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SYMPOSIUM INTRODUCTION

An Integrative Understanding of Evolutionary Convergence Across Organisms and Biological Scales

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From the symposium "Integrating research on convergent evolution across levels of biological organization, organisms, and time" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 2–6, 2024, at Seattle, Washington.

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Synopsis The extent to which evolution is predictable is a long-standing question in biology, with implications for urgent biological issues such as viral evolution, the emergence of antibiotic resistance in bacteria, and organismal responses to climate change. Convergent evolution, the phylogenetically independent evolution of similar phenotypes, provides biological replicates useful for exploring patterns of predictability in evolution. Understanding evolutionary convergence requires synthesizing findings across biological scales and organisms. To this end, we organized a SICB-wide symposium entitled "Integrating research on convergent evolution across levels of biological organization, organisms, and time." Our symposium showcased interdisciplinary research on evolutionary convergence across diverse study systems and levels of biological organization, while highlighting new techniques and comparative methods for identifying patterns of predictability in convergently evolved traits. Here, we introduce findings from papers included in this symposium issue and identify common themes, highlight emerging questions, and discuss how we can integrate new techniques, tools, and systems to expand our understanding of evolutionary convergence.

Introduction: harnessing evolutionary convergence to explore evolutionary predictability

"I call this experiment "replaying life's tape." You press the rewind button and, making sure you thoroughly erase everything that actually happened, go back to any time and place in the past—say, to the seas of the Burgess Shale. Then let the tape run again and see if the repetition looks at all like the original."—Stephen Jay Gould, *Wonderful Life: The Burgess Shale and the Nature of History* (1989).

More than 30 years later, Stephen Jay Gould's thought experiment (Gould 1989) continues to motivate a wealth of research programs addressing the extent to which contingency and determinism shape evolution (reviewed in Blount et al. 2018). Although we cannot replay the tape of life in natural systems, evolutionary convergence, or the repeated evolution of similar phenotypes, provides biological replicates useful for investigating the roles of contingency and determinism in evolution. For example, bioluminescence (Lau and Oakley 2021), viviparity (Blackburn 2015), and venom (Arbuckle 2020)—each of which likely evolved convergently over a hundred times across lifeforms—are statistically powerful systems for studying evolutionary predictability across biological scales. Studies of evolutionary convergence may use comparative approaches, which merge diverse scientific disciplines (e.g., evolutionary biology, molecular biology, physics, chemistry), to generate hypotheses surrounding the mechanisms underlying phenotypic convergence (i.e., behavioral, physiological, morphological, molecular). As such, furthering our understanding of evolutionary convergence requires synthesizing these findings across biological scales and diverse study systems.

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Fig. 1. Logo showcasing the diverse range of study systems featured in the 2024 SICB symposium on convergent evolution.

Evolution occurs at every level of biological organization, so investigating convergent evolution requires understanding evolutionary changes at each level and disentangling how levels of biological organization interact with one another. Classic studies of convergent evolution characterized large structures, as in the ecomorphs of *Anolis* lizards that converge on leg lengths and toepad morphology (Losos 2009). Histology revealed convergence in tissues (e.g., Tateoka 1959; Nyby and Thiessen 1971; Phillips and Tandler 1987; Wintrich et al. 2020), and the genomic revolution permitted the discovery of convergent cell types (Arendt et al. 2016). The once central question of whether convergent phenotypes rely on the same or different genes, tissues, or processes has been answered clearly with "both," and now the question is how and why these are recruited. Our understanding of convergent evolution continues to expand into additional levels of biological organization, but remains limited by our inability to investigate and intertwine evolutionary mechanisms at and between levels.

The goal of our symposium, "Integrating research on convergent evolution across levels of biological organization, organisms, and time" (Fig. 1) was to integrate interdisciplinary research on evolutionary convergence spanning across biological scales, timescales, and the tree of life. Ultimately, this symposium fostered discussions and syntheses on the evolutionary mechanisms that produce patterns of convergence through diverse and timely investigations into convergence across Metazoa. In this introduction, we first highlight findings from papers in this symposium issue (Table 1). Then, we identify common themes and emerging questions in convergent evolution research. Finally, we discuss the importance of integrating diverse techniques, tools, and systems for expanding research on evolutionary convergence. In the near future, we may gain a deeper understanding of the factors driving evolutionary convergence, as researchers continue to collaborate and synthesize emergent findings across study systems and levels of biological organization.

Topics and emergent themes in this issue

Convergent evolution varies within and across biological scales

Evolutionary convergence may vary across different levels of biological organization, which necessitates exploring convergent traits across biological scales. Recent advances in sequencing and large genomic datasets reveal that some traits may use distinct genetic mechanisms, while others may use conserved genes. For example, viviparous systems convergently evolved numerous times in vertebrates and use similar morphological structures and physiological mechanisms (Blackburn 2015), yet these convergent structures and functions may be encoded by different genes (Foster et al. 2022). Conversely, monogamous mating systems may have convergently evolved by using the same transcriptomic profiles (Young et al. 2019). These studies, illustrating contrasting patterns of genetic convergence, raise questions on when and why we may observe instances of genetic conservation in convergently evolved traits.

The extent of morphological convergence of a given trait may range from "complete" to "incomplete" (Herrel et al. 2004; Stayton 2006), depending on the degree of morphological similarity between convergently evolved traits. Incomplete convergence may result from the existence of multiple morphological solutions, phylogenetic constraints, differences in ecological and selective pressures, or simply because there has not been enough evolutionary time for convergence to occur (Losos 2011). This issue contains several studies examining the extent of morphological convergence in various systems, including transitions from saltwater to freshwater habitats in stingrays (Magnuson et al. 2024), dietary strategies in piranhas and pacus (Kolmann et al. 2024), and burrowing in crayfishes (Delekta and Kolmann 2024). For instance, Magnuson et al. (2024) reveal that, despite evolving under similar ecological conditions, repeated shifts to freshwater habitats in stingrays may result in morphological divergence rather than convergence. Similarly, Delekta and Kolmann (2024) identified cases of incomplete convergence in two traits of burrowing crayfishes, where claw shapes did not converge as strongly as carapace shapes. This pattern of incomplete convergence may stem from divergent selective pressures on the forms and functions of crayfish claws (e.g., feeding, mate competition, or defense) (Delekta and Kolmann 2024). Moreover, Stayton (2024) found that higher levels of phenotypic integration, or the correlation between

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Table 1. This symposium issue highlights research on evolutionary convergence across levels of biological organization and diverse systems.

Biological scale examined	System and findings	Reference
Physiology and behavior	Convergent physiological responses to heat tolerance in urban environments across taxa.	(Diamond et al. 2024)
	Foot flagging in frogs convergently evolved by repeatedly recruiting conserved physiological systems.	(Anderson et al. 2024)
Structural and skeletal morphology	Repeated transitions from salt to freshwater result in morphological divergence, not convergence, in stingrays.	(Magnuson et al. 2024)
	Repeated evolution of burrowing behavior promotes morphological convergence of carapace and claw shape in crayfishes.	(Delekta and Kolmann 2024)
	The extent of morphological convergence in piranhas and pacus may depend on feeding ecologies and dietary shifts.	(Kolmann et al. 2024)
	Higher levels of phenotypic integration in turtle shells, squirrel mandibles, and fishes are associated with higher levels of convergence.	(Stayton 2024)
	Different developmental patterns result in variation of form and function in one origin of toe pads in lizards.	(Griffing et al. 2024)
Molecular and genetic	Using "genetic toolkits" as a metaphor for understanding the repeated recruitment of conserved genes in convergent phenotypes.	(Oakley 2024)
	Using the bioinformatics program PhyloAcc to perform comparative genomics for identifying genes associated with convergent phenotypes.	(Thomas et al. 2024)

trait changes in the phenotype, may be associated with higher levels of convergence. These studies collectively raise fundamental questions—Why do some systems produce greater degrees of morphological convergence than others? What are drivers of phenotypic integration and morphological convergence at the physiological, developmental, and genetic levels?

Phenotypes may convergently evolve by recruiting similar and distinct pre-existing components

Evolution repurposes existing biological features, such as behaviors, organs, and genes, by co-opting them during the evolution of novel structures and functions. Convergent structures and functions may evolve by co-opting the same features, even across vast phylogenetic distances, but may also evolve by co-opting entirely different features. In this issue, Oakley (2024) outlines three stages for evolutionary co-option at a genetic level: genes must first originate, then be maintained in the absence of the derived trait, before being re-deployed. These three stages of genetic co-option may apply broadly across biological scales, providing a general framework for understanding how and why convergent evolution may recruit similar and distinct pre-existing components. For instance, foot flagging in frogs may have repeatedly recruited conserved mechanisms associated with pre-existing features of their sensory system (Anderson et al. 2024). In this example, a behavioral feature may have originated earlier, then was maintained for other organismal functions such as feeding, before being re-deployed for foot flagging.

Investigating the underlying mechanisms of convergently evolved traits may provide insight into whether certain features are more biased towards co-option during evolution. In this symposium issue, Anderson et al. (2024) hypothesize that certain highly conserved physiological and neurological mechanisms may be predisposed towards being repeatedly recruited in the convergent evolution of signaling behaviors, especially if the perceptual bias of the receiver is also conserved. Similarly, but at a different biological scale, Oakley (2024) discusses how, at the molecular level, the repeated co-option of homologous genes during evolutionary convergence may depend on the convergent structure or function and the possible molecular mechanisms that can produce it (Stern 2013; Lau et al. 2024). Across biological scales, in order for evolutionary convergence to recruit the same biological features, these features would have needed to remain conserved across taxa in the absence of the convergent trait. Emerging questions include: What conserved mechanisms underlie convergently evolved traits? To what extent did convergent traits evolve by recruiting the same biological features? If the same biological features are repeatedly recruited, were they maintained for the same organismal functions? What factors may drive these patterns of convergence?

Applying new systems, techniques, and tools to study evolutionary convergence

New systems, techniques, and tools have enormous potential for enhancing and expanding research in evolutionary convergence across organisms and timescales.

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In this issue, Diamond et al. (2024) discuss cities as an example of ecologically relevant incubators of rapid species change due to factors such as urban heat islands, pollution, habitat structural modification, and altered hydrology. Such environments provide new relevance to the question of whether evolution is reproducible in the face of climate change (Diamond et al. 2024).

New tools and techniques also allow us to connect precise molecular data to morphological structures and phenotypic functions. Over the last two decades, next- and third-generation sequencing decreased in cost and increased in efficacy, especially for non-model systems (Giani et al. 2020; Li and Wang 2021). This led to a spike in comparative genomics research into a variety of convergent phenotypes, such as bioluminescence (Pankey et al. 2014; Lau and Oakley 2021), venoms (von Reumont et al. 2022), and eyes (Oakley 2024). Some techniques, such as single-cell RNA-seq, ATAC-seq, and spatial transcriptomics, provide precise, detailed molecular information about transcription and downstream molecular functions (Vergara et al. 2021). This precision allows for more detailed connections between genotype and phenotype across biological levels of organization and through evolution (Hao et al. 2019), even within emerging model systems (Hulett et al. 2023) and across Metazoa more broadly (Tarashansky et al. 2021). To account for the influx of new data, and therefore new analytical possibilities, tools are being developed to explicitly connect molecular inferences to phenotypic traits, such as those that model rates of evolution for molecular loci and continuous traits simultaneously (Thomas et al. 2024). These also include tools that address challenges related to comparative analysis with new data types, such as those surrounding orthology assignment across taxa (Tarashansky et al. 2021).

Integrating new molecular tools with more traditional resources and data types is crucial for studying convergence across biological levels (Lau and Oakley 2021). In addition to generating sequence data, this approach also requires describing gross and tissue morphology across development and among taxa. In our symposium, we noted many instances of this integration, including techniques such as phylogenetic morphospace analyses (Delekta and Kolmann 2024; Kolmann et al. 2024; Magnuson et al. 2024), urban ecology and evolution (Diamond et al. 2024), isotope sampling across development (Griffing et al. 2024), or even assessments of phenotypic integration (Stayton 2024). The vast majority of these papers used natural history collections in their research, underscoring the invaluable role collections play as a rich resource for studies that integrate modern technologies with traditional techniques. Natural history collections are also useful resources for exploring the genetic architecture of convergent evolution (Lamichhaney et al. 2019) and establishing phylogenetic frameworks necessary for identifying instances of evolutionary convergence. By integrating new molecular techniques with more traditional types of data, research into evolutionary convergence is able to go deeper into the mechanisms of evolution than ever before. Emerging questions include: How do morphological and molecular changes interact across evolution to allow for convergently evolved traits? At what level of biological organization are patterns of convergence emerging and why? What challenges exist in integrating molecular and morphological techniques to investigate convergent evolution?

Concluding remarks

Research in evolutionary convergence, especially in non-model taxa, drastically expanded during the advent of next generation sequencing technologies, advancements in molecular biology and imaging techniques, development of new computational tools for phylogenetic comparative methods (Thomas et al. 2024), and establishment of new systems (Diamond et al. 2024). Applying these new technologies to research in convergent evolution revealed that evolutionary convergence may be similar at one level of biological organization yet radically different at others. The extent to which convergence extends across and within biological scales may be influenced by phenotypic integration (Stayton 2024), differences in selection pressures in form and function (Delekta and Kolmann 2024), trophic ecology (Kolmann et al. 2024), phylogenetic constraints (Magnuson et al. 2024), diversification after a convergent origin (Griffing et al. 2024), and whether certain biological mechanisms are predisposed towards evolutionary recruitment (Anderson et al. 2024; Oakley 2024). We anticipate research into evolutionary convergence will continue to expand, providing us with a deeper understanding of how contingency and determinism shape evolution. Aptly put, Gould's metaphorical thought experiment, "replaying the tape of life" (Gould 1989), continues to have a long-lasting impact on how we think about evolution, inspiring research programs to this day.

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Conflict of interest

The authors declare that there is no conflict of interest.

Data availability

No data was used in the preparation of this manuscript.

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