

Music as Art and Science
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An Evo-Devo Model for the Evolution of Music

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The Modern Synthesis (MS) is a well-established paradigm that continues to dominate theoretical accounts of biological evolution. Around eight decades ago, the MS integrated key concepts from Darwinian natural selection and Mendelian inheritance with the new science of genetics, bringing about the field of population genetics. Notwithstanding its major success among evolutionary biologists, this approach has been criticized for associating inheritance solely with genes and for neglecting other sources of evolutionary change besides mutation, natural selection, and fitness differences (for a critical analysis of the core principles of the Modern Synthesis, see Müller, 2017).

Despite these challenges, the neo-Darwinian approach has been widely used as a source of analogy for developing models of both cultural and musical evolution. Although cultural evolution has many parallels with genetic evolution, it also has clear differences from it (Creanza et al., 2017). This chapter critically reviews these neo-Darwinian approaches and highlights the shortcomings of their application to the evolution of music. Traditionally, the focus has been on the variation of rhythmic-melodic patterns (and, to a lesser extent, harmonic structures), interpreting those that persist in a musical tradition in ways similar to the neo-Darwinian concept of fitness. By contrast, here we argue that besides the transmission and variation of acoustic features, the evolution of music fundamentally

depends on a multiplicity of non-sonic components, including social, material, and functional elements, among others, requiring a broader theoretical framework that can accommodate these factors. We suggest that the perspective of evolutionary developmental biology (evo-devo) provides suitable theoretical tools for such an inclusive analysis.

Models of Cultural Evolution Based on the Neo-Darwinian Framework

Based on the idea that biological and cultural processes operate under similar rules, it is often argued that processes of cultural transmission and change can be analyzed using the same theoretical principles and methodological tools as applied to genetic inheritance. Thus, it has been suggested that the main tenets of Darwin's theory—(1) variation among individuals in a population; (2) inheritance of this variation across generations; and (3) the competitive selection of advantageous variants—are equally applicable to understanding cultural evolution (Mesoudi, 2011). One of these approaches is meme theory introduced by Dawkins (1977). In analogy with genes, Dawkins conceptualized memes as abstract units of cultural information that are transmitted from one individual to another, thereby facilitating the replication, transmission, and variation of information within a culture. Although memetic theory is no longer prominent in recent models of cultural evolution, the concept of culture as information stored in the brains of individuals, as well as the idea that imitation plays a key role in this process, remains central to these approaches. Mesoudi, for instance, formulates this view in the following way: "The skill required to use chopsticks, for example, is stored in the brains of virtually all Japanese people, is acquired from other people via imitation or teaching, and is expressed behaviorally in the form of chopstick use" (Mesoudi, 2011, p. 3). Thus, similar to how genes are regarded as heritable units encoding the information necessary to produce biological traits or phenotypes, the mind of an individual is seen as a repository of information, comprising

ideas and mental content that become manifest in behaviors and objects. Using the analytical tools of population genetics, cultural evolutionists aim to predict the frequency with which cultural expressions, mostly analyzed as isolated traits, are either retained or eliminated within a group of individuals (Boyd & Richerson, 2005). The “success” of one cultural item to be copied and transmitted more frequently than others is commonly seen as analogous to what is termed “fitness” in evolutionary biology.

This kind of evolutionary approach to culture suffers from several explanatory weaknesses, of which the following are particularly salient. First, the inclination to single out imitation as the primary driver of cultural transmission overlooks the complex, multifactorial pathways through which culture evolves across diverse spatial and temporal scales. Second, the understanding of culture as mental information fails to recognize the fundamental role played by the specific organization of the environment—including practices, social norms, and the use of artifacts—in processes of cultural reproduction and change. Third, the emphasis on analyzing cultural traits as independent entities black-boxes the crucial function of the processes through which these traits are generated, acquired, and transmitted both within and across generations. These shortcomings highlight the need for a model of cultural evolution that includes the generative, environmental, and transmissional components.

The Evolution of Music from a Neo-Darwinian Perspective

Despite the limitations described above, neo-Darwinian concepts of cultural evolution have been widely used in the study of musical evolution. The distinction between musicality and music is relevant for identifying the two main domains in which neo-Darwinian concepts have been applied in this terrain. As noted by Honing (2018) and other authors, musicality refers to the biological capabilities that enable us to both perceive and create music, while the notion of music refers to the cultural products—such as musical genres

and repertoires—developed by diverse groups around the world. This distinction has often been unclear, as many scholars when referring to musicality use it interchangeably with music. The foundational version of this conflation can be found in Darwin (1871), who hypothesized that the origins of music are linked to courtship behaviors observed in many species. He further suggested that, prior to the advent of human speech, our evolutionary ancestors used melodic intonations as a means of attracting mates for reproductive purposes. As an elaboration of such intonations, primordial forms of music would have been passed down across generations, because they conferred a survival advantage.

Contemporary versions of this hypothesis have expanded upon Darwin's original ideas by incorporating other aspects of music—and musicality—that are also considered to be part of sexual attractiveness, such as motor coordination in the form of bodily movements as well as a display of physical strength (Miller, 2000). Other scholars maintain that music's emergence can be attributed to its broader survival benefits beyond sexual reproduction, which includes caregiving, social bonding, collective coordination, and emotional communication (for a general review of these models see Savage et al., 2021). While these models have gained considerable acceptance, they suffer from their exclusive reliance on adaptationist explanations, which mostly disregard the intricate interplay of multifactorial components underpinning the human capacity for music. In other words, given the complex nature of human musicality—encompassing perceptual, cognitive, behavioral, and symbolic dimensions—scholars have argued that it is unlikely that music emerged as a unified adaptive package in response to specific environmental pressures (Savage et al., 2021). This debate has generated growing interest in exploring the relevance of different evolutionary approaches, such as niche construction theory and gene-culture coevolution, in models of the origins of human musicality (e.g., Tomlinson, 2015; Savage et al., 2021). However, in models focused on the evolution and transmission of musical genres and repertoires, the neo-Darwinian perspective remains dominant.

A key area in this research domain is what has been referred to as the evolution of tune families—groups of melodies that are thought to share a common ancestor and to have evolved over time across different cultures and musical traditions. The study of tune families has a long tradition that dates back to the early twentieth century (e.g., Sharp, 1907). In recent decades, it has incorporated techniques inspired by those of molecular biology, using automated analysis of shared melodic features and detecting divides across tune families (Savage & Atkinson, 2015; Jan, 2018). Research in this field typically characterizes musical evolution as the spread and transformation of specific motifs or themes over time, across different geographic areas, and through diverse styles, leading scholars to propose that, much like biological evolution, musical evolution follows specific overarching principles. For instance, Savage (2019) has argued that notes with pronounced structural roles, such as rhythmically accentuated notes, exhibit greater resistance to change, whereas melodic alterations are more likely to occur between neighboring notes than between those that are more distant.

Most studies in this field focus on examining what might be called the macroevolutionary relationships between distinct cultural traditions and musical genres, but scholars have also explored what they term “musical microevolution,” that is, processes of small-scale variation primarily studied in laboratory settings. In one experiment, for instance, researchers modeled a process analogous to sexual reproduction by combining and altering short audio sequences. They then employed an online survey where participants acted as a proxy for natural selection, evaluating and choosing features of the evolving music. Throughout several thousand generations, this process resulted in the emergence of music with aesthetically pleasing qualities from initially unstructured sounds, entirely shaped by listener preferences (Mac-Callum et al., 2012).

Although these studies have provided valuable insights into how the sonic characteristics of different musical traditions have evolved over time, a key limitation is the interpretation of these changes as analogous to genetic mutations, framing them exclusively as the

outcome of the random variation of gene-like units endowed with certain fitness qualities. By contrast, ethnomusicological research has rightly shown that musical genres are not merely products of sound variation but the result of active engagement with the social, cultural (Merriam, 1964), and material environment in which their development and transmission take place (Martínez & Villanueva, 2018). This requires characterizing the evolution of music as a multifactorial phenomenon that depends not only on the recombination of a set of sonic properties but also on the complex organization of norms, artifacts, and institutions in which this phenomenon is embedded. To explain this intricate process, a different framework is needed. We suggest that the research agenda of evolutionary developmental biology (evo-devo) can provide not only a new source of analogy for constructing explanatory models of cultural evolution that can be applied to music, but perhaps more important, a comprehensive theoretical approach to analyzing these processes from an interdisciplinary perspective.

Evolutionary Developmental Biology

Evo-devo is a field of evolutionary biology that has formed over the past four decades and has diversified into a wide variety of subfields, which have evolved numerous methodologies and concepts (Nuño de la Rosa & Müller, 2021). Its research focuses on two central questions: How do evolutionary mechanisms generate and modify developmental processes of (mostly multicellular) organisms? How, in turn, do the properties and structure of these developmental processes shape phenotypic evolution? Evo-devo demonstrates that the complex processes of development that multicellular organisms undergo guide phenotypic variation, which in turn channels evolutionary pathways. This perspective challenges the traditional view that associates evolution solely with genetic variation. From the evo-devo perspective, evolution is the reproduction and modification of developmental mechanisms that determine the generation of organismal form (Amundson, 2005).

This shift in perspective represents more than a simple change of emphasis. It marks a fundamentally different approach to understanding the process of phenotypic evolution. Whereas the received MS view concentrated on the fitness values of given genotypes or phenotypes, and consequently on how selection favors the minute variation and spread of traits, the evo-devo research program focuses on how traits are produced in the first place, and how their variation is a function of inherent developmental potentialities. A key aspect of this approach is the recognition that inheritance involves the reproduction of the entire developmental process, including its material and dynamical contexts, rather than merely the transmission of genes alone. Genes do not independently encode biological traits. Rather, they play an important role in a complex, multilevel system in which their products—such as structural and regulatory factors—interact with those of other genes, with environmental features, as well as with cellular, physical, and mechanical components. It is this interplay among multilevel properties that ultimately gives rise to organismal phenotypes. As a result, an organism's traits are not determined solely by its genes, but by the developmental context in which these genes are deployed. These mechanisms, molecular, physical, and process-based, constitute the material dimension of development, a view that differs substantially from the informational picture emphasized by the gene-deterministic approach.

The evo-devo-informed perspective enables novel explanations of evolutionary phenomena beyond the scope of classical population genetics, including “biases in the variation of morphological traits, rapid changes of form evident from the fossil record, the origin of nonadaptive traits, apparent dissociations between genetic and phenotypic evolution, and the origination of higher-level morphological organization such as homology, body plans, and novelty” (Müller, 2007, p. 500). It recognizes multiple levels of organization from molecules to genes, the self-organizing properties of cells and tissues that shape form, as well as the influence of external stressors on phenotypic variation. Crucially, all these properties are context-dependent. Developmental mechanisms are integrated within the overall generation of the organism, meaning not only that they

interact in a cohesive way, but also that they depend on environmental conditions. Some of these factors are general, such as the physical properties of cells and tissues, while others are lineage- and trait-dependent, originating in previous steps of evolution. Overall, evo-devo expands the scope of evolutionary thinking to encompass the origin, modification, and organization of phenotypes in evolutionary time. Together with other areas of reform in evolutionary theory, such as niche construction, epigenetic inheritance, and evolvability, evo-devo has become a principal contributor to a revised theoretical framework of evolution termed the Extended Evolutionary Synthesis (Müller, 2021; Lala et al., 2024).

Evo-Devo Approaches to the Study of Cultural Evolution.

Evo-devo-inspired ideas have been applied to studies of cultural evolution in recent decades. For instance, some models highlight the interplay between individuals and their environments in shaping evolutionary processes and assert that individuals inherit not only genes but also the development-environment interactions created in the past, along with the practices that drive these changes (Laland et al., 2000). Similarly, scholars advocating Developmental Systems Theory stress that it is the entire developmental system that evolves, encompassing the entire network of interacting elements involved in a life cycle and functioning as the unit for both development and evolution (Oyama et al., 2001). Research on technological innovation has also integrated the evo-devo perspective, emphasizing how alterations in the evolving relationship between agents and artifacts can result in new forms of human interaction, which, in turn, can produce a chain of reconfigurations across other areas of a cultural system (Anderson et al., 2014). These ideas are consistent with the “generative entrenchment” model, which suggests that items that are repeatedly reproduced and assembled become deeply embedded within a cultural system, acting as scaffolds or constraints for the generation of subsequent items (Caporael et al.,

2014; Wimsatt & Griesemer, 2007). These models emphasize the importance of generative and cumulative processes in cultural evolution, whereby certain cultural traits or practices become more firmly rooted in a broader system of mechanistic interactions and influence the future trajectory of those practices and their possibilities for innovation.

Approaches such as the ones mentioned above represent a significant advancement in the conceptualization of cultural evolution, framing it as a complex process driven by interconnected clusters of elements (e.g., cognitive, social, and material) that serve as reproductive generators for cultural traits. They also highlight that approaches to cultural evolution must not address this topic as disconnected from the sociomaterial structure that supports human learning and development. Instead, a comprehensive theory of cultural evolution should account for these dimensions and their reciprocal interactions (Wimsatt & Griesemer, 2007) alongside other biological underpinnings such as gene-culture coevolution, ecology, and demographics (Creanza et al., 2017). Although the evo-devo approach continues to inspire new models of cultural evolution, as well as significant reforms of evolutionary theory itself (Lala et al., 2024), the endeavor remains ongoing (Wimsatt, 2019). Evo-devo conceptual tools still have to be fully elaborated and applied to a wide range of cultural domains. The study of musical transmission and change represents an example of a complex cultural phenomenon to which such tools can be applied.

Toward an Evo-Devo Approach to Musical Evolution

What is recognized as music varies significantly around the world. In this cross-cultural context, music is typically not conceptualized solely by its sonic properties; it is also closely linked to the material and social practices that shape the complex settings in which it is performed and developed (Cross, 2001; Martínez & Villanueva, 2018). This suggests that processes of musical stabilization,

transmission, and change should be analyzed as a result of a variety of interrelated factors. We propose that so intricate a phenomenon can be more effectively addressed by our model. The following example illustrates this approach.

In the late 1970s and throughout the 1980s, a process of revitalization for *son jarocho*, a Mexican musical genre from southern Veracruz and its neighboring regions, started to take shape (García Díaz, 2022). Although *son jarocho* encompasses a rich array of elements, including a distinctive vocal style, popular poetry, and dance, our analysis will primarily focus on specific generative mechanisms driving the evolution and transformation of key aspects of its harmonic and melodic dimensions. By doing so, we aim to argue that this phenomenon entails more than a simple recombination of sonic properties.

This revival movement encompassed various initiatives, including the organization of musical festivals and workshops, the production of music recordings, and their promotion through local radio. However, from the outset, it was primarily driven by a renewed interest in fandangos—musical and dance celebrations integral to religious ceremonies as well as family and community festivities. Both *son jarocho* and fandangos were close to disappearing. Thus, the reactivation of the former implied the reactivation of the latter. Special emphasis was placed on the collective participation that had characterized fandangos in the past, which typically followed a specific structure. The musicians assemble around a *tarima* (a wooden platform), which demarcates the space for instrumentalists, singers, and other participants. Once the music begins, the dancers join the *tarima* in a spontaneous and usually alternating sequence. The number of musicians varies over the course of the fandango, which can last throughout the night. Percussion instruments such as the *tamborín* and the *quijada de burro* (donkey jaw) are commonly employed in these celebrations. The dance performed on a wooden platform also serves as a percussion instrument. Regarding string instruments, there is a wide variety of guitar-shaped, fretted local instruments. Due to the objective of this analysis, we will focus on two of them: the *jaranas jarocho*s and the *guitarras de son*.

The revival of *son jarocho* led to a process of standardization in the shape and tuning of the *jaranas jarochas*—traditional eight-string instruments resembling small guitars, typically used to play chords. The standardized designs facilitated chord execution, fostered collective participation, and constrained the tonalities used in interpreting the repertoire. The learning process for beginners was also supported by the standardized characteristics of these instruments and the social context of the fandangos. Novices had the opportunity to perform alongside more experienced musicians, playing basic chords and strumming patterns while learning from the complex performances of their skilled counterparts. A similar dynamic arose when they learned to play the other instruments as well as to sing and dance. In this way, collective practice became an essential part of the learning (developmental) process.

The *guitarra de son*, a small, four-string instrument similar to a guitar, carries the melodic line. Played with a small bone plectrum, it produces a distinctive, sharp articulation. A key element in the way the *guitarra de son* shapes the melody is the *tanguéo*, which can be defined as melodic sections that combine the use of the bass strings with the rhythmic articulation of higher notes. The proper execution of the *tanguéo* technique, and of the *guitarra de son* in general, relies on several factors including the tuning of the instrument, which features two lower-pitched strings and two higher-pitched strings; the dimensions, form, and weight of the bone plectrum, commonly held between the thumb and index finger, enable the musicians to strike or pluck the strings with different levels of force and speed; the physical characteristics of the *guitarra de son*, such as a comfortable neck, facilitate proper hand positioning and clean plucking, while the fingerboard's layout simplifies transitions between chords and melodic phrases.

During the period of musical recovery, innovative techniques for instrument construction were also developed, enabled by the use of more advanced tools. Notably, in the workshop of luthier Gilberto Gutiérrez, a groundbreaking five-string *guitarra de son* was created.

While the intricacies of the construction process and the physical characteristics of this novel instrument lie beyond the scope of this discussion, one pivotal change warrants attention: the addition of a higher-pitched string. This modification introduced a new tuning system, which, in turn, significantly influenced performance practices. The altered tuning reduced the frequency of *tanguéos* and fostered a shift toward more intricate melodic lines that spanned a wider tonal range, covering additional octaves. Furthermore, the five-string guitar expanded harmonic possibilities for *jaranas*, enabling performers to explore chords in diverse tonalities. This material innovation triggered a cascade effect, reshaping the characteristics of *son jarocho* music. Among them, it expanded harmonic possibilities, enriched melodic complexity, and broadened the tonal palette, while also influencing other aspects, such as the singing style, particularly by extending the range of tones employed in vocal performances.

This brief analysis provides only a very general overview of the ongoing revitalization of *son jarocho*. Currently, its musical repertoire continues to expand and diversify, driven by and contributing to the creation of new performative and learning spaces, the reappropriation of ancient instruments, the inclusion of new instruments, and the development of innovative forms of execution. Building on the above and through the lens of evo-devo, we can identify three major components and three forms of inheritance in the evolution of music: (a) the social settings (or niches) defined by the formal structures of ceremonies, celebrations, festivities, and so forth; (b) the material construction of instruments that define their acoustic properties and enhance the capacities for musical production and exploration; and (c) the functional techniques, which include performance practices, instrument production, and playing skills of the musicians. The relationships between these components are reciprocal (Figure 11.1). All three components possess largely (but not fully) independent inheritance processes that lead to the renewing development (learning) of musical repertoires in the next generation. It is worth noting that our

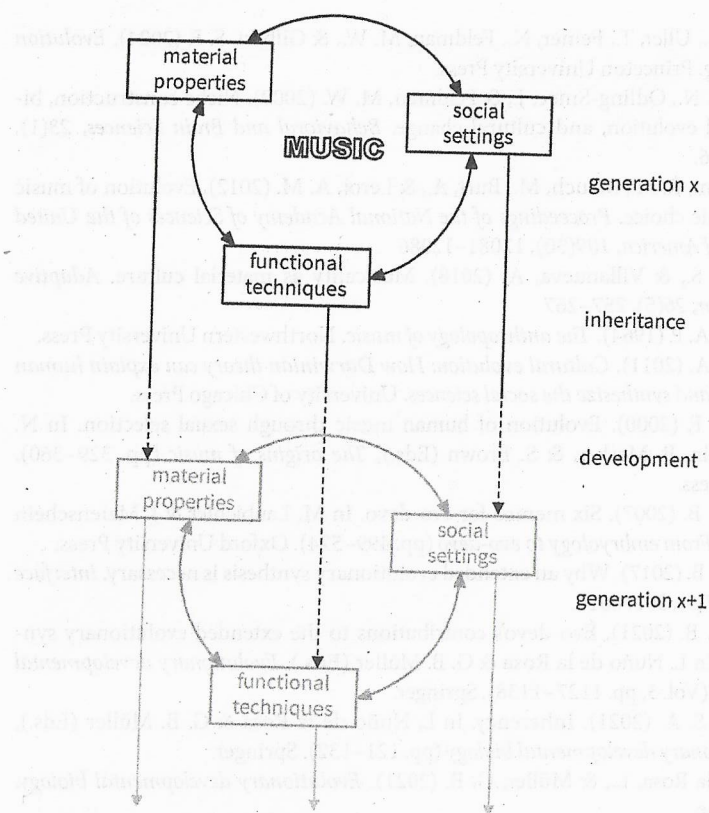


Figure 11.1 Evo-devo model of the non-sonic components of music evolution

model does not rule out its application to vocal musical traditions; in this context, the anatomical features of the vocal system may be regarded as analogous to the material characteristics of a musical instrument.

In this evo-devo view, the sonic architecture of a musical genre and its evolution over time arise not primarily from the external selection of sound-based properties but fundamentally also from the constellation of interconnected non-sonic factors (social setting, material components, performance practice) intrinsic to the generative context, a feature known as “inherency” in evo-devo and the philosophy of science (Newman, 2021).

Conclusions

The evo-devo model presented here identifies several generative components that are instrumental in the evolution of music. It illustrates that musical evolution is deeply dependent on the sociomaterial conditions and their interactions. The model is heuristic and is still far from a complete theory. However, its elements can be empirically tested and permit the formulation of new research questions. The concrete features of the pathways of inheritance and development, for instance, require further analysis. For other components empirical data are already available. The example of the musical revival is a case in point, showing that the organizational relations among non-sonic factors (material, functional, social) can either enable or constrain the potential for musical innovation. We also believe that ongoing analyses of automated sonic patterns can be further enriched, and their explanatory scope tested, by incorporating the elements highlighted in this approach. Thus, the model offers a theoretical framework for the further study of the complex processes underlying the evolution of music. This endeavor will require close interdisciplinary collaboration, fostering new dialogue between the humanities, the social sciences, and the natural sciences.

Overarching Research Questions

1. What limitations do current models of cultural evolution face in explaining processes of cultural transmission and change?
2. How do these limitations affect their application to understanding musical phenomena?
3. What is the payoff of applying an evo-devo framework to musical transmission and evolution?
4. How can the role of sociomaterial settings be incorporated into explanations of musical evolution?
5. Which kinds of interdisciplinary collaborations among the humanities, social sciences, and natural sciences can enhance our understanding of musical evolution?

Take-Home Messages

1. Cultural evolution studies of music were predominantly based on neo-Darwinian concepts.
2. New developmental approaches to evolution enrich the scope of cultural evolution studies, but they have not been applied to music yet.
3. The study of the evolution of music should extend beyond sound patterns to include the organization and restructuring of the sociomaterial systems in which it is embedded.
4. Such studies need to be supported by a cross-cultural perspective on music, informed by historical, anthropological, and sociological approaches.
5. The evo-devo approach provides theoretical tools for building interdisciplinary bridges that can support novel analyses of musical evolution from a broader perspective.

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