

Chapter 1

Introduction and Conceptual Framework

Ecology and evolution¹ are so closely intertwined as to be inseparable. This reality is obvious on long timescales given that different species are clearly adapted to different environments and have different effects on those environments (Darwin 1859). Yet, traditionally, evolutionary and ecological processes have been thought to play out on such different time scales that evolution could be safely ignored when considering contemporary ecological dynamics (Slobodkin 1961). However, the past few decades have seen a shift away from this “evolution as stage—ecology as play” perspective toward the realization that substantial evolutionary change can occur on very short time scales, such as only a few generations (reviews: Hendry and Kinnison 1999, Reznick and Ghalambor 2001, Carroll et al. 2007). If contemporary evolution can be this rapid, and if the traits of organisms² influence their environment, it follows that evolution will need to be considered in the context of contemporary ecological dynamics. This point is not a new one (e.g., Chitty 1952, Levins 1968, Pimentel 1968, Antonovics 1976, Krebs 1978, Thompson 1998) but the growing realization of its importance is crystalizing into a new synthesis that seeks to integrate ecology and evolution into a single dynamic framework (Fussmann et al. 2007, Kinnison and Hairston Jr. 2007, Haloin and Strauss 2008, Hughes et al. 2008, Pelletier et al. 2009, Post and Palkovacs 2009, Schoener 2011, Genung et al. 2011, Matthews et al. 2011b, 2014, Strauss 2014, Duckworth and Aguillon 2015).

According to Web of Science and Google Scholar, the earliest use of the term “eco-evolutionary” was Kruckeberg (1969) and the first use of the term “eco-evolutionary dynamics” was Oloriz et al. (1991); yet modern usage really began with a 2007 special issue of *Functional Ecology* (Fussmann et al. 2007, Carroll et al. 2007, Kinnison and Hairston Jr. 2007). To illustrate, Web of Science tallies 18 articles that used “eco-evolutionary” in the title, abstract, or keywords prior to 2007 and 445 articles since that time (as of Apr. 8, 2016). Consistent with that modern usage, I here define eco-evolutionary dynamics as *interactions between ecology and evolution that play out on contemporary time scales*, with

¹The Merriam-Webster definition will suffice for “ecology” (relations between a group of living things and their environment) whereas I offer my own definition for “evolution” (changes in the genetic composition—usually allele frequencies at particular places in the DNA sequence—of a population).

²When I refer to an “organism,” I mean the collection of individuals that make up a population or species, not a single “individual” within that population or species.

“contemporary” intended to encompass time scales on the order of years to centuries (or one to hundreds of generations). These interactions can work in either direction. In one, ecological changes lead to contemporary evolution (eco-to-evo), such as the ongoing adaptation of populations to changing environments. In the other direction, contemporary evolution can lead to ecological changes (evo-to-eco), such as when trait change in a focal species alters its population dynamics, influences the structure of its community, or alters processes in its ecosystem. Moreover, these interactions can feedback to influence one another: that is, ecological change can cause evolutionary change that then alters ecological change (Haloin and Strauss 2008, Strauss et al. 2008, Post and Palkovacs 2009, Genung et al. 2011, Strauss 2014). In this first chapter, I provide an overall conceptual framework for studying eco-evolutionary dynamics, and I explain how the rest of the book fits into that framework.

The style of this first chapter differs from those that follow. In this first chapter, I provide a very simple and general introduction that builds a framework on which to hang the more detailed deliberations that will follow later. I have therefore here written with a minimum of jargon, citations, and footnotes; and I have provided boxes that outline simple and clear examples. This writing style is intended to provide a stand-alone introduction accessible to all evolutionary biologists and ecologists, as opposed to only those already well versed in the topic. Rest assured, the subsequent chapters will be awash in enough jargon, citations, footnotes, and details to be of interest even to specialists.

Key elements of the book: phenotypes of real organisms in nature

When studying eco-evolutionary dynamics, one might focus on genotypes or phenotypes. My focus will be squarely on the latter: for two key reasons. First, selection acts directly on phenotypes rather than on genotypes. Genotypes are affected by selection only indirectly through their association with phenotypes that influence fitness. Understanding the role of ecology in shaping evolution therefore requires a phenotypic perspective. Second, the ecological effects of organisms are driven by their phenotypes rather than by their genotypes. Genotypes will have ecological effects only indirectly through their influence on phenotypes that have ecological effects. In some cases, eco-evolutionary dynamics might be similar at the genetic and phenotypic levels, most obviously so when a key functional trait is mainly determined by a single gene. However, this situation will be rare because most traits are polygenic and are also influenced by environmental (plastic) effects, topics considered at depth in later chapters. These two properties muddy (in interesting ways) the genotype-phenotype map and dictate that studies of eco-evolutionary dynamics should have, as their focus, organismal phenotypes. This focus does not mean that genotypes should be ignored and, indeed, genotypes are explicitly considered at many junctures in this book—but the central focus must be on phenotypes.³

³Here are some definitions of related terms as they will apply throughout the book. “Phenotypes” are physical characteristics, whether physiology, morphology, behavior, or life history, expressed by organisms in ways that can interact with the environment. “Traits” are phenotypes that can be defined and studied at least partly independently of other such traits, such as metabolic rate, body size, aggression, or fecundity. (Of course, such traits will often be correlated with each other.) Adaptive traits are traits whose particular values (e.g., larger or smaller) influence the fitness (survival and reproduction—more about this later) of organisms. Such traits are often called functional traits in the plant literature.

Eco-evolutionary dynamics can be studied in theory or in real organisms. Theoretical studies, such as those employing analytical (symbolic) math or computer simulations, are critical for helping to delineate the various possibilities that arise from an explicit set of assumptions. Theory also can help to formalize conceptual frameworks, develop analytical tools, and evaluate predictive structures for the study of real organisms. For these reasons, theory will make frequent appearances in the book, typically as a means of setting up expectations and for helping to interpret the results of empirical studies. In the end, however, theory is only a guide to the possible—it can't tell us what actually happens; and so an understanding of eco-evolutionary dynamics requires the study of real organisms.

Eco-evolutionary studies with real organisms could proceed in the laboratory or in nature. Advantages of the laboratory are manifold: populations can be genetically manipulated, environments can be carefully controlled, replicates and controls can be numerous, and small organisms with very short generation times (e.g., microbes) allow the long-term tracking of dynamics (Bell 2008, Kassen 2014). These properties dictate that eco-evolutionary studies in the laboratory are elegant and informative, yet only in a limited sense. That is, such studies tell us what happens when we impose a particular artificial environment on a particular artificial population and, hence, they cannot tell us what will actually happen for real populations in nature. Understanding eco-evolutionary dynamics as they play out in the natural world instead requires the study of natural populations in natural environments. I will therefore focus to the extent possible on natural contexts, although I certainly refer to laboratory studies when necessary.

The study of real populations in real environments is usually considered to be compromised in several respects. For instance, such studies have difficulty isolating a particular ecological or evolutionary effect because it might be confounded, or obscured, by all sorts of other effects that exist in the messy natural world. To me, this suggested weakness is actually a major strength because we obviously want to know the importance of a particular effect within the context of all other effects that also might be important. By contrast, it seems of limited value to isolate and evaluate a particular effect in a controlled situation if that effect is largely irrelevant in natural contexts. Moreover, elucidating causal effects and their interactions is possible even in nature through experimental manipulations (Reznick and Ghalambor 2005). However, the limitations of studying real populations and real environments are certainly real and important: replication and controls are harder to implement, experimental manipulations are less precise, and ethical and logistical concerns prevent some experiments. Yet such studies ultimately will be the key to developing a robust understanding of eco-evolutionary dynamics.

Conceptual framework and book outline

My primary goal in this first chapter is to provide a conceptual framework for eco-evolutionary dynamics. The framework will be presented in three parts. The first part (*eco-to-evo*) outlines how ecological change influences evolutionary change, and thereby amounts to a review and recasting of the classic field of evolutionary ecology. The second part (*evo-to-eco*) outlines how evolutionary change influences ecological change, and thereby amounts to the set of effects that have crystallized and driven the emergence of eco-evolutionary dynamics as a term and as a research field. The third part (*underpinnings*) considers the genetic and plastic basis of eco-evolutionary dynamics,

which can apply with equal relevance to our understanding of both preceding parts. Within each of these parts, important components of the framework will be presented sequentially and their correspondence to the various chapters will be explained. In the current presentation, I will only rarely refer to specific empirical results because those results will be discussed in detail in the chapters that follow. Rather, I will provide a series of linked examples drawn from a single empirical system: Darwin's finches on Galápagos (Grant 1999, Grant and Grant 2008). This choice of system doesn't imply that Darwin's finches provide the best illustration of every concept, but rather that they are suitable for explaining how different components of the conceptual framework fit together for a single well-known study system.

PART 1: ECO-TO-EVO

The eco-to-evo side of an eco-evolutionary framework obviously starts with ecology. By "ecology" in this context, I mean any combination of biotic or abiotic features of the environment that can impose selection on the phenotypes of some focal organism. In the context of a single population, I will generally refer to ecological *change*. In the context of multiple populations, I will generally refer to ecological *differences*. Either term might be used when generalizing to both contexts.

A single population in a stable environment should be characterized by phenotypes that are reasonably well adapted for that environment. Stated another way, the distribution of phenotypes in a population should correspond reasonably well to the phenotypes that provide high fitness (survival and reproductive success): that is, the distribution of phenotypes should be close to a fitness peak on the "adaptive landscape" (fig. 1.1). In this scenario, an obvious eco-to-evo driver is ecological change that shifts the fitness peak away from the phenotypic distribution. (A similar effect arises if the phenotypes shift away from the peak, such as through gene flow—see below.) This shift imposes selection on the population by increasing fitness variation among individuals with different phenotypes (Endler 1986, Bell 2008). If the phenotypic variation is heritable (passed on from parents to offspring), the next generation should see a phenotypic shift in the direction favored by selection: that is, toward the fitness peak. Under the right conditions, the phenotypic distribution should eventually approach the new peak and directional selection should disappear. In reality, peaks will be constantly shifting and populations might have difficulty adapting owing to genetic or other constraints as will be considered in detail later. Box 1 provides an illustrative example of directional selection and adaptation in Darwin's finches.

Selection is thus the engine that drives eco-evolutionary dynamics, and so the more detailed chapters of the book must begin there. Chapter 2 (Selection) starts with a description of how the mechanism works and how it is studied in natural populations. It then draws on recent meta-analyses to answer fundamental questions about selection in nature, such as how strong and consistent it is, how often it is stabilizing (disfavoring extreme individuals) or disruptive (favoring extreme individuals), what types of traits (e.g., life history or morphology) are under the strongest selection, and how selection differs when fitness is indexed as mating success (sexual selection) or survival/fecundity (natural selection).

The expected outcome of selection is adaptive phenotypic change (fig. 1.1), which should then shape eco-evolutionary dynamics. Chapter 3 (Adaptation) first outlines how to conceptualize and predict adaptive evolution based on information about selection

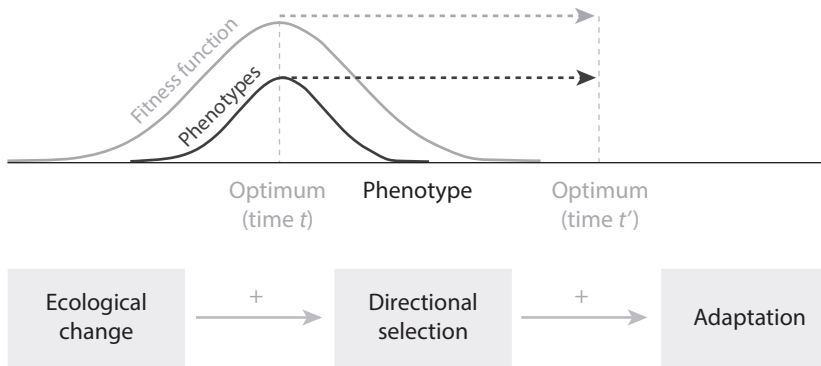
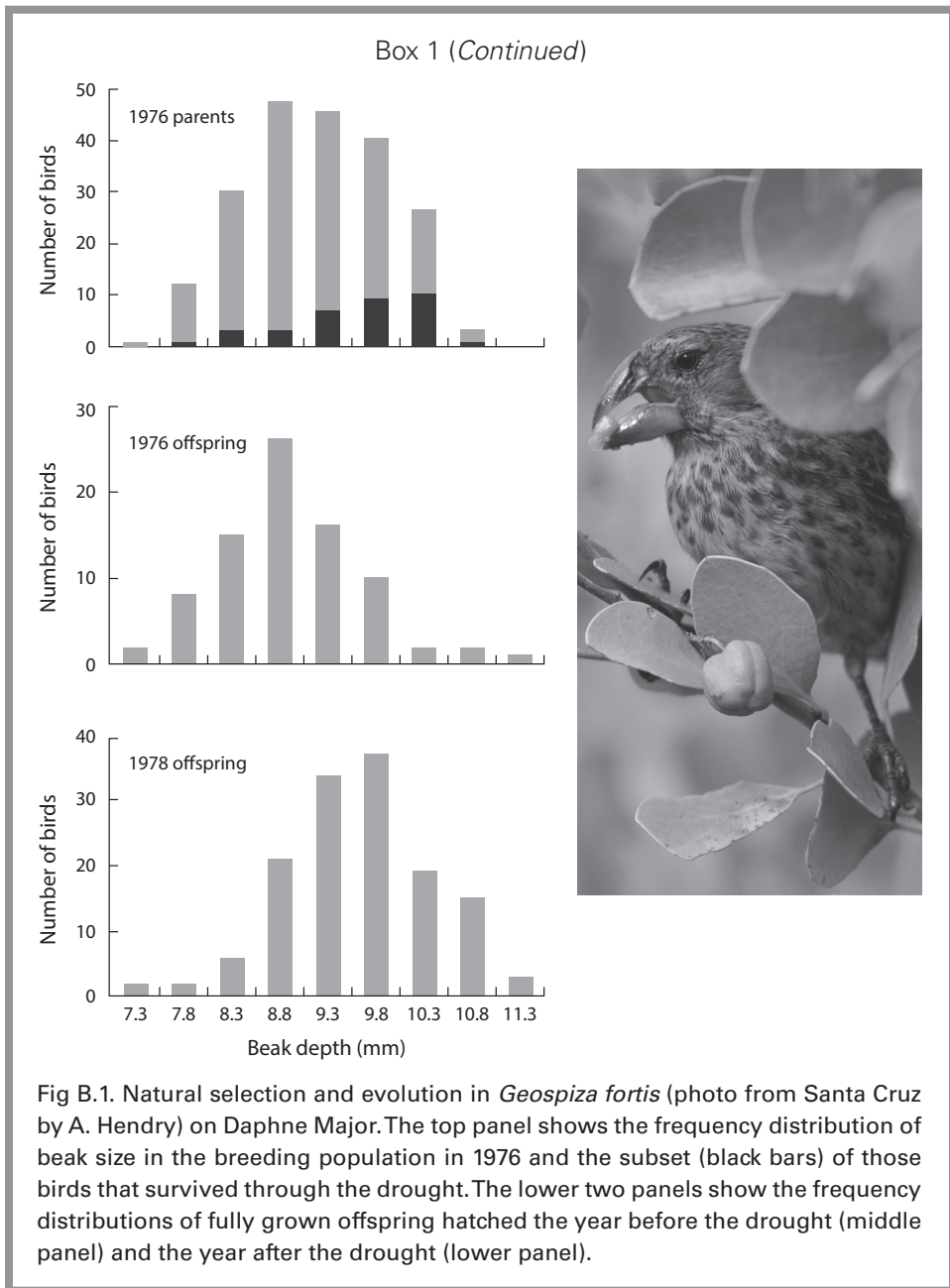


Fig 1.1. Graphical representation of ecological change, directional selection, and adaptation in a single population. Before ecological change (time t), the frequency distribution of phenotypes (lower curve) in a well-adapted population is centered near the phenotypic value that maximizes fitness (optimum). This optimum corresponds to the peak of the “fitness function” (upper curve) that relates phenotypes (x -axis) to fitness (y -axis). Ecological change occurring to time t' (upper dashed line) shifts the optimum phenotype to a new location, which imposes directional selection on the population, which should evolve toward the new optimum (lower dashed line). In reality, the fitness function is likely much wider than the phenotypic distribution. Also, this depiction assumes no constraints on evolution

Box 1

An example of natural selection and adaptation in Darwin’s finches on the small Galápagos island of Daphne Major (Boag and Grant 1981, Grant and Grant 1995, 2003). Conditions during 1976–1977 caused a drought that prevented reproduction by most plants. During this period, the resident population of medium ground finches (*Geospiza fortis*) rapidly depleted available seeds from the environment and many individuals starved to death, resulting in a population size decrease of about 85%. The depletion of seeds was nonrandom because all the finches can consume small/soft seeds whereas only finches with large beaks can consume large/hard seeds. As the drought progressed, the seed distribution therefore became increasingly biased toward larger/harder seeds, and the mortality of *G. fortis* became size-selective. Birds with larger beaks were more likely to survive, resulting in directional selection for larger beaks. When the rains commenced in 1978, the finches that had survived to breed were those whose beaks were larger (on average) than the population before the drought. Beak size is highly heritable (large-beaked parents produce large-beaked offspring) and, hence, the generation of birds produced after the drought had larger beak sizes than the generation of birds produced before the drought. Ecological change caused directional selection that led to adaptive evolution.

(Continued)



and genetic variation. It then introduces and explains adaptive landscapes (x -axis = mean phenotype; y -axis = mean population fitness), a concept that has proven useful in guiding our understanding of evolution. Finally, it reviews empirical data to answer fundamental questions about adaptation in nature, including to what extent short- and long-term evolution is predictable, how fast is phenotypic change, to what extent is adaptation constrained by genetic variation, and how well adapted natural populations are to their local environments.

Moving beyond selection and adaptation *within* populations, eco-evolutionary dynamics will be shaped by biological *diversity*: that is, different populations and species have different effects on their environment. This diversity arises when a single population splits into multiple populations that begin to evolve independently and could ultimately become separate species, which are then the roots of even the most highly divergent evolutionary lineages. Stated plainly, biological diversity at all levels has its initial origins in population divergence. Thus, the next step in developing a conceptual framework for eco-evolutionary dynamics is to expand our discussion from the evolution of single populations into the realm of population divergence.

The stage for population divergence is set when different groups of individuals from a common ancestral population start to experience different environments. These environmental differences could result from any number of factors, such as different abiotic conditions (temperature, pH, moisture, oxygen), different predators or parasites, different competitors, or different resources. Faced with this heterogeneity, selection will favor different phenotypes in the different groups, leading to *divergent (or disruptive) selection*. If the traits under selection are heritable, the expected outcome is adaptive divergence among the groups (now populations) that improves the fitness of each in its local environment (fig. 1.2) (Schluter 2000a). Box 2 provides an illustrative example from Darwin's finches.

Chapter 4 (Adaptive Divergence) focuses squarely on this process. It starts by explaining how the adaptive landscape concept can be extended from a single population in a single environment to multiple populations in multiple environments. Specifically, different environments produce different fitness peaks and divergent selection then drives different populations toward those different peaks (fig. 1.2). The chapter then outlines methods for inferring adaptive divergence with respect to both phenotypes (x -axis of the

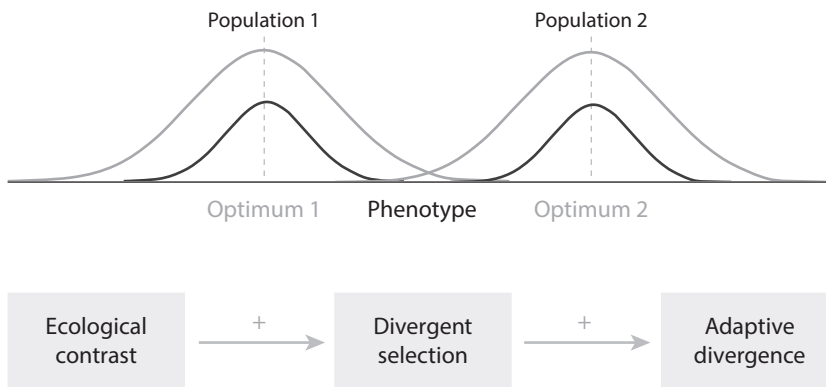


Fig 1.2. Graphical representation of an ecological contrast experienced by two populations in different environments, the divergent selection that this contrast imposes, and the adaptive divergence that is expected to result. Divergent selection occurs because the two environments have fitness functions (upper curves) with different optima. Adaptive divergence generates phenotypic differences (lower curves), such that each population becomes at least reasonably well adapted to its local optimum. As in figure 1.1, this depiction assumes no constraints on adaptive evolution

Box 2

The previous box described how one population of finches adapted to the seed resources that were locally available. Across populations, we would therefore expect average beak size to be correlated with the average size/hardness of available seeds. That is, adaptive divergence should take place as a result of differences in seed size/hardness distributions. To test this expectation, Schluter and Grant (1984) quantified the seed distributions on 15 Galápagos islands. They used these distributions to predict the mean beak sizes that would be expected for three seed-eating species: the small ground finch (*Geospiza fuliginosa*), the medium ground finch (*Geospiza fortis*), and the large ground finch (*Geospiza magnirostris*). These predictions (of what amount to adaptive landscapes) were then compared to observed beak sizes for the same species. Results for three of the islands are shown below and more complete results are provided in chapter 4. In many (although not all) cases, observed beak sizes closely matched predicted beak sizes. Adaptive divergence occurred in response to ecological differences.

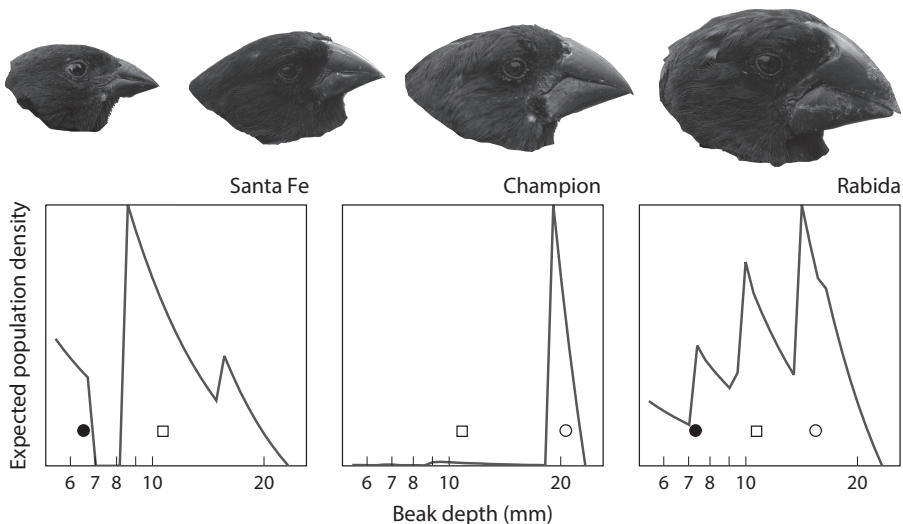


Fig B.2. Adaptive divergence. Beak size varies dramatically among populations and species of Darwin's finches in a manner that matches local food resources. The pictures at top show *Geospiza fuliginosa* (left), *Geospiza magnirostris* (right), and *Geospiza fortis* morphs with either small (center-left) or large (center-right) beak sizes (photos by A. Hendry). The figures at bottom show that mean beak sizes of the species present on each island (filled circle is *G. fuliginosa*, open box is *G. fortis*, and open circle is *G. magnirostris*) typically match the beak sizes expected based on the available seed types. Those expectations are shown as peaks depicting the expected density of finches of a given beak size. The data are from Schluter and Grant (1984), wherein further details are provided

adaptive landscape) and fitness (y -axis). The chapter then turns to a review of empirical data informing several key questions about adaptive divergence in nature, including how prevalent and strong it is, how many peaks adaptive landscapes have (ruggedness), how many of the peaks are or are not occupied by existing populations (empty niches), how predictable it is (parallel and convergent evolution), and what is the role of sexual selection in modifying adaptive divergence.

The above description might give the impression of populations inevitably evolving the phenotypes best suited for their local environments. The reality, however, is that many factors can constrain adaptation well short of optimality. Some of those factors are considered in chapter 4, but I here wish to draw special attention to the role of dispersal, which can take place for individuals, gametes, or propagules (eggs, seeds, or spores). If the dispersers successfully reproduce, the resulting genetic exchange (gene flow) can disallow independent evolution of the recipient populations. When this gene flow is high and occurs among populations in different environments, adaptive divergence can be strongly hampered (Lenormand 2002, Garant et al. 2007). The expected outcome is a balance between divergent selection pushing populations apart and gene flow pulling them together, such that adaptive divergence will occur but not to the degree expected in the absence of gene flow (fig. 1.3). Box 3 provides an example of how gene flow hampers adaptive divergence in Darwin's finches.

Chapter 5 (Gene Flow) starts by outlining empirical methods for quantifying gene flow and inferring its role in adaptive divergence. An important point made therein

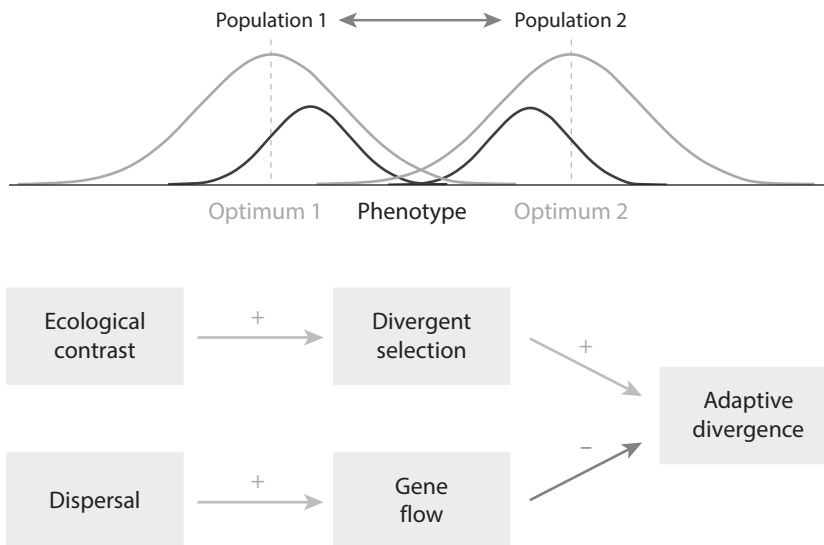


Fig 1.3. Graphical representation of how gene flow can constrain adaptive divergence. Dispersal between the populations (double-headed arrow) is expected to cause gene flow that prevents their independent evolution, and thus reduces adaptive divergence. The outcome is a balance between selection and gene flow: the populations show adaptive divergence (lower curves) but not as much as would be expected in the absence of gene flow (compare to fig. 1.2)

Box 3

As described in the previous box, multiple Darwin's finch species are present on many islands, and divergent selection has caused differences in their beak size: that is, they manifest adaptive divergence. A number of these species are very closely related and remain reproductively compatible, such that hybridization and introgression are not uncommon (Grant et al. 2005). Work on Daphne Major shows how this gene flow can reduce adaptive divergence between species. Starting in the 1990s, *G. fortis* showed increasing hybridization with *Geospiza scandens*, its pointier-beaked congener that mainly feeds on the pollen, nectar, and seeds of *Opuntia* cactus. The result was increasing introgression of *G. fortis* genes into *G. scandens*, which decreased differences between the species in both neutral genetic markers and adaptive phenotypic traits (Grant et al. 2004). Strikingly, the beaks of *G. scandens* became less pointed, thus starting to converge on the blunter beak shape of *G. fortis*. Increased gene flow reduced adaptive divergence.

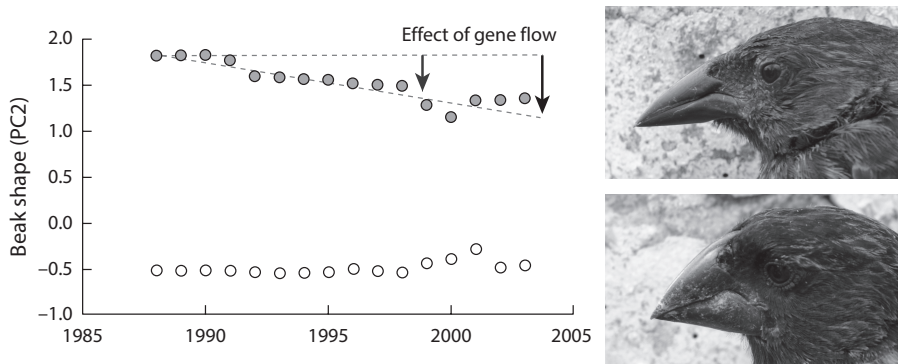


Fig B.3. Gene flow influences the beak shape of *Geospiza scandens* (top picture and dark circles in the figure) and *Geospiza fortis* (bottom picture and light circles in the figure) on Daphne Minor. The data are from Grant et al. (2004) and the photos from Santa Cruz are by A. Hendry and J. Podos. Gene flow is greater, and therefore its effects stronger, into *G. scandens* than into *G. fortis*

is that gene flow can sometimes *aid* adaptation, such as when it enhances the genetic variation on which selection acts. The key questions addressed with empirical data are therefore divided into the potential negative versus positive effects. On the negative side, questions include to what extent gene flow constrains adaptive divergence among environments, and how the resulting maladaptation might cause population declines and limit species' ranges. On the positive side, questions include whether gene flow has a special benefit in the case of antagonistic coevolution, and whether it can save (rescue) populations that would otherwise go extinct. Some of these questions begin to invoke evolutionary effects on demography, and thus grade into the evo-to-eco side of the story that we will take up later.

I earlier argued that divergent selection causing adaptive divergence is at the roots of evolving biological diversity, yet I have now just argued that gene flow hinders adaptive

divergence and should thereby constrain that evolution. The exuberant diversity of life makes clear that this potential impasse is often broken—but how? One obvious solution is the presence of physical barriers (mountains, rivers, oceans, deserts) that eliminate dispersal among populations, but the more interesting situation occurs when dispersal remains possible. A likely solution in this case is *ecological speciation*, whereby adaptive divergence causes the evolution of reproductive barriers that reduce gene flow (Schluter 2000a, Nosil 2012). This process starts because populations can begin to adapt to different environments even in the presence of some gene flow (fig. 1.3). This initial divergence will increase the fitness of residents relative to dispersers, which will reduce gene flow. This reduction in gene flow allows further adaptive divergence, which further reduces gene flow, which allows further adaptive divergence—and so on until adaptive divergence is high and gene flow is low (fig. 1.4). Under the right conditions, the populations can become so divergent and reproductively isolated as to be considered separate species. Box 4 provides an example from Darwin’s finches as to how this scenario might play out.

Chapter 6 (Ecological Speciation) starts by discussing how populations in different environments can fall at different stages along a continuum of progress toward ecological speciation. It then outlines how this variation can be used to infer ecological speciation through either of two general approaches: (1) integrated signatures of reproductive isolation based on measures of gene flow, and (2) confirmation of the ecological basis of reproductive barriers. The first two questions about ecological speciation in nature are

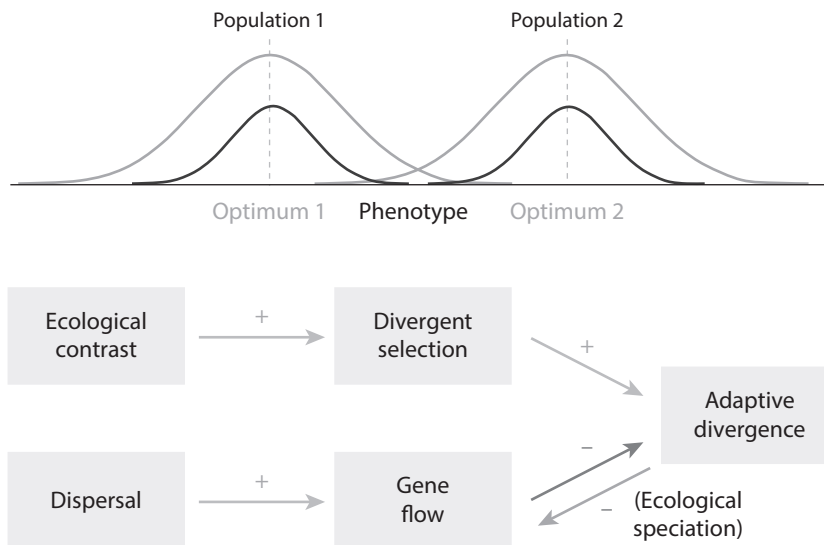


Fig 1.4. Graphical representation of how ecological speciation is expected to modify the balance between selection and gene flow that was previously illustrated in figure 1.3. Increasing adaptive divergence is expected to promote the evolution of reproductive barriers that reduce gene flow. This reduction in gene flow should allow increased adaptive divergence, potentially generating a positive feedback loop through which gene flow decreases to the very low levels characteristic of separate species

Box 4

As described in Box 2, adaptation to different seed distributions causes beak size divergence among populations and species of Darwin's finches. This divergence contributes to several reproductive barriers that influence ecological speciation. First, divergence in beak size (and bite force) causes divergence of the songs that males sing (Podos 2001, Herrel et al. 2009). Given that songs and beaks influence breeding behavior in Darwin's finches (Grant 1999, Grant and Grant 2008), populations diverging in beak size can begin to show positive assortative mating. Second, hybrids will show reduced survival if their intermediate beak sizes fall into valleys between the fitness peaks to which their parents were adapted (Grant and Grant 1993, 1996). To test these expectations, it helps to study populations in the early stages of speciation, such as *G. fortis* that are bimodal for beak size (Hendry et al. 2006). Studies of one such population confirmed the above expectations: large and small beak size morphs of *G. fortis* have different diets (De León et al. 2011), sing different songs (Huber and Podos 2006), respond most strongly to the songs

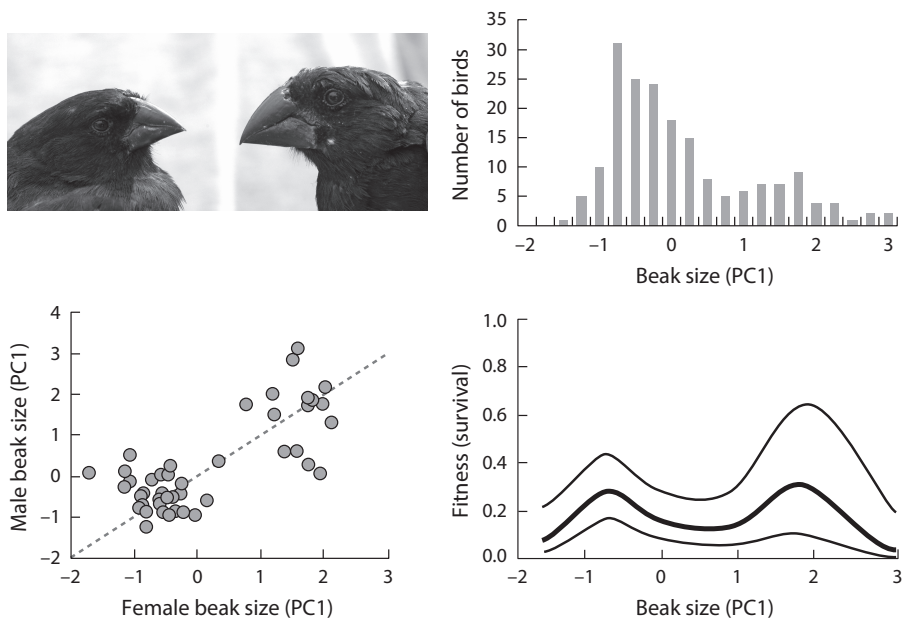


Fig B.4. Ecology drives diversification. The top left panel shows mature male *Geospiza fortis* morphs with small and large beak sizes: both birds were caught in the same mist net at the same time (photo: A. Hendry). The top right panel shows that beak sizes of this species at El Garrapatero fall into small and large modes, with relatively few intermediates (data from Hendry et al. 2009b). The bottom left panel shows that male-female pairing is assortative by beak size (data from Huber et al. 2007, provided by S. Huber). The bottom right panel shows that disruptive selection acts between the two modes (data from Hendry et al. 2009b). In all cases, beak size is PC1 from measurements of beak length, depth, and width. In the bottom right panel, the curves are a cubic spline with confidence intervals (see Hendry et al. 2009b for details)

Box 4 (*Continued*)

of the same morph (Podos 2010), show assortative mating by beak size (Huber et al. 2007), have higher survival than birds with intermediate beak sizes (Hendry et al. 2009b), and manifest genetic differences indicative of reduced gene flow (De León et al. 2010). Ecological differences within a species are driving the evolution of reproductive barriers that reduce gene flow.

these: When speciation occurs, how often is it ecological? And when ecological differences exist, how often do they cause speciation? Other questions consider the rapidity of ecological speciation (rapid speciation), at what point progress toward ecological speciation becomes irreversible (speciation reversal), to what extent ecological speciation is driven by competitive (adaptive speciation) or reproductive (reinforcement) interactions, and how many traits (magic traits) and selective pressures (dimensionality) are involved.

For this eco-to-evo part of eco-evolutionary dynamics, it would certainly be possible to add additional effects and processes, with more boxes and arrows; yet the above outline seems sufficient to lay the groundwork. First, selection (chapter 2) is the primary force driving the contemporary adaptation of populations (chapter 3). Second, divergent selection is the primary force driving adaptive divergence (chapter 4). Third, dispersal among populations in different environments can constrain adaptive divergence (chapter 5). Fourth, adaptive divergence can lead to reproductive barriers that reduce gene flow and thereby cause ecological speciation (chapter 6). Stated simply: ecology drives evolution! It is now time to consider the reverse: evolution driving ecology.

PART 2: EVO-TO-ECO

One way to outline the evo-to-eco side of eco-evolutionary dynamics would be to add arrows in figure 1.1 from adaptation back to ecological change (the single population case), and in figures 1.2–1.4 from adaptive divergence back to the ecological contrast (the multiple population case). As an example, the evolution of finch beaks will influence the seeds they consume and should therefore alter seed and plant distributions. In the end, however, presenting the key ideas will work more effectively through a different, although complementary, set of boxes and arrows. In particular, I now wish to specify interactions among different levels of biological variation: genes, phenotypes, populations (population dynamics), communities (community structure), and ecosystems (ecosystem function). Some of these levels refer to a particular focal organism: genes, phenotypes, and population dynamics (e.g., numbers, rates of increase, age structure, stability). Other levels refer to composite variables external to the focal organism: community structure (e.g., number and diversity of species, food web length, resistance to invasion) and ecosystem function (e.g., productivity, biomass, decomposition rates, nutrient fluxes).

How might change at each of these levels of variation influence change at the other levels? We can start from the simple recognition that interactions are sure to occur among the population dynamics of a focal organism, the structure of the community in which it is embedded, and the functions that exist in the encompassing ecosystem. For instance, changes in the abundance of a predator will influence the structure of prey communities and vice versa (populations ↔ communities), changes in the abundance

of an important herbivore will influence ecosystem productivity and vice versa (populations \leftrightarrow ecosystems), and changes in a community of herbivores will influence ecosystem productivity and vice versa (communities \leftrightarrow ecosystems). Thus, we can start by drawing three boxes (populations, communities, ecosystems) and connecting them all with arrows that go both ways.

We can next recognize that the properties of populations, communities, and ecosystems could each influence selection on phenotypic traits. For example, beak size in a Darwin's finch population will be influenced by the number of individuals (population dynamics influences seed availability and therefore selection), the community of seeds and other finches (community structure influences seed availability and therefore selection), and soil moisture and nutrients (ecosystem function influences plant reproduction and therefore selection). We can depict such effects with arrows connecting each of the ecological levels to the phenotypes of a focal organism. Then, if those phenotypes are to evolve in response to selection, we need arrows from phenotypes to genes (or, more generally, genomes) and back again. Alternatively, variation at the three ecological levels could plastically influence organismal phenotypes without causing genetic change. Combining all these effects (fig. 1.5), we have an alternative way of presenting the eco-to-evo sequence originally depicted in figure 1.1.

This new representation of eco-to-evo effects acting on phenotypes within a population can be extended to represent eco-to-evo effects acting on phenotypic divergence among populations. First, we need to recognize that dispersal influences not only gene flow but also population dynamics: for example, immigration can help to maintain population size, such as in the case of “source-sink” dynamics. Second, gene flow influences genetic divergence among populations, which then influences phenotypic divergence—as explained above. Finally, adaptive divergence can reduce gene flow through ecological

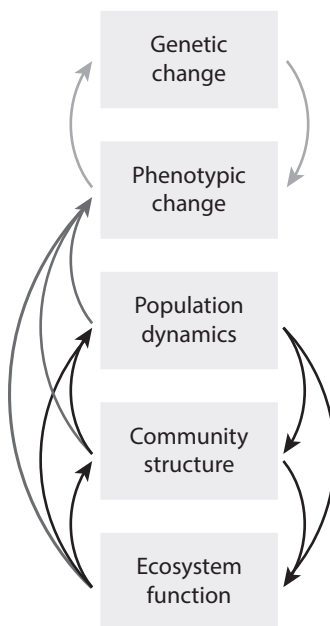


Fig 1.5. Graphical representation of the eco-to-evo side of eco-evolutionary dynamics for a population of a focal organism (top three boxes) in relation to composite aspects of its environment (bottom two boxes). This depiction is akin to that shown in figure 1.1, with the addition of separating three levels of ecological variation: population dynamics, community structure, and ecosystem function. Arrows indicate that these three levels can influence each other, as well as the phenotypes—and thereby genotypes—of the focal organism

speciation—also as explained above. Combining these effects (fig. 1.6), we have an alternative way of presenting the eco-to-evo effects originally depicted in figure 1.4.

To simplify presentation of the ideas that follow, I now fuse the within-population (fig. 1.5) and between-population (fig. 1.6) perspectives by simply referring to genes, phenotypes, populations, communities, and ecosystems. This concatenation means that references to a given level could refer to variation within a population or to variation among populations, with the latter implicitly including (but no longer explicitly represented with boxes and arrows) potential effects of dispersal and gene flow. To this new way of representing eco-to-evo effects, we can now add the reverse (evo-to-eco) side of the story (fig. 1.7). Specifically, phenotypes can influence population dynamics, community structure, and ecosystem function. I now discuss each of these potential effects in turn.

The phenotypes of a focal organism should have strong effects on its population dynamics. In particular, the mismatch between a population's current phenotypes and the phenotypes that would maximize fitness will influence population growth rate. Specifically, better-adapted populations (smaller mismatch) should have higher mean fitness, faster population growth, and perhaps larger population size (fig. 1.8). Thus, factors that change the mismatch should shape population dynamics. For instance, environmental change that increases the mismatch should precipitate population declines and extirpations. However, contemporary adaptation should decrease the mismatch and thereby promote population increases and range expansion: a process sometimes called “evolutionary rescue” (Gomulkiewicz and Holt 1995, Carlson et al. 2014). An example of adaptation influencing population dynamics in Darwin's finches is presented in Box 5.

Chapter 7 (Population Dynamics) starts with a more detailed outline of the various possibilities, including complexities that move beyond the above simplified scenario. It then evaluates various methods for inferring how phenotypes/genotypes influence population dynamics, including extensions of the year-by-year tracking approach illustrated

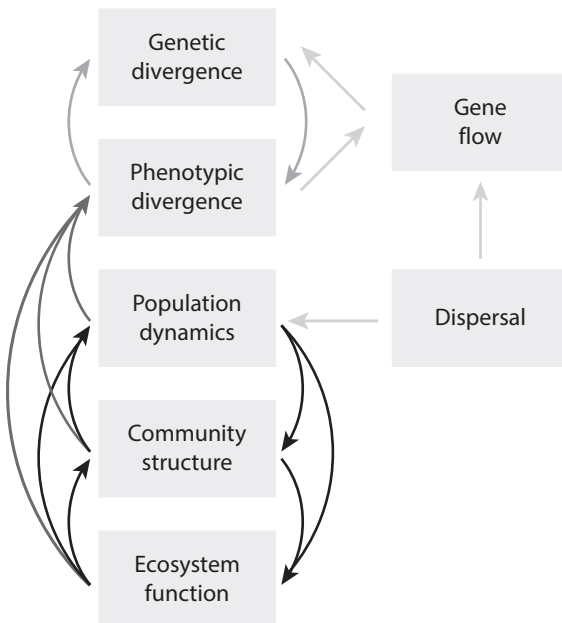


Fig 1.6. Graphical representation of the eco-to-evo side of eco-evolutionary dynamics taking into consideration multiple populations of a focal organism (akin to fig. 1.4). Extending the effects described in figure 1.5, ecological differences (at the population, community, or ecosystem levels) can influence, through selection or plasticity, phenotypic differences between populations of the focal species, which can cause genetic differences. In addition, dispersal between populations will influence population dynamics and gene flow, with the latter then influencing genetic divergence. Finally, phenotypic divergence can reduce gene flow through ecological speciation

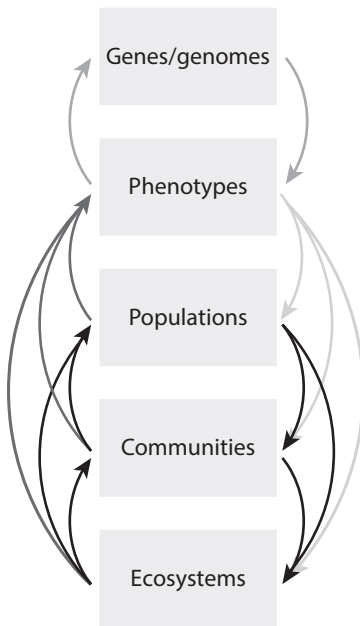


Fig 1.7. Graphical representation of a complete framework for considering eco-evolutionary dynamics. This representation fuses the within-population (fig. 1.5) and between-population (fig. 1.6) perspectives for eco-to-evo effects, and also adds the evo-to-eco realization that phenotypes can influence each ecological level. This representation also makes clear that feedbacks are expected between phenotypes and ecological variables. The effects of dispersal and gene flow (e.g., fig. 1.6) are implicit, but not explicit, in this representation

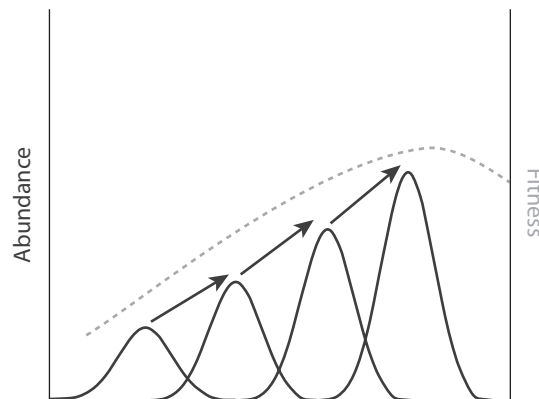


Fig 1.8. Graphical representation of how adaptation that reduces the mismatch between current phenotypes and optimal phenotypes can increase population size. The dashed curve shows mean fitness (y-axis at right) for populations with different phenotypes (x-axis) and the solid curves show the expected abundance of individuals (y-axis at left) with a given phenotype. The population starts far from the optimum where fitness is low and so too is population size. Adaptive evolution shifts (dashed arrows are time steps) the phenotypic distribution toward the new optimum, which thus increases fitness and so too population size. Nuances to this process are discussed in chapter 7

in Box 5. The key questions then provide an empirical assessment of the effects outlined above, starting with how maladaptation resulting from environmental change might decrease individual fitness and contribute to population declines, range contractions, and extirpations. The following questions consider the extent to which contemporary

Box 5

As noted in Box 1, the population size of Darwin's finches varies dramatically with rainfall, and mortality during the stressful drought periods is influenced

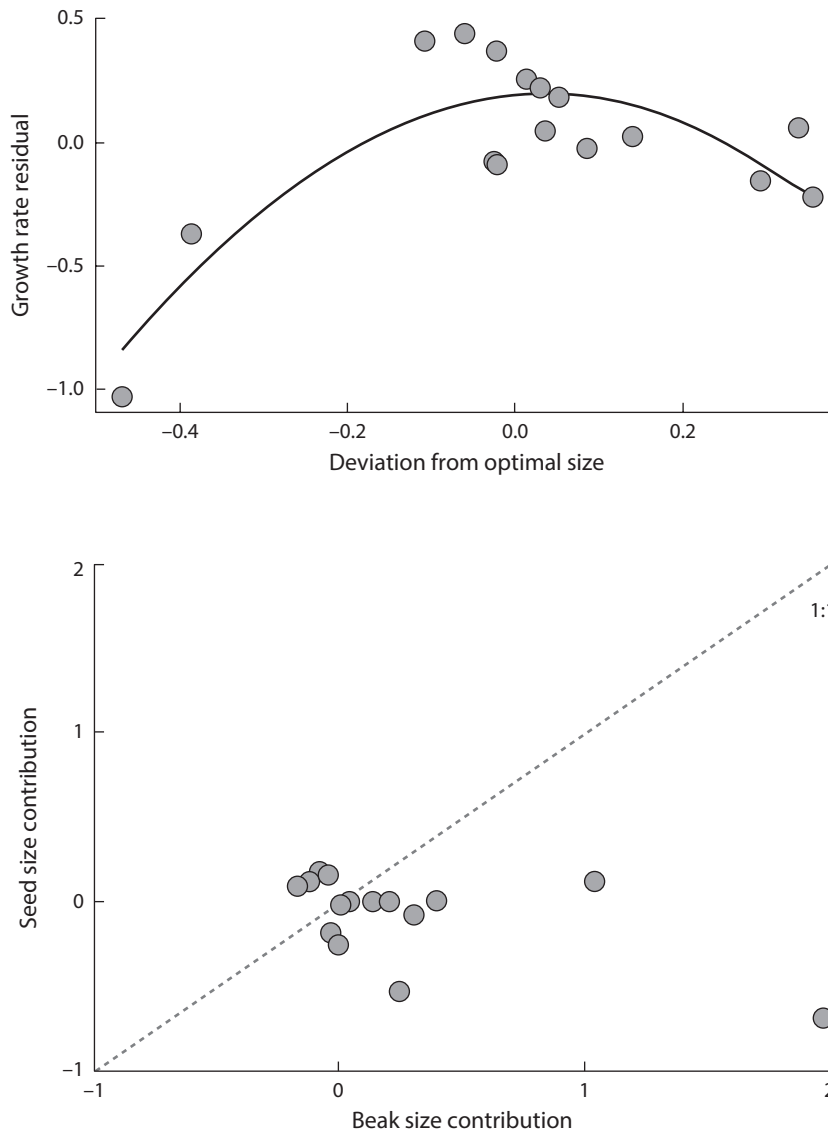


Fig B.5. Evolution influences population dynamics in *Geospiza fortis* on Daphne Major. The top panel shows the relationship between an estimate of the deviation of mean beak size from the optimal beak size (x-axis) and annual population growth rate “corrected” for effects of rainfall (growth rate residual, y-axis). The bottom panel shows the relative contributions to population growth rate of interannual changes in beak size (x-axis) and interannual changes in seed size (y-axis). The data are from Hairston Jr. et al. (2005), wherein more details are provided

(Continued)

Box 5 (*Continued*)

by beak size. Changes in population size from one generation to the next therefore should be related to how well existing beak sizes match the optimal beak sizes set by the seed distribution. In years when beaks are well adapted, population sizes should grow. In years when beaks are poorly adapted, population sizes should decrease. Hairston Jr. et al. (2005) tested these expectations by relating interannual changes in population size for *Geopsiza fortis* on Daphne Major to the degree of beak size adaptation, based on data from Grant and Grant (2002). The analysis showed that population growth rate was maximal at the estimated “optimal” beak size, and was lower if average beak sizes were larger or smaller. Hairston Jr. et al. (2005) further showed that this effect of variation in beak size on population growth rate was approximately twice as large (on average) as was the effect of environmentally driven variation in seed size. Evolution had an important influence on population growth.

evolution then helps to recover individual fitness and population size, which might then make the difference between persistence versus extirpation and range expansion versus contraction. A final question asks how phenotypic variation within populations and species influences population dynamics.

All discussion up to this point has considered effects on the properties (genotypes, phenotypes, population dynamics) of some focal organism, whereas I now transition to effects on composite ecological variables—starting at the community level. Phenotypic change in a focal organism could influence community structure through two basic routes, which I will refer to as “direct” and “indirect”.⁴ Through the direct route, the phenotypes of individuals could alter their per capita effects, depicted as the arrow from phenotypes to communities in figure 1.7. As an example, the foraging traits of a predator will influence the prey types it can consume and will therefore shape the prey community (Post and Palkovacs 2009). Box 6 provides a putative example for Darwin’s finches. In this route, phenotypic change in the focal organism will alter community structure even if the abundance of that organism remains constant. Through the indirect route, the above-described influence of phenotypes on population dynamics could cascade to influence community structure, depicted as the arrows from phenotypes to populations to communities in figure 1.7. In this case, phenotypic change in the focal organism will alter community structure even if the per capita effects of that organism remain constant. Importantly, direct and indirect effects can act in the same direction, thus “reinforcing” or “amplifying” the total effect, or in opposite or “opposing” directions, thus “offsetting” or “canceling” the total effect.

Chapter 8 (Community Structure) starts with an outline of mathematical approaches for evaluating how genotypes/phenotypes might alter community structure, which then points to predictions about when such effects should be strongest in nature. The chapter

⁴Alternative terms, such as trait-mediated versus density-mediated, might seem similar but they would not suffice in the present context. As will be made clear later, density-mediated effects could themselves be trait-mediated. In addition, other sorts of indirect pathway beyond “density mediated” will be considered.

Box 6

Darwin's finches deplete seeds from the environment in relation to their beak size. The evolution of finch beaks should therefore influence the seed distribution,

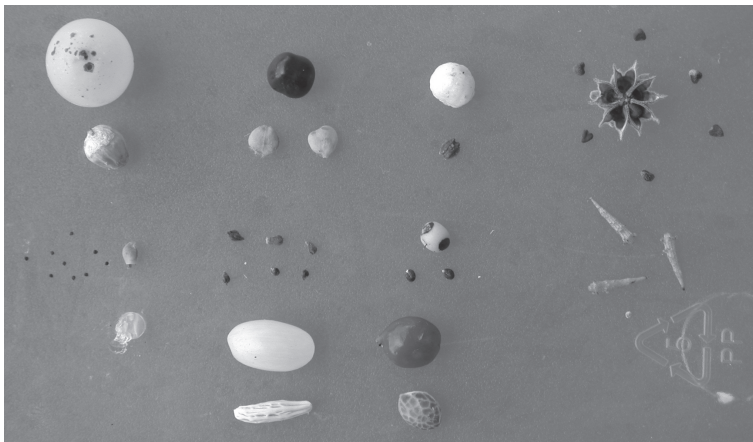
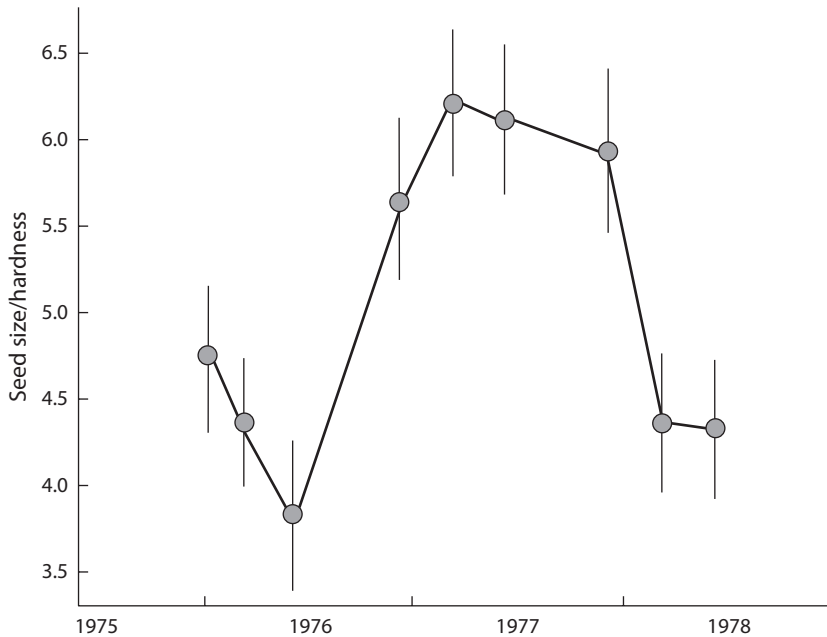


Fig B.6. Effects of finches on seed community structure. The graph shows the average size/hardness of seeds on Daphne Major from before to after the 1976–1977 drought. The data points are means and standard errors in fifty 1 m² quadrats sampled through time (from Boag and Grant 1981, wherein the details appear). The photograph shows some food types (fruits and seeds) available for consumption by *Geospiza* ground finches (on Santa Cruz). The top row shows *Cordia lutea*, *Scutia spicata*, *Tournefortia pubescens*, and *Bastardia viscosa*. The middle row shows *Portulaca oleracea*, *Cryptocarpus pyriformis*, *Tournefortia psilostachya*, and *Commicarpus tuberosus*. The bottom row shows *Vallesia glabra* and *Castela galapageia*

(Continued)

Box 6 (*Continued*)

which should then influence plant communities, which should then further influence finch beak sizes. This full eco-evolutionary feedback has been suggested (Post and Palkovacs 2009) but not formally demonstrated. However, the feedback can be inferred indirectly based on changes attending the colonization of Daphne Major in 1982 by the large ground finch, *Geospiza magnirostris*. As outlined in Box 1, drought conditions in 1976–1977 led to *G. fortis* depleting small/soft seeds from the environment. The remaining large/hard seeds led to selection on *G. fortis* for larger beaks. Another major drought occurred in 2003–2004 and selection was the opposite: *G. fortis* with smaller beaks were more successful than those with larger beaks (Grant and Grant 2006). It seems that, during the 2003–2004 drought, the larger-beaked *G. magnirostris* depleted the larger/harder seeds that *G. fortis* had used during the 1976–1977 drought. In short, the distribution of *Geospiza* beak sizes altered the seed distribution, which then fed-back to influence selection on the finches. Although the causal change in the beak size distribution here resulted from the addition of a new species, the situation remains a good proxy for variation within a species because *G. fortis* and *G. magnirostris* are very closely related and differ only in body/beak size. It remains to be determined to what extent a finch-induced change in the seed distribution alters plant communities.

then summarizes common approaches for empirical work, which might be broadly classed as (1) the effects of genotypes/phenotypes within and among populations, and (2) the year-by-year correspondence between phenotypic change and community change. The first two key questions that follow summarize the current state of knowledge for two classic applications of evolutionary thinking to community theory: predator-prey interactions and competition. The next question considers the importance of intraspecific genetic diversity for community structure, which echoes and extends the intense interest surrounding the effects of interspecific diversity (Loreau et al. 2001, Hooper et al. 2005). Other key questions relate to the relative strength of phenotypic/genetic effects, the time frames over which such effects play out, and whether they are direct or indirect in the sense described above.

The effects of genotypes/phenotypes on ecosystem function are a logical extension of the effects on community structure. For instance, such effects can be direct (when phenotypes differ in their per capita effects on ecosystem variables) or they can be indirect through several pathways: phenotypes to populations to communities to ecosystems, phenotypes to populations to ecosystems, or phenotypes to communities to ecosystems (fig. 1.7). Box 7 provides a concrete example by first suggesting how such effects might work in Darwin's finches and then showing how they actually do work in cottonwood trees (*Populus* spp.).

Chapter 9 (Ecosystem Function) first explains how the mathematical frameworks, empirical methods, and predictions introduced for community structure in chapter 8 can be extended to ecosystem function. Also outlined is an alternative conceptual framework (biological stoichiometry) for evaluating eco-evolutionary dynamics at

Box 7

No information exists on how the beaks of Darwin's finches influence ecosystem function, although such effects do seem likely. In particular, finch-induced changes in the seed community (Box 6) should have cascading consequences for ecosystem variables, such as decomposition rates, primary productivity, and nutrient cycling. Given that we don't know anything more for finches, we must switch to a different empirical system. Beavers (*Castor canadensis*) prefer to eat cottonwood genotypes with low levels of condensed tannin (Bailey et al. 2004). Cottonwood (*Populus*) stands subject to beaver activity thus become biased toward high-tannin genotypes. Condensed tannins influence many ecological properties, including soil microbial activity, and so a likely outcome of selection by beavers is reduced decomposition and nitrogen mineralization (Schweitzer et al. 2004). Thus, selection imposed by one species (beavers) can change the genetic composition of another species (cottonwoods), which alters ecosystem processes. Genetic variation within species, and presumably its evolution, influences ecosystem function.

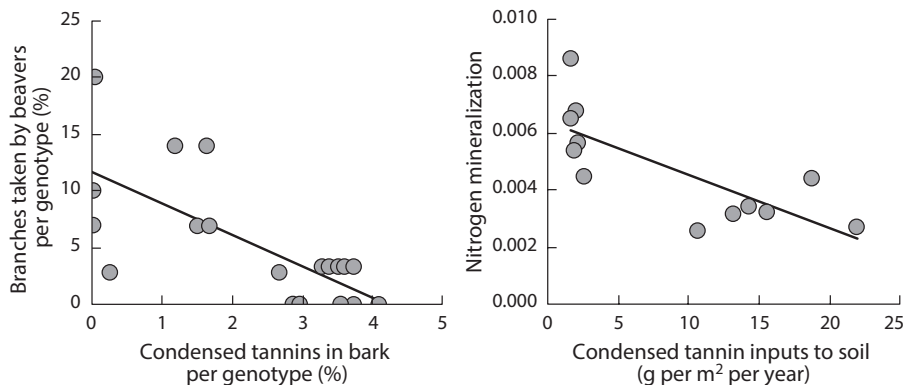


Fig B.7. Effects of selection by beavers (*Castor canadensis*) on ecosystem process. The left panel shows that beavers preferentially harvest cottonwood (*Populus*) genotypes that have low levels of condensed tannin (each data point is a cottonwood clone). The right panel shows that higher inputs of condensed tannin into the soil decrease rates of nitrogen mineralization (the data points are individual trees). The data were digitized from Whitham et al. (2006)

the ecosystem level (Elser 2006, Matthews et al. 2011b, Jeyasingh et al. 2014). Many of the key questions addressed in this chapter echo those first considered in the previous chapter: what is the importance of intraspecific diversity, what is the relative strength of the various effects, on what time scales do the effects play out, and to what extent are the effects direct or indirect? Also considered are some more synthetic questions: do the effects of genotypes decrease toward higher levels of complexity (from phenotypes to communities to ecosystems), and to what extent are feedbacks evident (traits influence ecosystems which then influence traits)?

At the end of these three evo-to-eco chapters, I hope that readers have an appreciation for the theoretical perspectives, empirical approaches, and key questions relating to this

side of eco-evolutionary dynamics. Given that much less work has been done on this evo-to-eco side of the equation than on the eco-to-evo side, the general conclusions I draw will be increasingly tentative and haphazard. The message that I hope comes across is that much more work needs to be done in this area, and that many opportunities exist for investigators to make novel and important contributions to the field's development.

PART 3: UNDERPINNINGS

As will be repeatedly emphasized throughout the book, phenotypes are the nexus of eco-evolutionary dynamics—because they (as opposed to genotypes) are influenced by, and have influences on, other organisms and the environment. Genes do not have these properties except indirectly through their association with phenotypes. All of the above chapters therefore focus—with a few exceptions—on phenotypic changes within populations and phenotypic differences among populations. Yet we can't ignore the sources of phenotypic variation because the role of phenotypes in shaping eco-evolutionary dynamics will depend on how they are influenced by genes and the environment. Thus, the final part of the book will consider in more detail the two major contributors to phenotypic variation: genetic variation and phenotypic plasticity.

Evolution occurs when allele frequencies change across generations within populations. When these evolutionary changes differ among populations, genetic divergence takes place. In some cases, a single gene might explain most of the phenotypic variation in a particular trait, such as wrinkled versus smooth peas, or *Cepaea* color patterns, or human blood types, or sickle cell anemia (Bell 2008). In such cases, phenotypic variation should closely mirror underlying genetic variation. Most traits, however, are influenced by many genes of small-to-modest effect and also by the environment, necessitating a quantitative genetic approach (Roff 1997, Lynch and Walsh 1998). In its simplest form, this approach asks how much of the variation within or among populations has a genetic (as opposed to environmental) basis, and to what extent this basis stems from the additive effects of alleles and genes (additive), interactions among alleles at a locus (dominance), and interactions among genes (epistasis). The resulting determinants of genetic variation influence phenotypic responses to selection and thereby contribute to eco-evolutionary dynamics.

Chapter 10 (Genetics and Genomics) first outlines common empirical methods for studying the genetics of adaptation: quantitative genetics, quantitative trait locus (QTL) linkage mapping, association mapping, genome scans, gene expression, and candidate genes. The key questions then address various aspects of adaptation, speciation, and eco-evolutionary dynamics. First, how much additive genetic variation exists in fitness-related traits, with the answer informing evolutionary potential? Second, to what extent does nonadditive genetic variation (dominance and epistasis) influence phenotypic variation? Third, how many loci are involved in adaptation and how large are their effects, with the extremes being “many-small” versus “few-large”? Fourth, to what extent does the adaptation of independent populations to similar environments involve parallel/convergent genetic changes? Fifth, is adaptation to changing environments driven mainly by new mutations or by standing genetic variation, and what do the resulting “adaptive walks” look like (how many steps and in what order)? Finally, to what extent are the ecological effects of individuals, considered in the context of

extended phenotypes, transmitted among generations—the so-called community heritability (Shuster et al. 2006)?

The other principal driver of phenotypic variation, and therefore eco-evolutionary dynamics, is phenotypic plasticity. Specifically, the environmental conditions experienced by an individual can cause developmental or behavioral changes in phenotype without any genetic change (Schlichting and Pigliucci 1998, West-Eberhard 2003). Some readers might wonder whether plasticity belongs in a book on *eco-evolutionary* dynamics, yet I can see several reasons why its inclusion is essential. First, the plasticity expressed by an individual has often evolved as a result of past selection, and so plasticity can be adaptive and can have a genetic basis. In essence, one can think of such plasticity as a current manifestation of past genetic change. Second, plasticity can evolve on contemporary time scales, and so phenotypic changes that accompany environmental change might partly reflect the *evolution* of plasticity. Third, plasticity modifies selection on genotypes, and thereby influences genetic responses to ecological change and ecological responses to genetic change. For all of these reasons, plasticity needs to be an integral part of any discussion of eco-evolutionary dynamics.

Chapter 11 (Plasticity) first outlines in more detail the nature of plasticity and how it can be studied, focusing in particular on the “reaction norm” approach. The subsequent key questions first evaluate whether or not plasticity is typically adaptive, with the main alternative being maladaptive physiological responses to stress. The next question informs the costs and limits to plasticity, without which any environment-phenotype mismatch could be easily bridged. The subsequent questions consider when adaptive plasticity should be strongest, such as when environments are variable in space or time, when gene flow is high, and when reliable cues exist. Also considered are alternative hypotheses for how genetic change and plasticity interact: that is, plasticity might enhance or constrain genetic evolution and ecological speciation. A final question considers how rapidly plasticity can evolve when populations experience new environments.

At the close of these two “underpinning” chapters, I hope that readers will agree that the phenotypic focus adopted in the book is valuable and appropriate. At the same time, I hope it remains clear that a phenotypic perspective on eco-evolutionary dynamics does not preclude rigorous investigations into its genetic and plastic basis.

What are eco-evolutionary dynamics—and what are they not?

Now that I have outlined a conceptual framework for eco-evolutionary dynamics, it is time to return to a consideration of just what they are and what they are not. I earlier defined eco-evolutionary dynamics as interactions between ecology and evolution that play out over contemporary time scales, such as decades or centuries. These interactions might be classified into five different categories.

1. Ecological change influences evolutionary change—but not vice versa.
2. Evolutionary change influences ecological change—but not vice versa.
3. Ecological change influences evolutionary change, which then influences ecological change—with the upstream ecological driver (e.g., population density) being different from the downstream ecological response (e.g., nutrient cycling).
4. Evolutionary change influences ecological change, which then influences evolutionary change—with the upstream evolutionary driver (a particular trait) being different from the downstream evolutionary response (a different trait).

5. Ecological and evolutionary change reciprocally influence each other through the same traits and ecological variables, inclusive of situations where intermediate traits or variables are involved. For example, a change in ecological variable A could cause a change in trait 1, which could then directly influence ecological variable B, which could influence ecological variable A.

Each of the five categories represents eco-evolutionary dynamics as long as the interactions occur in contemporary time. Further, categories 3 and 4 will be considered eco-evolutionary *feedbacks* in the broad sense and category 5 will be considered eco-evolutionary *feedbacks* in the narrow sense. These feedbacks can be positive (versus negative), such as when an increase in the level of ecological variable A causes the evolution of trait 1 in a manner that further increases (versus decreases) the level of ecological variable A. Positive feedbacks can reinforce (or “accelerate” or “enhance” or “exaggerate”) eco-evolutionary dynamics, whereas negative feedbacks can oppose (or “dampen” or “slow”) those dynamics. Note that all of the above designations focus on *change* as a driver of dynamics, whereas I will repeatedly emphasize that a *lack of change* as a driver of stability can just as easily (and perhaps even more importantly) be the result of cryptic eco-evolutionary dynamics, a phenomenon that might be called “eco-evolutionary stability.”

The above five options might seem so inclusive as to dictate that all changes, whether ecological or evolutionary, fall under the umbrella of eco-evolutionary dynamics. It is therefore useful to also suggest some scenarios that would *not* be considered eco-evolutionary dynamics.

1. Evolutionary changes that are not the result of ecological changes, such as many of those caused by genetic drift or genomic interactions unrelated to the ecological environment.
2. Ecological changes that are not the result of evolutionary changes, such as those resulting from geological forces such as volcanic activity or continental drift.
3. Evolutionary changes that do not cause ecological changes, such as in traits that have little influence on fitness and the environment (classically, bristle number in *Drosophila*).
4. Ecological changes that do not cause evolutionary changes in the focal organism under study.

In addition, we might not invoke eco-evolutionary dynamics if ecology and evolution are interacting on such long time scales as to be largely unchanging in contemporary time. (Although a full eco-evolutionary view of life will ultimately require integration across all time scales.) The extent to which these various alternatives occur in nature is an open empirical question. Perhaps most ecological and evolutionary change is eco-evolutionary, or perhaps not.

Some additional explanations and clarifications are helpful. First, every environmental change probably drives evolutionary change in at least some organism, whereas the above arguments are intended to apply to a particular focal organism. By this I mean that some species will not evolve in response to some ecological changes, even if other species are strongly affected. Second, I have phrased the above discussion as a yes-or-no proposition (eco-evolutionary dynamics are or are not occurring), which is not the real question of interest. Instead, we should be more concerned with quantifying *rates* of

eco-evolutionary dynamics and the *strength* of their effects. That is, eco-evolutionary effects may be fast or slow and strong or weak, or anything in between.

Limitations and scope

In attempting to provide a unified and comprehensive framework for studying eco-evolutionary dynamics, the book will end up covering a lot of ground. This broad scope made it impossible to go into great detail on any particular topic. I have instead tried to extract the most relevant considerations, the most critical questions, and the most informative empirical studies. For the same reason, I have not provided a detailed review of the many antecedents to eco-evolutionary dynamics or to alternative conceptual frameworks for its study. Instead, my goal was to integrate everything together, which led to the above framework that gives me the broadest possible scope for discussing interactions among genes, phenotypes, populations, communities, and ecosystems. More detailed work exists for particular subsets of these interactions, and I will reference these other efforts as the book unfolds.

I should also point out that this book does not represent, depict, or espouse a particular *hypothesis* or *theory*, such as the Ecological Theory of Adaptive Radiation (Schluter 2000a) or the Geographical Mosaic Theory of Coevolution (Thompson 2005). (Although I do suggest, in the final summary chapter 12, an emerging “Española-Isabela Hypothesis” for the eco-to-evo part of eco-evolutionary dynamics.) That is, I am not trying to marshal the evidence in support of a particular view of the world among potential alternative views. I am instead trying to review the evidence and tie together a series of disparate fields and subfields into a somewhat unified whole. No one disputes that ecology and evolution influence each other, but we lack a general conceptual framework and comprehensive empirical assessment of how these interactions play out in nature. That is what I am trying to achieve.