no society, only individuals and their families" while taking away welfare benefits for poor people. In evolution we hear almost exactly the same line in explanations of social behavior—it's all a side effect of individuals maximizing the fitness of their genes and those of their family members.

Certainly not everyone in these fields takes these extreme positions, and that is partly my point. These extensions of the theoretical models of evolution and economics are not dictated by the observations of naturalists and experimental economists (quite the contrary). They are a natural outgrowth of the Enlightenment philosophy of Voltaire, Locke, Laplace and their spiritual kin, who placed their faith in freedom, democracy and open exchange of ideas, looking forward to a great future in which man rules over nature by reason and tyranny is no more.

The failings of this ideology are becoming harder and harder to miss. Freedom and democracy are noble ideals, yet in the context of the culture of separation, hierarchy, and domination whose roots go much deeper, they have not been enough to prevent the paradoxes we encounter today: democracy subverted by the power of huge media monopolies, and the rhetoric of the free market used as a weapon by massive corporations to protect access to other countries' markets and stop them from making policy decisions autonomously. Most obviously, this faith in the power of reason, science, and technology, whether manifested in the putative free-market capitalism of Western societies or in the putative socialism of modern Eastern societies, has not stopped them from devastating the biosphere and

communities of innocent people all over the planet. These grand plans miss the embeddedness of humans in nature and the impossibility of making nature and communities of human beings embedded in their local ecologies conform to engineers' blueprints.

As time passes, we all seem to be more and more at the mercy of a few powerful people with fantasies of separation and control. Military planners appear to think that they can vanquish their enemies, and that they can set off atomic bomb tests and dust Iraq with depleted uranium powder without poisoning their own descendants; technocrats construct nuclear power plants without knowing where the radioactive waste will go; corporate executives pump communities full of useless, destructive products and the patterns of passive, alienated consumption that go with them, apparently imagining that they can do this without impoverishing their own lives; and biologists compete to cobble together strange new organisms for profit, with or without nightmares of what will happen if the world's ecological integrity is finally stretched beyond its limits as the transplanted genes escape from their makers' control.

I don't believe that the ideology of separation, control, and domination is inherent in the process of natural selection, or in the patterns of economic self-organization; it comes in in how the theories are constructed and used. Exploratory and idealized models are especially vulnerable to unconscious biases, because they often simply codify the modelers' preconceptions and are not subject to rigorous testing against observations.

Building on Levins' theory of model building as a heterogeneous process, Taylor (2000) identifies a number of "sites of sociality" where the model building process is not governed by the study system, and decisions must be negotiated by modelers on a social level. These sites include what idealized assumptions are considered reasonable; what level of correspondence with observations is considered sufficient confirmation for a model, and in what sense a model is considered to be "confirmed", whether as a conceptual pattern or a concrete prediction; what "degrees of freedom" are considered in constructing competing variant models—as ecologists commonly test their conclusions against the addition of spatial

heterogeneity, genetic heterogeneity, age structure and so on, whereas, for instance, models that assume that behavior is governed by economic or reproductive self-interest are rarely challenged on that basis; and what empirical observations are considered relevant, and how they are obtained, whether more passively or by actively constructing artificial conditions in which observations are taken.

Much of the modeling process consists of engaging with existing modeling projects on these levels and others. This process is heavily informed by all of our personal identities, social positions and non-rational beliefs, and it has a great impact on the social process of constructing the world, how we consider it to operate, the range of options visible to us, and how we act on it.

Ecologists, just by being ecologists, in a sense embody a way of perceiving the world and engaging with it that has the potential of growing into a source of hope for the future. We are in a unique position to challenge claims and patterns of living that go against our knowledge, and to construct alternative forms of knowledge.

In order to escape or mitigate the ecological and social disasters that seem more and more inevitable each year, we need more than clarity about the problems we face and the will to take them on. We need to work a transformation in the ways we relate to nature and to each other. More than that, we need to understand better how transformations happen and what kind of transformations result from what kinds of interventions. Ecologists, who study interactions, relationships, and transformations, are part of this crucial project. The more clearly we free ourselves from the narrow prejudices of individualism, competition, and separation, and think of ourselves as addressing problems that go beyond biology, and accept these challenges that occupy the realms beyond biology, the more effective we will be as citizens.

At the same time, the more we open our minds to multiple possibilities and free ourselves from outmoded stereotypes of economic competition and class division, the more ways we have to understand the systems we model while they still exist. Nature is not a

Dickens novel, and it is not a clockwork automaton (on whether it is a common harlot, I have no comment). If we look for alternative stories we will find them.

1.8 Introduction to the dissertation

The projects that I present in this dissertation are mathematical explorations of the patterns that emerge in simple models, and how that emergence happens. But of course there is more to it than that: they are connected to the larger process of science, by responding to the current state of theory and modeling practices and proposing new ideas and techniques. Chapter 3 introduces a framework for understanding adaptive dynamics models in terms of a tension between selection and constraints, and chapter 4 puts this framework to work to explore the behavior of adaptive dynamics models with multiple-dimensional phenotype variables. Chapters 5, 6 and 7 explore the effects of modifying the adaptive dynamics framework by changing the assumptions about mutation, and reveal a different kind of continuous diversification process than has been seen in unmodified models. Chapter 8 proposes a possible mechanism for an observed pattern of chemical concentrations in seawater, and chapter 9 looks at connections between natural selection and global ecological regulation and how the two might be compatible. Several of these chapters present new mathematical results that go beyond the particular modeling projects, especially the results on evolution on constraint surfaces (chapter 3) and the replacement and coexistence theorems presented in chapter 5. These results should be useful to modelers working on other problems.

Some of these models, particularly those of the central chapters, can also be read as critical responses to other models, even “interventions”, in Taylor’s terminology. The ecological models of chapters 4–6 participate in a current debate about the importance of mutualistic interactions in ecology, offering results that suggest that mutualism can be very common when biophysical constraints do not prevent it, and highlighting the possibility

that interactions can change from one type to another, for instance from competition to mutualism. In the analysis of chapter 5, mathematical results come out that suggest further that, in a sense, selection "wants" to reduce competition and increase cooperation, even when available genetic variation and tradeoffs do not allow it to actually do so. Chapter 7 transplants the conversion from antagonistic to mutualistic interactions into the standard game theory framework for evolution of cooperation, calling into question the assumption that cooperation is always vulnerable to exploitation and must be continually enforced.

Chapter 5 also presents a challenge to the conclusions of adaptive dynamics models that assume their ecological equations are continuous functions of continuously varying phenotype variables. When this assumption is relaxed, evolutionary motion is not smooth, and evolutionary branching does not happen at isolated singular points of the dynamics; branching can happen at any time, and may be an important part of the dynamics of evolutionary change at all points of the interacting populations' evolutionary trajectories. The smoothness assumptions make modeling much more tractable, but may paint the wrong picture about how evolutionary branching happens.

In a way, the models of chapters 5–7 can be seen as an instance of number (i) of Taylor's four points of intervention, or perhaps of number (ii). The interactions between individuals are made mutable rather than fixed (which is true in almost any evolutionary ecology model, but not in most game theory, in the sense that it is in chapter 7), and the network of relationships is made primary, rather than the characteristics of individuals in isolation. It is interesting how the changes in the models cluster together: how focusing on interactions rather than individuals produces a model in which the linear flow of evolutionary change is disrupted and cooperation is much more central than in most such models. These models were not constructed with these outcomes in mind (except the game theory one, which I made after I had a pretty good idea what would happen).

Turning finally to global patterns of ecological organization, in chapter 8 I present a simple model demonstrating how microorganisms in the ocean may control the chemical

balance of the ocean to suit their own biological needs. Then in chapter 9, in a more abstract model for biological control of geological processes, in particular the planetary temperature, I look at how ecological community structure can produce stable climate control or fail to control the climate, and how evolution affects these feedback systems. After looking at how natural selection, on a slow timescale, operates on the results of ecological dynamics, on a fast timescale, and observing the process that the slow dynamics of evolution goes through in this model, I am led to propose that on an even slower timescale, the process that is emergent from the dynamics of natural selection is not itself a member of the class of selection processes (or ecology-like processes), but is more closely related to learning processes—a case in which models from outside the natural sciences may be most appropriate to describe this biological process.

Chapter 2

Lotka-Volterra Dynamics

This chapter reviews published results about the behavior of Lotka-Volterra models. Relationships between these results and the invasion function, which is very important in adaptive dynamics, are explored, and specific results about invasion, extinction, and boundedness which are important to the analysis of adaptive dynamics in Lotka-Volterra systems are summarized.

2.0 Notation

Throughout this document, all points and vectors in $\mathbb{R}^n$ are column vectors. I will occasionally make vector comparisons, which are taken componentwise; for instance, $\mathbf{x} < \mathbf{y}$ means that $x_i < y_i$ for each i. A vector $\mathbf{x}$ is called positive when $\mathbf{0} < \mathbf{x}$.

When functions of vector variables come into play, I will at times make use of Jacobian matrices of partial derivatives, using the notation $\frac{\partial \mathbf{u}}{\partial \mathbf{v}}$ for the n-by-m matrix of partial derivatives of $\mathbf{u} : \mathbb{R}^m \to \mathbb{R}^n$ whose (i, j) entry is $\frac{\partial u_i}{\partial v_j}$. This notation makes it convenient to apply the chain rule for differentiation, as $\frac{\partial}{\partial \mathbf{w}}\mathbf{u}(\mathbf{v}(\mathbf{w}))$ expands out to $\frac{\partial \mathbf{u}}{\partial \mathbf{v}}\frac{\partial \mathbf{v}}{\partial \mathbf{w}}$. I will also use the notation $\partial_p f$ for the partial derivative of f with respect to its p'th argument (and $\partial_{pq} f$ for $\partial_q \partial_p f$, and so forth).[1]

The invasion function $\mathscr{I}(\mathbf{s}|\mathbf{s}_1, \ldots, \mathbf{s}_n)$ (represented by a script letter I), denoting the long-term growth rate of a rare type $\mathbf{s}$ in a community defined by resident types $\mathbf{s}_1$ through $\mathbf{s}_n$, is a function of $n+1$ variables, but can also be considered a function of one variable $\mathscr{I}(\mathbf{s})$ when the residents are held fixed. I will use these two versions of $\mathscr{I}$ interchangeably. Thus, for instance, $\partial_1 \mathscr{I}(\mathbf{s}_i)$ stands for $\frac{\partial}{\partial \mathbf{s}}\mathscr{I}(\mathbf{s}|\mathbf{s}_1, \ldots, \mathbf{s}_n)$ evaluated at $\mathbf{s} = \mathbf{s}_i$. When more complicated partial derivatives are being taken, I will be as explicit as necessary. Also, when strains can be identified in several ways, as in the case of the two phenotype variables $\mathbf{s}_i$ and $\mathbf{u}_i$ (section 3.6), $\mathscr{I}$ can be written as a function of any number of things that identify the strains in question, and I will be fairly casual about this.

In chapter 5 I use the notation $\mathbf{a}_{\cdot j}$ for the j'th column of the matrix $\mathbf{a}$, $\mathbf{a}_{i\cdot}$ for its i'th row, and $\mathbf{a}_{(i)}$ for the i'th row of $\mathbf{a}$ transposed into a column vector. Throughout this document, I will use n for the number of resident types and m for the length of the phenotype vectors

[1] Strictly speaking, the partial derivative is a linear operator on vectors rather than a vector quantity, that is, a contravariant rather than covariant tensor. The vector transpose operation that appears in the vector adaptive dynamics equations (as in equation 3.5) is more properly a tensor index-raising operation. In this treatment, I do not use objects with more than two indices, and more or less treat column indices as contravariant indices and row indices as covariant indices (see Abraham, Marsden, and Ratiu 1983 for a great deal of discussion of such things), and I will sometimes refer to the first partial derivative of $\mathscr{I}$ and the selection gradient (which is its transpose) interchangeably.

$\mathbf{s}_i$. Σ is the space of values phenotype vectors $\mathbf{s}_i$ are allowed to take on. Flagrant abuses of notation involving indices will occur in chapter 5; I ask forgiveness and I trust the meaning will be clear in context.

2.1 The Lotka-Volterra equations

The central chapters of this document study ecological dynamics using the classical generalized Lotka-Volterra equations for interacting populations (Scudo and Ziegler 1978). Mathematical ecologists have used Lotka-Volterra models for generations to study the behavior of networks of interacting populations because the simplicity of the equations—so similar in appearance to the systems of linear differential equations that are so important to understanding nonlinear dynamics—and complex richness of behavior they encode appear to promise an entry into understanding the emergence of ecosystem properties from individual interactions.

A model of this type involves n dynamic variables $X_1, X_2, \ldots, X_n$, which describe the size of n populations as they change through time. Individuals of populations i and j encounter each other at a rate proportional to the size of each population. These encounters have a positive or negative effect on population i described by the sign and magnitude of their *interaction term* a_{ij}, and an effect on population j described by the corresponding term a_{ji}. If a_{ij} is negative, encounters with j are detrimental to i, while if it is positive, these encounters are beneficial to i. When both a_{ji} and a_{ij} are negative, these populations are said to have a *competitive* interaction; when both are positive, it is a *mutualistic* interaction, and a pair with mixed signs is a *victim-exploiter* interaction, which may represent a predator-prey, host-parasite or similar relationship. Relationships with at least one negative term in the pair are *antagonistic*. Self-interactions a_{ii} are usually required to be competitive, representing an overcrowding or other negative density dependence effect which helps to prevent populations from growing without bound. In the absence of interactions, each population grows or declines at an intrinsic rate r_i.

The ecological community is thus summarized by an n-by-1 vector $\mathbf{r}$ of quantities r_i, giving the intrinsic growth rate of each population i, and an n-by-n matrix $\mathbf{a}$ of interaction terms a_{ij}, which are the parameters for a system of n nonlinear ordinary differential

equations:

$$\frac{dX_i}{dt} = r_i X_i + \sum_{j=1}^{n} a_{ij} X_i X_j, \quad X_i \geq 0, \quad i = 1, \ldots, n. \tag{2.1}$$

As the number of populations and complexity of their interconnections grow, the population dynamics rapidly becomes complex and mysterious.

Unfortunately, when there are a significant number of mutualistic interactions—populations helping each other via positive interaction terms—in the system, the population sizes tend to explode to infinity. In order to study the behavior of systems with mutualistic interactions, along with discussing the behavior of the Lotka-Volterra equations, I will also make use of a couple of modifications to the equations to avoid unbounded growth.

2.2 Analysis of Lotka-Volterra dynamics

When all species coexist, the Lotka-Volterra system (2.1) is at an equilibrium point $\hat{\mathbf{X}}$ when

$$r_i + \sum a_{ij} X_j = 0; \tag{2.2}$$

or, in vector form,

$$\mathbf{r} + \mathbf{a}\hat{\mathbf{X}} = \mathbf{0}.$$

Since this is a simple linear equation, when $\mathbf{a}$ is nonsingular and it is known that all species in the system coexist in the long term, the relevant equilibrium of the dynamics can be calculated directly:

$$\hat{\mathbf{X}} = -\mathbf{a}^{-1}\mathbf{r}.$$

However, the system also has numerous other fixed points at which some population sizes are zero and those that are not zero satisfy $\tilde{\mathbf{r}} + \tilde{\mathbf{a}}\tilde{\mathbf{X}} = \mathbf{0}$ for the smaller objects $\tilde{\mathbf{r}}$ and $\tilde{\mathbf{a}}$ representing the community of populations that are nonzero.

As we shall see, the behavior of Lotka-Volterra systems with complicated attractors is closely related to the behavior at these fixed points. Every possible permanently coexisting

collection of species must have a fixed point at the center of its dynamical attractor, the fixed points are connected to each other by isoclines, and the invasion function, which is closely related to coexistence, is determined by the relative locations of fixed points and isoclines. In an evolutionary model, the crucial questions of which strains invade and which go extinct are addressed by the invasion function. The connections between these various aspects of Lotka-Volterra dynamics are not fully worked out, but it is clear that they all work together in important ways.

2.3 One dimension

The one-dimensional Lotka-Volterra system is very simple, but it is useful to review the possible cases, because they help in analyzing the larger systems. The one-dimensional system is simply

$$\dot{X}_1 = r_1 X_1 + a_{11} X_1^2, \tag{2.3}$$

and there are four generic cases, determined by the signs of r_1 and a_{11}.

The most commonly considered case is $r_1 > 0$ and $a_{11} < 0$, since it is well behaved and biologically nontrivial. In this case, the growth rate $r_1 + a_{11}X_1$ is positive when X_1 is small and negative when X_1 is large, so the population X_1 is driven to a positive equilibrium value (which is easily seen to be $-r_1/a_{11}$). This is the standard logistic growth equation, often written $\dot{X} = rX(1 - X/K)$, using the equilibrium value $K = -r/a$.

If $r_1 < 0$ and $a_{11} < 0$, the growth rate $r_1 + a_{11}X_1$ is strictly negative for all $X_1 > 0$, so all positive-sized populations decline to 0. If $r_1 > 0$ and $a_{11} > 0$, the growth rate is positive for all positive X_1, so the population grows to infinity.

Finally, if $r_1 < 0$ but $a_{11} > 0$, the equilibrium $\hat{X}_1 = -r_1/a_{11}$ is positive, but the growth rate is negative below the equilibrium and positive above, making it an unstable equilibrium that repels nearby trajectories either to zero or to infinity, depending on which side they fall.

There are several degenerate cases as well, when one or both of the parameters is zero, but in general I intend to avoid degenerate cases as much as possible.

2.4 Two dimensions

A system of two interacting populations is governed by six parameters:

$$\mathbf{r} = \begin{pmatrix} r_1 \\ r_2 \end{pmatrix}, \quad \mathbf{a} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}.$$

The analysis of the dynamics comes in three parts: the dynamics of each population in isolation, and the dynamics of the two together. When species X_2 is not present, the dynamics of X_1 is simply the one-dimensional case (2.3) parametrized by r_1 and a_{11}; correspondingly, in the absence of species X_1, the system is the one-dimensional system described by r_2 and a_{22}. In geometric terms, this amounts to saying that the axes $\{\mathbf{X} \mid X_1 = 0\}$ and $\{\mathbf{X} \mid X_2 = 0\}$ of the X_1-X_2 plane are invariant manifolds of the dynamics (2.1). It follows that the interior positive cone, $\operatorname{int} \mathbb{R}^2_+ = \{\mathbf{X} \mid X_1 > 0,\ X_2 > 0\}$, is invariant as well. The dynamics of the two species taken together depends on how the interspecies interaction terms a_{12} and a_{21} change each species' population dynamics.

When each species separately is governed by standard logistic growth and all interactions are competitive, there are four standard cases for the dynamics, which are easily analyzed. First I will classify these cases using the zero-growth isoclines of the two species, and then I will discuss how they can be understood in terms of mutual invasibility.

The *zero-growth isocline* or *nullcline* for a species i is the set of points $\mathbf{X}$ for which $\dot{X}_i/X_i = 0$. A point where all species' nullclines intersect is a rest point of the dynamics. Due to the linear nature of the Lotka-Volterra equations, nullclines in these models are hyperplanes

$$Z_i = \{\mathbf{X} \mid r_i + \sum_j a_{ij} X_j = 0\};$$

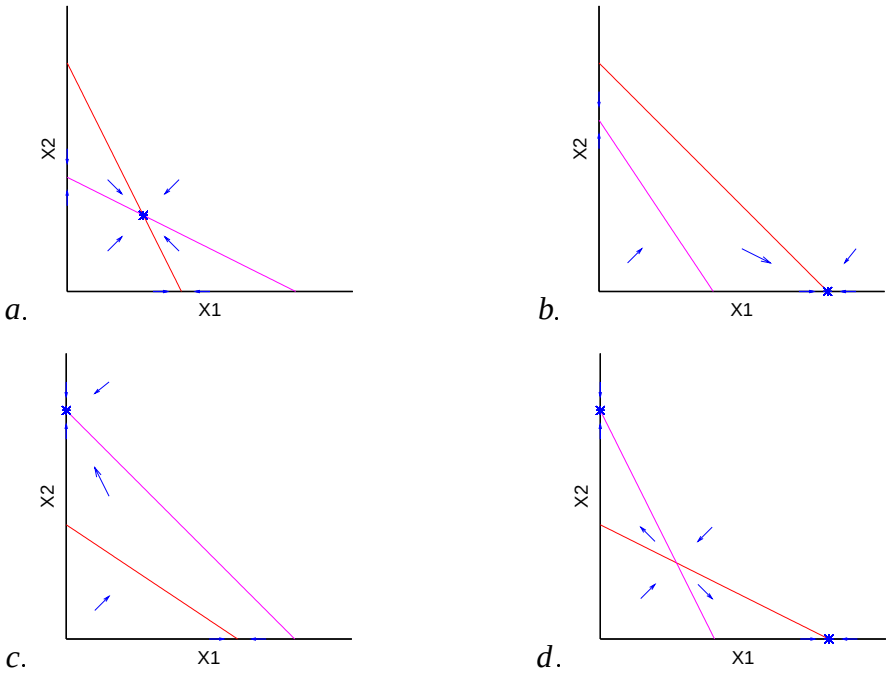


Figure 2.1: The four cases for competitive Lotka-Volterra dynamics in two dimensions: *a*. The two species X_1 and X_2 coexist at a stable equilibrium; *b*. Species X_1 outcompetes X_2; *c*. X_2 outcompetes X_1; *d*. The two species compete, and which survives depends on the initial conditions. The red and purple lines are the zero-growth isoclines of species X_1 and X_2, respectively.

in two dimensions, they are straight lines

$$Z_1 = \{\mathbf{X} \mid r_1 + a_{11}X_1 + a_{12}X_2 = 0\}$$
$$Z_2 = \{\mathbf{X} \mid r_2 + a_{21}X_1 + a_{22}X_2 = 0\}.$$

Each nullcline passes through the boundary equilibrium for its species, and there are two cases in which the two lines intersect in the first quadrant and two cases in which they do not. Since the nullclines and the axes are the only places where the populations' derivatives can change signs, the directions of motion can be extended continuously from the axes to the interior, giving a picture of the population dynamics as shown in figure 2.1.

The species 1 isocline meets the X_1 axis at $-r_1/a_{11}$ and the X_2 axis at $-r_1/a_{12}$; likewise the X_1- and X_2-intercepts of the species 2 isocline are $-r_2/a_{21}$ and $-r_2/a_{22}$. The four cases can be classified in terms of the relative positions of the X_1-intercepts and X_2-intercepts, giving the well known results for two species with logistic growth and competitive interactions:

Theorem 2.1. *Given two species with $r_i > 0$ and $a_{ij} < 0$,*

a. *When*
$$-\frac{r_1}{a_{11}} < -\frac{r_2}{a_{21}} \quad \text{and} \quad -\frac{r_2}{a_{22}} < -\frac{r_1}{a_{12}},$$
(2.1) has a unique positive equilibrium which is globally asymptotically stable for all solutions of (2.1) with positive initial values;

b. *When*
$$-\frac{r_1}{a_{11}} > -\frac{r_2}{a_{21}} \quad \text{and} \quad -\frac{r_2}{a_{22}} < -\frac{r_1}{a_{12}},$$
all solutions of (2.1) with positive initial values are globally attracted to the equilibrium $(-r_1/a_{11}, 0)$;

c. *When*
$$-\frac{r_1}{a_{11}} < -\frac{r_2}{a_{21}} \quad \text{and} \quad -\frac{r_2}{a_{22}} > -\frac{r_1}{a_{12}},$$
all solutions of (2.1) with positive initial values are globally attracted to the equilibrium $(0, -r_2/a_{22})$;

d. *When*
$$-\frac{r_1}{a_{11}} > -\frac{r_2}{a_{21}} \quad \text{and} \quad -\frac{r_2}{a_{22}} > -\frac{r_1}{a_{12}},$$
both fixed points $(-r_1/a_{11}, 0)$ and $(0, -r_2/a_{22})$ are asymptotically stable, and there is a positive saddle point which separates the positive trajectories of (2.1) into the basins of attraction of these two points.

In cases *b* and *c*, one of the two species goes extinct because it is entirely dominated by the other: its zero-growth isocline falls strictly below the other one, so that it is always in decline when the dominant species is at equilibrium, while the dominant species is always expanding when the dominated species is at equilibrium. Under these conditions the dominated species cannot persist in the long term, whether the dominant species does or not. Notice that when all r_i are equal, this happens exactly when all the entries in one row are larger than the corresponding entries in the other row. When the isoclines do cross (cases *a* and *d*), producing a fixed point within the positive cone, whether the fixed point is attracting or repelling depends on whether the fixed point falls above or below the line connecting the two single-species fixed points.

All the conditions of Theorem 2.1 can alternatively be written in terms of the *invasion exponent*: when species 2 is resident, the invasion exponent of species 1 is its growth rate when it is very rare:

$$\begin{aligned} \mathscr{I}(X_1|X_2) &= \lim_{X_1\to 0} \frac{\dot{X}_1}{X_1} \\ &= \lim_{X_1\to 0} (r_1 + a_{11}X_1 + a_{12}X_2) \\ &= r_1 + a_{12}\hat{X}_2 = r_1 - a_{12}\frac{r_2}{a_{22}}. \end{aligned}$$

Likewise, the invasion exponent of species 2 when species 1 is resident is

$$\mathscr{I}(X_2|X_1) = r_2 + a_{21}\hat{X}_1 = r_2 - a_{21}\frac{r_1}{a_{11}}.$$

(I will discuss the invasion exponent more thoroughly in chapter 3.) Classifying the signs of these two quantities gives the same four cases as above, and a compact summary:

> *Any species which can invade the other will be present at equilibrium; any species which cannot invade the other will be eliminated unless bistability allows it to eliminate the other instead.* (2.4)

Since by definition $r_1 + a_{11}\hat{X}_1 = 0$, the invasion condition for species 2, $r_2 + a_{21}\hat{X}_1 > 0$, is simply that r_2 or a_{21} is sufficiently larger than r_1 or a_{11}, and the opposite case works in the

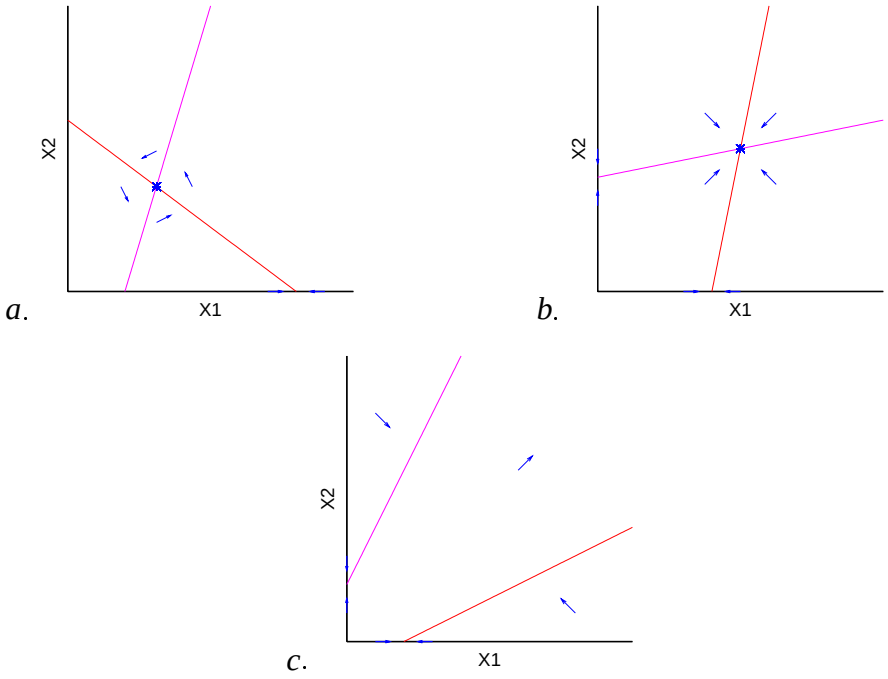


Figure 2.2: Some cases of Lotka-Volterra dynamics in two dimensions with positive interaction terms: *a*. Predator-prey dynamics ($a_{12} < 0 < a_{21}$; the fixed point is stable when $a_{11}, a_{22} < 0$); *b*. Mutualistic coexistence; *c*. Unbounded mutualism.

same way. In particular, when r_1 and r_2 are equal, the coexistence condition is simply that each off-diagonal term of **a** is larger than the diagonal term in the same column.

This is true even when one or both of the off-diagonal terms is positive, as long as the zero-growth isoclines intersect in the first quadrant. Figure 2.2 illustrates some cases with positive terms. As figure 2.2*c* shows, when the off-diagonal terms become too large—when a_{11} and a_{22} are negative, this happens when a_{12} and a_{21} are positive and $a_{11}a_{22} - a_{12}a_{21} < 0$—the population dynamics can grow to infinity, like the one-dimensional case with $a > 0$. Analysis of these cases requires knowledge of whether the dynamics is bounded from above, as well as the mutual invasibility conditions. Species that coexist permanently in two dimensions always settle to a fixed point, except in neutral cases, which are not

biologically realistic.

2.5 More than two dimensions

There are many basic unsolved questions about the behavior of the system (2.1) in more than two dimensions, and this is an area of active research. Much of the analysis of higher-dimensional Lotka-Volterra dynamics comes down to isoclines and boundedness of trajectories, in very similar ways to the previous section.

It is not clear whether general statements about coexistence and competition similar to the above statement (2.4) are waiting to be made. With this hope in mind, I will translate the various results into mutual invasibility conditions while I review them.

2.6 The time average

If we assume that all populations whose equilibrium value is zero have been removed from the equations, and that the population dynamics are bounded above, then each resident population X_i satisfies a weak permanence condition $0 < b < X_i(t) < B < \infty$ for $t > T$ (where the bounds b and B may depend on initial conditions). Given this minimal requirement, we can make use of the general fact that $\lim_{T\to\infty} \frac{1}{T}(\log X_i(T) - \log X_i(0)) = 0$ for each resident, which gives, for the Lotka-Volterra equations,

$$\lim_{T\to\infty} \frac{1}{T} \int_0^T \frac{d}{dt} \log X_i(t)\, dt \;=\; 0,$$

using angle brackets to represent the time average,

$$\begin{aligned} \left\langle \frac{d}{dt} \log X_i \right\rangle &= 0 \\ \left\langle \frac{1}{X_i} \frac{dX_i}{dt} \right\rangle &= 0 \\ \left\langle r_i + \sum_j a_{ij} X_j \right\rangle &= 0 \end{aligned}$$

$$r_i + \sum_j a_{ij} \langle X_j \rangle \quad = \quad 0. \tag{2.5}$$

It follows immediately that the vector $\langle \mathbf{X} \rangle$ of average population values is a solution of $\mathbf{r} + \mathbf{a}\langle \mathbf{X} \rangle = \mathbf{0}$; that is, it is a fixed point of the system, even if that fixed point does not attract actual trajectories of the dynamics. This implies that any given set of populations cannot coexist in the long term unless the dynamics has a fixed point at which they all coexist. It also makes it possible to analyze many aspects of the evolutionary dynamics of this system by ignoring complex attractor dynamics and simply computing invasion exponents (transversal eigenvalues) at fixed points, as we will see below. This lovely time-averaging property was known by Volterra (Scudo and Ziegler 1978).

2.7 The time average and the invasion function

When a variant population $X_{i'}$ is introduced, very similar in character to X_i, when the resident community is at equilibrium, its ability to invade, $\mathscr{I}(X_{i'}|X_j, j \neq i')$ or simply $\mathscr{I}(X_{i'})$, is governed by its per capita growth when its own population is approximately 0:

$$\mathscr{I}(X_{i'}) = \frac{1}{X_{i'}} \frac{dX_{i'}}{dt} = r_{i'} + \sum_{j \neq i'} a_{i'j} \hat{X}_j.$$

Subtracting out the terms of the equilibrium condition (2.2),

$$\begin{aligned} \mathscr{I}(X_{i'}) &= (r_{i'} - r_i) + \sum (a_{i'j} - a_{ij}) \hat{X}_j \\ &= \Delta r_{i'} + \sum \Delta a_{i'j} \hat{X}_j. \end{aligned}$$

The hopeful variant succeeds when $\mathscr{I} > 0$. Notice that if all the $n+1$ degrees of freedom $\Delta r_{i'}$, $\Delta a_{i'j}$ are unconstrained, successful variants can always be constructed by making enough of these values positive (increasing the effect on growth of everything at once is always beneficial).

If the resident populations are not at a fixed point, then the invasion exponent is a time average (see also chapter 3):

$$\begin{aligned}
\mathscr{I}(X_{i'}) &= \lim_{X_{i'}(0)\to 0} \lim_{T\to\infty} \frac{1}{T}(\log X_{i'}(T) - \log X_{i'}(0)) \\
&= \lim_{X_{i'}(0)\to 0} \lim_{T\to\infty} \frac{1}{T}\int_0^T \frac{d}{dt}\log X_{i'}(t)\; dt \\
&= \left\langle \frac{1}{X_{i'}}\frac{dX_{i'}}{dt} \right\rangle_{X_{i'}\to 0} \\
&= \left\langle r_{i'} + \sum_{j\neq i'} a_{i'j}X_j \right\rangle \\
&= r_{i'} + \sum a_{i'j}\left\langle X_j \right\rangle .
\end{aligned}$$

But because of the special properties of time averages, we can subtract out the time averages of the resident equations (equation 2.5) just as if they were the equilibrium conditions:

$$\begin{aligned}
\mathscr{I}(X_{i'}) &= (r_{i'} - r_i) + \sum (a_{i'j} - a_{ij})\left\langle X_j \right\rangle \\
&= \Delta r_{i'} + \sum_{j\neq i'} \Delta a_{i'j}\left\langle X_j \right\rangle ;
\end{aligned}$$

and note that the time average $\langle \mathbf{X} \rangle$ of the resident populations is in fact an equilibrium of (2.1).

Now we have that, regardless of the actual dynamics of the resident populations, the ability of the new variant to establish in the system is encapsulated by the simple formula

$$\mathscr{I}(X_{i'}) = \Delta r_{i'} + \sum_{j\neq i'} \Delta a_{i'j}\hat{X}_j \tag{2.6}$$

where $\hat{\mathbf{X}}$ is a fixed point of (2.1) with each $\hat{X}_j > 0$, which stands in for all the actual, possibly complicated and chaotic, dynamics of the resident populations. The variant can only establish if $\mathscr{I}(X_{i'}) > 0$. This formula makes $\mathscr{I}(X_{i'})$ a weighted sum of Δr and Δa values, which is positive when the positive Δ values in this sum outweigh any negative ones. (This condition has an especially strange property: if we pretend that some other population is the parent of the new variant, with corresponding—possibly large—Δ values, the above weighted sum of those Δ values gives just the same value as for the actual parent.)

2.8 Competitive systems

A number of researchers have presented analyses of coexistence and extinction in competitive systems that generalize the isocline analysis of figure 2.1*a*, *b* and *c*.

An extension of the two-species coexistence condition of figure 2.1*a* has been presented by Gopalsamy and others (Gopalsamy 1985; Tineo and Alvarez 1991):

Theorem 2.2. (Gopalsamy, Tineo, Alvarez). *Given system (2.1) in n dimensions, with* $r_i > 0$ *and* $a_{ij} < 0$ *for all i and j, let* $I_{ij} = -r_i/a_{ij}$ *be the* X_j*-intercept of the species i isocline, and suppose that*

$$\text{for each } i \leq n \qquad \sum_{j=1,j\neq i}^{n} I_{jj}/I_{ij} < 1. \tag{2.7}$$

Then there is a positive equilibrium point $\mathbf{X}^* = (X_1^*, \ldots, X_n^*)$ *which is globally attracting in the interior positive cone.*

This condition for coexistence can be interpreted in terms of invasibility as follows: since all $a_{ij} < 0$, the derivative of X_i is at most zero when $r_i + a_{ii}X_i = 0$, that is when $X_i = I_{ii}$, and is negative when X_i is larger. Therefore any equilibrium value of X_i is bounded above by I_{ii}. So when some set of species $j \in J$ (not including i) is resident, the invasibility of i is

$$\begin{aligned} \mathscr{I}(X_i|J) &= r_i + \sum_{j\in J} a_{ij} \left\langle X_j \right\rangle \\ &\geq r_i + \sum_{j\in J} a_{ij} I_{jj} \\ &\geq r_i + \sum_{j=1,j\neq i}^{n} a_{ij} I_{jj}, \end{aligned}$$

and that last quantity is positive when

$$\begin{aligned} 0 &< 1 + \sum_{j=1,j\neq i}^{n} \frac{a_{ij}}{r_i} I_{jj} \\ \sum_{j=1,j\neq i}^{n} I_{jj}/I_{ij} &< 1. \end{aligned}$$

Therefore the condition (2.7) guarantees that each species can invade any combination of the others. It seems that this mutual invasibility might be sufficient for coexistence (as is commonly assumed by adaptive dynamics modelers (Geritz et al. 1997; Metz, Nisbet, and Geritz 1992)), but mathematical analyses of the problem consistently require the stronger condition (2.7), either because it is defined straightforwardly in terms of **r** and **a**, or because it guarantees a fixed point attractor.

A theorem of M. L. Zeeman (1995) generalizes the competitive cases *b* and *c* of the two-dimensional system, showing that in a competitive system with logistic growth (that is, where all $r_i > 0$ and all $a_{ij} < 0$), the inequalities

$$I_{jj} < I_{ij} \text{ if } i < j \text{ and } I_{ij} < I_{jj} \text{ if } j < i \tag{2.8}$$

imply that the first species persists at a fixed point and all others go extinct. This isocline condition can be rewritten

$$I_{jj} < I_{ij} \text{ and } I_{ji} < I_{ii} \text{ if } i < j.$$

This implies that when any two species are taken apart from all the others (on the X_i-X_j plane where all other populations are zero) the larger-indexed species is dominated in the sense of figure 2.1*b*: when the X_i and X_j isoclines are intersected with this plane, the line belonging to the X_i isocline lies strictly below the line belonging to the X_j isocline. While no species need be entirely dominated by another in the sense that its entire isocline lies below the other, this is sufficient to construct an argument showing that each species but the first is dominated in a sense that guarantees it can not persist.

As in the two-dimensional case, these conditions can be translated into mutual invasibility conditions. When only two species are under consideration, invasibility and isocline intercept conditions are interchangeable:

$$\mathscr{I}(X_i|X_j) = r_i + a_{ij}I_{jj} = -a_{ij}(I_{ij} - I_{jj}),$$

so that $\mathscr{I}(X_i|X_j) > 0$ exactly when $I_{ij} > I_{jj}$ (as long as $a_{ij} < 0$). In terms of invasibility, then, Zeeman's condition is equivalent to the condition that for each pair of species $i < j$,

when no other species is present, species i can invade species j and species j can not invade species i. In this case, this kind of pairwise dominance hierarchy is sufficient to guarantee which set of species persists at equilibrium.

Zeeman's result is a natural extension of case b of Theorem 2.1, with the first species outcompeting a number of other species rather than just one. Another natural extension of the same result, where $n-1$ species persist and the last one is dominated, is presented by Ahmad and Lazer (1996):

Theorem 2.3. (Ahmad, Lazer). *Given system (2.1) in n dimensions, with* $r_i > 0$ *and* $a_{ij} < 0$ *for all* i *and* j*, suppose that*

$$\text{for each } i \leq n-1 \qquad \sum_{j=1, j\neq i}^{n} I_{jj}/I_{ij} < 1. \tag{2.9}$$

Then the first $n-1$ *species can coexist permanently at an equilibrium* $\mathbf{X}^* = (X_1^*, \ldots, X_{n-1}^*, 0)$ *when the nth species is absent. Further, if*

$$\mathscr{I}(X_n|\mathbf{X}^*) = r_i + \sum_{j=1}^{n-1} a_{ij} X_j^* < 0, \tag{2.10}$$

then $\mathbf{X}^*$ *is the globally attracting solution, that is, species n can not persist.*

The first part of the theorem is a variant of Gopalsamy's theorem for coexistence of $n-1$ species; in the second part, given that the first $n-1$ species are capable of permanent coexistence, Ahmad and Lazer's theorem tells us that if the nth species can not invade when rare, it can not persist under any conditions. This rules out bistability analogous to figure 2.1d in this case. However, this theorem does not make it clear whether having a positive invasion exponent rather than negative would be sufficient for species n to join the others in permanent coexistence, or whether, like the others, it would need to satisfy the stronger condition (2.9).

A number of results about coexistence and extinction are brought together and expanded in a theorem by Montes de Oca and Zeeman (1995):

Theorem 2.4. (Montes de Oca, Zeeman). *Given system (2.1) in n dimensions, with* $r_i > 0$ *and* $a_{ij} < 0$ *for all* i *and* j*, and* $m < n$*, suppose that*

$$\text{for all } i \leq m \qquad \sum_{j=1, j\neq i}^{n} I_{jj}/I_{ij} < 1 \tag{2.11}$$

and that

$$\text{for each } i > m \text{ there is a } k < i, \text{ such that for all } j \leq i \quad I_{ij} < I_{kj}. \tag{2.12}$$

Then (2.1) has a unique solution $\mathbf{X}^* = (X_1^*, \ldots, X_m^*, 0, \ldots, 0)$ *with all* $X_i^* > 0$ *(*$i \leq m$*), and every trajectory of (2.1) with initial conditions in* $\mathbb{R}^n_+$ *is asymptotic to* $\mathbf{X}^*$.

This theorem places the species into a sort of competitive hierarchy, in which the first m species persist at equilibrium and each of the remaining species is outcompeted by an earlier one. (Of course, like the previous ones, it also applies to any system for which the above conditions can be satisfied by reordering the species indexes.)

Condition (2.11), like (2.9), is a variant of (2.7). Condition (2.12) has each remaining species i dominated by an earlier species k, in the same way that species 2 is dominated by species 1 in figure 2.1*b*. The very last species is entirely dominated by an earlier one; its isocline lies completely above the dominating species' isocline, so that it must be extinct at any equilibrium that might be reached. In the absence of the very last species, (2.12) is is sufficient to make the second-to-last species dominated in the same way, and in this way, proceeding by induction, all species after the mth are shown to be doomed. Notice that when all r_i are equal, condition (2.12) is that each entry in row k (up to column i) is larger than the corresponding entry in row i.

Condition (2.12) seems to be stricter than (2.8). To my knowledge, a theorem combining (2.11) with (2.8) has not been published.

2.9 Noncompetitive systems

The above theorems do not apply to systems with any positive interaction terms, and are only applicable to some competitive systems as well. Hofbauer and Sigmund (1998) have some results for systems with positive terms. The system (2.1) is said to be *permanent* if there are a positive lower and upper bound b and B such that after some time T all trajectories of (2.1) are bounded by $b < X(t) < B$. (A subsystem is permanent if those populations become bounded by positive numbers when the others are not present.) A system for which all trajectories eventually satisfy $X(t) < B$ is said to have *uniformly bounded trajectories*. Permanence means that the boundary of the state space $\mathbb{R}^n_+$ (and "points at infinity") is a repellor. Both sufficient conditions and necessary consequences of permanence are presented, though none is both necessary and sufficient.

Some of the analysis of permanence is based on *transversal eigenvalues*. When (2.1) has a fixed point on the boundary of $\mathbb{R}^n_+$—that is, has a subsystem with a fixed point—the transversal eigenvalues at that point are the eigenvalues corresponding to directions involving species not present. A fixed point with no positive transversal eigenvalues is called a *saturated* fixed point. A fixed point in the interior of $\mathbb{R}^n_+$ is always saturated, trivially. An important theorem follows from a topological analysis of the flow of (2.1):

Theorem 2.5. (Hofbauer, Sigmund). *If (2.1) has uniformly bounded trajectories, then it has a saturated fixed point.*

Transversal eigenvalues are, in fact, the invasion exponents of the missing species, if the resident populations are held fixed at the fixed point. Thanks to the time average, if the resident populations fluctuate, these values are equal to the invasion exponents even so. Transversal eigenvalues characterize which assemblages of species are invasible by other species. An assemblage that is a stable destination of the ecological sorting-out process (that is, it is permanent and the species not present cannot invade) must be accompanied by a saturated fixed point containing the same combination of species, because of the time

average property of the dynamics. Unfortunately, the presence of such a point does not guarantee that that combination of species is permanent. The problem is that there may be an attracting heteroclinic orbit on the boundary of the space, in which case the dynamics can move away from stable coexistence and into a cycle in which different species replace each other in succession, coming closer and closer to extinction with each oscillation. These are difficult to analyze, and are not well understood, especially beyond three dimensions.

One necessary condition for permanence of all species, which follows from the time average property, is the presence of a fixed point in the interior positive cone. Permanence also implies that $\mathbf{a}$ is nonsingular (so that the fixed point is unique). Another necessary condition, which relies on some deep topological results, characterizes the determinants of the interaction matrix and Jacobian:

Theorem 2.6. (Hofbauer, Sigmund). *Let (2.1) be permanent and let* $\mathbf{J}$ *be the Jacobian at the interior fixed point* $\hat{\mathbf{X}}$*. Then*

$$|-\mathbf{a}| > 0, \quad |-\mathbf{J}| > 0, \quad \textit{and} \quad \operatorname{tr} \mathbf{J} < 0.$$

In many cases when analysis of invasibility of each fixed point is difficult, and for the construction of general proofs, it is more useful to construct an *average Lyapunov function*:

Theorem 2.7. (Hofbauer, Sigmund). *Given a dynamical system on* $\mathbb{R}^n_+$ *for which the boundary is invariant, let* $P : \mathbb{R}^n_+ \to \mathbb{R}$ *be a differentiable function vanishing on the boundary of* $\mathbb{R}^n_+$ *and strictly positive on the interior. If there exists a continuous function* Ψ *such that*

$$\frac{\dot{P}(\mathbf{X})}{P(\mathbf{X})} = \Psi(\mathbf{X}) \quad \textit{for } \mathbf{X} \in \textit{int } \mathbb{R}^n_+$$

and

$$\int_0^T \Psi(\mathbf{X}(t))\, dt > 0 \textit{ for some } T > 0 \quad \textit{for } \mathbf{X} \in \textit{bd } \mathbb{R}^n_+,$$

then the dynamical system is permanent.

This theorem is used to prove the following:

Theorem 2.8. (Hofbauer, Sigmund). *If the trajectories of (2.1) are bounded above and the set*

$$D = \{\mathbf{X} \in \mathbb{R}^n_+ \mid \mathbf{r} + \mathbf{aX} \leq \mathbf{0}\}$$

(where no X_i increases) is disjoint from the convex hull C of all boundary fixed points of (2.1), then (2.1) is permanent.

This condition generalizes the distinction between the two-dimensional cases *a* and *d*, and guarantees that all species' invasion exponents when absent are positive. However, it is not a necessary condition in more than two dimensions.

2.10 Invasion and extinction

Extinction can be thought of as invasion in reverse. Since the interior positive cone is an invariant region of the dynamics (2.1), for a species to go extinct means that its population asymptotically approaches zero (in many simulations, species are made to go extinct when their population falls below an arbitrary threshold value, but that makes things much more complicated and I am not talking about that here). If species *i* goes extinct while some set of species *J* remains permanently resident, this means that after a long time, when the resident species' dynamics have come arbitrarily close to their attractor, and the population of species *i* is very small, species *i* continues to decline on average:

$$\begin{aligned} \left\langle \frac{\dot{X}_i}{X_i} \right\rangle_{X_i \approx 0} &= \left\langle r_i + \sum_{j \in J} a_{ij} X_j \right\rangle \\ &= r_i + \sum_{j \in J} a_{ij} \left\langle X_j \right\rangle \quad < \quad 0. \end{aligned}$$

This expression is, of course, nothing but the invasion function, and the condition for extinction is the condition for invasion in reverse:

$$\mathscr{I}(i|J) < 0.$$

As invasion when rare requires a positive invasion exponent relative to the resident community, so extinction requires the same value to be negative. Both of these observations present necessary conditions for permanent coexistence or the lack thereof; neither is necessarily a sufficient condition to predict whether a species will in fact invade or go extinct, as they do not address what happens away from the boundary of the positive cone.

Nonetheless, it does suggest, for instance, that Ahmad and Lazer's Theorem 2.3 can be expanded to an if-and-only-if statement: since a species cannot go extinct unless its invasion exponent is negative relative to the surviving species, a positive invasion exponent is sufficient to prevent extinction; therefore, in Theorem 2.3 (assuming the invasion exponent is never exactly zero), species n is driven to extinction by the other species if and only if $\mathscr{I}(X_n|\mathbf{X}^*) < 0$. (But if species n is not driven to extinction in this way, it is not entirely clear whether all will coexist permanently or whether some other extinction may occur, with unknown consequences, though given the strong assumptions of the first part of the theorem this seems unlikely.)

2.11 Boundedness

When the matrix **a** contains all negative entries, all trajectories in $\mathbb{R}^n_+$ are bounded, as the quadratic terms dominate the linear terms when X values become large. However, when the matrix includes positive numbers, it is possible for some trajectories of the dynamics to become unbounded. Due to the positive quadratic terms $a_{ij}X_iX_j$, these trajectories actually grow faster than exponentially, rising to infinity in finite time, unlike the exponential growth that is seen in linear systems and systems well approximated by them. This hyperexponential growth is a feature of all Lotka-Volterra systems with unbounded trajectories (except in degenerate cases where the a terms drop out, leaving a positive r).

Lotka-Volterra systems can be classified into three cases: systems that include unbounded trajectories in the positive cone; uniformly bounded systems, that is, those in

which there is a bounded region within which all trajectories are eventually contained; and systems on the boundary between the other two cases. The condition for all trajectories of (2.1) to be uniformly bounded is for the matrix **a** to be a particular kind of matrix known as a *B-matrix*. I will refer to such a system as *B*-stable, and to the opposite kind of system as *B*-unstable (*B*-neutral systems are infinitely improbable when a values are chosen from a continuous distribution, but can appear as an endpoint of evolutionary self-organization, as we will see later in this chapter).

One condition for *B*-stability is given by Hofbauer and Sigmund (1998):

Theorem 2.9. (Hofbauer, Sigmund). *The system (2.1) is B-stable if and only if whenever*

$$X_i(\mathbf{aX})_i = \lambda X_i, \quad i = 1, \ldots, n$$

holds for some $\mathbf{X} \geq \mathbf{0}$ $(\mathbf{X} \neq \mathbf{0})$, *then* $\lambda < 0$.

This condition can be simplified as follows:

Theorem 2.10. *If* **a** *is nonsingular, the system (2.1) is B-unstable if and only if either it has a B-unstable subsystem or*

$$\mathbf{a}\bar{\mathbf{X}} = \mathbf{1}, \tag{2.13}$$

where **1** *is the n-by-*1 *vector of ones, admits a positive solution* $\bar{\mathbf{X}} \in \mathbb{R}^n_+$.

Proof. If a subsystem is *B*-unstable, then clearly the full system is as well. If (2.13) is satisfied, the previous theorem shows (2.1) is *B*-unstable.

Now suppose that no subsystem is *B*-unstable, but that the full system is *B*-unstable. Then there is a nonzero $\mathbf{X} \geq 0$ satisfying $X_i(\mathbf{aX})_i = \lambda X_i$ for all i with $\lambda > 0$ ($\lambda = 0$ would show the matrix to be singular). No X_i can be zero, for then the previous theorem would show a *B*-unstable subsystem. Therefore $\mathbf{aX} = \lambda\mathbf{1}$, and $\bar{\mathbf{X}} = \mathbf{X}/\lambda$ satisfies (2.13). □

Consequently we can test whether any given system is *B*-stable by applying Theorem 2.10 to **a** and each principal submatrix.

Hofbauer and Sigmund also show (Hofbauer and Sigmund 1998) that if **a** is nonsingular and hierarchically ordered—that is, if the species can be reindexed so that all positive entries appear below the diagonal, indicating that mutualistic effects flow only from earlier to later species—then **a** must be a *B*-matrix. This implies that the matrix of any *B*-unstable system must contain a *mutualistic cycle* of positive entries (a positive diagonal entry must be considered a mutualistic cycle by this definition). The presence of a mutualistic cycle, however, does not imply *B*-instability. The cycle must be in some sense strong enough to overwhelm the negative entries in the matrix. This condition is strongly reminiscent of the *hypercycle* studied in catalytic chemical systems (Eigen and Schuster 1979).

Chapter 3

Adaptive Dynamics

In this chapter I review what is known about modeling the adaptive dynamics of coevolving strains whose evolution is driven by ecological interactions, both in the case in which strains are characterized by one-dimensional phenotypes, which is the subject of most of the adaptive dynamics literature, and in the case in which phenotypes are represented by vectors, which is only more recently beginning to be covered in the literature. After this review, I reinterpret these known results in the case of evolution restricted to a constraint or tradeoff surface in a higher-dimensional space of possible phenotype values, or ecological parameters derived from phenotypic characters.

3.1 Adaptive dynamics

For most of the history of mathematical biology, the relationships between ecological interactions and changes in populations due to natural selection have primarily been studied by using population genetics formulas combined with ecological models, to predict how the gene frequencies of a number of alleles will change in response to fitness differences. A number of dynamic variables are needed for the gene frequencies of each population, in addition to the size of these population, which can add up to a large number of variables quickly. Since gene frequencies and population sizes change on similar time scales, these models become complex high-dimensional dynamical systems unless the assumptions are limited to small numbers of loci and populations.

More recently, some modelers have begun to use a simplified framework for evolutionary ecology, commonly known as adaptive dynamics. Unlike population genetics models, which often go into great detail about epistatic interactions, assortative mating, dominance, and other gene- or genome-level phenomena, these models simulate a greatly simplified version of evolution, considering only asexual reproduction with very rare and gradual mutations. The time scales of ecological and evolutionary dynamics are strictly separated, allowing the two aspects of the system's dynamics to be considered separately. Spatial heterogeneity and other complications also are generally not considered. The resulting models, while they does not address many important features of real-world biology, are simple and flexible and so may be able to approach some problems of more complexity than a more faithful model would be able to handle.

Adaptive dynamics as it is currently practiced also generally entails the assumption that the phenotypic characters undergoing mutational change are well represented by continuously varying numbers, and that the ecological interactions between an individual and its environment that give rise to selective pressure are well represented by a continuous function of those numbers. The result is a sort of differential calculus of adaptational change

with many interesting properties, in particular the emergence of continuous evolutionary branching events that may be able to shed light on actual sympatric speciation events. In subsequent chapters I will present models that share most of the basic assumptions of adaptive dynamics, but do not make these assumptions about continuous functions of phenotype values, and consequently do not exhibit the same smooth motion in phenotype space and predictable branching; in this chapter, I stay within the standard adaptive dynamics framework.

The fundamental assumption is that a population is composed of a number of strains, each of which is a lineage of organisms all having the same phenotype. A phenotype is a collection of numerical values, that is, a vector of a certain length m (infinite-dimensional phenotypes are occasionally considered as well). Reproduction is faithful within each strain, except for occasional mutations. A mutation event consists of the introduction of a new strain, whose phenotype is numerically very close to that of the parent strain.

The growth and death of the various strains in a population are governed by an ecological model:

$$\dot{X}_i = X_i f(\mathbf{s}_i, \mathbf{E}), \tag{3.1}$$

where X_i is the population size of the i'th strain, $\mathbf{s}_i$ is its phenotype, and $\mathbf{E}$ is some representation of the environment encountered by each individual (which can include information about the sizes and characteristics of the populations interacting with it) (Metz, Nisbet, and Geritz 1992; Metz and Meszéna 1999). A discrete-time ecological model can be represented in the same terms:

$$\Delta X_i = X_i f(\mathbf{s}_i, \mathbf{E}). \tag{3.2}$$

Now if a mutant strain is introduced, with phenotype $\mathbf{s}_{i'}$ very close to the parent phenotype $\mathbf{s}_i$, and population size too small to affect the environment, its success or failure is determined by its long-term growth rate when rare (Metz, Nisbet, and Geritz 1992; Rand,

Wilson, and McGlade 1994):

$$\mathscr{I}(\mathbf{s}_{i'}|\mathbf{E}) = \lim_{\substack{X_{i'}(0)\to 0 \\ T\to\infty}} \frac{1}{T}\log\frac{X_{i'}(T)}{X_{i'}(0)},$$

where $\mathbf{E}$ is partly determined by the collection of resident phenotypes $\{\mathbf{s}_1,\ldots,\mathbf{s}_n\}$. This function $\mathscr{I}$ is the *invasion exponent* or *invasion function*, the rate of exponential growth or decline of the mutant phenotype in the environment created by the resident types. It is defined for all possible mutant phenotypes, given any viable combination of resident types and state of the environment. Additionally, if the ecological model does not allow multiple attractors for the same ensemble of phenotypes, the long-term dynamics is entirely determined by the collection of phenotypes present in the ecosystem. In this case, the invasion function can be written $\mathscr{I}(\mathbf{s}_{i'}|\mathbf{s}_1,\ldots,\mathbf{s}_n)$. In the case of continuous-time dynamics, the invasion function is

$$\begin{aligned}
\mathscr{I}(\mathbf{s}_{i'}|\mathbf{s}_1,\ldots,\mathbf{s}_n) &= \lim_{\substack{X_{i'}(0)\to 0 \\ T\to\infty}} \frac{1}{T}\int_0^T \frac{d}{dt}\log X_{i'}(t)\,dt \\
&= \lim_{X_{i'}(0)\to 0} \left\langle \frac{d}{dt}\log X_{i'}(t) \right\rangle \\
&= \lim_{X_{i'}(0)\to 0} \left\langle \frac{1}{X_{i'}}\frac{dX_{i'}}{dt} \right\rangle \\
&= \lim_{X_{i'}(0)\to 0} \langle f(\mathbf{s}_{i'},\mathbf{E})\rangle ,
\end{aligned}$$

using angle brackets for the time average as in the previous chapter. If the resident population dynamics settles to a fixed point, the time average is simply $\mathscr{I}(\mathbf{s}_{i'}|\mathbf{s}_1,\ldots,\mathbf{s}_n) = f(\mathbf{s}_{i'},\mathbf{E})$ calculated when $\mathbf{E}$ is at the fixed point and $X_{i'} = 0$. For discrete-time models, the calculation is

$$\begin{aligned}
\mathscr{I}(\mathbf{s}_{i'}|\mathbf{s}_1,\ldots,\mathbf{s}_n) &= \lim_{\substack{X_{i'}(0)\to 0 \\ T\to\infty}} \frac{1}{T}\sum_{t=0}^{T}\log\frac{X_{i'}(t)+\Delta X_{i'}}{X_{i'}(t)}\,dt \\
&= \lim_{X_{i'}(0)\to 0} \langle \log(1+f(\mathbf{s}_{i'},\mathbf{E}))\rangle .
\end{aligned}$$

Every resident population, assuming only that it is bounded away from 0 and infinity, must have $\mathscr{I}(\mathbf{s}_i|\mathbf{s}_1,\ldots,\mathbf{s}_n) = 0$, while any population whose size asymptotically approaches zero in the deterministic model (3.1, 3.2) must have $\mathscr{I}(\mathbf{s}_{i'}|\mathbf{s}_1,\ldots,\mathbf{s}_n) < 0$. This is true whether the dynamics of (3.1) or (3.2) approaches a fixed point or a more complicated attractor.

Provided the long-term growth rate is a continuous function of each phenotype, the invasion exponent for a mutant phenotype very close to a resident phenotype is close to zero, and the invasion exponent for a mutation in the opposite direction must have the opposite sign, except at critical points of the $\mathscr{I}$ function. When the resident phenotypes are not critical points of $\mathscr{I}$, this invasion function cuts any small enough neighborhood of each resident phenotype into two halves, the mutants that can invade and those that can not.

Any mutant whose invasion exponent is negative must fail to establish itself in the environment; when the invasion exponent is positive, since each mutant population is initially very small, it also may fail to establish itself due to stochastic mortality. If the mutant strain is successful at invading the population, it often displaces its parent strain, which leads to a long-term dynamics in which a fixed number of strains move around the space of possible phenotypes by successive replacements.

The exact conditions under which a mutant strain replaces its parent rather than coexisting with it are not fully known. Continuity of the $\mathscr{I}$ function and its derivatives implies that when the mutant can invade the resident, the resident cannot invade the mutant (when the mutation size is small enough). If multiple attractors are not possible, inability to invade when rare implies that the parent will go extinct. However, a full analysis of this issue has yet to be published. Dercole (2002) presents an "invasion implies substitution" theorem (attributed to F. J. A. Jacobs) that applies to systems with one-dimensional phenotypes whose ecological dynamics always converge on a fixed point. When the phenotype is more than one-dimensional, in simulations with finite mutation sizes, temporary coexistence between parent and daughter strains is common, but in the long term the number of strains tends

to remain constant away from singular points. Most of the literature simply assumes that invasion implies substitution except at singular points, as this is a good approximation to what is observed in the simulations. (In chapter 5, I prove two theorems guaranteeing that invasion exponents predict coexistence and substitution more generally, in three-species Lotka-Volterra models; the two-species Lotka-Volterra version follows directly from Theorem 2.1.)

Under the assumption of successive replacements, the stochastic process of mutation and replacement has been analyzed and shown to converge, as the mutation step size approaches zero, to a mean path approximation (Dieckmann and Law 1996; Ma 2003), which is an ordinary finite-dimensional dynamical system governed by adaptive hill climbing. In a one-dimensional phenotype space, the approximation is

$$\begin{aligned} \dot{s}_i &= \gamma(s_i)\, \hat{X}_i\, \frac{\partial}{\partial s} \mathscr{I}(s|s_1,\ldots,s_n)_{s=s_i} \\ &= \gamma(s_i)\, \hat{X}_i\, \partial_1 \mathscr{I}(s_i) \end{aligned} \tag{3.3}$$

(using the partial derivative notation introduced in section 2.0), where $\gamma(s_i)$ is a scalar factor accounting for the rate and size of mutations and likelihood of stochastic extinction (γ is commonly taken to be constant, as I will generally do). Given n coevolving strains, this is a system of n ordinary differential equations whose dynamic variables are the n phenotypes. At each point, the values of $\hat{X}_i$ and $\partial_1 \mathscr{I}$ must be calculated by characterizing the attractor of the ecological dynamics given that particular ensemble of phenotypes. If the ecological dynamics ever has multiple alternative attractors, the evaluation of the adaptive dynamics can be much more difficult, and the above approximation may not apply (see Rand, Wilson, and McGlade 1994, VanDooren and Metz 1998 and Geritz et al. 2002).

When each species' phenotype is represented by a vector $\mathbf{s}_i$ of scalar traits, an evolving strain can drift randomly away from its expected path and across basin boundaries, subsequently diverging entirely from the mean path approximation (Dieckmann and Law 1996). Additionally, when the adaptive dynamics has a limit cycle or more complicated attractor,

the approximation can fail to predict the mean trajectory of the stochastic system well, as trajectories can wander away from the attractor in complex ways (Ma 2003). Still, if the mutation size is small enough, each trait in the phenotype vector is allowed to mutate independently of the others, and the evolutionary attractors are points, the expected path is a good approximation, giving the same expression for the expected evolutionary dynamics of each trait as before (Dieckmann and Law 1996):

$$(\dot{\mathbf{s}}_i)_k = \gamma_k(\mathbf{s}_i)\ \hat{X}_i\ \frac{\partial}{\partial(\mathbf{s})_k}\mathscr{I}(\mathbf{s}|\mathbf{s}_1,\ldots,\mathbf{s}_n)_{\mathbf{s}=\mathbf{s}_i}.$$

In vector notation, this can be written

$$\dot{\mathbf{s}}_i = \hat{X}_i\ \Gamma(\mathbf{s}_i)\ \partial_1\mathscr{I}(\mathbf{s}_i)^{\mathrm{T}}, \tag{3.4}$$

with $\Gamma(\mathbf{s}_i)$ a diagonal matrix. When mutations of the different traits are not independent, Γ may not be diagonal, reflecting correlations and tradeoffs between phenotypic characters. Differences in mutation processes reflected in Γ can change the qualitative behavior of the system (see Dieckmann and Law 1996; Doebeli and Dieckmann 2000). The *fitness gradient* or *selection gradient* $\partial_1\mathscr{I}(\mathbf{s}_i)^{\mathrm{T}}$, which I will also refer to as $\mathbf{S}(\mathbf{s}_i)$ or simply $\mathbf{S}$, can be viewed as representing the "preferred direction" of evolution, while $\Gamma(\mathbf{s}_i)$ represents the available phenotypic variation, and the two together determine the resultant direction of evolution. However, one also can often rescale the $\mathbf{s}_k$ axes to make γ_k equal, or assume they are equal to begin with, in which case the selection gradient encodes the actual direction of evolution:

$$\dot{\mathbf{s}}_i = \gamma\,\hat{X}_i\,\partial_1\mathscr{I}(\mathbf{s}_i)^{\mathrm{T}}. \tag{3.5}$$

3.2 Stable points and branching points

In either the one- or the many-dimensional case, this dynamical system can be analyzed in terms of stability of fixed points, bifurcations, and so forth. Fixed points, of course,

are found when $\hat{X}_i = 0$ or $\partial_1 \mathscr{I}(\mathbf{s}_i) = 0$ (or if $\Gamma(\mathbf{s}_i) = 0$—or, more often, as we will see, $\Gamma(\mathbf{s}_i)\ \partial_1 \mathscr{I}(\mathbf{s}_i)^{\mathrm{T}} = 0$) for each i. When $\hat{X}_i = 0$ the ith strain no longer exists. The other fixed point condition for (3.5), $\partial_1 \mathscr{I}(\mathbf{s}_i) = 0$, is closely related to the evolutionary game theory concept of the *evolutionarily stable strategy* (ESS). It has often been assumed that locating ESSs—phenotypes that, when resident, can not be invaded by nearby types—entails cataloguing the possible endpoints of evolution (Maynard Smith and Price 1973; Hamilton and May 1977). Since it has been discovered that an ESS may be unreachable by evolution from any other point (Eshel and Motro 1981), the ESS has been augmented by the idea of the *convergence stable strategy* or *continuously stable strategy* (CSS), an attracting fixed point of the evolutionary dynamics. (Here the game-theoretic or economic idea of adapting strategies merges with the ecological concept of evolving phenotypes; the theory is used flexibly in both domains.)

A fixed point of (3.3) or (3.4) that is both a CSS and an ESS is certainly an endpoint of evolution in this model. However, when a singular point is a CSS but not an ESS, mutant strategies near the singular point can invade and coexist with the singular strategy, producing a dimorphic population of two coexisting types. If these two types then evolve away from each other, the dynamics has a *branching point*, a fixed point which attracts a single phenotype, then splits the population into two coexisting phenotypes and repels them in opposite directions—a strange relative of the more familiar saddle point. After passing through a branching point, the system has more coexisting strains than before, and so its adaptive dynamics approximation is a system of more differential equations than before the branching. Extinction (and possibly convergence of two strains—the opposite of branching) can also change the dimensionality of the dynamical system.

A branching point (if strain i is the branching strain) is a fixed point that is attracting when the descendants of strain i are a single strain, and repelling when they are two strains. There are two conditions for a CSS to be a branching point: there must be a direction of mutation from the singular value of $\mathbf{s}_i$ in which mutants can *coexist* with the singular

strategy; and in the higher-dimensional dynamics of these coexisting strains, the fixed point must be *repelling*, that is, they must move apart from each other.

In the adaptive dynamics limit—that is, as the mutation step size becomes infitesimal—evolutionary branching can only happen at a branching point (Dieckmann and Law 1996), though with finite mutation sizes it is sometimes seen (at least temporarily) away from singular points.

3.3 Adaptive dynamics of one strain in one dimension

In a system governed by (3.3), when only one type is present, a fixed point s^* is characterized by $\partial_1 \mathscr{I}(s^*|s^*) = 0$. Since $\mathscr{I}(s'|s)$ is identically 0 along the line $s' = s$, we have as identities $\frac{d}{ds}\mathscr{I}(s|s) = (\partial_1 + \partial_2)\mathscr{I}(s|s) = 0$ and $\frac{d^2}{ds^2}\mathscr{I}(s|s) = (\partial_{11} + 2\partial_{12} + \partial_{22})\mathscr{I}(s|s) = 0$. From the first of these it follows that both first partial derivatives of $\mathscr{I}$ are zero at the fixed point, so the dynamics near the fixed point are determined by second derivatives.

The CSS condition is that for a resident near s^*, $\mathscr{I}(s'|s)$ is positive for mutants even closer to s^*, which works out to $(\partial_{11} + \partial_{12})\mathscr{I}(s^*|s^*) < 0$. The second of the above identities allows the CSS condition to be rewritten (Geritz et al. 1997) as

$$\partial_{11}\mathscr{I}(s^*|s^*) < \partial_{22}\mathscr{I}(s^*|s^*). \tag{3.6}$$

Coexistence requires that the fixed point be a local minimum of $\mathscr{I}$ along the line $(s', s) = (s^* + \Delta s, s^* - \Delta s)$ (Geritz et al. 1997), that is,

$$\partial_{12}\mathscr{I}(s^*|s^*) < 0. \tag{3.7}$$

The condition for the point to be repelling to two similar species, deduced by calculating eigenvalues (Ma 2003), is

$$\partial_{11}\mathscr{I}(s^*|s^*) > 0, \tag{3.8}$$

which is just the opposite of the ESS condition. A branching point is simultaneously a CSS and non-ESS, and since the repelling and CSS conditions taken together imply the

coexistence condition (since $\partial_{12}\mathscr{I} = (\partial_{11} + \partial_{12})\mathscr{I} - \partial_{11}\mathscr{I} < 0$) (Geritz et al. 1997), these two conditions are also sufficient. Consequently, when one strain is present and phenotypes are one-dimensional, a branching point is completely characterized by

$$\partial_1\mathscr{I}(s^*|s^*) = 0 \quad \text{and} \quad 0 < \partial_{11}\mathscr{I}(s^*|s^*) < \partial_{22}\mathscr{I}(s^*|s^*). \tag{3.9}$$

3.4 Adaptive dynamics of one strain in multiple dimensions

As with one-dimensional phenotypes, with m-dimensional phenotypes, an evolutionary fixed point occurs where $\dot{\mathbf{s}}_i = \mathbf{0}$, and the questions of most interest about such a point are whether it is attracting (*i.e.* CSS), and if so, whether it is a branching point. There are no special theorems about stability of a fixed point in this general case; in general, it must be calculated using eigenvalues of the linearization about the point, as in any other dynamical system.

However, it has been pointed out (Meszéna et al. 2000, attributed to O. Leimar) that a sufficient condition for a monomorphic CSS is that the matrix

$$\left(\frac{\partial^2}{\partial(\mathbf{s})_i\partial(\mathbf{s})_j}\mathscr{I}(\mathbf{s}'|\mathbf{s}) + \frac{1}{2}\left(\frac{\partial^2}{\partial(\mathbf{s}')_i\partial(\mathbf{s})_j}\mathscr{I}(\mathbf{s}'|\mathbf{s}) + \frac{\partial^2}{\partial(\mathbf{s})_i\partial(\mathbf{s}')_j}\mathscr{I}(\mathbf{s}'|\mathbf{s})\right)\right)\Bigg|_{\mathbf{s}'=\mathbf{s}=\mathbf{s}^*}$$

is negative definite; the multidimensional analog of the identity $\frac{d^2}{ds^2}\mathscr{I}(s|s) = 0$ is

$$\begin{aligned}\Bigg(\frac{\partial^2}{\partial(\mathbf{s}')_i\partial(\mathbf{s}')_j}\mathscr{I}(\mathbf{s}'|\mathbf{s}) + \frac{\partial^2}{\partial(\mathbf{s}')_i\partial(\mathbf{s})_j}\mathscr{I}(\mathbf{s}'|\mathbf{s}) \\ + \frac{\partial^2}{\partial(\mathbf{s})_i\partial(\mathbf{s}')_j}\mathscr{I}(\mathbf{s}'|\mathbf{s}) + \frac{\partial^2}{\partial(\mathbf{s})_i\partial(\mathbf{s})_j}\mathscr{I}(\mathbf{s}'|\mathbf{s})\Bigg)\Bigg|_{\mathbf{s}'=\mathbf{s}} &= \mathbf{0},\end{aligned}$$

which makes the above condition equivalent to having

$$\left(\frac{\partial^2}{\partial(\mathbf{s}')_i\partial(\mathbf{s}')_j}\mathscr{I}(\mathbf{s}'|\mathbf{s}) - \frac{\partial^2}{\partial(\mathbf{s})_i\partial(\mathbf{s})_j}\mathscr{I}(\mathbf{s}'|\mathbf{s})\right)\Bigg|_{\mathbf{s}'=\mathbf{s}=\mathbf{s}^*}$$

negative definite. These conditions, of course, reduce to the one-dimensional conditions $\partial_{11}\mathscr{I} + \partial_{12}\mathscr{I} < 0$ and $\partial_{11}\mathscr{I} - \partial_{22}\mathscr{I} < 0$, respectively, when $m = 1$. When $m > 1$, however, an evolutionary attracting point can occur without this matrix condition.

A branching point in multidimensional phenotype space has two conditions besides the CSS condition (Ma 2003):

Coexistence: When the stable strategy $\mathbf{s}^*$ is replaced by two strategies $\mathbf{s}_1,\ \mathbf{s}_2$ near $\mathbf{s}^*$ but on opposite sides of it, it must be possible for these two strategies to coexist; that is, $\mathscr{I}(\mathbf{s}_1|\mathbf{s}_2) > 0$ and $\mathscr{I}(\mathbf{s}_2|\mathbf{s}_1) > 0$ for some $\mathbf{s}_1 = \mathbf{s}^* + \Delta\mathbf{s},\ \mathbf{s}_2 = \mathbf{s}^* - \Delta\mathbf{s}$. Given that $\mathscr{I}(\mathbf{s}^*|\mathbf{s}^*) = 0$, this condition becomes

$$\sum_i \sum_j \frac{\partial^2}{\partial(\mathbf{s}')_i \partial(\mathbf{s})_j} \mathscr{I}(\mathbf{s}'|\mathbf{s})\Big|_{\mathbf{s}'=\mathbf{s}=\mathbf{s}^*} (\Delta\mathbf{s})_i (\Delta\mathbf{s})_j < 0.$$

If we introduce the (somewhat cumbersome) notation $D_{\mathbf{v}} f(\mathbf{x})$ for the directional derivative of $f(\mathbf{x})$ calculated by varying $\mathbf{x}$ in the direction of the vector $\mathbf{v}$, and $D_{(\mathbf{v},\mathbf{0})} f(\mathbf{x},\mathbf{y})$ for the directional derivative of $f(\mathbf{x},\mathbf{y})$ calculated by varying $\mathbf{x}$ in the direction of the vector $\mathbf{v}$, and so forth, this can be rewritten

$$D_{(\Delta\mathbf{s},\mathbf{0})} D_{(\mathbf{0},\Delta\mathbf{s})} \mathscr{I}(\mathbf{s}'|\mathbf{s})\big|_{\mathbf{s}'=\mathbf{s}=\mathbf{s}^*} < 0.$$

Repulsion: Given that the ecology can support a dimorphic population near the singular point, branching will occur provided the two types are driven away from the singular point rather than into it. The condition for this is

$$\sum_i \sum_j \frac{\partial^2}{\partial(\mathbf{s}')_i \partial(\mathbf{s}')_j} \mathscr{I}(\mathbf{s}'|\mathbf{s})\Big|_{\mathbf{s}'=\mathbf{s}=\mathbf{s}^*} (\Delta\mathbf{s})_i (\Delta\mathbf{s})_j > 0.$$

or

$$D_{(\Delta\mathbf{s},\mathbf{0})} D_{(\Delta\mathbf{s},\mathbf{0})} \mathscr{I}(\mathbf{s}'|\mathbf{s})\big|_{\mathbf{s}'=\mathbf{s}=\mathbf{s}^*} > 0,$$

for some $\Delta\mathbf{s}$ (which must also satisfy the coexistence condition). Such a direction $\Delta\mathbf{s}$ is a possible branching direction.

The above conditions are certainly satisfied if the matrix

$$\frac{1}{2}\left(\frac{\partial^2}{\partial(\mathbf{s}')_i\partial(\mathbf{s})_j}\mathscr{I}(\mathbf{s}'|\mathbf{s})+\frac{\partial^2}{\partial(\mathbf{s})_i\partial(\mathbf{s}')_j}\mathscr{I}(\mathbf{s}'|\mathbf{s})\right)\Bigg|_{\mathbf{s}'=\mathbf{s}=\mathbf{s}^*}$$

is negative definite and

$$\left(\frac{\partial^2}{\partial(\mathbf{s}')_i\partial(\mathbf{s}')_j}\mathscr{I}(\mathbf{s}'|\mathbf{s})\right)\Bigg|_{\mathbf{s}'=\mathbf{s}=\mathbf{s}^*}$$

is positive definite, though again these conditions are not necessary.

In general, in multiple dimensions, the CSS and non-ESS conditions do not imply coexistence; all three conditions must be checked to determine whether branching is possible (but among the stricter positive and negative definite conditions, the implication actually does apply).

A branching direction corresponds to an eigenvector of the dynamical system generated by considering the branching strain to be two similar strains, and the above positive directional derivative is the eigenvalue associated with it. If there are multiple branching directions, generically the one with the largest eigenvalue will dominate (though there can often be multiple equivalent branching directions corresponding to assigning different combinations of the same branching traits to the two branching strains) (Ma 2003). I will discuss this dimension doubling technique further in the next section.

3.5 Adaptive dynamics of coexisting strains

In the case of a polymorphic population, that is, when multiple strains are present, a fixed point is one at which all strains come to rest together. Stability (that is, the CSS—or maybe ‘convergence stable coalition’ or ‘convergence stable community’—condition) is a property of the entire system, not of each strain separately, and must be calculated in terms of eigenvalues of the Jacobian matrix of the system (3.3) at the fixed point.

A stable point of the dynamics of *n* strains (in *mn* dimensions) has *mn* eigenvalues λ_p,

all of which must have negative real part. In order to look at branching, we can make a $2mn$-dimensional system by including two copies of each strain, each pair of which may relax to the diagonal on which they are identical, or may diverge. A fixed point of the original system is a fixed point of the doubled system, and the diagonal subspace where $\mathbf{s}_i = \mathbf{s}'_i$ for all i is invariant, so that the eigenvalues λ_p of the original system are also eigenvalues of the doubled system. But the doubled system also has mn additional eigenvalues μ_p, which may indicate unstable directions prone to branching.

By doubling one strain at a time we can identify possible branching directions. If branching directions exist, a branching will occur, though as we will see, of the strains that satisfy the branching conditions, it may be that only some of them actually branch.

In one-dimensional phenotypes, Ma (2003) has shown that the n added eigenvalues are of the form $\mu_i = \hat{X}_i \, \partial_{11'} \mathscr{I}(s_i|s_1,\ldots,s_n)$ and, when positive, correspond to eigenvectors along which the two branching strains are repelled from the singular point in opposite directions, at equal speeds, and no other strains move. Thus, as in the monomorphic case, the post-branching repelling condition is the non-ESS condition $\partial_{11'}\mathscr{I}(s_i) > 0$. Unlike the monomorphic case, however, repelling does not imply coexistence. Coexistence of strain i with a nearby variant requires $\partial_{12'}\mathscr{I}(s_i) < 0$ (Ma 2003).

In multidimensional-phenotype systems as well, the repelling and coexistence conditions can be evaluated strain-by-strain. In either case, if the (unstable) dominant eigenvalue or eigenvalues μ_p all belong to one strain (and the coexistence condition is met), a separation of timescales argument shows that that strain will branch (Doebeli and Dieckmann 2000). If dominant eigenvalues belong to more than one strain this argument does not apply.

Once branching directions are identified, there can still be many complications in predicting what the actual branching behavior of the model will be. When multiple strains have possible branching directions, but one branching happens faster than another (having an eigenvalue with larger positive real part), the other branchings may not happen, as the

linearization no longer applies away from the singular point. It can also happen that the ecology does not support enough coexisting types to allow all the branchings indicated by the above calculations. Geritz and coworkers (Geritz et al. 1998) present an example of a three-patch metapopulation model that can support three coexisting types. One strain in this model branches into two, which then reach another branching point where both can branch. However, since four types cannot coexist, one strain can branch, but then the other cannot as it no longer has a region of coexistence near the branching point. Which branch is taken is determined arbitrarily by the stochastic mutation process. Ma (2003) presents a model based on competition for three resources that behaves in the same way.

Additionally, if two or more traits of the same strain are liable to branching, they can be assigned to the two descendant strains in various combinations, one of which ends up being arbitrarily chosen by the mutation process, and this can be an important path-dependence mechanism by which a very small random fluctuation is amplified into a crucial choice between subsequent trajectories of the system (Ma 2003).

3.6 Constraints on phenotypes

The foregoing calculations for the evolution of an m-dimensional phenotype presume that each entry in the phenotype vector is capable of evolving independently of the others. When tradeoffs or other forms of constraint restrict the range of realizable combinations of trait values, confining the motion of the phenotype vector $\mathbf{s}_i$ to a subset of the full space of possible vectors ($\mathbb{R}^m$), these calculations must be redone. When the set of realizable phenotypes, though possibly bounded, is m-dimensional, and the type in question occupies the interior of that set, the evolution of that type is unaffected by restrictions elsewhere in the space of possibilities, and proceeds as in (3.5). When evolution reaches the boundary of such a set, however, or when the set of realizable possibilities is of smaller dimension than the space of possible $\mathbf{s}_i$, the motion of $\mathbf{s}_i$ is confined to a lower-dimensional manifold

within $\mathbb{R}^m$, and its derivative must be recalculated accordingly.

A phenotype $\mathbf{s}_i$ restricted to a k-dimensional submanifold Σ of $\mathbb{R}^m$ can be parametrized, at least locally, as $\mathbf{s}_i = \mathbf{s}(\mathbf{u}_i)$, with $\mathbf{u}_i \in \mathbb{R}^k$. If the components of $\mathbf{u}_i$ are free to mutate independently, then we are in fact studying a k-dimensional adaptive dynamics problem in which $\mathbf{s}_i$ can simply be seen as a notational convenience. In this case, equation (3.5) can be applied directly to each $\mathbf{u}_i$:

$$\dot{\mathbf{u}}_i = \gamma \hat{X}_i \, \partial_{1:} \mathscr{I}(\mathbf{u}_i)^{\mathrm{T}}. \tag{3.10}$$

From this we can calculate the dynamics of $\mathbf{s}_i$ by means of the chain rule:

$$\begin{aligned} \dot{\mathbf{s}}_i &= \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i} \dot{\mathbf{u}}_i \\ &= \gamma \hat{X}_i \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i} \partial_{1:} \mathscr{I}(\mathbf{u}_i)^{\mathrm{T}} \\ &= \gamma \hat{X}_i \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i} \left(\partial_{1:} \mathscr{I}(\mathbf{s}_i) \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i} \right)^{\mathrm{T}} \\ &= \gamma \hat{X}_i \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i} \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}} \partial_{1:} \mathscr{I}(\mathbf{s}_i)^{\mathrm{T}}. \end{aligned} \tag{3.11}$$

Now what can be said about fixed points of this system? Clearly, as before, a phenotype $\mathbf{s}_i$ comes to rest when $\hat{X}_i = 0$ (which makes the phenotype irrelevant), or when $\mathbf{S}(\mathbf{s}_i) = \partial_{1:} \mathscr{I}(\mathbf{s}_i)^{\mathrm{T}} = 0$, that is, at a point which would be a fixed point of $\mathbf{s}_i$ even if its motion were not restricted. Since we have assumed nothing about $\mathscr{I}$ except smoothness, little can be said about the interpretation of this condition. In practice, as we shall see, when we have reason to choose a representation of the populations' phenotypes that is not maximally terse—writing the ecological equations in terms of m rather than k trait values—it is likely because that representation is well-matched to the form of $\mathscr{I}$, and this often leads to a form in which the selection gradient $\mathbf{S}$ is never zero.

However, it is also possible for the derivative of $\mathbf{s}_i$ to come to zero when neither of these conditions is met. Since the matrix $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}}$ is of dimension $k \times m$, there is a null space of dimension $m - k$ (if not more—let us assume the surface is smooth and well behaved)

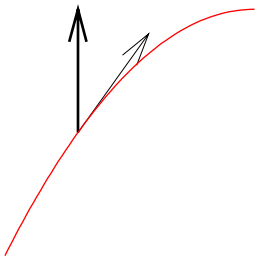


Figure 3.1: Illustration of evolutionary motion on a constraint curve. The selection gradient $\mathbf{S}$ points in some direction not tangent to the constraint curve; the component of $\mathbf{S}$ tangent to the curve is the direction of evolutionary motion.

of vectors $\mathbf{N}$ for which $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}} \mathbf{N} = 0$. To interpret this condition, notice that each row of this matrix is of the form $\left(\frac{\partial (\mathbf{s}_i)_1}{\partial (\mathbf{u}_i)_j}, \ldots, \frac{\partial (\mathbf{s}_i)_m}{\partial (\mathbf{u}_i)_j} \right)$, which summarizes the direction of change in $\mathbf{s}_i$ induced by increasing the jth component of $\mathbf{u}_i$. Linear combinations of these rows are vectors tangent to the surface $\mathbf{s}(\mathbf{u})$ at $\mathbf{s}(\mathbf{u}_i)$. A vector whose inner product with each of these tangent vectors is zero, that is, a vector in the null space of $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}}$, therefore must be normal to the surface at $\mathbf{s}(\mathbf{u}_i)$.

In fact, let us take this geometrical interpretation one step further. The rows of $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}}$ are a basis for the k-dimensional space tangent to the surface $\mathbf{s}(\mathbf{u})$ at $\mathbf{u}_i$. Whether it is zero or not, the vector $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}} \partial_1 \mathscr{I}(\mathbf{s}_i)^{\mathrm{T}} = \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}} \mathbf{S}(\mathbf{s}_i)$ is the projection of the m-dimensional vector $\mathbf{S}(\mathbf{s}_i)$ into that tangent space, expressed in the coordinates of that basis. Multiplication by $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}$ transforms that projected vector back into the coordinates of $\mathbf{s}_i$. (Since $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}$ is a matrix of rank k that operates on k-dimensional vectors, $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i} \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}} \mathbf{S}(\mathbf{s}_i)$ cannot be zero unless $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}} \mathbf{S}(\mathbf{s}_i) = \mathbf{0}$.)

Therefore, for any vector-valued phenotype $\mathbf{s}_i$ constrained to a manifold that can be locally parametrized (explicitly or not) by a smooth function $\mathbf{s}(\mathbf{u})$, the direction of motion of $\mathbf{s}_i$ on that manifold under the assumptions of adaptive dynamics is the projection of the

vector $\mathbf{S} = \frac{\partial \mathscr{F}}{\partial \mathbf{s}_i}^{\mathrm{T}}$—which is the direction that $\mathbf{s}_i$ would move if not constrained—onto the constraint manifold. Motion comes to rest when the selection gradient is zero or perpendicular to the constraint manifold.

Evolutionary motion on a phenotypic constraint curve, in the direction of the selection gradient $\mathbf{S}$ projected onto the curve, is illustrated in figure 3.1.

Notice the similarity between equation (3.11) and equation (3.4). In equation (3.11), as in (3.4), $\mathbf{S}(\mathbf{s}_i)$ represents the "preferred direction" of evolution, while $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}}$, in the place of $\Gamma(\mathbf{s}_i)$, filters the action of selection through a biased distribution of available phenotypic variation.

While the introduction of an intermediate variable $\mathbf{s}_i$, of course, does not produce a different dynamical system than would be found by writing the dynamics in terms of $\mathbf{u}_i$, it can make the adaptive dynamics much easier to interpret, and possibly easier to calculate as well. Additionally, such a constrained variable $\mathbf{s}_i$ can be used when the underlying parametrization is never made explicit.

3.7 Example

To illustrate how this constrained-vector approach can help simplify the treatment of evolutionary problems, consider the classic example of *K*-selection. Roughgarden's analysis of this example (Roughgarden 1976) uses a population genetics framework to study the dynamics of a population governed by

$$\Delta N = (\bar{W} - 1)N$$

where

$$\bar{W} = \bar{W}(p,N) = p^2 W_{11}(N) + 2p(1-p)W_{12}(N) + (1-p)^2 W_{22}(N)$$

and

$$W_{ij}(N) = r_{ij}\left(1 - \frac{N}{K_{ij}}\right) + 1,$$

and showed that selection drives the gene frequency p to whatever value maximizes the equilibrium population size $\hat{N}$. The proof occupies several pages and requires several applications of the implicit function theorem and explicit calculation of matrix eigenvalues.

The above expressions can be rewritten as

$$\bar{W} = r(p)\left(1 - \frac{N}{K(p)}\right) + 1$$

using the appropriate expressions for $r(p)$ and $K(p)$; in what follows we may use these or any other (positive) choice of $r(p)$ and $K(p)$. Take p to be a phenotypic character subject to mutation rather than a single-allele gene frequency, and then we can analyze evolution in this system in terms of

$$\mathbf{s} = \begin{pmatrix} r \\ K \end{pmatrix}$$

as a function of p.

Given a resident type $\mathbf{s}$ (in which case $\hat{N} = K$), the invasion function for a mutant $\mathbf{s}'$ is

$$\begin{aligned} \mathscr{I}(\mathbf{s}'|\mathbf{s}) = \left\langle \log \bar{W}(p', \hat{N}(p)) \right\rangle_{N' \to 0} &= \log\left[r'\left(1 - \frac{\hat{N}(p)}{K'}\right) + 1\right] \\ &= \log\left[r'\left(1 - \frac{K}{K'}\right) + 1\right]; \end{aligned}$$

so the direction of selection is

$$\left(\frac{\partial}{\partial \mathbf{s}'}\mathscr{I}(\mathbf{s}'|\mathbf{s})\right)^{\mathrm{T}}_{\mathbf{s}'=\mathbf{s}} = \begin{pmatrix} \frac{\partial}{\partial r'}\mathscr{I}(\mathbf{s}'|\mathbf{s}) \\ \frac{\partial}{\partial K'}\mathscr{I}(\mathbf{s}'|\mathbf{s}) \end{pmatrix}_{\mathbf{s}'=\mathbf{s}} = \frac{1}{r'\left(1 - \frac{K}{K'}\right) + 1} \begin{pmatrix} 1 - \frac{K}{K'} \\ \frac{r'K}{K'^2} \end{pmatrix}\Bigg|_{\mathbf{s}'=\mathbf{s}} = \begin{pmatrix} 0 \\ \frac{r}{K} \end{pmatrix}.$$

This vector points directly in the direction of increasing K. No matter what mapping we choose between p, r, and K (or what tradeoff between r and K), the projection of this vector onto the r-K curve must point in a direction that increases K (which is of course equivalent to increasing $\hat{N}$) . Therefore the evolutionary dynamics always moves $\mathbf{s}$ in whichever direction increases $\hat{N}$, and comes to rest when $\hat{N}$ is at a local maximum.

3.8 Attraction and branching on a constraint curve

Let us consider adaptive motion of one species on a curve in a higher dimensional space, since that is an application of the one-dimensional adaptive dynamics theory. Here we have a curve $\mathbf{s} = \mathbf{s}(u)$, with a vector $\mathbf{S}(\mathbf{s}) = \partial_1 \mathscr{I}(\mathbf{s}|\mathbf{s})^{\mathrm{T}}$ pointing the direction of evolution at each point. The equations of motion are

$$\dot{u} = \gamma \hat{X} \partial_1 \mathscr{I}(u|u) \tag{3.12}$$

and

$$\begin{aligned} \dot{\mathbf{s}} &= \gamma \hat{X} \mathbf{s}'(u) \mathbf{s}'(u)^{\mathrm{T}} \partial_1 \mathscr{I}(\mathbf{s}|\mathbf{s})^{\mathrm{T}} \\ &= \gamma \hat{X} \mathbf{s}'(u) \mathbf{s}'(u)^{\mathrm{T}} \mathbf{S}. \end{aligned}$$

A fixed point of the dynamics satisfies

$$\mathbf{s}'(u^*)^{\mathrm{T}} \mathbf{S} = \left\langle \mathbf{s}'(u^*), \mathbf{S} \right\rangle = 0. \tag{3.13}$$

The CSS condition is

$$\begin{aligned} (\partial_{11} + \partial_{12}) \mathscr{I}(u^*|u^*) &< 0 \\ \frac{d}{du} \partial_1 \mathscr{I}(u|u) &< 0 \\ \frac{d}{du} \left(\partial_1 \mathscr{I}(\mathbf{s}(u)|\mathbf{s}(u)) \, \mathbf{s}'(u) \right) &< 0 \\ \frac{d}{du} \left\langle \mathbf{s}'(u), \mathbf{S} \right\rangle &< 0, \end{aligned}$$

which, given $\langle \mathbf{s}', \mathbf{S} \rangle = 0$ at the fixed point, says that $\langle \mathbf{s}'(u), \mathbf{S} \rangle$ is positive when $u < u^*$ and negative when $u > u^*$, that is, that $\mathbf{S}$ points toward the fixed point, as one would expect. There are (assuming $\mathbf{S}$ does not vanish) two ways this can happen, and expanding out this expression shows that:

$$\frac{d}{du} \left\langle \mathbf{s}'(u), \mathbf{S} \right\rangle = \left\langle \mathbf{s}'(u), \mathbf{S}'(u) \right\rangle + \left\langle \mathbf{s}''(u), \mathbf{S} \right\rangle.$$

Figure 3.2: Illustration of conditions for a convergence stable strategy on a curve. Left, the selection gradient **S** turns toward the fixed point; right, the fixed point maximizes fitness on the curve while selection is constant.

If the first term of this expression is negative, it indicates that **S** is turned toward the fixed point at nearby points on the curve; if the second term is negative, it means that the curve $\mathbf{s}(u)$ curves away from **S** at the fixed point. These two situations are illustrated in figure 3.2. If only one of these two conditions is met, the other must fail weakly enough that the sum does not become positive.

Given the CSS condition, the branching condition is

$$\begin{aligned} \partial_{11}\mathscr{I}(u^*|u^*) &> 0 \\ \frac{d}{du}\partial_1\mathscr{I}(u|u^*) &> 0 \\ \frac{d}{du}\left(\partial_1\mathscr{I}(\mathbf{s}(u)|\mathbf{s}^*)\,\mathbf{s}'(u)\right) &> 0 \\ \left(\frac{d}{du}\partial_1\mathscr{I}(\mathbf{s}(u)|\mathbf{s}^*)\right)\,\mathbf{s}'(u) + \left\langle \mathbf{s}''(u), \mathbf{S}\right\rangle &> 0. \end{aligned}$$

The branching condition is simply that when the singular strategy is resident, all nearby variants on the curve are able to invade. On a curve, this condition also has two parts. The fixed point condition $\langle \mathbf{s}', \mathbf{S}\rangle = 0$ implies that to first order, points along the line tangent to the curve at a fixed point have invasion exponent 0. The first term of the expanded branching condition represents the second derivative of the invasion function along this direction; if it

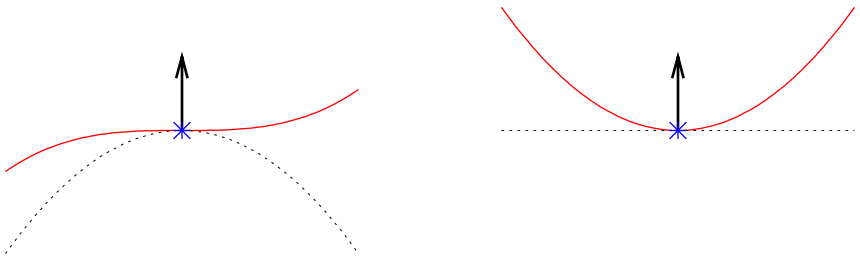


Figure 3.3: Illustrations of conditions for a branching point on a curve (assuming the point is convergence stable). The red line represents the constraint curve, while the dotted line represents the boundary between positive and negative fitness when the singular strategy is resident. Left, the second derivative of the fitness function makes fitness positive along the direction tangent to the curve; right, the second derivative of the constraint curve bends it into the region of positive fitness.

is positive (all else being equal) the condition will be satisfied. The second term expresses that if the curve is concave in the direction of positive fitness, the branching condition can be met even if $\mathscr{I}$ is constant along the tangent direction. These two conditions are illustrated in figure 3.3.

Similar diagrams can surely be drawn for higher-dimensional constraint surfaces, at least for the restricted cases of positive and negative definite matrices outlined above; they would, of course, be more complex and have more cases.

3.9 Discussion

The foregoing treatment of adaptive dynamics subject to ontogenetic or environmental constraints or tradeoffs, which as far as I know is original[1], is clearly reminiscent of Levins' fitness set formulation of the evolution of mutually constrained characters (Levins 1962;

[1]The use of constraint functions in this way is indicated in Rand and Wilson 1993, but is not developed mathematically.

Levins 1963), and both are, of course, descended from Sewall Wright's image of evolution as adaptive hill climbing of the fitness function (Wright 1932). Each of these earlier treatments, however, is limited to considering the adaptation of a single population governed by a fitness function that does not change.

In the current discussion, where $\mathscr{I}$ is the fitness function and the adaptive dynamics is clearly analogous to hill climbing in the sense of following the gradient of increasing $\mathscr{I}$, it is also clearly not hill climbing in the sense that the direction of increasing $\mathscr{I}$ changes continuously as the makeup of the community of resident types changes. This makes it possible for an adaptive dynamical system to exhibit limit cycle behavior (see Dieckmann, Marrow, and Law 1995, for example; even limit cycles that occupy different numbers of dimensions on different segments of the cycle, as in Kisdi, Jacobs, and Geritz 2000) and possibly chaos.

Any system that can be analyzed in this way can be analyzed directly, writing the ecological dynamics in terms of the most parsimonious representation $\mathbf{u}$ of the phenotypic characters in question, with no explicit consideration of how the ecological characteristics ($\mathbf{s}$) of each type are derived from its physical and behavioral characteristics ($\mathbf{u}$). All of the results are the same, but constructing such a derived representation can greatly simplify calculations, as we have seen, and can reveal much more about what ecological characteristics a population's environment is "selecting for" than simply predicting in what direction its phenotypes will change. In chapter 4 I will use this framework to present an analysis of a model system with an unspecified number of phenotypic dimensions that would be difficult or impossible without considering the phenotypes to be embedded in a constraint surface in a higher-dimensional space.

Chapter 4

Evolution of Phenotypes and Interactions

The first half of this chapter re-presents the adaptive dynamics results of Chapter 3 in the special case of Lotka-Volterra dynamics, and relates the dynamics of Lotka-Volterra interactions to the dynamics of the phenotypes from which they are derived. Evolutionary branching is shown to be characterized by the branches' inter-strain interactions being more favorable to them than their intra-strain interactions.

The second half of this chapter presents a simple model in which Lotka-Volterra interaction terms are derived linearly from populations' phenotypic traits. I use this model to explore adaptive dynamics on constraint surfaces, and to investigate how coevolution changes interactions, and in particular how competitive interactions can become less so, even to the point of converting into mutualistic interactions. Along the way, we see how the linearity of the model can make it both easier to analyze and more prone to unrealistic degenerate behaviors than more complex models. Finally, I introduce a nonlinearity into the model in order to avoid these degeneracies and look at its long-term behavior.

4.1 Adaptive dynamics in Lotka-Volterra systems

When an ecological model governed by Lotka-Volterra equations is used as the ecological model for an adaptive dynamics system, the r_i and a_{ij} values that parametrize the equations are taken to be functions of the interacting organisms' phenotypes, $r_i = r(\mathbf{s}_i)$ and $a_{ij} = a(\mathbf{s}_i, \mathbf{s}_j)$. As the phenotypes shift around in phenotype space, the entries in the **r** vector and the **a** matrix change, and the invasion function and equilibrium abundances are determined by the values of **r** and **a**. When a branching or extinction occurs, these objects expand or shrink to include more or fewer entries. The adaptive dynamics conditions we have discussed in terms of the $\mathscr{I}$ function can be restated in terms of the values of **r** and **a**, and vector and matrix properties emergent from them.

4.1.1 Phenotypes and interactions

The convention in adaptive dynamics and most population genetics is to use quantitative phenotypic characters as parameters to the population dynamics. For instance, if the evolution of body size is being considered, each organism's body size is represented by a number, and the population dynamics is written as equations describing the dynamics of n populations as a function of the populations' abundances and characteristic body sizes. From these dynamics, information about evolutionary changes in body sizes is derived. Genotypes are typically not explicitly considered in these models. This makes it possible to look at two levels of phenomena: population dynamics and changes to phenotypic characters. In more philosophical treatments of the matter, the point is made that fitness—the quantity from which all the effects of natural selection arise—is the result of the combination of all interactions between an individual of the population under consideration and that individual's external environment, where the 'external environment' is defined to include all abiotic factors, other populations in the system, and even the rest of the focal individual's own population. Sometimes (Metz and Meszéna 1999; Geritz et al. 1997) this concept is

made explicit by defining the *feedback environment* **E**, a mathematical quantity incorporating all the factors that determine the expected reproductive ability of an individual. Then in principle, all the population dynamics are determined by the ensemble of types present and the state of the environment; that is, the system has the form

$$\dot{X}_i = X_i f(\mathbf{s}_i, \mathbf{E})$$

where X_i is the size of population i and $\mathbf{s}_i$ is its phenotype. (The dimension of **E** then determines the number of types that can coexist, in a slight generalization of the known relationship between diversity and the number of controlling factors (Metz and Meszéna 1999; MacArthur and Levins 1964; Levin 1970; Tilman 1982).)

While it seems trivial to say that the effect of an organism's environment on its fitness is the sum of its interactions with the various organisms and abiotic factors in the environment, in a Lotka-Volterra model this is strictly true. The effect of each interaction with another organism is a number a_{ij}, the combined effect of interaction with everything else is a number r_i, and the function f described above is the sum of the expected number of these interactions. The explicit quantitative representation of interactions in the Lotka-Volterra equations makes them useful as an intermediate level between phenotypes and the result population dynamics. The flexibility of the Lotka-Volterra representation of interactions makes it natural to ask questions about, for instance, the conversion of competitive or predator-prey interactions into mutualistic interactions, where models using a more detailed representation of a particular form of interaction are thereby forced to study only one kind of interaction at a time (as in Dieckmann, Marrow, and Law 1995; Doebeli and Dieckmann 2000, etc.).

As we shall see, no matter what assumptions we make about the phenotypic traits characterizing the populations subject to evolutionary change in our models, the selective pressure on these populations is always decomposable into the selective pressure on the

ensemble of interaction terms and the mapping between phenotypic characters and interaction terms. I believe that this decomposition suggests some interesting questions about how interactions evolve and how evolution structures ecological communities (after all, the 'structure' of an ecological community is commonly taken to be synonymous with the network of interactions that defines the community).

The flexible, explicit representation of interactions in this way also provides an invaluable visualization tool which I will use extensively to analyze evolutionary dynamics in this thesis. Models of phenotypic evolution present at least two visualization problems: the common dynamical systems problem of representing motion in a phase space of more than three dimensions, and the problem that the number of dimensions of the phase space changes as the number of coexisting types changes. The adaptive dynamics community has developed two visual conventions: the branching display of phenotypic trait values against time, and the pairwise invasion plot indicating which phenotypes can invade which (see, for instance, Metz et al. 1996). While the phenotypes-against-time plot has no problem representing a changing number of types, it is really only suitable for one-dimensional phenotypes, and the pairwise invasion plot can only represent one resident type and one mutant, with one-dimensional phenotypes.

In a Lotka-Volterra model, no matter how complex organisms' phenotypes are taken to be, the interaction terms derived from them are always scalar quantities. By simply graphing all interaction terms against time on one graph, it is possible to display the results of coevolution in systems for which other forms of display are not available—such as systems with high dimensional phenotypes, and systems, as we shall see, in which phenotypes are not modeled at all.

Figure 4.1 is a typical plot of branching phenotypic trait values, generated by a model of asymmetric competition published by adaptive dynamics researcher Éva Kisdi (1999). This plot makes it clear that the initial strain evolves to a branching point (see chapter 3), at which it becomes two strains that separate from each other in aspect space. One of these

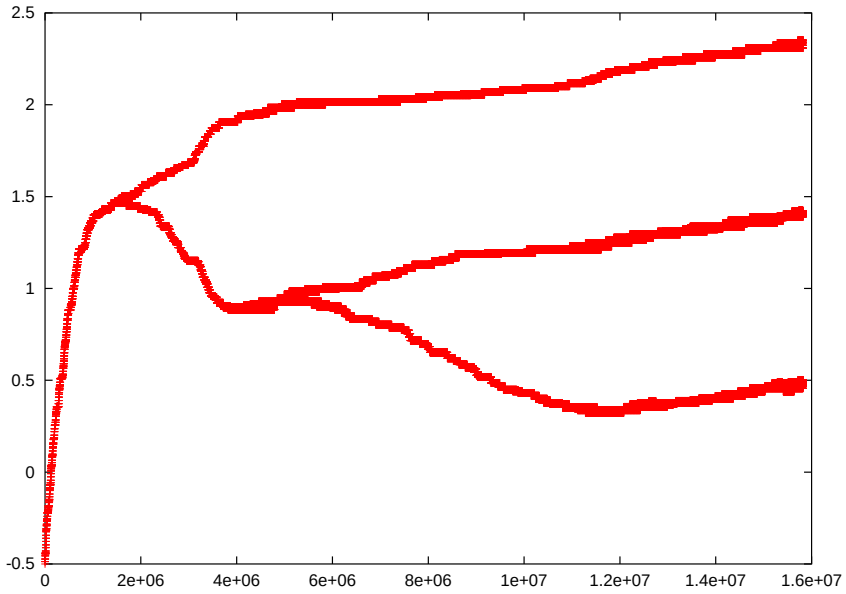


Figure 4.1: Evolution of phenotype values in asymmetric competition model (Kisdi 1999). One initial strain diversifies into two, one of which then branches again.

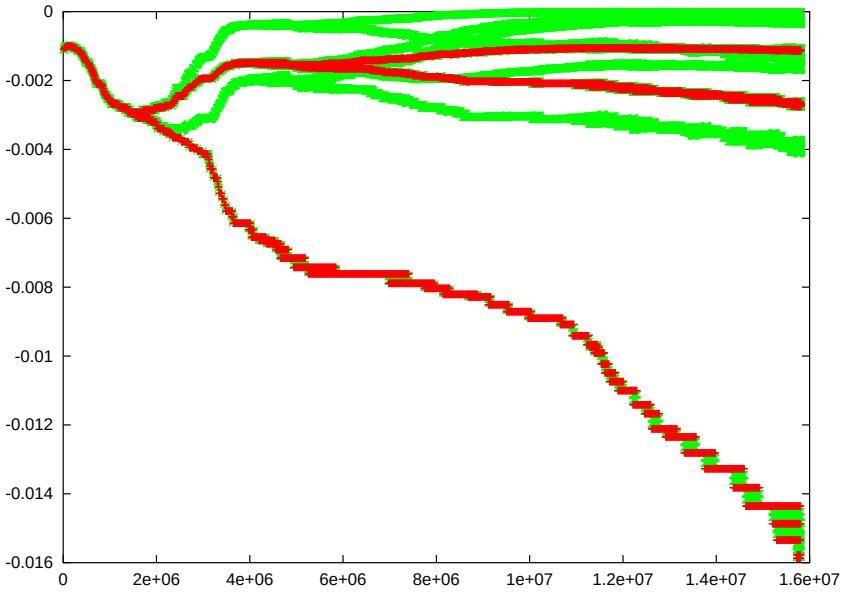


Figure 4.2: Evolution of interaction terms in asymmetric competition model (Kisdi 1999). Red points represent diagonal terms and green points represent all other terms.

two later branches again. Figure 4.2 displays the evolution of the interaction terms in this model, which uses Lotka-Volterra equations for its ecological dynamics. The branching of lineages can be read from this figure by following the red lines, which represent the diagonal terms of the **a** matrix. This plot also makes it clear at the first branching that as these lineages separate, the strengths of the interactions between separate lineages (the green lines) rise towards zero, indicating that these populations are evolving in such a way as to reduce competition between them. Being a model of competing populations, this model is defined in such a way that interaction terms can never become positive, and so this plot is bounded above by zero.

4.1.2 Lotka-Volterra adaptive dynamics formulas

As we have seen, in a Lotka-Volterra system the invasion function of a new variant strain works out to a linear sum of mutations in the strain's growth rate and interaction terms:

$$\mathscr{I}(\mathbf{s}_{i'}) = \Delta r_{i'} + \sum_{j \neq i'} \Delta a_{i'j} \hat{X}_j \tag{4.1}$$

where $\hat{\mathbf{X}}$ is a fixed point of (2.1) with each $\hat{X}_j > 0$. When the variant phenotype $\mathbf{s}_{i'}$ is very similar to its parent, of course, the invasion function is approximated by

$$\mathscr{I}(\mathbf{s}_{i'}) \approx \partial_1 \mathscr{I}(\mathbf{s}_i) \Delta \mathbf{s}_i$$

and the selection gradient is

$$\partial_1 \mathscr{I}(\mathbf{s}_i) = \partial_1 r(\mathbf{s}_i) + \sum \partial_1 a(\mathbf{s}_i, \mathbf{s}_j) \hat{X}_j.$$

In the case of one-dimensional phenotypes, the selection gradient is

$$\begin{aligned} \partial_1 \mathscr{I}(s_i) &= \partial_1 r(s_i) + \sum \partial_1 a(s_i, s_j) \hat{X}_j \\ &= \partial_1 r(s_i) + \partial_1 \mathbf{a}_{i\cdot} \hat{\mathbf{X}} \\ &= \partial_1 r(s_i) + \partial_1 \mathbf{a}_{i\cdot} (-\mathbf{a}^{-1} \mathbf{r}), \end{aligned}$$

where $\partial_1 \mathbf{a}_{i\cdot} = (\partial_1 a(s_i, s_1), \ldots, \partial_1 a(s_i, s_n))$ is the first partial derivative of the i'th row of $\mathbf{a}$. The known results for adaptive dynamics in one dimension are applicable. Evolution moves s_i in whichever direction $\partial_1 \mathscr{I}(s_i)$ is positive.

Evolutionarily singular points occur where $\partial_1 \mathscr{I}(s_i) = 0$ for all i at once (Ma 2003):

$$\partial_1 \mathbf{r} - (\partial_1 \mathbf{a}) \mathbf{a}^{-1} \mathbf{r} = \mathbf{0}. \tag{4.2}$$

This condition is stated entirely in terms of the a and r functions, and in principle can be expanded into an explicit equation whose roots are all possible evolutionarily singular configurations of phenotypes $(s_1, \ldots, s_n)$ for any n. While solving such an equation is not

a simple task, it may be that in cases where it can't be solved it can still be used to show that, say, there is no singular point with four populations (and thus four can never become more) or such things. Also, when r is constant, (4.2) becomes

$$(\partial_1 \mathbf{a})\mathbf{a}^{-1}\mathbf{r} = \mathbf{0}, \tag{4.3}$$

which may be far more workable. At least when $\mathbf{r}$ is nonzero, this condition requires $\partial_1 \mathbf{a}$ to be a singular matrix. This observation raises the possibility that additional singularities can occur when the $\mathbf{a}$ matrix becomes singular, in which case $\mathbf{a}^{-1}$ does not exist and the ecological dynamics (2.1) does not have a unique equilibrium.

The expanded representation of (4.2) is

$$\frac{\partial r(s_i)}{\partial s_i} - \sum_j \frac{\partial a(s_i, s_j)}{\partial s_i} \sum_k (\mathbf{a}^{-1})_{jk} r(s_k) = 0 \quad \forall i.$$

When $\mathbf{s}_i$ is a vector, the corresponding condition is

$$\frac{\partial r(\mathbf{s}_i)}{\partial (\mathbf{s}_i)_l} - \sum_j \frac{\partial a(\mathbf{s}_i, \mathbf{s}_j)}{\partial (\mathbf{s}_i)_l} \sum_k (\mathbf{a}^{-1})_{jk} r(\mathbf{s}_k) = 0 \quad \forall i \, \forall l, \tag{4.4}$$

which is essentially the same, but cannot be written so easily in matrix notation because $\partial_1 \mathbf{a}$ takes three indices.

In the case of vector phenotypes $\mathbf{s}_i$ constrained to a curve or surface parametrized by some $\mathbf{u}_i$, the evolutionary singular point condition is not simply $\partial_1 \mathscr{I}(\mathbf{s}_i) = \mathbf{0}$ for all i, as above, but $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}} \partial_1 \mathscr{I}(\mathbf{s}_i) = \mathbf{0}$ for all i, which can be expanded into an expression including all the above terms, if necessary.

4.1.3 Classification of singular strategies

In this section I assume r is a constant function and only a is subject to evolution, and look at how the CSS and branching conditions are determined by the a function in the case of one strain in one dimension. A fixed point s^*, as we have seen, is characterized

by $\partial_1 \mathscr{I}(s^*, s^*) = 0$; it is an (attracting) branching point if $0 < \partial_{11} \mathscr{I}(s^*, s^*) < \partial_{22} \mathscr{I}(s^*, s^*)$. Now we must rewrite these conditions in terms of a.

The first partial derivative of $\mathscr{I}$ is simply

$$\partial_1 \mathscr{I}(s'|s_i) = \hat{X}_i \, \partial_1 a(s', s_i),$$

and evaluated at the fixed point is

$$\partial_1 \mathscr{I}(s^*|s^*) = \hat{X}^* \, \partial_1 a^*,$$

where $a^* = a(s^*, s^*)$ is the interaction term at the singular point, $\hat{X}^* = -1/a^*$ is the equilibrium population at the singular point, and $\partial_1 a^*$ is the first partial derivative of a evaluated there. So the fixed point condition is just

$$\partial_1 a^* = 0.$$

The second derivatives are, in increasing order of complexity,

$$\partial_{11} \mathscr{I}(s'|s_i) = \hat{X}_i \, \partial_{11} a(s', s_i),$$

which at the fixed point is

$$\partial_{11} \mathscr{I}(s^*|s^*) = \hat{X}^* \, \partial_{11} a^*;$$

next,

$$\begin{aligned}
\partial_{12} \mathscr{I}(s'|s_i) &= \frac{\partial}{\partial s_i} \hat{X}_i \, \partial_1 a(s', s_i) \\
&= -\frac{\partial}{\partial s_i} \frac{\partial_1 a(s', s_i)}{a(s_i, s_i)} \\
&= -\frac{\partial_{12} a(s', s_i) \; a(s_i, s_i) - \partial_1 a(s', s_i) \; (\partial_1 + \partial_2) a(s_i, s_i)}{a(s_i, s_i)^2} \\
&= \hat{X}_i \, \partial_{12} a(s', s_i) + \hat{X}_i^2 \, \partial_1 a(s', s_i) \; (\partial_1 + \partial_2) a(s', s_i),
\end{aligned}$$

and at the fixed point

$$\partial_{12} \mathscr{I}(s^*|s^*) = \hat{X}^* \, \partial_{12} a^* + \hat{X}^{*2} \, \partial_1 a^* \; (\partial_1 + \partial_2) a^*;$$

because $\partial_1 a^* = 0$ this simplifies to

$$\partial_{12}\mathscr{I}(s^*|s^*) = \hat{X}^*\,\partial_{12}a^*;$$

and finally

$$\begin{aligned}\partial_{22}\mathscr{I}(s'|s_i) &= \frac{\partial^2}{\partial {s_i}^2}\hat{X}_i\,a(s',s_i)\\ &= -\frac{\partial^2}{\partial {s_i}^2}\frac{a(s',s_i)}{a(s_i,s_i)},\end{aligned}$$

which comes out to

$$\partial_{22}\mathscr{I}(s'|s_i) = -\hat{X}_i\,(\partial_{11}a(s',s_i)+2\,\partial_{12}a(s',s_i)) - 2\hat{X}_i^2\,(\partial_1 a(s',s_i)\,(\partial_1+\partial_2)a(s_i,s_i))$$

and

$$\partial_{22}\mathscr{I}(s^*|s^*) = -\hat{X}^*(\partial_{11}a^*+2\,\partial_{12}a^*).$$

It can easily be verified that $(\partial_{11}+2\partial_{12}+\partial_{22})\mathscr{I} = 0$.

Now the CSS condition

$$\partial_{11}\mathscr{I}(s^*|s^*) < \partial_{22}\mathscr{I}(s^*|s^*)$$

can be rewritten

$$\partial_{11}a^* < -\partial_{11}a^* - 2\,\partial_{12}a^*$$

or

$$\partial_{11}a^* < -\partial_{12}a^*.$$

Given the CSS condition, branching is equivalent to the non-ESS condition

$$\begin{aligned}0 &< \partial_{11}\mathscr{I}(s^*|s^*)\\ 0 &< \partial_{11}a^*.\end{aligned}$$

Therefore a branching point is completely characterized by

$$\partial_1 a^* = 0 \quad \text{and} \quad 0 < \partial_{11}a^* < -\partial_{12}a^*.$$

Notice that $\partial_2 a^*$ and $\partial_{22}a^*$ play no role in these conditions, so they can take on any values irrespective of whether the fixed point is attractive, branching or neither.

4.1.4 Evolution of phenotypes and interactions

As well as looking at how the interaction function a drives evolution, let us examine how evolution changes the interactions. In general, away from singular points, since interactions are derived directly from phenotypes, the motion of each interaction term is

$$\begin{aligned}
\dot{a}_{ij} &= \partial_1 a(\mathbf{s}_i, \mathbf{s}_j)\ \dot{\mathbf{s}}_i + \partial_2 a(\mathbf{s}_i, \mathbf{s}_j)\ \dot{\mathbf{s}}_j \\
&= \gamma\left(\partial_1 a_{ij}\ \hat{X}_i\ \partial_1 \mathscr{I}(\mathbf{s}_i)^{\mathrm{T}} + \partial_2 a_{ij}\ \hat{X}_j\ \partial_1 \mathscr{I}(\mathbf{s}_j)^{\mathrm{T}}\right) \\
&= \gamma\left(\hat{X}_i\ \partial_1 a_{ij}\ \sum_k \hat{X}_k\ \partial_1 a_{ik}^{\mathrm{T}} + \hat{X}_j\ \partial_2 a_{ij}\ \sum_k \hat{X}_k\ \partial_1 a_{jk}^{\mathrm{T}}\right).
\end{aligned}$$

When only one strain (call it $\mathbf{s}_i$) is present, there is only one interaction term a_{ii}, and its motion is controlled by

$$\begin{aligned}
\dot{a}_{ii} &= (\partial_1 + \partial_2) a_{ii}\ \dot{\mathbf{s}}_i \\
&= \gamma\ \hat{X}_i\ (\partial_1 + \partial_2) a_{ii}\ \hat{X}_i\ \partial_1 {a_{ii}}^{\mathrm{T}} \\
&= \gamma\ \hat{X}_i^2 (\partial_1 a_{ii}\ \partial_1 a_{ii}^{\mathrm{T}} + \partial_2 a_{ii}\ \partial_1 {a_{ii}}^{\mathrm{T}})
\end{aligned}$$

As the motion of $\mathbf{s}_i$ slows to zero on approach to a fixed point ($\partial_1 a_{ii} = \mathbf{0}$), of course the motion of a_{ii} does as well. The derivative of a_{ii} can also be zero when $(\partial_1 + \partial_2) a_{ii} = \mathbf{0}$, or when those two vectors are perpendicular, but this would not bring $\mathbf{s}_i$ to a stop, only a (which may be passing momentarily through a local extremum or inflection point).

Since we can assume nothing about the relative directions of $\partial_1 a$ and $\partial_2 a$, the sign of $\dot{a}_{ii}$ can be positive or negative, but as the first of the two terms of this expression ($\partial_1 a_{ii}\ \partial_1 {a_{ii}}^{\mathrm{T}}$) is clearly positive, we can imagine that all things being equal in some sense, we would expect the expression to be more often positive than negative, which would lead to an increase in a_{ii}. Assuming a_{ii} is negative (this is necessary for B-stability in a one-strain system), increasing a_{ii} means reducing density dependence and making the equilibrium population larger. Likewise, as the general expression for $\dot{a}_{ij}$ contains some positive terms and some terms about which we can say nothing, there is a slight indication that increase in a terms might be expected on average.

Now what happens at a branching point? Assume one strain at the singular point. Just after branching, the dynamics is dominated by the motion of the two branching strains away from each other. This is motion along an eigenvector of the expanded adaptive dynamical system, whose associated eigenvalue is $\lambda = \partial_{22}\mathscr{I}(s_i|s_i) > 0$ (Ma 2003). So near the branching point, we can write the system as

$$s_1 = s^* - \Delta s, \quad s_2 = s^* + \Delta s$$

with

$$\Delta s(t) = x_0 e^{\lambda(t-t_0)},$$

with x_0 very small, or write $s_j = s^* + d_j \Delta s$ with $d_1 = -1$ and $d_2 = 1$.

Now expanding out to the second order, the interaction terms look like

$$\begin{aligned} a(s_i, s_j) &= a^* + (s_j - s^*)\partial_2 a^* \\ &\quad + (s_i - s^*)^2 \partial_{11} a^* + 2(s_i - s^*)(s_j - s^*)\partial_{12} a^* + (s_j - s^*)^2 \partial_{22} a^* \\ &= a^* + d_j x_0 e^{\lambda(t-t_0)} \partial_2 a^* \\ &\quad + \left(x_0 e^{\lambda(t-t_0)}\right)^2 \left(\partial_{11} a^* + 2 d_i d_j \partial_{12} a^* + \partial_{22} a^*\right). \end{aligned}$$

Applying the appropriate values of d_1 and d_2, we can write out the dynamics of the **a** matrix close to the branching point:

$$\begin{aligned} \mathbf{a} &= \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix} a^* + x_0 e^{\lambda(t-t_0)} \begin{pmatrix} -1 & 1 \\ -1 & 1 \end{pmatrix} \partial_2 a^* \\ &\quad + \left(x_0 e^{\lambda(t-t_0)}\right)^2 \left(\begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix} (\partial_{11} + \partial_{22}) a^* + 2 \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix} \partial_{12} a^* \right). \end{aligned}$$

When $(t - t_0)$ is very small, the first and second columns of **a** diverge, one upward and one downward, at an exponential rate proportional to $\partial_2 a^*$; when the strains have branched enough to make quadratic terms significant, the entries in both columns curve together in the direction of $(\partial_{11} + \partial_{22})a^*$ and the off-diagonal terms separate from the diagonal terms.

It is immediately apparent from the nature of coexistence in the Lotka-Volterra system (as in chapter 2) that the off-diagonal terms must be larger than the diagonals; we can also verify this directly:

$$a_{21} - a_{11} = a_{12} - a_{22} = -4\left(x_0 e^{\lambda(t-t_0)}\right)^2 \partial_{12} a^*.$$

Since we know that $\partial_{12} a^* < 0$, we can see that the off-diagonal terms diverge upward from the diagonal terms at the branching point. This is illustrated by figure 4.2, and by figure 4.4 and others later in this chapter.

When a^* is negative, the cross terms becoming larger than the self-interaction terms signifies a lessening of interstrain competition compared to intrastrain competition. Character displacement among populations competing for the same set of resources is an example of this dynamic. If the cross terms continue to rise, they may actually change over to positive values, which signifies a conversion from interstrain competition to a mutualistic interaction. Figure 4.4 and others in the next section illustrate this process in a sample system.

4.2 A multi-dimensional evolutionary system

4.2.1 Deriving interactions from a vector of traits

Very little is published on adaptive dynamics of more than one-dimensional phenotypes. In this section, I present a very simple model that relates interactions to vector-valued phenotypes, in order to explore the relationships between phenotypic dimension, diversity, constraints, interactions, and community stability.

Vector-valued phenotypes represent populations characterized by a number of quantitative character traits which are subject to evolution. An interaction term, which summarizes the fitness effect of an interaction between two individuals, integrates, in some way, the effects of all the different trait values describing each individual into a single resultant number. The simplest possible way to combine these character traits into interaction terms

is to assume that they are all independent of each other, that each trait of one individual interacts with each trait of the other individual in a fixed way, and that all of these partial interactions simply combine linearly into the total interaction between individuals.

In this model, I assume m^2 constant values M_{pq}, each describing how ones pth character trait interacts with another individual's qth character trait. Given two individuals with m-dimensional phenotype vectors $\mathbf{s}_i$ and $\mathbf{s}_j$, the effect of an interaction between these two individuals—that is, the value of a_{ij}—is the sum of all the effects of pairwise interactions of the two individuals' traits,

$$a_{ij} = \sum_{p,q} (\mathbf{s}_i)_p M_{pq} (\mathbf{s}_j)_q.$$

Written in vector terms, the function constructing interaction terms from phenotype vectors is

$$a_{ij} = \mathbf{s}_i^{\mathrm{T}} \mathbf{M} \mathbf{s}_j,$$

where $\mathbf{M}$ is the $m \times m$ matrix of M_{pq} values. This formula can also be written as a vector inner product:

$$a_{ij} = \langle \mathbf{s}_i, \mathbf{M}\mathbf{s}_j \rangle.$$

In order to focus on the evolution of interactions, I fix all r_i equal to 1.

Since there are commonly biophysical tradeoffs constraining the simultaneous expression of phenotypic traits, the evolving populations are not allowed to optimize all the different traits independently, but are only allowed to have phenotype vectors of magnitude one. Thus the phenotype space Σ is the m-dimensional unit sphere.

4.2.2 Two dimensions

The simplest such case is the two-dimensional case, and while its behavior is not spectacularly complicated, it reveals most of what happens in more dimensions. Since the phenotype space, the unit circle, is in fact one-dimensional, the theorems for one-dimensional adaptive dynamics apply.

One strain

If we begin with just one strain in the system represented by $\mathbf{s}_i$, we have $a_{ii} = \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_i$ and $\hat{X}_i = -a_{ii}^{-1}$. When this strain spawns a mutant $\mathbf{s}_{i'}$, the success of the mutant is determined by

$$\begin{aligned}\mathscr{I}(\mathbf{s}_{i'}|\mathbf{s}_i) &= \Delta a_{i'i}\hat{X}_i \\ &= \Delta\mathbf{s}_{i'}^{\mathrm{T}}\mathbf{M}\mathbf{s}_i\hat{X}_i \\ &= \langle\Delta\mathbf{s}_{i'}, \hat{X}_i\mathbf{M}\mathbf{s}_i\rangle.\end{aligned}$$

The inner product is positive when the angle between the vectors is less than 90° and negative when the angle is greater than 90°. For a generic point on the circle, variants in one direction are successful and variants in the other direction are unsuccessful. Since $\mathscr{I}(\mathbf{s}_{i'}|\mathbf{s}_i)$ is continuous in $\mathbf{s}_i$, the community will undergo a series of replacements, in which $\mathbf{s}_i$ rotates in whichever direction brings it closer to $\mathbf{M}\mathbf{s}_i$.

To be more precise, the selection gradient is

$$\begin{aligned}\mathbf{S}(\mathbf{s}) &= \partial_1\mathscr{I}(\mathbf{s}|\mathbf{s}_1,\ldots,\mathbf{s}_n)^{\mathrm{T}} \\ &= \sum_j \hat{X}_j\left(\frac{\partial}{\partial\mathbf{s}}\mathbf{s}^{\mathrm{T}}\mathbf{M}\mathbf{s}_j\right)^{\mathrm{T}}.\end{aligned}$$

The terms of the vector partial derivative inside the parentheses are

$$\begin{aligned}\frac{\partial}{\partial(\mathbf{s})_k}\sum_{l,m}(\mathbf{s})_l\mathbf{M}_{lm}(\mathbf{s}_j)_m &= \sum_m \mathbf{M}_{km}(\mathbf{s}_j)_m \\ &= (\mathbf{M}\mathbf{s}_j)_k\end{aligned}$$

so

$$\frac{\partial}{\partial\mathbf{s}}\mathbf{s}^{\mathrm{T}}\mathbf{M}\mathbf{s}_j = (\mathbf{M}\mathbf{s}_j)^{\mathrm{T}},$$

and

$$\mathbf{S} = \sum_j \hat{X}_j\mathbf{M}\mathbf{s}_j$$

regardless of $\mathbf{s}$.

When $\mathbf{s}_i$ is the only strain in the system, the direction of evolution is $\mathbf{S} = \hat{X}_i \mathbf{M}\mathbf{s}_i$, constrained by the restriction to the unit circle. There are at most four points where its evolutionary motion comes to a stop—where $\mathbf{M}\mathbf{s}_i$ is normal to the unit circle:

$$\mathbf{M}\mathbf{s}_i = \lambda \mathbf{s}_i.$$

These points, of course, are the unit-length eigenvectors of $\mathbf{M}$, $\mathbf{v}_1$ and $\mathbf{v}_2$ (and their negatives), and their associated eigenvalues λ_1 and λ_2. The eigenvectors are singular points of the dynamics of $\mathbf{s}_i$. If $\mathbf{M}$ does not have real eigenvalues, the dynamics has no fixed points and if one strain is present it must revolve around the unit circle forever.

Assuming there are real eigenvalues and therefore fixed points at the eigenvectors, to understand what happens between the eigenvectors we write

$$\begin{aligned} \mathbf{s}_i &= \alpha_1 \mathbf{v}_1 + \alpha_2 \mathbf{v}_2 \\ \mathbf{M}\mathbf{s}_i &= \alpha_1 \mathbf{M}\mathbf{v}_1 + \alpha_2 \mathbf{M}\mathbf{v}_2 \\ &= \lambda_1 \alpha_1 \mathbf{v}_1 + \lambda_2 \alpha_2 \mathbf{v}_2. \end{aligned}$$

Let us assume without loss of generality that $\lambda_1 < \lambda_2$. Since $\langle \Delta\mathbf{s}_{i'}, \mathbf{s}_i \rangle = \langle \Delta\mathbf{s}_{i'}, \alpha_1 \mathbf{v}_1 + \alpha_2 \mathbf{v}_2 \rangle \approx 0$ when mutations are very small, then to first order,

$$\begin{aligned} \mathscr{I}(\Delta\mathbf{s}_{i'}) = \langle \Delta\mathbf{s}_{i'}, \hat{X}_i \mathbf{M}\mathbf{s}_i \rangle &= \langle \Delta\mathbf{s}_{i'}, \hat{X}_i (\lambda_1 \alpha_1 \mathbf{v}_1 + \lambda_2 \alpha_2 \mathbf{v}_2) \rangle \\ &= \langle \Delta\mathbf{s}_{i'}, \hat{X}_i (\lambda_1 \alpha_1 \mathbf{v}_1 + \lambda_2 \alpha_2 \mathbf{v}_2) \rangle - \lambda_1 \langle \Delta\mathbf{s}_{i'}, \mathbf{s}_i \rangle \\ &= \langle \Delta\mathbf{s}_{i'}, \hat{X}_i (\lambda_2 - \lambda_1) \alpha_2 \mathbf{v}_2 \rangle. \end{aligned}$$

The sign of α_2 places $\mathbf{s}_i$ on one side or the other of $\mathbf{v}_1$, and according to that sign mutations $\Delta\mathbf{s}_{i'}$ are successful that point toward whichever of $\mathbf{v}_2$ or $-\mathbf{v}_2$ is closer. Thus evolution of one strain proceeds to the eigenvector corresponding to the larger of the two eigenvalues of $\mathbf{M}$.

At either eigenvector $\mathbf{v}_k$, the value of a_{ii} is $\mathbf{v}_k^{\mathrm{T}}\mathbf{M}\mathbf{v}_k = \lambda_k \mathbf{v}_k^{\mathrm{T}}\mathbf{v}_k = \lambda_k$. If one or both of the eigenvectors is positive, as the one strain approaches $\pm\mathbf{v}_2$, as soon as its self-interaction term becomes positive, its population will explode to infinity. Since *B*-stability requires $a_{ii} < 0$, a well-behaved system must have $\lambda_1 < \lambda_2 < 0$. Actually, to guarantee $a_{ii} < 0$ for all $\mathbf{s}_i$, $\mathbf{M}^{\mathrm{T}} + \mathbf{M}$ must be negative definite, a stronger condition that implies the eigenvalue condition. In the rest of this chapter, I use matrices $\mathbf{M}$ generated by constructing a negative definite symmetric matrix and adding to it an antisymmetric matrix; this guarantees that each such matrix, while not symmetric, has the negative definite property that $\mathbf{s}^{\mathrm{T}}\mathbf{M}\mathbf{s} < 0$ for all $\mathbf{s}$.

Now under these assumptions, having established that $\mathbf{v}_2$ is a fixed point of the adaptive dynamics and that it is attractive to a monomorphic population, the clear next question is whether it stable to polymorphisms or will branch. As we have seen, given an attractive (that is, CSS) fixed point, branching of a single strain in one-dimensional phenotype space simply depends on whether $0 < \partial_{11} a(s,s)$ at the fixed point. To do this calculation, let

$$\mathbf{s}_i = \begin{pmatrix} \cos\theta_i \\ \sin\theta_i \end{pmatrix}.$$

Then we have

$$\partial_{11} a(\theta_{i'}, \theta_i) = \frac{\partial^2 \mathbf{s}_{i'}^{\mathrm{T}}}{\partial \theta_{i'}^2} \mathbf{M}\mathbf{s}_i.$$

Since

$$\frac{\partial^2 \mathbf{s}_i}{\partial \theta_i^2} = \begin{pmatrix} -\cos\theta_i \\ -\sin\theta_i \end{pmatrix} = -\mathbf{s}_i,$$

at the CSS we have

$$\partial_{11} a = -\mathbf{v}_2^{\mathrm{T}}\mathbf{M}\mathbf{v}_2 = -\lambda_2 > 0,$$

showing that this eigenvector is a branching point. Another way to see this is that since $\partial_1 \mathscr{I}(\mathbf{s}_i|\mathbf{s}_j) = \hat{X}_j \mathbf{M}\mathbf{s}_j$, there is no curvature of $\mathscr{I}$ associated with its first argument, and $\mathbf{S}(\mathbf{v}_2) = \lambda_2 \hat{X}_i \mathbf{v}_2$ points into the concavity of the constraint curve, just as in the right-hand picture of figure 3.3.

Two strains

After the branching, and in general, the motion of multiple strains in this system is always in the direction of $\mathbf{S} = \sum_j \mathbf{M}\mathbf{s}_j \hat{X}_j$, constrained to the unit circle or (hyper-)sphere.

To resolve what this expression means geometrically, we must resort to algebraic tricks. To begin with, since we have defined $a_{ij} = \mathbf{s}_i^{\mathrm{T}} \mathbf{M}\mathbf{s}_j$, it follows, in terms of the m-by-n matrix $\mathbf{s}$ whose ith column is $\mathbf{s}_i$, that

$$\mathbf{a} = \mathbf{s}^{\mathrm{T}} \mathbf{M}\mathbf{s}.$$

Further, in the same notation we can write

$$\mathbf{S} = \mathbf{M}\mathbf{s}\hat{\mathbf{X}},$$

and as the equilibrium population vector $\hat{\mathbf{X}}$ is defined by the equilibrium equation

$$\mathbf{a}\hat{\mathbf{X}} + \mathbf{r} = \mathbf{0},$$

by substituting we immediately obtain

$$\begin{aligned} \mathbf{s}^{\mathrm{T}} \mathbf{M}\mathbf{s}\hat{\mathbf{X}} + \mathbf{r} &= \mathbf{0} \\ \mathbf{s}^{\mathrm{T}} \mathbf{S} + \mathbf{r} &= \mathbf{0}. \end{aligned}$$

Since each $r_i = 1$, we therefore have $\langle \mathbf{s}_i, \mathbf{S} \rangle = -1$ for each i.

Since $\|\mathbf{s}_i\| = 1$, if we write $\theta(\mathbf{s}_i, \mathbf{S})$ for the angle between $\mathbf{s}_i$ and $\mathbf{S}$, this becomes

$$\|\mathbf{S}\| \cos\theta(\mathbf{s}_i, \mathbf{S}) = -1.$$

It follows that $\mathbf{S}$ makes the same angle with each phenotype vector $\mathbf{s}_i$, and that this angle is always obtuse. In the case of m strains in m dimensions, this geometric description uniquely determines the direction of $\mathbf{S}$, and therefore, the evolutionary trajectory of the community: there are two points on the unit hypersphere equidistant from all m phenotype vectors, and because of the obtuse angle, $\mathbf{S}$ points to the one further away. Therefore, the projection of $\mathbf{S}$ onto the constraint surface pulls the m vectors away from each other.

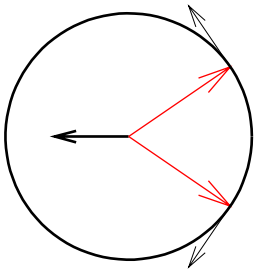


Figure 4.3: The selection gradient (thick black arrow) points away from the two phenotype vectors (red arrows) in two dimensions, making an equal angle with each. Its projection onto the constraint surface (thin black arrows) pulls the phenotypes away from each other.

For two strains, following the evolutionary branching, the two will move apart from each other at equal speeds until they are directly opposite one another (in the case of more than two strains, they will separate until they all lie on an $m-1$-dimensional plane or hyperplane passing through zero).

Degeneration

In two dimensions, as the angle between the two phenotype vectors $\mathbf{s}_1$ and $\mathbf{s}_2$ approaches 180° (at which point $\mathbf{s}_1 = -\mathbf{s}_2$), the Lotka-Volterra dynamics approaches the boundary of B-stability as the $\mathbf{a}$ matrix becomes singular (since the first row, $\mathbf{s}_1^{\mathrm{T}}\mathbf{M}\mathbf{s}$, becomes the negative of the second row, $\mathbf{s}_2^{\mathrm{T}}\mathbf{M}\mathbf{s}$).

At the singular point of the adaptive dynamics where the $\mathbf{a}$ matrix degenerates, the equilibrium equation $\mathbf{r} + \mathbf{a}\hat{\mathbf{X}} = \mathbf{0}$ no longer has a solution; the nullclines of X_1 and X_2 are parallel, and the population sizes rise exponentially to infinity.

In actual simulations, the pair of phenotypes approaches very close to opposite, then the next variant arises on the opposite side of the singular value, which produces a B-unstable system and population explosion. In either case, this is not realistic, and the model can no

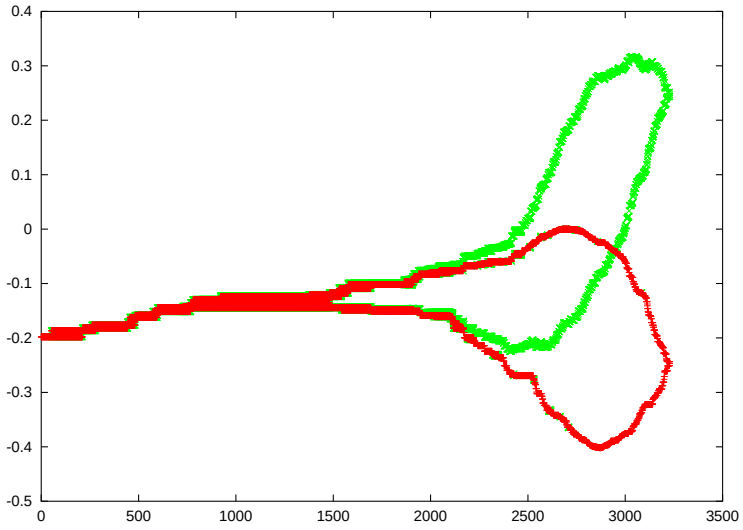


Figure 4.4: Evolution of a_{ij} values through time, on the unit circle, with $a_{ij} = \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_j$.

longer be used after this point.

Interactions

Figure 4.4 shows the evolution of interactions in this system, beginning with one strain that then branches into two. As the two variants approach opposite points, their self-interaction terms ($a_{ii} = \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_i$) approach the same negative number—in the realization pictured, about -0.25—while the cross interaction terms ($a_{ij} = \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_j = \mathbf{s}_i^{\mathrm{T}}\mathbf{M}(-\mathbf{s}_i)$) approach the opposite number—here, about 0.25.

4.2.3 More than two dimensions

On the unit hypersphere in any number of dimensions, the directions of evolutionary motion available to any given strain are all the directions perpendicular to the strain's phenotype vector. The constrained direction of motion of a phenotype $\mathbf{s}_i$ under the influence of the unconstrained selection gradient $\mathbf{S}$ is the component of $\mathbf{S}$ perpendicular to $\mathbf{s}_i$. The only way

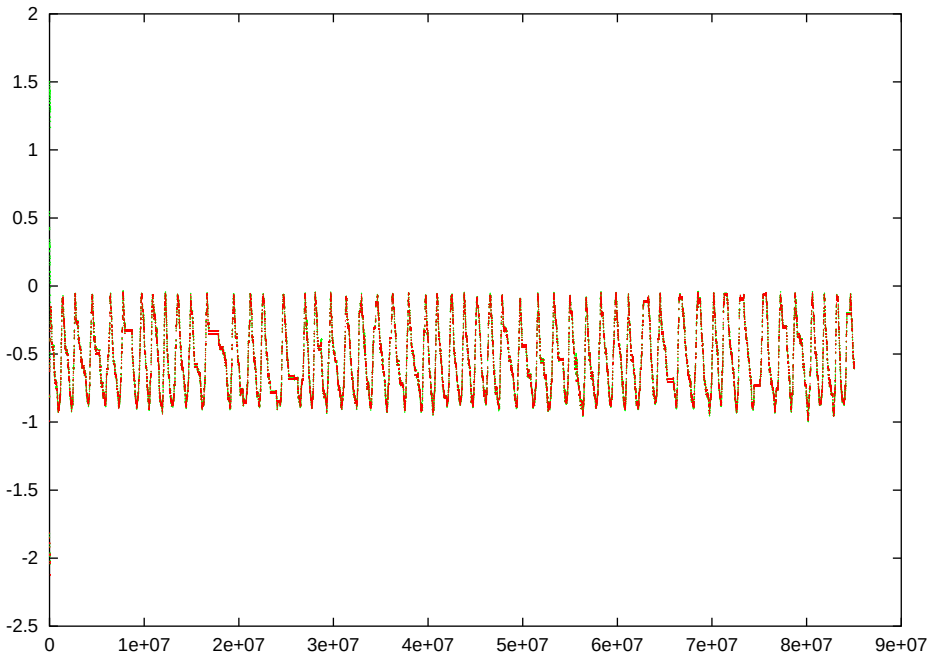


Figure 4.5: Evolutionary limit cycle involving one strain in three dimensions, with $a_{ij} = \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_j$.

an evolutionary fixed point can happen is when $\mathbf{S}$ is parallel to $\mathbf{s}_i$ or $\mathbf{S}$ is zero. Since by the foregoing calculations, $\langle \mathbf{s}_i, \mathbf{S} \rangle = -1$ whenever $\hat{\mathbf{X}}$ is well-defined, we cannot have $\mathbf{S} = \mathbf{0}$, and the evolutionary fixed point condition can only be satisfied when $\mathbf{S} = -\mathbf{s}_i$. Therefore the evolutionary fixed point condition, which is necessary for evolutionary branching, cannot be satisfied in this model when more than one strain is present, except where the interaction matrix becomes singular.

Beginning with one strain in *m* dimensions, either the model goes into a one-strain limit cycle, as shown in figure 4.5, or the one strain branches into two, and the two either go into a limit cycle together, or diverge until the system explodes as in the two-dimensional case. Quasi-periodic or chaotic attractors in one or two strains cannot be ruled out, but I have not observed them.

If we were to use some other constraint surface with the same a function, evolutionary singular points could happen where $\mathbf{S}$ is normal to the constraint surface at all points $\mathbf{s}_i$ at once, and surely in some such cases one strain would diversify into more than two. A more serious limitation of the model involves what happens when the number of strains exceeds the dimensionality of the phenotype space. Since

$$\mathbf{a} = \mathbf{s}^{\mathrm{T}}\mathbf{M}\mathbf{s},$$

the rank of $\mathbf{a}$ can be no greater than the rank of $\mathbf{M}$. Since the dimension of $\mathbf{M}$ is the dimension of the space of phenotype vectors, any time there are more strains present than there are entries in the phenotype vectors ($n > m$), the interaction matrix must be singular, and the equilibrium equation

$$\hat{\mathbf{X}} = -\mathbf{a}^{-1}\mathbf{r}$$

does not have a well-defined solution. A singular interaction matrix can do several things to the system: it can become B-unstable, or it can have a linear space of fixed points passing through the positive cone, or it can have no fixed point in the interior of the positive cone. When I have investigated the system by initializing it with more than m strains, I have simply found that some of them go extinct until there are m or fewer strains remaining.

4.2.4 Nonlinear variant model

The innocent simplifying assumption that character traits can be combined in a linear form to derive the overall effects of interactions between organisms has brought with it an unintended consequence—that the evolutionary dynamics of the community emergent from these interactions can support no more coexisting types than there are dimensions in the trait space. If I were to attempt to model a real ecological evolution problem by singling out a small number of character traits and using a simple linear model like this for interactions, the model would predict a very small amount of diversification, whereas a very

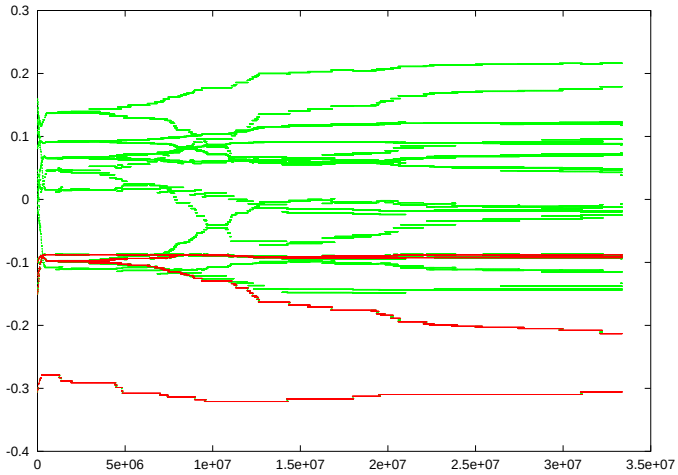


Figure 4.6: Evolution of a_{ij} values through time, on the two-dimensional unit circle, with $a_{ij} = 1 - e^{-10\ \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_j}$. The initial strain splits ultimately into not two but four strains.

similar model that includes other character traits, even if they appear to be entirely irrelevant, would not support that prediction. Adding evolution to a perfectly functional simple ecological model, apparently, can reveal serious weaknesses in the simplification.

If I modify this model by adding a nonlinearity in the construction of a_{ij} from $\mathbf{s}_i$ and $\mathbf{s}_j$, the connection between the phenotype dimension and the number of strains is broken. In particular, I have replaced

$$a_{ij} = \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_j$$

with

$$a_{ij} = 1 - e^{-k\ \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_j},$$

with $k = 10$, since that seems to produce interesting behavior. This function $1 - e^{-kx}$ maps negative numbers to negative numbers and positive numbers to positive numbers, while expanding negative numbers and shrinking positive numbers, so that the types of interactions are the same as they would be without this nonlinear mapping. At the same time,

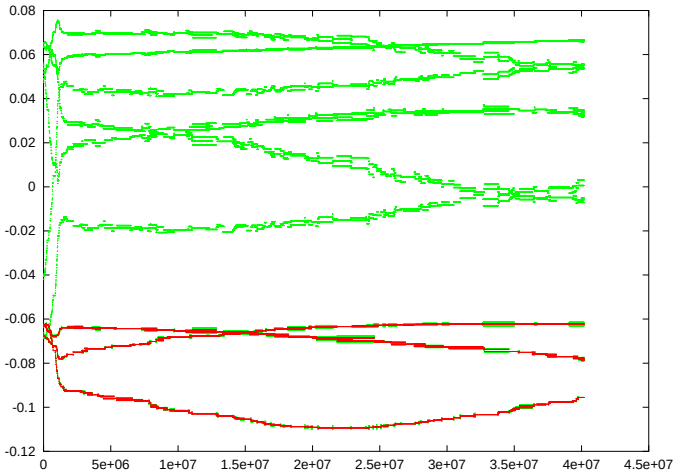


Figure 4.7: Coexistence of three strains on the two-dimensional unit circle, with $a_{ij} = 1 - e^{-10\ \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_j}$.

it fends off *B*-instability by making mutualistic interactions weaker and competitive interactions stronger than they are in the linear model. Figures 4.6–4.9 illustrate some of the evolutionary dynamics observed in this model, with various randomly chosen **M** matrices. Sometimes limit cycles arise, and at other times the community passes through a series of branching points, often producing more coexisting strains than the number of phenotypic traits. These systems often do not settle to an evolutionary attractor within the amount of time I have been able to run the simulations.

While the explosions of population that plague the linear model are not observed in this model, coexistence is still commonly associated with mutualism. Coexisting pairs commonly convert the interaction between them from competition to mutualism; the distinction between positive and negative interaction terms appears to make no difference to the evolutionary dynamics, as long as the population dynamics do not blow up.

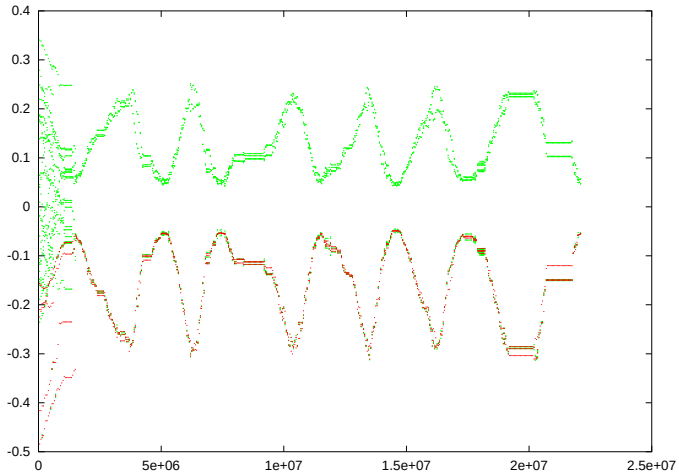


Figure 4.8: Dynamics of a values on the three-dimensional unit sphere, with $a_{ij} = 1 - e^{-10\ \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_j}$. Four strains are reduced by extinction to two, which have competitive self-interactions and mutualistic cross interactions, and which fall into a coevolutionary cycle in the spherical constraint manifold of the phenotype space.

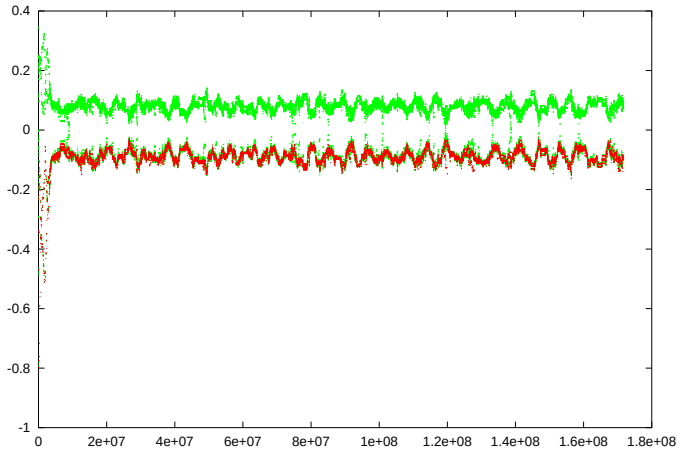


Figure 4.9: Evolution of a_{ij} values through time, on the six-dimensional unit hypersphere, with $a_{ij} = 1 - e^{-10\ \mathbf{s}_i^{\mathrm{T}}\mathbf{M}\mathbf{s}_j}$. The initial strain (with competitive self-interaction) splits quickly into a mutualistic pair, both of which then appear to orbit near a circle in the constraint manifold.

Chapter 5

Evolution Of Interactions Without Phenotypes

In this chapter I introduce a model in which interactions evolve directly, without explicitly modeling each strain's phenotype. This framework reveals how the selective pressure on phenotypes discussed in the previous chapter can be decomposed into the selective pressure on interactions that is emergent in the Lotka-Volterra representation of interacting populations, and the limitations on the available directions of evolution imposed by tradeoffs and constraints on available variation. In these terms, there appears to be a general pull towards reduced competition and increased mutualism. However, the evolution of interactions in this chapter's model, with no constraints imposed by phenotypic variation, cannot simply be seen as the result of the selective pressure identified above without any constraints. More complicated factors are at work, including higher-level selection. I discuss these results in the context of the literature on evolution of mutualism and self-organizing network dynamics.

Evolutionary ecologists have long been concerned with the effects of ecological community structure on the evolution of populations within a community, and many have also looked, through evolutionary branching and extinction events, at the effects of evolution on community structure. Both the older strain of evolutionary ecology, which is based on applying frequency dependent selection to population genetics models, and the newer adaptive dynamics, which abstracts out most of the genetics, focus on adaptive change in a small number of phenotypic characters. More recently, it has become popular to talk about network dynamics in an interdisciplinary way, asking in various kinds of systems how the actions of the components of the system affect the network of relationships between the components and vice versa. Models in this tradition tend to focus on the matrix or graph representing the network connecting the system together, and make the components of the system (the vertices of the graph) as simple as possible, if they have any characteristics at all other than the connections between them (Jain and Krishna 1998; Fontana and Buss 1996; Bak and Sneppen 1993).

Here I present a model created by blending aspects of these two approaches. Evolutionary change is layered on top of a simple ecological model just as in the adaptive dynamics framework, but rather than studying the motion of a few phenotypic parameters intrinsic to each population, I look directly at changes in the relationships between the populations. This choice highlights the connection between selective pressures induced by the ecological dynamics and constraints imposed by the genetic and physical structure of individuals and their environment on the available directions of evolution. Making this distinction explicit may be useful in both disciplines.

While Lotka-Volterra models are generally used to study competitive and predatory systems (and are particularly unsuited to modeling mutualism), when no constraint is placed on the range of possible interactions, evolution in this model tends to convert these antagonistic relationships into mutualistic relationships. This leads us to a discussion of the evolution of mutualism, and how this relates to the findings of other network dynamics

models.

5.1 The basic model

This model adds evolution to the Lotka-Volterra dynamics using most of the standard adaptive dynamics assumptions: the ecological dynamics

$$\frac{dX_i}{dt} = r_i X_i + \sum_{j=1}^{n} a_{ij} X_i X_j \tag{5.1}$$

is allowed to unfold until it has reached an attractor (at which time, all populations that are no longer viable have become very small and are removed); then a variant of one of the resident strains is introduced and the ecological dynamics is evaluated further, and this cycle repeats until the simulation is stopped. Thus while the population sizes change and adjust to each other following (5.1), the makeup of the community changes on a slower timescale by evolutionary replacement and diversification. The changing **a** matrix determines the ecological dynamics, while the ecological dynamics determine which strains succeed, which drives the changes in the **a** matrix.

While adaptive dynamics models generally consider each strain to be characterized by a small number of numerical characters, as we have seen in the previous chapter, this assumption can bias the results of such a model, for instance by limiting the number of strains that can coexist. The model presented in this chapter is an investigation of what might happen instead if the combinations of phenotypic characters that influence a strain's relationship with its environment are very complex and perhaps not capable of being captured by a smoothly differentiable function of continuous-valued quantities.

This question is being addressed from one particular angle by researchers connected to the Artificial Life tradition (Kauffman 1993; Schuster and Swetina 1988; van Nimwegen and Crutchfield 2000; Christensen et al. 2002), who model genotypes by long strings of binary digits, addressing such questions as stable quasispecies distributions, numbers of

evolutionary optima and evolutionary drift by neutral substitutions. Here I take a different angle, asking in a sense what might happen if genomes and the phenotypes they generate were infinitely complex, or at least too complex to model in any detail.

In this case, the scalar terms describing the effect of an interaction between two types would be described by a complex function of a great many values describing each type. When a slight change is made in one type, the changes introduced in the interaction terms would be constructed by combining the influences of a large number of small changes in its various phenotypic characters. When a large number of randomly distributed values combine in a complex way to produce a resultant value that cannot be computed explicitly, it is a common practice to model that value as a normally distributed random variable; that is the approach I follow in this chapter, replacing explicitly modeled phenotypes with normally distributed changes applied directly to the interaction terms.

As in mutating-phenotype models, in hope of observing more or less smooth changes in the community, I assume that a population produced by variation of an existing one is very similar to its parent; or more specifically, that its growth rate and interaction terms are very similar to those of its parent. In order to study the relationship between community dynamics and interactions, I fix all intrinsic growth rates r_i at 1 and only allow interaction terms to vary: if population i' is a variant of population i, then,

$$\begin{aligned} a_{i'j} &= a_{ij} + \Delta a_{i'j}; \\ a_{ji'} &= a_{ji} + \Delta a_{ji'}; \\ a_{i'i'} &= a_{ii} + \Delta a_{i'i'}, \end{aligned} \tag{5.2}$$

with all Δa values relatively small. When interaction terms are derived from phenotypic characters, these small changes in interaction terms follow from relations like

$$\Delta a_{i'j} = \partial_1 a(\mathbf{s}_i, \mathbf{s}_j)\Delta\mathbf{s}_i + O(\|\Delta\mathbf{s}_i\|^2).$$

Instead, having removed phenotypes from explicit consideration, I simply apply mutations

to the interaction terms directly, choosing Δa values independently from a normal distribution with mean zero and a small standard distribution. In this chapter, unless I note otherwise, I use a standard distribution of 0.02 for these numbers.

The simulation begins with one population with $\mathbf{r} = (1)$ and $\mathbf{a} = (-1)$ (the standard logistic equation), which then develops into

$$\mathbf{r} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \qquad \mathbf{a} = \begin{pmatrix} -1 & -1+\Delta a_{12} \\ -1+\Delta a_{21} & -1+\Delta a_{22} \end{pmatrix},$$

and onward from there, with whichever populations manage to persist.

5.2 Behavior of the basic model

When Δa values are chosen independently, the evolutionary behavior of the system is qualitatively different than the behavior of a standard adaptive model. Beginning with one initial strain, with one diagonal interaction term set to -1, as figures 5.1, 5.2 and 5.3 show, the descendants of that strain tend to split quickly into two distinct lineages; the self-interaction terms of each lineage (shown in red) tend to drift aimlessly, though with somewhat of an upward trend, while the interactions between the two lineages (shown in green) rise, essentially linearly, crossing from negative to positive, forming a mutualistic partnership that becomes stronger and stronger until the whole system loses stability and its population size explodes to infinity. When the community consists of two lineages, this happens when the product of "a_{12}" and "a_{21}", the green terms, exceeds the product of "a_{11}" and "a_{22}", the red terms.

While this long-term evolutionary splitting is not always seen, the general rise in average a values is always observed in the hundreds of simulations I have run, ultimately culminating in the loss of B-stability. As in the previous chapter, when the system loses B-stability and populations go to infinity, the system can not be evaluated after that point.

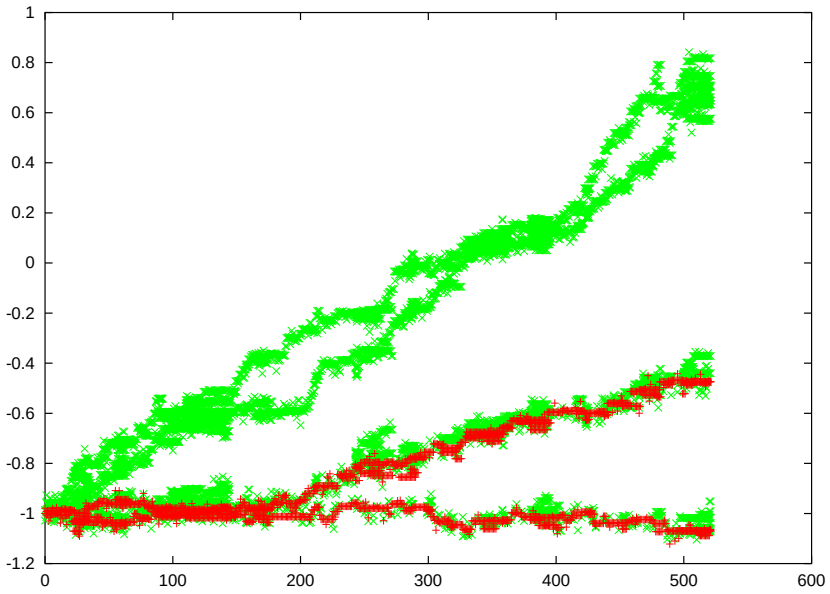


Figure 5.1: Evolution of the ensemble of a_{ij} entries through time, in a representative run of the simulation. The initial strain splits into two diverging lineages, with self-interaction terms (red) that often drift vaguely upward and cross-interaction terms (green) that rise steadily into positive values, forming a mutualistic partnership, until the system explodes.

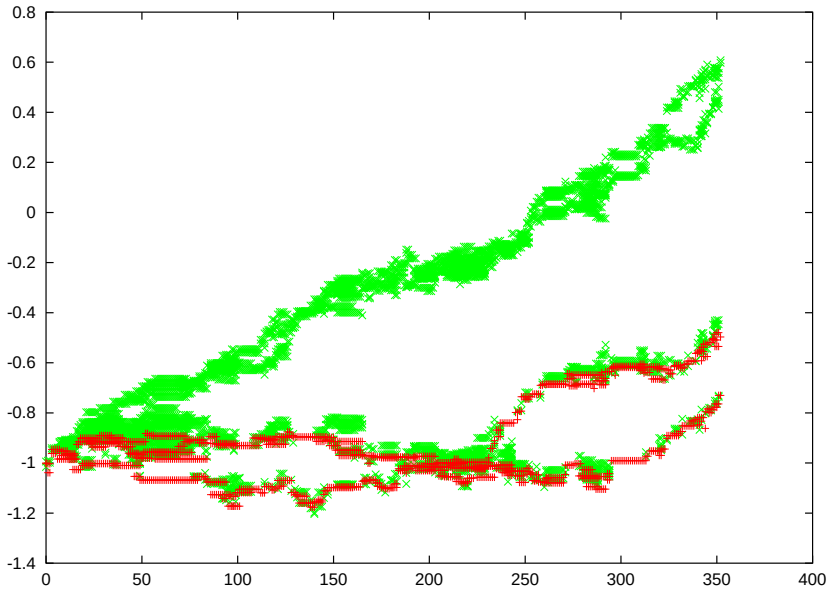


Figure 5.2: Evolution of the ensemble of a_{ij} entries through time, in another run of the simulation.

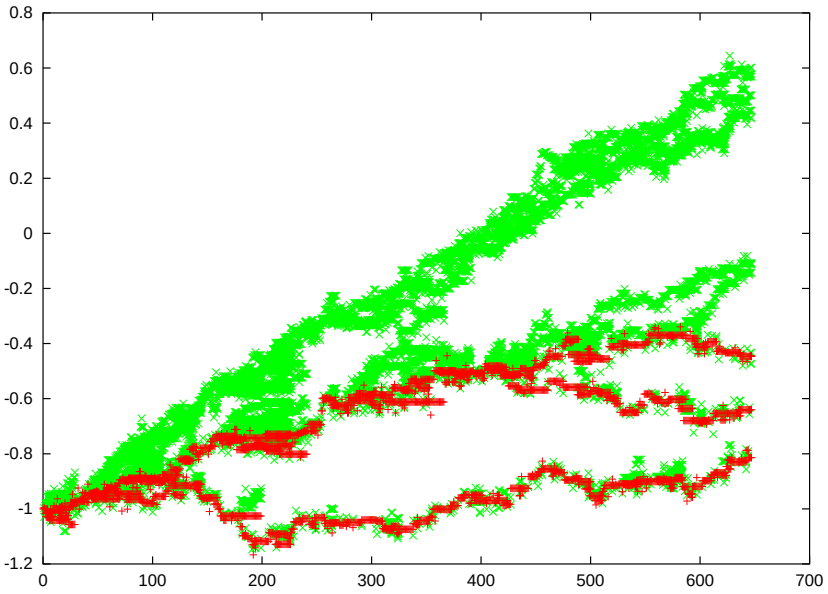


Figure 5.3: Evolution of the ensemble of a_{ij} entries through time, in another run of the simulation. Secondary splittings like this are fairly uncommon and tend to be short-lived.

5.3 Are *a* values like phenotypes?

When a_{ij} values are derived from phenotypes, the motion of a_{ij} values can be expressed in terms of the motion of the phenotypes following the standard adaptive dynamics equation (3.5), as in section 4.1.4. In this model, since there are no phenotypes, that equation cannot be applied directly. In this section I investigate the differences between these models and whether the no-phenotype model (5.2) can be approximated by a modification of the adaptive dynamics equations.

In a Lotka-Volterra adaptive dynamics model with phenotypes, the entries of the **a** matrix are calculated from the phenotypes much as the derived phenotype vectors $\mathbf{s}_i$ are calculated from 'underlying' phenotypes $\mathbf{u}_i$ in section 3.6. As in section 3.6, where the $\mathbf{u}_i$ vectors evolve in response to selective pressure that can be decomposed into selective pressure on $\mathbf{s}_i$ projected through derivatives of the function $\mathbf{s}(\mathbf{u})$ to $\mathbf{u}_i$, here too the action of selection on phenotypes $\mathbf{s}_i$ can be written in terms of selection on the entries of the **a** matrix projected through derivatives of $a(\mathbf{s}_i, \mathbf{s}_j)$. As the unconstrained adaptive dynamics equation (3.5) can be seen as a special version of the constrained equation (3.11) "with the constraints removed", by looking at the "constrained equations" for a_{ij} terms we can investigate what happens "when the constraints are removed" by dispensing with phenotypes and applying selection directly to **a**.

5.3.1 How *a* values are constrained by phenotypes

When a phenotype variable $\mathbf{u}_i$ is transformed into a derived phenotype variable $\mathbf{s}_i$, the selective pressure operating on $\mathbf{u}_i$ is

$$\begin{aligned} \mathbf{S}(\mathbf{u}_i) &= \partial_1 \mathscr{I}(\mathbf{u}_i|\mathbf{E})^{\mathrm{T}} \\ &= \left(\sum_j \frac{\partial \mathscr{I}(\mathbf{s}_i|\mathbf{E})}{\partial (\mathbf{s}_i)_j} \frac{\partial (\mathbf{s}_i)_j}{\partial \mathbf{u}_i} \right)^{\mathrm{T}} \end{aligned}$$

$$
\begin{aligned}
&= \left(\frac{\partial \mathscr{I}(\mathbf{s}_i|\mathbf{E})}{\partial \mathbf{s}_i}\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}\right)^{\mathrm{T}} \\
&= \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}} \partial_{1\cdot}\mathscr{I}(\mathbf{s}_i|\mathbf{E})^{\mathrm{T}} \\
&= \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}} \mathbf{S}(\mathbf{s}_i)
\end{aligned}
$$

in terms of $\mathbf{S}(\mathbf{s}_i)$, the selective pressure on $\mathbf{s}_i$.

In the Lotka-Volterra equations (with constant r), the invasion function is defined at each resident phenotype by

$$
\begin{aligned}
\mathscr{I}(\mathbf{s}_i|\mathbf{E}) &= r + \sum_j \hat{X}_j\, a_{ij} \\
&= r + \sum_j \hat{X}_j\, a(\mathbf{s}_i, \mathbf{s}_j),
\end{aligned}
\tag{5.3}
$$

and the selective pressure on the phenotype $\mathbf{s}_i$ is

$$
\begin{aligned}
\mathbf{S}(\mathbf{s}_i) &= \partial_{1\cdot}\mathscr{I}(\mathbf{s}_i|\mathbf{E})^{\mathrm{T}} \\
&= \sum_j \hat{X}_j\, \partial_1 a(\mathbf{s}_i, \mathbf{s}_j)^{\mathrm{T}} \\
&= \left(\sum_j \hat{X}_j \frac{\partial a(\mathbf{s}_i, \mathbf{s}_j)}{\partial \mathbf{s}_i}\right)^{\mathrm{T}}.
\end{aligned}
$$

Now observing from (5.3) that $\partial \mathscr{I}(\mathbf{s}_i|\mathbf{E})/\partial a_{ij} = \hat{X}_j$, we can formally substitute:

$$
\mathbf{S}(\mathbf{s}_i) = \left(\sum_j \frac{\partial \mathscr{I}(\mathbf{s}_i|\mathbf{E})}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial \mathbf{s}_i}\right)^{\mathrm{T}}.
$$

This expression involves only the a_{ij} terms found in the ith row of $\mathbf{a}$. If we introduce as a notational convenience a vector object $\mathbf{a}_{(i)} = (a_{i1}, \ldots, a_{in})^{\mathrm{T}}$ (that is, the i'th row of the $\mathbf{a}$ matrix, transposed into a column vector),

$$
\mathbf{S}(\mathbf{s}_i) = \left(\sum_j \frac{\partial \mathscr{I}(\mathbf{s}_i|\mathbf{E})}{\partial (\mathbf{a}_{(i)})_j}\frac{\partial (\mathbf{a}_{(i)})_j}{\partial \mathbf{s}_i}\right)^{\mathrm{T}}
$$

$$\begin{aligned} &= \left(\partial_{1,}\mathscr{I}(\mathbf{a}_{(i)}|\mathbf{E})\frac{\partial(\mathbf{a}_{(i)})}{\partial \mathbf{s}_i}\right)^{\mathrm{T}} \\ &= \frac{\partial \mathbf{a}_{(i)}}{\partial \mathbf{s}_i}^{\mathrm{T}} \partial_{1,}\mathscr{I}(\mathbf{a}_{(i)}|\mathbf{E})^{\mathrm{T}} \\ &= \frac{\partial \mathbf{a}_{(i)}}{\partial \mathbf{s}_i}^{\mathrm{T}} \mathbf{S}(\mathbf{a}_{(i)}), \end{aligned}$$

where

$$\mathbf{S}(\mathbf{a}_{(i)}) = \left(\frac{\partial \mathscr{I}(\mathbf{a}_{(i)}|\mathbf{E})}{\partial (\mathbf{a}_{(i)})_j}\right)_{j=1,\ldots,n} = \hat{\mathbf{X}}.$$

What is this saying? For one thing, it makes it clear that while all the entries of both the i'th row and the i'th column of $\mathbf{a}$ in some sense "define" strain i in terms of its interactions with the world, the only terms that directly affect the evolution of strain i are the terms in the i'th row, that is, the terms describing the effects the different strains in the environment have on strain i's growth. Second, it makes clear what the selective pressure on these interaction terms is: it is expressed by this "interaction selection gradient" $\mathbf{S}(\mathbf{a}_{(i)}) = \partial_{1,}\mathscr{I}(\mathbf{a}_{(i)})^{\mathrm{T}}$, which is in fact equal to the equilibrium population vector $\hat{\mathbf{X}}$ for every strain i. Since the entries of $\hat{\mathbf{X}}$ are always nonnegative, selection generally pulls the interaction terms a_{ij} upward, with a force acting on each a_{ij} proportional to the size of each population j being interacted with.

As in section 3.6, with the selection gradient pulling $\mathbf{s}_i$ along the surface parametrized by $\mathbf{s}(\mathbf{u})$, the "interaction phenotype" (the i'th row of the matrix) is pulled by its selection gradient $\mathbf{S}(\mathbf{a}_{(i)})$ along the surface parametrized by $\mathbf{a}_{(i)}(\mathbf{s}) = (a(\mathbf{s},\mathbf{s}_1),\ldots,a(\mathbf{s},\mathbf{s}_n))^{\mathrm{T}}$. Figure 5.4 illustrates the "interaction selection gradient" pulling on the "interaction phenotypes", producing motion along the curve parametrized by changes in the first variable $\mathbf{s}$.

Unlike the constrained phenotypes $\mathbf{s}(\mathbf{u})$, however, while $\mathbf{a}_{(i)}$ is moved in response to the pull of selective pressure in the direction dictated by $\mathbf{S}(\mathbf{a}_{(i)})$, it simultaneously moves in some other direction as well, as each entry a_{ij} is always varying with both $\mathbf{s}_i$ and $\mathbf{s}_j$. Figure 5.5 illustrates this situation: while selection "pulls" each strain along this "constraint curve" in interaction-phenotype space, the curve also moves—as the curve itself is defined by the values of the n phenotypes—and drags the strains' $\mathbf{a}_{(i)}$ vectors along with it. As we

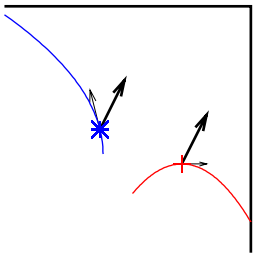


Figure 5.4: Action of the "interaction selection gradient" $\mathbf{S}(\mathbf{a}_{(i)})$ on rows of $\mathbf{a}$, in a 2×2 Lotka-Volterra system with one-dimensional phenotypes. Both strains are shown on the same graph. The X axis is $a(\cdot, \mathbf{s}_1)$, and the Y axis is $a(\cdot, \mathbf{s}_2)$, so that the two points shown represent the two rows of the $\mathbf{a}$ matrix. The curves passing through each point are the curves $(a(\cdot, \mathbf{s}_1), a(\cdot, \mathbf{s}_2))$ generated by varying the first argument to the a function in each place while keeping the two second arguments fixed. Each heavy arrow is $\mathbf{S}(\mathbf{a}_{(i)}) = \hat{\mathbf{X}}$, and the light arrows are its projections onto the constraint curves, which are the directions of motion of $\mathbf{a}_{(i)}$ induced by selection on strain i.

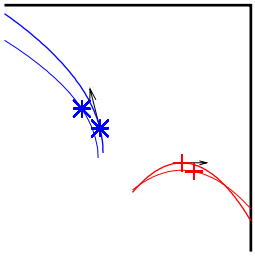


Figure 5.5: The situation a short time later than in figure 5.4. Both $\mathbf{a}_{(i)}$ rows have moved in response to selection, but have also been moved to the side by indirect consequences of the motion of $\mathbf{s}_1$ and $\mathbf{s}_2$, which moves the constraint curve itself.

have seen, the actual equations for the motion of a terms are

$$\dot{a}_{ij} \;=\; \partial_1 a(\mathbf{s}_i,\mathbf{s}_j)\;\dot{\mathbf{s}}_i + \partial_2 a(\mathbf{s}_i,\mathbf{s}_j)\;\dot{\mathbf{s}}_j,$$

where we would only have the first of these two terms if $\mathbf{a}_{(i)}$ were simply a function of $\mathbf{s}_i$, as in the $\mathbf{s}(\mathbf{u})$ case. Regardless, we can expand out this expression:

$$\begin{aligned}
\dot{a}_{ij} &= \gamma\left(\hat{X}_i\,\partial_1 a_{ij}\,\partial_1\mathscr{I}(\mathbf{s}_i)^{\mathrm{T}} + \hat{X}_j\,\partial_2 a_{ij}\,\partial_1\mathscr{I}(\mathbf{s}_j)^{\mathrm{T}}\right)\\
&= \gamma\left(\hat{X}_i\,\frac{\partial a_{ij}}{\partial \mathbf{s}_i}\frac{\partial \mathbf{a}_{(i)}}{\partial \mathbf{s}_i}^{\mathrm{T}}\,\mathbf{S}(\mathbf{a}_{(i)}) + \hat{X}_j\,\frac{\partial a_{ij}}{\partial \mathbf{s}_j}\frac{\partial \mathbf{a}_{(j)}}{\partial \mathbf{s}_j}^{\mathrm{T}}\,\mathbf{S}(\mathbf{a}_{(j)})\right)\\
&= \gamma\left(\hat{X}_i\,\frac{\partial a_{ij}}{\partial \mathbf{s}_i}\frac{\partial \mathbf{a}_{(i)}}{\partial \mathbf{s}_i}^{\mathrm{T}}\,\hat{\mathbf{X}} + \hat{X}_j\,\frac{\partial a_{ij}}{\partial \mathbf{s}_j}\frac{\partial \mathbf{a}_{(j)}}{\partial \mathbf{s}_j}^{\mathrm{T}}\,\hat{\mathbf{X}}\right).
\end{aligned}$$

The first term gives an expression for the "direct" effect on a_{ij} of selection on row i,

$$\dot{a}_{ij}^{(d)} = \gamma\hat{X}_i\,\frac{\partial a_{ij}}{\partial \mathbf{s}_i}\frac{\partial \mathbf{a}_{(i)}}{\partial \mathbf{s}_i}^{\mathrm{T}}\,\hat{\mathbf{X}},$$

and the second term gives an expression for the "indirect" effect of selection on row j,

$$\dot{a}_{ij}^{(i)} = \gamma\hat{X}_j\,\frac{\partial a_{ij}}{\partial \mathbf{s}_j}\frac{\partial \mathbf{a}_{(j)}}{\partial \mathbf{s}_j}^{\mathrm{T}}\,\hat{\mathbf{X}}.$$

5.3.2 When a values are not constrained

The adaptive dynamics framework for modeling evolutionary change, on which all the above calculations are based, depends centrally on the assumption that evolution proceeds by successive replacements, that is, that the number of strains remains constant away from branching points. As can be seen in figures 5.1–5.3, this assumption is not fulfilled with any accuracy by the no-phenotype model, but it is often true that the initial strain splits quickly into two descendant strains which do not diversify further, except for short-lived episodes. Actually, in adaptive dynamics simulations (with phenotypes) with finite mutation steps, the assumption of successive replacements is often temporarily violated, but the adaptive dynamics equations provide a good approximation to the observed dynamics anyway. So

let us consider the motion of the two strains seen in the no-phenotype model under the assumption that the rows of the matrix can be considered as moving phenotypes.

If this were strictly true, the motion of the matrix entries would be well modeled by the standard adaptive dynamics equations (3.5). Straightforward application of (3.5) would give

$$\begin{aligned} \dot{\mathbf{a}}_{(i)} &= \gamma \hat{X}_i \, \partial_1 \mathscr{I}(\mathbf{a}_{(i)})^{\mathrm{T}} \\ &= \gamma \hat{X}_i \, \hat{\mathbf{X}}, \end{aligned} \tag{5.4}$$

or

$$\dot{a}_{ij} = (\dot{\mathbf{a}}_{(i)})_j = \gamma \hat{X}_i \, \hat{X}_j.$$

Each row i, considered as a point in $\mathbb{R}^n$, would move upward and to the right in the direction of the equilibrium population vector $\hat{\mathbf{X}}$, with a speed proportional to the population of species i. This would imply, assuming the population sizes to be unequal at a given moment, that all the entries of one row would grow at a proportionally faster rate than the entries of the other row. Since we observe that the off-diagonal terms grow at an approximately equal rate, while the diagonal terms grow much more slowly, if they grow at all, this equation is not a good model for our system.

One correction to this model comes in looking more closely at how the process of successive replacements happens differently among the rows of the matrix than among phenotypic vectors. When a new variant is introduced to the matrix, a new row and column are added to the matrix, changing it from an $n \times n$ matrix,

$$\begin{pmatrix} a_{11} & \cdots & a_{1i} & \cdots & a_{1n} \\ \vdots & & \vdots & & \vdots \\ a_{i1} & \cdots & a_{ii} & \cdots & a_{in} \\ \vdots & & \vdots & & \vdots \\ a_{n1} & \cdots & a_{ni} & \cdots & a_{nn} \end{pmatrix},$$

to an $n+1 \times n+1$ matrix,

$$\begin{pmatrix} a_{11} & \cdots & a_{1i} & \cdots & a_{1n} & a_{1i}+\Delta a_{1i'} \\ \vdots & & \vdots & & \vdots & \vdots \\ a_{i1} & \cdots & a_{ii} & \cdots & a_{in} & a_{ii}+\Delta a_{ii'} \\ \vdots & & \vdots & & \vdots & \vdots \\ a_{n1} & \cdots & a_{ni} & \cdots & a_{nn} & a_{ni}+\Delta a_{ni'} \\ a_{i1}+\Delta a_{i'1} & \cdots & a_{ii}+\Delta a_{i'i} & \cdots & a_{in}+\Delta a_{i'n} & a_{ii}+\Delta a_{i'i'} \end{pmatrix}.$$

At this step the rows of the matrix become vectors of length $n+1$ instead of length n. The invasion function for strain i' is calculated using the first n terms of the bottom row of the matrix. To be more precise, let us write $\hat{\mathbf{X}}^{\{1,\ldots,n\}}$ for the equilibrium point of the population dynamics before strain i' is introduced; then the condition for successful invasion of strain i' is

$$\mathscr{I}(i'|\hat{\mathbf{X}}^{\{1,\ldots,n\}}) = \sum_{j\neq i'} \Delta a_{i'j} \hat{X}_j^{\{1,\ldots,n\}} > 0.$$

Assuming replacement, and assuming that no incidental extinctions are caused by the replacement, the population dynamics after the replacement will have its own equilibrium point $\hat{\mathbf{X}}^{\{1,\ldots,i-1,i',i+1,\ldots,n\}}$ (after rearranging the indices). As was discussed in section 2.10, the extinction of strain i requires

$$\mathscr{I}(i|\hat{\mathbf{X}}^{\{1,\ldots,i-1,i',i+1,\ldots,n\}}) = \sum_{j\neq i} (a_{ij} - a_{i'j}) \hat{X}_j^{\{1,\ldots,i-1,i',i+1,\ldots,n\}} < 0.$$

After the replacement (and reindexing) the matrix is once again $n \times n$:

$$\begin{pmatrix} a_{11} & \cdots & a_{1i}+\Delta a_{1i'} & \cdots & a_{1n} \\ \vdots & & \vdots & & \vdots \\ a_{i1}+\Delta a_{i'1} & \cdots & a_{ii}+\Delta a_{i'i'} & \cdots & a_{in}+\Delta a_{i'n} \\ \vdots & & \vdots & & \vdots \\ a_{n1} & \cdots & a_{ni}+\Delta a_{ni'} & \cdots & a_{nn} \end{pmatrix}.$$

Given small Δa values, this matrix is a slight perturbation of the original $\mathbf{a}$ matrix. Since the solution of the matrix equation $\hat{\mathbf{X}} = -\mathbf{a}^{-1}\mathbf{r}$ is a continuous function of each of the entries of $\mathbf{a}$ when $\mathbf{a}$ is not singular (this can be seen by writing out the entries of $\hat{\mathbf{X}}$ using Cramer's rule), the value of $\hat{\mathbf{X}}$ after replacement can be expected to be similar to its value before replacement (this corresponds to the assumption of chapter 3 that the invasion function is a continuous function of the resident phenotypes).

The necessary conditions for replacement of strain i by its daughter strain i' are then

$$\mathscr{I}(i'|\hat{\mathbf{X}}^{\{1,\ldots,n\}}) = \sum_{j\neq i'} \Delta a_{i'j}\hat{X}_j^{\{1,\ldots,n\}} > 0 \tag{5.5}$$

and

$$\begin{aligned}&\mathscr{I}(i|\hat{\mathbf{X}}^{\{1,\ldots,i-1,i',i+1,\ldots,n\}})\\ &\quad = \textstyle\sum_{j\notin\{i,i'\}}(-\Delta a_{i'j})\hat{X}_j^{\{1,\ldots,i-1,i',i+1,\ldots,n\}} + (\Delta a_{ii'} - \Delta a_{i'i'})\hat{X}_{i'}^{\{1,\ldots,i-1,i',i+1,\ldots,n\}} < 0.\end{aligned} \tag{5.6}$$

In the case of successive replacement of regular phenotype vectors which do not become longer and shorter during the process, all of the same Δ values would appear in both the invasion condition and the extinction condition. The stochastic dynamical system that gives rise to the adaptive dynamics equations (3.4) and (3.5) for motion of phenotypes is based on the assumption that those Δ values are introduced in an unbiased way, and biased by these requirements on the signs of their sums. The expected change in each phenotype vector component per unit time comes out to be proportional to the coefficient of each Δ in these expressions—in this case, to the various $\hat{X}_j$ values (which are the same before and after when $\max|\Delta a| \to 0$). These coefficients are in fact the components of the selection gradient $\mathbf{S} = (\partial\mathscr{I}/\partial\mathbf{s}_i)^{\mathrm{T}}$, or in this case, $\mathbf{S} = (\partial\mathscr{I}/\partial\mathbf{a}_{(i)})^{\mathrm{T}}$. If we were replacing a_{ii} by $a_{i'i}$, or $a_{ii'}$ by $a_{i'i'}$, this would probably work out fine and (3.5) would be a good approximation, but since we are replacing a_{ii} by $a_{i'i'}$ there is a disconnect between these two equations, and no clear indication what the sign or magnitude of $a_{i'i'} - a_{ii}$ might be.

This problem only applies to the diagonal terms, though; if we take apart equation (5.4)

into its component terms,

$$\dot{a}_{ij} = \gamma \hat{X}_i \hat{X}_j,$$

we can keep the rest of the terms while remaining skeptical about the trajectories of the diagonal terms:

$$\dot{\mathbf{a}} = \gamma \begin{pmatrix} ? & \cdots & \hat{X}_1\hat{X}_i & \cdots & \hat{X}_1\hat{X}_n \\ \vdots & \ddots & & & \vdots \\ \hat{X}_1\hat{X}_i & & ? & & \hat{X}_i\hat{X}_n \\ \vdots & & & \ddots & \vdots \\ \hat{X}_1\hat{X}_n & \cdots & \hat{X}_i\hat{X}_n & \cdots & ? \end{pmatrix};$$

for two strains,

$$\dot{\mathbf{a}} = \gamma \begin{pmatrix} ? & \hat{X}_1\hat{X}_2 \\ \hat{X}_1\hat{X}_2 & ? \end{pmatrix}.$$

Since selection does not appear to be acting directly on $\Delta a_{i'i'}$ in the way that it does on other $\Delta a_{i'j}$ terms, one possible approximate model for the system would simply be to place zeros on the diagonal where I have written ? signs. However, since numerous observations of simulations do indicate that diagonal terms do tend to grow more often than not, it seems that a better approximation may be possible. Equation 5.6 does provide a coefficient for $\Delta a_{i'i'}$ which has the appropriate sign; combining the two equations (and assuming the two $\hat{\mathbf{X}}$ vectors become identical in the limit of small Δa),

$$2 \sum_{j \notin \{i,i'\}} \Delta a_{i'j} \hat{X}_j + \Delta a_{i'i} \hat{X}_i + \Delta a_{i'i'} \hat{X}_i - \Delta a_{ii'} \hat{X}_i > 0.$$

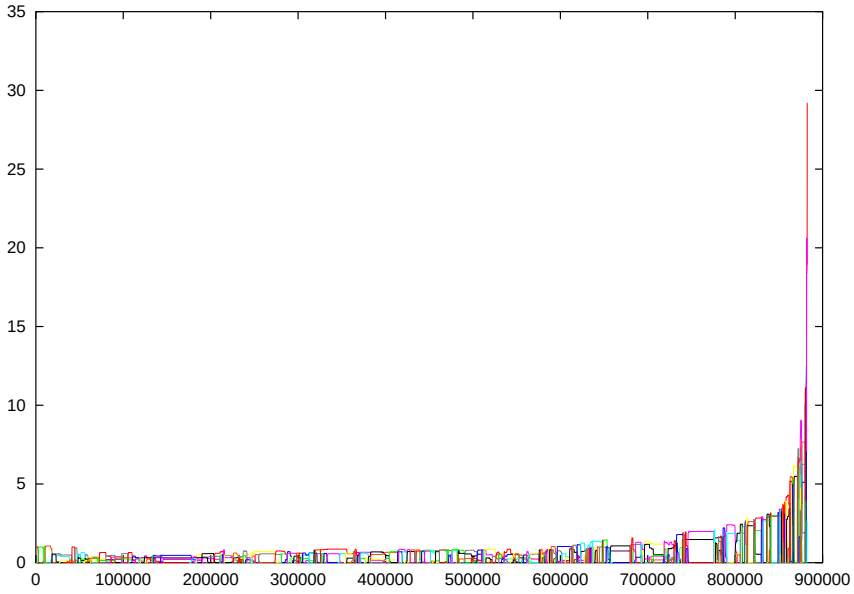


Figure 5.6: Population sizes against time in the same simulation as shown in figure 5.2. After the last equilibrium shown, the population becomes infinite.

This suggests that perhaps selection is acting on $\Delta a_{i'i'}$, half as strongly as on the off-diagonal terms:

$$\dot{\mathbf{a}} = \gamma \begin{pmatrix} \frac{1}{2}\hat{X}_1^2 & \cdots & \hat{X}_1\hat{X}_i & \cdots & \hat{X}_1\hat{X}_n \\ \vdots & \ddots & & & \vdots \\ \hat{X}_1\hat{X}_i & & \frac{1}{2}\hat{X}_i^2 & & \hat{X}_i\hat{X}_n \\ \vdots & & & \ddots & \vdots \\ \hat{X}_1\hat{X}_n & \cdots & \hat{X}_i\hat{X}_n & \cdots & \frac{1}{2}\hat{X}_n^2 \end{pmatrix};$$

and for two strains,

$$\dot{\mathbf{a}} = \gamma \begin{pmatrix} \frac{1}{2}\hat{X}_1^2 & \hat{X}_1\hat{X}_2 \\ \hat{X}_1\hat{X}_2 & \frac{1}{2}\hat{X}_2^2 \end{pmatrix}$$

(it also suggests that $\Delta a_{i'i}$ and $\Delta a_{ii'}$ are likely to be biased toward positive and negative numbers, respectively, by the replacement process, but since these terms are discarded when strain i goes extinct, this fact is not useful).

This model is appealing because it correctly suggests that a_{12} and a_{21} rise at the same rate, and makes it plausible that the diagonal terms grow more slowly than the off-diagonal terms. However, as figure 5.6 shows that both $\hat{X}_1$ and $\hat{X}_2$ grow as the matrix approaches the boundary of *B*-stability, while in figures 5.1–5.3 the off-diagonal terms appear to grow at a constant rate, this approximation also seems to be wrong.

Additionally, this approximation is still derived from the assumption that all changes in a values come from successive replacements, which preserve the number of strains of the system. Even if it is a good description of some realizations of the model, where this assumption more or less holds, as we will see shortly, the introduction of new strains that do not drive their parents to extinction can be very important in the development of diagonal terms. Since this half-strength selection term comes only from the extinction condition, where all the other terms come from both the invasion and the extinction conditions, a strain whose diagonal term does not increase will not fail to invade, it will only fail to displace its parent. The use of this term must be especially unsuited to situations in which these moments of coexistence are important.

I will return to the subject of coexistence and replacement among two and three strains after a discussion of how branching happens in this model.

5.4 A different kind of branching

In the adaptive dynamics literature, when strains are characterized by fixed-length phenotype vectors, the number of strains tends to remain constant, each evolving by successive replacements, except at singular points, where coexistence of a new strain with its parent and disruptive selection can lead to evolutionary branching. Coexistence of a parent and daughter strain is only possible at an evolutionary singular point where $\partial_1 \mathscr{I}(\mathbf{s}_i|\mathbf{s}_1,\ldots,\mathbf{s}_n) = 0$. If the model of this chapter were equivalent to an adaptive dynamics model with the rows of the **a** matrix serving as phenotypes, branching of one strain into two strains would only be

possible at special points where $\partial_1 \mathscr{I}(\mathbf{a}_{(i)}|\mathbf{a}) = 0$, that is, where $\hat{\mathbf{X}} = 0$. Since this is not possible in any model in which organisms continue to live, yet branching occurs in this model, it must be that branching happens in a different way than predicted by published adaptive dynamics theorems.

As we have seen above and in section 2.4, in a model based on phenotype vectors $\mathbf{s}_i$ in a vector space $\Sigma \in \mathbb{R}^m$, with $a_{ij} = a(\mathbf{s}_i, \mathbf{s}_j)$, when no other strains are present, a resident strain $\mathbf{s}_i$ can coexist with a mutant strain $\mathbf{s}_{i'} = \mathbf{s}_i + \Delta\mathbf{s}_{i'}$ when each can invade the other; in this specific model, when $a_{ii} < a_{i'i}$ and $a_{i'i'} < a_{ii'}$, or equivalently, when $0 < \Delta a_{i'i}$ and $\Delta a_{i'i'} < \Delta a_{ii'}$. When $\Delta\mathbf{s}_{i'}$ is small, we have

$$\begin{aligned}
\Delta a_{i'i} &= \sum_{k=1}^{m} (\Delta\mathbf{s}_{i'})_k \left.\frac{\partial a(\mathbf{s}, \mathbf{s}_i)}{\partial(\mathbf{s})_k}\right|_{\mathbf{s}=\mathbf{s}_i} + O(\|\Delta\mathbf{s}_{i'}\|^2); \\
\Delta a_{ii'} &= \sum_{k=1}^{m} (\Delta\mathbf{s}_{i'})_k \left.\frac{\partial a(\mathbf{s}_i, \mathbf{s})}{\partial(\mathbf{s})_k}\right|_{\mathbf{s}=\mathbf{s}_i} + O(\|\Delta\mathbf{s}_{i'}\|^2); \\
\Delta a_{i'i'} &= \sum_{k=1}^{m} (\Delta\mathbf{s}_{i'})_k \left.\left(\frac{\partial a(\mathbf{s}, \mathbf{s}_i)}{\partial(\mathbf{s})_k} + \frac{\partial a(\mathbf{s}_i, \mathbf{s})}{\partial(\mathbf{s})_k}\right)\right|_{\mathbf{s}=\mathbf{s}_i} + O(\|\Delta\mathbf{s}_{i'}\|^2) \\
&= \Delta a_{i'i} + \Delta a_{ii'} + O(\|\Delta\mathbf{s}_{i'}\|^2),
\end{aligned}$$

showing that the Δa term describing the interaction of the mutant with itself cannot be independent of the interactions between the mutant and its parent type. As $\Delta a_{ii'} - \Delta a_{i'i'}$ approaches $-\Delta a_{i'i}$, the two invasion conditions can not be met simultaneously as the mutation size goes to zero, except at a singular point where the first order terms vanish and the second order terms can come out in some other order.

But I am allowing these three terms to be chosen independently. With this assumption, since $\Delta a_{ii'} - \Delta a_{i'i'}$ is entirely independent of $\Delta a_{i'i}$, the resident and mutant have a 50% chance of coexisting, no matter what the value of $\mathbf{a}$ is. No singular point is required.

Thus it is not long after the introduction of the single initial strain that it develops into two coexisting strains. These two may be replaced by a single subsequent strain that outcompetes both of them, or they may evolve into a more stably coexisting pair—that is, one whose cross-interaction terms significantly exceed the self-interaction terms. As this

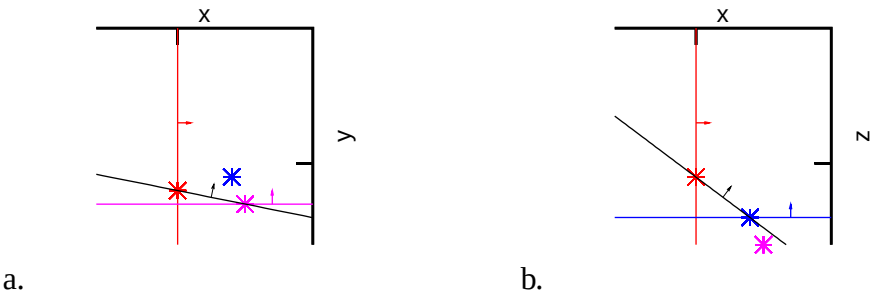
a. b.

Figure 5.7: (*a*) Coexistence of two strains; (*b*) replacement of strain 1 by strain 2, in terms of rows of the **a** matrix. The first row $\mathbf{a}_{(1)}$ and the region of invasibility when strain 1 is resident are shown in red; the corresponding objects for strain 2 are shown in purple.

reduction of interstrain competition proceeds, it becomes less likely that a mutant of one of the two coexisting strains will displace the other strain entirely. Evolutionary splitting in this model is characterized by these two green strands rising away from one of the red lines, both in the initial splitting which tends to be permanent and in the numerous short-lived later splittings, which tend to collapse almost immediately back to one strain.

5.5 A closer look at invasion and replacement

Let us look in more detail at how invasion, coexistence, and replacement affect the development of the interaction terms in the vector space of rows of the **a** matrix. Figure 5.7 illustrates the conditions for coexistence and replacement of one strain by a mutant strain. In the left-hand figure, the matrix shown is $\mathbf{a} = \begin{pmatrix} -1 & -1.08 \\ -0.9 & -1.13 \end{pmatrix}$. Each row of the matrix is plotted as a point in the (x,y) plane. For convenience, let us relabel the terms of the matrix as $\begin{pmatrix} x_1 & y_1 \\ x_2 & y_2 \end{pmatrix}$. Then strain 2 can invade strain 1 if $x_2 > x_1$, and strain 1 can invade strain 2 if $y_1 > y_2$ (continuing to assume that $r_i = 1$). The regions of points satisfying these



a. b.

Figure 5.8: Replacement of one of two coexisting strains. (*a*) When strains 1 and 2 coexist, strain 3 is able to invade. The black line and arrow show the region of (x,y) combinations that can invade when both strains 1 and 2 are resident. (*b*) Strains 1 and 3 can coexist, and strain 2 cannot invade this combination, since it is outside the region of (x,z) combinations that can invade when 1 and 3 are resident.

conditions are indicated in the figure, showing that in case *a*, both invasion conditions are met: the red point, representing strain 1, is above the purple line, and the purple point, representing strain 2, is to the right of the red line, so that these two strains can coexist.

The matrix shown in the right-hand figure is $\mathbf{a} = \begin{pmatrix} -1 & -1.08 \\ -0.9 & -1.02 \end{pmatrix}$. In this case, strain 2 can invade strain 1, but the reverse condition does not hold, so strain 2 must replace strain 1. After the extinction of strain 1, the community will be represented by the matrix (-1.02). Given invasion by the mutant strain 2, the distinction between coexistence and replacement is controlled by whether $y_2 > y_1$. While this condition clearly indicates that the parent is more likely to be replaced by a strain whose diagonal term is large, it does not guarantee that the original diagonal term will be replaced by a larger value, as the example shows.

Figure 5.8 illustrates two coexisting strains, and a third strain that invades and replaces

the second. The interaction matrix for these three strains is

$$\begin{pmatrix} -1 & -1.2 & -1.1 \\ -0.7 & -1.3 & -1.5 \\ -0.6 & -1.1 & -1.4 \end{pmatrix}.$$

Again, let us relabel these terms

$$\begin{pmatrix} x_1 & y_1 & z_1 \\ x_2 & y_2 & z_2 \\ x_3 & y_3 & z_3 \end{pmatrix}.$$

Before the invasion, the 2×2 matrix for the first two strains can be plotted on the (x,y) plane, just as in the previous example. Since the mutual invasibility conditions for these two strains are met, they coexist at equilibrium. The invasion function when both are resident is

$$\mathscr{I}(i|1,2) = 1 + \hat{X}_1 x_i + \hat{X}_2 y_i.$$

The set of points for which this quantity is zero is a straight line, and since $\mathscr{I}(1|1,2) = \mathscr{I}(2|1,2) = 0$, this line passes through (x_1,y_1) and (x_2,y_2), as shown in figure 5.8*a*. Since (x_3,y_3) lies above this light blue line, its invasion exponent is positive in this community. Conversely, when strains 1 and 3 are the resident strains, as shown in figure 5.8*b* (on the (x,z) plane), these two can coexist but the invasion exponent for strain 2 is negative.

Naturally, under these conditions we would expect that strain 3 will invade no matter how small its initial population is, and that strain 2 will certainly go extinct and strains 1 and 3 will then coexist permanently. This cannot be proven by any of the theorems presented in section 2.8, since the Gopalsamy condition (2.7) is not satisfied by the above matrix. The following theorem handles this case by being more general in terms of invasion and not requiring competitive interactions, but only applies to three dimensions.

Theorem 5.1. *Given system (5.1) in 3 dimensions, suppose that all* $r_i > 0$ *and* **a** *is nonsingular and B-stable. If the subsystem* $\{1,2\}$ *(that is, the subsystem in which only strains 1*

and 2 are present) and the subsystem $\{1,3\}$ *are both permanent, with positive fixed points* $\hat{\mathbf{X}}^{\{1,2\}}$ *and* $\hat{\mathbf{X}}^{\{1,3\}}$ *in the corresponding subspaces* $\mathbb{R}_+^{\{1,2\}}$ *and* $\mathbb{R}_+^{\{1,3\}}$ *of* $\mathbb{R}_+^3$*, and in addition, strain 3 can invade* $\{1,2\}$*,*

$$\mathscr{I}(3|1,2) = r_3 + a_{31}\hat{X}_1^{\{1,2\}} + a_{32}\hat{X}_2^{\{1,2\}} > 0, \tag{5.7}$$

while strain 2 can not invade $\{1,3\}$*,*

$$\mathscr{I}(2|1,3) = r_2 + a_{21}\hat{X}_1^{\{1,3\}} + a_{23}\hat{X}_3^{\{1,3\}} < 0, \tag{5.8}$$

then $\hat{\mathbf{X}}^{\{1,3\}}$ *is the globally attracting equilibrium.*

Proof. Trajectories in $\mathbb{R}_+^3$ can be attracted to solutions in the interior of $\mathbb{R}_+^3$, or in any of the various subspaces in the boundary of $\mathbb{R}_+^3$. As I will show, all of these possibilities can be ruled out except for the $\{1,3\}$ subspace, in which $\hat{\mathbf{X}}^{\{1,3\}}$ is the only possible attractor.

All three strains cannot go extinct, because each has a positive invasion exponent when nothing is present (the growth rate of X_i at $\mathbf{0}$ is $r_i > 0$). No one strain alone is a stable solution, since either strain 2 or 3 can invade strain 1, and strain 1 can invade either of the others (in two dimensions, permanent coexistence is equivalent to mutual invasibility). Since strain 3 can invade $\hat{\mathbf{X}}^{\{1,2\}}$, because of the time average theorem no attractor in int $\mathbb{R}_+^{\{1,2\}}$ can be attractive to trajectories with positive X_3. Therefore, all trajectories must be attracted either to $\{1,3\}$, to $\{2,3\}$ or to an attractor in int $\mathbb{R}_+^3$. If there is an attractor in the interior, there must be a fixed point $\hat{\mathbf{X}}^{\{1,2,3\}}$ in the interior. I will show first that there is no fixed point in the interior, and second that $\{2,3\}$ cannot be attracting whether it has a fixed point or not, so that $\hat{\mathbf{X}}^{\{1,3\}}$ must be the globally attracting solution.

The zero-growth isocline Z_i of each strain is a plane which cuts $\mathbb{R}_+^3$ into two regions: a region containing $\mathbf{0}$, in which X_i increases, and a region on the other side, in which X_i decreases. The invasion conditions (5.7) and (5.8) imply that $\hat{\mathbf{X}}^{\{1,2\}}$ is contained in the region 'below' Z_3 (containing $\mathbf{0}$) and $\hat{\mathbf{X}}^{\{1,3\}}$ is in the region 'above' Z_2, while the coexistence

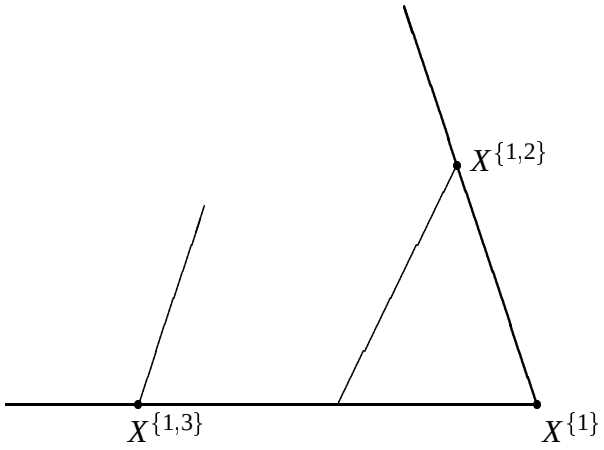


Figure 5.9: Sketch of part of the zero-growth isocline of strain 1, and its intersections with the other strains' isoclines.

conditions for $\{1,2\}$ and $\{1,3\}$ imply that $\hat{\mathbf{X}}^{\{1\}}$, the equilibrium point where only strain 1 is present, lies below both Z_2 and Z_3.

$\hat{\mathbf{X}}^{\{1\}}$, $\hat{\mathbf{X}}^{\{1,2\}}$ and $\hat{\mathbf{X}}^{\{1,3\}}$ are all contained in Z_1, the zero-growth isocline of strain 1, and any interior fixed point $\hat{\mathbf{X}}^{\{1,2,3\}}$ must also be contained in Z_1. Z_1 intersects the boundary of $\mathbb{R}^3_+$ at least in the $\{1,2\}$ and $\{1,3\}$ faces, since it passes through $\hat{\mathbf{X}}^{\{1,2\}}$ and $\hat{\mathbf{X}}^{\{1,3\}}$. The intersections of Z_2 and Z_3 with Z_1 are sketched in figure 5.9. Z_2 intersects the boundary of Z_1 in two points, one of which is $\hat{\mathbf{X}}^{\{1,2\}}$, and the other must fall between $\hat{\mathbf{X}}^{\{1\}}$ and $\hat{\mathbf{X}}^{\{1,3\}}$. Similarly, Z_3 includes $\hat{\mathbf{X}}^{\{1,3\}}$ and divides Z_1 into two regions, one of which includes both $\hat{\mathbf{X}}^{\{1,2\}}$ and $\hat{\mathbf{X}}^{\{1\}}$. Since both $Z_1 \cap Z_2$ and $Z_1 \cap Z_3$ are straight line segments, this implies that they cannot meet in the positive cone, and so there can be no positive fixed point.

Second, any fixed point in which strain 2 is present and strain 1 is not must lie in the intersection of Z_2 and the subspace $\mathbb{R}^{\{2,3\}}_+$ where $X_1 = 0$. Since the plane Z_2 intersects Z_1 in a line segment strictly disjoint from $\mathbb{R}^{\{2,3\}}_+$, and the corner point, $\hat{\mathbf{X}}^{\{1\}}$, occupies the region below Z_2, the part of Z_2 intersecting $\mathbb{R}^{\{2,3\}}_+$ must lie within the region in which strain 1 can invade. Therefore $\mathbb{R}^{\{2,3\}}_+$ cannot be attractive to trajectories in int $\mathbb{R}^3_+$. This leaves only trajectories in $\mathbb{R}^{\{1,3\}}_+$ as possible attractors, and Theorem 2.1 shows that $\hat{\mathbf{X}}^{\{1,3\}}$ is the only attractor in $\mathbb{R}^{\{1,3\}}_+$. □

This theorem shows that the relations shown in figure 5.8 are all that is needed to guarantee replacement of strain 2 by strain 3. The combination of coexistence of $\{1,2\}$ and $\{1,3\}$ and the invasion and replacement conditions (5.7) and (5.8) are both necessary for this replacement—as discussed in the previous section—and sufficient.

The opposite condition, in which strain 3 invades but does not replace strain 2, can also be proven.

Theorem 5.2. *Given all the assumptions of Theorem 5.1, except that*

$$\mathscr{I}(2|1,3) > 0,$$

all trajectories in int $\mathbb{R}^3_+$ *are attracted to a compact region in int* $\mathbb{R}^3_+$.

This theorem follows directly from the following general theorem for three dimensions:

Theorem 5.3. (Hofbauer, Sigmund). *Given a three-species ecological model*

$$\dot{x}_i = x_i f_i(x_1, x_2, x_3) \tag{5.9}$$

satisfying the following conditions:

(H1) the solutions of (5.9) in $\mathbb{R}^3_+$ *are uniformly bounded;*

(H2) all attractors on the boundary of $\mathbb{R}^3_+$ *are fixed points;*

(H3) the origin is hyperbolic, i.e. $f_i(\mathbf{0}) \neq 0$*, and there is at most one positive rest point on each axis;*

(H4) if there is a positive rest point on each axis and $\mathscr{I}(1|2)$, $\mathscr{I}(2|3)$, $\mathscr{I}(3|1) > 0$ *and* $\mathscr{I}(2|1)$, $\mathscr{I}(3|2)$, $\mathscr{I}(1|3) \leq 0$ *(or the other way around), then*

$$\mathscr{I}(1|2)\mathscr{I}(2|3)\mathscr{I}(3|1) + \mathscr{I}(2|1)\mathscr{I}(3|2)\mathscr{I}(1|3) > 0,$$

if none of the boundary rest points is saturated, then the system is permanent.

The fourth condition is necessary in order to rule out attracting heteroclinic cycles on the boundary. It is not relevant to the system of Theorem 5.2 because both $\mathscr{I}(1|2)$ and $\mathscr{I}(1|3)$ are positive.

As in the case of replacement of strain 1 in isolation, the conditions for replacement of strain 2 by strain 3 do not guarantee that a_{33} will be greater than a_{22}. a_{33} appears in two places in Theorem 5.1: in the coexistence condition for strains 1 and 3, which requires that $a_{13} > a_{33}$ in order that strain 3 does not displace strain 1, and in the extinction condition for strain 2, which involves

$$\hat{x}_1^{\{1,3\}} = \frac{a_{13} - a_{33}}{a_{11}a_{33} - a_{13}a_{31}} \quad \text{and} \quad \hat{x}_3^{\{1,3\}} = \frac{a_{31} - a_{11}}{a_{11}a_{33} - a_{13}a_{31}}.$$

Neither of these conditions affects whether the mutant strain 3 successfully invades into the community, only whether others are displaced by it. These effects are surely important to the development of the **a** matrix, but not in a straightforward way.

These two theorems cannot currently be generalized to more than 3 dimensions, since criteria for ruling out attracting heteroclinic cycles are not currently known. (If there are no heteroclinic cycles, the isocline argument of Theorem 5.1 generalizes nicely, and Hofbauer and Sigmund's theorem probably does as well.)

5.6 Diagonal terms and levels of selection

Since the coexistence of population n with the others hinges on its ability to enter the system when rare, the self-interaction term is left out of the calculation—a_{nn} does not affect the invasion exponent (5.5), so that when a new population enters the system, while all the other Δa values in its row are biased by the requirement that the sum (5.5) must come out positive, the Δa for the diagonal entry is not affected by this condition. Extinction also ignores the diagonal entries: when a population becomes very small, the extinction criterion (5.6) depends on whether it continues to shrink, which is independent of the self-interaction

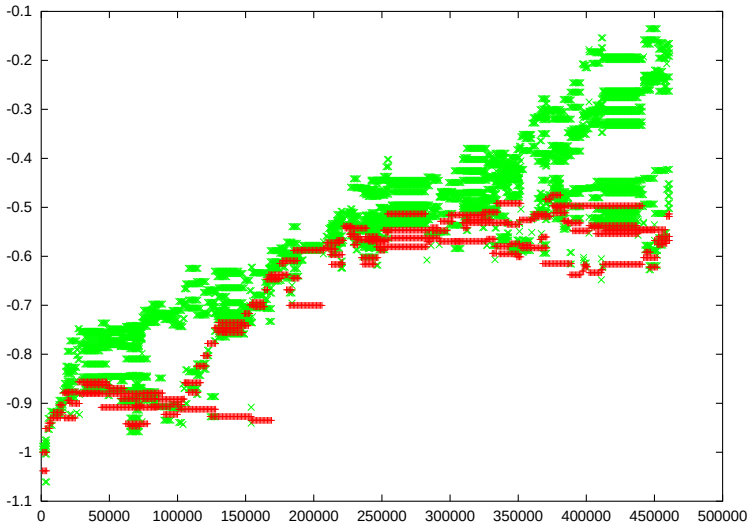


Figure 5.10: Increase of diagonal interaction terms, apparently due to 'species selection' in the Lotka-Volterra system (5.1). At about time 170,000, the upper red line collides with the green lines, which makes the strain represented by the lower red line unable to persist. The remaining strain then splits again and repeats the process, undergoing another extinction and splitting at about time 210,000.

just as the invasion criterion is. Diagonal entries, as mentioned in the previous section, do play a role in other strains' invasion and extinction criteria, but probably because of being essentially uncoupled from the success of the strain they belong to, the diagonal entries tend to drift freely where other terms of the matrix are pulled upward by selection.

However, as figures 5.1–5.3 reveal, diagonal terms do tend to grow, though not as quickly as the terms that descend from them. This may be due to a more subtle form of selection: populations with larger self-interaction terms, especially when the matrix is small, tend to equilibrate at larger population sizes, and so produce mutant offspring more frequently. As a result, the self-interaction terms of variant populations tend to fall toward the upper end of the distribution of self-interaction terms among resident populations, causing the distribution of these terms to rise over time even though they are not subject to selection in the direct sense.

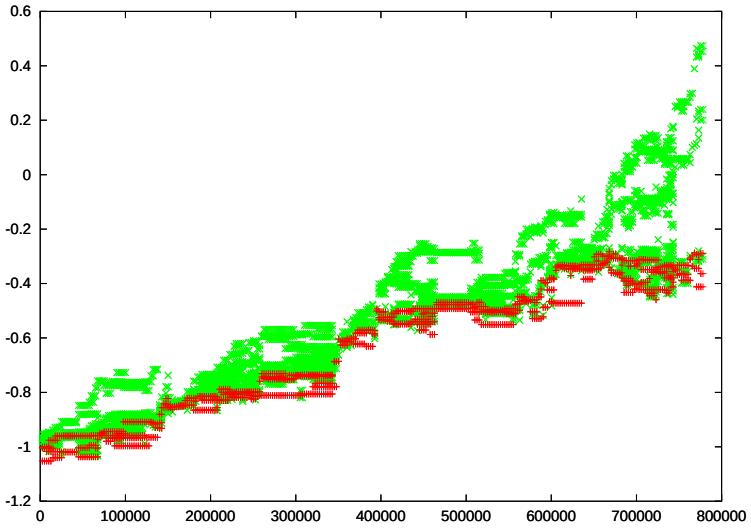


Figure 5.11: Increase of diagonal interaction terms by repeated splitting and extinction.

Another source of increase in diagonal terms may be due to a process that is essentially species selection, as seen in figure 5.10. As we have seen, two populations in this system coexist when $a_{12} > a_{11}$ and $a_{21} > a_{22}$. When the community consists of one strain which splits into two lineages, its self-interaction term splits into four lineages of interactions, two diagonal and two off-diagonal, with the off-diagonal terms larger than the corresponding diagonal terms, as is necessary for coexistence. After the split, if one of the lineages of self-interaction terms (red lines in the graphs) rises up to meet the line of cross-interaction terms (one of the green lines) above it, disrupting the relative ordering of terms, the conditions for coexistence are no longer met and the other strain is driven to extinction. When this happens, the surviving strain tends to have self-interaction terms larger than those of the extinct lineage. (This is kind of an extreme case of the previous case: when the red line rises all the way up to the green line, the difference in population sizes is so extreme that the other population size is zero.)

It may be that a form of this branching-extinction process is at work on short time scales

in this system as well as at long and intermediate time scales: very short-lived periods of coexistence end with the survival of one strain with larger self-interaction than the other or others, on average, and as the process repeats, the ensemble of red points gradually rises toward positive values. Figure 5.11 appears to illustrate this process on an intermediate scale.

5.7 How to model this system

It might be possible to derive from the invasion and extinction criteria a differential equation model for the motion of the four terms of a 2×2 interaction matrix, under the (false) assumption of long periods of coexistence of exactly two strains moving by successive replacements, using the stochastic modeling techniques used by adaptive dynamics modelers. Even if this model were able to match well with the observed motion of these terms in the periods when the community is made up of two lineages, it would not teach us anything about the more interesting aspects of this system—the nonstandard splitting events, the rises in average self-interaction terms due to higher-level selection, why one strain dependably splits into two when it is alone in the community but splittings rarely persist when other strains are present, and why, as we will see in the next chapter, this last fact is not true when the model is changed a little.

An analysis of the system that is able to address these questions would have to face head-on the fact that the community does not behave like an assemblage of moving points in phenotype space, that the number of strains present at equilibrium can change with every mutation event. I believe (without rigorous proof) that the dynamical system is autonomous with respect to **a**, that there is no need to worry about metastability in the ecological dynamics making it indeterminate which strains will persist and which will go extinct at each step, so that the evolution process can be understood, in principle, as a well-defined stochastic dynamical system with **a** as the state variable (see Law and Morton 1993 for a preliminary

discussion of using invasion and extinction to construct a Markov process of transitions between permanent subsystems of (5.1)). But this can not be done in terms of calculus-like motion of each entry of **a**. The matrix must be considered as a point in a space that includes 1×1, 2×2, 3×3 matrices and so on, with a metric under which the dynamics can be seen as a map that can take a 2×2 matrix to a 'nearby'—appropriately defined—3×3 matrix, and then back again in the next step.

To define such a map would require a fuller analysis than we have of which strains persist after each invasion. It might suffice to assume without proof that the various invasion exponents imply what they seem to imply—in particular, that the replacement and coexistence theorems of section 5.5 which formalize the conditions illustrated in figures 5.7 and 5.8 can be generalized to n dimensions, though there are surely cases where this is not true. This might make it possible to write some useful things about this map and make some predictions about the motion of diagonal terms and off-diagonal terms, and possibly to look for useful summary quantities that make predictions about qualitative changes in the overall community makeup. The calculations defining the invasion and extinction criteria can be quite complicated, especially when more than two strains are resident. It would be interesting to pursue these questions further.

5.8 Discussion

5.8.1 Comparison to related models

Lev Ginzburg and two coworkers (Ginzburg, Akçakaya, and Kim 1988) use this mutation-of-interaction-terms technique to study evolution in all-competitive communities. They found that one species diversifies into several, and that off-diagonal terms become larger than diagonal terms. Since they do not allow any terms to become positive, they do not find any mutualism, and they do not discuss the nature of the branching event.

Peter Taylor (before his transformation to student of scientific discourses; see chapter 1) (1988) describes the pattern of accumulation of positive matrix entries followed by populations exploding to infinity in a model in which immigrant species are added to the Lotka-Volterra matrix one by one, by choosing interaction coefficients independently from a continuous distribution. That paper does not involve gradual evolutionary changes to populations, and does not discuss the nature of the explosion in any detail, focusing on what happens before that. Taylor does find a trend toward increase in the proportion of mutualistic interactions in the community before the explosion.

Others who have used evolutionary simulations and Lotka-Volterra dynamics together, using phenotype schemes of varying levels of complexity, and observed a gradual buildup of mutualistic terms, include Kauffman (1993), Christensen and coworkers (2002), and Shimada and coworkers (Shimada, Yukawa, and Ito 2003). None of these look at phylogeny or how diversification happens, or analyze how and why positive terms accumulate. Tokita and Yasutomi (2003), using a significantly more complicated model than mine with a mix of phenotypes and mutations of interactions, find the emergence of mutualists and do look at their phylogeny, but do not analyze the branching event or the evolutionary pressure driving species toward mutualism. I have not come across anything resembling my analysis of the branching event and the selective pressure on interaction terms.

The transition to a cooperative community that causes the explosion in the Lotka-Volterra dynamics is reminiscent of the emergence of hypercycles (Eigen and Schuster 1979) and autocatalytic sets (Farmer, Kauffman, and Packard 1986; Kauffman 1993) in models of prebiotic evolution. The appearance of the chemical hypercycle, which is similar to the transition seen here, is seen as a crucial step in the origin of life. In particular, this model's results echo those seen by Sanjay Jain and Sandeep Krishna in a series of models of chemical network formation.

Jain and Krishna (1998, 1999) model a community of chemical species which can catalyze the formation of other chemical species, described by a directed graph of catalytic

relationships. The graph is represented by a matrix of zeros and ones. Each time the population dynamics comes to equilibrium, one of the least successful species is removed and replaced by one with randomly assigned connections in the graph. There is a period in which no qualitative change occurs, followed by the emergence of an autocatalytic set—a subgraph containing a cycle—which causes a population explosion very much like the one reported here; following which populations not participating in the autocatalytic set are gradually replaced until the autocatalytic set encompasses all species in the model. A later model (Jain and Krishna 2001) replaces the ones in the matrix with real values between -1 and 1, and produces generally the same results.

An obvious difference between the Jain and Krishna models and the present one is that those describe inanimate chemicals while this one describes interacting biological populations; this is reflected in the fact that their birth terms are linear while the corresponding terms in the present model are quadratic. While this difference makes the Lotka-Volterra model harder to analyze in some ways, it does not seem to make much difference in the qualitative description of the different phases of community formation. Other differences between the models may be more significant.

One important difference is that in the present model extinctions are endogenous, with species disappearing whenever their population approaches zero. In the Jain and Krishna model, at each evolutionary time step one of the smallest populations is removed without regard for whether many or no species have zero population. Since the authors transform their variables into relative population sizes to construct the standard replicator equation form, the model does not clearly distinguish between well-behaved systems and those whose dynamics approach zero. This difficulty can be resolved by assuming an outside supply term that is not visible in the replicator dynamics—like the r_i term in the present model—but this leaves the question of why a newly innovated chemical species is supplied from outside after it appears but not before. (A related question is how a newly introduced chemical species is produced by the catalytic action of older species which did not produce

it before.)

When the autocatalytic set has come to include all species in the system, so that all populations are nonzero at equilibrium, the Jain and Krishna model chooses one of them for extinction regardless and replaces it with a new random species. This is the cause of the occasional collapses of cooperation that are observed after the transition to cooperation in their models. In the present model these collapses do not happen, as species are only removed when they naturally go extinct.

5.8.2 Conversion to mutualism in biology

Most ecological-evolutionary models fix the types of the interactions between the populations they study, and studies of evolution and ecological community structure, other than the above ones, tend to focus on food webs, including only competition and predation (such as Post and Pimm 1983; Ginzburg, Akçakaya, and Kim 1988; Drossel, Higgs, and McKane 2001). However, not only is mutualism common in natural communities—one author (Janzen 1985) estimates that every organism participates in an average of one mutualism—it is accepted that most mutualisms developed from competitive or exploitative relationships, and changes between the commonly identified types of interactions, particularly changes to mutualism, have been the cause of many or all of the major transitions of evolution (Leigh and Rowell 1995; Leigh 2001), and go on in less dramatic ways throughout natural history.

Pollen and seed dispersal relationships were probably once predator-prey interactions, which gradually adapted to benefit the plants more. Many mutualistic relationships are in fact thought to change back and forth between mutualism and exploitation fairly commonly in evolutionary time. Yucca moths of the genus *Tegeticula*, which pollinate yucca plants, have lost the pollination behavior in two lineages and become parasites (Pellmyr, Leebens-Mack, and Huth 1996; Pellmyr and Leebens-Mack 2000), and the same shift to

parasitism has been identified in at least one fig wasp species (Compton et al. 1991). Within parasitic lineages of fig wasps, a shift to mutualistic pollination has apparently developed independently in several different species (Jousselin, Rasplus, and Kjellberg 2001).

Such a shift has also been observed in laboratory ecosystems: microbiologist Kwang Jeon, studing amoebae, found his populations infected by small parasitic bacteria, which at first debilitated the amoebae; but after a few years the amoebae became able to thrive with the bacteria within, and then lost the ability to live without them (Margulis 1982; Margulis and Sagan 1986).

5.8.3 Mutualism, unboundedness and the Lotka-Volterra equations

As we have seen, a Lotka-Volterra system whose dynamics are bounded is one in which any cooperative interactions are overwhelmed by competitive and victim-exploiter interactions. Correspondingly, studies of community structure and dynamics that use Lotka-Volterra or similar equations (Dieckmann, Marrow, and Law 1995; Kisdi 1999; Kisdi, Jacobs, and Geritz 2000; Kisdi and Geritz 2001, for example) tend to study competition and predation relationships, excluding mutualism from consideration. Many discussions of Lotka-Volterra dynamics begin by assuming uniform boundedness—"obviously a minimal concession to reality" in the words of Hofbauer and Sigmund (1998). But of course any real ecosystem has upper bounds on population sizes, no matter how much individuals may cooperate with each other. Reality demands that mutualistic systems behave reasonably, not that mutualisms be excluded. This is a failure of the Lotka-Volterra model, which should be addressed by questioning the model and considering alternative models, not by altering our assumptions about the world in order to work around the model's weaknesses. In the next chapter, I will examine some modified models that are able to explore systems dominated by mutualism, and whether such systems may behave differently than competitive systems.

5.8.4 The replacement and coexistence theorems

The adaptive dynamics equations (3.3,3.5) rely on the assumption that the invasion function predicts which strains live and die following each mutation event. A mutant strain i' can only invade if $\mathscr{I}(i'|i) > 0$. Away from critical points of $\mathscr{I}$, continuity of its first and second derivatives is sufficient to guarantee that this implies $\mathscr{I}(i|i') < 0$, which suggests that when the mutant becomes resident its parent i will go extinct. This reasoning also applies when the strain undergoing mutation is one of several resident strains. The question of extinction is not so simple, however. A negative invasion exponent guarantees that when strain i is very small, it will go extinct, but if it does not become very small, the population dynamics may be drawn to some other attractor at which it does not go extinct. In general, the assumption that mutants replace their parents away from singular points of $\mathscr{I}$ is made without proof.

Dercole's "invasion implies substitution" theorem (2002) applies when the population dynamics attractors are fixed points and mutations are applied to a single scalar phenotypic trait, in the limit of small mutation steps, and may be able to be generalized to vector phenotypes and more complex population dynamics. My theorem 5.1 is only applicable to Lotka-Volterra systems of two resident strains and one mutant (I have also proven the one-resident, one-mutant case, but I do not call it a theorem because it is so obvious from theorem 2.1). However, it does not require equilibrium population dynamics, thanks to the time-averaging property, and makes no assumptions about phenotypes. The two theorems 5.1 and 5.2 together provide exhaustive criteria for determining whether the new mutant will replace its parent or coexist with it, based only on their invasion exponents (as long as the dynamics are away from any bifurcation points where, for example, the other resident goes extinct). As the criteria for distinguishing permanent communities from those with heteroclinic cycles come to be understood in systems of more than three dimensions, I expect these two theorems will be able to be extended straightforwardly to more dimensions.

Chapter 6

Variant Models Without Phenotypes

In this chapter I offer several models that continue the previous chapter's approach of applying mutations to interactions rather than phenotypes, some with modifications to the ecological dynamics and some exploring constraints on available combinations of interactions. First I look at two ways to avoid the explosion to infinite populations that makes the Lotka-Volterra system useless for strongly mutualistic situations. Next I explore the effect of restricting the system to competitive interactions by forcing all interaction terms to be negative. Then I look at evolution in a food web model, by generating the interaction matrix entries from a weighted directed graph of predation relationships and applying evolution to the weights of the graph. These variant models both propose ways to apply this new class of models to different specific evolutionary problems, and contribute insights into how to understand the entire class of models.

Since the model for mutations of complex entities presented in the previous chapter produces an interesting form of evolutionary branching that is qualitatively different from the branching observed in adaptive dynamics models, and avoids the restrictive assumption that populations are characterized by a small number of quantifiable character traits, it is of interest to explore the space of similar systems other than that simple model with no constraints on the evolution of interactions.

Constraints can be applied to the evolution of interactions in other ways than deriving interactions from explicit phenotypes. In addition, this model for the evolution of interactions can be paired with ecological models other than the standard Lotka-Volterra model. First I will look at two modifications of the Lotka-Volterra equations, which allow positive interactions to accumulate without reaching an unrealistic explosion in the population dynamics, and then I will present two different ways of restricting the types of available interactions, first to competition only, and then to predation relationships. Each of these models is interesting in different ways, and each may be responsive to further research.

6.1 Replicator dynamics

The accumulation of mutualistic interactions in the standard Lotka-Volterra equations leads to an explosive instability, as seen in the previous chapter, in which population sizes grow to infinity, making it impossible to use those equations to study ecosystems dominated by mutualism. Of course, in the real world populations do not become infinite no matter how mutualistic they may be. In order to look at what happens after the matrix becomes B-unstable, the model must be modified. One common way to do this is to make the assumption that any amount of organisms exceeding a certain capacity are discarded, for instance that the populations are swimming in a small puddle from which any excess production

spills over and is lost. This produces the equations

$$\frac{dX_i}{dt} = r_i X_i + \sum_{j=1}^{n} a_{ij} X_i X_j - \Phi(t) X_i, \quad i = 1, \ldots, n,$$

where $\Phi(t)$ is a loss term, independent of i, sufficient to keep the populations bounded. Then, since the positive r_i terms guarantee that the total population will not vanish, we can simply consider relative population sizes

$$x_i = \frac{X_i}{\sum_k X_k}.$$

The x_i equations are

$$\frac{dx_i}{dt} = x_i \left(r_i + \sum_j a_{ij} x_j - \left(\sum_k r_k x_k + \sum_k x_k \sum_j a_{kj} x_j \right) \right),$$

and with the special assumption $r_i \equiv 1$, since $\sum_k x_k = 1$, this reduces to the classic replicator equation

$$\frac{dx_i}{dt} = x_i \left((\mathbf{ax})_i - \mathbf{x} \cdot \mathbf{ax} \right). \tag{6.1}$$

As in the Lotka-Volterra case, the invasion exponent of a new mutant n reduces to $\mathscr{I}(n) = \sum_{j=1}^{n-1} \Delta a_{nj} \hat{x}_j$, where $\hat{\mathbf{x}}$ is a fixed point of (6.1) (even if the fixed point is not an attractor of the dynamics (Hofbauer and Sigmund 1998)). This point $\hat{\mathbf{x}}$ is of course not the same point as the fixed point $\hat{\mathbf{X}}$ of the Lotka-Volterra dynamics, so the invasion exponent, which characterizes the selection pressure, is not perfectly preserved by this change in the model assumptions. However, it can easily be calculated (given $r_i \equiv 1$) that when the Lotka-Volterra equations (5.1) have a positive fixed point, that point and the fixed point of (6.1) are scalar multiples of one another, so that the selective pressure is in fact the same; but in (6.1) the populations stay bounded and continue to undergo selection after interactions become mutualistic.

Figure 6.1 displays the development of the interaction matrix in this model over a much longer time than figures 5.1–5.3. There is no qualitative change as the interaction terms

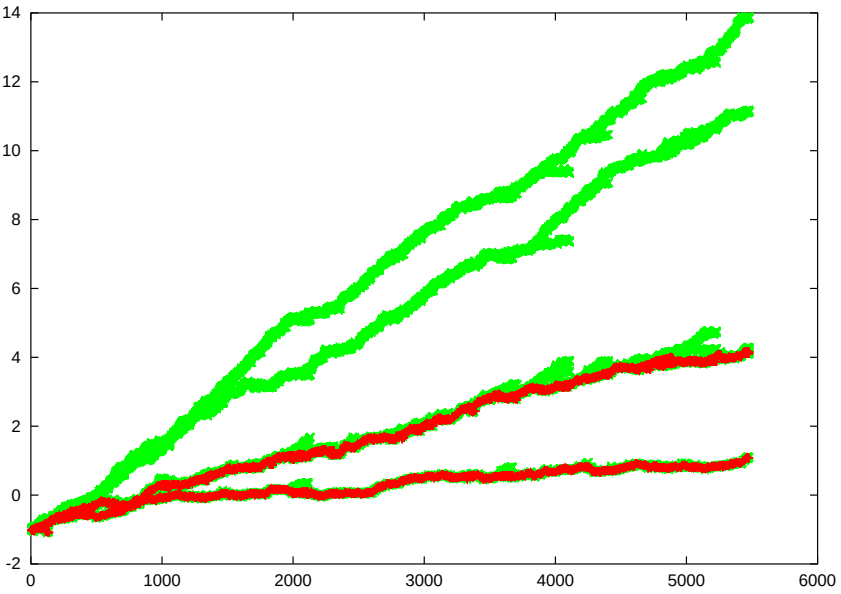


Figure 6.1: Long-term evolution of the ensemble of a_{ij} entries through time, using the replicator equation (6.1).

shift from negative to positive; since the dynamics of the replicator equation is insensitive to addition of a constant to any column of the interaction matrix (or to the entire matrix), mutualistic systems behave just like competitive systems. However, there is still a real difference in biological meaning between negative and positive terms, with populations consistently adjusting their interactions to become less and less competitive, and more and more mutualistic.

This figure makes the regularities of the dynamical system of figures 5.1–5.3 especially apparent. Despite relatively short-lived branchings of either of the two lineages, no more than two lineages are able to coexist sustainably, and viewed over the long term, the diagonal interaction terms, as well as the off-diagonal terms, are clearly moving upward at a constant linear rate. As in chapter 5, how to explain the linear motion of these four values, whether by an idealization that treats these occasional extra branchings as extraneous, or by an explanation that relies centrally on a continual cycle of coexistence and higher level selection, is an open question.

6.2 Space limitation

Another way to keep populations finite, rather than by removing excess population, is to restrict birth rates by forcing all populations to compete for space in addition to the interactions defined by the **a** matrix entries:

$$\frac{dX_i}{dt} = r_i X_i + \sum_{j=1}^{n} X_i L(a_{ij} X_j), \quad i = 1, \ldots, n, \tag{6.2}$$

where

$$L(Y) = \begin{cases} Y\left(1 - \frac{1}{K}\sum_k X_k\right), & \text{if } Y > 0, \\ Y, & \text{if } Y \leq 0 \end{cases} \tag{6.3}$$

limits the total population in the system to K by restricting birth when the population becomes large. These equations approach the standard Lotka-Volterra model (5.1) as $K \to \infty$,

so that when K is very large, the two systems are effectively the same until (5.1) becomes unbounded.

Figures 6.2 and 6.3 show how the **a** matrix develops using (6.2), with $K = 10000$. The initial development of the system is the same, but instead of exploding to infinity when the matrix loses B-stability, the total population size rises to nearly K, illustrated in figure 6.4, and the system can still be integrated further. The transition is clearly visible in figures 6.2 and 6.3. The development of the a entries is much slower after the transition, and the two populations diversify into at least four or five.

The slowing down of evolutionary speed may be an artifact; the software takes longer to detect equilibria when both very large and very small populations are present. On the other hand, there is probably real slowing down as well, because invasion exponents become small when the total population size is close to K.

Unfortunately, this model also begins to behave badly at a later time, when rows of positive numbers begin to appear. Figures 6.5, 6.6 and 6.7 show the development of the **a** matrix and population sizes in (6.2), with $K = 1$ instead of 10000. At the final time shown in figure 6.5, the row of the population corresponding to the one red point above 0 consists of all positive entries. This is a population that can never decline, no matter how much its growth is limited, since all the terms in its dynamical equation (6.2) are non-negative. As a result, this population grows until the total population is exactly K, and when this happens all population growth rates are at most 0. Some of this population's variant offspring have invasion exponents less than 0, and some variants' invasion exponents are exactly 0, but none can be positive, and there can be no further selection, only neutral drift. Thus this model also becomes unusable, though at a later time than (5.1).

Nonetheless, this model has some interesting things to say about qualitative transitions in the ecological dynamics before it degenerates. Figure 6.8 shows the same data as figure 6.6, but with populations on a log scale. In this figure one can see that after the population explosion the range of population sizes is notably larger, with very small populations

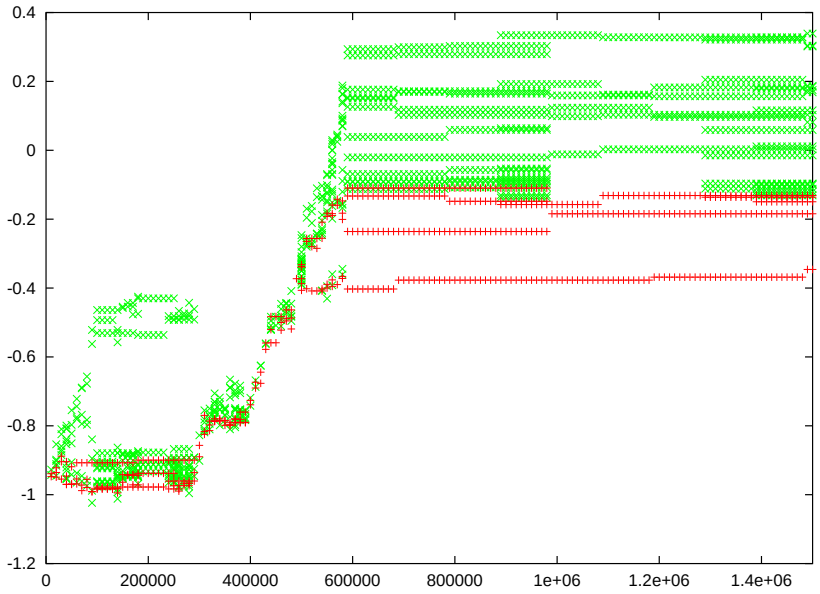


Figure 6.2: Early evolution of interaction matrix in the space-limited system (6.2) with $K = 10,000$. Space limitation comes into play when the first positive term appears, but becomes a major factor when the matrix becomes B-unstable and the total population becomes much larger, at about time 590,000.

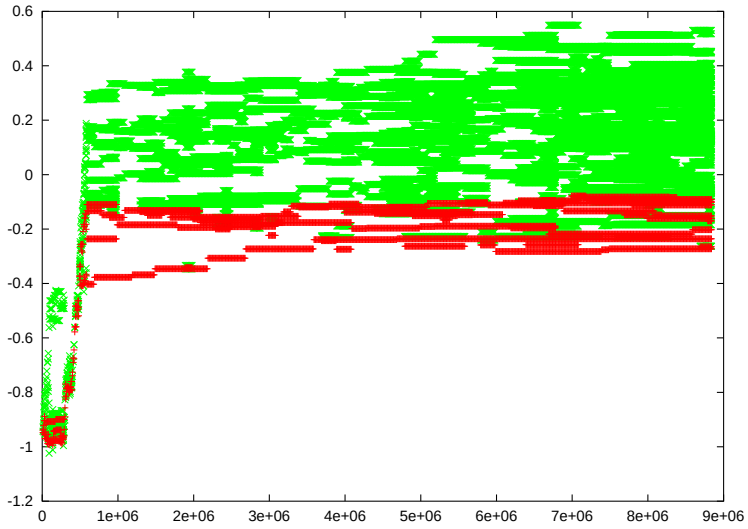


Figure 6.3: Long-term evolution of interaction matrix in the same simulation as figure 6.2.

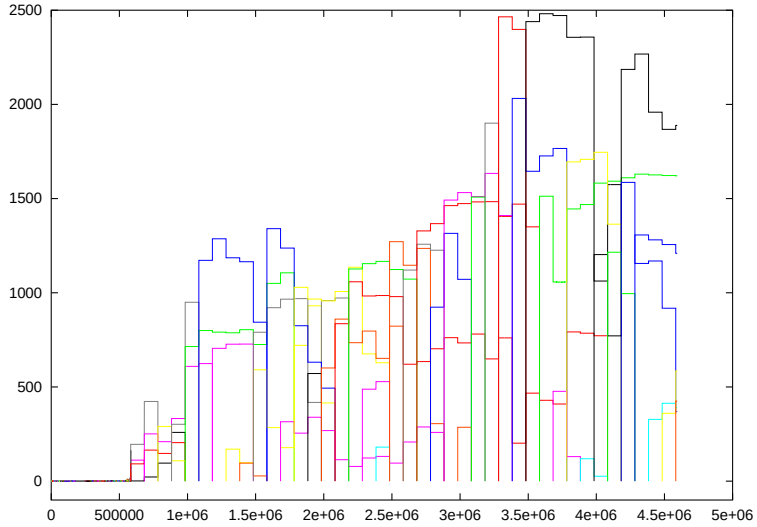


Figure 6.4: Evolution of population sizes in the same simulation as figure 6.2. Population sizes expand by several orders of magnitude when the matrix loses *B*-stability.

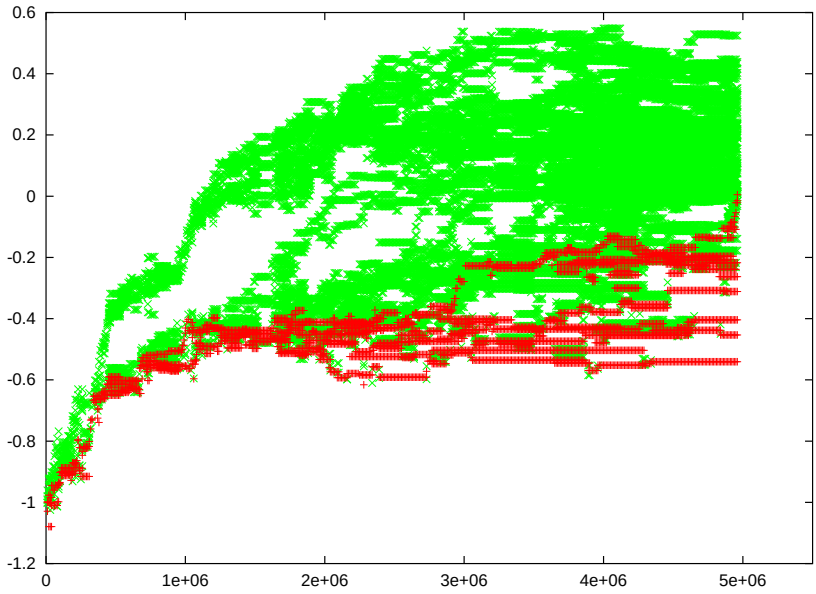


Figure 6.5: Evolution of interaction matrix in the space-limited system (6.2) with $K = 1$. Space limitation first becomes a factor when positive terms appear, at around time 1,000,000; the total population grows to K and the invasion function becomes entirely zero or negative when an all-positive row appears, at the last time shown.

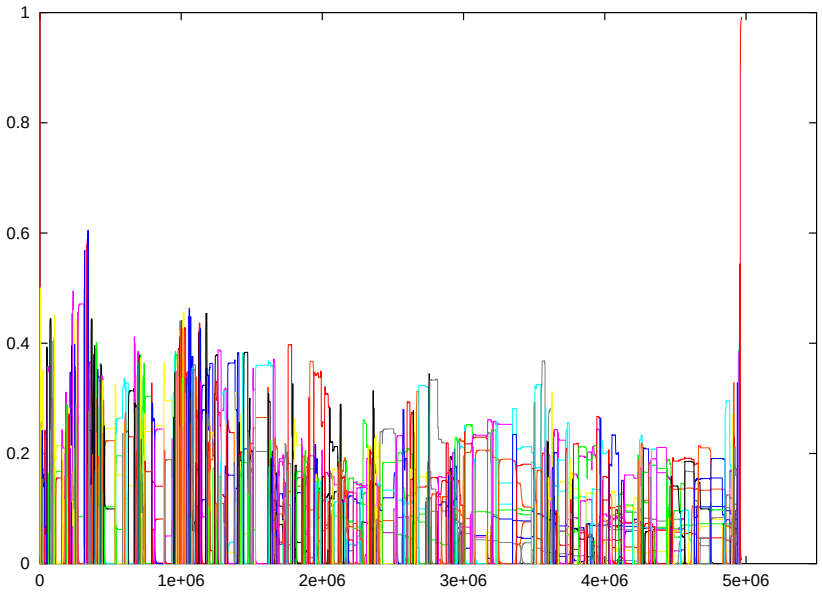


Figure 6.6: Population sizes in the space-limited system (6.2) with $K = 1$.

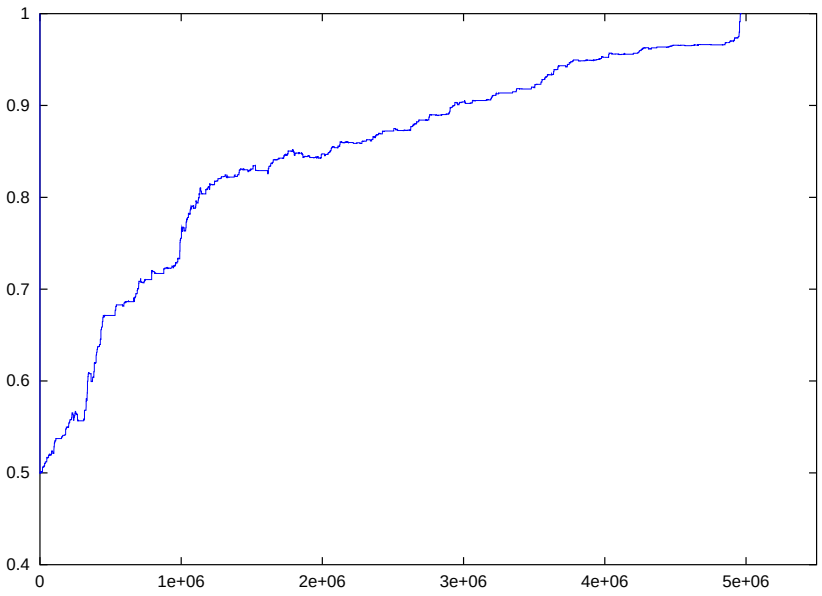


Figure 6.7: Total population size in the space-limited system (6.2) with $K = 1$.

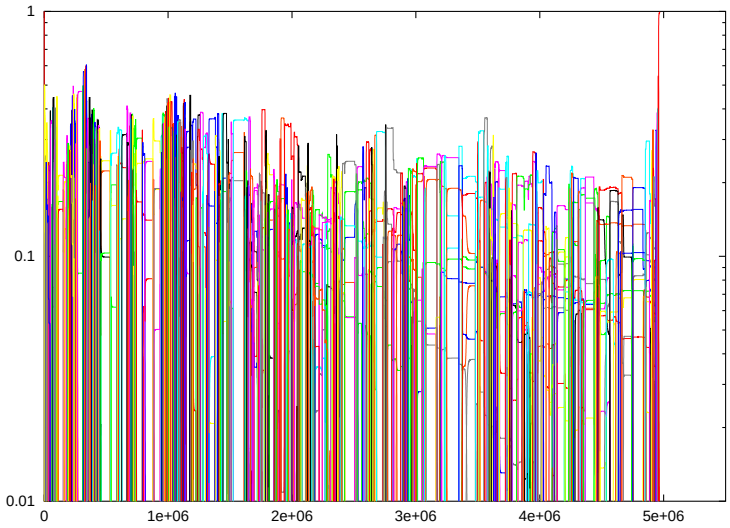


Figure 6.8: Population sizes in the space-limited system (6.2) with $K = 1$, plotted on a log axis. In this and the next two figures it can be seen that the sizes of coexisting populations have a much larger range at later times, after mutualism becomes a factor.

coexisting with relatively very large ones. Figures 6.9 and 6.10 show magnifications of figure 6.8 at early and late stages of the system's evolution, so that the range of population sizes can be seen more clearly.

This observation, which is consistently seen in numerous runs of the simulation, suggests that the dynamics and makeup of communities in which mutualism plays a major role may be qualitatively different than in communities dominated by antagonistic interactions. (Of course, the standard Lotka-Volterra model, by diverging to infinity when mutualism predominates, also suggests this, but in a less convincing way.) If this is true, predictions made by models that presume that community structure is defined by competition and predation relationships may be qualitatively wrong for many real systems.

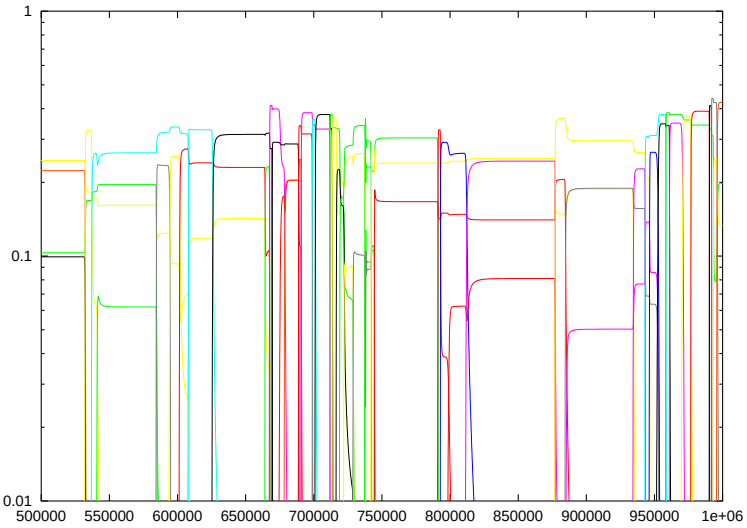


Figure 6.9: Close-up view of population sizes in the space-limited system (6.2) with $K = 1$, plotted on a log axis, at an early stage of the evolution of the system. Population sizes range from about 0.05 to about 0.5.

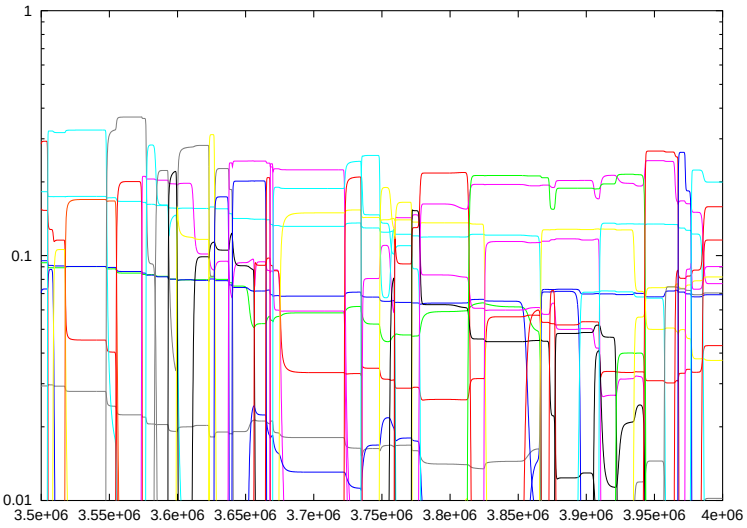


Figure 6.10: Close-up view of population sizes in the space-limited system (6.2) with $K = 1$, plotted on a log axis, at a late stage of the evolution of the system. Here population sizes range from about 0.01 or less to about 0.3.

6.3 Competition

While the two systems presented above address the inability of the Lotka-Volterra equations to accommodate mutualism by modifying the equations, the more common "minimal concession to reality" modelers make is simply to restrict the amount of mutualism modeled, and consider primarily competitive and victim-exploiter relationships. In this section and the next one I follow this strategy, considering first competitive systems, and finally evolution in food webs made up, of course, of predation interactions.

Recalling how I made a model prone to *B*-unstable accumulations of mutualistic interactions into a more compliant one in chapter 4 by applying a nonlinear transformation to all the interaction terms, I could construct a strictly competitive system in a somewhat similar way by maintaining an **a** matrix just as in chapter 5, with the same mutation process, but then using a negative "effective interaction"

$$A_{ij} = -e^{-a_{ij}}$$

with

$$\frac{dX_i}{dt} = r_i X_i + \sum_{j=1}^{n} A_{ij} X_i X_j.$$

Large positive a_{ij} terms would be transformed into interaction terms approaching zero from below, while large negative a_{ij} terms would be transformed into large negative interaction terms. Interaction terms A_{ij} approaching zero would change less and less as a result of mutation, since the size of a mutation to an interaction term in this model is proportional to the size of the term:

$$\begin{aligned} A_{i'j} &= -e^{-a_{ij}-\Delta a_{i'j}} \\ &= A_{ij} e^{-\Delta a_{i'j}} \\ &= A_{ij} + A_{ij}(e^{-\Delta a_{i'j}} - 1) \\ \Delta A_{i'j} &= A_{ij}(e^{-\Delta a_{i'j}} - 1). \end{aligned}$$

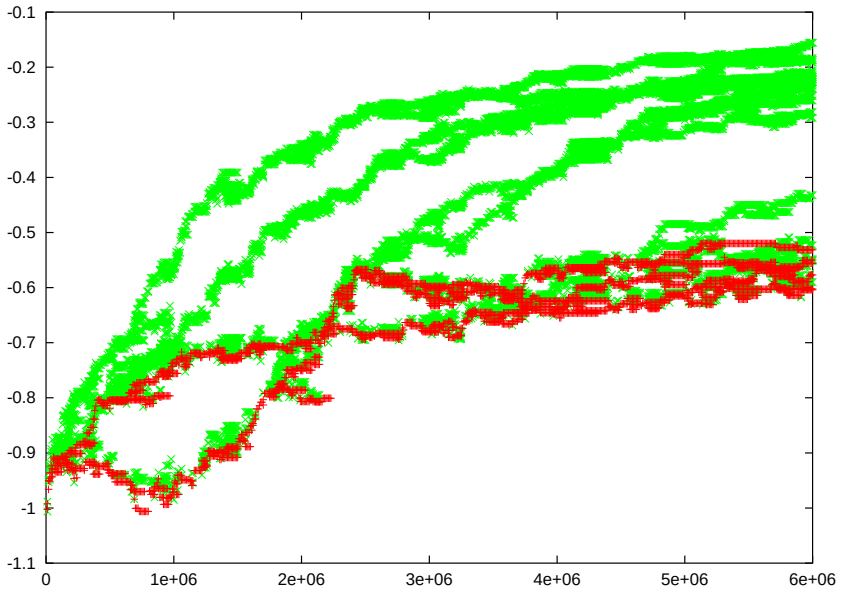


Figure 6.11: Evolution in the Lotka-Volterra system (5.1) with competition-preserving mutation. All a values are mutated by choosing a Δa values from a normal distribution with mean 0 and standard deviation 0.02 and changing a to $(1+\Delta a)a$.

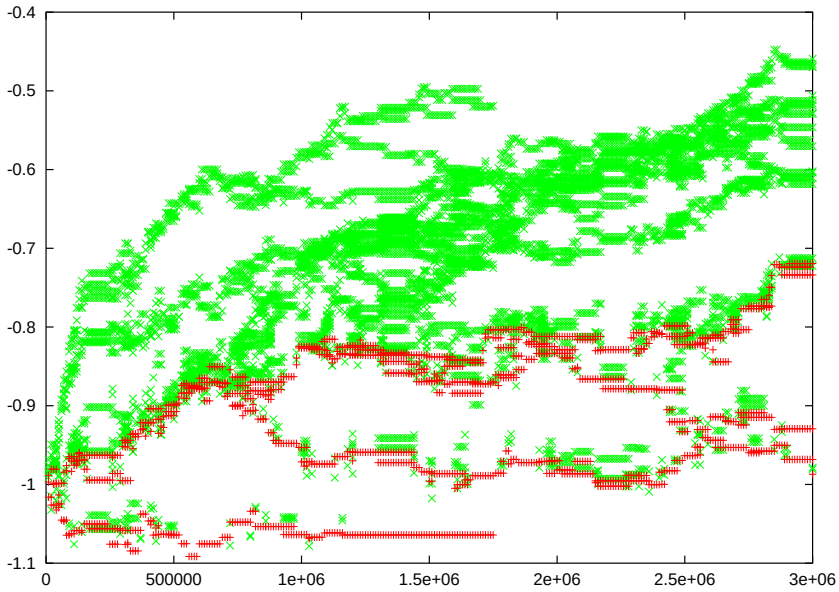


Figure 6.12: Evolution in the Lotka-Volterra system (5.1) with competition-preserving mutation.

Since $e^{-\Delta a_{i'j}}$ is very close to $1-\Delta a_{i'j}$ when $\Delta a_{i'j}$ is small, we can construct a very similar model which doesn't use an intermediate variable A_{ij}, and is interesting in its own right: simply use

$$a_{i'j} = a_{ij}(1+\Delta a_{i'j})$$

with small, normally distributed $\Delta a_{i'j}$ (and the corresponding expressions for $a_{ji'}$ and $a_{i'i'}$).

Figures 6.11–6.14 display the effects of evolution on interaction terms using this process. Instead of rising linearly, interaction terms appear to approach zero asymptotically (that is, acting like $-e^{-k(t+t_0)}$ instead of like $k(t+t_0)$). Initially the behavior is similar to the model of the previous chapter, with one strain splitting into two, and the green cross terms rising upward while the red density dependence terms drift vaguely upward. The two coexisting lineages differentiate themselves by reducing the competition between them, just as predicted by classic models of niche differentiation. But then when the green curves begin to level off as they approach zero, these two lineages branch further, developing into third and fourth permanently coexisting lineages. Sometimes lineages produced by earlier branchings are eliminated by later ones, as in figure 6.12, and sometimes they are not. This process can apparently go on forever.

An interesting thing about this model is that no explicit constraints have been imposed on the interaction terms a_{ij}, whether by placing them in a subspace parametrized by phenotypes, as in chapter 4, or parametrized by anything else; the only thing changed from the model of chapter 5 is that a bias has been introduced into the distribution of mutations, making mutations smaller when an interaction term is closer to zero. The fact that this change to the mutation process produces an important change in the branching behavior of the model suggests that the exact distribution of mutations must be important in understanding the behavior of this class of models, much as changes to the phenotypic variance-covariance matrix Γ of equation 3.4 without changing the phenotype space or ecological model can dramatically change the qualitative behavior of an adaptive dynamics model.

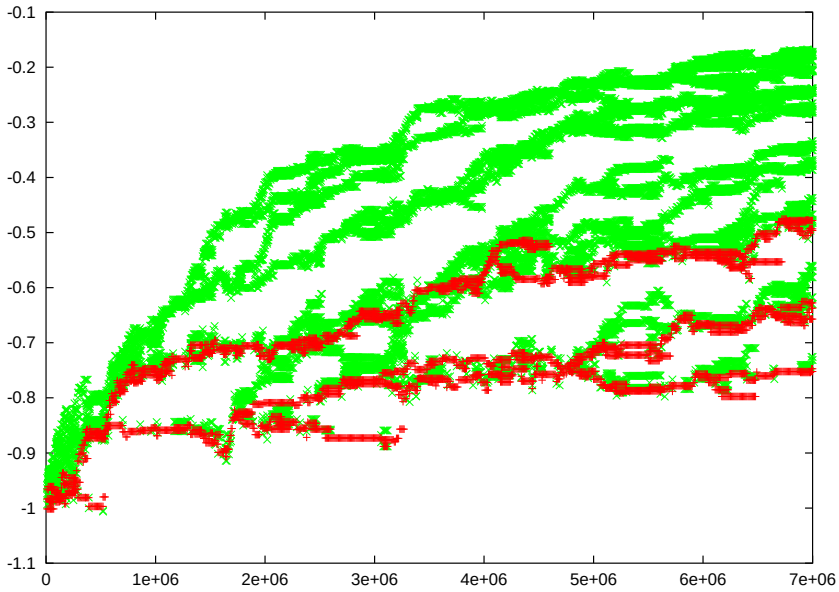


Figure 6.13: Evolution in the Lotka-Volterra system (5.1) with competition-preserving mutation.

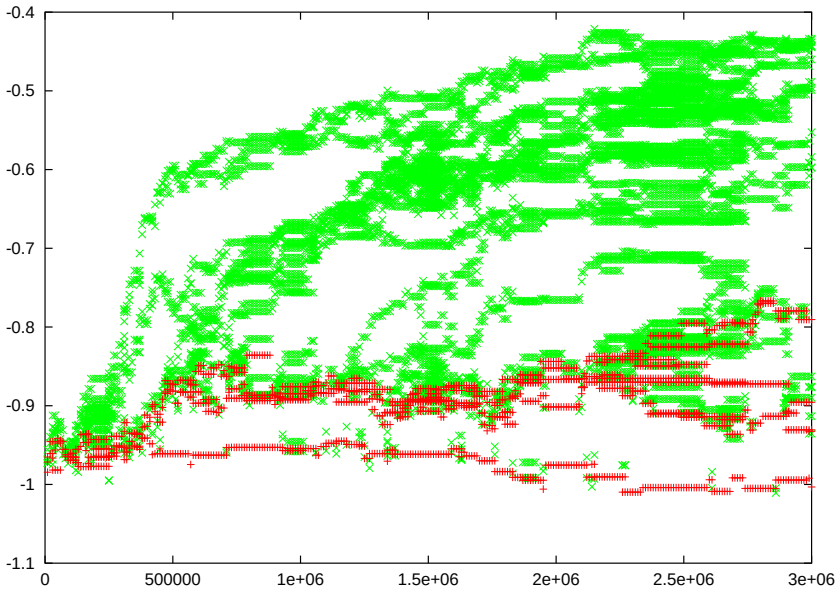


Figure 6.14: Evolution in the Lotka-Volterra system (5.1) with competition-preserving mutation.

6.4 Food webs

Finally, since the primary focus of most work on Lotka-Volterra models over the years has been on the relationship between food web structure and community dynamics, and this was in fact the original intent of my investigations into all these Lotka-Volterra evolution models, I now return to the subject, equipped with the perspective I have developed in the last few chapters.

Most studies of evolution in predator-prey dynamics either fix the place of each species in the trophic network and look at evolutionary changes in intensity of predation and co-evolutionary arms races (Dieckmann, Marrow, and Law 1995), or model a process of community assembly by adding new species unrelated to those in residence (Post and Pimm 1983; Taylor 1988). While it is possible to construct a framework in which a strain's position in the network of competitive, predatory, and mutualistic interactions that makes up the community is derived from a compactly defined phenotype (Christensen et al. 2002, for example), it is difficult to do so in a simple, flexible, continuous way, and even more difficult to do so while focusing on predation and competition rather than mutualism, as we saw in chapter 4.

The no-phenotype model of chapter 5 was intended to escape from the limitations of low-dimensional phenotypes and allow the interactions between each pair of species to adjust themselves independently. That model turned out to be too unconstrained to really study competition and predation relationships, since it simply converts just about everything into mutualism.

Here I present a model which is constrained, but not by phenotypes. This model uses a weighted directed graph to represent a food web. Mutations are applied to the entries of the food web graph, and interaction terms are generated from the graph structure.

Let $\mathbf{Q}$ be the matrix representing the food web graph, with $Q_{ij} > 0$ when strain i is eaten by strain j and $Q_{ij} = 0$ otherwise, and the magnitude of Q_{ij} determining the strength of the

predation interaction (so either Q_{ij} or Q_{ji} can be positive, but not both). The simplest way to make this graph structure into an ecological model is to make these predation links into Lotka-Volterra interaction terms:

$$a_{ij} = \begin{cases} -Q_{ij} & \text{if } Q_{ij} > 0, \\ cQ_{ji} & \text{if } Q_{ji} > 0 \end{cases} \tag{6.4}$$

with conversion efficiency c defining how much a predator population increases after consuming one unit of prey.

There are some complications that must be attended to before this model is complete. A prey species that is not a predator must have $r_i > 0$ in order to survive, while if the predators die a population with $r_i > 0$ can grow to infinity unless the interactions include negative density dependence terms as well as predation terms. This problem can be fixed by setting $a_{ii} = -1$, at least when i is not a predator.

We cannot simply place -1 terms on the diagonal, though. If a prey strain i gives birth to a slight variant i', if $a_{i'i} = 0$ while $a_{ii} = -1$, all such variants will be successful regardless of whether they are otherwise better or worse adapted. Density dependence must be conserved between parent and daughter strains, or at least change gradually. On the other hand, if we simply include equal density dependence and growth terms everywhere, it can become impossible for predators and prey to coexist:

$$\begin{aligned} \dot{X}_1 &= X_1(1 - X_1 + (-Q_{12} - 1)X_2) &= 0 \\ \dot{X}_2 &= X_2(1 + (cQ_{12} - 1)X_1 - X_2) &= 0, \end{aligned}$$

for example, has no positive solution for $Q_{12} > 0$.

There is surely any number of ways to complicate this model, to make it behave acceptably well. I have chosen the following: $r_i = 1$ when i is a 'basal species'—that is, one that does not prey on anything and so must get all of its growth from its r_i term—and $r_i = -1$ for all others, so that predators cannot survive without predating; $a_{ij} = -1$ when both i and j are basal, a_{ij} defined by Q_{ij} as in (6.4) when one is a predator on the other, and $a_{ij} = 0$ otherwise.

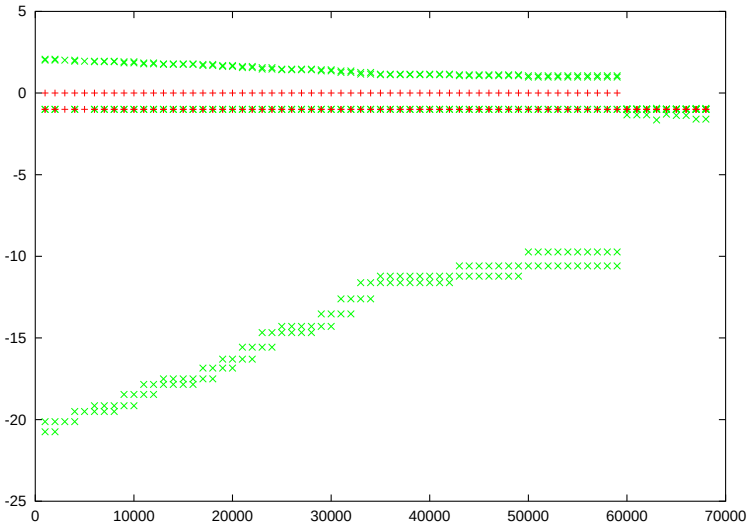


Figure 6.15: Evolution of interactions derived from food web graph, beginning with $Q_{12} = 20$. Selection reduces the strength of predation until the predator goes extinct.

Mutations are applied to the **Q** matrix, making existing Q_{ij} terms larger or smaller by a small normally distributed amount ΔQ_{ij}, including possibly changing positive Q_{ij} terms into zero. Additionally, small positive Q_{ij} terms can be introduced where previously there was only a zero. When a basal strain gives birth in this way to a predatory daughter strain, the r term for the daughter strain is set to -1 rather than 1. When a predator changes into a non-predator, its r is not changed from -1 to 1; it is simply allowed to die.

In all that follows, I take $c = 0.1$.

Figure 6.15 displays the outcome of the evolutionary process in a system initialized with

$$\mathbf{Q} = \begin{pmatrix} 0 & 20 \\ 0 & 0 \end{pmatrix},$$

that is, with one predator, species 2, and one prey, species 1. The predation term Q_{12}, manifested in the pair of interaction terms beginning at -20 and 2, decreases in intensity until the predators go extinct when $Q_{12} \leq 10$.

The Lotka-Volterra equations for this pair are

$$\begin{aligned}\dot{X}_1 &= X_1(1 - X_1 - Q_{12}X_2)\\ \dot{X}_2 &= X_2(-1 + cQ_{12}X_1),\end{aligned}$$

which has a fixed point at $X_1 = \frac{1}{cQ_{12}}$ and $X_2 = \frac{1}{Q_{12}}(1 - X_1)$. This fixed point is positive when $X_1 < 1$, which is the case when $cQ_{12} > 1$. In the absence of the predator, species 1 can always persist at $X_1 = 1$; at this boundary fixed point, the predator can invade exactly when $\mathscr{I}(X_2|X_1) = cQ_{12} - 1 > 0$, which is the same condition. When $cQ_{12} = 1$, the two fixed points merge into one. This is a classic transcritical bifurcation, where the coexistence equilibrium takes stability from the boundary equilibrium as it crosses the boundary into the interior of $\mathbb{R}^2_+$.

Evolution of the prey species looks like this: let Q be the above value Q_{12} before mutation, and Q' the value after mutation. If we label the mutant strain as strain 3, then the **Q** matrix after mutation is

$$\mathbf{Q} = \begin{pmatrix} 0 & Q & 0 \\ 0 & 0 & 0 \\ 0 & Q' & 0 \end{pmatrix},$$

and the equations for all three strains are

$$\begin{aligned}\dot{X}_1 &= X_1(1 - X_1 - QX_2 - X_3)\\ \dot{X}_2 &= X_2(-1 + cQX_1 + cQ'X_3)\\ \dot{X}_3 &= X_3(1 - X_1 - Q'X_2 - X_3).\end{aligned}$$

When X_1 and X_2 are at equilibrium, the mutant prey X_3 can invade when

$$\mathscr{I}(X_3|\hat{X}_1, \hat{X}_2) = 1 - \hat{X}_1 - Q'\hat{X}_2 - X_3 = (Q - Q')\hat{X}_2 > 0.$$

Likewise, when X_2 and X_3 are resident, the invasion condition for X_1 is exactly the opposite, and the prey with smaller Q replaces the other. Thus evolution of prey reduces Q_{12} in this system.

Evolution of the predator is just the opposite: when X_3 is a mutant predator, its invasion function is $c(Q'-Q)\hat{X}_1$, so that it can succeed in invading, and replacing the parent, when $Q' > Q$. This is no surprise; predators benefit from more predation and prey benefit from less predation.

If only the prey were evolving, we could consider Q to be a phenotype variable for the prey, and it would in fact evolve according to the standard adaptive dynamics equation:

$$\begin{aligned} \dot{Q}_{12} &= \gamma\hat{X}_1 \frac{\partial \mathscr{I}(Q'|Q)}{\partial Q'} \\ &= -\gamma\hat{X}_1\hat{X}_2. \end{aligned}$$

If only the predator were evolving, it would move Q in the opposite direction:

$$\dot{Q}_{12} = \gamma c\hat{X}_1\hat{X}_2.$$

The difference in rates comes from the fact that successful invasion is less likely when a positive invasion exponent is smaller. Since both processes are operating at once, Q_{12} increases whenever the predator strain is replaced and decreases whenever the prey strain is replaced. Q_{12} behaves like a phenotype variable that belongs to both strains at once and is pulled in both directions:

$$\dot{Q}_{12} = \gamma(c-1)\hat{X}_1\hat{X}_2.$$

Since c is always smaller than 1, selection on the predator affects Q_{12} less than on the prey, and Q_{12} always decreases in this two-species system. When it crosses the bifurcation value ($Q_{12} = 1/c = 10$), the predators go extinct.

In the more general case, for any given resident strain k, whose population dynamics is

$$\dot{X}_k = X_k(r_k + \sum_i cQ_{ik}X_i - \sum_j Q_{kj}X_j - \sum_l D_{lk}X_l)$$

(where D_{ik} is the density dependence interaction, one if both i and j are basal strains and

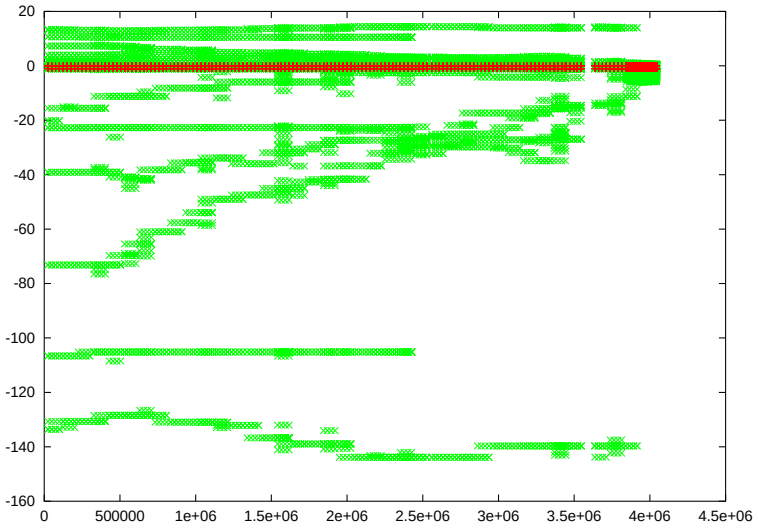


Figure 6.16: Evolution of interactions derived from food web graph, beginning with **Q** as given in the text.

zero otherwise), we have

$$\frac{\partial \mathscr{I}(k|\mathbf{E})}{\partial Q_{ij}} = \begin{cases} c\hat{X}_i & \text{if } k = j, \\ -\hat{X}_j & \text{if } k = i, \\ 0 & \text{otherwise.} \end{cases}$$

Since any nonzero term Q_{ij} in the matrix is adjusted by selection on the predator strain j and on the prey strain i, its evolutionary motion always has two terms:

$$\begin{aligned} \dot{Q}_{ij} &= \gamma \hat{X}_i \frac{\partial \mathscr{I}(i|\mathbf{E})}{\partial Q_{ij}} + \gamma \hat{X}_j \frac{\partial \mathscr{I}(j|\mathbf{E})}{\partial Q_{ij}} \\ &= -\gamma \hat{X}_i \hat{X}_j + \gamma c \hat{X}_i \hat{X}_j \\ &= \gamma (c-1) \hat{X}_i \hat{X}_j. \end{aligned}$$

This value is always negative, just as in the simple predator-prey system, predicting that selection generally reduces predation in this model.

Figure 6.16 displays the evolutionary motion of interactions in a food web with three prey and three predator species. This community was constructed by beginning with a large

(200 species) **Q** matrix and seeing what is left after most of the populations go extinct. The initial **Q** matrix for this community is

$$\mathbf{Q} = \begin{pmatrix} 0 & 0 & 0 & 106.617 & 0 & 22.7472 \\ 0 & 0 & 0 & 0 & 133.584 & 20.1719 \\ 0 & 0 & 0 & 39.1045 & 0 & 73.1555 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}.$$

In this system, species 1, 2, and 3 are prey, species 4 consumes species 1 and 3, species 5 consumes species 2, and species 6 consumes all three of the prey species. As in figure 6.15, the green lines are cQ_{ij} and $-Q_{ij}$ for each Q_{ij}, and all the red lines overlap at 0 and -1.

Most of the interaction terms in the figure move toward zero while some appear to drift, and eventually there are a number of extinctions, ultimately leaving only one prey, as in figure 6.15.

The fact that the Q values do not all move monotonically toward zero is partly because each Q_{ij} is being pulled in opposite directions by the two species affected by it. When one is replaced, it tends to move one way, and when the other is replaced, it tends to move the other way. It is probably also due to another form of stochastic variation common to simulations of adaptive dynamics models involving multiple characters, which can be quite noisy. This is because while selection favors a particular direction for each character, a mutation moving one character in the "right" direction and another one in the "wrong" direction can do just fine, so that each character can wander back and forth quite a bit while tending overall in the direction indicated by the selection gradient. Since in this system, all but species 5 are undergoing selection on multiple Q values, this is probably a significant factor. As the mutation step shrinks to zero, the trajectories of all the Q terms should converge on the mean path predicted by the adaptive dynamics equations.

Despite the apparent hostility to diversity evident in the behavior of this model, I believe

that the use of a Q matrix to represent community structure is an interesting alternative to modeling based on explicit phenotypes. Many different ecological models could be built on top of the same matrix or similar structures, and the simplicity and flexibility that this approach brings may prove quite useful.

Chapter 7

Evolution Of Mutualism As An Alternative To Reciprocal Altruism

This chapter departs from ecological models and applies the novel mutation technique introduced in chapter 5 to the famous prisoner's dilemma model of game theory. When 'strategies' available to players evolve by changes to the payoffs they receive, as 'strains' in the Lotka-Volterra system evolve by changes to their interaction terms, the same conversion to positive, cooperative interactions can occur. Simple (non-repeated) game players who converge on mutual defection gradually transform that interaction into something mutually beneficial, and players with memory who can enforce cooperation by means of retaliation subsequently convert cooperation into something more desirable than defection, so that retaliation (and memory) are no longer necessary.

When choosing between two evils, I always like to pick the one I never tried before.

– Mae West

7.1 The evolution of cooperation

While mutualism between individuals of different species, such as plants and pollinators, hosts and endosymbionts, and so forth, is clearly a kind of cooperation in any standard usage of the word, the term ‘cooperation’ in the biological literature is commonly taken to mean mutually beneficial behavior between individuals of the same species, and treated in a different way.

In the study of mutualism, while attention is certainly given to the problem of ‘cheating’ on the exchange of favors between species, it is also well accepted that helping behavior need not have an associated cost and may also be the behavior that most benefits the helping individual (Leigh 2001). When this is the case, there is no temptation to cheat and no need to explain how cooperation is maintained.

The coincidence of selfish and cooperative behavior is certainly possible in within-species interactions as well (Dugatkin, Mesterton-Gibbons, and Houston 1992), and most researchers in this field recognize this possibility and take care to distinguish cooperation from altruism, or ‘costly cooperation’, which is cooperation that cannot be explained by direct self-interest because one can benefit more by not cooperating (Axelrod 1984; Sober and Wilson 1998; Leigh 2001). Even so, the appearance of the word ‘cooperation’ in a journal like *Journal of Theoretical Biology* has become a sure sign of a paper on the evolution of altruism, and some go so far as to make claims like “We know that any form of mutual aid is threatened by exploitation” (Sigmund and Nowak 1997) or

> The evolution of stable patterns of mutually beneficial interaction, particularly among selfish, unrelated individuals, appears paradoxical because such behavior is so clearly vulnerable to exploitation. The Prisoner’s Dilemma is the mathematical framework for the study of cooperation, and had led to [sic] a large number of theoretical investigations. (Wahl and Nowak 1999)

As a result of the widespread conflation of cooperation and altruism in the study of

behavior, many people, like the authors of the above quotations, have come to think of cooperation as a mysterious anomaly whose existence is difficult to explain because of the universal temptation to defect. Prisoner's dilemma and tragedy of the commons scenarios, which embody these assumptions, appear in the mass media as authoritative scientific statements legitimizing a bleak Hobbesian picture of humans as selfish, greedy individualists whose antisocial tendencies must be kept in check by coercive social forces (Picardi and Seifert 1976; Whitfield 2002, for example). This characterization is not justified by these models, which ignore the range of non-costly cooperation situations, thus obscuring the possibility of easy, stable mutualistic behavior.

This bias has been pointed out and is being addressed by a few animal behavior researchers making the distinction between by-product mutualism and altruism (Mesterson-Gibbons and Dugatkin 1997; Dugatkin, Mesterton-Gibbons, and Houston 1992; Connor 1995), and modeling how mutualistic interactions can arise among particular organisms (Mesterson-Gibbons 1991; Clutton-Brock 2002). In this chapter I adapt the model of chapter 5, which depicts the transformation of antagonistic ecological interactions into cooperative ones, to game theory, constructing a variant of the standard model for costly cooperation, in which mutual defection can be transformed into stable mutualistic cooperation.

7.2 The prisoner's dilemma

The prisoner's dilemma (Rapoport and Chammah 1985; Axelrod 1984) is the *Drosophila* of costly cooperation models, the center of a massive research program modeling it in any number of settings and variations in search of techniques for maintaining cooperation in the face of temptation to defect. The story from which it takes its name is of two prisoners who are being questioned separately by police about a crime (Luce and Raiffa 1957; Taylor 1976). Each has two options, to confess or to keep quiet. If both prisoners keep quiet ("cooperate"), both will go free since the police have no evidence. If both confess and

implicate one another ("defect"), both will receive a reduced sentence for cooperating with the police. If one prisoner agrees to provide incriminating evidence while the other remains silent, the first will be set free and rewarded, while the other will suffer the full wrath of the law. By manipulating rewards and punishments in this way, the police create a situation in which each player benefits more from defecting than from cooperating, whether the other chooses to cooperate or not. If the other prisoner confesses, you will do better if you confess as well; while if she does not, you can go free either way, but you can also collect the payoff for collaborating if you turn her in. As a result, when the prisoner's dilemma is made into an evolutionary game theory model, mutual defection is a convergence stable ESS and mutual cooperation is an unstable equilibrium (Maynard Smith 1982; Boyd and Lorberbaum 1987). By seeking to maximize their own rewards, both prisoners betray their own interests and condemn themselves to long jail sentences unnecessarily.

The prisoner's dilemma is considered to be a succinct summary of the problem of how humans and other organisms can be induced to help each other in the face of temptations to take a short-term benefit at the expense of long-term collective well-being. When expanded into an *n*-player social dilemma, it takes the form of the tragedy of the commons scenario (see chapter 1), which represents the problem of managing a commonly held resource or other public good, such as a fishery or the world's atmosphere, when individuals can profit by overexploiting it at the expense of sustainability. Since human beings and other organisms "cooperate" continually and promiscuously, and sometimes even behave altruistically, the failure of cooperation in the prisoner's dilemma is seen as a problem to be solved, to explain how cooperation—or rather altruism—is sustained (May 1981).

The most famous solution to this "paradox", developed by Robert Axelrod (Axelrod 1984), is to model the prisoner's dilemma as a repeated game in which players can make their choice to cooperate or defect based on what the other player did previously. In this scenario, the famous Tit-for-Tat strategy, invented by psychologist Anatol Rapoport, which simply returns whatever the other player did previously, and variants are very successful,

suggesting the importance of "reciprocal altruism" (Trivers 1971) in stabilizing cooperation. Cooperation can also be maintained by spatial locality (Axelrod 1984; Nowak and May 1992; Oliphant 1994), kin selection (Wade and Breden 1980), group selection (Boyd and Richerson 2002; Boyd and Richerson 1990), mutual recognition based on arbitrary characteristics (Holland 1993), or probably any of many possible mechanisms that allow players to cooperate preferentially with others who are likely to have similar strategies to themselves (Cohen, Riolo, and Axelrod 1999; Pepper and Smuts 2002). Additionally, punishment (Boyd and Richerson 1992; Henrich and Boyd 2001), communication (Miller, Butts, and Rode 1998) and other social norms, including simple conformity (Boyd and Richerson 1985), can stabilize cooperation in these models.

Mathematically, the prisoner's dilemma, in its basic form, is represented by a two-player game with a payoff matrix summarizing the outcomes of the four combinations of choices to cooperate or defect:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \left(\begin{array}{cc} R & S \\ T & P \end{array} \right). \end{array}$$

The entries of this matrix represent the payoff to the player whose choice appears in the left-hand column, given the other player's choice in the top row. The prisoner's dilemma is characterized by the fact that the "reward" R exceeds the "punishment" P, while the "temptation to defect" T is greater than the reward, and the "sucker's payoff" for the cooperator who is betrayed, S, is even worse than the punishment:

$$S < P < R < T.$$

Additionally, it is common to require $S + T < 2R$, so that two players cannot do better by taking turns "cheating" each other than by cooperating (Rapoport and Chammah 1985). This matrix encapsulates the paradox of the prisoner's dilemma, since the entries in the D

row strictly dominate those above them, making defection always better rewarded, while mutual defection leads to the inferior outcome *P*.

7.3 Game theory dynamics

It is very common, especially in the biology literature, to model the search for well-adapted behaviors in game theory models by considering the various possible behaviors to be heritable phenotypic characters of the game-playing individuals, whose frequency in the population changes as the game players reproduce and are selected. Under these assumptions, adaptive dynamics models can be constructed and inspected for evolutionary fixed points and the like. The same models can be justified by saying that game players do not reproduce and die, but rather replace their chosen strategies with others' in a sort of mental epidemiological process. This interpretation is not an especially well-motivated model for social learning, and seems more like a retrospective justification of the evolutionary model.

Not wishing to contribute to the preponderance of literature that considers behavior to be caused by genes, I will not use these assumptions in this chapter, using instead a simple model in which players try out various behaviors and learn from the results.

The learning model I use in place of evolution was introduced by biologist Calvin B. Harley (1981), who showed that if there is an ESS, that will be the strategy learned by this rule. It is as simple as any evolutionary model, though it is less easy to reduce to differential equations. Since the system I study in this chapter can not be analyzed mathematically in any case and must simply be simulated, this is not an issue. I combine this learning model with a standard game theory framework, constructing a dynamic model of game players who learn from experience how to increase the payoffs they receive.

Given two or more possible *behaviors*, for instance "*C*" and "*D*", each game player's current *strategy* is a vector of probabilities, adding up to one, describing how likely the player is to choose each behavior. In each round, each player plays with a randomly chosen

partner and then takes the payoff as a reward or punishment for the behavior that was chosen, increasing or decreasing the future likelihood of choosing that behavior. If s_i is the player's probability of choosing behavior i, when behavior i is chosen and receives payoff p, s_i is adjusted in accordance with the payoff, using a small multiplier c that makes the process of learning more or less gradual,

$$s_i \quad \mapsto \quad \frac{s_i + cp}{1 + cp},$$

so behavior i becomes more likely if p is positive and less likely if p is negative. The rest of the strategy vector is adjusted to maintain a total probability of one:

$$s_j \quad \mapsto \quad \frac{s_j}{1 + cp}, \quad j \neq i.$$

All these probabilities are constrained to remain between zero and one. As this process is iterated, players learn to favor whichever behaviors are likely to yield the greatest payoff given the other players' strategies. Since the expected payoff associated with each behavior changes as all the other players change their strategies, the population of players may or may not converge on an optimum.

7.4 Evolution of behaviors and their interactions

As I have described it so far, this iterated learning model is not especially new or interesting. When it is applied to the prisoner's dilemma, players behave selfishly and converge on total mutual defection. What I now add to this model is the possibility of innovating new variations on the existing "behaviors".

The learning model, in which the frequency of each behavior in the population rises or falls as players learn, settling on an equilibrium or fluctuating attractor, with some behaviors possibly going extinct, can be thought of as the "ecology" of the behaviors. As with the Lotka-Volterra model used in previous chapters, the ecological model can be paired with an evolutionary model that introduces variant behaviors.

Here I use an evolutionary model very similar to the one presented in chapter 5. The entries of the payoff matrix, which characterize each behavior in terms of how it interacts with all the other behaviors, are perturbed by small numbers to represent the introduction of a new, innovative behavioral option which is a slight variant of one of the existing behaviors. For instance, given the standard prisoner's dilemma options C and D, if a variation on the D behavior is introduced, the resulting payoff matrix is

$$\begin{pmatrix} R & S & S+\Delta p_{13} \\ T & P & P+\Delta p_{23} \\ T+\Delta p_{31} & P+\Delta p_{32} & P+\Delta p_{33} \end{pmatrix}$$

with each Δp value chosen from a continuous distribution of small values centered on zero.

Periodically, when the learning dynamics have unfolded for a long time, a variant behavioral option is introduced in this way, with a small probability of use by each player, and the players' learning dynamics then determine whether the new option is adopted and whether older members of the behavioral repertoire are abandoned. On a slower timescale than the learning dynamics, the set of behaviors currently in use undergoes evolutionary change and the payoff matrix, like the Lotka-Volterra interaction matrix in chapter 5, undergoes slow qualitative changes.

7.5 Conversion of defection to cooperation

All the simulations of this chapter are done beginning with a prisoner's dilemma payoff matrix whose exact values are

$$\begin{pmatrix} 3 & -2 \\ 4 & -1 \end{pmatrix}.$$

Ten players are simulated, with $c = 0.01$. All players begin with 90% probability of choosing the C behavior. A new variant behavior is introduced after every one million rounds of game play, made by choosing one of the existing behaviors with probability proportional to

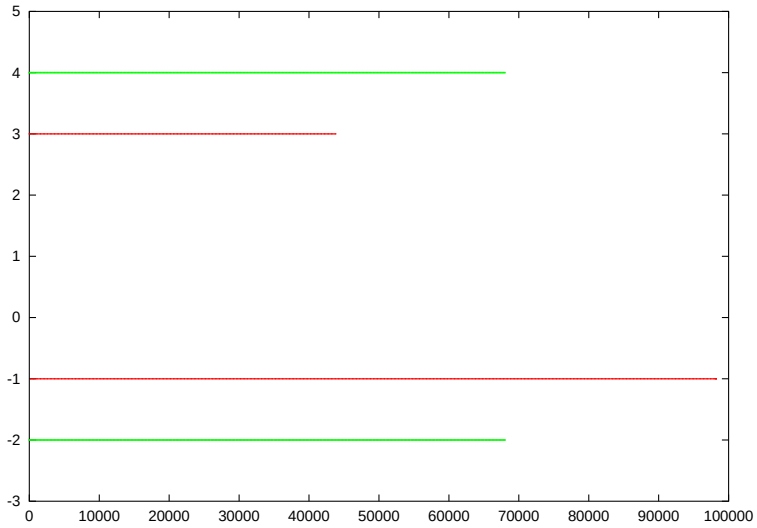


Figure 7.1: Changes in the distribution of payoffs over time in the standard prisoner's dilemma.

its current popularity among game players, and perturbing the payoffs using Δp values chosen independently from a normal distribution with mean zero and standard deviation 0.2.

Figure 7.1 is a graph of the entire contents of the payoff matrix against time, just like the red and green graphs of the interaction matrix used in previous chapters. This figure illustrates what happens before any mutations are introduced. The diagonal terms R and P (3 and -1) are shown in red and the off-diagonal terms T and S (4 and -2) are shown in green. Payoffs that occur less than 1% of the time are not shown. As the game players learn that cooperation does not pay as well as defection, they shift their strategies to pure defection. As the probability that a player will choose the C behavior declines to zero, first the probability of a C-C interaction becomes vanishingly small, so that the red line at 3 disappears, and then the probability of a C-D interaction does as well, so that the green lines at -2 and 4 also disappear, leaving only -1, the payoff given to each of a pair of defectors.

Figure 7.2 displays the probability of cooperation in the same system. The initial 90%

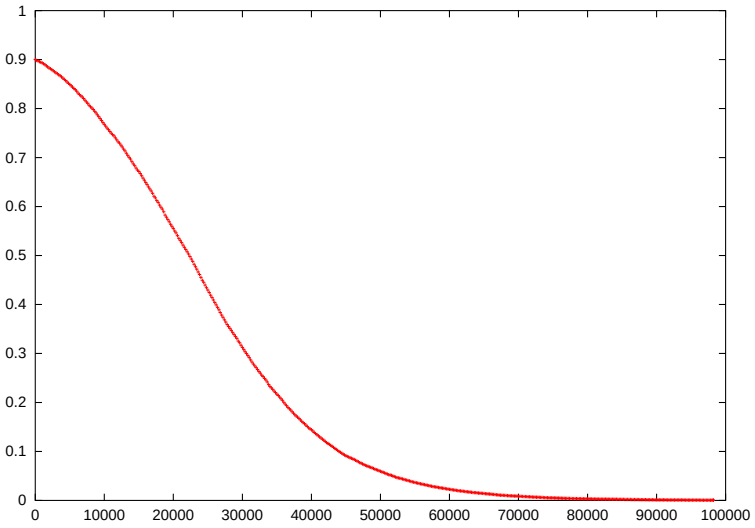


Figure 7.2: Probability of cooperation over time in the standard prisoner's dilemma.

probability of cooperating declines to zero. In this graph, probability of cooperating is simply the probability of choosing the *C* behavior, but when the system includes any number of different behaviors generated by mutation, it is not so simple to separate 'cooperative' behaviors from 'non-cooperative' behaviors, and a more carefully defined measure of cooperation must be used. The quantity I use here and in the other 'probability of cooperation' graphs in this chapter is the probability, over the complete distribution of payoffs, that the second player receives a positive payoff (the probability of the payoff in position (i, j) of the payoff matrix is the probability that the second player chooses behavior i multiplied by the probability that the first player chooses behavior j). In the un-mutated prisoner's dilemma game, this is equivalent to the probability that the first player chooses *C*, but in general, cooperation cannot be defined so simply. The definition I am using here is the probability of *achieved* cooperation, in that the first player's choice is only considered cooperative if it actually benefits the second player; I could also consider *intended* cooperation by counting any behavior that has the *potential* of benefiting the second player (depending on the second

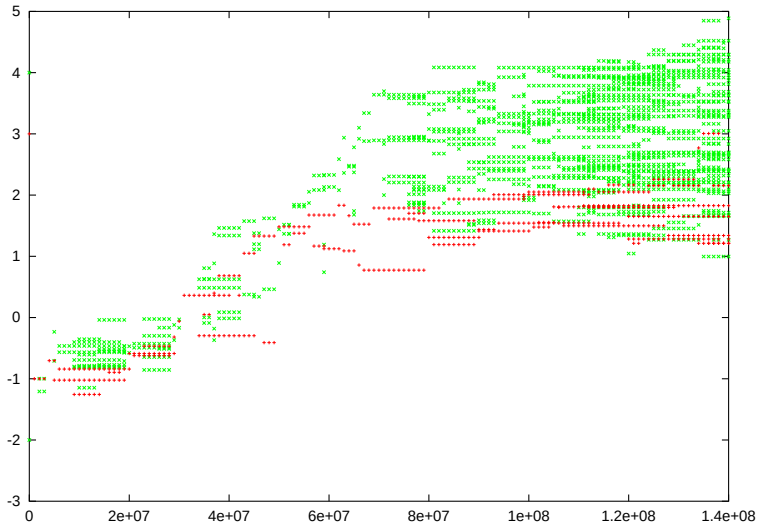


Figure 7.3: Evolutionary development of the payoff matrix in one realization of the simulation. After the "defection" behavior becomes dominant, it transforms by gradual improvements into a behavior whose effect benefits both players, and then splits into several coexisting lineages of behaviors whose payoffs in combination are even better than any of their effects in isolation.

player's choice), which would clearly give a higher estimate of the amount of cooperation in the system.

Figures 7.3–7.12 show what happens to the game in the long term, as variant behaviors are introduced and selected. Figures 7.3 and 7.4 illustrate an especially optimistic outcome. After the initial equilibration, in which all players settle on mutual defection, they begin to experiment with slight variations on the defection behavior. Soon this process produces a pair of variant behaviors that coexist because, just like closely related strains in the Lotka-Volterra system of chapter 5, each benefits from the presence of the other: each of the two behaviors yields a higher payoff when the two are combined than in isolation. This coexisting pair then collapses when one of the self-interaction terms (diagonal payoffs) exceeds the corresponding off-diagonal term in its column. A series of repetitions of this branching-extinction cycle produces progressively less harmful ways of interacting, until at

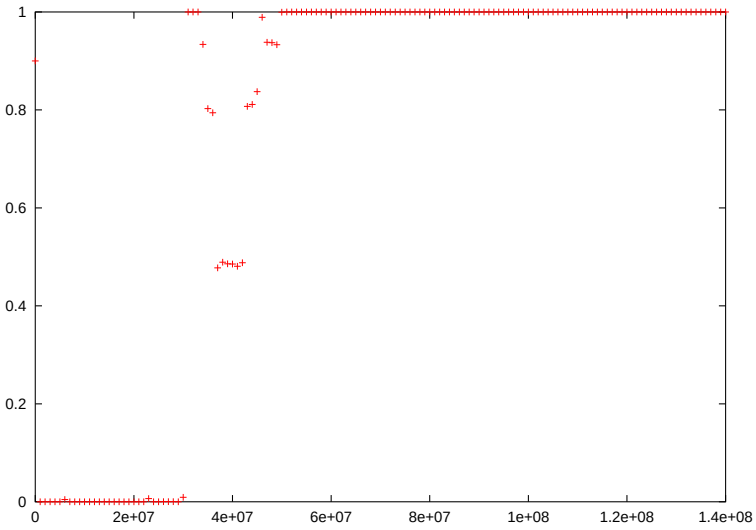


Figure 7.4: Probability of achieved cooperation in the simulation shown in figure 7.3.

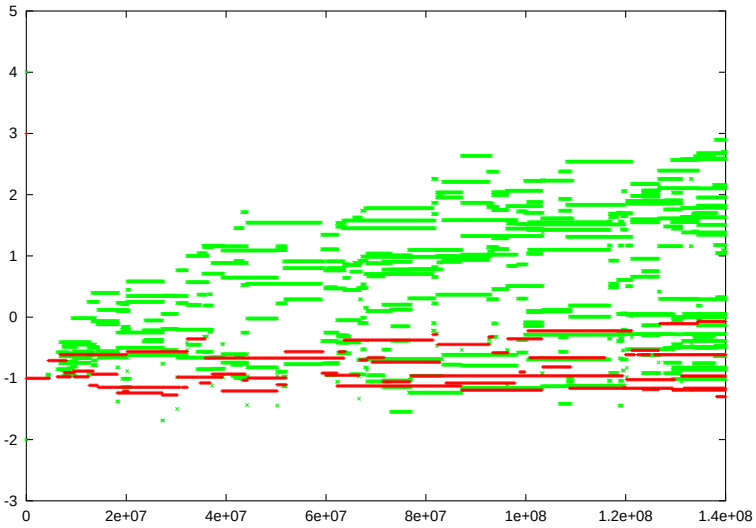


Figure 7.5: Development of the payoff matrix in another realization.

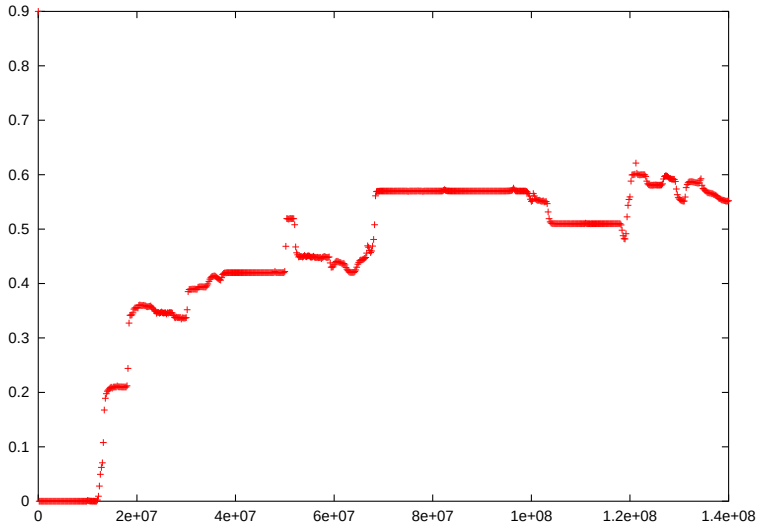


Figure 7.6: Probability of achieved cooperation in the simulation shown in figure 7.5.

some time shortly after time 3×10^7, all players are exclusively using a behavior, descended from the behavior initially known as "defection", which gives a positive payoff to both players who use it. That behavior splits again into two, which collapse into an even better one, which then diversifies into a whole variety of cooperating behaviors. The payoffs for each of these, when paired with itself, mostly remain steady between 1 and 2, but when two are paired with each other, each can yield a payoff more than twice that large.

In figures 7.5 and 7.6, the *D* behavior splits early and does not collapse back to a single type, so that diagonal payoffs stay around -1 and never become positive. The off-diagonal pair of payoffs, however, rise directly across 0 into positive numbers, and off-diagonal terms created by subsequent splittings do as well. Through this diversification, the population of players is able to achieve a more than 50% rate of cooperation, even though each of these behaviors would do badly on its own. Figures 7.7 and 7.8 are similar to figures 7.5 and 7.6, but in this case some of the diagonal payoffs become positive as well as most of the off-diagonal ones. As a result, the rate of cooperation is much higher.

Figures 7.7 and 7.8 also illustrate that, since the evolutionary motion of payoffs, like the motion of interaction terms in previous chapters, is not strictly upward, the rate of cooperation can decline again after reaching 1. Slight declines from 1 can be seen in figures 7.9–7.12 as well. Since the motion is generally upward, though, these declines are not likely to be nearly as large as the preceding rise from 0 to 1 (and the rate of cooperation is certainly not likely to go back to 0), and in the longer term are also fairly likely to be followed by an eventual rise back to 1, as even diagonal terms do tend to rise eventually.

7.6 Discussion

I am aware of only a little published work on conversion of prisoner's dilemmas to other game structures, such as the non-dilemma games that evolve here. One such contribution is a model of reproducing insects presented by Michael Mesterson-Gibbons (1991). These insects, looking for sites to lay their eggs, have to choose whether to lay in sites where an egg is already placed, which is an action that hurts the chances of both eggs but gives, of course, a better chance than not laying an egg. If the insects are capable of distinguishing their own eggs from those laid by others, then the problem has the structure of the prisoner's dilemma, and insects are expected to defect by aggressively laying eggs on sites others have used, unless reciprocity or another such mechanism intervenes to make cooperation stable. However, if insects are not capable of identifying their eggs, defection is no longer a favorable option and evolutionary game theory predicts that they will cooperate by sticking to unused sites.

Considering the provision of public goods as an n-player prisoner's dilemma, Mancur Olson, in his venerable text *The Logic of Collective Action* (1965), asserts that collective action problems are less likely to occur in smaller groups. This is certainly evident if one considers a group of size one, in which "defection" is clearly not a favorable option. If the cost of contributing remains constant, while the benefit of cooperation (relative to

defection) becomes less and less significant as the group size increases, the balance will gradually shift from favoring cooperation to discouraging it.

These examples point to the existence, even if only occasionally, of “degrees of freedom” along which interactions that have the prisoner’s dilemma structure can be changed into more favorable arrangements. Where this is possible, it presents an alternative solution to the dilemma, in contrast to the well-known mechanisms of reciprocal altruism, kin selection and so on that presume the necessity of working within the prisoner’s dilemma structure.

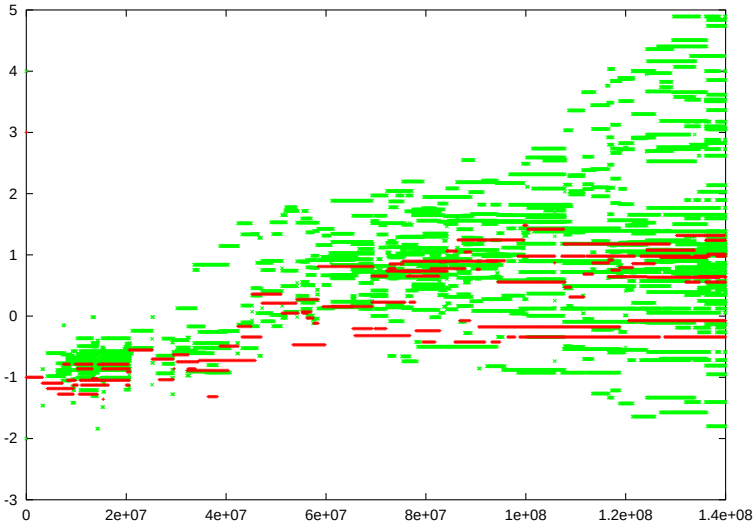


Figure 7.7: Development of the payoff matrix in another realization.

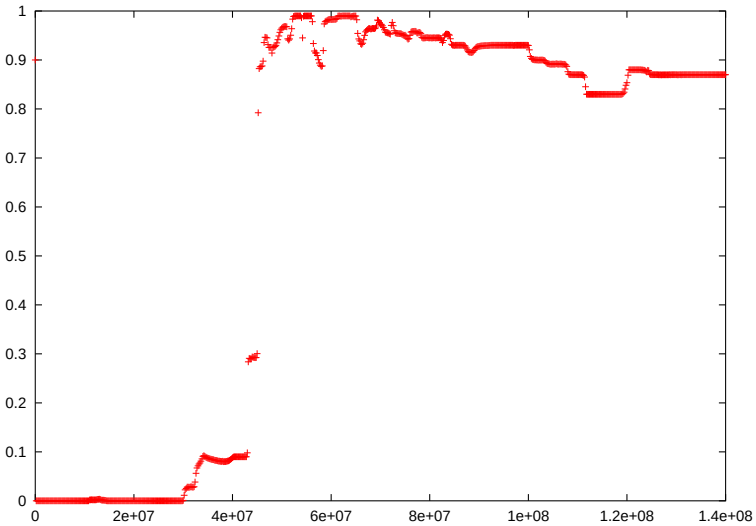


Figure 7.8: Probability of achieved cooperation in the simulation shown in figure 7.7.

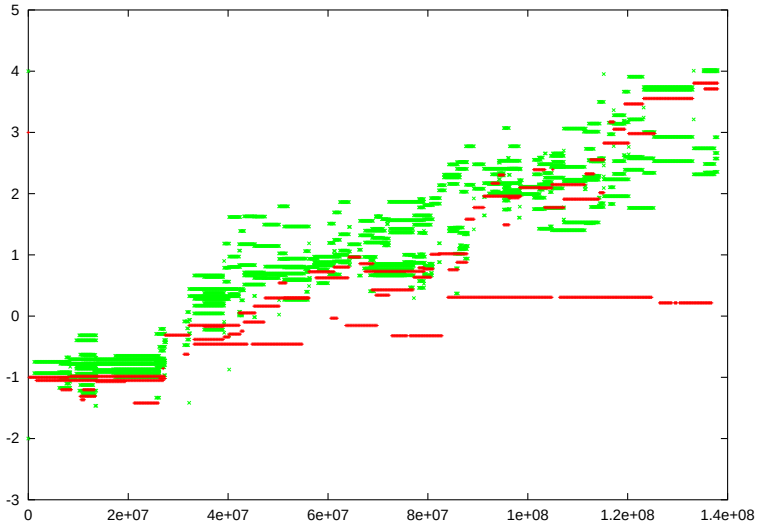


Figure 7.9: Development of the payoff matrix in another realization.

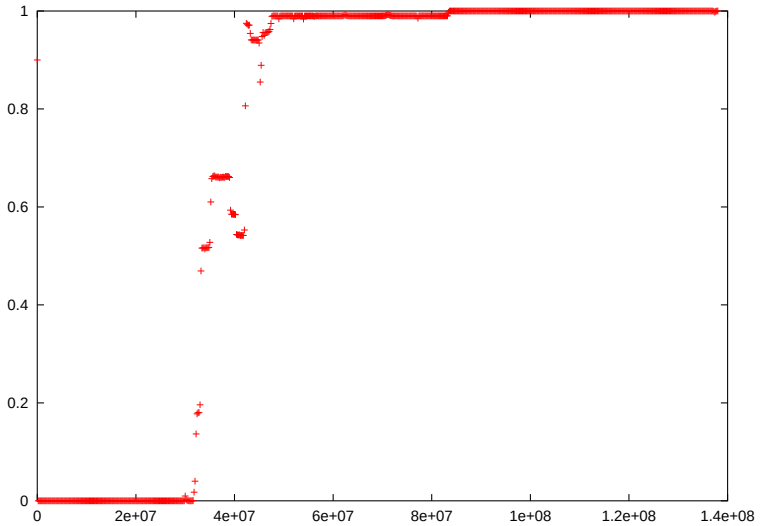


Figure 7.10: Probability of achieved cooperation in the simulation shown in figure 7.9.

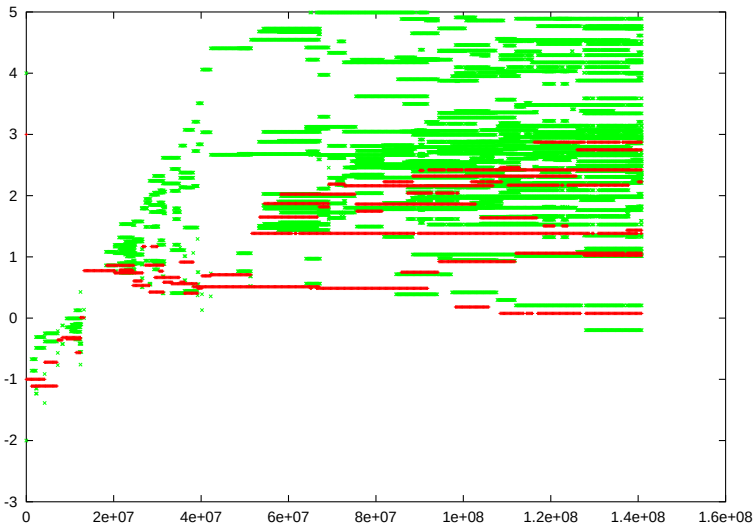


Figure 7.11: Development of the payoff matrix in another realization.

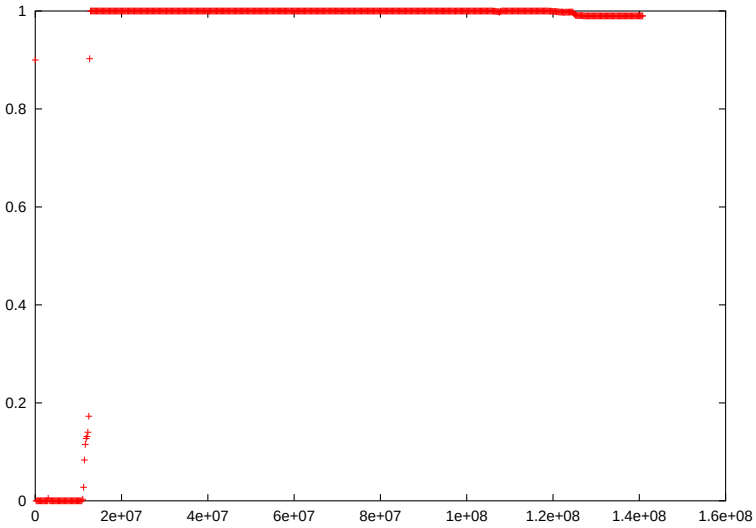


Figure 7.12: Probability of achieved cooperation in the simulation shown in figure 7.11.

Chapter 8

Biological Control of Seawater Composition

This chapter presents a simple mechanism by which oceanic microorganisms might be able to control the environmental balance of trace nutrients that have the potential to be limiting to their population growth. When the diversity of metabolic processes is sufficient, coexisting populations are able to bring the external concentrations of trace nutrients into balance so that none is more limiting to population growth than the others. This process may account for the observed ratios of metals in seawater, which have been seen to correlate better with organisms' uptake rates than with their rates of supply from inorganic sources.

8.1 Introduction

Biogeochemist François M. M. Morel and coworkers have studied sea-water concentrations of various trace metals used by phytoplankton, and found a strong predictive relationship between these elements' external concentrations and the ease with which they are absorbed by the populations that require them (Morel, personal communication). In particular, the relationship is a simple inverse one, so that the effective availability—concentration multiplied by uptake rate—is approximately *the same* for all elements studied.

This paper uses a set of mathematical models to present a possible mechanism producing this regularity. We show that the concentrations of resources in the environment can be controlled by the dynamics of populations that consume those resources, so that differences in resources' effective availability are removed.

We can model differences in nutrient limitation by giving the plankton a sort of biochemical pathway that depends on several functions; each function requires a certain nutrient, as it would if there were a particular enzyme required which is based on a particular mineral. The association of functions and nutrients is different from one population to another.

For instance, if there are three functions and two available nutrients, one population might need iron for one of these functions and manganese for two of them. Another might require manganese for two functions and iron for one. Thus when iron is scarce relative to manganese, the first population would fare better than the second, and would grow faster; when conditions change the second might begin to have an advantage.

But if the first population were to grow faster than the other, it would also take up more manganese than iron, and the two resource concentrations would be brought into balance. In the simple models we describe here, that balance is determined by the biological rates of uptake of the respective resources.

8.2 Resource-consumer model

I model this problem by considering k species of plankton dependent on n nutrients, represented respectively by population sizes N_i and concentrations R_j. Each population N_i dies at a constant per capita rate m, and grows at a rate g_i which depends on the availability of needed resources:

$$\dot{N}_i = N_i \left(g_i(R_1, \ldots, R_n) - m \right).$$

The interaction between populations and resources can be modeled in various ways, and I will present two simple alternative models. The central feature of these models, though, is that there is some fixed number of biological functions that must be performed by each organism, that each of these functions requires one of the n resources for its performance, and that the different species are distinguished by the substitution of different resources for the performance of the same functions. The assignment of resources to functions by each species is summarized by each species' overall resource requirements b_{ij}, each of which is a number defining, in some sense, how many units of resource j are required by one unit of population i. As I am only studying the effects of substitution, I require that the total requirement per unit growth of each species be the same. In the examples below, I use a simple model system where the first population (called population 0) requires one unit of resource 0 and two units of resource 1, and the other (population 1) requires two units of resource 0 and one unit of resource 1; that is, $b_{00} = 1$, $b_{01} = 2$, $b_{10} = 2$, and $b_{11} = 1$.

Since each unit of N_i can be considered to be constructed from b_{ij} units of each resource R_j, we can write the equations for R_j correspondingly:

$$\dot{R}_j = S(R_j) - \sum_i b_{ij} N_i \left(g_i - m \right), \tag{8.1}$$

where $S(R_j)$ can represent an external supply of the resource. This formulation assumes that all relevant nutrients taken up by an organism are returned to the pool of available nutrients after its death, but as we will see, that assumption could be relaxed without altering the

conclusion, as long as the supply rates S are sufficient to keep the system from running out of resources. The simulations I will show are of closed systems, with $S(R_j) = 0$, but the mathematical analysis makes no assumptions about S except that it is sufficient.

8.3 Collision model

Here we model the reproduction of the population as a sort of chemical reaction, where one individual and the indicated number of units of resources all need to come together to make a new individual. If the availability of resource j is R_j, and the rate at which it can be absorbed is r_j, then we can say that population i encounters resource j at rate $r_j R_j N_i$. Since we need several things at once, we can write it as a kind of n-way collision:

$$\begin{aligned} g_0 &= \gamma r_0 R_0 (r_1 R_1)^2 \\ g_1 &= \gamma (r_0 R_0)^2 r_1 R_1 \end{aligned}$$

or

$$g_i = \gamma \prod_j \left(r_j R_j\right)^{b_{ij}} \tag{8.2}$$

where b_{ij} expresses the requirement of population i for nutrient j (in the example system, b_{ij} is either 1 or 2).

The balance of resources at equilibrium comes from the first equation. Here I solve for the example system, for simplicity.

$$\begin{aligned} N_i (g_i - m) &= 0 \\ \gamma r_0 R_0 (r_1 R_1)^2 &= m \\ \gamma (r_0 R_0)^2 r_1 R_1 &= m \\ r_0 R_0 &= r_1 R_1. \end{aligned}$$

Numerical simulation shows that this equilibrium is stable, as in figure 8.1. This simulation has $r_0 = 1$ and $r_1 = 2$. Thus the final value of R_0 is twice that of R_1.

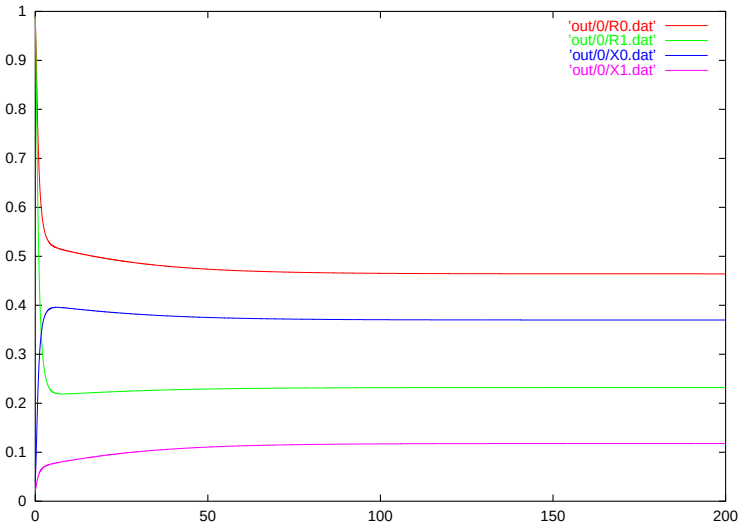


Figure 8.1: Dynamics of resources and populations in collision model. Resources 0 and 1 are red and green, respectively, and species 0 and 1 are blue and purple, respectively.

8.4 Waiting time model

Alternatively, let us say that the time it takes an individual (or one unit) of population i to collect one unit of resource j is $\frac{1}{r_j R_j}$, and so the time to collect all the things needed for an offspring is $\sum_j \frac{b_{ij}}{r_j R_j}$. Then the resultant reproductive rate is

$$g_i = \frac{1}{\sum_j \frac{b_{ij}}{r_j R_j}}. \tag{8.3}$$

Leaving the rest of the equations as above, we can recalculate the balance at equilibrium.

Again we solve the N equations at equilibrium for the example system:

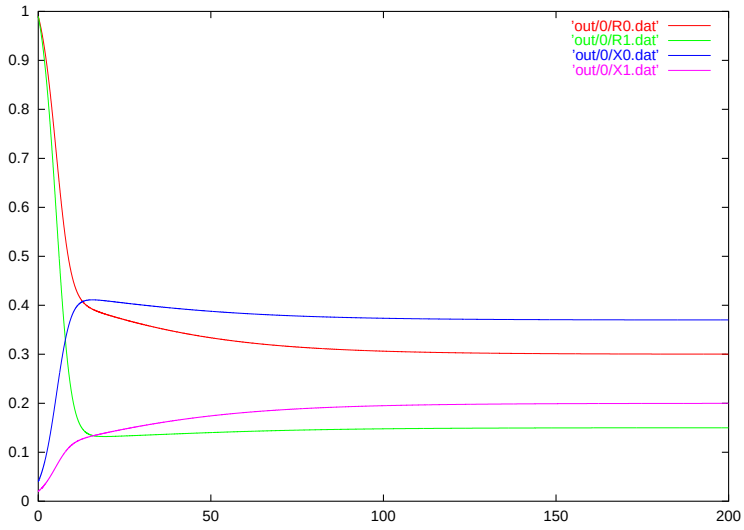


Figure 8.2: Dynamics of resources and populations in waiting time model. Colors as in figure 8.1.

$$\begin{aligned}
\frac{1}{\frac{1}{r_0R_0}+\frac{2}{r_1R_1}} &= m \\
\frac{1}{\frac{2}{r_0R_0}+\frac{1}{r_1R_1}} &= m \\
\frac{1}{r_0R_0}+\frac{2}{r_1R_1} &= \frac{2}{r_0R_0}+\frac{1}{r_1R_1} \\
\frac{1}{r_0R_0} &= \frac{1}{r_1R_1};
\end{aligned}$$

which gives the same result as before. Figure 8.2 shows the result of simulation. Again the final value of R_0 is twice that of R_1.

8.5 Generalized results

8.5.1 Unspecified number of species and resources

The equilibrium results presented above can be generalized to k species interacting via n resources. First, in the case of the collision model (8.2), the equilibrium condition is k equations

$$\prod_j \left(r_j R_j\right)^{b_{ij}} = \frac{m}{\gamma},$$

Taking the logarithm of both sides and substituting $s_j = \log r_j R_j$ gives

$$\sum_j b_{ij} s_j = \log \frac{m}{\gamma}. \tag{8.4}$$

Second, in the waiting time model (8.3), the equilibrium condition is k equations

$$\left(\sum_j \frac{b_{ij}}{r_j R_j}\right)^{-1} = m,$$

or, with $s_j = \frac{1}{r_j R_j}$,

$$\sum_j b_{ij} s_j = \frac{1}{m}.$$

In either case, we have the additional requirement that the total amount of resources required per unit of growth is the same for each species, that is, $\sum_j b_{ij} = c$ for each i. It is this condition that gives us the main result of this paper, that the equilibrium conditions can be satisfied by equalizing the effective availabilities $r_j R_j$ of all resources. This can be seen by setting $s_j = \frac{1}{c} \log \frac{m}{\gamma}$ in the first case, and $s_j = \frac{1}{mc}$ in the second case, each of which demonstrates the existence of the desired solution.

To see whether that solution is unique, it is simple enough to analyze these two systems of linear equations. First of all, if there are the same number of equations as unknowns s_j (that is, n species and n resources), there will be a unique solution as long as the n-by-n matrix (b_{ij}) is nonsingular. Since the ecologically balanced equilibrium $s_1 = s_2 = \ldots = s_n$

is always a solution, in this case it is the only solution. If there are fewer species than resources, there will not be enough equations in this system to determine the equilibrium balance of resources, and the ecologically balanced solution will only be one of many possible equilibria. This demonstrates that n species are needed to bring n resources into balance. Additionally, when n species are present, the requirement that the matrix be nonsingular can be interpreted as meaning that those species must be ecologically distinct in the sense that for each species, the vector of numbers b_{ij} describing the resource requirements of that species must be linearly independent of all the others. The ensemble of species, in a sense, needs to be able to 'span' all the different directions the environment might diverge from the balanced equilibrium, in order to be able to keep it in balance.

If there are more species than resources, there will be more equations in s_j than there are unknowns s_j. In general, such a system has no solution. However, in this case, the system can always be solved by setting all the effective availabilities equal. This implies that, unlike most ecological systems, this system can support more than n species on n resources at equilibrium (Levin 1970). Since the species equilibrium is determined by the resource equations (8.1), of which there are only n, when there are more than n species, their equilibrium population sizes are not uniquely determined. However, any equilibrium they may find will have the property of equalizing all resources' effective availabilities, provided the ensemble of species includes n which are ecologically distinct, in the sense described above (that is, provided that the rank of (b_{ij})—in this case a k-by-n matrix—is n).

This result is in a way the reverse of the standard ecological result that it takes n "controlling factors", such as resources or predators, to stabilize n populations at equilibrium; the result here is that it takes n independent populations to stabilize n resources at equilibrium. The linear algebra principle behind these results is the same, of course.[1]

[1]Both are similar to Ashby's (1956) "Law of Requisite Variation": the regulating system must have as much variety in the actions it can take as there is in the system being regulated. However, Ashby's use of the term "variety" is defined in terms of communication theory and the amount of information exchanged by

8.5.2 General functional form

These results can be generalized to any system for which the equilibrium conditions for the k species, $g_i - m = 0$, can be written in a form

$$F(\sum_j b_{ij} f_j(R_j)) = 0, \quad i = 1, \ldots, k,$$

provided each f_j is an invertible function (our two examples are $f_j(R_j) = \log r_j R_j$ and $F(x) = \gamma e^x - m$, and $f_j(R_j) = \frac{1}{r_j R_j}$ and $F(x) = 1/x - m$), and provided there is an X satisfying $F(X) = 0$. If these conditions are satisfied, then in order to achieve equilibrium each resource must satisfy

$$\sum_j b_{ij} f_j(R_j) = X$$

for some such X, and it follows that $f_j(R_j) = X/c$, for all j, is a solution (as long as X/c falls within the range of f_j). If these functions are of the form $f_j(R_j) = f(r_j R_j)$, this solution will have the characteristic that $r_j R_j$ is equal for all j. Uniqueness and interpretation of this solution are determined by the size of k relative to n, and by the rank of the matrix (b_{ij}), as before, though with possible complications in the case where there might exist multiple equilibrium values of X.

8.6 Discussion

In this wide class of models of coexisting populations distinguished by substitution of different nutrients for equivalent biological functions, the interaction of consuming populations brings external resource concentrations into balance, such that $r_j R_j$ is equal for all resources. This means that the effective availability of all resources is the same, so that no one resource is limiting for any of the populations.

systems choosing from a discrete set of responses, and so this does not appear to subsume the later results on equilibria of continuous dynamical systems (though he uses it to discuss such systems (Ashby 1960)), even if they can potentially be shown to be instances of a single, general principle. (This reference is thanks to Elinor Ostrom (2001).)

This result depends strongly on the assumption that the uptake rate r_j is equal for all populations, for each j. If it depended also on i, the result would be much more complicated; however, if all uptake rates for a given resource were roughly the same, the resulting balance should also be roughly in proportion.

It also requires that substitution be perfect: if one species were to require a different nutrient for one purpose than another, and also in a different quantity, the total requirement c would not be conserved, and the equilibrium would not have the equal effective availability property. Also, if substitution were to change other characteristics of a species, such as the value of γ or m for that species, the result would no longer hold, though if these were small differences, the result would in many cases be close to the equal-effective-availability solution.

Chapter 9

Nutrient Cycles and Global Homeostasis

This chapter uses simulations of populations exchanging nutrients and waste products to look at the interplay between ecology, geophysical processes, and evolution. When biological communities indirectly control global temperature, evolution can either stabilize or destabilize the emergent pattern of control. In the discussion of the model results, a process is proposed that works on a longer timescale than natural selection, which may be able to select stable global systems over unstable ones.

These models were developed jointly with Juan Keymer.

9.1 Global self-regulation and the Gaia hypothesis

The planet Earth is the biggest ecological system around. Innumerable different forms of organisms find ways to coexist, adapting to their surroundings and each other, and modifying their environments in countless ways at the same time. How this big, essentially materially closed ecosystem functions has been the subject of scientific study at least since geologist Vladimir Vernadsky developed his theories emphasizing the important role of life among the geological forces shaping the planet, in the early twentieth century (Vernadsky 1986). More recently, James Lovelock and Lynn Margulis have been the central figures in this area of science, with debate focusing on their controversial Gaia hypothesis (Lovelock and Margulis 1974; Lovelock 1979).

Lovelock proposed the Gaia hypothesis as a response to the observation that the chemical balance of the earth's atmosphere is very different from what it would be at equilibrium in the absence of life, but is in fact much better suited to the needs of the Earth's inhabitants than the equilibrium atmosphere would be. Lovelock's hypothesis is that living species have taken control of the atmosphere, regulating its composition to make it more suitable to their needs.

This proposal has met with a number of objections. Prominent criticisms have included Doolittle's claim that the Gaia hypothesis implies teleology, which would make the hypothesis require a great deal of explaining to justify it scientifically (Doolittle 1981), and Dawkins's objection that it cannot be justified in terms of natural selection, since organisms that contribute to global regulation are engaging in a form of altruism, which is vulnerable to being undermined by "cheaters" that take advantage of global regulation but do not contribute to it (Dawkins 1983). Dawkins wrote that a pattern of homeostasis on the planetary level cannot be a result of natural selection unless the planet is a unit of selection, which would require it to reproduce.

The Daisyworld model (Lovelock 1983; Watson and Lovelock 1983) responds to the

claim that teleology is required by offering, as a "parable", a model in which organisms cooperate to control the planetary temperature in a purely mechanistic way. In this model the temperature is determined by the amount of solar flux absorbed by the planet, which is a function of the reflectivity, or albedo, of the planet's surface. White daisies increase the planet's albedo, and black daisies increase it. Since white daisies are cooler in the hot sun, they thrive at higher temperatures than black daisies, and so when the temperature increases, the resulting increase in white daisies lowers the global temperature. Likewise, when the planet cools, the rise in the black daisy population returns the temperature to an intermediate value at which both populations are at equilibrium.

Variants of the Daisyworld model that include evolution have been proposed, addressing the problem of cooperation and "cheaters". In Robertson and Robinson's version (Robertson and Robinson 1998), daisies' optimal temperature, that is, the global temperature at which growth rate is maximized, adapts over time by approaching the current global temperature. They find that when the optimal temperatures converge, the ability of the daisies to regulate the global temperature is lost, since they no longer respond differently to changes in temperature (Sugimoto (2002), however, claims that temperature regulation is not in fact lost in this model). Lenton and Lovelock (2000) also find this destabilization, and then show that by adding an evolutionary tradeoff it is possible to demonstrate a model in which evolution does not subvert the self-regulation process, and can even strengthen it. This is done by attaching a multiplier to each population's growth rate that declines as the population's optimal temperature moves away from its initial optimal temperature.

Here we explore these same overall questions in a different framework from the Daisyworld family of models. We construct a model in which any number of species can coexist by consuming different resources, and producing other resources as waste. When some of these resources are "greenhouse gases" that alter the global temperature, and different species' growth rates are affected differently by the global temperature, feedback loops are set up and a pattern of self-regulation similar to the one in the Daisyworld model is possible.

The opposite pattern, of self-destabilization, is also possible. Evolution of the optimal temperature can undermine a temperature-stabilizing feedback loop, just as in the Daisyworld models, but when we look at what happens in the longer term, a hypothesis is suggested that might explain how a stable, Gaia-like system of feedbacks can be constructed without requiring natural selection on the planetary level.

9.2 Introduction of basic model

Our intention is to investigate the relationships between ecology, evolution and homeostasis on the simulated planetary scale, using a network structure that can describe very simple or very complex ecological communities.

We propose, as an idealization of the problem, a collection of different species, each of which consumes a single resource and produces as waste a single other resource. The environment consists of a number of pools of different resources R_j. Each species i consumes resource $R_{c(i)}$ and produces as waste resource $R_{p(i)}$, transforming each unit of resource $R_{c(i)}$ that it consumes into γ_i units of biomass and $1-\gamma_i$ units of $R_{p(i)}$. Organisms that die are decomposed back into the same single resource $R_{c(i)}$ that is consumed to make them.

Our model is based on Tilman's work (Tilman 1982) on competition among two or more plant species for a single resource, which provides the following equations for species and resource dynamics:

$$\frac{dN_i}{dt} = \frac{r_i R}{k_i + R} N_i - m_i N_i \tag{9.1}$$

$$\frac{dR}{dt} = a(S-R) - \sum_{i=1}^{N} \frac{1}{\gamma_i} \frac{r_i R}{k_i + R} N_i. \tag{9.2}$$

This is a special case of the more general form

$$\begin{aligned} \frac{dN_i}{dt} &= \mu_i(\vec{R}) N_i - m_i N_i \\ \frac{dR_j}{dt} &= g_j(\vec{R}) - \sum_{i=1}^{N} \mu_i(\vec{R}) h_{ij}(\vec{R}) N_i, \end{aligned}$$

with $\mu_i(\vec{R}) = \frac{r_i R}{k_i+R}$, $g(\vec{R}) = a(S-R)$, and $h_{ij} = \frac{1}{\gamma_i}$; here N_i and R_j are the abundance of species i and resource j, respectively; m_i is the mortality rate of species i; μ_i describes the dependence of the net per capita reproductive rate of species i on resource availability; g_i is the supply rate of resource i as a function of resource concentrations; h_{ij} is the function describing the amount of resource j required to produce a single individual of species i; and N and P are the number of species and resources respectively.

In this system the major result is that for each species i one can derive a quantity $R_i^* = \frac{m_i k_i}{r_i - m_i}$, which predicts the outcome of interspecies competition in a very simple way. The value of R_i^* is the amount of the resource R that is present at equilibrium if species i is the only species present, and in the presence of multiple species, whichever species has the smallest R^*, that is, whichever can survive on the smallest nutrient concentration, excludes all others and is the only surviving competitor at equilibrium. Corresponding but more complicated results hold in the case of species competing for two or more resources.

The full equations are then

$$\frac{dN_i}{dt} = \gamma_i \frac{r_i R_{c(i)}}{k_i + R_{c(i)}} N_i - m_i N_i \tag{9.3}$$

$$\frac{dR_j}{dt} = g_j(\vec{R}) + \sum_{\{i|c(i)=j\}} m_i N_i + \sum_{\{i|p(i)=j\}} (1-\gamma_i) \frac{r_i R_{c(i)}}{k_i + R_{c(i)}} N_i - \sum_{\{i|c(i)=j\}} \frac{r_i R_{c(i)}}{k_i + R_{c(i)}} N_i. \tag{9.4}$$

If $g_j(\vec{R}) = 0$ for all resources, the system is closed since all the above terms taken together sum to zero. We have given a great deal of attention to the closed case, since we are interested in the planetary ecosystem, which is materially closed (to first order). Notice that we do not assume the system is energetically closed, since our model does not consider energy: behaviors that seem like perpetual motion may in fact be reasonable given a constant influx of energy.

Thus the entire system is characterized by the values of $c(i), p(i), \gamma_i, r_i, k_i$ and m_i for all species i and $g_j(\vec{R})$ for all resources j.

9.3 Continuous and discontinuous evolution

In addition to the above dynamics, we introduce evolution into the model by numerically integrating the equations in a computer system, and stopping the evaluation at certain times to add and subtract species and resources from the list, reconstructing the dynamical equations according to (9.3) and (9.4) before continuing.

The evolutionary algorithm works as follows:

- Numerically compute values of all $N_i(t), R_i(t)$ from current time t_0 to some time t_1

- Choose a random 'time to next speciation' τ, exponentially distributed with mean M (τ and M have units of biomass multiplied by time); find the time of speciation t_s by solving
$$\int_{t_0}^{t_s} \sum_i N_i(s)\,ds = \tau$$
(integrating beyond time t_1 if necessary). Then choose at random which species i is to speciate at that time, weighted by population.

- With probability P_c, produce a *"continuous mutation"* event: create a daughter species i' identical to the parent species, but with $r_{i'}$ or $k_{i'}$ (with probability P_r, $1-P_r$ respectively) altered by a small amount (and kept within the allowable range—see table 9.1). Currently we do this by multiplying by a number uniformly distributed in an interval near 1, and then comparing to maximum and minimum values for that parameter. Both r and k are kept above a small minimum, usually 10^{-3}, to avoid numerical instability.

- With some probability $1-P_c$, produce a *"discontinuous mutation"* event: construct a daughter species i' with a completely different $p(i')$ or $c(i')$ from its parent, with metabolic rate constants r_i, k_i chosen umiformly from the range of

γ_i	0.5
m_i	0.5
initial r_i	2
initial k_i	0.01
$g_j(\vec{R})$	0
Mutation rate (per unit mass per time step)	
	0.2 (*i.e.*, $M = 5$)
P_c	0.5
P_r	0.5
Range of continuous mutations	$[1 - maxmut, 1 + maxmut]$
maxmut	0.1
Range of r_i	$[10^{-3}, 4]$
Range of k_i	$[10^{-3}, 0.1]$
Extinction threshold	10^{-6}
Fraction of biomass assigned to daughter species	
	Uniform on $[0, 10^{-4}]$

Table 9.1: Standard values of numeric parameters.

possible values. The resource chosen to replace $p(i)$ or $c(i)$ comes from a list of all resources except the current $p(i)$ and $c(i)$, with one resource that is not yet part of the network added to the list.

- Reconstruct the dynamical equations from the new list of species and resources, and construct new initial conditions from the old final conditions. Assign a small amount of biomass taken from the parent species to the new daughter species.

- Remove all species whose populations have fallen below a small minimum threshold value at time t_s. Construct new initial conditions and reconstruct the dynamical equations from the new list of species and resources, and restart the numerical integration at time t_s.

Unless indicated otherwise, all model results discussed below are obtained using the

values listed in table 9.1. Simulations begin with a total mass of 1 unit, assigned randomly among all species and resources. If the system is closed, the total mass remains 1 at all times.

9.4 Equilibrium solutions

***N* equations** Since our population equation (9.3) is essentially identical to Tilman's (9.1), we derive the same quantity

$$R_i^* = \frac{m_i k_i}{\gamma_i r_i - m_i},$$

by setting $\frac{dN_i}{dT} = 0$ and solving for a nonzero equilibrium value of $R_{c(i)}$. Each species' population N_i is at equilibrium when $R_{c(i)} = R_i^*$ (or when $N_i = 0$).

Consequently, if two species have the same food resource but different R^* values, they can not coexist at equilibrium. Tilman's proof that the lowest-R^* species always excludes the rest does not transfer to our system, since there are cases (when the growth functions $\mu_i(\vec{R})$ cross) in which the competition depends on the supply rate of the resource, and supply rate in our system can depend circularly on the competing species themselves, making this a difficult question which we haven't solved.

We also haven't shown that the system always comes to a point equilibrium at all, rather than a limit cycle or other attractor, but in practice we have always seen it do so, for all network graphs and choices of parameters (in the absence of temperature feedback, that is, which we will introduce below). Further, while it is possible to construct a time-varying supply rate for a shared resource which will cause a species with higher R^* to outperform its competitors, the supply function required seems unnatural and extreme, and the supply rates we actually observe are slow-changing and relax directly to equilibrium with few oscillations. In our simulations we consistently see classical R^* competition, and can count on it to produce a steady decline in R^* for each species due to continuous mutation (discussed below). In the next few sections we will discuss results with the assumption that the

ecological dynamics always come to a stable fixed point, and that the lowest-R^* species in each niche is the dominant competitor.

R equations Assuming the N_i equations are all at equilibrium (either because $R_{c(i)} = R_i^*$, *i.e.* $\gamma_i \mu(R_{c(i)}) - m_i = 0$, or because $N_i = 0$) we can replace $m_i N_i$ by $\gamma_i \mu(R_i^*) N_i$ in (9.4) at equilibrium:

$$\begin{aligned} 0 &= g_j(\vec{R}) + \sum_{\{i|c(i)=j\}} \gamma_i \mu(R^*_{c(i)}) N_i + \sum_{\{i|p(i)=j\}} (1-\gamma_i)\, \mu(R^*_{c(i)}) N_i - \sum_{\{i|c(i)=j\}} \mu(R^*_{c(i)}) N_i \\ &= g_j(\vec{R}) + \sum_{\{i|p(i)=j\}} (1-\gamma_i)\, \mu(R^*_{c(i)}) N_i - \sum_{\{i|c(i)=j\}} (1-\gamma_i)\, \mu(R^*_{c(i)}) N_i. \end{aligned}$$

Each of these expressions $(1-\gamma_i)\, \mu(R^*_{c(i)}) N_i$ is the net flow of matter from resource $c(i)$ to resource $p(i)$ due to species i at equilibrium. This equation simply expresses that the flow into each resource j must equal the flow out of resource j at equilibrium.

This result implies that any resource that supports a nonzero population of consumers at equilibrium, naturally enough, must have a source. If there is an external supply of one resource ($g_j(\vec{R}) > 0$) a chain of species can bridge from that resource, through any number of neutral resources, to one that is a sink ($g_j < 0$); if there is no external source, the only stable configuration is a closed loop of species (or several disjoint loops) endlessly circulating matter.

9.5 Ecological results

From the above results we can predict the fate of any network, as long as we are willing to suspend disbelief and assume stable fixed points and Tilman-style R^* competition.

First we remove any species that shares its food resource with a superior (lower R^*) competitor. Then the remaining network will be made up of (zero or more) disjoint cycles and chains. All cycles survive, and chains survive only when supplied by a source nutrient

(and if the resource at the downstream end of a chain is not drained out of the system it will grow without bound).

9.6 Evolution results

Continuous mutations and R^* If the continuous mutation operator produces a daughter species with lower R^* than its parent, that species will replace its parent. If not, it will not. Consequently, all species gradually evolve lower and lower R^*, at a rate dependent on the current r and k, and also on the species population.

Discontinuous mutations, competition and destruction Discontinuous mutation can produce a new species that consumes a previously unused resource, or consumes a known resource but produces something new, or one that connects two resources that are already in use. If the new species shares its food resource $c(i')$ with another species, it must outcompete the other species in order to survive. If the new species displaces a species that is part of a cycle and breaks that cycle (and no matter is supplied from outside the system), all species in the cycle (which may make up the entire ecosystem) are in danger of extinction, and can only be rescued if a later speciation event creates a species that closes the loop before any species in the loop become extinct. This 'drain' phenomenon very commonly kills all the species in our simulations of closed systems, which is very frustrating.

An analogy to this phenomenon on our planet may be the action of coccolithophores such as *Emiliania huxleyi*, which convert dissolved carbon to calcium carbonate shells which are then deposited on the ocean floor and become chalk and limestone deposits. Clearly, unless this material is pushed up to the surface by geological activity and recycled into the biosphere in time, the planet will eventually face a crisis of carbon limitation.[1]

[1] In fact, this carbon is occasionally returned to circulation by volcanic activity (Lovelock 1991).

Canalization and beating the drain Since the accumulation of continuous mutations constantly optimizes the R^* of long-lasting species, while all species are created by the discontinuous mutation operator with the same initial distribution of R^*, as a particular configuration of species persists, it becomes harder and harder to invade. Actually, in our model, any species that lasts long enough will attain the optimal R^* allowed within the given maximum and minimum values of r and k, after which it cannot be displaced. If we were to remove these strict boundaries, it would seem that invasion is always possible, but as an ecosystem becomes older it becomes more and more resistant to invasion.

If we begin our model with the simplest possible sustainable closed system, a cycle of two species, each producing the other's food resource, with the parameter values given in the table above, the system can not last long before being killed by a 'drain' species, typically less than 2000 time steps. If we increase the rate of evolutionary optimization, on the other hand, by increasing *maxmut* (see table 9.1) to 0.25, the system can sometimes resist invasion until both species become fully optimized and uninvasible, around 100,000 time steps.

In this way, by increasing the rate of evolutionary optimization we can sometimes get an ecosystem that resists extinction, but at the cost of being able to accomodate change of any kind. The network structure present early in the system's natural history becomes fixed in stone for all time.

Open vs. closed It is possible to stop the system from extinguishing itself quite so often, by making the system materially open with a source at, say, resource 1 ($g_1(\vec{R}) > 0$), and possibly a sink somewhere else in the system to keep the total mass from growing too large. In this case the long-term tendency of the system is to evolve a linear chain of species head-to-tail beginning at whatever resource is supplied. From time to time the head species is replaced by a mutant with lower R^* and a different product resource, which kills all the species downstream, and then another chain gradually grows feeding off the new

head species. This is the scheme we have used to look at climate regulation (below), but at least one of us (LW) finds the materially open system esthetically unsatisfying.

9.7 Chemistry

One possible reason that the terrestrial biosphere does not seem more vulnerable to mutations that convert essential resources to unusable compounds is that beyond a certain complexity, new compounds tend to be unstable and break down spontaneously into more familiar substances. This would make such a mutation harmless, since its useless product would convert automatically into usable resources.

Indeed, it turns out to be very easy to rescue our model from extinction, without sacrificing dynamically changing network graph structures, by adding this assumption.

We have only played a little with this possibility, using a very simple idealization of chemistry. We assume that every compound R_j spontaneously reduces to compound $R_{\lfloor j/2 \rfloor}$ (writing $\lfloor x \rfloor$ for the integer part of x), at rate 1 for lack of a reason to use any other rate. Resource 1 does not reduce to anything, and all other resources eventually flow into resource 1 unless biology intervenes.

Generalizing a little to write $red(j)$ for the reduction product of resource j (here $\lfloor j/2 \rfloor$) and ρ_j for its reduction rate (here 1), we rewrite our equations with a few new terms:

$$\frac{dN_i}{dt} = \gamma_i \frac{r_i R_{c(i)}}{k_i + R_{c(i)}} N_i - m_i N_i \tag{9.5}$$

$$\frac{dR_j}{dt} = g_j(\vec{R}) - \rho_j R_j + \sum_{\{j' | red(j') = j\}} \rho_{j'} R_{j'} + \sum_{\{i | c(i) = j\}} m_i N_i + \sum_{\{i | p(i) = j\}} (1 - \gamma_i) \frac{r_i R_{c(i)}}{k_i + R_{c(i)}} N_i - \sum_{\{i | c(i) = j\}} \frac{r_i R_{c(i)}}{k_i + R_{c(i)}} N_i. \tag{9.6}$$

Now the simplest ecosystem is a single species feeding on resource 1 and producing anything else, for example resource 2. This system, while completely self-contained, provides an empty niche for a species feeding on resource 2 to arise and extend the ecological

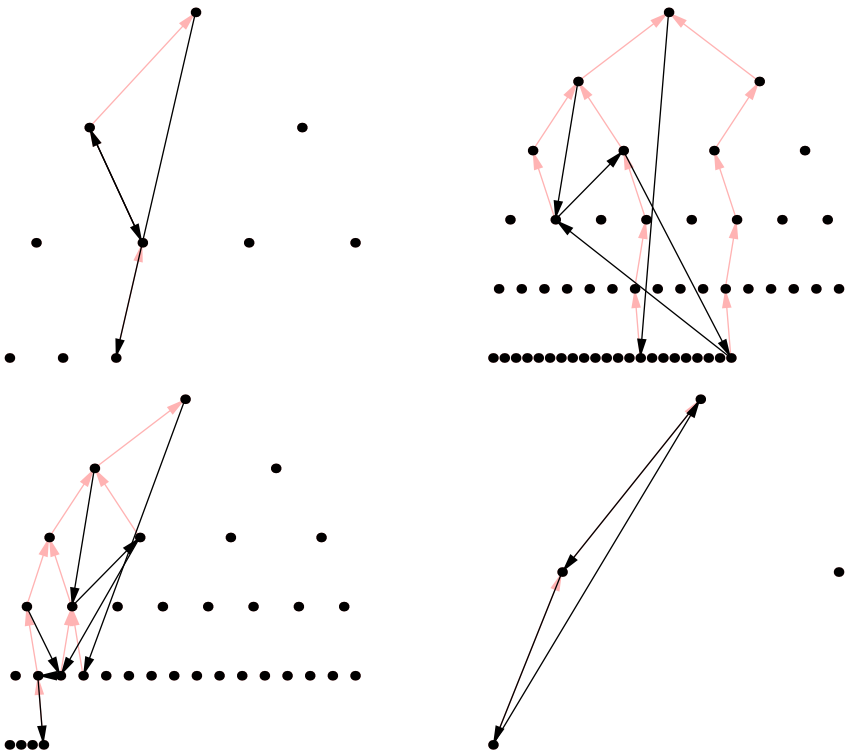


Figure 9.1: Networks evolved from single species ($R_1 \rightarrow R_2$) with inorganic chemistry. Black arrows represent species; pink arrows represent spontaneous chemical reduction. Resource numbers count from top to bottom, left to right. Notice only the last network is immune to invasion, or would be if all species' R^* were optimal.

network into other previously undiscovered niches.

It is possible for an ecosystem in this environment to become uninvasible, for instance if the second species in the system were to transform resource 2 back into resource 1 and this configuration could last long enough for both species' R^* to be optimized. However, the disruptive action of discontinuous mutations, which usually kills everything in our system without chemistry, now tends to produce a more interesting system and open new niches.

Figure 9.1 shows some networks that have evolved from this initial single-species system. Evolution in this model appears to be open-ended, without the tendency to crash and become lifeless that plagues the earlier model. This appears to be a promising way to get interesting long-term behavior from the model, at the expense of a bit more complexity.

9.8 Temperature regulation

To return to the question of global homeostasis, we consider homeostasis to be a question of temperature only. Here, instead of using chemistry, we augment the simple model by considering the resources to be atmospheric gases, which trap solar heat at varying rates, and closing the feedback loop by introducing temperature-dependent mortality to each species:

$$m_i = \delta_i + \beta_i (T - \bar{T_i})^2$$

giving modified equations:

$$\frac{dN_i}{dt} = \gamma_i \frac{r_i R_{c(i)}}{k_i + R_{c(i)}} N_i - \left(\delta_i + \beta_i (T - \bar{T_i})^2\right) N_i \tag{9.7}$$

$$\frac{dR_j}{dt} = g_j(\vec{R}) + \sum_{\{i|c(i)=j\}} \left(\delta_i + \beta_i (T - \bar{T_i})^2\right) N_i + \sum_{\{i|p(i)=j\}} (1-\gamma_i) \frac{r_i R_{c(i)}}{k_i + R_{c(i)}} N_i - \sum_{\{i|c(i)=j\}} \frac{r_i R_{c(i)}}{k_i + R_{c(i)}} N_i. \tag{9.8}$$

Temperature in this model is also a dynamic variable, which rises at a rate dependent on the concentration of greenhouse gases and dissipates into space at a fixed rate. Each atmospheric resource R_j is assigned a coefficient α_j between 0 and 1 describing how effectively

Φ	75
Λ	0.45
α_1, α_3	0
α_2	1
δ_i	0.25
β_i	0.0003
$\bar{T}_1$	40
$\bar{T}_2$	60
$g_1(\vec{R})$	$1 - R_1$
$g_j(\vec{R})$, $j \neq 1$	$-0.1R_j$
k_1	$1/3$

Table 9.2: Values for temperature regulation experiments.

it traps solar radiation; Φ is the rate at which radiation arrives from the sun, and Λ is the rate of temperature dissipation:

$$\frac{dT}{dt} = \Phi \frac{\sum_j \alpha_j R_j}{\sum_j R_j} - \Lambda T. \tag{9.9}$$

The mutation operators are expanded to operate on $\bar{T}_i$ as well as r_i and k_i.

To avoid the problem of recurrent total extinction, we have so far been looking at this model using a materially open setup. We have not put the temperature and chemistry equations together to date. The results discussed below use the parameter values listed in table 9.1, with the changes listed in table 9.2.

Temperature regulation enables coexistence In this version of the model, it is possible to construct a simple system, similar in concept to Lovelock's Daisyworld model (Lovelock 1979), which regulates the temperature by controlling the populations of warming and cooling species (figure 9.2). Resource 1 is supplied from outside the system. Species 1 transforms resource 1 into resource 2, which captures heat and warms the planet. Species 2 transforms resource 1 into resource 3, which does not capture heat and so tends to cool the planet as it accumulates. Species 1 has a lower optimal temperature than species 2, and so

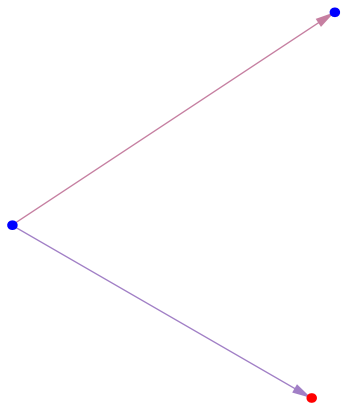


Figure 9.2: Simple network for temperature regulation. Resource 1 (left) is supplied. Species are color-coded by optimal temperature ($\bar{T}_i$), blue = 0, red = 100. Resources are color-coded by rate of heat absorption (α_j), blue = 0, red = 1. Species colors appear similar because their $\bar{T}$ values (40, 60) are close together. Notice that the cold-adapted species produces the warming resource, and vice versa.

by raising the temperature, the overall effect of an excess of species 1 is to suppress itself and encourage growth of species 2, and vice versa. In this way the system comes to an equilibrium in which the temperature is held constant at a compromise value between the two species' optima.

Since the expression for R_i^* for each species depends on m_i, which we have now made a function of temperature, what these two species actually do is to find the unique value of T that makes R_1^* and R_2^* equal, allowing the two species to coexist sharing the same resource. While this result may appear to contradict Tilman's results, the more general result is that two controlling environmental factors (here R_1 and T) can allow as many species to coexist (Levin 1970).

Evolution destabilizes temperature regulation The effect of natural selection on the system of figure 9.2 is still to gradually make the resource utilization of each species more and more efficient, which is very much as before when T does not change much. At the same time, though, it also brings each species' optimal temperature $\overline{T}_i$ progressively closer to the actual temperature. If either species' $\overline{T}$ actually becomes equal to T, the two-species community can no longer control the temperature, and it can wander upward or downward, killing one or both of the species. This problem is very simple and general, and seems like one that must be almost universal in this general kind of system.

In full simulations of the model, with discontinuous mutations included, the results are more complicated.

Results of full simulation Figure 9.3 shows species populations, optimal temperatures, and global temperature in one simulation, beginning with the two-species system of figure 9.2. Up to time 5250, the makeup of the system is qualitatively the same, although each of the two species is replaced from time to time by one with different optimal temperature, r, etc., giving different equilibrium temperatures. Around time 2700, in fact, the system does not find an equilibrium temperature at all, going into what appears to be a limit cycle (figure 9.4). At time 5250, a macroevolutionary event produces a species that transforms resource 2 into resource 3, which apparently destroys the ability of the species on resource 1 to use temperature to maintain coexistence by equalizing their R^*s. The temperature drops and the species connecting R_1 to R_3 goes extinct. Subsequent succesfully establishing species appear at the end of the chain beginning with R_1 and R_2. At time 7486, R_7, which has been accumulating for some time faster than it is removed from the system, and has very little warming effect, is suddenly transformed into R_2 in great quantity, causing a catastrophic temperature change. Almost everything goes extinct, and then the system slowly starts to rebuild itself, at which time the simulation was stopped.

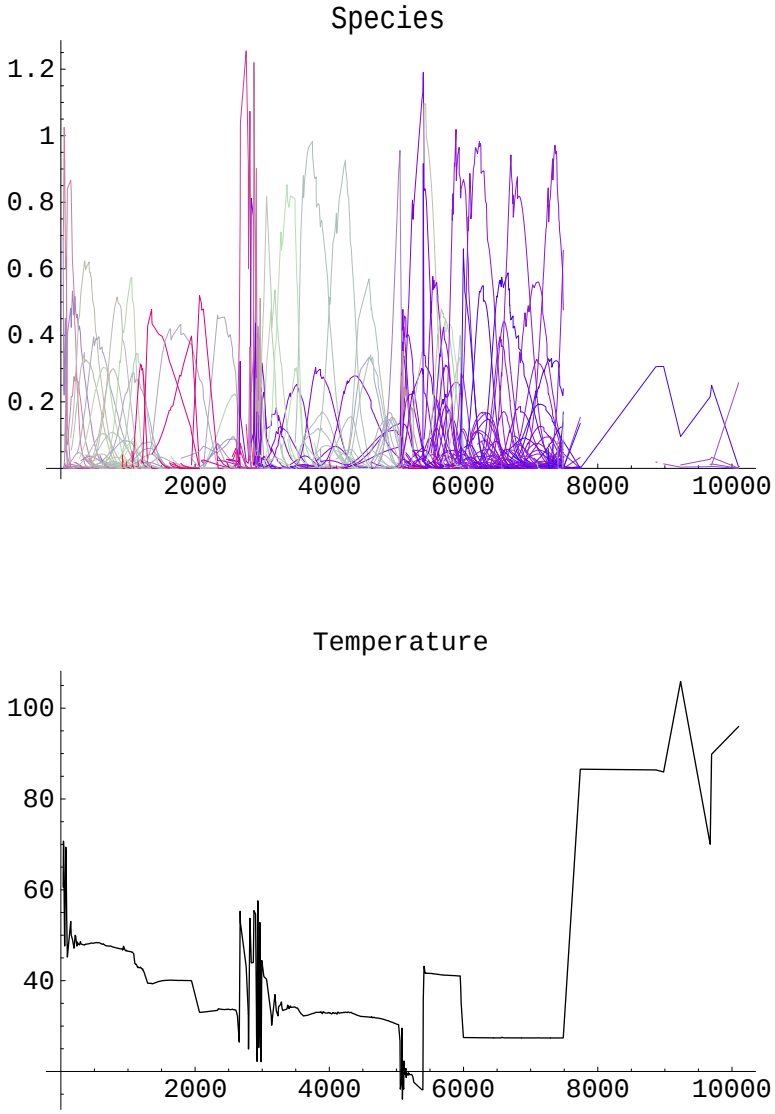


Figure 9.3: Species abundances and temperature in simulation of equations (9.7, 9.8, 9.9) from initial configuration described in text. Species graphs are color-coded by optimal temperature $\overline{T}_i$.

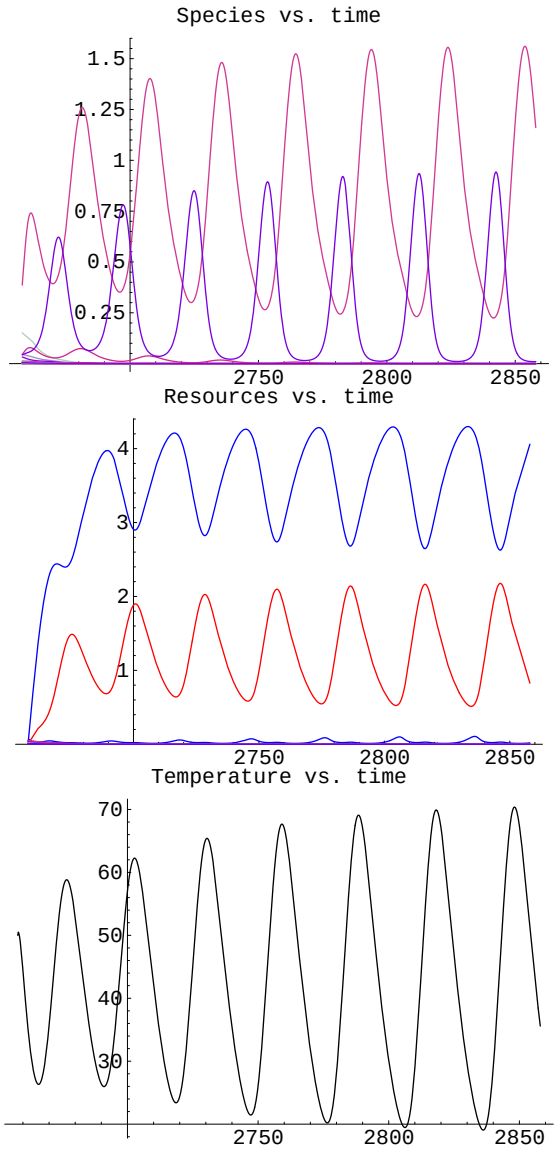


Figure 9.4: Apparent limit cycle at time 2658 of figure 9.3. Figure generated by reconstructing the system as it was at time 2658, and evaluating for 200 time steps without evolution, from randomized initial conditions.

9.9 Conclusions

Though these observations are very preliminary and rudimentary, they suggest some hypotheses about evolution and global regulation.

The problem of the basic model is very simple and clear: if something interrupts the cycle of nutrients through the ecosystem by transforming something usable into something unusable, it threatens everything in that cycle. This has to be true in all ecosystems. Why this has not happened to our planet is not obvious. Perhaps the detailed nature of real-world chemistry makes it hard for existing organisms to produce anything stable that they can't metabolize. Perhaps organisms have been lucky, and have been able to evolve ways to metabolize new, problematic compounds before each such problem becomes severe enough to destroy life. The ecological crisis that apparently occurred when photosynthesizing organisms appeared and flooded the atmosphere with oxygen, followed by the appearance of aerobic metabolic processes (Margulis and Sagan 1986), would appear to be an example. It could also be that such a process is happening, only slowly enough that we don't know it yet.

The global temperature model, like the Daisyworld model, demonstrates that global self-regulation is possible, but it also shows that when the system is stable, as the species involved adapt to current conditions (by adjusting their optimal temperatures), they undermine the negative feedback that provides regulation. Lenton and Lovelock's model (Lenton and Lovelock 2000) demonstrates that evolution can reinforce global regulation rather than undermine it; this is done by imposing a tradeoff or correlation between several characters that are undergoing selection, so that the optimal temperatures are pulled away from the actual temperature as well as toward it, and do not converge fully. In our model, we could also make $\overline{T_i}$ a function of r_i and k_i, or make the growth rates favor some particular temperatures, as Lenton and Lovelock do, in such a way that selection for higher growth rates and lower R^* would control $\overline{T_i}$ and steer it away from the actual T. On the other hand, we could just

as well construct a function that would make $\bar{T}_i$ converge on the global temperature even faster than if it were left alone, or cross right over it to make the negative feedback into an especially unstable positive one. Selection pushes each species in a particular direction, steered by whatever helps individuals of that species thrive. A side effect of that selection is to modify that species' contribution to the general well-being. Whether that contribution is strengthened or weakened depends on whether the constraints governing evolution are lined up in a way that makes each species' self-interest correlate positively or negatively with the greater good. It would seem to be a matter of luck whether they line up so as to make global self-regulation stable.

The possibility that some globally self-regulating ecosystems are stable to evolutionary change and some are not raises (in the realm of speculation) a possible sort of selection-like process that might produce stable self-regulating planets. This possible process goes something like this: If the planetary community responds to its environment in a way that generates unstable feedback, the temperature or other quantities will change until the community changes, either by extinction or by changing the geographical distributions of species, or by other means. In this way it will find its way to a stable system of feedbacks. If a self-regulation scheme arises that is not stable to evolutionary change, because the correlation between "selfishness"- and "generosity"-related characters does not line up correctly, that system will quickly collapse. The system that replaces it might collapse as well, but when this process of trial and error settles on a stable configuration, that system will not collapse and may become permanent. Periods of "punctuated climate equilibrium" are expected, something like those seen in figure 9.3, interrupted at times when stability breaks down and the planetary system goes searching for another equilibrium. In this way, the planet will eventually develop a Gaia-like property.

This process seems to have a lot in common with natural selection—a number of different variants are produced, and those that are more successful are more likely to persist—but there is nothing corresponding to a population, or even to reproductive success. It would

probably be best to call this a non-selective process of adaptation, more akin to a kind of learning. At any rate, it is very different from the idea of reproducing planets that Dawkins invokes in order to discredit the Gaia hypothesis.

Actually, it has much more in common with a class of systems proposed by cybernetics theorist W. Ross Ashby as a mechanistic model for animal learning (Ashby 1960). An animal needs to maintain a number of quantities near equilibrium levels, such as body temperature, blood sugar level, and so forth, but there are many situations in which the animal is not born not knowing how to do so: how to forage for food, how far to stand from a fire, etc. If an animal were a simple machine, how would it be designed to handle these situations? Ashby proposes a design he calls the *ultrastable system*.

This is a system in which feedback happens on two levels, as it does in our Gaia model, with the ecological climate regulation process nested within a natural selection process that changes the ecological feedbacks. On the inner level, the idealized animal is governed by a set of behavioral processes that work more or less well for surviving in the world. That is, they serve to keep the *essential variables* within the range of values that is biologically acceptable. On the outer level, there is an adaptive process that changes the animal's rules for behavior when a situation arises where they don't work. The simplest ultrastable system is a machine that does the following: whenever any of the essential variables escapes from the acceptable range, change the rules in some random way. If the first thing this machine tries doesn't work, it will keep making changes until it finds a scheme that does work.

The punctuated climate equilibrium process I have proposed above works essentially this way. Whenever the temperature or another biologically important characteristic of the environment exceeds the ecological community's limits of tolerance, the community undergoes a reorganization. As long as not everything goes extinct, it seems that this process should be able to find a stable solution. If this is true, the answer to Dawkins' complaint may be that a planet doesn't evolve the Gaia property, it learns it.

Chapter 10

Discussion

This chapter ties together the various subjects of the preceding chapters. I discuss in more detail how important phenotypic constraints are in determining evolutionary dynamics, with the implication that evolutionary dynamics cannot be considered emergent from ecological interactions. In particular, cooperation is neither necessarily favored nor necessarily destabilized by evolution; either outcome is possible, depending on the structure of the constraints shaping the variation available to the selection process. This chapter also reiterates the new results of the thesis, including new theorems on coexistence and replacement in Lotka-Volterra systems, a branching event that is fundamentally different from the branching that occurs at singular points in known adaptive dynamics models, and the proposal that the system of planetary homeostasis central to the Gaia hypothesis may be constructed by a process similar to learning processes in animals or organizations.

In the preceding chapters I have offered a number of mathematical results that I hope others will find useful. The calculations about adaptive dynamics on constraint surfaces, and their counterparts in more dimensions, can make the relationships between selection and ecological parameters easier to interpret, and can make calculations simpler and more tractable.

The theorems about replacement and coexistence in three species (theorems 5.1 and 5.2) help to fill a gap in adaptive dynamics modeling that has been conspicuous. Adaptive dynamics modelers often simply assume that positive and negative invasion exponents are sufficient to predict which species will invade and which will go extinct, although it is in fact possible in many systems for a species whose invasion exponent is negative in a given environment to avoid going extinct, due to the presence of multiple stable attractors of the population dynamics. These theorems make it clear that invasion exponents are, in fact, sufficient to predict which species will live and which will die in three-species competitive Lotka-Volterra systems. (I have also shown that this is true in two-species Lotka-Volterra systems, though this is too trivial to be labeled a theorem.) Systems with more than three species, unfortunately, are much harder to analyze, so that is work yet to be done, as is the case in which not all interactions are competitive.

The calculations I have presented relating selection and the Lotka-Volterra interaction terms, in chapters 4 and 5, may also be of use to others working on Lotka-Volterra systems. Additionally, a similar analysis may be possible for models other than the Lotka-Volterra ones, such as those using ratio-dependent predation, or those exploring various functional forms for predation, parasitism, and mutualism.

Beyond those specific results, there are two major themes that tie the different chapters together: the emergence and maintenance of cooperation, and the difference between modeling evolution by applying mutations to phenotype vectors and doing it by applying mutations to the numbers describing interactions. These two subjects are separate and independent, as shown by the models of chapter 4, where competition transforms into cooperation as a result of the evolution of phenotypes, and chapter 6, where systems without

phenotypes are restricted to competitive or predatory interactions.

It is the analysis of the basic model of Lotka-Volterra evolution without phenotypes, though, that motivates the decomposition of the selective pressure on phenotypes into the selective pressure on interactions and the mapping between phenotypes and interactions, which shows that the selective pressure on interactions always favors cooperation, though the phenotype-interaction mapping may in fact drive the actual evolutionary motion in some other direction. When I began working on the no-phenotype model of chapter 5, I had no intention of studying mutualism or cooperation. The unexpected behavior of that model forced me to think about this relationship between selective pressure and phenotypic constraints on interactions. Even so, I did not expect mutualism to emerge in the models of chapter 4; then I began to think it might be a common outcome of models that do not assume it away by studying phenotype-interaction mappings that make it impossible. This led me to see whether the prisoner's dilemma model could have the potential for the same transformation of interactions, which chapter 7 demonstrates that it does have.

10.1 Constraints and cooperation

I have been using the words constraints, tradeoffs, and correlations somewhat interchangeably, because they play the same role in my analysis. The important thing is that in each case, selection acting on two or more qualities of the individuals in question is unable to act on each independently, because they vary together. For instance, among the Darwin's finches of Galápagos (Boag and Grant 1981), birds with larger bills are better able to eat large seeds and birds with smaller bills are better able to eat small seeds. Depending on what kinds of seeds are most available, selection will favor larger or smaller bills. When many different-sized seeds are available, one might say that selection favors having both a large bill and a small bill, since that would surely be best, all other things being equal, but this is clearly not an option. A choice has to be made. I would call this a tradeoff.

Birds with large bills tend to be large birds, and there are additional selection pressures on body size, particularly relating to energetic requirements and dominance-related behavior (Boag and Grant 1981). Consequently, even when birds with larger bills might do better, selection for smaller body size can cancel out that advantage and cause the population to stabilize at an intermediate size of both bodies and bills. I would call this a correlation. In either case, the effect on selection is that not all combinations of values of these characters are possible; this is why I refer generally to constraints. When two or more characters are subject to a tradeoff, correlation or constraint, they must be considered together before one can say what the effect of selection on those characters might be. The case of a lower-dimensional constraint surface that I treat in chapter 3 is an extreme case, useful in modeling because it is more simple and tractable than a case in which characters are partially correlated and partially independent.

If we were to arrange a population of finches on a two-dimensional graph whose axes are ability to eat large seeds and ability to eat small seeds, they would presumably line up more or less along a curve reaching from the upper left to the lower right, since increasing one of these measures decreases the other. Since fitness is increased by increasing either of these two abilities, the fitness gradient at each point points somewhere in the upper right direction. On the other hand, if we graph bill size versus body size, the finches will line up from lower left to upper right, and at points where selection for larger bills is balanced by selection for smaller bodies, the fitness gradient will point to the upper left.

Any place on this curve where the fitness gradient is perpendicular to the tradeoff curve, if the adaptive dynamics equations are a good description of evolutionary change in this population, and the population is in fact confined to to this tradeoff curve, is an evolutionary fixed point. Whether an intermediate fixed point exists, or selection drives the population to one extreme or the other, depends as much on the shape of the curve as on the direction of the selective pressure, as represented by the fitness gradient.

One of the convenient aspects of the Lotka-Volterra equations is that the interactions

between populations are represented by single numbers (though such numbers can also be assigned in other models, I'm sure). If we put these numbers on the axes, as I did in chapter 5, plotting a_{i1} and a_{i2} for each strain i, then we are looking at, for each strain, how it is affected by strain 1 and how it is affected by strain 2, and how these two quantities are related. Often these quantities are related, since they are both determined by body size, flying speed, or other individual characters.

How these two values change with evolution, as in the above cases of more traditional phenotypic characters, is determined by the interaction between the constraint curve relating a_{i1} and a_{i2} and the direction of the fitness gradient on this graph (and, in this case, the evolutionary motion of strains 1 and 2 as well). Depending on the shape of the constraint curve, evolution may increase one of the two interaction coefficients for a given strain (making it more beneficial to that strain) and decrease the other, or it may cause all the strains to stop at some intermediate value. The constraints that determine the range of possible combinations of interaction terms can produce any number of different kinds of evolutionary outcomes.

When I decompose the selective pressure on phenotypes, though, in chapter 5, separating the selective pressure on interactions from the constraints on interactions imposed by phenotypes, that decomposition reveals that the fitness gradient operating on interactions always points upward and to the right, in the direction of reduced competition and increased cooperation. Because of constraints, interactions do not always evolve in the direction of the fitness gradient, and so competition is not always reduced and cooperation is not always increased. But as the model presented in chapter 4 shows, when a set of constraints is proposed that does not limit interactions to competitive or predatory values, antagonistic interactions can change into cooperative ones quite easily. While competition does not always change into cooperation, this is because of constraints and not because of something inherent in the selection process.

I believe this is a fairly general and even obvious point: all other things being equal,

cooperation is always more beneficial than other options. The reason cooperation is not universal is that it often comes with tradeoffs, such that increasing cooperation requires sacrificing something else. For a plant, participating in a mutualistic exchange with a pollinator requires providing nectar to feed the pollinator. If the cost of providing nectar is prohibitive, the plant will find a way to get by without a pollinator. In the prisoner's dilemma and tragedy of the commons models, choosing to cooperate means giving up a bigger payoff that one could get by defecting. This is a matter of constraints, since if it were possible to cooperate without sacrificing anything, everybody would do it, and everybody would benefit. Because of this, I believe that questions about the evolution of cooperation are not universal questions, they are questions about constraints: what makes cooperation possible within a certain set of constraints, and what kind of constraints make cooperation possible. One might even say that the central question is not how cooperation manages to arise, but in cases where it does not, what is standing in the way[1].

The model of chapter 5 is, in a way, a model that allows that upward selective pressure to operate without constraints, making all populations as generous and cooperative as possible. But of course, there is no such thing as complete freedom from constraints. The strict constraint curves or surfaces that I have been discussing are special cases of a more general condition: the direction of evolution is limited by the available variation. The projection matrix $\frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i} \frac{\partial \mathbf{s}_i}{\partial \mathbf{u}_i}^{\mathrm{T}}$ that appears in the equations for motion on a constraint surface is a special case of the more general variance-covariance matrix $\Gamma(\mathbf{s}_i)$ of the more general equation (3.4), which describes all the correlations and variances governing the distribution of mutations of the different traits. Compare the "basic model" of chapter 5 with the model for competition described in chapter 6. The only difference is in the distribution from which the mutations are chosen that are added to the a_{ij} terms, and the outcome of the models is very different. In the latter model, all interactions are competitive, and more branching is observed than in the basic model. How these models behave, and whether they result in

[1] and, where appropriate, what might be done to change the constraints.

cooperation and what kinds, as in models that use phenotypes, depends on the distribution of available variation.

When I first thought of applying mutations to the interaction matrix and coding up the model of chapter 5, I imagined I would be finding out what kind of evolutionary motion is inherent in the Lotka-Volterra model, without imposing any bias on it. I now believe that that is not possible. Evolutionary motion is always constrained and shaped by the range of variation it is given to work with. If changing the distribution of mutations produces different outcomes, which is the "natural" behavior of the ecological model? As I will discuss more below, the question of how mutations are distributed is central to the different kinds of branching as well as to cooperation.

10.2 Dilemmas and non-dilemmas

When the prisoner's dilemma is modified in the way that I do in chapter 7, the same issues about constraints and available variation come out. In the unmodified prisoner's dilemma, the issue of constraints does not seem relevant. There are only two choices, and one has to choose one. Constraints have to do with available variation, so they come into play when there is a range of different behaviors available. For instance, in some "continuous prisoner's dilemma" models (Wahl and Nowak 1999, for instance), players are allowed to choose a degree of cooperation between 0 and 1. The fundamental feature of the prisoner's dilemma is preserved, though: defection pays better than cooperation, or else it wouldn't be a dilemma. This is a constraint in the sense I have been using. Cooperation, which means behavior that benefits the other player, benefits oneself less than defection. While a whole range of behaviors is possible, it is not possible to change to a behavior that increases the benefit to both the other player and oneself. One comes at the expense of the other.

When that constraint is removed, in the model I have presented, the model players that I have presented with a dilemma find their way out of the dilemma by devising behaviors

that benefit both players more than the other options, so that nobody is "tempted to defect", that is, attracted to an option that hurts somebody else. Following the animal behavior literature, I refer to this kind of behavior as "byproduct mutualism", since each player ends up behaving generously to other players as a byproduct of selfishly seeking the largest payoff. When byproduct mutualism is an option, mechanisms such as indirect reciprocity, kin selection, group selection, punishment, communication, and the like are not necessary since the mutually optimal outcome is easily achieved without them.

Contrary to the opinions of many cooperation researchers, this easy route to cooperation can also be important in social and economic systems. In the mid-twentieth century heyday of cultural anthropology, cultural anthropologist Ruth Benedict did a comparative study of a number of different societies that she and her colleagues had studied around the world, investigating differences in how societies are organized and the different qualities they take on. Focusing on aggression, meaning behavior aimed at hurting, expelling, or humiliating another person, "from all comparative material", she concludes, "the conclusion that arises is that societies where nonaggression is conspicious have social orders in which the individual by the same act and at the same time serves his own advantage and that of the group" (Maslow and Honigman 1970).[2]

Sometimes it is possible to arrange a confluence between what people want to do and what everybody else wants them to do, and sometimes it is not.[3] The prisoner's dilemma and tragedy of the commons models represent the most difficult and intractable possibilities. It is important to understand how best to handle such situations, but it is equally crucial to recognize that there are many other ways to achieve cooperative interactions, so that we are alert to possibilities of transforming a dilemma into something more promising. Emphasizing the difficulty of achieving cooperation in prisoner's dilemma, social dilemma and tragedy of the commons situations without acknowledging the existence of other situations

[2] I am indebted to Derrick Jensen (2000) for this reference.

[3] This echoes Sewall Wright's point (1980) that group selection can be much more successful when it coincides with the effects of selection for individual advantage than when the two are in conflict.

in which cooperation is much easier can lead us to make overly pessimistic and destructive policy decisions, and cause us to overlook opportunities to construct easy forms of cooperation, as well as making it more difficult to explain the ubiquity of cooperative human behavior.

10.3 Cooperation in ecosystems

The connection between constraints and cooperation arises in the Gaia hypothesis model of chapter 9 as well. When there are two species working together to regulate the global temperature, as in figure 9.2, the actions that make this regulation possible, specifically the act of responding to any change in temperature with changes in population that counteract that change, can be called cooperation. Temptation to defect, then, would be an opportunity for mutant populations to increase their fitness by abandoning this behavior, for instance by shifting their optimal temperature to match the target temperature, which destroys their ability to respond differentially to increases and decreases in temperature. Whether this temptation exists is a question of constraints, since such changes in optimal temperature only confer a fitness advantage if they do not entail associated changes in other characters that cause a net decrease in fitness. If correlations between characters make such "defection" undesirable, we could say there is a "temptation to cooperate".

Therefore, since we have seen that some combinations of constraints can make Gaia-like global regulation possible and even reinforce it, and other combinations of constraints can undermine it, it seems that the central question is not whether evolution can produce a globally self-regulating system, but under what conditions of organismal constraints and correlations, and how the emergence of systemwide qualities proceeds from these constraints.

10.4 Continuous phenotypes and branching

When mutations are applied to the terms of the Lotka-Volterra interaction matrix in the way that they are in chapter 5, populations can diversify at any point of their evolutionary trajectory. In the adaptive dynamics field, this is not considered to be possible. If each population is a point in a finite-dimensional vector space and the invasion exponent is a smooth function of trait values, diversification can only occur at isolated branching points where the first partial derivatives of the invasion function vanish (in the limit as mutation size approaches zero).

As we saw in chapter 5, this haphazard branching happens because the mutation associated with the new diagonal term ($\Delta a_{i'i'}$) is uncoupled from the other two mutations applied to the parent's diagonal term ($\Delta a_{i'i}$ and $\Delta a_{ii'}$). When the interaction terms are derived smoothly from phenotype vectors of any dimension, the first of these is always correlated with the other two.

The strange-seeming assumption of this model, that the interacting entities involved are so complex that there are always enough degrees of freedom for all the different interactions to change independently of each other, is hardly more realistic than the common idealization of only one or two continuous-valued traits. However, it is not noticeably less realistic either. Organisms are complex, and their interactions are determined by many factors. Phenotypic traits are not continuous functions of genetic mutations (I don't even know how to make that a meaningful concept), and interactions are (often) not continuous functions of phenotypes. The different models are simply different oversimplifications of reality, which yield different predictions about emergent pattern, and the differences between the two classes of models present an opportunity to clarify our understanding of both, and of how the world resembles and differs from each.

The branching process that appears here is qualitatively different from the evolutionary branching found in continuous-phenotypic adaptive dynamics models. As chapters 6

and 7 show, this new kind of branching can be observed in a range of different models, including, in the game theory chapter, a very different ecological model from the others. Since I see no reason to assume that the biological world is more faithful to simple adaptive dynamics models than to these models, I think this other kind of branching may be a useful description of some biological diversification processes. It may even be possible to find this other kind of branching in simulations of standard adaptive dynamics models, in regions of phenotype space where the first derivatives of the invasion function nearly vanish, so that second derivatives become significant and can put those three Δa values out of order. When mutations are not infinitely small, which is realistic, this seems possible, and if it does happen, even if the branchings are short-lived, they may play an important role in the longer-term dynamics, as they appear to do in the motion of the red lines in chapter 5.

10.5 The learning model

In chapter 9 I discuss Dawkins's evolutionary objection to the Gaia hypothesis: how can there be cooperation on a planetary scale, when there is no selection between planets to overpower the temptation to cheat and not cooperate? Dawkins's logic is based on making an analogy between cooperation among species on the planet and cooperation among cells in an organism. It asserts that cooperation is always accompanied by a temptation to defect, and that cooperation can only be achieved by Darwinian evolution on a level that subordinates the interests of the parts to the interests of the whole. (Curiously, this claim appears to contradict Dawkins's more famous position, that all selection reduces to the level of individual genes.)

The response to Dawkins's question that I have proposed does not validate these assumptions. Beginning from the assumption that whether a particular pattern of living comprises "cooperation" or not may have little or nothing to do with whether it is favored by

selection, I theorize that the pattern of evolutionary catastrophes encountered by the planetary ecosystem can comprise a sort of search process that will settle on a system in which cooperation is favored by natural selection on the individual level, and not undermined by it.

Identifying this process as closely related to Ashby's model for animal learning, I propose that to investigate further how this process might work, one of the best places to look is at what else Ashby and others have written about processes of learning in machines, animals, humans, and organizations. I see this possibility as validating my proposal, in the introduction to this document, to abandon the reductionist hierarchy of systems of knowledge, and particularly to partially reverse the flow of information between the natural sciences and other disciplines, such as the behavioral sciences.

The process of selecting between different complex feedback patterns to find an arrangement that is stable against being undermined by incentives to defect may happen differently on different levels of organization where such a conflict can exist. On the organismic level, the same function can be fulfilled by selection, apparently; while selfish genes do exist and in some cases are controlled by cellular policing mechanisms, other types of selfish genes tend to kill the whole organism and so are defeated by selection on the whole-organism level, which trumps gene selection in this case. The role of weeding out unstable arrangements is occupied by natural selection on the organismic level, and, in my proposal, by this process of ecological learning by trial and error, instead of selection, on the planetary level.

Ecological learning by trial and error may occur on other levels than the planetary, for instance in smaller ecosystems that need to stabilize their environments—the ocean, for example, or isolated watersheds. The same process may also operate in some systems where selection also operates. For instance, on the organismic level, while selection weeds out gene combinations that make the organism inviable, other combinations may cause trouble that can be repaired by a series of adjustments in the developmental process, restoring the

organism's ability to regulate itself and parts of its environment, though in different ways than employed by its parents.

10.6 When is a simple model too simple?

I have made some abortive attempts to construct a new version of the temperature control model where species can change smoothly from living on one resource to another. It is simple enough to write equations in which one strain can consume purely resource 1 and a nearby mutant strain can have all the same parameters except that it requires 95% resource 1 and 5% resource 2, and so forth. Unfortunately, all these strains turn out to be evolutionary neutral. This linear tradeoff between one resource and the other is *too* linear.

The plankton model of chapter 8 has the same problem. Since any combination of species brings the seawater to the same equilibrium, and any number of them can coexist at that equilibrium, any mutant strain that might be introduced will also be at equilibrium, and so the mutation-"selection" process will simply produce large numbers of mutant strains with very small populations, neutrally coexisting. The model needs to be made more complicated before it can be reasonably combined with an evolutionary process.

In the temperature control model, changing the linear tradeoff curve between the requirement for one resource and the requirement for the other to a nonlinear curve gets rid of the degeneracy and produces somewhat reasonable-looking evolutionary motion. A curve that bends one way produces motion toward a superspecies right in the middle that consumes as many resources as it is allowed to, while a curve that bends the other way produces bistability such that nothing but specialization on a single resource is viable. Take your pick: what you put in is what you get out.

Others have had this problem. What the system does depends on the choice of constraint curve, and there is little reason to choose one over another, unless one is studying a particular biological system. For this reason, many adaptive dynamics papers simply make

an arbitrary choice, and then end with a claim that a particular kind of evolutionary motion may be possible.

Sometimes mathematically degenerate situations are not so easy to get rid of. For instance, in the model of chapter 4 that ends up at a point where the interaction matrix becomes singular, measures such as adding a uniform amount of density dependence to all the interactions do no good. The model seems to be determined to become degenerate, and if the population dynamics do not explode, it becomes evolutionarily neutral anyway. To make it behave, it seems to be necessary to make it nonlinear in a deeper way.

With the space limitation model described in chapter 6, I have no idea how to change the model to one that does not become degenerate when positive rows appear. I am sure it is possible, but I suspect it requires a significant nonlinearity, like in chapter 4.

Of course, the standard Lotka-Volterra model has as many problems as these strange members of its family. Mutualism makes it explode. This is the problem that the space limitation model is only partially successful in circumventing. To study differences between competition, predation and mutualism, we need reliable models, and it is not clear what to use. Perhaps there is no model that is both flexible enough and as simple as the Lotka-Volterra one, and we will just have to study more specific cases.

10.7 Other questions about models

In my introduction, I called on ecologists to look beyond the boundaries of biological ecosystems and ask more encompassing questions about process, interaction and transformation. Of course, many ecologists are committed to working on specific questions of great importance to particular biological communities, and have no use for such proposals. Rather than talking about the role of ecologists, I may just be trying to revive the ideas of cybernetics and general systems theory of the postwar 20th century. These intellectual movements had multiple branches, and many of them ended up subsumed into military

planning, engineering, artificial intelligence research and the development of computers and the internet. However, they also had a more contemplative side, and many of the approaches I have advocated, such as to study patterns of interaction and relationships that are common to multiple kinds of material systems, are essentially theirs. The influence of these researchers, such as von Bertalanffy, Bateson, and Ashby, though the cybernetics and general system theory movements are no longer visible under those names, has only spread through a great range of different disciplines and been incorporated into accepted theories and techniques.

In this light, many ecologists also work as system theorists some of the time, and many people doing system theories may in fact be a sort of variant kind of ecologists, including many who do not study biology. Perhaps rather than asking ecologists to become system theorists, I am hoping for people who are system theorists to identify with that tradition and bring it back to life.

Some of the approaches championed by system theorists seem to be immanent in the process of modeling and how our minds work. We have a consistent desire to abstract our models and try to generalize them to a wider range of systems; when a model of some aspect of population dynamics suggests a general pattern our minds immediately try to apply the pattern to other realms of life. This tendency has possibly always been there, and the people who made a program out of it in the last century were part of a long tradition of holistic theorizing.

Making analogies and metaphors is a complex process, and in the introduction I included a few critiques of current approaches to the construction of general models. Some of the models I have presented fit with these critiques in certain ways. The entire project of modeling coevolution, that is, how populations' evolution is guided by their interactions with other populations, as an alternative to the older tradition that holds fitness fixed and looks at how evolution finds fitness peaks, is a way of "viewing embeddedness as primary"

and “allowing the system’s dynamics to be mutable”. Making the system’s dynamics mutable and giving up the presumption that the nature of individuals’ interactions is given at the outset is the point of the game theory model of chapter 7, which demonstrates how these interventions can undermine the conclusions of prisoner’s dilemma models.

These approaches, plus shifting the emphasis from “atomized individuals” to the networks that connect them, are the difference between the ecological models of chapters 5 and 6 and the body of otherwise similar modeling projects. Those changes in approach are the source of the different outcomes of the altered models, both the different process of branching and the pattern of weakening of competition and strengthening of cooperation, which exposes the connection between constraints and the evolution of cooperation.

Of the various sites of intervention identified by Taylor, Deleuze and Guattari and others, I have only engaged with a selected few. For instance, I have not taken on the assumption of “systemness”, that is, the assumption that the relationships and processes within “the system” can be considered in isolation from all the other processes that intersect “the system”. In this case I have made the standard modeling assumption that models that ignore such intersections can isolate particular patterns and understanding what happens when more processes are active is helped by understanding models of the processes in isolation from each other. “Examining diverse intersecting processes”, we hope, is at least partially facilitated by having simpler models to combine together.

Another issue I have not engaged with is the adaptive dynamics assumption of clonal reproduction, which is an abandonment of sociality and embeddedness if there ever was one. This choice makes phylogenetic trees primary and declines to engage with the questions raised by lateral gene transfer of what evolution looks like when ones genetic makeup comes from many sources including multiple species. To the extent that Lotka-Volterra models are models for many systems, including biological, economic and cultural ecologies, my models comment on all those systems as well; but if lineages do not work the way I model them, the model could be wildly inaccurate. This problem may be acute in

modeling cultural ecologies as well as biological ones.

I also have not addressed the problem of whether individuals are selfish actors. All of these models of byproduct mutualism essentially make the point that "altruism" often does not need to be explained, because cooperation can be compatible with self-interest. They do not help anyone who wishes to talk about why people do often behave altruistically and challenge the assumptions of individualism and self-interest that appear to make this a paradox. Even the assumption that preferences and utility can be located on a well-ordered numerical scale, which is fundamental to game theory, is not questioned, let alone the idea that behavior is predicted by payoffs.

These are difficult modeling questions. What kind of mathematical model would one use to look for the patterns of evolution where gene exchange is continual and voluminous? This requires a number of assumptions about how genes interact and the networks of gene transfer. It seems like a project that cannot help but be very complex. The other problem, of addressing how communities of people behave when people's choices are not determined by individual preference functions but by socially embedded processes, seems even more daunting. Mathematics may simply be the wrong way to describe such things. I have stayed within the framework of economic self-interest, not because I have an interest in promoting these assumptions, but because the available techniques of applying mathematics to these questions seem to require it.

I am sure there are probably ways around this conflict; mathematics can do more things than it is currently used for. It is worth asking, though, whether the strengths and weaknesses of mathematics itself force us into problematic philosophical limitations. For instance, whether it is an inherent requirement of mathematics or a convention of usage that can be abandoned, it is currently much easier to model things by a finite combination of numbers than by a continuum (it goes almost without saying that it is easier to study things that can be represented by real numbers than by elements of other spaces). This is why we have been looking at populations as points in finite-dimensional vector aspect spaces,

which is the source of the model for evolutionary branching that I have shown to be incomplete.

Did the historical rise of Protestantism and capitalism in Europe lead to models of economics based on individuals maximizing their economic utility, obscuring the traditions of common property, social conventions and face-to-face economic relationships that were being overturned at that moment in history? Or did the conceptual power of such ways of thinking accelerate the spread of these new social forms? The causation may go both ways. Is is possible that the use of mathematics itself may be a hindrance to forms of engaged epistemology that we need to turn toward? Are mathematical models an appropriate tool for studying human cooperation? I'm sure they are, and will continue to be, when done well, but I think it is worth asking the question. If our analytical tools make us see people as selfish machines, and nature as a dead repository of resources, and that line of thinking channels us into social forms that make people into selfish machines and wilderness into a wasteland, we may be advised to look for other ways to make progress.

These questions are easier to ask than to answer. Perhaps someday we will have answers to some of them. I hope we will agree to ask them. We are all responsible for looking clearly at the consequences of the choices we make. But it is not a question of sacrificing scientific progress to good citizenship. Openly questioning all aspects of our work is the only way to approach the full possibilities of the work. If we have the courage to take on the hard questions, we will all benefit.

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