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SYMPOSIUM INTRODUCTION

Sex Across Origins: Questioning Animal-Centric Assumptions and Developing Integrative Frameworks

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From the symposium "Sex Across Origins: Questioning Animal-Centric Assumptions and Developing Integrative Frameworks" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7th, 2026.

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Synopsis Sex encompasses a suite of concepts and phenomena that are important for many biological processes and manifest differently across organismal diversity. Scientific progress in understanding sex, across taxonomic and disciplinary specializations, has substantially expanded knowledge of sexual diversity and complexity. This expansion is arguably transformative; however, its accessibility to and impact on nonspecialists remains limited. Common understandings of sex are often centered in human experience and a narrow subset of organismal diversity, shaped by entwined social/scientific histories. Meanwhile, political efforts to define "biological truth" and limit understanding of sexual diversity harm people and science. Improving the integration of knowledge about sex can increase its accessibility, offer new insights, and serve as a foundation for future research. Our symposium brought together researchers across disciplinary and taxonomic expertise to consider sex broadly, decentering animals and working toward broader integrative frameworks. It also included an education workshop and session of talks aimed to improve teaching about sex-related biology. Here, we discuss the symposium contributions and key themes, introducing the papers in this issue. We suggest ways to move forward, informed by discussions at the symposium.

Introduction

Sex encompasses multiple biological concepts describing phenomena that occur across a vast diversity of organisms, including but not limited to differentiated sexes (Warkentin et al. 2026). Biological understanding of the diversity and complexity of sex is growing rapidly. However, much of this information remains siloed within organismal and conceptual subfields, limiting the scope of comparative research, the larger insights that could emerge from integration, and the dissemination of this information to students and the public. Meanwhile, an oversimplified version of "biological sex" has been politically weaponized to justify harmful, discriminatory practices and limit education and inquiry (e.g., The Florida Legislature 2026; Exec. Order No. 14168 2025; Whitford 2025). Calls for researchers to define how they are using the word *sex* (Cell Press 2026; Eppley et al. 2026) and for educators to teach the diversity of sex (Long et al. 2021; Štrkalj and Pather 2021; Zemenick et al. 2022; Casper et al. 2025b) highlight important actions, but more is necessary. To improve research, teaching, and public understanding, scientists must build and share a better and more broadly integrative understanding of the biology of sex, in all of its complexity and diversity (Fig. 1). We organized this symposium as a contribution to this large-scale, ongoing community project.

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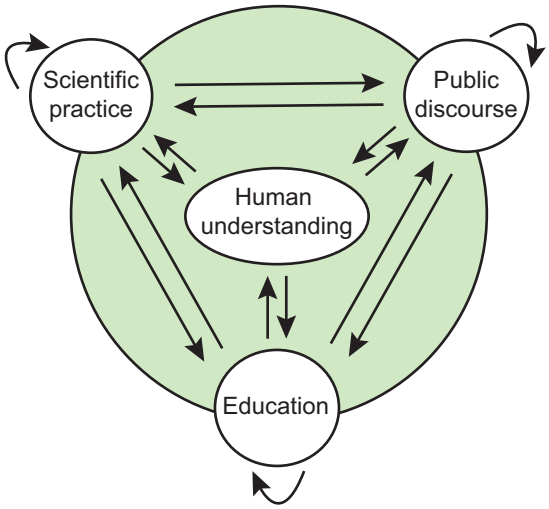


Fig. 1 As a social process, science builds on and contributes to human understanding directly and indirectly, through impacts on education and public discourse. It is also deeply shaped by these things. Work to improve understanding of sex-related topics, including in this symposium, faces a tripartite challenge. One element is improving biological understanding and practice, integrating and building on current knowledge while recognizing and addressing gaps and limitations shaped by history, social context, and our inherent biases, including as human organisms. The second is improving communication about sex-related topics to more effectively share our growing knowledge with students, colleagues, and the broader public. The importance and the challenge of studying and teaching the diversity of sex are both heightened by the challenges of navigating the current sociopolitical attacks on science, education, and sex and gender diversity.

While western scientific and social conceptions of sexes have shaped each other throughout their entwined histories (Massa 2026), understandings of sex have also been shaped and limited by a focus on canonical animals—centering human biology, model organisms, and a limited subset of natural diversity. Building a more complete and accurate understanding of sex requires recognizing the assumptions and biases generated by this limited and zoocentric frame of reference, sharing and engaging with knowledge across organismal silos, and testing hypotheses and theoretical frameworks across the breadth of organismal diversity. For instance, understandings of sexes are contested, with some stressing the foundational concept of an evolved, binary difference in gamete size (Goymann et al. 2023) while others focus on the complexity of multivariate sexual phenotypes and the common use of nongametic characteristics to assign sex in biological research and medicine (McLaughlin et al. 2023; Eppley et al. 2026). However, gamete evolution has a rich and complex history, with many convergent origins and some losses of size differences, as well as divergence and convergence in other traits in ways that are not always aligned with gamete size (Gorelick et al. 2016; Henshaw et al. 2023; Warkentin et al. 2026). Anisogamous gametes are extremely diverse across lineages, and anisogamy is just one of many binary and nonbinary mechanisms that structure reproductive compatibility (Billiard et al. 2026; Falk 2026). This diversity challenges assumptions underlying established theory, suggests ways to build more inclusive theory, and provides opportunities to test it (Constable and Liu 2026).

Beyond sexes, the diversity of sex in biology ranges from forms of genetic recombination to spatial arrangements of male and female gamete production within and among bodies (i.e., sexual architectures) and from reproductive modes to gamete-transfer strategies. A broad consideration of sex across organismal diversity complicates traditional definitions of gametes, sexes, reproduction, and sexual behaviors. The "Sex Across Origins" symposium brought together an interdisciplinary group of biologists spanning taxa and fields of biology to engage with this multifaceted complexity, build bridges and synthesize knowledge across areas of specialization, develop integrative frameworks, and identify key areas and opportunities for further work. The symposium included 11 talks, a round-table discussion, and an education workshop, as well as 18 complementary talks addressing sex-related topics in biology and education. The papers in this issue address multiple challenges related to more effectively studying, communicating and teaching about sex-related topics. They address the language and conceptions of sex, situate sex among other types of biological variation, use organismal diversity to test theory and identify disconnections and gaps in understanding, and provide insights aimed to improve teaching about sex-related biology. Collectively, they contribute to vital and synergistic efforts to build and support better understanding of the biology of sex.

Biological complexity, context, and scientific imaginaries: Language and conceptions of sex

A series of papers in this issue address how language shapes our understanding of the biodiversity and complexity of sex (Casper 2026; Casper and Warkentin 2026; Massa 2026; McDonough-Goldstein et al. 2026; Warkentin et al. 2026). In different ways, they address the entwined histories of scientific and societal understandings of sex and the challenges of this moment, in which growing scientific and public understanding of the complexity of sex is juxtaposed with regressive oversimplifications of biology for political ends. While the biological scope of sex is broader, sexes are particularly

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contested. Focusing on sexes, Massa (2026) contextualizes the recent US history of science defunding and legislative attacks on queer and trans rights, justified by claims of "biological truth," within the history of western scientific and social thinking about sex, showing how sex has always been political. She discusses how the changing scientific knowledge and discourse addressing the complexities of sexes is expanding scientific imaginaries (i.e., capacities to imagine scientific questions, methods, meanings, and possibilities; Van Anders 2014) and building new conceptual tools, offering an example of "everyday scientific creativity" to both improve scientific rigor and sidestep political restrictions on allowable questions and language. When general concepts and common language are too contested and historically burdened to serve scientific aims, more specific concepts and technical language can enable continued research and the generation of new knowledge.

Two papers address the breadth of biological phenomena encompassed by *sex*, their manifestations across the evolved diversity of life, and the linked challenges this breadth and diversity pose to communication and understanding (McDonough-Goldstein et al. 2026; Warkentin et al. 2026). Warkentin et al. (2026) present a framework of seven sex concepts, or biological phenomena called sex, including cellular processes, alternative states, and organismal actions. They use this framework to discuss the relationships among and multifaceted diversity and complexity within each of these aspects of biology, highlighting ways that evolutionary and developmental processes both generate and disrupt categorical boundaries while addressing multiple challenges in communicating about sex. The distinctions, anchor points, connections, and organismally inclusive approach of this framework offer ways to represent the breadth and complexity of sexual biology, contextualize simplifications and focal subsets, and communicate more clearly. McDonough-Goldstein et al. (2026) address the challenges of terminology for comparative research on reproductive trait evolution and discuss the community-based efforts of the Tree of Sex 2.0 consortium (Jeffries et al. 2025) toward building an ontology of sex, with context-embedded definitions. They acknowledge the complexity and imperfections of scientific terminology, including ways that it is insufficient to communicate sexual variation and inconsistencies across taxa and research areas; however, this terminology has enabled a rich body of research and biological insight. They show how scientific knowledge about sex has been shaped by the construction of language and suggest ways to move forward.

In another paper considering the organismal and conceptual scope of sex in biology, Casper and Warkentin (2026) use master narrative theory, from social science (McLean and Syed 2015), to identify some normative assumptions that are often implicit in biology, based on the human experience of diplontic life cycles, unitary and gonochoristic body plans, and obligately amphigonic reproduction. If unaddressed, these animal/vertebrate/mammalian biases can constrain thinking about organisms unlike ourselves and conceptualizations of biology more broadly. Casper and Warkentin (2026) discuss the value of simply naming our implicit assumptions and the specific contexts in which they apply, framed within the broader realm of organismal diversity. They suggest broader applications for "specialized" conceptual frameworks that were developed for organisms with greater complexity of body plans, life cycles, and reproduction, but can accommodate organisms with simpler lives. To facilitate the conceptual integration of sex across unitary and modular organisms, they offer a diagraming system to depict and compare how gamete production is structured across body plans encompassing any number of levels of modular organization (Casper and Warkentin 2026).

The collective scientific process of clarifying concepts and improving the terminology of sex will take time. Meanwhile, Casper (2026) offers a resource for better use of the language we have now, situated between oversimplified introductions and dense specialist texts. Ze identifies areas where oversimplification of biology and misuse of terms have blurred the meaning of words as well as areas where more conceptual work is needed to adequately describe known biology.

Sexes are not unique: Sex in the context of biological variation

Another set of papers in this issue examines sex/es in the broader context of variation. Phenotypic and genetic variation are the raw material for and products of evolution. While sexes are often treated as special and distinct from other kinds of variation, a repeated theme of the symposium was treating sexes as physical and behavioral phenotypes among other types of variation—i.e., just one type of variation among the many encompassed within a species. Falk (2026) examines sexes in the broader context of phenotypic polymorphisms, a type of variation that involves distinct alternative morphs. Sexes have long been understood to be a type of polymorphism (Ford 1945; Ah-King and Nylin 2010), but the full extent and implications of their similarity with other polymorphisms is rarely addressed. Falk (2026) considers the genetic, developmental, and evolutionary mechanisms underlying sexes and other polymorphisms, as well as their role in repro-

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duction, showing that in each case sexes fit within the broader realm of polymorphisms. Both sexes and other polymorphisms can be determined by structural mutations and alteration of regulatory mechanisms, be maintained by balancing selection, and shape reproductive options and strategies. Viewing sexes as polymorphisms focuses attention on their dynamic flexibility, with traits converging and diverging over evolutionary time, and encourages application of the same conceptual and analytical tools we use for other types of organismal variation (Falk 2026).

Billiard et al. (2026) use a similar strategy, situating anisogamy as one of a suite of self-incompatible *mating class* systems that dictate reproductive compatibility across eukaryotes, based on molecular, developmental, morphological, and behavioral mechanisms at the gametic and organismal levels. Comparing across many such systems, Billiard et al. (2026) examine the evolution of mating classes and their underlying genetic architectures to address the longstanding, unresolved question: Why do so many mating systems involve binary classes? They discuss patterns of transitions among multiple types of genetic architecture and their relationship to the number of mating classes, as well as the common emergence of multiple mating class layers which may be synergistic or independent. For example, genetic incompatibility between mating types can be reinforced by the evolution of anisogamy, yet the two can co-occur in a species without linkage, as can the morphological and molecular self-incompatibility systems of flowering plants (Billiard et al. 2026). Recognizing and tracing the evolution of these layers and their interactions allows for explicit testing of classic hypotheses more broadly than is possible with anisogamy alone.

As sexes are just one of many types of intraspecific variation, so sex-specific mating is just one type of mate discrimination. Nonetheless, different-sex mating has often been assumed as a default and same-sex sexual behavior (SSB) considered an anomaly. Lerch (2026) reviews SSB in the context of sexual behavior more broadly, showing how variation in sex discrimination fits within the broader context of random versus choosy mating. In this light, understanding SSB does not necessarily require new frameworks, explanations, or models. Rather, the application of classic theory on the evolution of mate choice and sexual signals can explain the widespread occurrence of SSB as well as variation in its prevalence in the context of adaptive sex-discrimination functions. In addition to his analysis of adaptive mating strategies, Lerch (2026) reviews the evolution of adaptive SSB, considering potential nonreproductive functions in parallel with the nonreproductive adaptive functions of different-sex mating. The accumulating empirical documentation of SSB requires a shift in perspective; Lerch (2026) highlights gaps where more research is needed while emphasizing the strong theoretical and empirical foundation available to fully integrate SSB into our understanding of sexual behavior.

Situating sex within the full scope of an organism's phenotype can lead to novel perspectives and more precise analyses. Massa (2026) discusses the scientific history of sex as a binary variable in biology and its current political weaponization. As an antidote, she calls for development of new tools that avoid the assumption of sexual differences in favor of more direct testing. To illustrate, Massa (2026) discusses work in which she and her colleagues needed a way to test for the effect of estrogen on neuronal responsiveness (Massa et al. 2023). Rather than assuming estrogen expression was higher in females, the researchers developed a more precise comparison that measured transcriptomic proxies of estrogen levels, finding surprising patterns.

In a similar vein, Griffith et al. (2026) reviewed the modern literature on hormonal influences on sexual color differences in birds and found that estrogen and testosterone have extremely complex, family- and species-specific associations with male and female coloration. They discuss varying interactions with luteinizing hormone, corticosteroids, and thyroid hormone, as well as gene-hormone interactions that likely play a critical and understudied role. Since the last major review of sexual dichromatism in avian plumage (Kimball 2006), research has moved toward more complex models to address the variation in plumage dichromatism among and within species. Age and season matter, and specific hormones may influence certain color types—or even color patches—more than others. Through a phylogenetic analysis across Aves, Griffith et al. (2026) identify evolutionary patterns as well as crucial gaps in our understanding of the proximate mechanisms underlying sexual dichromatism, highlighting key areas likely to reward further investigation and the risks of assuming mechanistic similarity across taxa.

Chen et al. (2026) explicitly tested common assumptions about animal behavior, that sexes differ in their level and targets of aggression and overall dominance rank. By observing mixed-sex flocks of monk parakeets (*Myiopsitta monachus*), they found that males and females were similar in aggression level and dominance rank within groups and sex had little explanatory power in predicting aggression toward other individuals of either sex. Their results emphasize that sex differences in dominance hierarchies should not be assumed, suggesting sex similarities in aggression are likely when competition for resources or social status affect sexes similarly.

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Sex through the lens of organismal diversity

The diversity of living organisms challenges simplifications and generalizations about sex and offers many ways to test ideas and expand our understanding, through both broadly comparative work and focal studies of clades or species whose lives differ from canonical animals. Many papers in this special issue take such approaches (Billiard et al. 2026; Casper and Warkentin 2026; Constable and Liu 2026; dos Santos et al. 2026; Fitzwater et al. 2026; Griffith et al. 2026; Van Etten and Johnson 2026).

Although genetic recombination through meiosis and syngamy is restricted to eukaryotes, DNA exchange occurs far more broadly through a variety of mechanisms. Van Etten and Johnson (2026) offer a primer and broadly integrative framework for understanding horizontal gene transfer (HGT) in prokaryotes and eukaryotes, considering ecological context and cellular and genomic mechanisms as well as the evolutionary dynamics, effects, and fates of transferred DNA. They note the many ecological processes, beyond eukaryotic sex, that increase opportunities for DNA transfer and point out that adaptive HGTs, which have been the focus of most research, represent just a small fraction of the DNA transfer dynamics in ecological communities. While meiosis and syngamy have specific properties and effects that have massively impacted the evolution of eukaryotes, an appreciation for HGT decenters and contextualizes these processes within a broader, older, and more inclusive realm of mechanisms of DNA exchange and recombination.

Constable and Liu (2026) approach the longstanding problem of the "paradox of sex"—i.e., how the benefits of sexual reproduction can outweigh its costs—through the lens of four well-studied unicellular eukaryotes whose life cycles, in different ways, exhibit stress-induced sex, dormancy, and multicellularity. Facultative, stress-induced sex has often been explained as a form of condition dependence in which well-adapted individuals avoid the cost of recombination by reproducing clonally, while poorly adapted ones use sex to produce more fit offspring. However, this logic fails for the many microbial eukaryotes in which resource limitation induces both sex and dormancy, then reproduction resumes when resources are available. Constable and Liu (2026) model evolutionary responses to such resource-based population growth cycles, showing how declining resources can select for dormancy, increased cell size via fusion (i.e., syngamy), and genetic recombination (i.e., syngamy + meiosis). By breaking down sex into its component stages (gametogenesis, syngamy, and meiosis) and considering them in the context of other life-cycle events (mitosis, dormancy, aggregation), they highlight the species-specificity of the costs of sex and show that its occurrence and timing may be more about minimizing costs than maximizing benefits, providing new insights into a longstanding question (Otto 2009; Constable and Liu 2026).

As familiar, complex, multicellular organisms with ancestral anisogamy whose life cycles, body plans, and sexual systems differ profoundly from canonical animals, plants challenge common conceptions of sex and offer excellent opportunities to build more comprehensive, integrated knowledge (Sandford 2023; Casper and Warkentin 2026). Land plants include bryophytes and tracheophytes, sister clades that diverged in life cycles, body plans, and ecological niches and independently diversified their sexual systems (Harris et al. 2022). In their review of sexual architectures in mosses, the most diverse bryophytes, dos Santos et al. (2026) show how sexual systems are evolutionarily dynamic reproductive phenotypes, shaped by ecological context, that impact habitat usage, environmental control of sex expression and phenology, and resilience to climate change. Rather than simply the capacity of physical or genetic individuals to express one versus both sexes, the continuously variable spatial distribution of male and female gamete production interacts with the availability of free water for microgamete movement to constrain or facilitate sexual reproduction, impacting population structure and dispersal (dos Santos et al. 2026). These insights reveal how environmental conditions structure bryophyte diversity and, as climate change alters these conditions, how sexual system architecture can predict population vulnerability. They also focus attention on the complexity of sexual variation in plants, showing how overly simple categorization limits the predictive value of sexual information for ecological and evolutionary questions.

Turning to tracheophytes, Chen and Pannell's (2025a, 2025b, 2025c, 2026) work provides insights into the evolution of sexual systems based on experimental manipulations of two species of flowering plants. Taking advantage of "leaky dioecy" to generate a continuous distribution of sex allocation from female to male in a wind-pollinated annual (*Mercurialis annua*), they found that inbreeding depression alone was enough to generate disruptive selection favoring males and females over hermaphrodites, even without benefits of sexual specialization (Chen and Pannell 2025a). Mapping reproductive success onto sex allocation landscapes in an insect-pollinated perennial (*Pulsatilla alpina*) revealed two fitness peaks, which were differentially accessible based on resource level (Chen and Pannell 2025b). Their fitness landscape explains this species' complex sexual system combining andromonoecy, in which individu-

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als produce both male and bisexual flowers over their lifetime, and gender diphasy, switching between male and hermaphrodite phases between seasons (Chen and Pannell 2025c). Together, their studies exemplify experimentally feasible approaches to study the evolution of sexual system transitions and the complex sex allocation patterns of hermaphrodites (Chen and Pannell 2025a, 2025b, 2025c, 2026).

In animals, males and females are often thought to differ in immune system function. Fitzwater et al. (2026) examine parasite diversity, abundance, and prevalence across sexes beyond the gonochoristic male–female binary, focusing on an androdioecious fish with primary males and self-fertilizing hermaphrodites that can outcross with males and facultatively transition to secondary males. Comparing across populations that differ in the prevalence of males, they found parasitism varied in complex, interacting ways with population, host size and sex, and parasite species; contrary to predictions, males were not more heavily parasitized. A meta-analysis of sex differences in immunity in animals (Kelly et al. 2018) also challenges the generality of greater female immunity and testosterone-mediated immunosuppression, suggesting species diversity and mechanistic complexity; however, we know little about the effects of sex on parasitism in species other than gonochorists.

Teaching the complexity of sex

The symposium contributions above describe a complexity in sex-related topics that is rarely integrated into how biology is taught. In light of this disconnect, many educators, biologists, gender studies scholars and science education researchers have called for improvements in teaching the complexity and variation in sex-related biology (Ah-King 2013; Mercer-Mapstone et al. 2021; Zemenick et al. 2022; Casper et al. 2025b). Both the harms of teaching sex-related biology topics from a normative oversimplified binary and the benefits of teaching diversity are well documented (Long et al. 2021; Štrkalj and Pather 2021; Casper et al. 2022, 2025b; Zemenick et al. 2022; Eddy et al. 2026b). Yet, developing approaches to teach the complexity of sex is often challenging, in multiple ways. At a systemic level, the siloed nature of academic fields artificially separates biology from social science, history, and other entangled topics, including the influence of socio-political context on biology teaching practices (Ah-King 2013; Lewis and Sharpe 2023; Casper et al. 2025b; Choi et al. 2025; Whitford 2025; Duran et al. 2026). Within biology, oversimplified perspectives are entrenched in textbooks and course materials (Bazzul and Sykes 2011; Fuselier et al. 2018; Donovan et al. 2019; Spaulding and Fuselier 2023; 2024), particularly at the introductory level, structurally reinforcing the teaching of specific content and exclusion of other information and frameworks. Thus, instructors often need to personally acquire knowledge and create course materials to accurately integrate the complexity of biology into sex-related topics in their courses (Casper et al. 2025a). Moreover, at state and institutional levels, instructors now face constraints on academic freedom to teach about sexual diversity and complexity, with political imposition of bioessentialist framings of sex and gender (Beatty et al. 2023; The Florida Legislature 2026; Choi et al. 2025; Whitford 2025). Even without such constraints, what is considered appropriate, relevant, or important for biologists to teach about such topics may be limited (Driessen et al. 2024; Casper et al. 2025a, 2025b). This symposium issue is a step toward addressing some of these challenges. All of the papers provide information about complexity and variation in aspects of sex, and the two education papers provide additional teaching-specific insights. Discussions at the symposium roundtable and teaching and learning workshop (TAL-X) demonstrated both the need for such materials and concern about the harmful influence of the current socio-political context on instructors' ability to teach accurate biology.

A growing body of research demonstrates how teaching sex-related topics from a diversity-centric perspective supports knowledge of biological diversity for all students (Eddy et al. 2026b; Casper and Dockendorf 2023; Casper et al. 2026a). In contrast, teaching from a cisheteronormative perspective harms queer students, contributing to the "chilly climate" in STEM that queer students experience and likely also to their lower persistence in STEM fields (Hughes 2018; Forbes 2020; Hughes and Kothari 2021; Casper et al. 2022; Maloy et al. 2022; Schneider et al. 2025). Based on their TAL-X workshop, Eddy et al. (2026c) summarize research-based guidance from biology education researchers and suggestions from biologists about teaching sex-related complexity. The paper includes specific insights from the five authors' teaching experiences, ranging from individual portable activities to the design of entire courses, with extensive supplementary materials designed to help others working to integrate diversity and variation into their own courses.

Casper et al. (2026b) provide insights on pathways to teaching the diversity of sex-related topics. They revised the sex determination unit of a developmental biology course and found that students largely thought it was important to learn accurate biological complexity about the variation of sex, gender, and reproduction. However, they also found that students struggled to learn some of the content, particularly material about topics that are commonly oversimplified in

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public discourse. Their findings demonstrate the challenges that students can have navigating the contrast between oversimplified information about sex-related topics and the biological diversity-centric content that is taught in a class, highlighting the importance of teaching practices that specifically help students navigate this challenge.

In addition to these two papers, several speakers in the education-focused complementary session shared key insights and discussed new research demonstrating the importance of teaching the biological diversity of sex-related topics. Several speakers addressed how teaching about sex-related biological diversity reduces students' belief in bioessentialist fallacies and supports both student learning and belonging across a range of identities, including gender and sexual minorities and majorities (Blake et al. 2026a; Eddy et al. 2026a, 2026b; Casper et al. 2026a). Other presenters discussed ways that instructors' approaches to teaching were influenced by their beliefs about if and how sex-related content, including gender, fit within their subject area (Driessen et al. 2024, 2026). Moreover, they reported instructors' concerns about how students would respond to sex-related content taught from a biological diversity perspective, including the potential for harmful student discussions in small groups (Driessen et al. 2024, 2026, Casper et al. 2026a, 2026b). Others shared classroom-tested teaching strategies for integrating sex diversity content (Blake et al. 2026a, 2026b; Otter 2026).

Integrative and comparative biologists, individually and collectively, have extensive knowledge about biological complexity and ways the diversity of sex exceeds a simple binary. Substantial discussion at the roundtable session and TAL-X workshop focused on the need for support in developing ways to help students and others understand the complexity of sex-related biology, particularly in the context of political efforts to promote inaccurate bioessentialism and restrict knowledge of sexual diversity. In preparing to teach about sex-related topics, we (the symposium organizers) have frequently encountered research literature outside our specialties that upended our prior understanding of a topic. These confrontations have revealed that what we understood and had taught—what was in our course materials—was wrong. Sometimes our knowledge and material was incomplete or biased such that, with the necessary framing, it could be considered relatively accurate for a subset of organisms. Sometimes the errors and omissions, when revealed, called into question more foundational issues—broad conceptual frameworks, overarching perspectives and approaches. Facing this, calls to "teach the diversity" seemed insufficient to the challenge without a deeper examination and integration of the underlying science.

Moving forward

Building an integrated understanding of the biology of sex across organismal diversity poses challenges, in part, because of how deeply entrenched particular, limited understandings of sex are in human societies. This is especially evident and politicized now, but it is not new. Although assumptions and biases about sex have shaped scientific questions and approaches, slowing the discovery of diversity and integration of knowledge, both scientific and social understandings of sex have expanded dramatically. Sex is a fascinating, complex, and diverse part of the larger diversity and complexity of life; building and sharing a better, more integrative and inclusive understanding of this biology is a multifaceted challenge. The papers in this issue exemplify some ways to approach it.

The foundation of this work is empirical research. There are still many organisms whose reproductive and sexual biology is poorly or entirely unknown, and basic discovery science will continue to yield important surprises. Species that differ from expectations based on theory or related species are particularly valuable to test and build our understanding. Comparative research on sexually diverse clades is important to integrate and synthesize knowledge and reveal larger patterns (e.g., Umen and Coelho 2019; dos Santos et al. 2026). Understanding how change occurs, and sometimes why it does not, also requires mechanistic research focused on variation in sex-related traits within and among species.

Integrative and comparative research at a much larger scale will be crucial to better understand and share the rich body of empirical knowledge that already exists, as well as contextualize new discoveries and call attention to important gaps. The first Tree of Sex database (The Tree of Sex Consortium et al. 2014) enabled substantial advances. The new Tree of Sex 2.0 project (treeofsex.org; Jeffries et al. 2025) is building a more expansive open database to compile knowledge on reproductive traits across eukaryotes and enable broader analyses. One crucial part of this integration is navigating disciplinary and taxonomic variations in terminology and meanings, as well as shifts in language over time, to enable accurate comparisons of biological variation. Another will be finding effective ways to incorporate variation at the fuzzy edges between and around available categories, maintaining contextual information to enable the parsing of data in different ways appropriate to specific questions (McDonough-Goldstein et al. 2026). We look forward to the new understandings that will emerge from this eukaryote-wide integration.

We also need integrative conceptual syntheses across organismal diversity to build frameworks that facilitate

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Box 1. Biology un/bounded: A beautiful mess

Karen M. Warkentin (2024)

We seek boundaries, sharp lines of rupture, neat categorization.
We impose them, forcing a fit, struggling to classify.

We know organismal variation is not homogenous, not
a smooth continuum, nothing like
the spectrum of electromagnetic wavelength that generates colors of the rainbow.
We see the spectrum and name categories.
Language shaping our brains changes how we process stimuli, making us see
named distinctions better, faster, more than unnamed, making them more
real
to us.[1]

But neither is organismal variation discrete, not
sharply categorical, nothing like
the elemental structures of atoms, stably arrayed in the periodic table.
One proton makes the difference between solid carbon and gaseous nitrogen.
They bond, but nothing exists to bridge the gap, fill the space between their different natures.

Life has "joints"—evolutionary bifurcations create species,
developmental switches differentiate tissues or alternative phenotypes.
Life occupies zones of phenotypic space and leaves others unoccupied,
whether by historical accident or selective elimination.
Life has coherence and conformity and identifiable distinctions.

But life is also
messy.

Organisms vary. They don't stay in their places. They innovate.
The beauty of biodiversity messiness of edges fuzziness of categories
are inextricably
interlinked.

The speciating lineage is neither one nor two.
It was one and may become two but now it is
a beautiful mess.

The developmental variant may be ephemeral, a unique nonconformist, or
it may be the start of some new form, a small adjustment or
a radical innovation. It may reshape the world.
Photosynthesis. Eukaryotic endosymbiosis. Sex. Multicellularity.

Our inability to make unequivocal, clear, consistent and general distinctions is not
a failing of biologists.
It is a property of life.

Life generates and crosses boundaries. Life builds boxes then invents ways to climb out.
Life fills spaces in non-random, structured, and
indiscrete patterns.

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We need
better words, better concepts to understand to discuss
all the kinds of variation,
recognizing the reality and utility of categories and simultaneously the fact
that life bridges and inhabits spaces between categories, occupies and discards them.

We need
to recognize how names, our constructed categories, make things we think we see
real (for us[1]); we need to
test test test
our ideas against all the variation,
seek the life that doesn't fit doesn't make sense
breaks
what we think are the rules.

Well-behaved organisms seldom make evolutionary history.

Or, although most life fits categories and understandings based on common forms,
lives that do not are
fundamental in the nature of life
necessary for diversification of nature
critical for advancing our understanding.

thinking about sex more broadly (Warkentin et al. 2026). For instance, an accessible framework integrating variation in sexual systems across diversity in life cycles and body plans would be useful to connect work across algae, plants, modular animals and more, and situate unitary, diplontic animals like vertebrates in this larger organismal context rather than centering ourselves as an unnamed norm (Casper and Warkentin 2026). Similarly, a synthesis across patterns of sexual variation, from intraspecific intersex variations to diverse forms of hermaphroditism, mixed sexual systems, and interspecific variation would be useful to link the development and evolution of sex-related traits. Moreover, we need syntheses that consider sex as just one of many kinds of intraspecific variation (e.g., Billiard et al. 2026; Falk 2026); such contextualizations can highlight alternative evolutionary solutions to common problems, reveal larger patterns of which sex is a part, and disrupt perceptions of sex as a special and more fundamental type of variation.

Many symposium participants are currently working in a polarized and contentious social context that exacerbates the challenge and highlights the need to develop more inclusive and integrated understandings of sexual diversity and more accessible ways to share them. Research on sex has revealed more variation and complexity than anticipated, in multiple dimensions, and such discoveries are likely to continue. Grasping and making sense of such complexity is indeed a challenge. Yet there is another disconnect between specialists' knowledge and broader perceptions among nonspecialists, including biologists with other specialties: The awareness that common, accessible ways to understand sexual variation are inadequate to accommodate the known diversity. Under such frameworks, phenomena, individuals, and species that do not fit may be rendered invisible or else othered and set aside as anomalies, rather than understood to reveal limitations or errors in the initial understanding. Shifts in understanding are a normal and exciting part of science as knowledge expands, revealing errors and insufficiencies in prior understandings. Integrating these changes builds the foundation for further research. Effectively sharing this integrated, expanded understanding is also necessary for advances in scientific knowledge to be useful in a broader sociocultural context.

Finally, as with other aspects of biodiversity, the complexity and diversity of sex can be a source of joy and deep wonder, as well as a challenge that inspires creativity as we struggle to understand it and share our knowledge. In Box 1, we share one such struggle in the form of a poem, "Biology un/bounded: A beautiful mess." Engaging with biodiversity creatively, as well as technically, can help to build understanding and expand our communication modalities.

1 Language affects visual perception (Winawer et al. 2007; Lupyan et al. 2020) and contributes to gender/sex bioessentialism (Saguy et al. 2021).

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Author Contributions

Karen M. Warkentin (Conceptualization, Funding acquisition, Project administration, Resources, Visualization, Writing—original draft, Writing—review & editing), Jay J. Falk (Conceptualization, Funding acquisition, Project administration, Resources, Writing—original draft, Writing—review & editing), and A.M. Aramati Casper (Conceptualization, Funding acquisition, Project administration, Resources, Writing—original draft, Writing—review & editing)

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Data Availability

No new data were created or analyzed in the preparation of this manuscript.

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