The role of socially transferred materials in translating and mediating the effects of global change

Reitsema-Wang, Y.[1*], Berasategui, A.[2]; Koene, J.M.[2]; Margalef, M[2]; Matte, A.[1]; Perry, J.[3]; Pollux, B.J.A.[4]; Saito, T.[2]; Schulte, L.M.[5]; Skerrett-Byrne, DA[6]; Stynoski, J.L.[7]; Hakala, S[8§]; LeBoeuf, A.C.[1§]; Groothuis, T.G.G[9§]

[1] Department of Zoology, University of Cambridge, Cambridge, United Kingdom

[2] Amsterdam Institute for Life and Environment, Vrije Universiteit Amsterdam, Amsterdam, the Netherlands

[3] Department of Biology, St. Francis Xavier University, Antigonish, Nova Scotia, Canada

[4] Experimental Zoology Group, Wageningen University, Wageningen, the Netherlands

[5] Department of Wildlife, Zoo-Animal-Biology and Systematics, Faculty of Biological Sciences, Goethe University Frankfurt, Frankfurt am Main, Germany

[6] School of Environmental and Life Sciences, College of Engineering, Science and Environment, The University of Newcastle, Callaghan, Australia

[7] Instituto Clodomiro Picado, Facultad de Microbiología, Universidad de Costa Rica, Costa Rica

[8] Department of Ecology and Evolution, Faculty of Biology and Medicine, University of Lausanne, Switzerland

[9] The Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, the Netherlands

[*] corresponding author: yuqi.reitsema.wang@gmail.com

[§]These authors contributed equally

Abstract

Almost all animal species transfer endogenously produced substances to conspecifics, either horizontally or vertically, through eggs, seminal fluid, milk, or other specialized materials. These socially transferred materials (STMs) can have substantial evolutionary consequences, are exceptionally plastic, and may enable organisms to adapt to environmental change. The world is facing rapid anthropogenic environmental changes that challenge the adaptive capacity of most species, with important consequences for biodiversity and ecosystem functioning. We suggest that STMs should be urgently investigated as functional traits, as diagnostic biomarkers for negative responses to environmental change, and as potential channels for mitigation. Here, we first outline the three main types of STMs and how global change is influencing their production, transmission, and effects on recipients. Then we discuss theory-based predictions about the role of STMs in potential translation, mitigation and adaptation. Finally, we outline an interdisciplinary research program to provide insights into the roles of STMs in addressing the biodiversity crisis in a rapidly changing world.

Terminology box

Socially transferred materials (STMs): materials transferred between conspecifics that (i) include components metabolized by the donor, (ii) induce a direct physiological response in the receiver, bypassing sensory organs, and (iii) benefit the donor on an evolutionary timescale[1]. STMs are taxonomically widespread and show broad diversity.

Primary component: material being transferred, such as nutrition, genetic material, or symbionts, that is the evolutionary driver for the origin of the transfer.

Secondary components: over evolutionary time, materials that supplemented the primary component. The functions of the various secondary components are not necessarily related to the functions of the primary components.

Global change: the suite of environmental changes that are occurring due to human activities (**Figure 1**)

1. Introduction

Human activities have fundamentally altered the earth's environments at unprecedented scales and rates. This **global change**—encompassing climate warming, pollution, habitat fragmentation, species invasions, and altered biogeochemical cycles—challenges the adaptive capacity of most organisms[2–7]. Understanding how animals cope with these changes has become perhaps the most important challenge of ecological and conservation research.

Socially transferred materials (STMs) offer a novel framework for studying animal adaptation in the face of global change. STMs, such as eggs, milk, ejaculates, and social regurgitates, differ from sensor-based communication channels in that STMs involve direct transfer of biochemical substances that induce physiological responses in recipients with long-lasting effects[1]. Unlike other communication channels, STMs serve multiple functions beyond signalling: they transfer nutrients, genetic material, symbionts, hormones, and immune factors that can fundamentally alter recipient phenotypes[1].

The composition of STMs often reflects donor condition and environment[8], making them both responsive to environmental change and influential in translating the environment to conspecifics, increasing their impact by either detrimental effects or enabling adaptation. Transfer occurs between parents and offspring[9], between sexes[10] and between nestmates[11] mediating interdependence and influencing evolutionary dynamics[1]. Particularly, STMs enable parents to buffer offspring[12] or prepare offspring for environmental challenges through phenotypic plasticity[13](**Figure 1**). However, when environmental changes are too recent for evolution to have realized adaptation, or exceed adaptive capacity, STMs may negatively impact survival and reproduction.

Global change can disrupt the composition of STMs, as observed across diverse species, including humans, and across ecosystems from deserts to Antarctica[14–16]. Yet we lack a comprehensive understanding of how STMs, as private physiological channels, modulate animals' risks and adaptation potential in the face of environmental challenges[17].

The objectives of this perspective paper are to 1) characterize how STMs are affected by changing environments and lead to adaptive or maladaptive responses; 2) pose hypotheses of short- and long-term consequences for adaptive capacity through STMs; and 3) indicate future directions and potential fruitful study systems for understanding STMs under global change. By highlighting the importance of STMs in evolutionary adaptation, we aim to inspire researchers to adopt the STM framework to study adaptive plasticity and inform conservation and management strategies. We call on researchers to prioritize STM studies in three areas: (1) establishing baseline STM compositions in threatened species before they are lost, (2) testing whether adaptive STM responses can buffer populations against ongoing environmental change, and (3) developing STM-informed conservation interventions while there is still time to implement them effectively. Overall, we hope this perspective paper will lead to increased awareness of STMs as tools for research, biodiversity conservation, and environmental change mitigation strategies.

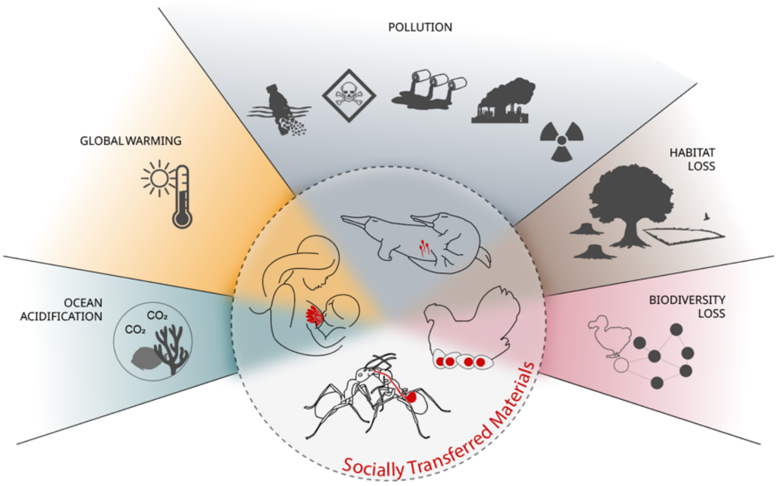

Figure 1. The socially transferred materials (STM) framework can help in understanding animal responses to global change. Animal populations and their various STMs are shaped by a complex web of environmental factors that can affect STM composition, their function, and their transfers between individuals (shown in the center, indicating in red STM transfer by milk, regurgitation, eggs and ejaculate). Some direct stressors, such as changing temperature and different types of pollution, have already been demonstrated to affect STMs, as we discuss in section 2 of this paper. Others, such as habitat degradation and biodiversity loss, may have more cascading effects through ecological communities and the loss of genetic diversity of each population. All the stressors may affect the plasticity and adaptation potential of the STMs, in ways we discuss in section 3.

2. How global change impacts STMs and phenotypic outcomes

Broadly, STMs can provide a read-out of individual physiology[1]. They are often excellent indicators of donor condition, environment, phenotype, and fitness. Environmental change, such as rising temperature[18], pollution[16], and land and water use change[19] has been demonstrated to affect STMs, either via alteration of STM composition or the behaviors that facilitate their transfer. Here, we address the consequences of global change on three main classes of STMs: genetic material, nutritional factors, and symbionts. Although most studies focus on maladaptive and short-term consequences of STMs, we also highlight examples of how STMs enable adaptive responses to environmental change, underscoring the need for future studies on the long-term evolutionary responses to ecological challenges.

The ***transfer of genetic material*** through sperm, eggs and their associated fluids serves as the primary vehicle for genetic and epigenetic information transfer between generations and all can be profoundly affected by environmental factors[20]. Eggs contain not only genetic material but also the molecular machinery, nutrients, and signalling molecules necessary for embryonic development[21]. Environmental stressors can disrupt this complex transfer system at multiple levels, affecting fertilization success, embryonic gene expression, and long-term offspring fitness. Both maternal and paternal environmental conditions have been repeatedly linked to offspring fitness[4].

Rising temperatures have been shown to have negative effects on the transfer of genetic material in both eggs and sperm, leading to distorted sex ratios[22] or increased offspring mortality[23]. Yet, some evidence suggests that STMs may support animals in adapting to higher temperatures[24]. In wild guinea pigs (*Cavia aperea*), males exposed to increased temperature produced offspring with distinct DNA methylation changes in the liver and testis, reflecting the fathers' epigenetic response to heat[25]. This paternally induced epigenetic shift is hypothesised to modulate gene expression in ways that enhance thermal tolerance in the whole organism beyond just gametes, potentially offering an adaptive advantage in a warming climate. In *Takydromus septentrionalis*, offspring from parents exposed to experimental warming survived well under simulated warming climate conditions but not under present climate scenarios, demonstrating anticipatory parental effects that prepare offspring for predicted thermal environments through epigenetic mechanisms in eggs[26]. Heat stress during pregnancy in dairy cattle affected not only immediate offspring but persisted through the maternal lineage for at least three generations[27]. In sheepshead minnows (*Cyprinodon variegatus*), offspring grew best when their rearing temperature matched the thermal experience of their parents[28]. Growth was poorest under mismatched conditions, indicating strong transgenerational plasticity via epigenetic mechanisms in sperm and eggs, which may buffer against climate-induced stress.

Environmental changes disrupt the transfer of genetic material through multiple pathways: direct DNA damage, alteration of ejaculate components, interference with fertilization mechanisms, and systematic alteration of epigenetic programming. For example, the presence of per- and polyfluoroalkyl substances in adult humans has been directly associated with reduced sperm motility, sperm concentration, and total sperm count, affecting male fertility[29]. Heavy metals accumulate in both sperm and eggs, with consequent impacts on fertility[30]. Chemicals in microplastics are also known to impact sperm quality, reducing sperm count and motility[31]. Many pollutants preferentially accumulate in egg yolks due to their lipophilic nature, creating concentrated exposure of genetic material during the vulnerable period of early embryonic development[32]. Thus far, animals are thought to cope with anthropogenic pollutants poorly, as the pollutants have increased at a faster rate than animals can adapt. Long-term research on most pollutants is still lacking, and new substances are continuously being created.

Transfers of nutritional materials—such as in eggs, milk, social regurgitation, and viviparity—are critical for offspring survival in species that rely on them. Compositions of nutritional STMs are highly variable and shift with donor environment and condition[1].

Many nutritional STMs are enriched with secondary components (components with functions beyond nutrition), including hormones and microRNAs, which play essential roles in regulating physiology. For example, in many taxa, mothers transfer thyroxine—a hormone essential for normal development—along with nutritional materials to their offspring[33]. This process relies on adequate environmental iodine. Both excessive iodine (e.g., due to nuclear pollution) and iodine deficiency (e.g., from habitat degradation leading to malnutrition) can have detrimental effects on offspring development[34]. In aphids, females transfer hormones and other molecules to embryos, causing a developmental switch that leads to later-season nymphs being born with wings, and some of them male, unlike all-female early-season nymphs. This allows these aphids to disperse and reproduce sexually[35].

Such regulation relies on environmental cues and hence is sensitive to rising temperatures and ecological change. As a final example, environmental disruptors (e.g., feminizing herbicide[36]) can interfere with hormone receptors, affecting sexual differentiation and population dynamics.

Further, nutritional STMs are often contaminated by anthropogenic pollutants, such as herbicides[37], pharmaceuticals[38], and even microplastics[39], leading to negative effects on the offspring[37,40]. Also in this case, species that might have STM-based mechanisms to fine-tune offspring phenotypes might be especially at risk of perturbations by anthropogenic substances. For instance, mothers sometimes adjust the quantity of nutrients and hormones transferred to offspring to optimise development in a specific environment[41]. This balance can be disrupted by plastic additives, which mimic hormonal activity, leading to mismatched developmental outcomes and impaired fitness[5].

Nutritional transfers occur not only in the parent-offspring contexts, but they also happen in other situations, such as when an animal gives a "nuptial gift" metabolized by the donor to a mate or when social insects, birds, and other species regurgitate for each other with processed external materials[1]. Such behaviors extend the potential impacts of anthropogenic change to other conspecifics. For example, increased temperature affects nuptial-gift-related behaviours in *Drosophila subobscura*, impacting sex-specific mate choice and population dynamics[42]**.**

Transfer of symbionts can be critically important for many animals relying on the metabolic capabilities of their associated microbes or microbiomes. Usually, these associations enhance the nutritional or defensive physiology of their host animals[43].

Some socially transferred symbionts are highly sensitive to changes in temperature[44], with a critical effect on host fitness[45,46]. For example, *Hamiltonella defensa*, a facultative, vertically transmitted symbiont of aphids that protects against parasitoids, becomes less effective in defending its host at higher temperatures[47]. Interestingly, the few instances where another aphid endosymbiont *Buchnera* has been replaced by a novel microbe have occurred in especially warm climates[46].

Microbes in STMs can also underlie and facilitate the survival of insects in a pesticide-rich environment. Female *Nilaparvata lugens* planthoppers vertically transmit *Wolbachia* symbionts to their offspring that aid in the detoxification of insecticides. However, rising temperatures reduce bacterial titers, hindering insect resistance to pesticides[48]. These studies highlight how the transferred symbionts can be replaced over evolutionary time, fuelling adaptation and ecological novelties, especially under environmental change[49,50].

3. Building hypotheses about short- and long-term consequences for adaptive capacity

Although we now know that anthropogenic environmental changes can profoundly affect STMs (see previous section), an integrative approach of chemical, physiological, and eco-evolutionary studies is needed to predict how environmental effects on STMs will influence short- and long-term adaptive capacity across levels of biological organization. In this section, we discuss several concepts relevant to predicting how the effects of environmental change on STMs will impact fitness and scope for adaptation (**Figure 2**).

In contrast to many behavioral signals, ***STMs are private channels*** of communication between donors and receivers. Because STMs are transferred through direct contact, there is reduced environmental interference. This might make STM signals more efficient and effective in some systems compared with, for example, birdsong masked by urban noise. However, due to their more personalized transmission modes, STM signals are less efficient for communicating with large groups. Depending on the network of transfer, STMs may induce larger individual differences within a population, creating scope for evolution and adaptation.

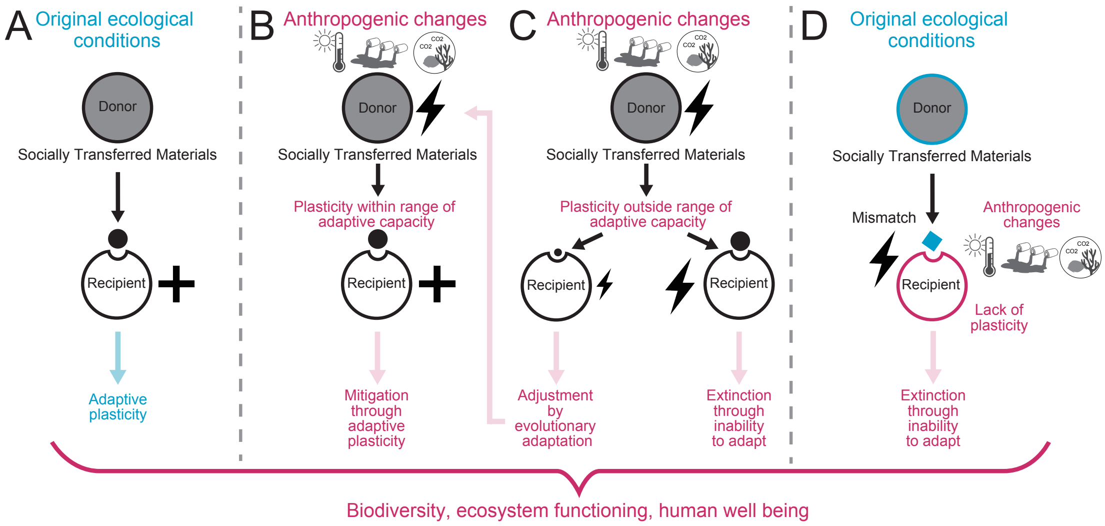

Figure 2. Modes by which organisms can respond plastically to their environments and to anthropogenic changes through the use of and response to socially transferred materials (STM). ***(A)*** *Under original ecological conditions, donors produce STMs and recipients respond to them, with adaptive plasticity maintaining the interaction without detrimental effects.* ***(B)*** *When anthropogenic changes (elevated CO_2, temperature, pollution) occur, plasticity within the range of adaptive capacity in both donor and recipient allows mitigation of environmental impacts through adjustment of STM production and response.* ***(C)*** *When the anthropogenic changes push the organisms outside the range of adaptive plasticity, two outcomes are possible: if the environmental change is moderate and sufficient genetic variation exists, adjustment by evolutionary adaptation can occur over generations, potentially restoring adaptive capacity; alternatively, if the change is too severe or rapid, extinction can occur due to the inability to adapt.* ***(D)*** *Under conditions where there is a mismatch between the donor's ecological conditions and anthropogenic changes, a lack of plasticity in either donor or recipient (or both) to adjust STM production or response leads to extinction through inability to adapt. The outcomes depicted across all scenarios have consequences for biodiversity, ecosystem functioning, and human well-being.*

All organisms can respond to environmental change through developmental or phenotypic plasticity. Whether and how plasticity via STMs helps organisms adapt to the recent anthropogenic challenges[51]? This largely depends on the extent the regulation of STMs is independent of the environment and even anticipatory.

Mechanistically, if and when donors can regulate STM components or volumes somewhat independently from the donor's own condition and exposure, the scope for beneficial effects increases[52]. For example, nutritional transfers can buffer environmental stress[53–55] when donors modulate STM composition (such as lipids[55], proteins, hormones, and immune factors[56]) independent from their environmental conditions, and there is some evidence that this can also occur in the receiver[56–58]. In *Gallus gallus*, males being chased away by stronger males may transfer more sperm and ejaculate proteins with each mating because they cannot secure many matings [59]. Receivers may also exert some control by avoiding the intake of harmful STMs, but this is limited when classical senses do not detect anthropogenic contaminants and there has been insufficient time to evolve aversion to novel anthropogenic substances. Recipients can also show adaptive behavioural plasticity in responding to changes in the donor's STM strategy (e.g., females that receive fewer nuptial gifts/less seminal protein increase their mating frequency[60]).

When STM provision or response is decoupled from the donor's environment or when donor STMs are adjusted to an environment that is dissimilar to that of the receiver, it has the potential to create mismatches between STM-based signals and lived environments when the physiological systems lack plasticity. This can be especially problematic for long-lived organisms and under increasing anthropogenic unpredictability (e.g., climate change, food availability, parasite loads). These mismatches are most harmful when STMs act early in development, hardwiring consequences into place and reducing potential for later plasticity. A well-studied example of such a mismatch in humans is the effect of the Dutch hunger winter. Epigenetic alterations of the insulin growth factor led to a suite of detrimental health effects in children born during this winter, despite the later prosperity, because they were exposed to much better food conditions after the winter than where they were prepared for[61].

On the other hand, STMs may reflect and depend on the environmental concentration, potentially constraining recipient development and fitness and creating cascading effects across generations[62]. For example, poor condition may lead to altered STM composition and decreased STM transfer[8]. For receivers, poor condition may lead to a less effective response to STMs, affecting growth (e.g. poor-condition offspring might gain less growth per unit of nutrition received)[63], or mating strategies (e.g. poor-condition females might respond less to fecundity stimulation from male seminal proteins)[20].

Inherent vulnerability of certain types of STMs is another concept relevant to predicting how the effects of environmental change on STMs will impact fitness and scope for adaptation. For example, hormonal signals in STMs, are particularly vulnerable due to their deep conservation, pleiotropy, and strong sensitivity to environmental cues in their production in the donor. In addition, hormones act via well-conserved receptors in almost all animal species and have a wide array of pleiotropic effects, making the likely impact of global change-induced modification relatively strong. Well-known cases include environmental disruptors, such as the feminizing herbicide atrazine[47], which acts on steroid receptors, affecting sexual differentiation and leading to population declines. Similarly, immune factors that are ratcheted with STMs are also vulnerable to environmental changes[64].

Generalists versus specialists. STMs often require physiological and behavioral specialization, such as offspring depending on a sole STM source of nutrition for a proportion of their development, which reduces potential for plasticity. Evolutionary theory predicts that specialists thrive in stable, optimal habitats, while generalists dominate in homogenized or changing environments (e.g., urban areas)[65]. Consistent with these predictions, habitat specialists struggle to colonize urban areas to the same degree as generalists[66,67], and are more likely to suffer population declines in urban settings[68,69]. These predictions can be extended to some STMs, and it remains to be tested whether the specialization associated with STMs also reduces population growth in non-optimal habitat conditions. Possible population declines and extinction due to an inflexible reliance on specialized STMs could have dramatic spillover effects in community-level food webs[70].

STM systems can also be viewed through the theoretical lens of ***Indirect Genetic Effects (IGEs)***, in which genetic variation in social partners influences an individual's phenotype[58]. For instance, in simultaneously hermaphroditic flatworms, partner genotype affects ejaculate composition and postcopulatory behavior, influencing receiver traits[71]. Such heritable social influences can constrain or accelerate evolutionary trajectories under the effect of a changing environment[58]. In a meta-analysis, trait heritability increased from 0.27 to 0.45 due to the influence of IGEs[72], indicating higher adaptation capacity to changing conditions. However, if negative IGE covariance in a social partner is strong enough, even maladaptive traits can evolve[73], in which case STMs could become an adaptive burden.

4. Future directions and appropriate study systems

Understanding environmental effects on STMs and the adaptive capacity of species requires studying both plastic and evolutionary change and their interplay on survival and reproduction. The physiologically different transfers of genetic material, nutrition, and symbionts vary in adaptive potential due to different levels of STM reliance and different balances of costs and benefits. Vertical transfers may cause particularly fast change via plasticity, which can later become genetically assimilated[74]. In this section, we advocate a multifaceted approach to disentangle the ecological and evolutionary processes.

Studying populations of the same species in different conditions is one way to investigate STM plasticity. Comparisons are valuable between populations affected by recent environmental changes (e.g., pollution, habitat fragmentation, climate shifts) and those in pre-industrial environments[75]. Also, invasive species or populations that have recently undergone range expansions offer contrasts to historical populations for assessing changes in STMs under a new ecological context[64,76]. Where feasible, museum specimens can provide historical data for tracking phenotypic change and STM dynamics over time, for example, via changes in secretory gland morphology and protein composition[77].

Urban ecology is particularly fruitful for studying STMs under multiple stressors like heat, light, pollutants, and altered diets. It is unknown to what extent these conditions affect STM systems and cause divergence between urban and rural populations, but since most of humanity already lives in urban conditions, this is an especially important study direction. Urban-adapted birds, rodents and pet mammals such as cats and dogs are promising models, and lessen the ethical and practical constraints of studying humans directly[78]. It is already known that at least chemical communication is often altered in cities via shifts in gland morphology[79], signal composition[80], or frequency of social contact[81]. The same selection pressures are likely affecting STM-producing tissues, signals, and behaviors.

While STM plasticity alone may lead to short-term adaptation, understanding the underlying genetics is key to distinguishing it from evolutionary change and long-term adaptation. Although many of the mechanisms that underpin STM plasticity may be taxon- and context-specific, a search for commonalities in the molecular composition and evolutionary dynamics of STMs using multi-omics and phylogenetic tools might reveal universal mechanisms. For example, STMs may harbour protein families that specifically facilitate (or constrain) how organisms cope with environmental change (e.g. heat-shock proteins like HSP90[82]). To further bridge the gap between plastic and evolutionary outcomes, we should monitor STM-related traits across generations, linking short-term function to long-term genomic changes. As mentioned in the second section of this paper, research is also needed on social immunity[83] and how STMs facilitate dependency on symbionts[84,85], regarding impacts of temperature or pollutants on nutritional and defensive physiology. Taking such an approach in a multi-generational context enables bridging of short- and long-term consequences.

Comparative studies of taxa across gradients (e.g., lactation duration, placenta complexity, use of love darts) can establish dose-response relationships and their consequences in the face of disturbance. Furthermore, some systems are ripe for paired designs among families, species, or populations with and without an STM, such as urban birds that feed offspring with crop milk (i.e. pigeons) or do not (i.e. sparrows), viviparous or oviparous reptiles[86]or fish[87], and amphibians that exchange courtship proteins through sensory organs or the skin[88] in comparison to related species that do not. Comparative studies of the variation in responses of many species or clades that have the same STM and are influenced by similar environmental disturbances, for example, pollutants in eggs, would answer many of our open questions about the evolutionary potential of STMs. It is important to note that it will be challenging to disentangle the co-evolutionary effects of social dynamics from the direct effects of the STM, especially in natural populations. To mitigate the confusion, experiments with cross-fostering designs could be used to quantify the IGE, or STM composition could be manipulated directly with match-mismatch designs[89].

5. Concluding remarks

Given the accelerated pace of environmental change and the extinction risk faced by many taxa[90], time is of the essence to generate knowledge to fill the gaps discussed in this paper. Thus, we must prioritize and innovatively use existing long-term datasets, short-generation systems, and incorporate underrepresented taxa to maximize insight before critical natural history knowledge is lost. Given the rapid expansion of methodological and technical tools in different research fields, it is now possible to integrate and join forces from different fields such as biology, chemistry, toxicology, medical and veterinary sciences, theorists and others in focused interdisciplinary programs to address the important societal challenges and take our responsibility to help preserve the planet for future generations. Ultimately, a better understanding of convergent patterns in STMs' function across species will allow us to apply the precautionary principle more broadly, in such key research areas as fertility, nutrition, and exposure to human-generated chemicals or extreme heat. The aim of these studies is not only to advance knowledge of STMs but to create actionable knowledge. By illuminating how STMs mediate adaptation, we can inform conservation strategies and environmental policy in our rapidly changing world, for the benefit of all species, including our own.

Acknowledgement

We are grateful to the Lorentz Center and the European Society for Evolutionary Biology (ESEB) for providing funding that enabled a workshop on socially transferred materials in November 2024. We thank all attendees of the workshop, especially Elva Robinson, for valuable insights and participation, and all participants of the online Bring-Your-Own-Fluid (BYOF) seminars. Y.R-W and ACL were supported by Human Frontiers Science Program grant RGP0023/2022 to ACL. TGG was supported by the University of Groningen.

Reference

1. Hakala, S. M. *et al.* Socially transferred materials: why and how to study them. *Trends in Ecology and Evolution* vol. 38 446–458 Preprint at https://doi.org/10.1016/j.tree.2022.11.010 (2023).

2. Pizzol, D. *et al.* Pollutants and sperm quality: a systematic review and meta-analysis. *Environmental Science and Pollution Research* **28**, 4095–4103 (2021).

3. Petrlik, J. *et al.* Monitoring dioxins and PCBs in eggs as sensitive indicators for environmental pollution and global contaminated sites and recommendations for reducing and controlling releases and exposure. *Emerg Contam* **8**, 254–279 (2022).

4. Walsh, B. S. *et al.* The impact of climate change on fertility. *Trends Ecol Evol* **34**, 249–259 (2019).

5. Kirkok, S. K., Kibet, J. K., Kinyanjui, T. K. & Okanga, F. I. A review of persistent organic pollutants: dioxins, furans, and their associated nitrogenated analogues. *SN Appl Sci* **2**, 1729 (2020).

6. De Toni, L., Finocchi, F., Jawich, K. & Ferlin, A. Global warming and testis function: A challenging crosstalk in an equally challenging environmental scenario. *Front Cell Dev Biol* **Volume 10-2022**, (2023).

7. Willmott, N. J., Wong, B. B. M., Lowe, E. C., McNamara, K. B. & Jones, T. M. Wildlife Exploitation of Anthropogenic Change: Interactions and Consequences. *Q Rev Biol* **97**, 15–35 (2022).

8. Mousseau, T. A. & Fox, C. W. The adaptive significance of maternal effects. *Trends Ecol Evol* **13**, 403–407 (1998).

9. Wijenayake, S. *et al.* The contributions of parental lactation on offspring development: It's not udder nonsense! *Horm Behav* **153**, 105375 (2023).

10. Zizzari, Z. V., Smolders, I. & Koene, J. M. Alternative delivery of male accessory gland products. *Front Zool* **11**, 32 (2014).

11. Negroni, M. A. & LeBoeuf, A. C. Metabolic division of labor in social insects. *Curr Opin Insect Sci* **59**, 101085 (2023).

12. Mashoodh, R., Trowsdale, A. T., Manica, A. & Kilner, R. M. Parental care shapes the evolution of molecular genetic variation. *Evol Lett* **7**, 379–388 (2023).

13. Engqvist, L. & Reinhold, K. Adaptive trans-generational phenotypic plasticity and the lack of an experimental control in reciprocal match/mismatch experiments. *Methods Ecol Evol* **7**, 1482–1488 (2016).

14. Matei, M. *et al.* Persistent Organic Pollutants (POPs): A Review Focused on Occurrence and Incidence in Animal Feed and Cow Milk. *Agriculture* **13**, (2023).

15. Chen, M., Koekkoek, J. & Lamoree, M. Organophosphate ester metabolites in human breast milk determined by online solid phase extraction coupled to high pressure liquid chromatography tandem mass spectrometry. *Environ Int* **159**, 107049 (2022).

16. Calvert, L. *et al.* Assessment of the Emerging Threat Posed by Perfluoroalkyl and Polyfluoroalkyl Substances to Male Reproduction in Humans. *Frontiers in Endocrinology* vol. 12 Preprint at https://doi.org/10.3389/fendo.2021.799043 (2022).

17. Samuel, P. *et al.* Effects of chemical contaminants on the ecology and evolution of organisms a review. *Chemistry and Ecology* **39**, 1–37 (2023).

18. van Heerwaarden, B. & Sgrò, C. M. Male fertility thermal limits predict vulnerability to climate warming. *Nat Commun* **12**, 2214 (2021).

19. Choe, S.-A. *et al.* Land use and semen quality: A fertility center cohort study. *PLoS One* **16**, e0255985- (2021).

20. Perry, J. C., Sirot, L. & Wigby, S. The seminal symphony: how to compose an ejaculate. *Trends Ecol Evol* **28**, 414–422 (2013).

21. Berg, C., Sieber, M. & Sun, J. Finishing the egg. *Genetics* **226**, iyad183 (2024).

22. Pérez-Crespo, M., Pintado, B. & Gutiérrez-Adán, A. Scrotal heat stress effects on sperm viability, sperm DNA integrity, and the offspring sex ratio in mice. *Mol Reprod Dev* **75**, 40–47 (2008).

23. Sales, K. *et al.* Experimental heatwaves compromise sperm function and cause transgenerational damage in a model insect. *Nat Commun* **9**, 4771 (2018).

24. Puisay, A., Hédouin, L., Pilon, R., Goiran, C. & Pujol, B. How thermal priming of coral gametes shapes fertilization success. *J Exp Mar Biol Ecol* **566**, 151920 (2023).

25. Weyrich, A. *et al.* Paternal intergenerational epigenetic response to heat exposure in male Wild guinea pigs. *Mol Ecol* **25**, 1729–1740 (2016).

26. Sun, B.-J., Wang, Y., Wang, Y., Lu, H.-L. & Du, W.-G. Anticipatory parental effects in a subtropical lizard in response to experimental warming. *Front Zool* **15**, 51 (2018).

27. Gershoni, M. Transgenerational transmission of environmental effects in livestock in the age of global warming. *Cell Stress Chaperones* **28**, 445–454 (2023).

28. Chang, S. L., Lee, W. S. & Munch, S. B. Separating Paternal and Maternal Contributions to Thermal Transgenerational Plasticity. *Front Mar Sci* **8**, (2021).

29. Sun, F. *et al.* Per- and Polyfluoroalkyl Substances in Semen Associated with Repeated Measures of Semen Quality in Healthy Adult Men. *Environ Sci Technol* **59**, 256–267 (2025).

30. Ding, J. *et al.* Variations in tree sparrow (Passer montanus) egg characteristics under environmental metal pollution. *Science of The Total Environment* **687**, 946–955 (2019).

31. Zhang, C. *et al.* Association of mixed exposure to microplastics with sperm dysfunction: a multi-site study in China. *EBioMedicine* **108**, (2024).

32. Alava, J. J. *et al.* Loggerhead sea turtle (Caretta caretta) egg yolk concentrations of persistent organic pollutants and lipid increase during the last stage of embryonic development. *Science of The Total Environment* **367**, 170–181 (2006).

33. Burrow, G. N., Fisher, D. A. & Larsen, P. R. Maternal and Fetal Thyroid Function. *New England Journal of Medicine* **331**, 1072–1078 (2025).

34. Glinoer, D. & Delange, F. The Potential Repercussions of Maternal, Fetal, and Neonatal Hypothyroxinemia on the Progeny. *Thyroid®* **10**, 871–887 (2000).

35. Chen, Y. *et al.* Differential wing polyphenism adaptation across life stages under extreme high temperatures in corn leaf aphid. *Sci Rep* **9**, 8744 (2019).

36. Hayes, T. B. *et al.* Demasculinization and feminization of male gonads by atrazine: Consistent effects across vertebrate classes. *J Steroid Biochem Mol Biol* **127**, 64–73 (2011).

37. Yang, Z. *et al.* Prenatal endocrine-disrupting chemicals exposure and impact on offspring neurodevelopment: A systematic review and meta-analysis. *Neurotoxicology* **103**, 335–357 (2024).

38. Mailho-Fontana, P. L. *et al.* Milk provisioning in oviparous caecilian amphibians. *Science (1979)* **383**, 1092–1095 (2024).

39. Ragusa, A. *et al.* Plasticenta: First evidence of microplastics in human placenta. *Environ Int* **146**, 106274 (2021).

40. Christian, S. *et al.* Is Bone Mineral Composition Disrupted by Organochlorines in East Greenland Polar Bears (Ursus maritimus)? *Environ Health Perspect* **112**, 1711–1716 (2004).

41. Groothuis, T. G. G., Hsu, B.-Y., Kumar, N. & Tschirren, B. Revisiting mechanisms and functions of prenatal hormone-mediated maternal effects using avian species as a model. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20180115 (2019).

42. Pembury Smith, M. Q. R., Latkova, L. & Snook, R. R. Elevated temperatures have sex-specific effects on nuptial gift behavior. *Behavioral Ecology* **36**, araf049 (2025).

43. Koch, H. & Schmid-Hempel, P. Socially transmitted gut microbiota protect bumble bees against an intestinal parasite. *Proceedings of the National Academy of Sciences* **108**, 19288–19292 (2011).

44. Wernegreen, J. J. Mutualism meltdown in insects: bacteria constrain thermal adaptation. *Curr Opin Microbiol* **15**, 255–262 (2012).

45. Yoshitomo, K. *et al.* Collapse of Insect Gut Symbiosis under Simulated Climate Change. *mBio* **7**, 10.1128/mbio.01578-16 (2016).

46. Zhang, B., Leonard, S. P., Li, Y. & Moran, N. A. Obligate bacterial endosymbionts limit thermal tolerance of insect host species. *Proceedings of the National Academy of Sciences* **116**, 24712–24718 (2019).

47. Dean, L. L., Whiting, J. R., Jones, F. C. & MacColl, A. D. C. Reproductive isolation in a three-way contact zone. *Mol Ecol* **33**, e17275 (2024).

48. Zhang, Y. *et al.* Decline in symbiont-dependent host detoxification metabolism contributes to increased insecticide susceptibility of insects under high temperature. *ISME J* **15**, 3693–3703 (2021).

49. Koga, R. & Moran, N. A. Swapping symbionts in spittlebugs: evolutionary replacement of a reduced genome symbiont. *ISME J* **8**, 1237–1246 (2014).

50. Herrera, M. *et al.* Temperature transcends partner specificity in the symbiosis establishment of a cnidarian. *ISME J* **15**, 141–153 (2021).

51. Chirgwin, E., Marshall, D. J., Sgrò, C. M. & Monro, K. How does parental environment influence the potential for adaptation to global change? *Proceedings of the Royal Society B: Biological Sciences* **285**, 20181374 (2018).

52. Groothuis, T. G. G. & Schwabl, H. Hormone-mediated maternal effects in birds: Mechanisms matter but what do we know of them? *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 1647–1661 (2008).

53. Buckley, J. *et al.* Biparental mucus feeding: a unique example of parental care in an Amazonian cichlid. *Journal of Experimental Biology* **213**, 3787–3795 (2010).

54. Nadimpalli, M. L. *et al.* Can breastfeeding protect against antimicrobial resistance? *BMC Med* **18**, 392 (2020).

55. Razzaghi, A., Ghaffari, M. H. & Rico, D. E. The impact of environmental and nutritional stresses on milk fat synthesis in dairy cows. *Domest Anim Endocrinol* **83**, 106784 (2023).

56. Wang, Y. *et al.* Plasticity in metabolism of maternal androgens in avian embryos. *Sci Rep* **13**, 8083 (2023).

57. Wang, Y. *et al.* Dynamics of maternal androgens and its metabolites during early embryonic development: embryonic modification of a maternal effect. *Journal of Endocrinology* **258**, e220299 (2023).

58. Baud, A., McPeek, S., Chen, N. & Hughes, K. A. Indirect Genetic Effects: A Cross-disciplinary Perspective on Empirical Studies. *Journal of Heredity* **113**, 1–15 (2022).

59. Lelono, A., Riedstra, B. & Groothuis, T. G. G. The relationship between male social status, ejaculate and circulating testosterone concentration and female yolk androgen transfer in red junglefowl (Gallus gallus). *Horm Behav* **116**, 104580 (2019).

60. Gwynne, D. T. Sexual Conflict over Nuptial Gifts in Insects. *Annu Rev Entomol* **53**, 83–101 (2008).

61. Schulz, L. C. The Dutch Hunger Winter and the developmental origins of health and disease. *Proceedings of the National Academy of Sciences* **107**, 16757–16758 (2010).

62. Lindström, J. Early development and fitness in birds and mammals. *Trends Ecol Evol* **14**, 343–348 (1999).

63. Groothuis, T. G. G., Kumar, N. & Hsu, B.-Y. Explaining discrepancies in the study of maternal effects: the role of context and embryo. *Curr Opin Behav Sci* **36**, 185–192 (2020).

64. Partecke, J., Hegyi, G., Fitze, P. S., Gasparini, J. & Schwabl, H. Maternal effects and urbanization: Variation of yolk androgens and immunoglobulin in city and forest blackbirds. *Ecol Evol* **10**, 2213–2224 (2020).

65. Büchi, L. & Vuilleumier, S. Coexistence of Specialist and Generalist Species Is Shaped by Dispersal and Environmental Factors. *Am Nat* **183**, 612–624 (2014).

66. Magura, T., Ferrante, M. & Lövei, G. L. Only habitat specialists become smaller with advancing urbanization. *Global Ecology and Biogeography* **29**, 1978–1987 (2020).

67. Clavel, J., Julliard, R. & Devictor, V. Worldwide decline of specialist species: toward a global functional homogenization? *Front Ecol Environ* **9**, 222–228 (2011).

68. Devictor, V., Julliard, R. & Jiguet, F. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* **117**, 507–514 (2008).

69. Ibarra, J. T. & Martin, K. Biotic homogenization: Loss of avian functional richness and habitat specialists in disturbed Andean temperate forests. *Biol Conserv* **192**, 418–427 (2015).

70. Dyer, L. A., Richards, L. A., Short, S. A. & Dodson, C. D. Effects of CO2 and Temperature on Tritrophic Interactions. *PLoS One* **8**, e62528- (2013).

71. Marie-Orleach, L. *et al.* Indirect genetic effects and sexual conflicts: Partner genotype influences multiple morphological and behavioral reproductive traits in a flatworm. *Evolution (N Y)* **71**, 1232–1245 (2017).

72. Santostefano, F., Moiron, M., Sánchez-Tójar, A. & Fisher, D. N. Indirect genetic effects increase the heritable variation available to selection and are largest for behaviors: a meta-analysis. *Evol Lett* **9**, 89–104 (2025).

73. Murray, M., Wright, J. & Araya-Ajoy, Y. G. Evolutionary rescue from climate change: male indirect genetic effects on lay-dates and their consequences for population persistence. *Evol Lett* **8**, 137–148 (2024).

74. Fox, R. J., Donelson, J. M., Schunter, C., Ravasi, T. & Gaitán-Espitia, J. D. Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20180174 (2019).

75. Donihue, C. M. *et al.* Hurricane-induced selection on the morphology of an island lizard. *Nature* **560**, 88–91 (2018).

76. Buczkowski, G. & Wossler, T. C. Controlling invasive Argentine ants, Linepithema humile, in conservation areas using horizontal insecticide transfer. *Sci Rep* **9**, 19495 (2019).

77. Schmitt, C. J., Cook, J. A., Zamudio, K. R. & Edwards, S. V. Museum specimens of terrestrial vertebrates are sensitive indicators of environmental change in the Anthropocene. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20170387 (2018).

78. Schell, C. J. *et al.* The ecological and evolutionary consequences of systemic racism in urban environments. *Science (1979)* **369**, eaay4497 (2020).

79. Idris, M. & Prakash, I. Scent marking in the Indian gerbil,Tatera indica in response to conspecific odours. *Proceedings: Animal Sciences* **95**, 89–96 (1986).

80. Whittaker, D. J. *et al.* Songbird chemosignals: volatile compounds in preen gland secretions vary among individuals, sexes, and populations. *Behavioral Ecology* **21**, 608–614 (2010).

81. Alexander, K. A. & Nichols, C. A. Behavior - Landscape Interactions May Create Super-Spreader Environments: Vigilance-Olfactory Interactions Across Land Type and Disease Transmission Potential in the Banded Mongoose. *Front Ecol Evol* **Volume 8-2020**, (2020).

82. Rutherford, S. L. & Lindquist, S. Hsp90 as a capacitor for morphological evolution. *Nature* **396**, 336–342 (1998).

83. Cotter, S. C. & Kilner, R. M. Personal immunity versus social immunity. *Behavioral Ecology* **21**, 663–668 (2010).

84. Rowe, M., Veerus, L., Trosvik, P., Buckling, A. & Pizzari, T. The Reproductive Microbiome: An Emerging Driver of Sexual Selection, Sexual Conflict, Mating Systems, and Reproductive Isolation. *Trends Ecol Evol* **35**, 220–234 (2020).

85. Murphy, K. M., Le, S. M., Wilson, A. E. & Warner, D. A. The Microbiome as a Maternal Effect: A Systematic Review on Vertical Transmission of Microbiota. *Integr Comp Biol* **63**, 597–609 (2023).

86. Pettersen, A. K. *et al.* Maternal behavioral thermoregulation facilitated evolutionary transitions from egg laying to live birth. *Evol Lett* **7**, 351–360 (2023).

87. Blackburn, D. G. & Hughes, D. F. Phylogenetic analysis of viviparity, matrotrophy, and other reproductive patterns in chondrichthyan fishes. *Biological Reviews* **99**, 1314–1356 (2024).

88. Schulte, L. M., Martel, A., Cruz-Elizalde, R., Ramírez-Bautista, A. & Bossuyt, F. Love bites: male frogs (Plectrohyla, Hylidae) use teeth scratching to deliver sodefrin precursor-like factors to females during amplexus. *Front Zool* **18**, 59 (2021).

89. Groothuis, T. G. G. & Taborsky, B. Introducing biological realism into the study of developmental plasticity in behaviour. *Front Zool* **12**, S6 (2015).

90. Butchart, S. H. M. *et al.* Measuring trends in extinction risk: a review of two decades of development and application of the Red List Index. *Philosophical Transactions of the Royal Society B: Biological Sciences* **380**, 20230206 (2025).