PERSPECTIVE

doi:10.1111/evo.14268

SSE 75th anniversary SOCIETY for the STUDY of EVOLUTION

EVOLUTION INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

Neo-darwinism still haunts evolutionary theory: A modern perspective on Charlesworth, Lande, and Slatkin (1982)

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Received April 20, 2021
Accepted May 14, 2021

The Modern Synthesis (or "Neo-Darwinism"), which arose out of the reconciliation of Darwin's theory of natural selection and Mendel's research on genetics, remains the foundation of evolutionary theory. However, since its inception, it has been a lightning rod for criticism, which has ranged from minor quibbles to complete dismissal. Among the most famous of the critics was Stephen Jay Gould, who, in 1980, proclaimed that the Modern Synthesis was "effectively dead." Gould and others claimed that the action of natural selection on random mutations was insufficient on its own to explain patterns of macroevolutionary diversity and divergence, and that new processes were required to explain findings from the fossil record. In 1982, Charlesworth, Lande, and Slatkin published a response to this critique in *Evolution*, in which they argued that Neo-Darwinism was indeed sufficient to explain macroevolutionary patterns. In this *Perspective* for the 75th Anniversary of the Society for the Study of Evolution, we review Charlesworth et al. in its historical context and provide modern support for their arguments. We emphasize the importance of microevolutionary processes in the study of macroevolutionary patterns. Ultimately, we conclude that punctuated equilibrium did not represent a major revolution in evolutionary biology – although debate on this point stimulated significant research and furthered the field – and that Neo-Darwinism is alive and well.

KEY WORDS: Evolutionary theory, Gould, macroevolution, microevolution, punctuated equilibrium, species selection.

> "…there is, after all, no need to placate the ghost of neo-Darwinism; it will not haunt evolutionary theory much longer."
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> –Rosen (1986), *Evolutionary Theory: Paths into the Future*

In the first half of the 20th century, the effort to reconcile Darwin's research on evolution by natural selection with Mendel's work on the mechanics of inheritance gave rise to the Modern Synthesis (MS), which unified such disparate fields as genetics, systematics, embryology, and paleontology. Since its cohesion, the MS has faced regular challenges from diverse evolutionary fields (e.g., Eldredge and Gould 1972; Pollard 1984; Laland et al. 2014). Arguably, much of this controversy has arisen from the fact that, its name notwithstanding, the authors of the MS were not always working in conjunction; they often disagreed on the driving factors in evolution, and did not publish a conclusive, definitive summary of their work (although there were colloquia to discuss their work; Gayon and Huneman 2019). Even after the publication of *Evolution: The Modern Synthesis* (Huxley 1942), in which Huxley attempted to join the work of all the key players together, the MS continued to evolve as academic descendants of Fisher, Wright, Haldane, Dobzhansky, Simpson, Stebbins, and others refined and updated its principles. Even today, many papers that argue for the continuing relevance of the MS are not consistent in their definitions of what it actually is, often choosing to emphasize the factors or researchers most important to a particular field of study. This lack of cohesion also means that new knowledge may appear to be outside the scope of the MS.

Given the convoluted history of its development, the modern student of biology could be forgiven for being puzzled at what the MS actually is. For one, the MS has gone by several other names, including "neo-Darwinism" and simply the "evolutionary synthesis." Further, some definitional fuzziness may have arisen because the tenets of the MS are so widely accepted among today's practicing biologists that they are no longer identified with any particular synthetic framework. But for our purposes here, a clear and concise definition is necessary. Ultimately, the MS is based on a few core principles: (1) genetic variation is the source of phenotypic variation; (2) this variation arises due to mutations that are random with respect to fitness; (3) accumulated mutations selected over time are the basis of evolution within a taxon (gradualism); (4) adaptation is solely the result of natural selection; and (5) evolution occurs at the population level (Futuyma 2017).

A few decades after the formalization of MS, Gould and Eldredge challenged one of its foundational pillars: gradualism. Examining the fossil record of invertebrates, Gould and Eldredge hypothesized, first in 1972, and then more explicitly in 1977, that "stasis was data"; the consistency with which some species were found to persist through time indicated that phyletic evolution was slow. Further, explosions of new species at given periods in the fossil record suggested that the bulk of evolutionary change occurred in punctuated bursts at speciation events (or cladogenesis), a theory they called "punctuated equilibrium" (PE). To Eldredge and Gould (1972), this invalidated the idea suggested by the MS that most evolutionary change was gradual and occurred at the population level. Instead, they put forth the idea that specific traits and epistatic networks conferred an advantage on some macroevolutionary lineages while dooming others to extinction. Key to this argument were the notions that evolution (and therefore selection) is hierarchical and that natural forces shaping populations will also act at the species level. Their critique culminated in the famous Macroevolution Conference at the Field Museum in 1980, which was attended by both detractors and supporters of the MS (Lewin 1980; Futuyma et al. 1981). Of the meeting, Lewin (1980) wrote that it was "at times unruly and even acrimonious" in his article "Evolutionary Theory Under Fire."

Published in 1982, "A Neo-Darwinian Commentary on Macroevolution," by Brian Charlesworth, Russell Lande, and Montgomery Slatkin, provided a comprehensive rebuttal to Gould and Eldredge's critique of the Modern Synthesis. In this tour-de-force defense of Neo-Darwinism, Charlesworth, Lande, and Slatkin (CLS) presented, and proceeded to defang, each of the major tenets of punctuated equilibrium. In this Perspective, we return to this paper, which was published at the midpoint between Huxley's *Modern Synthesis* (1942) and the 75th anniversary of the journal *Evolution* (2021) and take the opportunity to re-examine and engage with ideas old and new in the light of discoveries made into the 21st century. While the flames of many of the original MS versus PE debates have faded, the question of whether microevolutionary processes are sufficient to explain macroevolutionary trends is still hotly debated to this day.

We have organized this *Perspective* around CLS's refutation of the major points of PE, and we will revisit their arguments in light of modern evidence. First, we discuss the PE and MS interpretation of stasis in the fossil record, concluding with CLS that stabilizing selection is the force most likely to explain the pattern. Second, we evaluate the proposed association of morphological change with speciation and Mayr's "genetic revolutions," which Eldredge and Gould (1972) used to explain this pattern. We conclude that this association is dependent on the speciation process itself, and that evidence from molecular phylogenetics does not support genetic revolutions as the means by which populations or species cross to new adaptive peaks. Third, we examine the claim that selection acting above the species level is necessary to explain phylogenetic trends, and that "clade-level mutations" can effectively decouple micro- and macroevolution. We contend that no such decoupling can be done, that there are no clade-level mutations that are analogous to genetic mutations, and that ignoring microevolution can distort the interpretation of macroevolutionary data. Finally, we conclude by examining the philosophical evolution of PE in light of Kuhn's (1962) view of scientific revolutions. Like biological evolution, the development of PE was largely the result of gradualism and descent with modification.

STASIS

The interpretation of the observed pattern of stasis in the paleontological record was one of the principal areas of contention between proponents of the PE and those of the MS. Punctuated equilibrium held that if morphological stasis over macroevolutionary timescales was the norm, then rates of phyletic evolution (i.e., gradualistic change within a lineage) must be "orders of magnitude" lower than the rate of morphological change occurring at speciation (Gould and Eldredge 1977). Below, we examine stasis through the lens of CLS's review of PE, describing its centrality in PE critiques of the MS, CLS's responses to those critiques, and modern research that sheds light on this argument.

PE: Developmental constraints and gene flow mitigate divergence

The pattern of stasis in the fossil record indicated, in Eldredge and Gould (1972)'s view, that phyletic evolution (i.e., evolutionary change within species) is unimportant, because most change is happening at speciation. Their argument was that the MS viewed evolution as a population-level process, with change happening in allele frequencies over successive generations, and that it therefore could not explain long-term stasis, or the apparent *lack* of evolution in populations (Gould and Eldredge 1977). Gould and Eldredge (1977) asserted that this shortcoming arose from the fact that the MS had historically ignored developmental constraints that act to limit a population's adaptive potential. An extreme example of developmental constraints might be the vertebrate four-limb body plan; once tetrapods started down the developmental pathway to four limbs, it became impossible for them to evolve six. Therefore, even if it would be beneficial for a tetrapod to have six limbs instead of four (imagine the time saved carrying-in groceries!), such variation cannot arise for selection to favor. This example of developmental constraints highlights what PE claimed was an issue for the MS. Gould (1981) wrote that the MS views an organism as a sphere, equally likely to be molded by natural selection in any direction and therefore infinitely plastic. If this were true, he contended, then natural selection should not be limited by available variation, and the fossil record should reveal gradual patterns of morphological change within populations. Speciation should have little to no impact on overall patterns. Instead, Gould and Eldredge viewed the observed pattern of stasis in the fossil record as clear evidence that developmental constraints circumscribe the direction in which natural selection can drive morphological evolution. Therefore, they argued, the MS was unable to explain existing patterns, and other forces outside the scope of the MS must be at play in generating them.

Gene flow was an alternative mechanism of morphological stasis proposed by other adherents of PE. The idea that gene flow could swamp local differentiation and therefore maintain species morphological stasis through time was first suggested by Mayr 1963 and was later promoted by Stanley (1979), although not Eldredge and Gould (1972). Stanley's reasoning was that gene flow, coupled with spatial variation in selection pressures, would essentially cancel out any directional evolution in the species metapopulation as a whole, resulting in stasis. This argument invoked Wright's theoretical result (1931) that even a single migrant per generation can prevent differentiation at neutral loci.

MS: Stabilizing selection as a cause of stasis

In their defense of the MS, CLS argued Gould and Eldredge's characterization of the MS was a caricature, that microevolutionary processes were sufficient to explain macroevolutionary patterns, and specifically that the pattern of stasis was the result of stabilizing selection. They argued that Gould's (1981) analogy of the infinitely plastic sphere was a "severe distortion" of the MS, and that, at least going back to Muller (1949), limitation in the directions of phenotypic change was already understood by proponents of the MS. Furthermore, CLS reasoned, developmental constraint was an inadequate explanation of stasis, as it ignored the incredible phenotypic varieties that have been produced by artificial selection. For example, any student of biology (or vegetable enthusiast) will be familiar with the wild mustard plant (*Brassica oleracea*), which is the ancestral phenotype for diverse crops such as brussel sprouts, kale, cabbage, kohlrabi, broccoli, and cauliflower. That such extreme artificial selection is possible relies on the fact that population-level variation exists to be selected upon, even if that variation is very rare. There continue to be excellent empirical examples of systems in which developmental constraints clearly do not stand in the way of rapid morphological diversification. Even for such a canonical example of stasis as the allometric scaling of *Drosophila* wing shape, which is highly conserved over macroevolutionary timescales, there is experimental evidence that selection can rapidly escape developmental constraints (Bolstad et al. 2015).

Charlesworth et al. next turned their critique to Stanley's proposed mechanism of stasis, gene flow (Stanley 1979). They argued that gene flow is, in most cases, an insufficient factor for maintaining morphological similarity across a widespread species. Further, they pointed out that Wright's result on gene flow preventing differentiation only pertains to neutral loci, and that alleles under even moderate local selection can overcome the homogenizing effects of gene flow (Haldane 1930; Slatkin 1973). While there are certainly cases of gene flow acting counter to local adaptation (e.g., Sambetti and Rice 2006), there are also many empirical examples of striking divergence in the presence of gene flow (e.g., Gonzalo-Turpin and Hazard 2009; Moody et al. 2015; Butlin et al. 2014). For example, there is minimal genome-wide divergence between the light and dark morphs of two White Sands lizards (*Aspidoscelis inornata* and *Sceloporus cowlesi*) (Rosenblum 2006; Laurent et al. 2016).

Instead of developmental constraints or gene flow, CLS believed that the MS explanation for the pattern of morphological stasis over macroevolutionary time is stabilizing selection. This mechanism acts to maintain an optimal mean phenotype by selectively culling those that deviate too far from it (Haldane 1957; Maynard Smith 1968). Evidence for this was first observed by Darwin (1859), who noted that vestigial features are far more variable than functional ones. Charlesworth et al. noted that it is a "common observation" for morphological characters in longitudinal studies to show decreasing phenotypic variance as the age of the cohort increases.

There continues to be strong evidence today for stabilizing selection as a mechanism of stasis. In a large-scale study of over 2,600 species, Estes and Arnold (2007) evaluated a variety of different models of phenotypic evolution on timescales ranging from hundreds to millions of generations. These models included a wide range of scenarios, including stabilizing selection, genetic constraints, and neutral evolution. They found that stabilizing selection was consistently chosen as the model with the most explanatory power. Furthermore, over the entire range of heritability values for most models (which ranged from 0.001−0.999), genetic constraints had negligible impacts on results (Estes and Arnold 2007). These findings are in agreement with other observations in nature, such as the rapid evolution of antibiotic resistance in bacteria (Davies and Davies 2010), herbicide resistance in many pest insects (Manalil et al. 2011), and others, which suggest that phenotypic evolution in natural populations may only rarely be restricted by mutations. Taken together, there appears to be an abundance of support for stabilizing selection as an effective mechanism of stasis.

MORPHOLOGICAL CHANGE ASSOCIATED WITH SPECIATION

Gould and Eldredge believed that most morphological evolution occurs in bursts between long periods of stasis, that bursts of evolution occur at speciation events, and that speciation itself facilitates rapid morphological change via the relaxation of developmental constraints (1972, 1977). In their model, speciation proceeds via founder events, which then allow populations to cross adaptive valleys to new peaks. This idea was first proposed by Mayr (1954), who thought that these "genetic revolutions" could be the result of large-scale reorganization of the genome, such as chromosome inversions or duplications. Alternatively, in the MS perspective, speciation is itself not a cause of morphological divergence, which instead arises due to the cessation of gene flow by some intrinsic or extrinsic force coupled with the gradual accumulation of genetic differences. Gould and Eldredge (1977) argued that the view of the MS was inadequate to explain the trends of punctuated morphological change at speciation events given that it did not assume speciation to be a driving force of evolution.

Below, we review the concept of the "genetic revolution" as a driver of morphological change at speciation. While we provide CLS's rebuttal, we note that we are largely rehashing a closed debate, as Mayr's theory of genetic revolutions is no longer accepted in mainstream evolutionary biology. However, the idea was central to the theory of PE and is interesting in a historical context. Furthermore, while the mechanism itself is no longer seriously discussed, the questions regarding rates of evolutionary change and mechanisms of speciation that it sought to answer are (e.g., Uyeda et al. 2011; Matute and Cooper 2021). In this context, we evaluate the predictions of genetic revolutions in light of molecular phylogenetics, concluding that there is no evidence for an association between population bottlenecks and rapid evolution.

Evolution by revolution

Proponents of PE argued that "genetic revolutions" occurring at speciation were necessary for morphological evolution to overcome developmental constraints (or the homogenizing effects of gene flow; Stanley 1979). The term "genetic revolution" was introduced to the lexicon of evolutionary biology by Ernst Mayr, who postulated that speciation most often occurs when small populations near the edges of a species' range become isolated from the rest of the range, and eventually evolve into a novel species (1954). Because these founding populations are bottlenecked, genetic drift is more free to sample morphological space that might otherwise have been restricted by stabilizing selection (or gene flow; Stanley 1979) in large populations. The colonizers are expected to quickly reach a new adaptive peak, allowing their numbers to exponentially grow such that inbreeding does not lead to extinction. Eldredge and Gould (1972) proposed that genetic revolutions were a mechanism that could generate rapid phenotypic change at cladogenesis.

In their critique of the idea of genetic revolutions, CLS noted several difficulties in identifying correlations between morphological change and speciation from fossil data alone; these have been echoed in a recent review by Pennell et al. (2014). First, evaluating such associations requires the assumption that we have sampled direct ancestors of descendant taxa, which is very unlikely. Secondly, it requires that the fossil record is sufficiently well-sampled that we can adequately rule out gradualistic evolution. Given the sheer number of individuals that have died in the history of life relative to the number of those preserved in the fossil record, our ability to justify this second assumption seems tenuous at best. Thirdly, testing this hypothesis require strong taxonomic assumptions about the extent of identifiable morphological change that constitutes a new species designation. This latter point has become particularly problematic over the last decade given the increased appreciation of the prevalence of cryptic species (e.g., Bickford et al. 2007; Fišer et al. 2018) that presumably would not be identifiable from even the best-preserved fossils. Indeed, as CLS pointed out, "[t]here seems to be no way in which systematists can arrive at a certain classification of closely related, allopatric taxa as separate biological species on the basis of purely morphological criteria." Coyne and Orr (2004) extended this argument further, noting that, outside of direct breeding trials, it is almost impossible to deduce whether allopatric populations are distinct biological species. Furthermore, as noted by Levinton and Simon (1980), the use of morphology for species identification introduces a tautology into Gould and Eldredge's arguments, as any change observed in the fossil record will merit a new species designation, which means that all changes will be correlated with inferred cladogenesis events.

Charlesworth et al. argued that the physical evidence in the fossil record cannot provide sufficient support for the theory of punctuated equilibrium, but we can further evaluate whether Mayr's concept of genetic revolutions is even theoretically plausible. Barton and Charlesworth (1984) evaluated Mayr's and other's models that rely on founder events (e.g., Carson 1968; Templeton 1980) and found theoretical flaws. For example, they noted that the rate of genetic drift is slow; a neutral mutation takes on the order of $4N_e$ generations to reach fixation in a population (where N_e is the effective size of the population). Phenotypic evolution due to drift is therefore likely to be very slow relative to the action of selection and thus, drift alone is unlikely to rapidly shift a population through a valley between adaptive peaks.

Any signatures of bottlenecks?

If genetic revolutions were generally responsible for rapid adaptive change, then we should be able to identify signatures of population bottlenecks that correspond to periods of evolutionary bursts. Charlesworth et al. raised the Hawaiian radiation of *Drosophila* as an example of a system in which Mayr's genetic revolutions could have occurred; after all, the system is characterized by repeated colonizations of new islands and extensive morphological divergence with reproductive isolation via mate discrimination. However, they noted that it is unlikely that a genetic revolution is responsible because there seems to be little evidence that these species have the reduced heterozygosity expected after a founder event (Templeton 1980). Furthermore, the existence of ring-species undermines the notion that genetic revolutions are necessary to generate reproductive isolation. In ring species, speciation is the result of the gradual cessation of gene flow and accumulated divergence between demes that meet at the edge of the ring (e.g., Mortiz et al. 1992; Wake and Schneider 1998; Irwin et al. 2001; Cacho and Baum 2012). In addition, there are numerous empirical examples of systems in which genetic divergence does *not* correlate with phenotypic divergence. For example, Fišer et al. (2015) reported that species of the amphipod crustacean *Niphargus* were widely genetically diverged but morphologically indistinguishable. These cases reflect a "lack of correlation between low heterozygosity and rapid speciation" (CLS), or between speciation and morphological change, as would be predicted if genetic revolutions were the principal mechanism of speciation. Indeed, the existence of cryptic species alone challenges the notion that genetic revolutions are the main means by which speciation occurs.

The incorporation of coalescent theory into phylogenetic methods (Maddison 1997; Degnan and Rosenberg 2006; Liu et al. 2009; Degnan and Rosenberg 2009) has facilitated the use of molecular phylogenetics to test for signatures of bottlenecks in rapidly evolving clades. On average, bottlenecks are expected to reduce incomplete lineage sorting and gene-tree/species-tree discordance. A recent simulation-based study (Hancock et al. 2021) suggests that this reduction in the proportion of discordant gene-trees is expected to be particularly striking under a peripatric speciation model like that proposed by Mayr (1954). Therefore, if peripatry is the dominant form of speciation, especially in the case of rapid morphological evolution, then across the Tree of Life we would expect to see increased gene tree concordance at the shortest nodes or nodes leading to dramatic morphological change. However, the exact opposite pattern has been observed and is well documented for many major radiations (e.g., Takahashi et al. 2001; Smith et al. 2019; Doronina et al. 2015). Parins-Fukuchi et al. (2021) recently found that, across six major clades ranging from angiosperms to mammals, the periods of the most phylogenomic conflict corresponded with bursts of rapid phenotypic evolution. If population sizes had been depressed following a founder event, and this depression allowed for genetic drift to shift populations between adaptive peaks, then we would expect *less* gene tree conflict associated with phenotypic change, not more.

PHYLOGENETIC TRENDS

A major claim of PE was that population-level processes (microevolution) could not adequately explain macroevolutionary trends. The proponents of PE suggested instead that a hierarchical view of evolution was necessary, and that processes acting on clades were separate from (though analogous to) those acting at the population level. Below, we first provide the arguments of PE and the modern advocates of species selection. Next, we summarize CLS's response to the claim that the MS was inadequate to explain higher-level patterns and offer our own perspective on the continuity of microevolution and macroevolution. We conclude that macroevolutionary processes such as species selection likely play a relatively minor role in the evolutionary history of biological diversity and that population-level perspectives offer more satisfactory explanations of phylogenetic patterns.

Sometimes Darwin and sometimes Dracula

Gould (1981) described the separation of macroevolution and microevolution with an analogy of packing books. When packing books, he was concerned with their size and shape, but not the publisher or the print size, because "the books, as morphological entities, are irreducible as objects to be packed." Gould did not deny that the books have "micro-level properties" that he cared about; he wrote "sometimes I read Darwin and sometimes I read *Dracula*."

The theory of PE not only recognized a macroevolutionary *pattern* in the fossil record (organization of books in boxes), but also claimed that macroevolutionary *processes* (act of arranging books into boxes) distinct from those at the population level were responsible (Stanley 1979; Eldredge and Gould 1972;

Gould and Eldredge 1977). Importantly, the PE arguments concerning macroevolutionary trends were predicated on two key points: (1) morphological change occurs at speciation and (2) that these changes are random with respect to the direction of macroevolution (what they referred to as "Wright's rule"; Wright 1940). If these two postulates hold true, they argued, then directional macroevolutionary patterns, such as the general trend toward increased body size in mammals or parallel evolution, could not be explained by traditional microevolutionary processes contained within the MS. Instead, these trends suggested the action of some higher-level mechanism.

The mechanism that advocates of PE believed was generating macroevolutionary trends is called species selection (Stanley 1979; Vrba 1984; Gould 1998), which is defined as lineage-level selection acting on the emergent traits of species. As with Gould's example of packing books, these traits cannot be reduced to or predicted by their component parts, so their effects only act at the species level or above. For example, range size is often considered an emergent trait because it cannot be predicted by any individual-level property, such as dispersal distance (see Grantham 2007, who designated range size as "weakly emergent"). Species selection occurs when lineages that possess a trait – which must be inheritable by descendent lineages – have a higher net diversification rate, either due to an increase in speciation rate, a decrease in extinction rate, or both. Crucially, species selection was defined by PE as a force that could not be explained by microevolutionary processes, and was therefore outside the purview of the MS.

Cannot see the trees for the forest

The Neo-Darwinian stance on macroevolutionary patterns, as presented by CLS, is that they "are due to natural selection acting in each species." Because CLS had already rejected the premises that morphological change was linked to speciation events and that the direction of that change was random, their approach was to instead point out the ways in which microevolutionary processes are perfectly capable of generating macroevolutionary patterns. First, they pointed out that parallel evolution could be explained by natural selection acting within species that were in similar ecological circumstances. There are numerous compelling empirical examples of this type of parallelism, including the light coloration of the different White Sands lizard species mentioned above (Rosenblum 2006), or the striking convergence of sand-diving lizards found in the North America West and in Namibia (in the genus *Uma* and *Meroles*, respectively, Robinson and Barrows 2013). Similarly, CLS argued that if the fitness of individuals with heritable traits that were more diverged from that of their co-occurring competitors was higher, divergent evolution could also be explained by natural selection acting to differentiate species due to their ecological interactions. As an example, CLS referenced the canonical example of *Anolis* lizards, which have repeatedly differentiated into different niches following their colonization of new Antillean islands (Williams 1972; Losos 1994); trait divergence in sympatry has been documented in many other empirical systems, including canine size in desert felids (Dayan et al. 1990) and floral scent in California jewelflowers (Weber et al. 2018). In each of these cases, the pattern of species divergence can be explained by invoking microevolutionary processes alone.

These examples of ecological character displacement offer strong support for the MS idea that species divergence can be explained by natural selection and ecological interactions, but this idea can also receive support from a *lack* of divergence. For example, vicariant speciation would not be expected to produce dramatic morphological changes because the resulting sister species would still largely be in the same environment as the ancestral populations from which they descended and experiencing ecological interactions with the same competitors (or mutualists). Cryptic species present compelling evidence for this process playing out in nature. For example, in the Gulf of Mexico, multiple vicariant zones have been identified with sister species on either side that are minorly differentiated or completely cryptic (Portnoy and Gold 2012). This lack of divergence in the absence of ecological interactions that might otherwise drive trait evolution in sympatry also supports CLS's argument that microevolutionary processes are responsible for macroevolutionary patterns.

In 1982, there were few papers that invoked the action of species selection, leading CLS to write, "…there is as yet no evidence that species selection has been effective in producing major morphological trends." In the decades since, the increased availability of large, time-calibrated phylogenies, coupled with advances in statistical methods to detect diversification rate shifts (e.g., Maddison et al. 2007; Moore and Donohue 2009; Rabosky 2014; although see also Louca and Pennell 2020) have generated numerous convincing examples of "species-level" selection (e.g., Weber and Agrawal 2014) and widespread community acceptance of the idea (Jablonski 2008; Rabosky and McCune 2009; Pennell et al. 2014). However, it is important to note that although there is now evidence that a lineage's traits may affect its net diversification rate, the mechanism by which this species selection is understood to occur is microevolutionary: e.g., self-incompatibility decreases extinction rates due to avoidance of inbreeding depression at the population level (Goldberg et al. 2010).

As further validation of CLS's defense of the MS, we should note that Charlesworth et al. did not argue that species selection is nonexistent, but rather that it would be inefficient and is likely to be less important than microevolutionary processes. The problem that CLS had with species selection is that the number of lineages within a clade and their relative turnover rates is necessarily less than the number of individuals in a population, which makes selection on the individual a much more powerful force than selection on the species (Lewontin 1970; Slatkin 1981). Despite the proposed inefficiency of species selection, CLS recognized that the vast majority of life on Earth has gone extinct, which "evidently provides a large opportunity for stochastic events or selection between species and higher taxa." The question that remains to be answered is how important is species selection in evolution? As pointed out by Dietrich (2010), the debate between micro- and macroevolutionary processes is not a winner-take-all, but rather a question of degree. Given the immensity of past biological diversity, no one would dispute that species selection at some point in time may have driven diversification within a clade. But is it efficient enough to approach the efficacy of natural selection acting at the individual level?

We have argued above that micro- and macroevolution cannot be easily decoupled. But beyond this, we believe that doing so reduces our explanatory power of the trends themselves. Charlesworth et al. wrote that an attempt to decouple these "seems to neglect the fact that every living or fossil organism owes its existence to a continuous line of descent going back generation by generation into the remote past" and that while species selection "may provide a convenient description of macroevolutionary patterns, these terms should not be identified with the genetic and ecological mechanisms causing the changes." Many empirical studies have shown that there is a clear link between microevolutionary processes and resulting macroevolutionary patterns (e.g., Kane et al. 2011; Okamoto et al. 2015; Rolland et al. 2018; Costa et al. 2019). A classic example comes from Sewall Wright's work on artificial selection in guinea pigs. All species in the family Caviidae have three toes on their back foot, but through artificial selection on slight variation between individuals Wright was able to breed laboratory populations with four toes (Wright 1960). Orzack (1981) noted that if these four-toed individuals had been discovered in the fossil record, paleontologists would likely have designated them as a new species (or even a new family!). At the genomic level, Kane et al. (2011), evaluating protein evolution in the Asteraceae, found that purifying selection was the norm at the interspecific level, with positive selection only obvious at microevolutionary scales. Furthermore, the targets of purifying selection remained the same across both scales. This led Kane et al. (2011) to conclude that macroevolution "looks very much like 'repeated rounds of microevolution'" (quoting Erwin [2000]).

Other studies have gone further, showing that when macroevolutionary studies ignore microevolution they may come to incorrect conclusions (e.g., Wakeley 2000; Edwards and Beerli 2000; Li et al. 2018). For example, Li et al. (2018) evaluated the macroevolutionary pattern of latitudinal diversity gradients (LDG) using the protracted speciation model, which allows for different rates of lineage splitting, merging, and conversion. They demonstrated the same patterns of species richness could be obtained in different ways at the population level; for example, species at high latitudes may "experience chronic divergent selection and often yield sister species pairs" or may undergo constant "population fragmentation but low completion of species" (Li et al. 2018). They note that either scenario is consistent with producing the LDG but invokes very different population-level processes. Boiling these processes down to speciation and extinction rates obscures the underlying mechanisms driving these trends. Ultimately, framing macroevolutionary patterns as the result of species selection simplifies, but fails to elucidate, the actual processes that underpin these patterns.

We would like to return to Gould's book-packing analogy. Instead of thinking of the relationship of micro- to macroevolution as books to be packed with words that are unrelated to their packing, we promote a view of the relationship like that of trees in a forest. We can study the dynamics of a forest – its scale, its ecosystem services, soil community composition, etc. – but we must recognize that a forest only exists as a collection of individual trees. We can understand all of these trees together as a forest in aggregate, but alterations to the forest topology is a result of processes occurring at the level of the tree. If across vast timescales we find that larger forests tend to survive longer than smaller ones, we should not ask about selection on forest size, but rather inquire as to the conditions promoting tree growth in one but not the other. In reversing the common phrase, we suggest that adopting a macroevolutionary perspective divorced from a microevolutionary one is akin to missing the trees for the forest.

Conclusions: Is PE Kuhnian or Darwinian?

In the original paper proposing a punctuational view of evolution, Eldredge and Gould (1972) quoted P.B. Medawar (1969): "Innocent, unbiased observation is a myth." In this work, and more forcefully in Gould and Eldredge (1977), they argued that much of Neo-Darwinism was a product of the philosophical positions held by 19th century Victorians. Indeed, they quoted Irvine (1959), a biographer of Darwin's, who wrote that Darwin was "…adding Hooker and Burke to Bentham and Adam Smith." Above, we have largely ignored the philosophical perspectives of both Darwin and the neo-Darwinists, instead focusing our attention on the theoretical support for the view that macroevolution is "repeated rounds of microevolution" (Erwin 2000). It is difficult to untangle the web of history around what *is* and *is not* the MS, especially given that none of the authors of this perspective are historians or philosophers of science. But we would like, in conclusion, to evaluate whether PE, as Gould and Eldredge (1977) suggested, represents a major revolution in evolutionary biology.

In the concluding paragraphs of "A Neo-Darwinian Commentary on Macroevolution", CLS, like Eldredge and Gould (1972), referenced Kuhn's conception of science: "Science progresses more by the introduction of new worldviews… than by the steady accumulation of information." In this punctuational view of history, science – like society – is largely conservative and resistant to change, until a rapid, intense struggle forces a paradigm shift. One of us (ZBH), who, unlike Gould, may not have "learned his Marxism literally at his daddy's knee" but nevertheless managed to absorb it elsewhere, is sympathetic to this view (Gould and Eldredge 1977). But it is unclear whether PE – admittedly with the power of hindsight – caused either a major paradigm shift or was even that revolutionary.

Ironically, the historical development of PE was gradual. The roots of the critiques of the MS that would form the basis of PE were laid decades before Eldredge and Gould (1972), with the works of von Kölliker (1864), Galton (1892), and Goldschmidt (1940). Indeed, the concept of species selection was discussed by Fisher (1958). Rapid, saltational changes that result in speciation – the cornerstone of PE – are not that far from the mutational theories of evolution espoused by Hugo de Vries (1905), Thomas Hunt Morgan (1905), and William Bateson (1894) in the late 19th and early 20th centuries. Therefore, if PE can be considered a revolution at all, it was a protracted one. Furthermore, as recently concluded by Pennell et al. (2014), while PE generated interesting discussion, most of its assumptions (such as the supremacy of cladogenetic change relative to phyletic) have been abandoned. Irrespective of whether Kuhn's conception of scientific progress is correct, CLS ultimately concluded that "…it does not appear… that the theory of punctuated equilibrium should be accepted as a major revolution in evolutionary biology."

Punctuated equilibrium, we contend, represents a lineage of evolutionary thought along a tree of gradual evolution predating even Darwin. The ancestors of PE include not only de Vries' *Mutationstheorie* and Goldschmidt's "hopeful monsters," but also Wright (1940)'s thoughts on the directionality of morphological evolution with respect to speciation and his concepts of inter-deme selection. It even contains traces of hybrid ancestry with Mayr's ideas on genetic revolutions and his general disdain for "beanbag genetics" (see Haldane 1964). These philosophical phenotypes predated PE by decades and were undoubtedly transitional forms as Gould and Eldredge (1977) frequently cited them as such. Viewed in isolation – say, without reference to the lineages that had explored the same state space but gone extinct – PE would appear as a "revolution", even if one doomed to extinction. But taken in historical context, the development of PE appears quite gradual, with slight modifications on ancestral conceptions.

Charlesworth et al.'s commentary on macroevolution remains an important defense of the explanatory power of the MS. In each section, we have extended their arguments with modern support, demonstrating the staying power of their conclusions. And though the heated debates of PE have largely faded, contention surrounding the MS and its various detractors remain (see Laland et al. 2014; Futuyma 2017). The arguments put forward by CLS – and extended by many others – therefore remain relevant today and are worth revisiting on this 75th anniversary of the founding of SSE. Despite Gould's (1980) proclamation that the MS was "effectively dead" and Rosen (1986) assuring us that the MS would not still be haunting us, it seems we are left in the company of Felsenstein (1986), patiently "waiting for a post-neo-Darwinian theory that has not appeared."

Box 1: Hybridization, the Modern Synthesis, and me

– E.S. Lehmberg

The ubiquitous and ongoing nature of hybridization, especially in Animalia, is perhaps one of the more surprising recent discoveries of the Next Generation Sequencing era. Hybridization and subsequent genomic introgression have a variety of outcomes; some of the more fascinating results are the formation of new species or the passage of sequences from one lineage to another. Hybridization, particularly between deeply divergent taxa, causes us to question where the firm boundaries between taxa lie and how to even operationally define species. Despite its pervasiveness, we still know little about how hybridization interacts with natural and sexual selection, providing the opportunity for development of new models and concepts to account for what was once considered a quirk of nature rather than an evolutionary force.

Sexual selection has especially interesting consequences with respect to hybridization: while a chooser can mate with a partner from another species, isolating mechanisms such as sexual conflict (competing fitness outcomes between males and females) can serve to accelerate lineage isolation. In my own work, I use phylogenetics to answer questions about the long-term consequences of sexual conflict and its relationship to frequency of hybridization, and my PhD project lies somewhere on the boundary of both macroevolution and microevolution. My research is focused on exploring the idea that, while traits under strong selection as a result of sexual conflict might cause increased rates of diversification (and species selection), hybridization also has genetic consequences that are explicitly addressed in the Modern Synthesis (Haldane's cline theory; Bateson-Dobzhansky-Muller Incompatibilities) and can be either immediate or long-term. While we still struggle to link macroevolutionary patterns with microevolutionary processes, drawing on foundational concepts from both MS and PE allows me to comprehensively view the interaction between these two natural evolutionary forces.

When I first read CLS, I immediately recognized its importance for my research, and, after several re-readings, I have realized the power of the paper is not only in the explicit links the authors make between macro- and microevolution but also in the authors' ability to deconstruct an argument and place it within a pre-existing framework. As an early career researcher, this skill is something I am still developing, so this paper is doubly valuable to me, both in its structure and its content. Finally, re-examining CLS 39 years after it was written gives me perspective on where we are now as a field and where we could, and should, go. It is truly wild to me that – a little less than a hundred years after Huxley's *Modern Synthesis* – not only can we take this once-revolutionary set of ideas for granted, but we can now directly test the theory laid out in the modern synthesis on massive scales; our ability to generate massive genomic data presents an opportunity to firmly and empirically link micro- and macroevolution and further explore the universes contained within our own genomes.

We know *so much* and yet so little. That is what keeps me here and searching and learning, on the shoulders of giants who came before us.

Box 2. Speak, Ancestors!*: The continuity of all life*

–Z.B. Hancock

From the opening pages of Nabakov's 1947 autobiography, *Speak, Memory!*, we are filled with the chronophobiac's dread of existence as a "brief crack of light between two eternities of darkness." But this ignores that, within each of us, is written the entire history of life – that all of existence is connected via our shared ancestry. I became an evolutionary biologist because it provided me a way to step-out of Nabakov's nightmare. Viewed through the lens of Darwin, existence becomes a vast expanse of light, a 3.5-billion-year thread that connects all life, living and extinct. Nevertheless, there seems to be a persistent trend within the community of neatly partitioning timescales into "micro" or "macro". While this may at times be for convenience, others (reviewed in this *Perspective*) have argued that this disjunction is *real* – that evolutionary processes between these timescales are fundamentally different.

The 75th anniversary of the founding of the Society for the Study of Evolution is an excellent time to appreciate the "grandeur in this view of life" that there is an inseparable thread of existence between all levels of biological organization. And I can think of no better promotion of this view than Charlesworth, Lande, and Slatkin's (1982) paper in *Evolution*. Despite punctuated equilibrium as a theoretical framework having largely been discarded, their paper remains influential as it foreshadowed much of the work on the continuity of evolution into the 21st century. As a young graduate student, I appreciated not only their ardent defense of the MS, but the elegant way in which they dissected each argument of PE in light of population-level processes.

Encountering CLS as a graduate student inspired me to reject the artificial division between micro- and macroevolution; ultimately, this worldview of the continuity of life led me to find ways to demonstrate the reliance of macroevolutionary trends on processes acting within populations in my own thesis work. Using amphipod crustaceans, I found that differences in beach partitioning, likely due to competition between species occupying the same beach, led to differences in dispersal distances and ultimately greater rates of speciation (Hancock et al. 2019). In a second study, combining simulations and an empirical dataset of Brazilian endemic lizards, I found that a history of isolation-by-distance in the ancestral population of descendant species left a signature on inferred node ages across the tree (Hancock and Blackmon 2020). Finally, in a review on the impacts of continuous space on phylogenetics, we showed that spatial processes within populations impacted all facets of inference, clearly linking the dynamics of the population with trends between species (Hancock et al. 2021). As a postdoc, I have expanded my research to include the study of the more recent past, working to develop demographic models that accommodate both spatial and temporal aspects of genetic drift. But coalescence is both a within and between population process, and a future goal will be to extend these models to incorporate modes of speciation and, ultimately, project lineage survivability and dispersal trajectories on changing landscapes into the future.

This *Perspective* is, in many ways, a homage to CLS as the torchbearers of the past, but also a celebration of a view of evolution promoted by them and other defenders of the MS: that evolution is a bottom-up process, driven by populations of individuals each interacting with one another and their environment, and ultimately that these dynamics are written in the genes of all life.

ACKNOWLEDGMENTS

We would like to extend a special thanks to the Society for the Study of Evolution and all of its members over the years who have worked hard to make the society an open and welcoming place: to 75 more years of evolutionary biology! We would also like to thank Tracey Chapman and an anonymous reviewer for the time dedicated to our manuscript. Research reported in this publication was supported by the National Institute Of General Medical Sciences of the National Institutes of Health under Award Number R35GM137919 (awarded to G.S.B.). E.S.L. is supported by funding from the National Science and Engineering Research

Council. The content is solely the responsibility of the authors and does not necessarily represent the official views of the NIH.

LITERATURE CITED

Barton N H, Charlesworth B. 1984. Genetic Revolutions, Founder Effects, and Speciation. Annual Review of Ecology and Systematics 15 (1): 133 –164. https://doi.org/10.1146/annurev.es.15.110184.001025.

Bateson, William. 1894. Materials for the study of variation. London: The Macmillan Co.

Bickford, David, Lohman, David J., Sodhi, Navjot S., Ng, Peter K.L., Meier, Rudolf, Winker, Kevin, Ingram, Krista K., and Das, Indraneil. 2007. Cryptic species as a window on diversity and conservation. 22(3): 148–155.

Bolstad, G., J. A. Cassara, E. Márquez, T. F. Hansen, K. Linde, D. Houle, and C. Pélabon. 2015. Complex constraints on allometry revealed by artificial selection on the wing of *Drosophila melanogaster*. Proc. Natl, Acad. Sci. USA 112:13284–13289.

Butlin, R. K., M. Saura, G. Charrier, B. Jackson, C. André, A. Caballero, J. A. Coyne, J. Galindo, J. W. Grahame, J. Hollander, et al. 2014. Parallel evolution of local adaptation and reproductive isolation in the face of gene flow. Evolution 68:935–949.

Cacho, N. I., and D. A. Baum. 2012. The Caribbean slipper spurge *Euphorbia tithymaloides*: the first example of a ring species in plants. Proc. R. Soc. B 279:3377–3383.

Carson, H. L. 1968. The population flush and its genetic consequences. Population biology and evolution123–137.

Charlesworth, B., R. Lande, and M. Slatkin. 1982 A Neo-Darwinian commentary on macroevolution. Evolution 36:474–498.

Costa, C. L. M., P. Lemos-Costa, F. M. D. Marquitti, L. D. Fernandes, M. F. Ramos, D. M. Schneider, A. B. Martins, and M. A. M. de Aguir. 2019. Signatures of microevolutionary processes in phylogenetic patterns. Sys. Bio 68:131–144.

Coyne, J., and H. A. Orr. 2004. Speciation. Oxford Univ. Pres, Oxford, U.K.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection. John Murray, London, U.K.

Davis, J., and D. Davies. 2010. Origins and evolution of antibiotic resistance. Microbiol. Mol. Biol. Rev 74:417–433.

Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov. 1990. Feline Canines: Community-wide character displacement among the small cats of Israel. Am. Nat 136:39–60.

Degnan, J. H., and N. A. Rosenberg. 2009. Gene tree discordance, phylogenetic inference and the multispecies coalescent. Trends Eco. Evol 24:332–340.

de Vries, Hugo. 1905. Species and varieties. Their origin by mutation, Chicago: Open Court Publishing Co.

Degnan, J. H., and N. A. Rosenberg. 2006. Discordance of species trees with their most likely gene trees. PLoS Genet 2:e68.

Dietrich, M. R. 2010. Microevolution and macroevolution are governed by the same processes. In Contemporary Debates in Philosophy of Biology. Eds. F. J., Ayala, and R. Arp. Wiley-Blackwell, West Sussex, U.K.

Doronina, L., G. Churakov, J. Shi, J. Brosius, R. Baertsch, H. Clawson, and J. Schmitz. 2015. Exploring massive incomplete lineage sorting in Arctoids (Laurasiatheria, Carnivora). Mol. Biol. Evol 32:3194–3204.

Edwards, S. V., and P. Beerli. 2000. Perspective: Gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. Evolution 54:1839–1854.

Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: An alternative to phyletic gradualism. In Models in paleobiology. Eds. T. J. M., Schopf F. Reeman, Cooper, San Francisco, CA, USA.

Erwin, D. H. 2000. Macroevolution is more than repeated rounds of microevolution. Evol. Dev 2:78–84.

Estes, S., and S. J. Arnold. 2007. Resolving the paradox of stasis: Models with stabilizing selection explain evolutionary divergence on all timescales. Am. Nat 169:227–244.

Felsenstein, J. 1986. Waiting for Post-Neo-Darwin. Evolution 40:883–889.

Fisher, R. A. 1958. The Genetical Theory of Natural Selection. 2nd Ed. Dover, N.Y.

Fišer, Z., F. Altermatt, V. Zakšek, T. Knapič, and C. Fišer. 2015. Morphologically cryptic amphipod species are “ecological clones” at regional but not local scales: A case study of four *Niphargus* species. PLoS ONE 10:e0134384.

Fišer Cene, Robinson Christopher T., Malard Florian. 2018. Cryptic species as a window into the paradigm shift of the species concept. Molecular Ecology 27 (3): 613 –635. https://doi.org/10.1111/mec.14486.

Futuyma, D. J. 2017. Evolutionary biology today and the call for an extended synthesis. Interface Focus 7:20160145.

Futuyma, D. J., R. C. Lewontin, G. C. Mayer, J. Seger, J. W. Stubblefield, A. R. Templeton, L. Val Giddings, H. L. Carson, E. C. Olson, J. E. Armstrong, et al. 1981. Macroevolution conference. Science 211:770–774.

Galton, F. 1892. Finger prints. Macmillan and Co London, U.K.

Gayon, J., and P. Huneman. 2019. The Modern Synthesis: Theoretical or institutional event? J. Hist. Biol 52:519–535.

Goldberg, E. E., J. R. Kohn, R. Lande, K. A. Robertson, S. A. Smith, and B. Igić. 2010. Species selection maintains self-incompatibility. Science 330:493–495.

Goldschmidt, R. 1940. The Material Basis of Evolution. Yale Univ. Pres Hanover, Massachusetts.

Gonzalo-Turpin, H., and L. Hazard. 2009. Local adaptation occurs along altitudinal gradient despite the existence of gene flow in the alpine plant species *Festuca eskia*. J. Ecol 97:742–751.

Gould, S. J., and N. Eldredge. 1977. Punctuated equilibria: The tempo and mode of evolution reconsidered. Paleobiology 3:115–151.

Gould, S. J. 1980. Is a new and general theory of evolution emerging?. Paleobiology 6 119–130.

Gould, S. J. 1981. But not Wright enough: Reply to Orzack. Paleobiology 7:131–134.

Gould, S. J. 1998. Gulliver’s further travels: the necessity and difficulty of a hierarchical theory of selection. Phil. Trans. R. Soc. B 353:307–314.

Grantham, T. 2007. Is macroevolution more than successive rounds of microevolution? Paleontology 50:75–85.

Haldane, J. B. S. 1930. A mathematical theory of natural and artificial selection. VI. Isolation. Proc. Camb. Phil. Soc 26:220–230.

Haldane, J. B. S. 1957. The cost of natural selection. J. Genet 55:511–524.

Haldane, J. B. S. 1964. A defense of beanbag genetics. Perspect. Biol. Med 7:343–360.

Hancock, Z. B., and H. Blackmon. 2020. Ghosts of a structured past: Impacts of ancestral patterns of isolation-by-distance on divergence-time estimation. J. Hered 111:573–582.

Hancock, Z. B., E. S. Lehmberg, and H. Blackmon. 2021. Phylogenetics in space: How continuous spatial structure impacts tree inference. In review.

Huxley, J. 1942. Evolution: The Modern Synthesis. The MIT Press, Cambridge, Massachusetts, USA.

Irvine, William. 1959. The influence of Darwin on literature. Proceedings of the American Philosophical Society 103(5): 616–628.

Irwin, D. E., J. H. Irwin, and T. D. Price. 2001. Ring species as bridges between microevolution and species. In: A. P., Hendry and M. T. Kinnison (eds) Microevolution Rate, Pattern, and Process. Contemporary Issues in Genetics and Evolution, vol 8. Spinger, Dordrecht.

Jablonski, D. 2008. Species selection: Theory and data. Annu. Rev. Ecol. Evol. Syst 39:501–524.

Kane, N. C., M. S. Barker, S. H. Zhan, and L. H. Rieseberg. 2011. Molecular evolution across Asteraceae: Micro- and macroevolutionary processes. Mol. Biol. Evol 28:3225–3235.

Kölliker, R. von. 1864. Über die Darwinische Schöpfungstheorie. Zeitschrift für wissenschaftliche Zoologie 14:74–86.

Kuhn, T. S. 1962. Historical structure of scientific discovery. Science 136:760–764.

Laland, K., T. Uller, M. Feldman, K. Sterenly, G. B. Müller, A. Moczek, E. Jablonka, J. Odling-Smee, G. A. Wray, H. E. Hoekstra, et al. 2014. Does evolutionary theory need a rethink? Nature 514:161–164.

Laurent, S., S. P. Pfiefer, M. L. Settles, S. S. Hunter, K. M. Hardwick, L. Ormond, V. C. Sousa, J. D. Jensen, and E. B. Rosenblum. 2016. The population genomics of rapid adaptation: disentangling signatures of selection and demography in white sands lizards. Mol. Ecol 25:306–323.

Levinton, J. S., and C. M. Simon. 1980. A critique of the punctuated equilibrium model and implications for the detection of speciation in the fossil record. Syst. Zool 29:130–142.

Lewontin, R.C. 1970. The units of selection. Annual Review of Ecology and Systematics 1 1–18.

Lewin, R. 1980. Evolutionary theory under fire. Science 210:883–887.

Li, J., J. Huang, J. Sukumaran, and L. L. Knowles. 2018. Microevolutionary processes impact macroevolutionary patterns. BMC Ecol. Evol 18:123.

Liu, L., L. Yu, L. Kubatko, D. K. Pearl, and S. V. Edwards. 2009. Coalescent methods for estimating phylogenetic trees. Mol. Phylogenet. Evol 53:320–328.

Losos, J. B. 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. Annu. Rev. Ecol. Syst 25:467–493.

Louca, S., and M. W. Pennell. 2020. Extant timetrees are consistent with a myriad of diversification histories. Nature 580:502–505.

Maddison, W. P. 1997. Gene trees in species trees. Syst. Bio 46:523–536.

Maddison, W. P., P. E. Midford, and S. P. Otto. 2007. Estimating a binary character's effect on speciation and extinction. Syst. Bio 56:701–710.

Manalil, S., R. Busi, M. Renton, and S. B. Powles. 2011. Rapid evolution of herbicide resistance by low herbicide dosages. Weed Sci 59:210–2017.

Matute, D. R., and B. S. Cooper. 2021. Comparative studies on speciation: 30 years since Coyne and Orr. Evolution 75:764–778.

Maynard-Smith, J. 1968. "Haldane's Dilemma" and the rate of evolution. Nature 219:1114–1116.

Mayr, Ernst. 1963. Animal species and evolution, London: Harvard University Press.

Mayr, E. 1954. Change of environment and evolution. *In* Evolution as a Process. Eds. J., Huxley, A. C., Hardy, and E. B. Ford. Allen and Unwin, London, U.K.

Medawar, P. B. 1969. Induction and Intuition in Scientific Thought. American Philosophical Society, Philadelphia, Pennsylvania, U.S.A.

Moody, K. N., S. N. Hunter, M. J. Childress, R. W. Blob, H. L. Schoenfuss, M. J. Blum, and M. B. Ptacek. 2015. Local adaptation despite high gene flow in the waterfall-climbing Hawaiian goby, *Sicyopterus stimpsoni*. Mol. Ecol 24:545–563.

Moore, B. R., and M. J. Donohue. 2009. A Bayesian approach for evaluating the impact of historical events on rates of diversification. PNAS 106:4307–4312.

Morgan, Thomas Hunt. 1905. Evolution and adaptation, London: The Macmillan Co.

Mortiz, C., C. J. Schneider, and D. B. Wake. 1992. Evolutionary relationships within *Ensantina eschscholtzii* complex confirm the ring species interpretation. Syst. Bio 41:273–291.

Muller, H. J. 1949. Redintegration of the symposium on genetics,paleontology, and evolution. *In* Genetics, Paleontology, and Evolution. Eds. G. L., Jepsen, G. G., Simpson, and E. Mayr. Princeton Univ. Pres, Princeton, New Jersey, U.S.A.

Okamoto, K. W., R. B. Langerhans, R. Rashid, and P. Amarasekare. 2015. Microevolutionary patterns in the common *Caiman* predict macroevolutionary trends across extant crocodilians. Biol. J. Linn. Soc 116: 834–846.

Orzack, S. H. 1981. The Modern Synthesis is partly Wright. Paleobiology 7:128–134.

Parins-Fukuchi, C., G. W. Stull, and S. A. Smith. 2021. Phylogenomic conflict coincides with rapid morphological innovation. PNAS 118:e2023058118.

Pennell, M. W., L. J. Harmon, and J. C. Uyeda. 2014. Is there room for punctuated equilibrium in macroevolution? Trends Ecol. Evol 29:23–32.

Pollard, J. W. 1984. Evolutionary Theory: Paths into the Future. Academic Press, London, U.K.

Portnoy, D. S., and J. R. Gold. 2012. Evidence of multiple vicariance in a marine suture-zone in the Gulf of Mexico. J. Biogeogr 39:1499–1507.

Rabosky, D. L. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. PLoS ONE 9:e89543.

Rabosky, D. L., and A. R. McCune. 2009. Reinventing species selection with molecular phylogenies. Trends Ecol. Evol 25:68–74.

Robinson, M. D., and C. W. Barrows. 2013. Namibian and North American sand-diving lizards. J. Arid Env 93:116–125.

Rolland, J., D. Silvestro, G. Litsios, L. Faye, and N. Salamin. 2018. Clownfishes evolution below and above the species level. Proc. R. Soc. B 285:20171796.

Rosen, Donn. J. W. Pollard, 1986. Hierachies and history. Evolutionary theory: Paths into the future, London: Academic Press.

Rosenblum, E. B. 2006. Convergent evolution and divergent selection: Lizards at the White Sands ecotone. Am. Nat 167:1–15.

Sambatti, J. B. M., and K. J. Rice. 2006. Local adaptation, patterns of selection, and gene flow in the Californian serpentine sunflower (*Helianthus exilis*). Evolution 60:696–710.

Slatkin, M. 1973. Gene flow and selection in a cline. Genetics 75:733–756.

Slatkin, M. 1981. A diffusion model of species selection. Paleobiology 7:421–425.

Smith, S. A., N. Walker-Hale, J. F. Walker, and J. W. Brown. 2019. Phylogenetic conflicts, combinability, and deep phylogenomics in plants. Syst. Biol 69:579–592.

Stanley, S. M. 1979. Macroevolution: Patterns and Processes. W. H. Freeman and Co San Francisco, California, U.S.A.

Takahashi, K., Y. Terai, M. Nishida, and N. Okada. 2001. Phylogenetic relationships and ancient incomplete lineage sorting among cichlid fishes in Lake Tanganyika as revealed by analysis of insertion of retrotransposons. Mol. Biol. Evol 18:2057–2066.

Templeton, A. R. 1980. The theory of speciation via the founder principle. Genetics 94:1001–1038.

Uyeda, J. C., T. F. Hansen, S. J. Arnold, and J. Pienaar. 2011. The million-year wait for macroevolutionary bursts. PNAS 108:15908–15913.

Vrba, E. S. 1984. What is species selection? Syst. Zool 33:318–328.

Wake, D. B., and C. J. Schneider. 1998. Taxonomy of the plethodontid salamander genus *Ensatina*. Herpetologica 54:279–298.

Wakeley, J. 2000. The effects of subdivision on the genetic divergence of populations and species. Evolution 54:1092–1101.

Weber, M. G., and A. A. Agrawal. 2014. Defense mutualisms enhance plant diversification. PNAS 111:16442–16447.

Weber, M. G., N. I. Cacho, M. J. Q. Phan, C. Disbrow, S. R. Ramírez, and S. Y. Strauss. 2018. The evolution of floral signals in relation to range overlap in a clade of California jewelflowers (*Strepthanus* s.l.). Evolution 72:798–807.

Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evol. Biol 6:47–49.

Wright, S. 1940. Breeding structure of populations in relation to speciation. Am. Nat 74:232–248.

Wright, S. 1960. The genetics of vital characters of the guinea pig. J. Cell Comp. Physiol 56(Suppl.1): 123–151.

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