

Sisyphean evolution in Darwin’s finches

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ABSTRACT

The trajectory of speciation involves geographic isolation of ancestral populations followed by divergence by natural selection, genetic drift or sexual selection. Once started, the process may experience fits and starts, as sometimes diverging populations intermittently reconnect. In theory populations might cycle between stages of differentiation and never attain species status, a process we refer to as Sisyphean evolution. We argue that the six putative ground finch species (genus *Geospiza*) of the Galápagos Islands represent a dramatic example of Sisyphean evolution that has been confused with the standard model of speciation. The dynamic environment of the Galápagos, closely spaced islands, and frequent dispersal and introgression have prevented the completion of the speciation process. We suggest that morphological clusters represent locally adapted ecomorphs, which might mimic, and have been confused with, species, but these ecomorphs do not form separate gene pools and are ephemeral in space and time. Thus the pattern of morphological, behavioural and genetic variation supports recognition of a single species of *Geospiza*, which we suggest should be recognized as Darwin’s ground finch (*Geospiza magnirostris*). We argue that instead of providing an icon of insular speciation and adaptive radiation, which is featured in nearly every textbook on evolutionary biology, Darwin’s ground finch represents a potentially more interesting phenomenon, one of transient morphs trapped in an unpredictable cycle of Sisyphean evolution. Instead of revealing details of the origin of species, the mechanisms underlying the transient occurrence of ecomorphs provide one of the best illustrations of the antagonistic effects of natural selection and introgression.

Key words: adaptation, Darwin’s finches, Darwin’s ground finches, *Geospiza*, Sisyphean evolution, speciation.

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I. INTRODUCTION

‘The gods had condemned Sisyphus to ceaselessly rolling a rock to the top of a mountain, whence the stone would fall back on its own weight.’—

Albert Camus

The origin of new species has a generally well understood timeline. First, populations with heritable variations become isolated geographically (Mayr, 1942). In isolation, drift, natural selection or sexual selection act on these variations over time to yield recognizably new units of biodiversity, or species (Coyne & Orr, 2004). The process, however, may have fits and starts. Isolation might prove incomplete (Nosil, 2012), establishing an antagonistic interaction between the divergent effects of selection and the homogenizing effects of gene flow. In some cases, especially where geographic isolation is long-standing, divergence may ‘win out,’ leading to the evolution of new species. Alternatively, gene flow may persist, leading to the reversion of diverging populations into a single panmictic species. However, because the strength and direction of selection pressures often fluctuate over time (Siepielski, DiBattista & Carlson, 2009), populations could remain in an extended cycle of divergence and reticulation, a process we term Sisyphian evolution. Our use of a Sisyphian analogy is not meant to imply that speciation is inevitable or that populations strive to reach species status, rather that the relative strengths of divergence and reticulation fluctuate, sometimes moving in the direction of speciation and other times moving in the opposite direction. During this Sisyphian period, speciation *per se* cannot easily be studied because the outcome of the process (i.e. whether or not it will lead to new species) is unpredictable, thereby confounding adaptive divergence and the origin of species (Mayr, 1963). We suggest that for almost a century, a dramatic example of Sisyphian evolution has been confused with the standard model of species divergence in one of the most famous examples in evolutionary biology, the finches of the Galápagos Islands, now popularly referred to as Darwin’s finches.

II. OVERVIEW OF DARWIN’S GROUND FINCHES (GEOSPIZA)

(1) A brief systematic history of *Geospiza*

Darwin’s finches have become textbook icons of evolution (Freeman & Herron, 2003; Futuyma, 2005) and one of the most famous examples of an adaptive radiation (Futuyma, 2005, p. 62). The best-known members of this famous radiation are the ground finches (*Geospiza*), which, after 40 years of intensive long-term study, provide one of the most cited examples of natural selection in the wild (Grant, 1999) as well as a picture

of the early stages of speciation (Grant & Grant, 2008*b*). More controversially, studies of *Geospiza* have suggested that hybridization may have played a creative role in facilitating animal speciation (Grant & Grant, 2008*b*). These evolutionary inferences depend on a sound understanding of Darwin’s finch systematics, but systematic problems have plagued the finches since their discovery (Zink, 2002).

Originally described as 10 species (Gould, 1837), ground finch populations have been rearranged in various combinations into 6 (Lack, 1947), 9 (Swarth, 1931; Snodgrass & Heller, 1904), 11 (Salvin, 1876), 12 (Rothschild & Hartert, 1902), 23 (Ridgway, 1896), and 27 (Sharpe, 1909) species with a total of 33 taxonomic names (i.e. species or subspecies) applied within the genus. This in part reflects changing taxonomic philosophies; when the subspecies concept became prevalent, many allopatric species were ‘demoted’ to subspecies status. However, not all taxonomic disputes involved the status of allopatric forms. Ridgway (1896) identified at least eight (and possibly nine) different ground finch species on Santiago Island, but these eight species have been considered subsequently to represent five species. To illustrate some of the taxonomic confusion, a single series of specimens was classified as *Cactornis hypoleuca* (Ridgway, 1890), *Camarhynchus pallidus* (Ridgway, 1896), *Geospiza pallidus* (Rothschild & Hartert, 1902; Sharpe, 1909), *Cactospiza pallida pallida* (Swarth, 1931; Hellmayr, 1938; Lack, 1945), and *Camarhynchus pallidus pallidus* (Lack, 1969; Paynter, 1970).

Difficulties in distinguishing species were acknowledged by many early students of the group. Ridgway (1896, p. 508) lamented that his species were ‘so gradually connected by intermediate types that there seems no possibility of satisfactorily subdividing [*Geospiza*] into two or more sections.’ Similarly, Swarth (1931) suggested that one could arrange all museum specimens from smallest to largest without revealing a morphological gap. Thus, generations of avian taxonomists failed to produce a consistent classification of Darwin’s finches. Although systematics entered an era of character-based numerical and phylogenetic analyses, the last assessment of species limits was Lack’s (1947) intuitive classification over 60 years ago.

Intensive long-term studies over the ensuing 60 years have revealed new aspects of ground finch ecology and evolution that provide perspective on their evolutionary history. Drawing on this new evidence, we show that the six putative species of ground finch fail standard criteria for species recognition under all species concepts, lending more understanding to past taxonomic flux. We argue that morphological variants within *Geospiza*, which are more consistent with the definition of ecomorphs, have been prevented from completing the speciation process by the dynamic and unpredictable environment of the Galápagos, which has constrained the ground finches in a process of Sisyphian evolution.

(2) A review of the differences among putative species

Ground finches do not differ discretely in characteristics that typically delimit avian species, such as plumage patterns, song, or breeding behaviour (Lack, 1947; Ratcliffe, 1981; Grant & Grant, 2008b), and surveys of neutral genetic variation have uncharacteristically revealed genetic homogeneity among all species in the genus (Ford, Ewing & Parkins, 1974; Polans, 1983; Freeland & Boag, 1999; Sato *et al.*, 1999). In fact, the F_{ST} value across the genus was not significantly different from zero (Zink, 2002), an unprecedented observation for six species in a single genus. An in-depth DNA sequence study (Freeland & Boag, 1999, p. 1560) concluded that their results 'must call into question the suitability of designating the ground finches as six distinct species.' In addition, nuclear microsatellite studies have reported no species-specific diagnostic alleles within *Geospiza* (Petren, Grant & Grant, 1999; Grant *et al.*, 2004; Grant, Grant & Petren, 2005; Petren *et al.*, 2005; Grant & Grant, 2010). Thus, neither organellar nor nuclear data supported the six-species classification.

Body size and bill size and shape vary within the ground finches (Lack, 1947; Grant & Grant, 2008b), and could provide species-recognition cues. It was believed that ground finch species overlapped morphologically (e.g. Ridgway, 1896), but a principal component analysis (PCA) of external traits led Grant *et al.* (1985, p. 25) to conclude, '... the morphological classification of museum specimens of Darwin's finch species is sound.' However, Grant *et al.* (1985) analysed character means for each island and thus did not take into account size and shape variation within island populations.

(3) A re-evaluation of principal component evidence

We reassessed the distinctiveness of the six putative *Geospiza* species using a PCA that incorporated within-island variation. Measurement data were taken by H. S. Swarth and consisted of six measurements (wing length, tail length, tarsus length, culmen length, bill width, and bill depth) from 501 male specimens representing the six putative *Geospiza* species. Specimens were collected from 16 different islands and included approximately 10 individuals per species per island (50 populations total). All measurements were made to the nearest 0.1 mm. Measurements were log-transformed, and a PCA based on a covariance matrix was used to reduce morphological variables into fewer, independent dimensions. All statistical analyses were performed using the program SPSS v. 20.0.

Results showed that putative *Geospiza* species occupied overlapping, contiguous regions of principal component space (Fig. 1). The first three principal components explained 99% of the variation. All factor loadings on PC1, which explained 92.0% of the variation, were positive, indicating PC1 was an overall size axis. PC2 (5.2% of variation) and PC3 (1.6% of

variation) had factor loadings for bill dimensions that were of mixed sign, suggesting that PC2 and PC3 were axes of bill shape. The first two principal components from our analysis were essentially the same as the two principal components recovered by Grant *et al.* (1985).

One might argue that, because morphological overlap is generally confined to the edges of putative species clusters, these data support the six currently recognized ground finch species. However, this result would obtain simply because specimens were initially identified using body size and bill shape. Therefore it would be circular to conclude that those specimens formed dispersed but overlapping clusters based on an analysis of those same body size and bill shape characters. We suggest that, given these data, the real test of species limits is determining the extent to which specimens form multiple morphological clusters when *a priori* specimen identifications are ignored.

Owing to substantial interisland variation within, and overlap among, putative species (Figs 1 and 2), without *a priori* identification of individuals to species (Fig. 1A, C), it is difficult to discern six morphological clusters of individuals (Fig. 1B, D). Thus, we concluded that our PCA of morphological measurements did not support the existence of six discrete entities within *Geospiza*. Instead our analysis (Fig. 2) supports Swarth's (1931) hypothesis that the species taxa grade continuously in size and shape from the smallest *G. fuliginosa* to the largest *G. magnirostris*.

(4) Ground finch phenotypes over time

Island-specific morphologies show temporal instability. Studies on the islands of Daphne Major (Grant & Grant, 2002) and Genovesa (Grant & Grant, 1989) have documented significant morphological change in ground finch morphology over short time intervals, which results from temporally unstable, and reversible, selection pressures driven by the El Niño-Southern Oscillation phenomenon (Grant & Grant, 2002). From 1976 to 1983, available food resources on Daphne Major did not favour intermediate phenotypes between two putative species (*G. scandens* and *G. fortis*). Following the El Niño event of 1982–1983, the distribution of food resources changed and phenotypically intermediate individuals survived as well or better than parental 'species' (Grant & Grant, 2002). Subsequently, high intermediate fitness caused morphological convergence of the putative species suggesting to Grant & Grant (2006b, p. 99) that the two forms were 'despeciating'. More recently, however, environmental conditions have shifted again, and the two 'species' appear to be in the process of re-diverging, prompting Grant *et al.* (2004, p. 1596) to conclude that 'the two species on Daphne may approximately follow a 25-year periodicity in alternately converging through hybridization and selection and diverging through selection alone.' Given that gene flow both among islands and among putative species

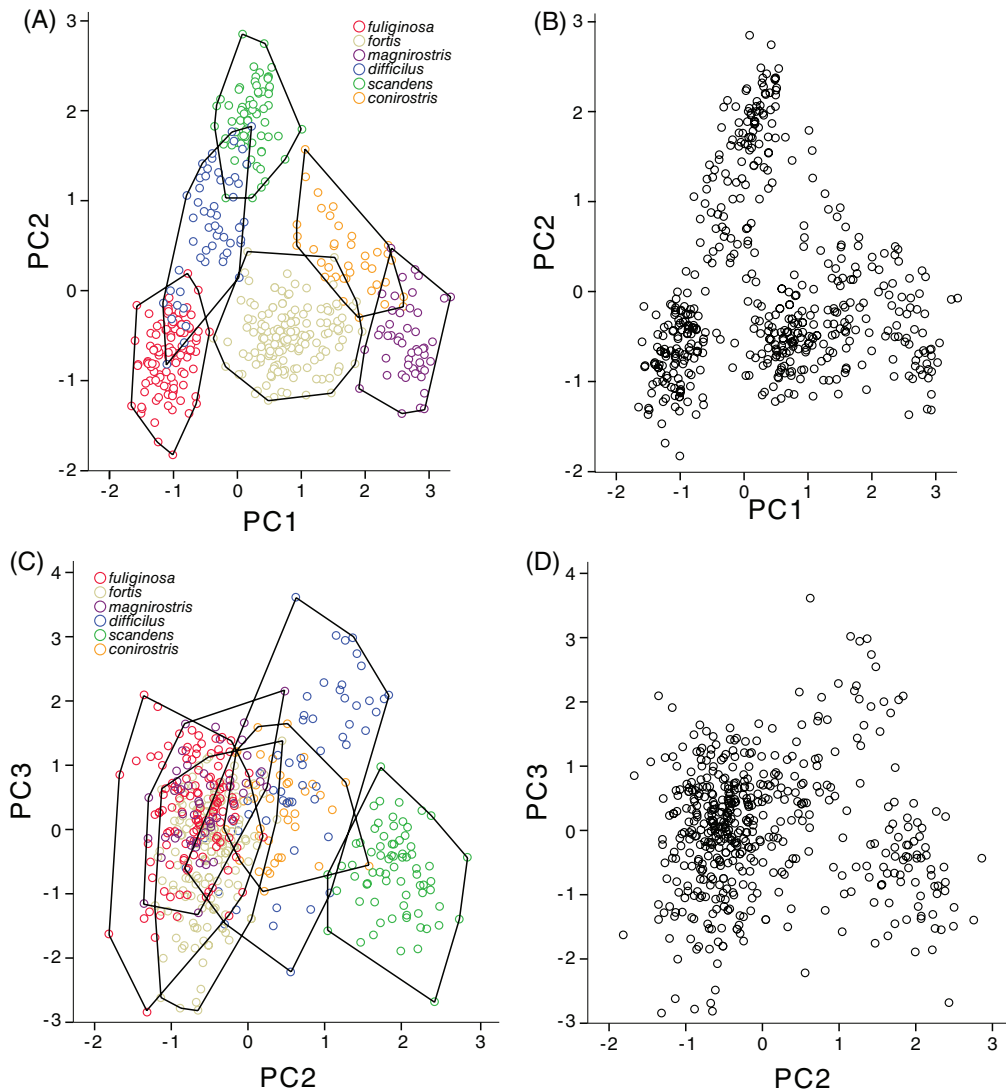


Fig. 1. Results of a principal components analysis of six morphological measurements made from *Geospiza* specimens. These measurements include the principal external attributes known to vary among *Geospiza* species. Principal component (PC) 1 was an overall size component, whereas PC2 and PC3 were bill-shape components. Because individual finches were identified to species using the same morphological features that were used to create principal components, it is inevitable that samples cluster by putative species. When species envelopes (A, C) are removed, it is difficult to discern six different clusters of individuals (B, D).

is widespread, Grant & Grant (2008a) suggest that this fusion–fission dynamic may be a general phenomenon. We suggest that this phenomenon has been wrongly equated with the standard allopatric model of speciation and instead represents the process of Sisyphian evolution.

III. SPECIES LIMITS AND THE EVIDENCE

All prior interpretations of speciation and adaptive evolution in Darwin's finches assumed that the species classification correctly represented evolutionary history.

Thus, the six species should clearly be species under at least one species concept. Using a published list of major species concepts and the criteria employed for recognizing species (i.e. de Queiroz, 2007), we evaluated whether each ground finch species met requirements for species status. This assessment is possible only because of the wealth of new ecological and behavioural information on the finches, but has not been previously attempted.

(1) Biological species concepts

Lack (1947) divided *Geospiza* into six biological species because he thought hybridization among species was

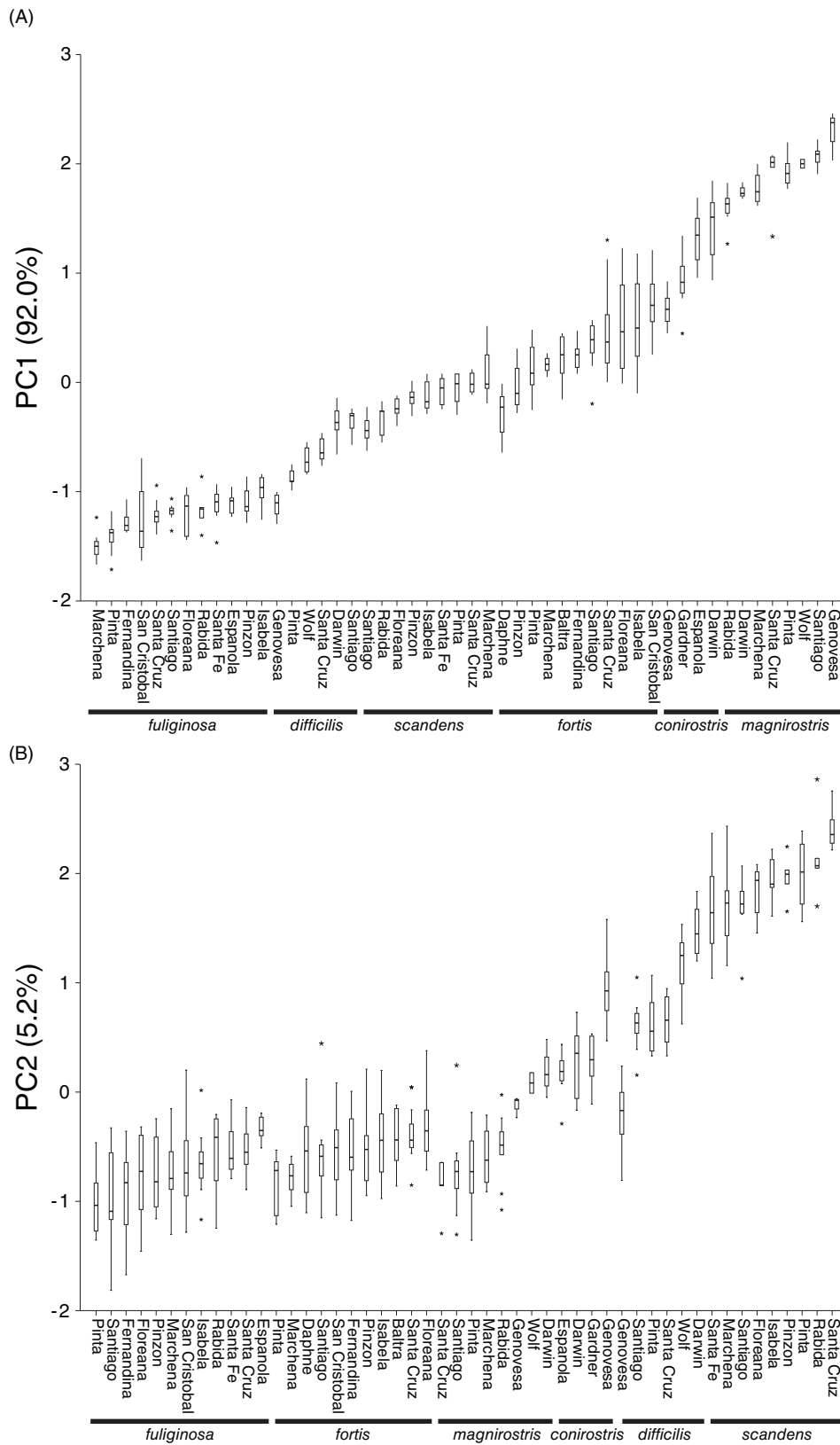


Fig. 2. (A, B) The first two principal components of six morphological measurements of *Geospiza* grouped by species and by island. Note that there is high individual variation within island populations as well as high population variation within species.

extremely rare, if not completely absent. This view prevailed for several decades, but it is now known that mispairings among the six putative species occur regularly and that 'hybrid' offspring are viable and fertile (Grant & Grant, 1997). Under a strict interpretation of the biological species concept (e.g. Dobzhansky, 1937; Mayr, 1942), production of viable and fertile hybrids invalidates the six ground finches as species.

Some proponents of the biological species concept relax criteria for species recognition. Coyne & Orr (2004, p. 30) characterize biological species as having 'substantial but not necessarily complete reproductive isolation.' They later state (p. 31) that biological species cannot be 'distinct at only a few loci but freely exchange genes in the rest of the genome.' Grant & Grant (2006*b*) estimated that 'hybrid' pairings make up 1–2% of those observed on Daphne Major, although rates as high as 73% have been reported (Grant, 1993). Introgression among putative species is persistent across years, and Grant *et al.* (2005) suggest that it is widespread across the archipelago. Further, introgression is not confined to a hybrid zone, and occurs haphazardly in space and time. Gene flow is a powerful force (Wright, 1931), and although natural selection might yield statistical differences in the frequencies of genes associated with body and bill size, there are seemingly no mechanisms preventing putative *Geospiza* species from freely exchanging genes in the rest of their genomes through widespread and persistent introgression.

Paterson (1978, p. 369) proposed that 'members of a species share a common specific mate recognition system.' Mate-choice experiments have demonstrated that putative ground finch species do not possess range-wide mate-recognition systems. Males presented with models from foreign islands did not preferentially choose supposed conspecifics over heterospecifics (Ratcliffe & Grant, 1983), and there is no indication that they consistently recognize allopatric populations of their own 'species' as conspecific. There is also no species-specificity in song (Ratcliffe, 1981, p. 1), which is culturally inherited (Grant & Grant, 2008*b*); Ratcliffe & Grant (1985, p. 290) stated that 'The songs of the six different species of Darwin's ground finches (*Geospiza*) on the Galápagos Islands are difficult to distinguish unambiguously because of high levels of intraspecific variation and interspecific similarity in some cases.' This rare, if not unprecedented, observation for an avian genus is perhaps unsurprising, however, considering that different island populations of the same named species do not necessarily share a common ancestor and many similar phenotypes are believed to have evolved through convergence (Petren *et al.*, 2005).

Podos (2001) suggested that birds with large beaks sing songs with low rates of syllable repetition that span a narrow frequency range, whereas the opposite was true for small-beaked birds. He further suggested that birds mated assortatively based on these song (and beak)

characteristics. Although this might provide a mechanism for assortative mating of birds with similar morphologies, the ground finches are not either small or large but instead represent a gradation from small to large size, thereby eliminating the prospect of maintaining discrete morphological types through song- or beak-based mate-choice cues.

Some might argue that although species limits are obscured when considered across the Galápagos archipelago as a whole, species limits are more clear-cut when comparing sympatric species (Grant & Grant, 2008*b*). For example, song differences (Ratcliffe, 1981) and song discrimination (Ratcliffe & Grant, 1985) are statistically stronger between sympatric species pairs than between allopatric species pairs. However, countering this trend, Grant (1984) reported that female *G. conirostris* on Genovesa avoid mates with songs similar to their fathers, which Goodale & Podos (2010) suggest is a result of selection to avoid inbreeding (see also Vagvolgyi & Vagvolgyi, 1989).

The expectation under any biological species concept is that the six putative ground finch species comprise six distinct and isolated gene pools. The question then becomes whether observed local isolating mechanisms are sufficient for maintaining six reproductively cohesive gene pools across the islands. We argue that the weight of evidence suggests they are not. In fact, there is a growing body of evidence indicating that the breakdown and reversal of local isolating mechanisms may be common (Grant & Grant, 2008*b*; Grant & Grant, 2014; Kleindorfer *et al.*, 2014). This combined with the widespread interisland movement of individuals that are seemingly immune to any existing local isolating mechanisms seriously undermines the hypothesis that ground finches distributed across the Galápagos Islands are organized into six distinct and isolated gene pools. As we argue below, the available evidence is more consistent with a paradigm of ecologically driven morphs, selectively maintained collections of adaptive body size and bill shape alleles, that are formed, rearranged, and broken down dynamically within the sea of a single gene pool.

(2) Ecological species concept

Given their well-studied ecological differences, one might think Darwin's ground finches would be ideal candidates for ecological species. Van Valen (1976, p. 233) defined an ecological species as 'a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range.' Even if one set aside the fact that there is considerable morphological overlap among species to argue that the six *Geospiza* species occupy different adaptive zones, invoking the lineage criterion remains an obstacle. Van Valen (1976, p. 233) defined lineages *sensu* Simpson (1961) as 'an

ancestral-descendent sequence of populations.' This requirement was meant to keep populations that had independently evolved the same adaptation from being lumped as the same species. However, there is evidence that *Geospiza* populations do independently evolve the same morphological adaptations (Petren *et al.*, 2005), so the six currently recognized ground finch species are not population lineages and therefore cannot be ecological species.

(3) Evolutionary and phylogenetic species concepts

Evidence that *Geospiza* species are not evolutionary lineages invalidates them as species under the evolutionary (Simpson, 1951; Wiley, 1978) and Hennigian (Hennig, 1966; Meier & Willmann, 2000) species concepts. Templeton's (1989) cohesion species concept emphasized intrinsic mechanisms that promote the genetic relatedness of individuals and populations within a species, but it also defined species as evolutionary lineages. Phylogenetic species concepts use character evidence to predict common history. Monophyletic definitions (Donoghue, 1985; Mishler, 1985) require derived characters (apomorphies). Genealogical definitions (Avice & Ball, 1990; Baum & Shaw, 1995) require exclusive coalescence of alleles. Diagnosable species definitions (Cracraft, 1983; Nixon & Wheeler, 1990) require diagnostic (i.e. fixed) characters. The six currently recognized *Geospiza* species are not known to possess apomorphies, exclusive coalescence of any genes, or fixed character differences; thus, they cannot qualify as species under any of these concepts.

(4) Phenotypic and genotypic cluster concepts

The phenetic species concept defines species as 'a group of organisms not itself divisible by phenetic gaps resulting from concordant differences in character states ... , but separated by such phenetic gaps from other such groups' (Michener, 1970, p. 28). Mallet (1995, p. 296) defined genotypic cluster species as 'identifiable genotypic clusters ... recognized by a deficit of intermediates, both at single loci (heterozygote deficits) and at multiple loci (strong correlations or disequilibria between loci that are divergent between clusters).' It is not possible to reconcile the current six species paradigm with either phenetic or genetic cluster species concepts. The ground finches do not form six morphological clusters (Fig. 1). Furthermore, if statistical differences among populations were equated with clusters, then ground finches would represent many more than six species because most allopatric island populations have statistically different average phenotypes (Fig. 2) (Grant, Grant & Petren, 2000). Intraspecific 'morphs' of the same species on the same island, such those described for *G. fortis* on Santa Cruz Island (Hendry *et al.*, 2009) would also have to be recognized as species under cluster concepts. Therefore, under cluster concepts,

Geospiza would either be considered a single variable species or dozens of cluster species, but not six species.

(5) A new species taxonomy for the ground finches

Barring evidence for multiple species, a single species of *Geospiza* should be recognized. *Geospiza magnirostris* was the first taxon mentioned in Gould's (1837) original description, and we refer the formerly recognized six species of *Geospiza* to a single species, Darwin's ground finch (*G. magnirostris*). This highly variable species consists of non-random clusters of individuals within and among islands but these are not congruent with genetic data nor do they qualify as evolutionarily independent taxa (Freeland & Boag, 1999) or species by any prior definition. We characterize these clusters as evolutionarily transient ecomorphs. Given this view, we note that the process of morph generation is ongoing. For example, two phenotypic clusters of individuals on Santa Cruz Island are considered to be morphs of *G. fortis* (Ford, Parkin & Ewing, 1973; Huber *et al.*, 2007; de Leon *et al.*, 2010). Two morphs of *G. conirostris* were reported earlier on Genovesa (Grant & Grant, 1979). Identifying all phenotypic clusters within *Geospiza* as morphs is a more consistent way to characterize variation, although each morph does not require or deserve a separate Linnaean name.

IV. WHY HAVE GROUND FINCH ECOMORPHS NOT BECOME SPECIES?

Widespread introgression and oscillating selection pressures, hallmarks of the Sisyphean process, are likely the primary reasons for a lack of speciation within *Geospiza*. Ground finch individuals move among islands and establish immigrant populations that interbreed with local residents (Grant & Grant, 2008b), sometimes at high rates (Grant, 1993). Divergent selection that might reinforce allopatric divergence or cause sympatric speciation (Nosil, 2012) is unstable, and replaced periodically by convergent selection. As a result, ecomorphs track local adaptive peaks that are ephemeral in space and time (Fig. 3). Populations on some islands might be extirpated by droughts, but with later amelioration of ecological conditions, these islands are recolonized by individuals from other (perhaps several different) islands, and natural selection rapidly fits new populations to existing resource peaks. The ever-changing adaptive landscape combined with pervasive introgression among ecomorphs prevents completion of the speciation process and the maintenance of discrete, isolated gene pools or evolutionarily independent lineages. Thus, the observed pattern of divergence at any one time represents one of many possible ephemeral states on a dynamic adaptive landscape (Fig. 3). An example of this process can be found in the analysis by Vagvolgyi &

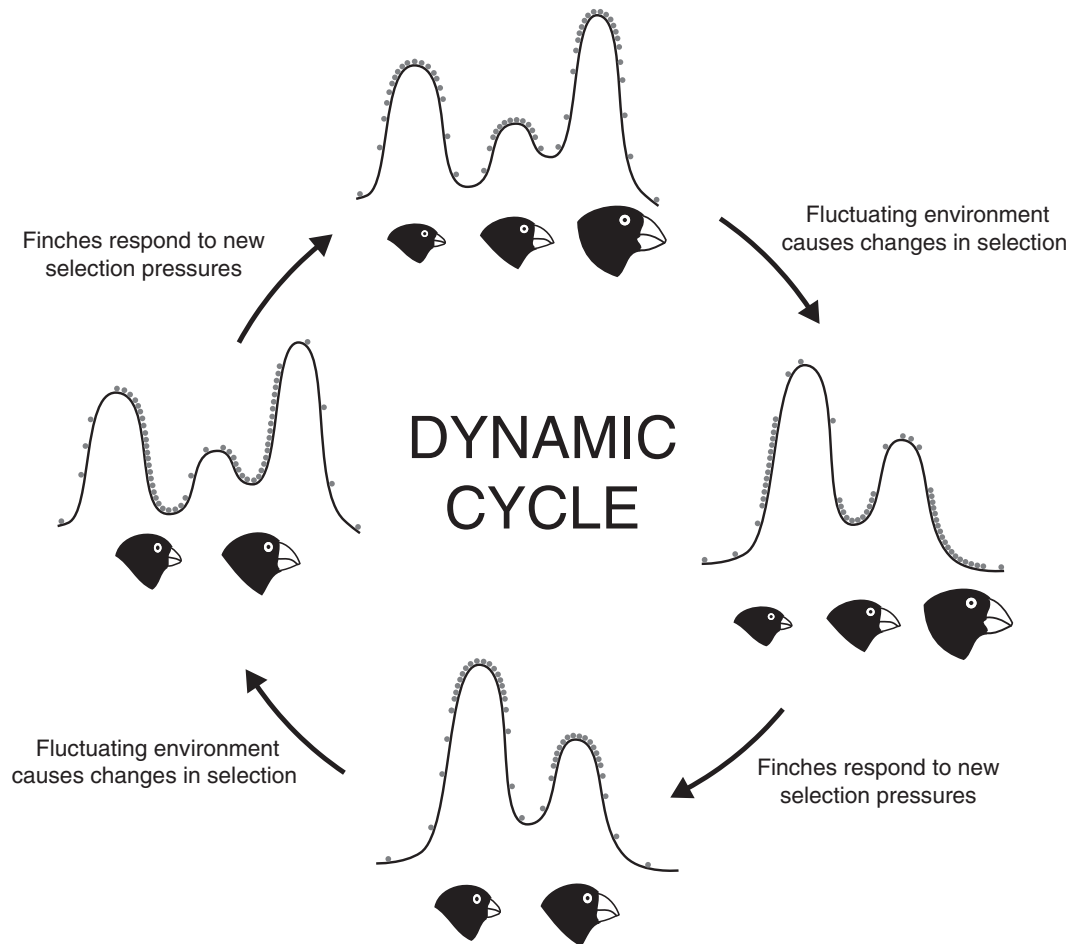


Fig. 3. A conceptual diagram illustrating the evolutionary dynamics ongoing within *Geospiza* on the Galápagos Islands. Curved peaks represent the distribution of food resources, and grey circles represent where the morphology of finch individuals falls along resource peaks. The fluctuating environment of the Galápagos changes the temporal distribution of food resources. After some time, finch populations (represented by multiple individuals), which we consider to be ecomorphs, adapt to the new environment. The environment changes again and so on, resulting in a dynamic cycle whereby cyclical environmental change is followed by a corresponding cyclical change in the morphology of finch populations. The ephemeral nature of phenotypic clusters within *Geospiza* is consistent with a paradigm of intraspecific polymorphisms and not multiple species. In terms of speciation, the net result of this process, which we call Sisyphian evolution, is unpredictable, but has not yet led to more than one species of *Geospiza*.

Vagvolgyi (1989, p. 147): ‘... Genovesa supports *G. difficilis* which, in the absence of the competing species *G. fuliginosa*, underwent profound changes in its diet and morphology to become deceptively similar to the absent competitor.’

V. CONSEQUENCES OF THE NEW PARADIGM

Recognizing a single species of *Geospiza* affects many evolutionary conclusions drawn from prior studies. Darwin’s finches as a whole represent a less-impressive adaptive radiation from the standpoint of species diversity. That is, instead of 14 species, there are only nine; however, species status in the genus *Camarhynchus* has

also been challenged (Zink, 2002; see also Kleindorfer *et al.*, 2014), and it seems likely that the same Sisyphian processes occur in that genus as well. Importantly, it should be recognized that the process of local morphological adaptation within *Geospiza* does not necessarily represent the speciation process, as speciation has not yet occurred. One might ponder whether the processes of divergence driven by natural selection does not in fact provide information about the speciation process, irrespective of whether there are 1 or 6 or 30 species of *Geospiza*. We suggest that we know about speciation because there are species. Therefore, if all six previously recognized species are in fact ecomorphs of a single species, then the evolutionary processes that influence them are those that result in geographic variation and local adaptation, but are not necessarily

those that lead to 'good' species. That is, the nature of morphological differences among the major lineages of Darwin's finches are of a different quality than the continuously varying ones within *Geospiza* (and possibly *Camarhynchus*). Mayr (1942) noted that although species might evolve through a subspecies stage, not all subspecies become species; the same could be said of ecomorphs. An ecomorph caught in a Sisyphean process might eventually give rise to additional species if the divergent effects of selection overcome the homogenizing forces of gene flow. However, the future environmental conditions and genetic backgrounds from which new species might eventually emerge are unpredictable, so it is counter-productive to formally recognize ecomorphs as species.

The single-species paradigm reverses the hypothesized role of introgression within ground finches (Seehausen, 2004). If *Geospiza* is a single species, introgressive hybridization had no role in promoting speciation. In fact, high rates of interisland immigration and persistent introgression among ecomorphs retards the speciation process, as is thought to be the case in the majority of animal systems (Dowling & Secor, 1997). Our model (Fig. 3) predicts the observed phenotypic overlap and lack of genetic differentiation (Freeland & Boag, 1999), and reinforces the homogenizing effect of introgression.

The existence of but one species in *Geospiza* compromises phylogenetic reconstructions and interpretations of prior hypotheses. Phylogenetic studies using various methods and sources of data (Lack, 1947; Yang & Patton, 1981; Schluter, 1984; Freeland & Boag, 1999; Petren *et al.*, 1999, 2005; Sato *et al.*, 1999) yielded 12 resolved phylogenetic trees, each of which supports a different pattern of ground finch relationships. Because a group of species has a singular evolutionary history, this result is disconcerting, although it helps understand the inconsistent classifications of previous taxonomists working with museum specimens. Given that the morphs do not have independent evolutionary histories, phylogenetic mapping of traits within *Geospiza* will be misleading. For example, Abzhanov *et al.* (2006) found no concordance between the expression of calmodulin, a gene implicated in bill development, and a phylogenetic tree. In retrospect, this observation is understandable given that there has been no phylogenetic evolution within *Geospiza*.

Conclusions about the workings of natural selection within the ground finches would not change under a single-species paradigm. In fact, it is the driving force in our view of the process of Sisyphean evolution. Populations within *Geospiza* clearly adapt to changing environmental conditions and the ground finches are still among the best examples of natural selection in nature, illustrating both the magnitude and rate of adaptive morphological change. However, character displacement in the ground finches (Grant & Grant,

2006a) needs to be reinterpreted in the context of intraspecific polymorphisms rather than in the context of interacting species.

VI. SYNTHESIS

Some might argue that we have provided simply an alternative explanation for the patterns of morphological, genetic and behavioural variation in *Geospiza*. However, alternative explanations exist when there is strong evidence supporting contrasting viewpoints. We find no convincing evidence supporting the existence of six species of *Geospiza*, and conclude that the most parsimonious explanation is that there is a single species. Hence, the evolutionary history of *Geospiza* has been misunderstood. It does not support the standard textbook model of insular allopatric speciation, as speciation has not occurred, but instead has been continually stalled or reversed. This view of ongoing evolutionary processes explains the observed patterns of morphological and genetic variation, and demands a thorough conceptual reinterpretation of the evolution of the ground finches of the Galápagos.

Islands are generally regarded as providing a clearer understanding of ecological and evolutionary processes owing to their relative simplicity compared to continental ecosystems (Losos & Ricklefs, 2009). The antagonistic forces of natural selection and gene flow operate in all ecosystems but are perhaps nowhere better revealed than in *Geospiza*. Sympatric morphs adapted to different food resources are not uncommon in vertebrates (Skúlason & Smith, 1995), although Darwin's ground finch represents a particularly dramatic example. Given the complexity and uniqueness of the patterns of morphological and genetic variation, it is perhaps unsurprising that it has taken decades to unravel the ground finch's history and to reconcile the historically unstable taxonomic history with an evolutionary explanation. We suggest that this new paradigm redefines the iconic nature of this group and makes the finches even more important to our understanding of the evolutionary process.

VII. CONCLUSIONS

(1) The six widely recognized species of Darwin's ground finch (*Geospiza*) from the Galápagos do not satisfy criteria for species status under any modern definition of species. We suggest they should be considered instead as a single species, Darwin's ground finch (*G. magnirostris*).

(2) Instead of a standard allopatric model of speciation, evolution within Darwin's ground finch is better characterized as a dynamic and unpredictable process, whereby morphological clusters, or ecomorphs, track

local adaptive peaks that are ephemeral in space and time. Thus, the observed pattern of divergence at any one time represents one of many possible ephemeral states on an ever-changing adaptive landscape.

(3) As a result of oscillating selection pressures, frequent dispersal, and pervasive introgression, ecomorphs are constantly cycling between stages of differentiation, although not-as-yet becoming separate species. We refer to this cyclical condition as Sisyphian evolution.

(4) Our new paradigm redefines the iconic nature of the group and makes the finches even more important to our understanding of the evolutionary process.

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