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**Peter R. Grant & B. Rosemary Grant: How and Why Species Multiply**

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## CHAPTER ONE

# The Biodiversity Problem and Darwin's Finches



Now it is a well-known principle of zoological evolution that an isolated region, if large and sufficiently varied in topography, soil, climate and vegetation, will give rise to a diversified fauna according to the *law of adaptive radiation* from primitive and central types. Branches will spring off in all directions to take advantage of every possible opportunity of securing foods.

*(Osborn 1900, p. 563)*

I have stated that in the thirteen species of ground-finches, a nearly perfect gradation may be traced, from a beak extraordinarily thick, to one so fine, that it may be compared to that of a warbler.

*(Darwin 1839, p. 475)*

## BIODIVERSITY

**W**E LIVE IN A WORLD so rich in species we do not know how many there are. Adding up every one we know, from influenza viruses to elephants, we reach a total of a million and a half (Wilson 1992, ch. 8). The real number is almost certainly at least five million, perhaps ten or even twenty, and although very large it is a small fraction of those that have ever existed; the vast majority has become extinct. Knowledge of the world's biological wealth is constantly expanding—for example, new species of marine fish are found each week. Nevertheless the rate of discovery of fundamentally different organisms is slowing down, and the discovery of a new order, class, or phylum is an extremely rare event. New findings are incorporated into an existing Linnean framework, and rarely change it. In short, incomplete as the biological inventory of life on earth is, enough is known to

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pose a strong challenge to evolutionary biologists. Explain it! Why are species as diverse as they are, and why are there so many?

The challenge is currently being met in numerous and diverse studies, for example in studies of butterfly wing pattern (Jiggins et al. 2006), plant phylogenies (Soltis et al. 2005), and fossil whales (Gingerich 2003), to name just three. Our own way of addressing the challenge is to start low down in the Linnean hierarchy, at the level of populations, species, and genera, reasoning that they contain the seeds of differences at the higher levels of classes, phyla, and kingdoms. The lessons learned at lower levels can then be extrapolated to higher levels where evolutionary pathways connecting related taxa are less clear. We choose a single group of related species for close scrutiny, and attempt to answer the following questions: where did they come from, how did they diversify, what caused them to diversify as much as they did (and no more), and over what period of time did this happen?

### THE CHOICE OF ORGANISMS

Ideally, as well as for convenience, the group should be more than a few but less than a multitude. Preferably they should live in the same geographical location in which they evolved as this helps us to interpret their past evolution. They should be easy to study in captivity and in nature, and they should have left a good, recoverable, and interpretable fossil record of their history.

Organisms that come closest to meeting all these needs are members of adaptive radiations. An adaptive radiation is the rapid evolution from a common ancestor of several species that occupy different ecological niches (Givnish and Sytsma 1997, Schluter 2000). The organisms are numerous enough for quantitative comparisons, similar enough to enable us to reconstruct their routes of diversification, and they live in environments where those routes can be interpreted adaptively (or otherwise).

Prime candidates for study are species-rich genera that live in the same region. There are many of these. Some of the best known and impressively diverse are the cichlid fish of African Great Lakes (Kocher 2004, Joyce et al. 2005, Seehausen 2006), *Anolis* lizards (Losos 1998) and *Eleutherodactylus* frogs (Hedges 1989) of the Caribbean and Central and South America, and *Drosophila* (DeSalle 1995) and the Silversword alliance of Composite plant species (Barrier et al. 1999) of the Hawaiian archipelago. Several groups

comprise hundreds of species, literally: more than 700 in the single genus of *Eleutherodactylus* alone (Crawford and Smith 2005), and the total is closer to a thousand in the case of Hawaiian *Drosophila* (Kaneshiro et al. 1995, Kamby-sellis and Craddock 1997). Then there are numerous Central and South American species of butterflies in the genus *Heliconius* (Mallet et al. 1998), *Partula* snails in Polynesia (Johnson et al. 2000), dipterocarp trees in Asia (Ashton 1982), figs and fig wasps distributed widely in the tropics (Weiblen 2002), likewise orchids and orchid bees (Pemberton and Wheeler 2006), etc., etc. The list goes on and on, and whether the groups of species meet strict or relaxed criteria for being recognized as adaptive radiations (Schluter 2000) they are certainly rich in species and diverse.

A more compact and manageable group than all of these is a small number of remarkable birds known as Darwin's finches (Plates 1 and 2). They are unique in what they offer biologists. They are so similar to each other that transformation of one species into another can be reconstructed easily. They are accessible; their behavior can be studied easily because they are tame. And importantly, no species has become extinct through human activities.

### DARWIN'S FINCHES

Apart from a single species on Cocos island, Darwin's finches (subfamily Geospizinae) are confined to the Galápagos islands of Ecuador (Fig. 1.1). Depending on how they are classified there are 14 or 15 of them (Table 1.1), which is a convenient number for complete study. They constitute a classical case of adaptive radiation (Fig. 1.2), having been derived from a common ancestor, and diversified relatively rapidly in morphology and ecology. They live in the same, largely undisturbed, environment in which they evolved, consequently whatever we can learn about their ecology and evolution gives us insights into the process of speciation and adaptive radiation under entirely natural conditions. For instance, populations of the same species occur on different islands (Table 1.2), and in some cases they have different ecologies. This enables us to investigate the reasons for their divergence. Then again, closely related species occur together on the same island, and differ. This allows us to investigate the nature of the reproductive barrier between them, and the question of how and why species stay apart. So, considering populations across the entire archipelago, it is as though the whole process of

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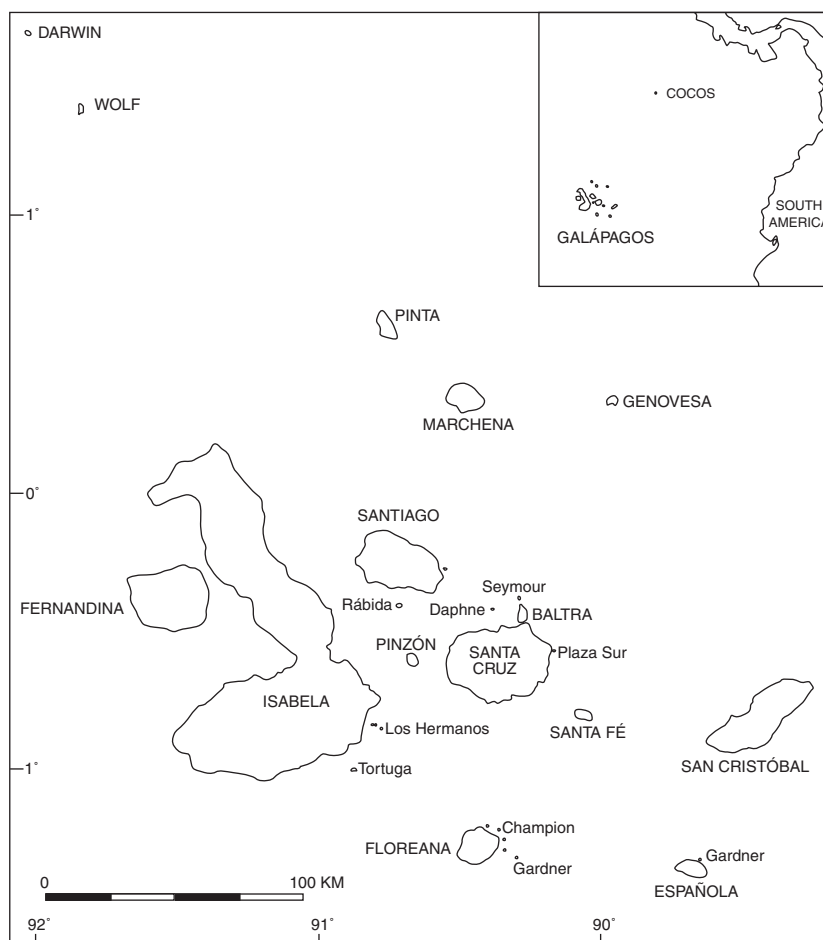


Fig. 1.1 Map of the Galápagos islands. From Grant et al. (2005a).

speciation is represented in all of its stages from start to finish: from an initial divergence to reproductive isolation, repeated many times.

These are very large advantages for their study. They are offset to some extent by two disadvantages: by the limited degree to which finches can be used experimentally, and by the absence of fossils except for very recent ones. As we shall see, some experimental investigations are possible, and molecules can sometimes help where fossils fail.

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TABLE 1.1

Darwin's finch species. *C. olivacea* could be considered two species on the basis of genetic evidence (Fig. 2.1).  
The woodpecker and mangrove finches have been considered members of a separate, weakly differentiated genus *Cactospiza* (Grant 1999).

<i>Scientific Name</i>	<i>English Name</i>	<i>Approximate Weight (grams)</i>
<i>Geospiza fuliginosa</i>	Small Ground Finch	14
<i>Geospiza fortis</i>	Medium Ground Finch	20
<i>Geospiza magnirostris</i>	Large Ground Finch	34
<i>Geospiza difficilis</i>	Sharp-beaked Ground Finch	20
<i>Geospiza scandens</i>	Cactus Finch	21
<i>Geospiza conirostris</i>	Large Cactus Finch	28
<i>Camarhynchus parvulus</i>	Small Tree Finch	13
<i>Camarhynchus pauper</i>	Medium Tree Finch	16
<i>Camarhynchus psittacula</i>	Large Tree Finch	18
<i>Camarhynchus pallidus</i>	Woodpecker Finch	20
<i>Camarhynchus heliobates</i>	Mangrove Finch	18
<i>Platyspiza crassirostris</i>	Vegetarian Finch	35
<i>Certhidea olivacea</i>	Warbler Finch	8
<i>Pinaroloxias inornata</i>	Cocos Finch	16

DIVERSITY OF DARWIN'S FINCH SPECIES

As a starting point for a discussion of their evolution we have followed the classification of species developed by Lack (1945, 1947) on the basis of an exhaustive study of museum specimens. Samples of specimens from the same island tend to fall into discrete groups: different species. Differences between species persist, even if they interbreed rarely, which is the essence of the biological species concept (Wright 1940, Mayr 1942).

The species differ in plumage and morphology (Plate 2). Those differences are summarized as follows. Six species of ground finches (genus *Geospiza*) are alike in having brown and streaked female plumage and unstreaked black male

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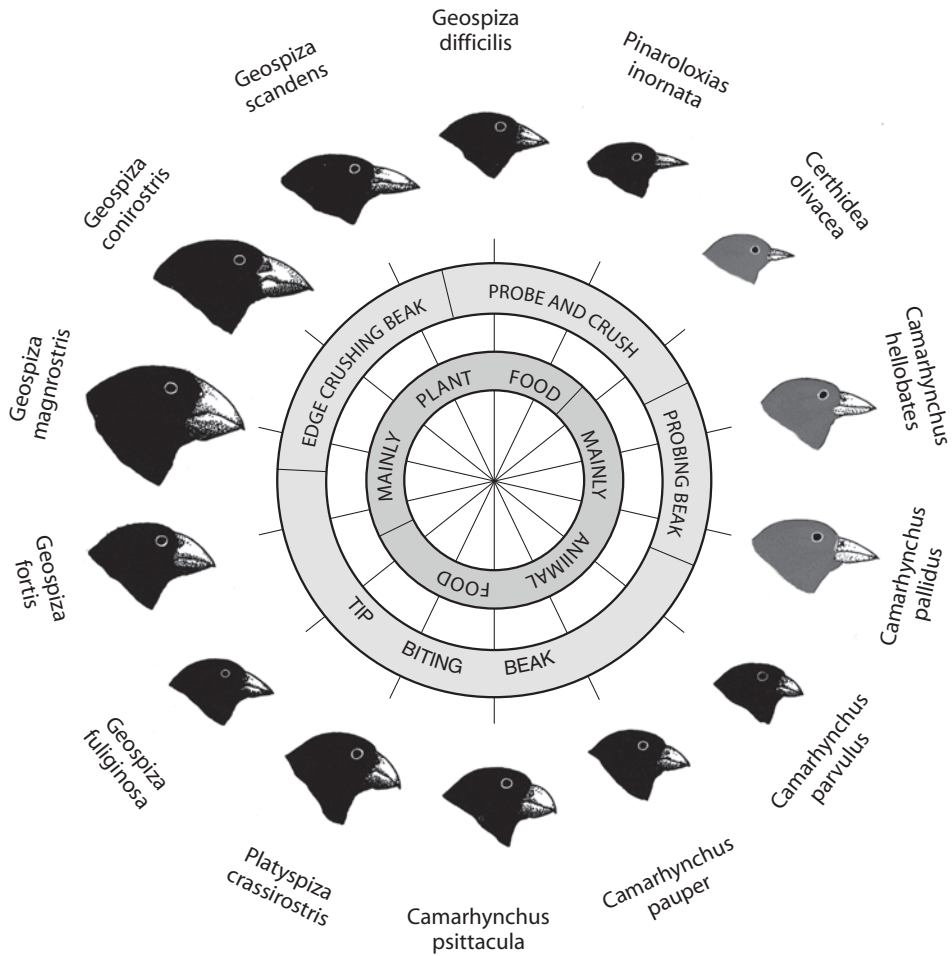


Fig. 1.2 Darwin's finches portrayed to emphasize the radiation, and not their genealogy (see Plate 1), like the canopy of a tree viewed from above. From Grant (1999).

plumage. Plumage traits set them apart from a group of five species of tree finches (*Camarhynchus*), which have a more olive-green than brown tone and few or no streaks. Males of three of them have black heads, shoulders, and chest, whereas males of the other two (*C. pallidus* and *C. heliobates*) have no black color, and nor do warbler finches (*Certhidea*). The vegetarian finch (*Platyspiza*) combines the color of ground finches with the limited expression



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of black of the male in three of the *Camarhynchus* tree finches. Finally the single species on Cocos (*Pinaroloxias*) shares the plumage features of the Galápagos ground finches.

Species in each of the ground finch and tree finch groups differ from each other to some extent in body size, but more so in beak size and shape (Fig. 1.2). That is how we can tell them apart: by their appearance. Furthermore the warbler, vegetarian, and Cocos finches possess beak morphologies quite unlike any of the others. As a result no two species in the entire group of Darwin's finches have the same beak morphology.

These few remarks capture the essence of three axes of variation in the radiation of Darwin's finches; a major beak axis, and lesser axes of body size and plumage. The variation is continuous in the case of beak and body size variation, and discrete and clustered in the case of plumage. An important feature is the placement of the species on the axes. Some species are surprisingly close together, such as the small, medium, and large ground finches (Plate 2). Others are more distant, and the warbler finch is distant from all others. Considered as a whole, Darwin's finches vary from a warbler-like bird of 8 g to a grosbeak-like bird of 35 g.

Their feeding ecology matches their morphological diversity, which is why the radiation of Darwin's finches is described as adaptive (Lack 1947, Bowman 1961). The ground finches feed often on the ground, consuming a variety of seeds, arthropods, as well as the fruits and seeds of prickly pear (*Opuntia*) cacti. Tree finches are more arboreal and insectivorous. The vegetarian finch is well-named for its vegetarian diet, and warbler finches feed on nectar and a variety of spiders as well as insects of small size.

### SPECIES AND POPULATIONS

The simple morphological descriptions above belie complexity in the assignment of some populations to species. Although species are discrete when co-occurring on the same island, the boundaries between species are not always clear-cut when considered across the archipelago. This is to be expected in young, ongoing, adaptive radiations, and more will be made of it in later chapters. Blurring of the discrete morphological boundaries is what makes the finches such a promising but challenging group for the study of speciation.

Darwin (1842) wrote about this seven years after he, FitzRoy (Captain of the *Beagle*), and their assistants collected the first specimens in 1835:

The most curious fact is the perfect gradation in the size of the beaks of the different species of *Geospiza*.

which led him to a prophetic evolutionary conjecture:

Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might fancy that, from an original paucity of birds in this archipelago, one species has been taken and modified for different ends.

Translated into the language of evolutionary biology, “modified for different ends” means adaptation by natural selection.

Complexity in the assignment of some populations to species occurs in two ways. First, populations of the same species differ from one island to another (Fig. 1.3). Although species are discretely different on the same island, as illustrated with ground finch species on Marchena in Figure 1.3, a large member of a small species on one island can be very similar to a small individual of a larger species on another island (Lack 1945, 1947, Grant et al. 1985). For example, medium ground finches on Santa Cruz are larger on average and vary much more than elsewhere. As a result the largest individuals of this population have larger beaks than the smallest of the large ground finches (*G. magnirostris*) on Rábida (Fig. 1.3). Thus, where to draw the line between the species is not always easy to decide. Nevertheless, despite some confusing similarities, individuals on an island are rarely difficult to classify (Lack 1947).

Second, well-differentiated populations on two islands could be considered separate species. There is no clear, unambiguous way of deciding whether members of such populations would interbreed and therefore whether the populations merit recognition as one species (conspecific) or two (heterospecific). The two prime examples are in the ground finch group. Six populations of sharp-beaked ground finches (*G. difficilis*) are united by shared features of beak shape but differ from each other in size enough to raise that question. For example, on Genovesa the average weight is 12 g, whereas on Santiago it is 27g! Populations of the large cactus finch (*G. conirostris*) on Genovesa and Española are morphologically similar to each other more than either is to the cactus finch (*G. scandens*), but they do

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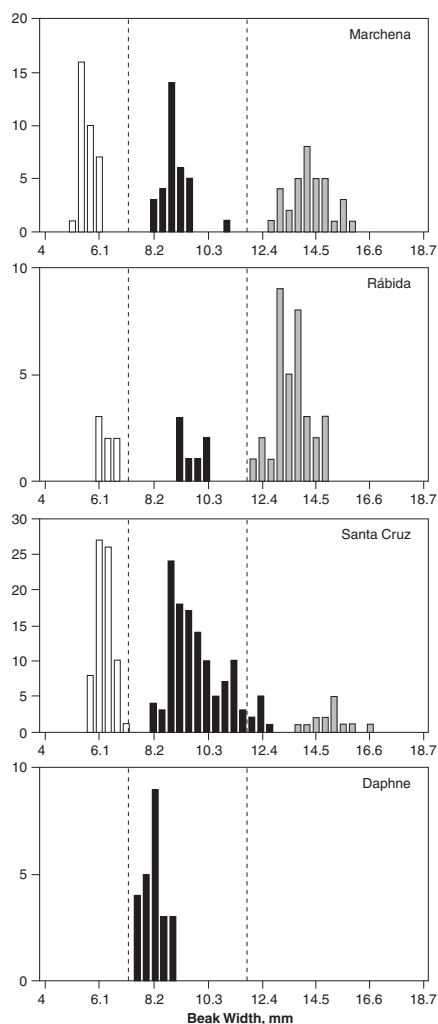


Fig. 1.3 Frequency distributions of beak widths of three species of ground finches, *G. fuliginosa* (white), *G. fortis* (black), and *G. magnirostris* (grey). They are approximately symmetrical and widely spaced apart on most islands (e.g., Marchena and Rábida), but not on Santa Cruz. Here *G. fortis* is exceptionally variable, and the largest individuals are larger than the smallest *G. magnirostris* on Rábida. The possibility of hybridization of *G. fortis* and the much rarer *G. magnirostris* on Santa Cruz is suggested by the shape of the *G. fortis* distribution, which is strongly skewed towards *G. magnirostris*. On Daphne Major the distribution of *G. fortis* beak sizes is shifted in the opposite direction, in the virtual absence of the other two species (chs. 5 and 6). Based on measurements of male specimens in museums (Grant et al. 1985).

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not coexist with the cactus finch anywhere, so possibly they should be considered conspecific with it.

The first of these complications raises questions about the identity of individuals, the second raises questions about the identity of species. They are not just classificatory conundrums. They are manifestations of the core Darwinian problem of understanding how species form. Paraphrasing Dobzhansky (1937) and Mayr (1942), that problem is how one population of interbreeding individuals splits into two with little or no interbreeding between them: how they multiply and diversify, and why.

## OVERVIEW OF THE BOOK

In this book we attempt to explain the evolutionary diversification of Darwin's finches in terms of geography, behavior, ecology, and genetics. The explanation involves natural and sexual selection, random genetic drift, exchange of genes through hybridization (introgression), and cultural as well as genetic evolution. Linking all these factors together is the frequent and strong fluctuation in climatic conditions, with droughts on the one hand and extremely wet (El Niño) conditions on the other. An important conclusion will be that environmental change is an observable major driving force in the origin of new species. Using information from the study of contemporary finches, we then turn to questions of how and why the radiation unfolded in the way that it did. We focus on how environmental change in the past has guided the multiplication of finch species, and how some properties of the finches may have predisposed them to diversify.

We start (chapter 2) by using molecular genetic data to estimate phylogenetic relationships, that is the genealogical relationships between populations and species of Darwin's finches, and between them and possible relatives in Central and South America. Changes in the environment that have occurred since the finches arrived on Galápagos are described. This information sets the scene for considering how speciation could have taken place in theory (chapter 3). Subsequent chapters explore the steps with data. First we use ecological information to describe what happens when an island is colonized and a new population becomes established (chapter 4), how adaptation through natural selection occurs (chapter 5), and how competition for resources contributes to natural selection and evolution (chapter 6). Then we address the important

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question of how individuals choose mates and what constitutes the barrier to interbreeding between species (chapter 7). Sometimes the barrier is breached, and interbreeding ensues. We examine the causes and consequences of hybridization in chapter 8. Chapter 9 uses the information and ideas developed so far to confront the issue of how species should be recognized. Chapter 10 focuses on the differences between species formed early and late in the radiation, and attempts to explain them in terms of responses to changing ecological opportunities and the balance between speciation and extinction. In chapter 11 we offer some explanation for why Darwin's finches radiated when other birds in the same environment did not. We place the radiation of Darwin's finches in a wider context in chapter 12 by outlining three stages that radiations pass through. Darwin's finches exemplify the first stage. We conclude this chapter with a short synthesis: a synthetic theory of adaptive radiation. Chapter 13 summarizes the main features of the Darwin's finch radiation, highlights what we do not know, and suggests some directions for future study.