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Founder Events: Foundational in Rapid Post-Flood Diversification

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Abstract

A biblical view of natural history begins in Genesis. God created plant and animal life according to their kinds, telling them to reproduce and fill the earth. Another important historical event was the global Flood, where terrestrial and flying animal numbers were severely reduced. Again, the creatures preserved on the ark went on to reproduce and fill the earth. Although creationists reject universal common ancestry on biblical grounds, they still need to adequately account for the diversification and speciation that has occurred within the various kinds of animals since the Flood. Because a biblical model demands the rapid diversification of creatures into forms filling different ecological niches, or adaptive radiation, creationists have the opportunity and responsibility to contribute to our understanding of this important topic and thus show the relevance of the biblical model.

Many biologists recognize three sources of adaptive variation: environmentally based sorting of ancestral alleles, mutation, and hybridization. Conditions following the Flood would have led to an inordinate number of founding events, potentially contributing to environmentally based sorting of alleles. Evolutionists have done considerable work to understand the effect of founding events on subsequent populations. Much of that work is reviewed here. Yet a blind spot remains, as most techniques intended to identify the founder effect assume it is random and that founders do not select the new environment or niche. It is concluded that founder events were foundational in the rapid post-Flood diversification that has taken place in history, setting the stage for other processes that contributed to rapid speciation. There is a tremendous need for creation research to further elucidate key details and promote a biblical understanding of natural history.

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Introduction

The Bible presents crucial details of natural history. God created life on earth "according to their kinds" (Gen. 1:11–13, 20–31). He pronounced a blessing on them, directing them to reproduce and fill the earth (v. 22 and perhaps implied in v. 28). Humans, who were created in the image of God rather than according to their kinds, started with just two individuals (Gen. 1:26–28; 2:7–29). We are not given any specific figure for the number of individuals in any of the animal or plant created kinds. However, if it was two for the sexually reproducing animals that Adam was required to name, it would have highlighted to Adam the fact that he did not have a suitable helper prior to God creating Eve (Gen. 2:20).

Another pivotal event in natural history was the Flood (Gen. 6–8). In this event, eight humans and two animals from each created kind among flying and terrestrial creatures were preserved; all other creatures in these groupings died (Gen. 7:20–23). This describes what biologists call a population bottleneck, a sharp reduction in the size of a population due to environmental factors. This historical information makes it clear that within any specific kind of land animal or bird, the diversity we see today can be attributed to the diversity carried by the two individuals[1] on the ark and any diversity that has arisen within the thousands of years since the Flood.

The evolutionary worldview assumes a very different history: the diversity of all life descended naturalistically from a single common ancestor. Unfortunately, the distinction between the worldviews is often muddled since the word "evolution" has several meanings, ranging from the change in allele frequency in a population over time (which creationists recognize) to the idea that all life shares a common ancestor (which contradicts the history in Genesis). The latter would not only involve the formation of novel functional genes but also the placement of these genes into the complex, well-integrated networks that are characteristic of life—all by naturalistic processes.

Despite their differences, both evolutionists and creationists need to account for diversification and speciation in animals. Examples of diversification, such as changes in coat color or adaptation to high altitudes, do not involve the formation of new genes or regulatory networks. Instead, they involve adjustments in what already exists to allow for adaptation (Lightner, 2008; Lightner, 2014). Despite this, these types of examples are often promoted at the popular level as examples of evolution (implying it extends to universal common ancestry); the evolutionists who do so seem to be particularly blind to the fact that these examples *require* preexisting complex, well-integrated networks that were specifically designed to allow for such changes (Lightner, 2016a; Lightner, 2016b).

Ideas about the mechanisms involved in speciation have historically been dominated by theoretical work. This is because the mechanisms are normally inferred, based on observations of what currently exists today. Thus, the mechanisms are controversial, both in how they work and to what extent they contribute to speciation. Natural selection, genetic drift, and founder effect have all been debated for decades, and ideas have shifted as new evidence has come to light (Provine, 1989).

Based on extensive fieldwork, such as Peter and Rosemary Grant's prospective study of finches on the island of Daphne Major in the Galápagos (Grant and Grant, 2014), another mechanism has been demonstrated to affect allele frequencies in a population, and at times speciation—namely, hybridization. Other studies and molecular data appear to support this as well (Mallet, 2005; Berner and Salzburger, 2015; Pease et al., 2016). Currently, some biologists are now identifying three major mechanisms that play a role in rapid diversification and speciation (including adaptive radiations): (1) environmentally based sorting of ancestral alleles, (2) mutation, and (3) hybridization (Hedrick, 2013; Pease et al., 2016).

Regarding the environmentally based sorting of ancestral alleles, many people influenced by evolutionary ideology might think first of Darwin's idea of natural selection. While natural selection is a potential mechanism, it is not the first one that should come to mind in a biblical worldview (Lightner, 2015). The Bible lists two times in history when populations spread out from a localized place: after Creation and again after the Flood. Thus, through migration there may have been an unprecedented amount of environmentally based sorting, more than evolutionists would expect with their model. To understand how founder events affect the diversity we see today, we first need to examine how the concept of founder effect has been developed by the evolutionists.

Development of the Concept

Though Ernst Mayr first mentions the idea of the founder principle in his 1942 book (Mayr, 1942), the first significant discussion of the concept appeared years later in a book chapter entitled "Change of Genetic Environment and Evolution" (Mayr, 1954). The discussion was an attempt to address a peculiar pattern noted by taxonomists, where there are conspicuous differences in the most peripherally isolated populations that

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[1] Seven (or seven pairs) of the clean animals were brought on board (Gen. 7:2–3), but the extra animals were necessary for sacrifice and possibly for food for humans after the Flood (Gen. 8:20; 9:3). Though there may be isolated exceptions where more than two animals contributed to the gene pool, the repetition of "two" in the narrative makes it clear that two was the norm (Gen. 6:19–20, 7:2).

do not appear obviously attributable to natural selection alone.

Mayr pointed to the paradise kingfishers (*Tanysiptera hydrocharis-galeta* complex) as one example. On the New Guinea (now Western New Guinea and Papua New Guinea) mainland, three subspecies were recognized that were all very similar in appearance. Yet when members of this group were found on the surrounding islands, they were different enough to be regarded as separate species. Ironically, the mainland has extremely different environments in different regions, yet morphologically the kingfishers are nearly identical. In contrast, kingfishers on the various islands are morphologically different from those on the nearest coast, which generally has very similar environmental conditions.

Mayr proposed that the islands had been invaded by a small number of breeding individuals. Due to the distance from the mainland, there was essentially no migration between the islands and mainland, and thus no gene flow. This contrasts with the mainland, where gene flow is known to occur between different populations and is ostensibly a major factor in maintaining phenotypic similarities between them (for a different view, see Lande, 1980). Mayr posited that the immigrants to the islands would carry only a fraction of the genetic diversity present in the original population.

Mayr argued that the genetic environment (or genetic background) is changed profoundly by a founder event, since many alleles present in the populations on the mainland were now absent. This would mean the alleles still present may have dramatically different selective values. Combining this with the effects of environmental and biotic factors, he postulated a rapid change in gene frequencies simultaneously at many loci, or in other words, a genetic revolution.

Mayr referenced the work of Sewall Wright, a cofounder of the field of population genetics. Wright introduced the concept of a fitness landscape, which compares fitness to a topographic map (Figure 1). Theoretically, natural selection would favor adaptive alleles and drive the population to an adaptive peak (Wright, 1932). The problem was that if there were a higher peak nearby, natural selection would prevent the population from crossing the intervening valley to reach it.

Wright pointed out that in smaller populations—even in the absence of selection, mutation, or migration—allele frequencies would be expected to drift from previous values. This is because, assuming Mendelian inheritance, offspring carry a random sampling of the alleles of the parents. When the population is small, the random sample can easily differ from the parental population. Thus, alleles could be lost or fixed in a population by this random process, without the necessity of natural selection. This effect becomes negligible in a large population where individuals freely interbreed (Wright, 1931, confirmed by many since including creationists Carter and Powell, 2016).

So, genetic drift (from the random sampling of alleles from the parent population) became the mechanism proposed for knocking a population off a theoretical adaptive peak. If it landed at the base of a different adaptive peak, natural selection would carry it up that peak, which might be higher. Now evolutionists had two naturalistic mechanisms for significantly changing allele frequency in a population (which they commonly call evolution): natural selection and genetic drift. In Wright's shifting balance theory, both play an important role.

It is not uncommon for people to view Mayr's founder principle as a special case of Wright's shifting balance theory. Mayr suggested that a founding event would naturally result in a new population that carried a random sampling of alleles from the parent population, and thus it is an example of genetic drift. Mayr wrote of a shift from one set of coadapted alleles (in the parent population), through a period of instability to another equilibrium of balanced integration. This can be compared to traveling from one adaptive peak through an intervening valley to a second adaptive peak. However, several authors have cautioned that despite superficial similarities, considering Mayr's founder effect as merely a special case of Wright's shifting balance theory is overly simplistic (Provine, 1989; Templeton, 2008).

William L. Brown proposed an alternative that he felt would make a greater

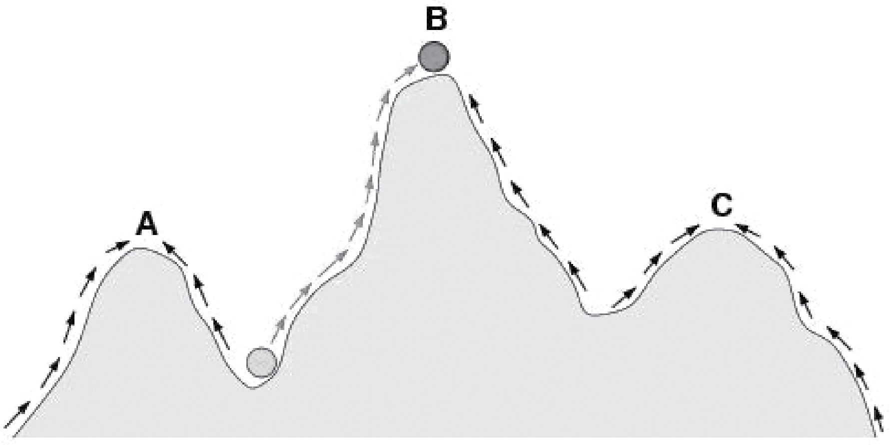

Figure 1. Simplified diagram of Sewall Wright's "fitness landscape." Original illustration by Claus Wilke used by courtesy of Wikipedia Commons.

contribution to speciation; he called it centrifugal speciation. He recognized that many populations have been observed to expand their geographical range into less favorable peripheral regions, only to later contract into more favorable refuges. He suggested that during the contraction there may be small breeding populations that remain in restricted pockets or on islands that are favorable enough for survival (Brown, 1957). This is essentially a founder event when they represent a small sample of the larger population, since gene flow is cut off between those remaining in the peripherally isolated pockets and the parental population.

Brown considered his hypothesis stronger than Mayr's because the characters providing the basis for speciation were derived from the more central regions of the population, where variability is naturally expected to be higher (Brown, 1957). In contrast, Mayr had stressed the loss of variability that he believed characterized the founders (Mayr, 1954), causing some to question their ability to further adapt. Both Mayr and Brown cited specific examples in nature where they believed the mechanisms they proposed might be operating.

Hampton L. Carson (1967) further developed the concept by introducing the term "population flush." This is a rare, rapid population growth usually mediated by environmental factors and accompanied by relaxed selection. During this time, an initially variable population could increase available variation dramatically through extensive recombination. Eventually the population would crash, and less favorable combinations of genes would be removed. Similar to Brown's hypothesis, occasional pockets of breeding individuals might remain after the crash and potentially provide the basis of new species.

Both Brown and Carson recognized the cyclic oscillations characteristic of many populations, incorporating it into their models. Both emphasized the importance of initial variability and a role for natural selection. Both recognized that small breeding populations left in the peripherally isolated pockets after the population size contracted could end up being swamped later during the next increase in population size. This, of course, would not lead to speciation. Yet Carson's proposal of relaxed natural selection during the flush theoretically allowed for considerable recombination to break apart previous gene associations that supposedly had been maintained during periods of stronger selection.

Interestingly, Carson discusses an example of a population flush involving inbred laboratory *Drosophila* strains maintained under constant conditions. A dramatic increase in population size was precipitated by the introduction of a single hybrid whose mother was from the population but whose father was from an unrelated laboratory strain. The population size nearly tripled even though the amount of food was kept constant. Carson recognized that this type of hybridization could occur when peripherally isolated pockets of an organism were brought back into contact with the parent population during a subsequent population increase, though he did not consider it as important as other factors (Carson, 1967, pp. 126–127).

Based on Carson's model, Alan R. Templeton developed the concept of "genetic transilience," a rapid shift in a multilocus complex that influences fitness, in response to a sudden perturbation in genetic environment (Templeton, 1980). As with Mayr's proposal, the emphasis was the change in the genetic environment (commonly known as genetic background) leading to altered selection. However, because Templeton postulated the involvement of a smaller number of epistatic genes, he chose to avoid the term "genetic revolution." Based on experimental work, he proposed that loci affecting fundamental development, physiologic, and life history processes were most commonly involved (Templeton, 1980, p. 1013).

Templeton (1980) discusses the various population structures, sampling patterns, and other variables that influence the probability of genetic transilience. As with many after Mayr, he recognized the importance of heterozygosity in the founders to allow for adaptation to the new environment; yet he places importance on inbreeding, which results in homozygosity at some loci. He incorporated both population genetics modeling and laboratory and field observations to develop his model in a way to give it predictive power.

One point of particular note is that Templeton (1980) states that there is no *one* model of founder speciation, a detail that often seems to be ignored in discussions of the topic (p. 1030). Indeed, it is impossible for there to be only one, since there are numerous circumstances, both genetically within the founders and in the environment, which can affect the outcome. These circumstances will vary between different populations. Thus, realistic population genetic modeling would need to be tailored to the specific situation.

There is really no debate that founder events occur. It is well established that a very small number of founders, even a fertilized or pregnant female, can go on to produce a population that can survive and reproduce. In the laboratory, isofemale lines are created by capturing a single wild fertilized female and breeding the offspring together. What has been debated is under what conditions a founder event will lead to speciation (Carson and Templeton, 1984; Lande, 1980; Barton and Charlesworth, 1984; Charlesworth and Smith, 1982; Templeton, 2008).

Empirical Evidence from Colonizations

There are many known colonizations that have not resulted in speciation.

Mayr (1954) mentions starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*) that were introduced to the United States from Europe. Examples such as these are believed to be generalist or "weedy" species that can colonize new territories but show little change as they do so (Carson and Templeton, 1984, p. 103). Nevertheless, information on colonizations of all types is important to understand how founding events affect the subsequent population. An accumulating number of empirical studies provide some key details in this regard.

In the studies that assess genetic differences, "neutral genetic variation" is generally used. This means short DNA segments that do not code for proteins are sequenced, and from this data, inferences are made. While there are many examples where genetic diversity decreased because of a founding event, there are others where no decrease was detected. Further, even in cases where decreased genetic diversity was identified, it was generally considered moderate (Clegg, 2009; Colautti and Lau, 2015).

Two measures of genetic diversity are often used: allelic diversity (the actual number of alleles at a locus) and heterozygosity (proportion of individuals who are heterozygous at a locus). It is common to find a greater decrease in the first measure than the second. This is because it is relatively easy for rare alleles in the parent population to be lost when a limited number of individuals found a new population. However, loss of rare alleles does little to affect overall heterozygosity. Heterozygosity is considered important in providing a basis for future adaptation of the population (Clegg, 2009).

In addition to the generally mild loss of diversity, there are a surprising number of examples suggesting that rapid adaptation has taken place (Bock et al., 2015; Colautti and Lau, 2015). One particularly interesting example involves the artificial introduction of the brown anole lizard, *Anolis sanrei*, onto seven small Caribbean islands where previous populations had been destroyed when the islands were submerged during a hurricane (Kolbe et al., 2012). This experimental colonization is worth discussing in more detail.

Hind limb length varies adaptively in anole lizards. Those with relatively longer legs can run faster on broad substrates, such as tree branches or trunks. Those with shorter legs in relation to their body size maneuver more deftly on narrower vegetation. The researchers randomly chose seven pairs of lizards from a population adapted to large vegetation and introduced one male and one female to each of the islands with small, scrubby vegetation. Each year they returned to take measurements and tissue samples for genetic analysis.

A clear founder effect was observed, with an average 46% decrease in allelic diversity and 23% in heterozygosity. Each of the new populations increased dramatically during the first two years and fluctuated thereafter. Within three years there was a highly significant decrease in relative hind limb length as the lizards adapted to the smaller vegetation on the islands. Yet despite this rapid adaptation, the genetic and phenotypic traits of the founders were still evident in each population.

One might propose that phenotypic plasticity was involved in this adaptive change, yet that seems unlikely given that the first generation had mean values that completely overlapped those of the founders. By the third generation, the mean relative hind limb length was nearly nonoverlapping. In the end, this study shows that founder effects can play an important role in island divergence, even in cases where adaptation occurs (Kolbe et al., 2012).

Not all introduced species have been observed to undergo such a rapid increase in population size from the outset. In fact, among invasive species it is commonly accepted that a lag phase occurs before a dramatic increase in growth rate (Bock et al., 2015). A variety of reasons have been proposed for this phenomenon. First, it may be that repeated colonization to increase standing variation is a necessary prerequisite in some cases. Second, it is possible that selection can take a while to act on standing variation. Additionally, the lag may be related to the time it takes for a suitable adaptive mutation to occur.

There are also nongenetic factors that may be involved in the lag phase associated with invasive species. These include a sudden change in environmental conditions or dispersal to a more suitable area. However, there may sometimes seem to be a lag phase because no one was really monitoring the population as it grew, and once it is noticed, it is subsequently reported in many new places. While this is an area where more research would be helpful, it is challenging because one cannot generally predict which species will become invasive so they can be monitored from the time they are first introduced (Bock et al., 2015).

Founder Mutations

The term "founder effect" is often used to refer to the loss of genetic variability in a new population (compared to the parent population) resulting from a founder event. It can also refer to the change in allele frequency resulting from the event, or to unique traits of the founders. In human medicine there is interest in specific mutations carried by the founder(s) (Ankala et al., 2015; Norcliffe-Kaufmann et al., 2016; Ossa and Torres, 2016).

Under most conditions, a new mutation can easily be lost from a population by genetic drift. This is because it starts out so rare, found only in a single individual. The probability of loss is greatest when the population size is large but declining. However, in the case of a founder event where one or more individuals carry a mutation, an increase in population size will result in the mutation becoming quite prevalent even in the absence of selection (Patwa and Wahl, 2008).

The NIH National Cancer Institute dictionary defines a founder mutation as a "genetic alteration observed with high frequency in a group that is or was geographically or culturally isolated, in which one or more of the ancestors was a carrier of the altered gene" (National Cancer Institute, n.d.). Founder mutations are generally recognized as a recurrent mutation seen on the same haplotype background in a specific population (Ankala, et al., 2015). In other words, the mutation shows up repeatedly in the population within the same neighboring DNA sequence.

Founder mutations can be used to trace ancestry, migration, and growth of populations; however, they are primarily of interest in human medicine because they are associated with a high frequency of recessive diseases in some populations (Ankala, et al., 2015). Examples range from mutations in BRCA1 and BRCA2 genes associated with breast cancer to the rare neurologic disorder familial dysautonomia, seen among the Ashkenazi Jews (Ossa and Torres, 2016; Norcliffe-Kaufmann et al., 2016). As genetic studies continue, more examples are continually being identified (Ankala et al., 2015).

Sorting Out the Variables

In many of the studies involving colonization, the biologists are interested in differentiating between random mechanisms involved in differentiation (i.e., founder effect and genetic drift) and natural selection. Natural selection is generally regarded to be the only mechanism to explain the adaptive differences that are identified. Yet there are other potentially confounding factors that need to be considered. Habitat choice and meiotic drive, for example, may be nonrandom and bias the conclusions.

Generally, evolutionists have assumed that habitat choice that matches adaptive traits to the environment is not involved in colonization. For example, Carson (1967) argued that it is not, perhaps partially because he was attempting to explain the existence of putatively "nonadaptive" characters in certain species. Yet Grant and Grant (2014) clearly documented a colonization where the genetic makeup of the birds that chose to stay and breed on the island was different from those that chose to leave before breeding. This emphasizes the fact that founding events are not necessarily random and that current methods to detect the founder effect are insufficient. The extent to which choice of a suitable environment affects the environmentally based sorting of ancestral alleles remains to be elucidated.

A second potentially confounding factor is meiotic drive. Meiotic drive refers to any of a variety of mechanisms that result in a non-Mendelian inheritance pattern. One example is biased gene conversion, where one allele (version of a gene) is preferentially copied onto the second allele during gene conversion. While evolutionists are aware of this phenomenon, their worldview motivates them to assume it is random with respect to fitness. Yet given the mathematical modeling showing natural selection is not usually very effective at fixing beneficial alleles, meiotic drive may well be a designed mechanism that would normally facilitate the spread of adaptive alleles in the population (reviewed in Lightner, 2015).

There has been discussion of the complexity of adaptive divergence by some in the field. For example, there are several potential sources for the adaptive alleles that natural selection is believed to work on. In addition to the standing variation in the founders, multiple introductions and hybridization can affect the allele distribution. Novel mutations can also be involved, and some authors even discuss the possibility of preadaptation (Bock et al., 2015; Colautti and Lau, 2015). However, currently used statistical methods are not able to identify the founder effect of preadapted organisms; instead, it is attributed to natural selection based on its nonrandom pattern.

Importance in the Creation Model

Understanding founder events is foundational in reconstructing a plausible natural history using a biblical perspective. After the Flood, there would have been massive global seed germination, since the land was cleared of previous plant life. Scripture mentions that plant regrowth commenced prior to anyone exiting the ark (Gen. 8:11–12). Observational evidence supports the fact that many seeds can germinate after extended exposure to water, even saltwater. In other cases, seeds transported in carcasses (e.g., the crops of dead birds) or sheltered in mats of vegetation would have opportunity to germinate as well (Howe, 1968). Additionally, vegetative propagation could have played a role in plant regrowth (Woodmorrape, 1996).

Not only would the organic matter left after the Flood have provided for vigorous plant growth, but many pollinators are flying creatures (insects, birds) that would have reached these open regions relatively quickly. Thus, by the time land animals migrated out to these regions of the world, there would already be well-established plant communities. Not only would migration and the founding of new populations have been a common occurrence in the years that followed the Flood, but conditions also would naturally be set up for the founder-flush phenomenon proposed by Carson.

As various creatures spread out, founding new populations, there would have been a tremendous amount of sorting of ancestral alleles, the first major component believed to be a part of adaptive radiations. Most of these ancestral alleles would likely have been part of the diversity initially created by God. It is important to note that evolutionary models assume there was no such thing as created heterozygosity, which introduces a bias in their models. This is the reason they make the ill-founded claim that humans must have descended from a group of several thousand individuals (Carter and Powell, 2016; Carter and Lightner, 2016; Hössjer et al., 2016). Yet given the command of God to fill the earth (Gen. 1:22; 8:17) and the importance of heterozygosity in allowing creatures to do so, considerable heterozygosity would logically have been present from the Creation.

There appear to be several factors associated with the environmentally based sorting of ancestral alleles. First, there is commonly some loss of variability when a new population is founded, especially when there are only a few individuals involved. Thus, not all alleles carried through the Flood would become a part of each new population. Much of this loss could be completely by chance, especially when there were many favorable habitats to exploit. At other times, however, the animals could have chosen environments they found most favorable, and thereby carried in alleles that were adaptive in that environment.

Interestingly, in a situation where a few animals carry in adaptive alleles by choosing the environment they find most favorable, it should increase the probability of future speciation. Templeton showed this in his correlated sampling example (Templeton, 1980, pp. 1022–1023). While the initial level of variability is reduced, adaptive alleles are already present. If the population remains isolated, inbreeding would accumulate at a faster rate, increasing chances of changes resulting in speciation. Currently, studies by evolutionists miss this because of the underlying assumption that animals do not choose new environments based on how well they are already adapted to them (e.g., Price, 2008, p. 49).

In summary, while many variables can play a role in diversification and speciation, the multiple founding events that occurred in the years following the Flood would have played a foundational role. In each of the newly founded populations, mutations, genetic drift, natural selection, and meiotic drive would have played variable roles in the process, depending on the specific conditions a particular population encountered. The degree of isolation also likely varied over time, allowing repeated colonization and hybridization to play a role in many cases.

Now it is incumbent on creationists to further develop our models to provide a more detailed, realistic understanding of natural history and how the factors described in the previous paragraph have contributed, under various circumstances, to the pattern of life we see today. This will require an integration of fieldwork, particularly prospective studies that track genetic (and epigenetic) changes through time, DNA analysis, and development of statistical tools and models that more closely reflect the complex reality involved in diversification and speciation.

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