Introduction

Darwin's Galápagos finches in modern biology

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One of the classic examples of adaptive radiation under natural selection is the evolution of 15 closely related species of Darwin's finches (Passeriformes), whose primary diversity lies in the size and shape of their beaks. Since Charles Darwin and other members of the *Beagle* expedition collected these birds on the Galápagos Islands in 1835 and introduced them to science, they have been the subjects of intense research. Many biology textbooks use Darwin's finches to illustrate a variety of topics of evolutionary theory, such as speciation, natural selection and niche partitioning. Today, as this Theme Issue illustrates, Darwin's finches continue to be a very valuable source of biological discovery. Certain advantages of studying this group allow further breakthroughs in our understanding of changes in recent island biodiversity, mechanisms of speciation and hybridization, evolution of cognitive behaviours, principles of beak/jaw biomechanics as well as the underlying developmental genetic mechanisms in generating morphological diversity. Our objective was to bring together some of the key workers in the field of ecology and evolutionary biology who study Darwin's finches or whose studies were inspired by research on Darwin's finches. Insights provided by papers collected in this Theme Issue will be of interest to a wide audience.

Keywords: Darwin's finches; evolution; speciation; adaptive radiation

1. INTRODUCTION

The most curious fact is the perfect gradation in the size of the beaks in the different species of *Geospiza*, from one as large as that of a hawfinch to that of a chaffinch, and ... even to that of a warbler. ... Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends.

(Darwin 1839, pp. 379–380)

High above the cliffs of the Darwin Bay on Isla Genovésa (Tower Island), one of the Galápagos archipelago islands in the Pacific Ocean, jumping around the sharp lava rocks on the ground, perched on the branches of the yellow geiger (*Cordia lutea*) and croton (*Croton scouleri*) bushes and flying around large yellow flowers of prickly pear cactuses (*Opuntia helleri*), are small black and brown birds. These birds look similar to each other in plumage and song, yet closer observation reveals that they all differ from one another in how their beaks look and work. One of them is called a warbler finch (*Certhidea fusca*) and, as its name suggests, it looks and behaves like a warbler from the

mainland. It has a very thin and pointed beak, which is used to probe leaves of the palo santo trees (*Bursera graveolens*) to catch small insects and their larvae. Another species feeding nearby on a small bush is the sharp-beaked finch (*Geospiza difficilis*), which has a slightly larger and more cone-shaped beak that is used to collect a more varied diet of both insects and small seeds. On the neighbouring small island of Wolf, members of the same species (*G. difficilis septentrionalis*) use their sharp arrowhead-shaped beaks to cut wounds on large sea birds, such as the Nazca and blue-footed boobies, and drink their blood. These same populations also feed on booby eggs by pushing and rolling them into rocks until they break, revealing remarkable behavioural adaptations that match their beak morphology. Two larger species of finches on Genovésa feed and nest in close proximity to the warbler and sharp-beaked finches. One of them, the large ground finch (*G. magnirostris*), has a massive, extremely deep and broad bullfinch-shaped beak that can be deployed to crush the large and hard seeds that no other bird on the island can handle. Lastly, there is the large cactus finch (*G. conirostris*) that has a more elongated yet still robust beak adapted for penetrating the firm covers of cactus fruits and closed cactus flower buds that contain protein- and sugar-rich parts inside (figure 1). All these species and 10 more across other islands of the Galápagos archipelago and Cocos Island do not belong to different families, as their extreme differences in beak

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One contribution of 13 to a Theme Issue 'Darwin's Galápagos finches in modern evolutionary biology'.

Figure 1. (a) Galápagos Islands, such as Isla Floreana, are volcanic islands visited by Charles Darwin in 1835; (b) bushes of the prickly pear cactuses (*Opuntia helleri*) on Isla Genovesa (Tower Island); (c) flowers of the yellow geiger (*Cordia lutea*); (d) male of the large ground finch (*Geospiza magnirostris*) singing during the rainy season; (e) female of the large ground finch (*G. magnirostris*) on Isla Genovesa; (f) female of the medium ground finch (*G. fortis*) on Isla Santa Cruz; (g) male large cactus finch (*G. conirostris*); (h) male sharp-beaked finch (*G. difficilis*) feeding on cactus flowers on Isla Genovesa; (i) male warbler finch (*Certhidea fusca*) singing next to its nest.

morphology and specializations would suggest, but are all part of a tightly linked and relatively recent group that diverged within the last 2–3 Myr called Darwin's finches (formerly known as the Galápagos finches) (Grant 1986, 1999; Petren *et al.* 1999; Sato *et al.* 1999). How was such morphological and behavioural diversity generated and how is it being maintained?

Several populations of the same species of Darwin's finches reside on different islands, and different species often share the same islands, as the situation on Genovesa (Tower) described above illustrates. Explaining such patterns has been an enduring challenge ever since Charles Darwin, in a brilliant insight, first attempted to explain the diversity and distribution of these species as a result of adaptation by

natural selection some 20 years before the publication of the book '*On the Origin of Species*' (Darwin 1859). More specifically, he wrote: 'Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends' to explain the mechanisms of evolution in this 'most singular group of finches' (Darwin 1839). The study of Darwin's finches began in 1835 when they were first collected by an expedition of the HMS *Beagle* that included young Charles Darwin. He later described them and asked John Gould of the Museum of the Zoological Society in London to study and catalogue them. It was Gould who realized

that all of these species, though extremely diverse in terms of their shapes and sizes, which presumably reflected differences in diets, were otherwise closely related to each other and, more distantly, to species on the South American mainland (Bowman 1961). Such key 'case studies' combined with the crucial insights gleaned from other evidence, such as the fossil record, artificial selection and world biogeography, eventually led Charles Darwin to conclude that biological species are subject to change and such change is not random, but is driven by continuous adaptation to the environment (Lack 1947; Bowman 1961). Many species of living organisms are being studied to understand a multitude of important aspects of evolutionary biology but few other species have as much historical, symbolic and scientific importance to the evolutionary theory as Darwin's finches (Darwin 1859; Lack 1947; Grant 1986, 1999; Grant & Grant 2008). As these birds were studied by Charles Darwin himself and their significance for evolutionary biology only increased over time, this Special Issue commemorates the anniversary of the bicentennial of Darwin's birth and celebrates 150 years since the anniversary of the publication of '*On the Origin of Species*' in 2009 (when this Special Issue was organized). It brings together researchers working on Darwin's finches on topics that range from historical species and population diversity to conservation status of the mangrove finch, the most rare species of the group, to evolution of cognitive behaviours, to the role for hybridization and gene flow in finch speciation and to the development and biomechanical significance of beak shapes. It also includes several highly related evolutionary and ecological studies on other avian species from researchers inspired by insights from Darwin's finches.

2. OVERVIEW OF THE SPECIAL ISSUE

The paper by Petren *et al.* (2010) is the first to report a genetic analysis of specimens collected by Charles Darwin and his shipmates on the voyage of the HMS *Beagle*. The authors use modern genetic tools, such as cloning and sequencing ancient DNA and multilocus microsatellite markers, to genotype modern and historical finch samples and populations from the Galápagos, to investigate the loss of diversity in this island ecosystem since the visit of Darwin in 1835. This study revealed that much more biodiversity has been lost in the Galápagos than was previously acknowledged, despite the fact that these island habitats are considered to be among the least influenced by humans owing to a relatively late exploration and low settlement activity. In addition, this paper makes another important contribution by shedding light on some of the (infamously!) unknown origin of some of Darwin's finch specimens as the authors were able to successfully determine the location and species of a number of unknown finches collected by Charles Darwin and others during early collecting expeditions over the last 175 years.

Despite the apparent loss of several island populations of Darwin's finches (above), none of the species have gone extinct. However, in recent years

owing to a combination of increased human activity, habitat loss and invasion by introduced species, the mangrove finch (*Camarhynchus heliobates*) is now on the brink of extinction, with a total population of around 100 individuals, and is among the rarest birds on the planet. The paper by Fessl *et al.* (2010) provides the much-needed new quantitative information on this endangered species, and discusses it in the context of conservation efforts and techniques. It is clear that the mangrove finch is very low in numbers in all of the small mangrove patches that it inhabits and its very existence is threatened by rats and parasitic flies. Using software for population projection analysis, the authors perform a useful analysis to show just how vulnerable the populations are under current regimes of predation, and how the vulnerability could be lessened with an elevation of breeding success and suppression of predation. Such information should be very useful and valuable for conservation of this and other species. While the prime focus of this paper is ecology and conservation of the mangrove finch and not its evolution, it is an important reminder of what can happen to an endemic island species that is pushed beyond its adaptive capabilities.

The next paper by Podos (2010) examined whether members of the medium ground finch *Geospiza fortis* population at a particular location, called El Garrapatero, on Santa Cruz Island discriminate between two beak-size morphs based on song alone, and also additionally tested whether these birds can discriminate the songs of local and distant (24 km away) singers of the same species. The first question is a particularly interesting one, as these two morphs are known to mate assortatively and thus may provide a good model for studying the formation of species boundaries through sympatric differentiation. The author provides evidence that they respond differently to local songs produced by different morphs but do not discriminate between small-morph songs recorded from different locations, counter to the results of a previous playback study in which local and distant songs elicited different responses (Podos 2007). The higher significance of the morph of the singing male (morph discrimination) than that of a location where the song was produced (acoustic preference) thus supports the hypothesis that song in Darwin's finches can serve as a behavioural mechanism for assortative mating and sympatric evolutionary divergence.

A related paper by de León *et al.* (2010) studied the factors that mediate gene flow between divergent populations/species of Darwin's finches. This is a study of morphological divergence and reproductive isolation in the presence of gene flow. The rationale is that ecological differences may work to maintain or even promote differentiation and reproductive isolation when directional selection is strong enough to counteract the homogenizing effects of gene flow. Such a scenario has been suggested some time ago by Felsenstein (1981) and Smith (1989). The authors take advantage of variable populations of medium ground finch by comparing genetic differences (allelic variation at 10 microsatellite loci in about 1000 individuals) among such populations with morphological

differences and geographical separation between populations. In addition, they perform a similar comparative analysis on several ground finch species (medium ground finch *G. fortis*, small ground finch *G. fuliginosa* and large ground finch *G. magnirostris*) from the same island (Santa Cruz Island). The key finding is that population (genetic) structure is associated with beak morphology but less so with geographical separation. That is, populations with similar beak sizes showed less genetic differentiation than populations with different beak sizes. Moreover, *G. fortis* with the greatest divergence in beak size also showed the greatest divergence at neutral markers. This pattern is also similar for the interspecific comparisons among the ground finches, and consistent results at these two biological scales (intra- and interspecific variation) suggest that ecological differentiation (disruptive selection and assortative mating) may be important in driving speciation. Finally, the study adds to the growing body of evidence indicating that the speciation can occur despite gene flow between populations.

The next paper by Temeles and co-workers (2010) touches on related issues of morphological adaptation and speciation in a different group of birds, the hermit hummingbirds (Phaethornithinae). In this paper, the authors studied the evolution of sexual dimorphism in bill size and shape on a group of hummingbirds combining morphological data obtained from hundreds of specimens from 30 distinct genera from museum collections with the recently published phylogenetic information on these species. Such extensive beak-shape dimorphism adapted for resource partitioning does not exist in Darwin's finches or in many other bird groups, but understanding its origin and function in groups where it does occur, such as hummingbirds, contributes greatly to our understanding of beak morphological evolution. The authors obtained interesting results on the evolution of sexual dimorphism within this group showing, for example, that moderate female-biased sexual dimorphism in bill curvature was the ancestral condition in hermit hummingbirds (Phaethornithinae), and that it was greatly amplified in several species, such as *Glaucis hirsutus* and *Phaethornis guy*, where bills of females are 60 per cent more curved than bills of males, which could be explained by differences in the usage of food plants. Their data suggest that hermit hummingbirds could provide a valuable model for studies of ecological causation as a mechanism for the evolution of sexual dimorphism for any species in which there are differences in trophic morphology or other such morphological differences owing to sex-specific resource use.

A paper by Grant & Grant (2010) provides an intriguing look at patterns of gene flow between species of Darwin's finches on Daphne Major Island, as well as gene flow owing to immigration of con- and heterospecifics. The main result, that gene flow from heterospecifics appears to be higher than gene flow from conspecifics on different islands, is quite fascinating and thought-provoking, as it challenges our usual conceptions regarding species boundaries and the role of gene flow in keeping populations of the same

species cohesive and populations of different species separate. The authors used very comprehensive methods combining pedigrees obtained through observation and genotyping with morphometric measurements and even behavioural observations, such as song structure and repertoire. These careful observations allowed the authors to successfully estimate such relatively small amounts of gene flow. They concluded that conspecific gene flow as a result of immigration into Daphne Major was insufficient to negate the strong effects of both hybridization and local selection, and that conspecific and heterospecific gene flow in combination are sufficient to counteract random genetic drift. One major implication of the findings by Grant & Grant (in press) is that gene exchange between populations is complex, heterogeneous and a dynamic process in time measured over decades revealing population genetic structure that is often used to calculate average rates of gene flow at the assumed steady state. Complex patterns of gene exchange can lead to the formation of a barrier to interbreeding during speciation.

Clegg & Phillimore (2010) contributed a paper that provides interesting information on how phenotypic and genetic divergence can be decoupled in species of island birds. The paper is a serious attempt to disentangle the evolutionary forces that shape the origin of biological diversity by studying the population genetic structure and phenotypic divergence between two co-distributed congeneric bird species from the genus *Zosterops* inhabiting the Vanuatu archipelago. The authors took advantage of this island system to address the relative role of drift and gene flow in shaping genetic variation within populations, while correlating patterns of genetic variation with phenotypic differences among populations. Comparative analysis of these features between the two bird species with similar ecologies but differing histories in the islands proved particularly revealing. It was found that influence of migration on population genetic structure appeared to persist for very long time periods (up to hundreds of thousands of years) in their archipelago setting. At the same time, the expected transition to a condition of a drift-mediated system as island populations become increasingly isolated owing to reduced dispersal ability was found to only partially occur in an endemic species, despite a long evolutionary history on the archipelago (millions of years). The approach and conclusions described in this paper will form an important background to consider in the future while studying island speciation in Darwin's finches and other species.

Darwin's finches are most famous for the differential use of their distinct beaks, whose shapes and sizes are believed to be maximally effective for their respective diets. One of the most important aspects of beak function is the ability to convey and withstand biomechanical stress during the beak usage, which is particularly important for species cracking large and/or hard seeds. The biomechanical output of the integrated beak/jaw and cranial musculature system should be matched by the physical and geometrical properties of the beak. A paper by Soons *et al.* (2010) is an interesting study that uses a compilation

of empirical data to perform a computational analysis on the mechanical and adaptive significance of beak shape in Darwin's finches. More specifically, the authors used finite-element modelling to test the fracture-avoidance hypothesis. Using a sound methodology and a well-constructed computational analysis, the authors produced a study that should be broadly informative to biologists in the fields of ecomorphology, craniofacial biomechanics and evolution. This paper illustrates that deep and wide beaks in ground finches allow for reduction of areas with high stress and peak stress magnitudes, allowing birds to crack hard seeds while limiting the risk of beak failure. These results help to explain deep and wide beak morphologies among the seed-eating ground finches when compared with similarly sized species of Darwin's finches pursuing dissimilar diets, such as the cactus finches, and correlation of such morphology with the increased bite force reported earlier (Herrel *et al.* 2005).

A paper by Tebbich *et al.* (2010) is addressing adaptive evolution of behavioural traits in Darwin's finches. While differently shaped beaks allow for a more efficient (and safe) handling of different types of food sources by Darwin's finches, one remarkable and often overlooked feature of their biology is a range of behavioural adaptations that these birds display while searching and accessing those food sources. Ground finches explore the soil and large rocks for seeds, cactus finches penetrate cactus flowers and fruits with their pointed beaks, Warbler finches probe leaves of trees and bushes for small arthropods and sharp-beaked finches peck on feather buds to drink blood from boobies or crack their eggs by pushing them over rocks. In one of the most extraordinary examples in all birds, woodpecker finches will make a tool from a twig or branch to remove an insect larva from a crevice in the tree trunk when they are unable to reach it with their beak (Lack 1947; Bowman 1961). Such diverse and neophilic behaviours probably have a profound genetic component, but how and when such behaviours evolved in Darwin's finches remained a matter of speculation. The authors tested the 'flexible stem hypothesis' to explain the variation observed among Darwin's finches by connecting individual adaptability to species richness. This hypothesis would suggest that the ancestral finches were flexible and therefore able to adapt to the new and harsh environment they encountered on the Galápagos by exploiting new food types and developing new foraging techniques. It also predicts that high levels of cognitive capacities should be expected in all species of Darwin's finches, not only the ones using innovative techniques, such as woodpecker finches. The authors compared several components of cognitive behaviours such as operant and reverse learning, innovativeness, cane and seesaw tasks in multiple individuals of woodpecker finches and small tree finches and found evidence that innovative behaviours are phylogenetically primitive in Darwin's finches.

Badyaev (2010) contributed a paper that represents an extensive body of data on beak-shape variation within a single species of house finches (*Carpodacus*

mexicanus), another example of ongoing adaptive radiation, and offers a thoughtful overview of contemporary phenotypic evolutionary thinking and includes ideas that only recently emerged from other related studies. The author is focusing on the possible mechanisms that enable precise adaptation in beak morphology and its adaptability during rapid evolution and diversification of avian beaks. In particular, he is interested in explaining the observed rapid evolutionary changes in beak morphology in light of the neo-Darwinian model that necessitates coordinated changes in developmentally distinct precursors and correspondence between functional and genetic modularity in beak morphogenesis, which has recently been elucidated (Abzhanov *et al.* 2004, 2006; Schneider 2006; Badyaev *et al.* 2008). This study focuses on the first 19 generations of house finches colonizing a particular site in Montana and which display a wide array of distinct and presumably adaptive beak morphologies—a result of compensatory developmental interactions between beak length and width in accommodating microevolutionary change in beak depth. It was found that directional selection has largely eliminated phenotypic extremes formed by these compensatory developmental interactions, while long-term stabilizing selection along a single axis (beak depth) was mirrored in the structure of beak additive genetic covariance. Among the most interesting interpretations of the data provided by Badyaev (2010) are that the adaptive equivalence of beak configurations shields genetic and developmental variation in individual components from depletion by natural selection and that compensatory developmental interactions among beak components can generate rapid and extensive reorganization of beak morphology under novel conditions, thereby facilitating evolution of precise local adaptation and contributing to overall diversification.

A paper from the Keller group (Hoeck *et al.* 2010) looks at another group of Galápagos land birds, which were also very important to Charles Darwin and his early thinking about evolutionary theory, the Galápagos mockingbirds. Mockingbirds' small and isolated island populations offer an ideal model to study the effects of limited population size, genetic drift and gene flow on genetic diversity. The authors measured genetic diversity within and differentiation among 19 mockingbird populations on most Galápagos islands, covering all four endemic species, using putatively neutral microsatellite loci. The authors examine these loci for signs of drift and gene flow, and they also used historic specimens to assess genetic change over the last century, revealing some clear and striking patterns of differentiation and diversity consistent with strong genetic drift and limited gene flow. This is in contrast to Darwin's finches who display widespread interisland migration levels and have low levels of isolation-by-distance (Petren *et al.* 2005; Tonnies *et al.* 2005). It thus appears that phenotypic divergence among populations of Galápagos mockingbirds is due in large part to isolation and genetic drift.

Finally, a paper by Ricklefs (2010) proposes host–pathogen coevolution as a possible explanation for reduced secondary sympatry, and thus rates of

diversification, in related sister species inhabiting island archipelagos. While being highly relevant to understanding mechanisms of speciation in Darwin's finches, this study also provides a complement to the niche studies of Peterson *et al.* (1999), who concluded that niches of sister species do not change for a long time after speciation. The hypothesis proposed by Ricklefs (2010) is based on the observed pattern among selected taxa, which shows that remote archipelagos reveal higher levels of secondary sympatry than archipelagos nearer to continental landmasses. The author suggests that secondary sympatry might be prevented by apparent competition mediated through pathogens that coevolved with host populations but are pathogenic in sister populations. The absence of numerous pathogens in remote archipelagos, therefore, would allow sister populations to achieve secondary sympatry more readily and accelerate diversification. By the same reasoning, species should accumulate relatively slowly within continental regions as well. This is a novel idea proposed to explain apparent levels of reduced secondary sympatry in certain geographical locations such as remote archipelagos. Given the relatively recent emergence of the study of diseases in natural populations of any species, it is understandable that this paper does not present a strict test of the proposed hypothesis, but an overall description of the 'pathogen hypothesis', which will surely open the field to a series of field and experimental studies.

In summary, Charles Darwin and his shipmates from the HMS *Beagle* were the first to collect small songbirds, now known as Darwin's (Galápagos) finches, exactly 175 years ago (Darwin 1839). These birds were later recognized as being closely related to each other but having evolved beaks of distinct shapes and sizes as adaptations for different food sources. As such, they became a classic example of many different evolutionary processes and continue to provide us with valuable insights into principles of evolutionary change. As this Special Issue illustrates, the new and exciting discoveries being made from studies on Darwin's finches and related groups are a true celebration of Darwin's legacy to modern science. It is certain that we will continue to use these iconic birds to educate, train and inspire future generations of researchers for a long time to come.

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