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Editorial

New frontiers in avian physiology: what's migration got to do with it?

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For over a century the study of bird migration has attracted both scientists and the wider public. This fascination comes from the extraordinary distances covered by migratory species, the precision of avian navigation and the near clockwork timing punctuality on arrival times, all of which continue to inspire awe. At the same time the physiological adaptations that enable these journeys remain an active frontier of research. Early studies revealed that migratory birds change their body composition and remodel their internal organs during their migratory flights (Odum and Connell 1956, Piersma and Gill Jr 1998). Flight energetics, metabolic adjustments and endocrine features were explored in studies in wind tunnels and in migrants captured *en route* and at stopover sites (Wingfield and Farner 1978, Jenni-Eiermann and Jenni 1991, Pennycuick et al. 1996). Research on captive birds further demonstrated that migratory physiology was organised by inherited spatio-temporal programmes (Helbig et al. 1989, Gwinner 1996). This pioneering work laid the foundation for ensuing research. It encouraged migration ecologists to pursue mechanistic approaches, and physiologists to pay attention to bird migration. Thereby, the fascination of migration motivated great strides towards a fundamental understanding of avian physiology, and more broadly of animal behaviour.

While classical approaches continue to reveal major insights (Maggini et al. 2022, Shochat et al. 2022), more recently, studies using molecular methods (e.g. genomics (Bossu et al. 2022, Sokolovskis et al. 2023)) or new imaging tools (Elowe et al. 2023) offer new pathways towards understanding the proximate mechanisms of avian migration. This research helps us not only to understand migratory behaviour itself but also the physiological basis of extreme endurance and phenotypic plasticity. However, we still only partly understand the proximate mechanisms of migration, while pressure on migratory birds is increasing due to climate change, habitat loss and other anthropogenic disturbances (Cooke et al. 2024). Improving our understanding of the underlying

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physiology of avian migration will thus not only be key from a fundamental perspective but also for predicting species resilience and informing conservation strategies in a rapidly changing world (Klaassen et al. 2012, Van Gils et al. 2016).

The special issue brings together studies addressing both new and well-established physiological systems in relation to avian migration. Our goal is to provide an updated overview of several fields of migration physiology, and to serve as a base for future research on this fascinating aspect of avian biology. The thematic issue features 15 studies that span a diverse range of physiological aspects, with several cutting across fields. Although aspects partly overlap, we grouped them as follows: thermoregulation, metabolism and bioenergetics, oxidative stress physiology, immune system and body coordination systems (Fig. 1). Additionally, we feature an outlook on linking migration physiology to an emerging field, the study of the microbiome. The contributions cover a vast array of approaches, including wind-tunnel, field-based and captive studies, experimental approaches, comparative studies and literature reviews. They highlight the dynamic physiological strategies that migratory birds use to face the unique energetic, oxidative, and immunological challenges derived from their journeys. The order Passeriformes is the most represented taxonomic group in the special issue, accounting for 67% of the empirical studies, while among flyway systems, the African-Eurasian Flyway is the most frequent (Fig. 1). Although we expect some general patterns of the migratory phenotype to hold across species (Piersma et al. 2005), there are significant gaps remaining in our understanding of underrepresented flyways, e.g. the East Asian-Australasian Flyway, which host a remarkable diversity of migratory species and is increasingly under threat (Yong et al. 2021).

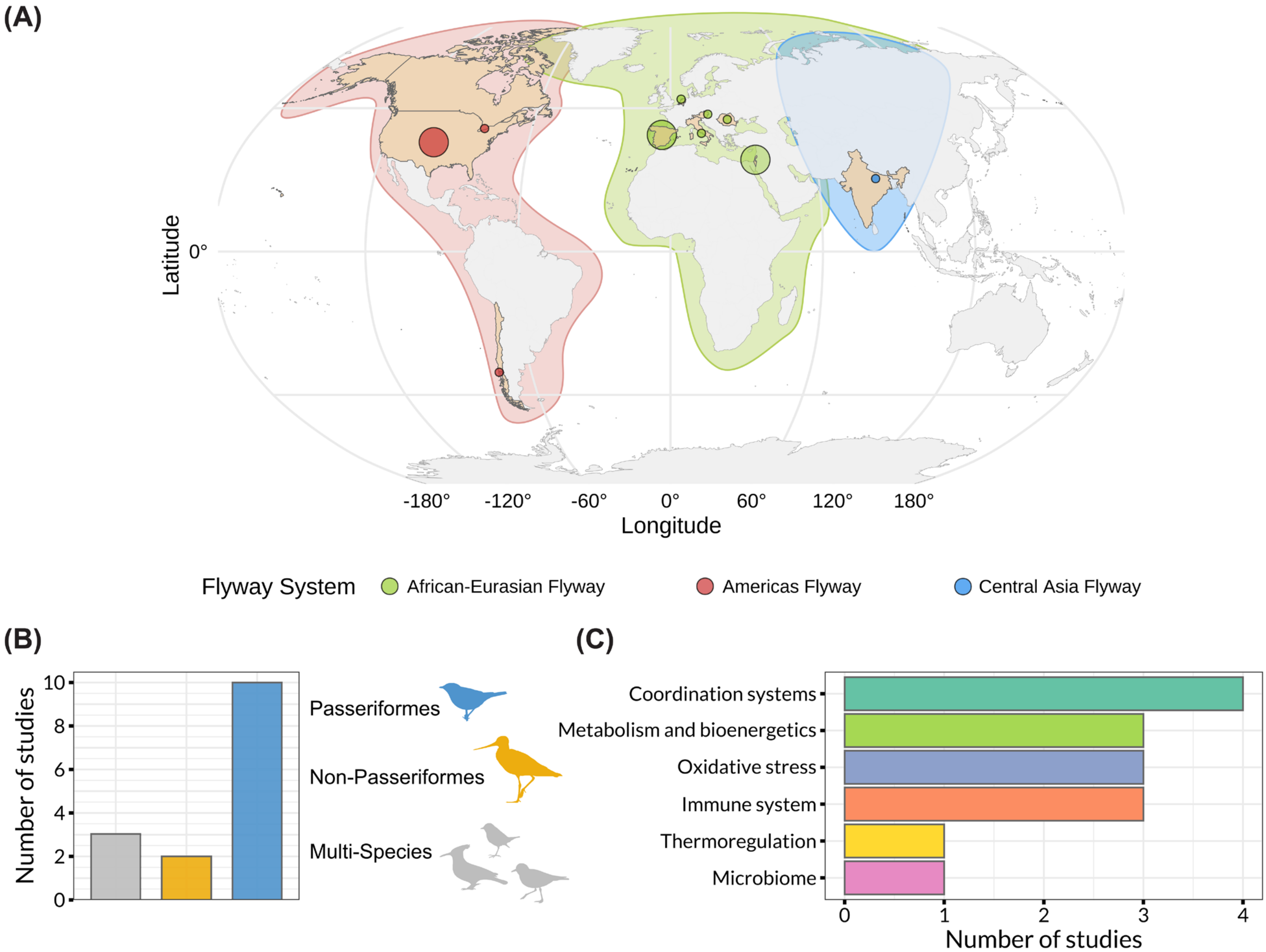

Figure 1. Features and topics of the studies included in the Special Issue. (A) Global distribution of studies with Flyway System boundaries and names defined according to BirdLife International (Americas, African-Eurasian, and Central Asian; BirdLife International 2025). The circle size represents the number of studies per country. (B) Taxonomic composition of studies grouped into broad species categories. (C) Distribution of studies across physiological domains addressed in this issue. Each category represents a primary focus, although several studies span multiple topics (see text for details). Silhouettes adapted from PhyloPic (www.phylopic.org), used under Creative Commons licenses.

Thermal resilience across hot frontiers

Thermoregulation places a fundamental demand on endothermic vertebrates to maintain their internal homeostasis. Exposure to temperatures exceeding an individual's body temperature imposes challenges, i.e. heat stress (McNab 2002, Bradshaw 2003). In theory, species experiencing greater climatic variability should also exhibit greater phenotypic flexibility in their thermoregulatory traits and broader thermal tolerance (Bozinovic et al. 2011, Stager et al. 2021). While desert specialist species are adapted to hot environments, temperate species might be more vulnerable to increasingly hot and dry conditions (Jiguet et al. 2006). The extent of migration further influences the range of thermal environments that species experience, exemplified by temperate-breeding species crossing the Sahara Desert twice per year. **Hasenbichler et al.** (2025) address thermal tolerance by comparing panting onset temperatures in 14 short- and long-distance migrant species studied during autumn migration in Austria, before facing major thermal barriers. Supporting their predictions, trans-Saharan migrants began panting at higher ambient temperatures, suggesting a physiological predisposition to cope with the high temperatures they will encounter during their migratory journeys. Studies like Hasenbichler et al. (2025) are increasingly valuable for understanding the physiological limits of migratory species and projecting the potential impacts of climate change on migratory performance.

Fuelling the migratory journey from metabolome to the organelle

Migration is one of the most energetically demanding phases of a bird's annual cycle as flight itself is metabolically costly (Butler 2016), as are the physiological adjustments that make sustained flight possible. These adjustments include for example rapid fuel accumulation, efficient storage and precise mobilisation of energy reserves to support migratory journeys across unpredictable environments. In the special issue, **Zimin et al.** (2025) and **Domer et al.** (2025) both studied the plasma metabolome of migratory songbirds at similar field sites, offering complementary insights into metabolic flexibility. These represent some of the earliest contributions of metabolomic regulation in the context of avian migration. Zimin et al. (2025) focused on Eurasian blackcaps *Sylvia atricapilla* during spring migration, demonstrating that variation in fat and muscle stores is reflected in the metabolome, with larger fuel reserves associated with increased reliance on lipid metabolism, alongside reduced protein catabolism. In addition, they also found a shift in the metabolome as time passed from sunrise, i.e. decreased fuel utilisation likely reflecting nutrient influx. Adding a complementary perspective, Domer et al. (2025) examined Eurasian blackcaps and lesser whitethroats *Curruca curruca* during autumn migration across contrasting stopover sites, either dominated by fat-rich or nectar-producing trees and representing different stages of stopover, such as resting or refuelling. This study highlights the spatial variation in metabolic responses compared to previous metabolomics studies. While lipid metabolism remains a primary energy pathway during endurance flight (Guglielmo 2018), Domer et al. (2025) found that blood lipid profiles contained many lipophilic compounds not directly related to exercise metabolism and traditional indicators such as triglycerides and β-hydroxybutyric acid did not reliably reflect site quality (Eiermann and Jenni 1992, Guglielmo et al. 2005). The study further suggests that glucose cycling from protein catabolism supports post-flight recovery, and transient insulin resistance and hyperglycaemia may represent adaptive responses to endurance exercise and fasting, similar to trauma recovery in other vertebrates. These findings underscore the context-dependent nature of metabolic markers, shaped by species, feeding ecology, and local food resources, and highlight the challenges of inferring physiological processes from natural observations. Taken together, these two studies illustrate the potential of metabolomic analyses to reveal the complex physiological pathways involved in migration, and as reference datasets will continue to grow, metabolomic information will become a powerful complement to traditional biomarkers.

Circulating metabolites capture systemic energy status, however, studies at the tissue level can provide a deeper insight into organ-specific resilience. Flight muscle metabolism and performance are central for successful migration (see also the contribution by **Schlinger et al.** (2025) to the special issue). Therefore, understanding how migratory flights affect mitochondrial function, the powerhouse of the cell, and muscle morphology can provide valuable information on migratory endurance. **Coulson et al.** (2025) used wind tunnel flights to simulate multi-hour endurance flights in blackpoll warblers *Setophaga striata* and measured flight muscle mitochondrial function, reactive oxygen species (ROS) emission and fibre ultrastructure. Their results indicate that endurance flight did not induce any dysfunction on muscle mitochondrial functioning, nor did they affect oxidative phosphorylation capacity and ROS emission. Similarly, the area of flight muscle fibres did not change between pre- and post-endurance flights. However, under experimentally induced energy deprivation, mimicking the fasting conditions that birds experience during flight, birds selectively catabolised digestive organs but not tissues essential for flight, including flight muscle. These results illustrate the prioritisation of critical organs under energy stress and suggest a remarkable robustness of the flight apparatus against metabolic and oxidative challenges. At a molecular level, seasonal and circadian mechanisms further coordinate metabolic processes across time and annual-cycle stage, as detailed below in the article of **Kumar et al** (2025).

Flight, food and free radicals: flexibility in oxidative defences

The high metabolic demands of avian flight tend to shift the oxidative balance, i.e. the equilibrium between the generation of the damaging ROS and the protective antioxidant defences, resulting in increased ROS generation

(McWilliams et al. 2021), but see Coulson et al's (2025) contribution in the special issue. A way for many birds to boost their antioxidant defences is to selective forage on antioxidant-rich fruits (Cooper-Mullin and McWilliams 2016). However, in the special issue, **DeMoranville et al.** (2025) question the generality of dietary antioxidants buffering oxidative stress during exercise. Using an experimental design involving flight training and diet manipulation in captive European starlings *Sturnus vulgaris*, they demonstrate that flying itself stimulated antioxidant defences, while dietary antioxidant supplementation (anthocyanins) did not mitigate and, counterintuitively, may have increased oxidative damage. The data suggest that birds flexibly manage oxidative stress through mechanisms not solely dependent on dietary intake and that energy expenditure during sustained flight dynamically shapes antioxidant capacity.

Conversely, in support of an important role of dietary antioxidants, **Jiménez-Gallardo et al.** (2025), show that blackcaps infected with haemosporidians preferentially selected anthocyanin-rich food during stopover. This adaptive foraging strategy suggests that individuals under elevated oxidative pressure, whether due to infection or low energy stores, actively forage on components that can enhance antioxidant capacity. Taken together, these studies illustrate the context-specific regulation of oxidative balance that integrates infection status, energy state and dietary availability, and that may depend on species characteristics.

In a further step towards shedding light on context-specificity, **Pap et al.** (2025) present a comparative study across 113 European species that examines links between oxidative lipid damage, uric acid levels and characteristics of species and their migratory journeys. They find that migration distance is positively associated with oxidative lipid damage and uric acid levels, whereas wing morphology or flight muscle traits, serving as proxies of flight energetics, are not. Their phylogenetic analysis suggests that migratory distance *per se* imposes a cumulative oxidative toll. Interestingly, this study was conducted during the breeding season. Therefore, it does not only challenge the assumption that oxidative costs are tightly coupled to morphological adaptations for flight efficiency, but it also highlights the need to consider carry-over or correlated effects of migration on subsequent life-history stages.

Balancing immune defence and energy on the move

Migration not only exposes birds to physiological challenges in terms of energy and oxidative balance but also in maintaining immune function. The immune system is fundamental for self-maintenance and survival, reducing the probability of disease-related mortality (Lochmiller and Deerenberg 2000). In relation to migration, two contrasting hypotheses have been proposed. On one hand, migrants need to downregulate their immune function because of an energetic trade-off with other physiological systems (Hasselquist 2007, Eikenaar et al. 2018). On the other hand, the exposure to novel pathogens and the high densities at stopover sites might favour the opposite strategy, i.e. an upregulation of the immune system (Møller and Erritzøe 1998, Van Dijk et al. 2014). In the special issue, **Valdebenito et al.** (2025) investigated the largely unexplored immune dynamics during the non-breeding and non-migration season in Hudsonian godwits *Limosa haemastica*, a long-distance migrant between the Arctic and Southern Patagonia. The authors found that three constitutive immune system parameters (bacterial killing capacity, haemolysis and haemagglutination) did not differ between recently arrived and pre-migratory birds, indicating that these aspects of the innate immune system remain stable across the non-breeding season. However, when each period was analysed separately, bacterial killing ability and, to a lesser extent, agglutination increased within pre-migratory birds as they prepared for breeding, particularly in males. This suggests limited immunomodulation toward the end of the non-breeding season, with some sex-specific adjustments before migration.

A complementary perspective is offered by **Palacios et al.** (2025), who examined partially migratory populations of Eurasian hoopoe *Upupa epops* in Iberia. The authors compared the innate and adaptive immunity of migrant and resident individuals under the same environmental conditions (during breeding). They found that resident birds had higher IgY levels, which are antibodies associated with long-term adaptive immunity, as well as larger energy stores than migrants. These results suggest that resident birds might invest more in long-term immune protection, while migrants may allocate more resources towards the energetic demands of migratory journeys, indicating a link between migratory strategy and immune investment.

To migratory birds, stopover locations could serve for refuelling as well as for restoring immune balance. Several studies indicate that constitutive immune function recovers after endurance flights (Buehler et al. 2010, Eikenaar et al. 2023). Thus, in addition to refuelling needs, immune status at arrival of migratory birds may determine the duration of their subsequent stopover. **van Mastrigt et al.** (2025) explored this idea of time needed for physiological recovery in radio-tracked Eurasian blackbirds *Turdus merula* that used the island of Vlieland in the Dutch Wadden Sea as stopover. Opposite to their expectations, they did not find any correlation between their indices of immune status upon arrival and the duration of stopover. Instead, departure decisions were mainly affected by environmental components like tailwind and low cloud cover, as well as by an individual's fuel load. Apparently, immune status as captured by the metrics of the study played a subordinate role for migratory decisions of blackbirds.

Altogether these studies suggest both the resilience and flexibility of the avian immune system during migration. Based on these findings, future work should integrate immune measures not only with energetic status but also with pathogen exposure and environmental conditions, to better understand how migratory birds balance immune function with the many competing demands of migration.

Timing and tuning: coordination of the migratory phenotype

Birds meet the high demands of migratory performance by controlled up- and down-regulation of the many involved physiological systems. Regulations proceeds on different timescales, ranging from advance seasonal preparations (such as fuel deposition or muscle build-up), through diel preparations (such as shifts from anabolism to catabolism), to instantaneous adjustments in response to acute internal or external demand. Several body coordination systems, orchestrate or modulate regulatory changes, implicating biological rhythms and endocrine and neural systems. Although the overall integration and regulation of migration still remains elusive, the extent of regulatory changes is all but daunting. In the special issue, **Kumar et al.** (2025) explores the regulation of migratory states from a biological timekeeping perspective. Much of their extensive work over four decades on Palearctic-Indian buntings as models for songbird migratory physiology have remained largely inaccessible to migration researchers, despite integrating behavioural, tissue-level, endocrine, neural and molecular approaches. Here, they present their findings from black-headed bunting *Emberiza melanocephala* and red-headed bunting *Emberiza bruniceps* by first reviewing the extensive changes the birds undergo. They then summarise that fat accumulation, activity rhythms and endocrine signals orchestrate fuel mobilisation across the annual cycle of migratory species and suggest conceptualisations of the regulatory networks. Their review also highlights differences between autumn and spring migrations, and how these reflect interactions between environmental context, physiological states and metabolic demands, exemplifying the intricate timing underlying migratory physiology and its concomitant metabolic processes.

Schlinger et al. (2025) also take a widely integrative perspective on coordination within the migrant body, but they focus on skeletal muscle and its two-way interaction with endocrine control. They first characterise the general physiology, biochemistry, and energetics of avian muscle in a migration context. Drawing on decades of their research on migratory white-crowned sparrows *Zonotrichia leucophrys*, they explain how populations with different migratory phenotypes vary in muscle dynamics across the annual cycle and in endocrine-muscle interactions. Schlinger et al. (2025) then review modulation of neuromuscular systems in other annual-cycle contexts (namely, courtship) and argue that some of the mechanisms may be highly relevant for dynamically regulated migratory performance. They also also emphasise bi-directional signalling between muscle, brain, and other tissues, e.g. involving myokines, and ultimately recommend embracing systems-biology approaches to understand such complex interactions.

Two additional contributions put greater emphasis on field data to explore endocrine interactions with migration. **Ketterson and Greives** (2025) also used long-term comparative studies of a taxon with a wide range of migratory phenotypes to investigate endocrine coordination of the birds' annual cycles. Their field, captive and experimental studies of dark-eyed juncos *Junco hyemalis* in spring demonstrate that endocrine responses to identical environmental conditions are linked to migratory phenotype. Increasing daylength, signals residents to prepare for breeding, leading to gonadal activation, while co-occurring migrants prepare for their homeward journeys and deposit fuel. Ketterson and Greives (2025) track down the birds' responses to differences in photoperiodic thresholds, to profiles of testosterone and corticosterone, and to gene expression in muscle and blood. They show that gonadal development and fattening aligned with estimated migration distance, as inferred from stable isotope analyses. They also confirmed a partial genetic control and local adaptation based on persistent differences between the migratory phenotypes under identical captive conditions (i.e. common garden experiments). Taking an evolutionary perspective, they engage with possible implications of a changing climate to the distribution and future strategies of the migratory phenotypes.

Last but not least, **Calabretta et al.** (2025) examined corticosterone (CORT) dynamics in two trans-Saharan migrants, the garden warbler *Sylvia borin* and the common whitethroat *Curruca communis*. Using correlational approaches, they examined CORT and fuel reserves in migrants soon after arrival on an island following the crossing of the Mediterranean Sea in spring. Despite variation in tailwind conditions and air temperature during the study period, baseline and stress-induced CORT levels after arrival remained largely stable in individuals with sufficient energy reserves. This result indicates the resilience of the endocrine system, suggesting that long non-stop flights over a geographical barrier are not necessarily stressful for long-distance migratory passerines. As long as energy reserves are sufficient, these species might be capable of anticipating and meeting ecological challenges within a certain range. However, the magnitude of challenges is likely to increase through effects of climate change, especially through higher variability and more extreme events.

From gut to flight: microbiome dynamics in migratory birds

Over the past decades, there has been an increase of interest in animal microbial ecology, including in avian systems (Bodawatta et al. 2022). However, relatively little attention has been paid to how migration influences the dynamics of host-associated microbial communities. The gut microbiome, which is a diverse community of symbiotic microbes that produce rare nutrients, fatty acids and immune compounds, is expected to play an important role in helping birds meet the physiological demands of migratory journeys. **Capilla-Lasheras and Risely** (2025) review the current knowledge on the gut microbiome during migration, highlighting how microbial composition and function could influence energy balance and immune function, and thereby ultimately influence migratory performance. They also emphasise the need for more empirical studies correlating microbiome composition with physiologically relevant traits, as well as more experimental approaches to better understand the functional role of these microbial communities.

Conclusions

The contributions in the special issue highlight the integrative nature of avian migration physiology. From thermoregulatory adaptations, metabol-ism/-omics and oxidative balance to immune function, endocrine regulation and the microbiome, the ability to accomplish migratory journeys depends on the coordination of these multiple physiological systems. Altogether these studies demonstrate that migratory birds are highly adapted to the challenges of their current environments, displaying remarkable flexibility and resilience. At the same time, the limits of this flexibility remain largely unknown, and understanding them is critical for predicting how species will cope with ongoing environmental change and habitat loss along the major migratory flyways. A persistent bias in our understanding lies in the underrepresentation of migratory systems in the Global South, where many species undertake extraordinary movements across diverse and changing landscapes. Expanding physiological research to these regions is crucial to build a complete picture of how migration operates globally and across the annual cycle, as many migratory birds that breed in the Northern Hemisphere spend up to three quarters of their lives in the Global South. Next to the challenges of studying the ephemeral phenomenon of birds on the move, many new and exciting opportunities are at hand. Several articles highlight novel physiological tools, and many more are ready to be embraced by migration researchers. Furthermore, we hope that the collection of articles can cross-inspire towards integrating some of the physiological systems presented here. Such an integration, alongside the use of emerging tools in physiology, ecology and bio-logging, and data integration from long-term demographic studies (e.g. reproductive success and survival), will help to identify the proximate and ultimate causes of migration across the annual cycle. We hope that this collection will encourage further research and reinforce the need for interdisciplinary approaches. Ultimately, our aim is to deepen our understanding of the extraordinary phenomenon of bird migration whilst protecting what fascinates us the most, the birds themselves.

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Author contributions

Pablo Salmón: conceptualization (equal); writing – original draft (lead); writing – review and editing (equal). **Tiia Kärkkäinen**: conceptualization (equal); writing – original draft (supporting); writing – review and editing (equal). **Barbara Helm**: conceptualization (equal); writing – original draft (supporting); writing – review and editing (equal).

Data availability statement

Data sharing is not applicable as no new data were created or analysed in this editorial.

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