Review

Writing the pause: epitranscriptomics in the eco-evolutionary logic of dormancy

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Abstract

Dormancy has been widely recognized as an evolutionarily conserved strategy that enables cells and organisms to endure environmental stress, resource scarcity, or developmental arrest. While transcriptional regulation has been extensively studied in this context, increasing attention is being directed toward post-transcriptional mechanisms that allow rapid and energy-efficient control of gene expression. Among these, epitranscriptomic modifications, chemical marks added to RNA, have emerged as dynamic and reversible regulators of mRNA fate. In this perspective, it is proposed that RNA modifications can play a central role in establishing and maintaining dormancy across diverse biological systems. Evidence from plant seeds, microbial persisters, stem cells, and dormant cancer cells suggests that specific RNA marks, such as N6-methyladenosine (m6A), influence mRNA stability, translation, and localization in a context-dependent manner. It is argued that these modifications serve as a molecular interface between environmental signals and cellular responses, fine-tuning the transition between active and paused states. By examining dormancy through an

epitranscriptomic lens, a unifying model is presented in which RNA modifications contribute to the evolutionary flexibility of dormant programs. This article highlights key mechanistic insights, evolutionary parallels, and outstanding questions at the intersection of RNA regulation and cellular dormancy.

Keywords:

Dormancy, Epitranscriptomics, RNA modifications, Cellular quiescence, Eco-evolutionary adaptation

1. Introduction

Dormancy has been recognized as a widespread and evolutionarily conserved strategy that enables cells, tissues, and entire organisms to withstand periods of environmental or physiological stress (Miller, Brown, Enderling, Basanta, & Whelan, 2021; Webster & Lennon, 2025). Across the tree of life, from unicellular bacteria to multicellular plants and mammals, dormancy has been employed as a temporally controlled mechanism that promotes survival during unfavorable or unpredictable conditions (McDonald et al., 2024; Özgüldez & Bulut-Karslioğlu, 2024; Wilsterman, Ballinger, & Williams, 2021). Rather than representing a passive shutdown, dormancy has been increasingly understood as a highly regulated, energy-conserving state that involves distinct molecular, metabolic, and structural features (Alekseev & Vinogradova, 2019; Klupczyńska & Pawłowski, 2021; Montrose, López Cabezas, Paukštytė, & Saarikangas, 2020; Pranzini, Raugei, & Taddei, 2022; Sajeev, Koornneef, & Bentsink, 2024; S. Yang et al., 2025). Its prevalence across phylogenetically distant organisms has been interpreted as evidence of strong selective pressure favoring phenotypic plasticity and reversible growth arrest under stress (Constant, Dobson, Habold, & Giroud, 2023; Webster & Lennon, 2025; Wilsterman et al., 2021). In prokaryotes, dormancy has been observed in the form of spore formation or persister cell states, where replication is halted and metabolic activity is drastically reduced, allowing survival in the presence of antibiotics or immune

responses (McDonald et al., 2024; Walker, Sanabria, & Youk, 2024). In plants, seed dormancy has evolved as a developmental pause that is tightly regulated by environmental cues such as temperature, light, and moisture (Klupczyńska & Pawłowski, 2021; Sajeev et al., 2024). In animals, dormancy-like states, including diapause in invertebrates and quiescence in adult stem cells, have been shown to underlie developmental timing and tissue regeneration (Wilsterman et al., 2021). Similarly, in oncology, a dormant phenotype has been increasingly attributed to disseminated tumor cells that evade chemotherapy and remain clinically undetectable for years before reactivation (S. Yang et al., 2025).

Despite their varied contexts, all forms of dormancy are characterized by a shift in cellular priorities: from active proliferation or differentiation to survival and maintenance (Considine, 2024; Gomis & Gawrzak, 2017; Pshennikova & Voronina, 2022). This transition is achieved through global suppression of biosynthetic processes, reduced transcriptional output, and highly selective translation of stress-adaptive proteins (Amissah, Combs, & Shevtsov, 2024; Buijs, Vogelzang, Nijveen, & Bentsink, 2020; Jobava et al., 2021; Koli & Shetty, 2024; Tognacca & Botto, 2021). Such states are not only reversible but are often poised for rapid reactivation upon re-exposure to permissive conditions (Özgüldez & Bulut-Karslioğlu, 2024; Pshennikova & Voronina, 2022). This reversibility has underscored the need for regulatory mechanisms that can efficiently toggle gene expression without relying solely on genomic or transcriptional alterations. Given the limitations of transcription-based regulation in energy-restricted environments, it has been hypothesized that post-transcriptional control plays a central role in dormancy (Collignon et al., 2023; Craft et al., 2020; Luján-Soto & Dinkova, 2021; Pi et al., 2022; Reynolds, 2019; Tognacca & Botto, 2021). Recent studies have pointed to the significance of mRNA stabilization, selective translation, and RNA-protein granule formation in sustaining the dormant state (Collignon et al., 2023; Escalante & Gasch, 2021; Ignatov et al., 2015; Lorenzo-Orts & Pauli, 2024). These mechanisms allow cells to preserve transcripts for future use, degrade non-essential messages, or modulate translation rates in a transcript-specific manner. However, the emerging field of epitranscriptomics has introduced an additional layer of regulation that may operate as a rapid and reversible switch during dormancy transitions (Collignon et al., 2023; Dhingra, Gupta, Gupta, Agarwal, & Katiyar-Agarwal, 2023; Shao, Wong,

Shen, & Yu, 2021). Thus, dormancy can be viewed not merely as a passive delay in growth, but as a highly evolved, dynamically regulated, and energy-efficient survival program. Its recurrence across evolutionarily distant lineages suggests the existence of conserved molecular frameworks, among which RNA-based regulation is increasingly considered to be fundamental. In this context, the role of RNA modifications as part of the dormancy machinery is now gaining attention as a key mechanistic and evolutionary feature of this ancient adaptive state.

2. Dormancy-regulating signaling pathways across biological kingdoms

Plant dormancy, particularly in seeds and buds, is governed primarily by the abscisic acid (ABA) and gibberellin (GA) signaling pathways (Tuan, Kumar, Rehal, Toora, & Ayele, 2018). ABA induces and maintains dormancy under stress by promoting desiccation tolerance and repressing growth-related genes (Maia, Dekkers, Dolle, Ligterink, & Hilhorst, 2014), while GA promotes dormancy release and germination by activating growth-promoting gene expression (Ogawa et al., 2003). Sugar signaling, mediated through the SnRK1 kinase pathway, also plays a crucial role in energy sensing and metabolic adjustment during dormancy (Choudhary, Kumar, Kaur, & Kaur, 2022). Additional regulation comes from auxin and cytokinin signaling, which influence bud dormancy and reactivation (Matilla, 2020; Qiu et al., 2019; Schaller, Street, & Kieber, 2014). Recent research has demonstrated that m^6A RNA methylation plays a key role in regulating these hormone pathways: m^6A marks affect the stability and translation of ABA and GA pathway transcripts, thereby modulating the timing and sensitivity of dormancy induction and release (Amara, Shoaib, & Kang, 2022; Shen & Yu, 2025; J. Tang, Yang, Duan, & Jia, 2021; Huihui Wang et al., 2025; X. Wu et al., 2024). This indicates a functional epitranscriptomic layer fine-tuning the plant's dormancy transitions (Figure 1A).

In animals, dormancy (often termed quiescence in stem cells or latency in cancer) involves a complex interplay of metabolic and stress-related pathways (Dias, Bouma, & Henning, 2021; Özgüldez & Bulut-Karslioğlu, 2024). The mTOR and AMPK pathways are central: mTOR promotes growth and biosynthesis under favorable conditions (Alhasan et al., 2021; Bulut-Karslioglu et al., 2016), while AMPK becomes activated during energy stress to conserve

resources and promote dormancy (Kadekar & Roy, 2019; Kamata, Yamada, & Sekijima, 2023; Rider, 2015). FOXO transcription factors support dormancy through stress resistance and cell cycle arrest (van der Weijden et al., 2024), while pathways like TGF-β, Notch, and Wnt/β-catenin regulate stem cell quiescence and dormancy plasticity in cancer (Abravanel et al., 2015; Dias et al., 2021; R. Fan et al., 2020; Herrick, Lin, Peterson, Schnittke, & Schwob, 2017; Prunier, Baker, ten Dijke, & Ritsma, 2019; van der Weijden & Bulut-Karslioglu, 2021). Increasingly, evidence highlights a significant role for m^{6}A RNA methylation in modulating these pathways. For instance, m^{6}A regulates mTOR and AMPK signaling by affecting the translation of key metabolic genes (G. Li et al., 2021; J. Liu et al., 2023). FOXO mRNAs are also subject to m^{6}A-dependent stabilization or decay, influencing stress adaptation (X. Li et al., 2023; Lin et al., 2020; Xi Liu et al., 2024). In cancer cells, m^{6}A modification of Wnt pathway transcripts modulates self-renewal and exit from quiescence (K. Li et al., 2023; Shouyi Zhang et al., 2023). Similarly, TGF-β pathway components are regulated by m^{6}A-dependent RNA decay or translational control, fine-tuning cell cycle arrest and reactivation (W. Fan et al., 2024; Feng Zhang et al., 2024). These recent findings suggest that epitranscriptomic mechanisms are deeply embedded in the regulation of dormancy decisions in animal cells (Figure 1A).

Fungal dormancy is most commonly observed in spores and quiescent vegetative states, regulated primarily by nutrient-responsive pathways like TOR, cAMP-PKA, and AMPK-like kinases (Plank, 2022; G. Sun, Qi, & Wilson, 2019). When nutrients are scarce, TOR signaling is inhibited, prompting a shift from proliferation to dormancy; cAMP-PKA signaling similarly balances growth and stasis. While epigenetic regulation in fungal dormancy is well-established, epitranscriptomic regulation is an emerging field. Recent studies in *Saccharomyces cerevisiae* have identified m^{6}A modifications in transcripts related to metabolic adaptation and stress resistance, though specific pathway interactions are still being uncovered (Scutenaire et al., 2023; Hong Wang, Zhao, Cheng, Bi, & Zhu, 2022; Yadav & Rajasekharan, 2017). There is preliminary evidence that m^{6}A affects mRNAs involved in the TOR and stress response pathways (Bodi, Bottley, Archer, May, & Fray, 2015; Z. Ren et al., 2022), likely influencing the timing of sporulation or quiescence. However, unlike in plants and animals, these interactions remain under-characterized and necessitating deeper mechanistic study.

Bacterial dormancy, including sporulation, persistence, and latency, is regulated by unique prokaryotic pathways such as the stringent response (via (p)ppGpp), toxin-antitoxin systems, and two-component regulatory systems (Abid et al., 2025; McDonald et al., 2024). These networks help cells survive antibiotic stress, nutrient deprivation, and immune evasion by shutting down transcription, translation, and replication. Unlike in eukaryotes, epitranscriptomic regulation in bacteria is less extensively studied, though it is gaining attention (Tan et al., 2024). Some studies have identified bacterial RNA modifications, including m^6A and m^5C, in transcripts related to dormancy, persistence, and stress response (Antoine et al., 2021a; Riquelme-Barrios et al., 2025; Vargas-Blanco & Shell, 2020). However, direct crosstalk between specific dormancy pathways (e.g., RelA and SpoT-mediated stringent response) and RNA methylation remains speculative and largely unexplored (Pletnev et al., 2020; Yu et al., 2025). Current evidence suggests that while bacteria may use RNA modifications for fine-tuning gene expression during dormancy, detailed molecular mechanisms are still emerging.

3. Beyond transcription: the need for post-transcriptional control in dormancy

Dormancy has traditionally been explored through the lens of transcriptional regulation, with many studies focusing on stress-responsive transcription factors, chromatin remodeling, and promoter-level silencing. While such mechanisms have provided foundational insights, accumulating evidence suggests that transcriptional repression alone does not fully account for the dynamic, flexible, and energy-efficient control required during dormancy. In many systems, dormancy has been shown to persist even when transcription is globally reduced, pointing to the existence of additional regulatory layers acting downstream of gene transcription. This has led to increased interest in the post-transcriptional landscape, where RNA molecules and their processing, stability, and translation are tightly regulated in response to dormancy-inducing conditions (Collignon et al., 2023; Luján-Soto & Dinkova, 2021; Pi et al., 2022; Tognacca & Botto, 2021).

A compelling need for post-transcriptional control in dormancy arises from the metabolic constraints faced by cells in the dormant state (Storey & Storey, 2004; Tognacca & Botto, 2021).

Transcription is an energy-intensive process, and its global suppression under stress is both adaptive and necessary (Logan, Wu, & Storey, 2019; Ramnanan, Allan, Groom, & Storey, 2009; Storey & Storey, 2012). However, survival during dormancy still requires the production of selective proteins involved in stress resistance, metabolic rewiring, and the maintenance of cellular architecture (Bezrukov, Prados, Renzoni, & Panasenko, 2021; Lorenzo-Orts et al., 2023; Sajeev, Bai, & Bentsink, 2019). To resolve this paradox, many organisms rely on stored transcripts, which are preserved in a translationally silent state and selectively activated when needed (Bai et al., 2020; Bazin et al., 2011; Ignatov et al., 2015; Sano, Rajjou, & North, 2020)(ref). This allows cells to maintain a minimal yet responsive proteome without initiating new transcription. Moreover, the spatial and temporal regulation of mRNA adds another layer of control that transcription cannot achieve on its own. For example, in plant seeds, bacteria and certain invertebrates, mRNAs critical for germination, sporulation or developmental progression are localized to specific subcellular compartments and remain untranslated until favorable conditions return (Iwańska et al., 2024; Lorenzo-Orts & Pauli, 2024; Özgüldez & Bulut-Karslioğlu, 2024; Sano et al., 2020; Stuckas, Mende, & Hundsdoerfer, 2014; Xingzhuo Yang, Zhao, Zhao, & Du, 2024). In stem cells and cancer cells, stress granules and P-bodies serve as reservoirs for silenced mRNAs, whose fate is determined by post-transcriptional cues rather than promoter activity (Fefilova et al., 2022; Lavut & Raveh, 2012; J. Ren, Zhang, Zong, Zhang, & Zhou, 2022). These structures exemplify how dormancy involves dynamic mRNA regulation at the cytoplasmic level, where storage, decay, and translation are finely tuned. Post-transcriptional regulation has also been observed to interact with metabolic signaling pathways known to control dormancy, such as TOR (target of rapamycin) (Alhasan et al., 2021; Bulut-Karslioglu et al., 2016; Yeh & Yong, 2020) and AMPK pathways (Ramnanan, McMullen, Groom, & Storey, 2010; Teraoka et al., 2006; You et al., 2022). These kinases regulate the activity of translation initiation factors and RNA-binding proteins, thereby influencing which mRNAs are translated under dormancy-inducing conditions. Interestingly, both of these metabolic pathways are known to have extensive regulatory crosstalk with epitranscriptomic mechanisms in the same cells that they control dormancy (An & Duan, 2022; T. Chen et al., 2024; G. Li et al., 2021). Thus, post-transcriptional control is not an isolated layer but is functionally integrated

with upstream signaling and environmental sensing. Finally, other post-transcriptional mechanisms playing important role in dormancy such as microRNAs (Huo, Wei, & Bradford, 2016; Ruksha, 2019) and alternative splicing (J. Li et al., 2021; Penfield, Josse, & Halliday, 2010) are tightly regulated by epitranscriptomic mechanisms such m6A RNA modification (Erson-Bensan & Begik, 2017; Mei et al., 2023; Zhu, Huo, Zhang, Shan, & Pei, 2023).

4. The reversible nature of dormancy and RNA modifications

A hallmark feature of dormancy is its reversibility, the ability of cells or organisms to return to an active, proliferative, or developmental state upon receiving appropriate stimuli (Miller et al., 2021; Özgüldez & Bulut-Karslioğlu, 2024; Pshennikova & Voronina, 2022). This reversibility distinguishes dormancy from terminal differentiation or senescence and underpins its adaptive value in fluctuating environments (Fujimaki & Yao, 2020). Mechanistically, such plasticity requires the existence of regulatory systems that are dynamic, sensitive to environmental changes, and energetically conservative. In recent years, RNA modifications have emerged as prime candidates fulfilling these criteria, offering a versatile means of regulating gene expression without permanent genomic changes.

The best-characterized RNA modification to date, N6-methyladenosine (m6A), has been shown to influence a wide array of post-transcriptional processes, including mRNA stability, splicing, nuclear export, and translation efficiency (Meyer, 2019; Meyer & Jaffrey, 2014). Importantly, m6A is installed by "writer" complexes such as METTL3/METTL14, removed by "eraser" enzymes like FTO and ALKBH5, and interpreted by "reader" proteins (e.g., YTH domain-containing proteins) (Zaccara, Ries, & Jaffrey, 2019). This tripartite system enables dynamic and reversible control over RNA fate (Fu, Dominissini, Rechavi, & He, 2014; Leighton et al., 2018; Xiong, Yi, & Peng, 2017), which is particularly advantageous in dormant cells that must remain in a poised but inactive state. The reversibility of RNA modifications mirrors the reversible entry and exit from dormancy observed across biological contexts. For instance, in hematopoietic stem cells, m6A levels are dynamically regulated during transitions between quiescent and active states, with specific m6A readers promoting the translation of cell cycle regulators upon

activation (Chang et al., 2024; Hu Wang et al., 2018; Yao et al., 2018). Similarly, in cancer biology, dormant tumor cells exhibit altered expression of m6A machinery, and changes in m6A status have been linked to both entry into dormancy and metastatic reawakening (Collignon et al., 2023). These findings underscore that RNA modifications act as regulatory switches, not only marking transcripts for degradation or translation, but doing so in a context-sensitive and reversible manner. This molecular flexibility is ideally suited to the demands of dormancy, where a rapid shift in cellular state must be achieved without de novo transcription. Furthermore, the reversibility of RNA modifications offers potential for fine-tuning gene expression thresholds, enabling cells to "test the waters" before fully committing to reactivation. It has also been proposed that external cues, such as hypoxia, nutrient availability, or oxidative stress, can modulate the activity of RNA-modifying enzymes, thereby linking the extracellular environment directly to RNA fate (Ahi & Singh, 2024; Cayir, Byun, & Barrow, 2020). This positions epitranscriptomic machinery as a sensor–effector interface that transduces environmental signals into changes in the translational landscape, an essential capability for reversible dormancy (Buijs et al., 2020; Ramnanan et al., 2009). Altogether, the reversible nature of both dormancy and RNA modifications points to a deep mechanistic compatibility between these two phenomena. By harnessing the inherent flexibility of RNA chemical marks, cells are able to execute reversible gene expression programs that underpin survival, latency, and reactivation, traits that are evolutionarily selected and biologically indispensable.

5. Mechanistic insights: epitranscriptomic marks that modulate translation, stability, and localization

RNA modifications have gained increasing recognition for their role in modulating the functional fate of transcripts (Arzumanian, Dolgalev, Kurbatov, Kiseleva, & Poverennaya, 2022; Moshitch-Moshkovitz, Dominissini, & Rechavi, 2022; Motorin & Helm, 2022; Zhao, Roundtree, & He, 2016). These modifications, which decorate coding and non-coding RNAs, have been observed to influence three major post-transcriptional processes highly relevant to dormancy: mRNA stability (Basbouss-Serhal, Pateyron, Cochet, Leymarie, & Bailly, 2017; Vargas-Blanco &

Shell, 2020), translation efficiency (Basbouss-Serhal, Soubigou-Taconnat, Bailly, & Leymarie, 2015; Lorenzo-Orts & Pauli, 2024), and subcellular localization (C. L. K. Nguyen et al., 2025; Xia et al., 2019). Each of these regulatory dimensions contributes to how cells manage their protein output in states of low metabolic activity, making them particularly relevant to dormant conditions where selective protein synthesis is required.

Among the various known RNA modifications, m6A is the most extensively characterized in eukaryotic systems (Meyer, 2019; Meyer & Jaffrey, 2014). It has been shown to mark mRNAs for differential decay rates; for instance, methylation near the 3' untranslated region can facilitate transcript degradation via recruitment of YTHDF2 (Sikorski, Selberg, Lalowski, Karelson, & Kankuri, 2023). In contrast, methylation in coding sequences or near the 5' UTR can enhance translation through recognition by other reader proteins, including YTHDF1 and YTHDC2 (Sikorski et al., 2023). This context-dependent interpretation of RNA marks allows a single modification to produce opposing functional outcomes depending on its placement and associated readers (Shi, Wei, & He, 2019). Such a system permits dormant cells to selectively stabilize or degrade transcripts involved in stress resistance, metabolic adaptation, or reactivation readiness (Collignon et al., 2023).

Epitranscriptomic marks also control translation efficiency (Meyer, 2019), which is especially critical when dormancy is accompanied by global downregulation of protein synthesis (Buijs et al., 2020; Koli & Shetty, 2024; Ramnanan et al., 2009). Through direct modification of the mRNA or via reader-mediated recruitment of translation machinery, these marks can determine which transcripts bypass translational repression. For example, specific m6A modifications have been associated with cap-independent translation initiation, a mechanism that is favored under stress or when eIF4E-mediated cap binding is inhibited (Coots et al., 2017; Meyer et al., 2015). This permits dormant cells to synthesize a small number of survival-critical proteins even when canonical translation is suppressed.

In terms of localization, modifications like m6A and pseudouridine have been found to guide mRNAs into stress granules or P-bodies; cytoplasmic sites involved in mRNA storage or decay (Eyler et al., 2019; Fu & Zhuang, 2020; Loedige et al., 2023; Vaidyanathan, Alsadhan, Merriman, Al-Hashimi, & Herschlag, 2017; Zlotorynski, 2024). These compartments have been repeatedly

observed in dormant or quiescent cells across different organisms (Davies, Stankovic, Vian, & Wood, 2012; Kearly, Nelson, Skirycz, & Chodasiewicz, 2024; Koli & Shetty, 2024; Lee, Cheng, Chao, & Leu, 2016; Shah et al., 2014; M. Zhang, Joyce, Sullivan, & Nussenzweig, 2013). The inclusion or exclusion of mRNAs from these compartments appears to depend, in part, on their modification status (Anders et al., 2018; L. Sun et al., 2023). Thus, RNA modifications act as sorting signals, governing the spatial organization of the transcriptome in a way that aligns with dormancy-associated translational priorities.

Beyond m6A, other modifications such as 5-methylcytosine (m5C) and pseudouridine (Ψ) are also gaining attention for their potential roles in dormancy (Blanco et al., 2011; David et al., 2017; Gkatza et al., 2019; Lorenzo-Orts & Pauli, 2024; S. Song & Wood, 2020; Soto, Ortiz, Contreras, Soto-Rifo, & González, 2022). m5C has been implicated in RNA export and stability, while pseudouridine is thought to influence RNA folding and translational fidelity (Wiener & Schwartz, 2020). The full functional scope of these modifications in dormant states remains underexplored, though early findings suggest that they contribute to the precise tuning of RNA behavior required for long-term survival. Taken together, RNA modifications function not only as passive chemical marks but as active regulatory signals that orchestrate the life cycle of individual transcripts. Their capacity to govern stability, translation, and localization in a selective manner makes them ideally suited to control gene expression during dormancy. These mechanisms provide a flexible yet specific mode of regulation that does not depend on ongoing transcription or permanent genetic changes, features that align closely with the core requirements of the dormant state.

6. Studies linking epitranscriptomics to dormancy in diverse organisms

Across living organisms, diverse forms of dormancy, including seed and bud dormancy in plants, diapause in animals, quiescence in stem cells, sporulation and cyst formation in microbes, and hibernation or estivation in animals, represent distinct but functionally analogous survival strategies (Özgüldez & Bulut-Karslioğlu, 2024; Webster & Lennon, 2025; Wilsterman et al., 2021). Though these states differ widely in their molecular mechanisms and evolutionary

origins, they are unified by their role in pausing growth and conserving resources in response to unfavorable conditions. Common physiological traits include metabolic downregulation, increased stress tolerance, and reversible developmental arrest. Rather than reflecting a shared molecular toolkit, dormancy across life forms represents a conserved strategy at the level of life history and ecological function, enabling organisms to endure environmental stress and resume activity when conditions improve. However, certain molecular mechanisms, such as RNA chemical modifications, are emerging as key candidates that may contribute to this convergent strategy across domains of life.

Examples from multiple biological systems have begun to demonstrate a functional intersection between epitranscriptomics and dormancy. These case studies provide crucial validation of the hypothesis that RNA modifications may participate in regulating entry into, maintenance of, and exit from dormant states. Though much of the mechanistic detail remains under active investigation, current findings across plants (Z. Li et al., 2024; J. Tang et al., 2021; J. Wang et al., 2024), animals (Rehman, Varma, Gupta, & Storey, 2023; Wade, Hadj-Moussa, & Storey, 2023), microbes (Antoine et al., 2021b; Kouvela, Zaravinos, & Stamatopoulou, 2021; Fan Zhang et al., 2024), and cancer and stem cell biology (Blanco et al., 2011; Collignon et al., 2023; Gkatza et al., 2019; Feng Zhang et al., 2024) reveal regulatory patterns that support a potentially important role for epitranscriptomic control.

In plant biology, dormancy is most prominently observed in seeds, which must survive long periods in a metabolically inactive state. Recent transcriptome-wide mapping in the plant model, *Arabidopsis thaliana*, has revealed dynamic changes in m6A methylation patterns during the activation of germination. Also an m6A mRNA eraser (demethylase) and a reader found to be involved in the transition from dormancy to germination in this species (Z. Li et al., 2024; J. Tang et al., 2021). These modifications are correlated with altered stability and translatability of transcripts involved in hormone signaling, particularly abscisic acid and gibberellin pathways (Amara et al., 2022; Y. Li et al., 2025; Shen & Yu, 2025; Huihui Wang et al., 2025; S. Yin et al., 2022), which are known to regulate dormancy depth and release in plants (X. Wang et al., 2024; Zheng et al., 2015). Moreover, a recent study has demonstrated the involvement of m6A RNA modification in regulation of bud dormancy in plants (J. Wang et al., 2024). m6A marks were

also enriched in transcripts associated with desiccation tolerance, suggesting a potential role in stress preparedness during dormancy (Han, Shoaib, Cai, & Kang, 2023; X. Wu et al., 2024).

In the microbial world, *Mycobacterium tuberculosis* (Mtb) provides a compelling example of long-term dormancy in the form of latent infection (Gengenbacher & Kaufmann, 2012). During the latent phase, Mtb enters a non-replicative but metabolically active state. Although much attention has been placed on transcriptional regulators such as DosR (Boon & Dick, 2012), new evidence points to RNA-based mechanisms as well. Pseudouridine and m6A modifications have been identified to play role in mechanisms contributing to Mtb dormancy (Ma et al., 2024; Tomasi, Kimura, Rubin, & Waldor, 2023), with indications that they may influence the stability of stress-response transcripts under hypoxia or nutrient starvation, conditions characteristic of granulomatous dormancy.

In animals, metabolic rate depression (MRD) is a unifying physiological state underlying various forms of dormancy, including hibernation, estivation, torpor, and diapause (Staples, 2016; Storey & Storey, 2004). Characterized by a profound, reversible reduction in energy consumption and biochemical activity, MRD enables animals to conserve resources, maintain cellular integrity, and survive prolonged periods of environmental stress such as cold, heat, or food scarcity. Despite differing triggers and durations, these dormant states converge on MRD as a shared metabolic adaptation for endurance. Recent studies in animals revealed MRD related mechanisms involving m6A RNA modification such as hypoxia-induced MRD condition in naked mole-rats, *Heterocephalus glaber* (Ingelson-Filpula, Kadamani, Ojaghi, Pamenter, & Storey, 2024), freezing and anoxia-induced brain MRD in wood frogs, *Rana sylvatica* (Wade et al., 2023), and dehydration induced whole-body MRD in the African clawed frog, *Xenopus laevis* (Rehman et al., 2023). Another study also revealed changes in RNA A-to-I editing as a mechanism underlying cold induced MRD during hibernation in the brain of the ground squirrel (Riemondy et al., 2018). During the diapause of bivoltine silkworm (*Bombyx mori*), a m6A reader has been shown to play pivotal role in regulation of the mRNA stability of genes in ecdysone synthesis pathway, which are required for this process (Y. Chen et al., 2022; Y. H. Chen et al., 2023). Although intriguing, these examples highlight that our understanding of RNA modification–mediated mechanisms in animal dormancy remains in its early stages, with much

still to uncover. They point to a promising frontier in organismal biology, where future research may reveal how epitranscriptomic regulation shapes dormancy across diverse animal systems.

In hematopoietic stem cells (HSCs), quiescence serves as a protective mechanism that preserves the long-term regenerative capacity of the cell population. Several studies have shown that the m6A writer METTL3 is essential for HSC activation, while its depletion promotes prolonged quiescence and impairs hematopoietic recovery (Hu Wang et al., 2018; Yao et al., 2018; R. Yin et al., 2022; Zuo et al., 2024). Specific targets of m6A-mediated regulation include mRNAs encoding cell cycle drivers and metabolic regulators. These findings suggest that RNA methylation contributes to the timing and coordination of dormancy exit, enabling a precise transition back to proliferation. In cancer biology, tumor cell dormancy represents a major clinical challenge due to its link to therapy resistance and metastatic relapse. RNA modifications have been found to be dysregulated in dormant cancer cells (Collignon et al., 2023). For instance, high expression of the demethylase ALKBH5 has been correlated with increased dormancy in glioblastoma stem-like cells, partly through the stabilization of transcripts encoding quiescence-associated transcription factors (Q. Cui et al., 2017; Sicong Zhang et al., 2017). Other cancers, including breast and melanoma, show alterations in the balance of m6A writers and erasers during periods of therapeutic dormancy (Z. Yang et al., 2022), suggesting that the epitranscriptome is actively remodeled to support survival without proliferation.

Each of these case studies points to a shared theme: the selective remodeling of RNA modifications is associated with transitions into and out of dormancy. Whether through controlling transcript decay in plants, translational priming in stem cells, or stress adaptation in pathogens and tumor cells, epitranscriptomic mechanisms appear to serve as regulatory switches that operate across a wide range of biological contexts. This broad applicability hints at an evolutionarily conserved function and demonstrate the potential of RNA modifications as targets for modulating dormancy-related processes.

7. Epitranscriptomics as a fast, flexible toolkit for adaptation

The persistence of dormancy across distant branches of the evolutionary tree has suggested that this trait provides a substantial adaptive advantage (Constant et al., 2023). In fluctuating or hostile environments, dormancy allows cells and organisms to temporarily suspend growth while remaining viable (Gianinetti, 2023; Jobava et al., 2021; Măgălie, Schwartz, Lennon, & Weitz, 2023; Roberts, Szejner-Sigal, & Lehmann, 2023). The regulatory systems supporting such plasticity must operate efficiently under low-energy conditions, respond quickly to environmental changes, and remain evolutionarily adaptable. Within this context, epitranscriptomics presents itself as a regulatory system capable of fulfilling all these criteria, functioning as a post-transcriptional toolkit that is both fast-acting and evolutionarily flexible (Ahi & Singh, 2024; Dannfald, Favory, & Deragon, 2021; Xiangbo Yang, Patil, Joshi, Jamla, & Kumar, 2022). Unlike changes at the DNA or chromatin level, RNA modifications do not require permanent alterations to the genome; instead, they provide rapid and reversible control over gene expression at the RNA level (Fu et al., 2014; Leighton et al., 2018; Xiong et al., 2017). This form of regulation minimizes energetic cost and allows for tight, transcript-specific responses. Such characteristics are advantageous for survival in variable environments, where immediate and graded responses to stress or resource scarcity may determine evolutionary fitness.

From an evolutionary standpoint, RNA-modifying enzymes and reader proteins are conserved across a wide range of organisms. For example, homologs of METTL3 and FTO, the m6A writer and eraser enzymes, have been identified in plants, animals, and fungi (Kim, Hu, Kang, & Kim, 2024; C. Liu, Cao, Zhang, & Yin, 2022; Sibbritt, Patel, & Preiss, 2013; Wong & Eirin-Lopez, 2021). This conservation indicates that RNA modifications were likely present in early eukaryotes and may have been co-opted to support dormancy-related processes in different lineages. Yet, despite this conservation, considerable functional diversification has occurred, allowing RNA modification pathways to be tailored to specific ecological niches and developmental programs (C. Liu et al., 2022; H. Sun, Li, Liu, & Yi, 2023; Wilkinson, Cui, & He, 2022). In microbial species, RNA modifications may provide a means for bet-hedging, where subpopulations enter dormancy even in the absence of external cues, enhancing survival against unpredictable threats (Antoine et al., 2021a; Hou, Masuda, & Foster, 2020; Morawska, Hernandez-Valdes, & Kuipers, 2022). In plants, seed dormancy has evolved in multiple lineages, often in response to

local or global climatic pressures (Jaganathan & Phartyal, 2025; Jayasuriya & Phartyal, 2024; Koutouan-Kontchoi, Phartyal, Rosbakh, Kouassi, & Poschlod, 2020; Rosbakh et al., 2023). The ability to adjust the sensitivity of dormancy-related transcripts through epitranscriptomic mechanisms may offer a tunable system that enhances fitness across diverse environments (Tognacca & Botto, 2021; Xiang et al., 2024). In higher organisms, the evolutionary adaptation of epitranscriptomic systems has been associated with lifespan extension (McMahon, Forester, & Buffenstein, 2021; Wagner & Schosserer, 2022), tissue regeneration (G. Cui et al., 2023; Weng et al., 2018), and cancer resistance (L. Tang et al., 2024), all of which involve quiescent or dormant cellular states (Heyman, Kumpf, & De Veylder, 2014; Rumman, Dhawan, & Kassem, 2015; Stuart & Brown, 2006). For instance, long-lived mammals exhibit distinct expression patterns of RNA-modifying enzymes in tissues known to harbor dormant cells (e.g., skeletal muscles, brain, hair follicles and bone marrow) (Jiapaer et al., 2022; Ogbe et al., 2024; Ozkurede et al., 2019; Z. Wu et al., 2023; R. Yin et al., 2022). These patterns suggest that selection has acted not only on the presence of RNA modifications but on their context-dependent deployment to support long-term cellular maintenance and delayed reactivation.

Taken together, the flexibility of RNA modifications also makes them ideal candidates for integration into complex regulatory networks. By interacting with stress pathways, metabolic sensors, and signaling cascades, RNA marks can serve as modular units that plug into pre-existing systems without requiring extensive genetic rewiring. This modularity may explain their frequent repurposing across taxa to regulate dormancy under diverse physiological and environmental conditions. Therefore, the epitranscriptome can be viewed as a core regulatory infrastructure that enhances the evolutionary adaptability of dormancy. It operates with speed, specificity, and minimal energetic demand, properties that are consistently favored under conditions where survival depends on reversible growth arrest and precise reactivation timing.

8. Toward a unified model: the epitranscriptomic regulation of the dormant state

As evidence accumulates from different systems, a conceptual framework has begun to emerge in which the epitranscriptome is positioned as a central regulator of dormancy. In this unified model, RNA modifications function as key molecular signals that mediate the transition between active and dormant states; modulate transcript fate in response to environmental inputs; and support reactivation when conditions improve. Within this model, the initiation of dormancy involves both transcriptional and post-transcriptional changes. As transcription slows, a subset of transcripts is selectively marked by modifications such as m6A, which either stabilize them for later use or direct them toward silencing in granules (Alriquet et al., 2021; Collignon et al., 2023; Heck & Wilusz, 2019; Loedige et al., 2023; Feng Zhang et al., 2024). These decisions are governed by RNA-binding proteins that recognize specific modifications and coordinate the recruitment of decay factors, translational machinery, or storage compartments (Loedige et al., 2023; D. Song, Chen, Wang, Cheng, & Shyh-Chang, 2024; Zuo et al., 2024).

Maintenance of the dormant state is achieved through continued repression of translation, paired with selective access to pre-existing transcripts that remain protected and responsive (Collignon et al., 2023; K. Li et al., 2023; Lorenzo-Orts & Pauli, 2024). RNA marks serve as molecular bookmarks, allowing the cell to preserve information without active transcription. This preservation ensures that essential stress-response or metabolic genes can be re-engaged quickly when conditions change, without the need for new RNA synthesis (Zhou et al., 2015). Upon exit from dormancy, RNA modifications are reinterpreted by shifts in the expression or activity of writer, eraser, or reader proteins. External signals such as nutrient availability or temperature change may influence enzyme localization, substrate affinity, or cofactor availability, leading to a rewiring of the RNA modification landscape (Collignon et al., 2023; K. Li et al., 2023; Lorenzo-Orts & Pauli, 2024; Zhou et al., 2015). This transition permits a rapid and energy-efficient ramp-up of protein synthesis that is essential for re-entering the cell cycle or resuming development.

The unified model also accommodates context-specific variations, such as differences in which transcripts are modified or how modifications are interpreted. These variations arise from differences in tissue type, developmental stage, or organismal lineage but are underpinned by the same general principles of reversible, mark-driven regulation. Importantly, the model

supports integration with other regulatory layers, including chromatin state, transcription factors, and metabolic cues. By uniting disparate observations under a single framework, the model reinforces the idea that epitranscriptomic regulation is not a peripheral feature of dormancy but a central organizing mechanism. It explains how dormancy can be sustained without genetic alterations; how cells remain responsive during inactivity; and how reactivation is executed with speed and precision. This perspective not only aligns with known biological data but also provides a useful guide for future investigations, enabling the formulation of testable hypotheses regarding the timing, specificity, and function of RNA modifications in dormant states.

9. Open questions and future directions

While significant progress has been made in identifying RNA modifications and their potential roles in dormancy, many questions remain unresolved. Addressing these gaps will be essential for fully understanding how the epitranscriptome contributes to the establishment, maintenance, and reversal of dormancy in diverse biological systems. One of the most immediate challenges is the limited resolution of current epitranscriptomic mapping techniques, particularly in dormant cells, which often yield low RNA quantities. Advances in single-cell and low-input RNA modification detection (Bresnahan et al., 2023; Tegowski, Prater, Holley, & Meyer, 2024) are needed to determine the transcript-specific landscape of modifications during dormancy transitions. Such tools would enable researchers to determine whether unique epitranscriptomic signatures define dormant states or predict reactivation potential. The temporal dynamics of RNA modifications during dormancy remain poorly understood. It is not yet clear whether these marks are deposited before dormancy entry as a preparatory measure; added during dormancy to modulate transcript fate; or rapidly rewritten during reactivation. Controlled time-course studies using inducible dormancy models could provide insight into the sequence and causality of these events.

Another open question involves the specificity of reader protein interactions. While several readers of m6A and other marks have been identified, their binding preferences under

dormancy-inducing conditions are not well characterized. It is possible that shifts in reader expression or post-translational modifications influence how RNA marks are interpreted, leading to different outcomes even with identical modification patterns (T. K. H. Nguyen & Kang, 2024). Furthermore, the extent to which RNA modifications interact with other novel emerging mechanisms of dormancy state regulation in various organisms and cells, such as small or long non-coding RNAs (Reynolds, 2019), enhancer RNAs (So et al., 2022; Tremblay et al., 2024), RNA G-quadruplexes structuring (Zuurbier et al., 2024), intra-cellular phase separation processes (Xin Liu, Zhu, & Zhao, 2023; Xu, Zheng, Lu, Song, & Zhang, 2021), and codon usage bias (Feng, Wang, Guo, Liu, & Long, 2025; Kanduc, 2021; Small-Saunders et al., 2024), is still unclear. Interestingly, all of these novel players in regulation of dormancy are known to have extensive regulatory crosstalk with m6A RNA modifications (Figure 1B). The role of feedback loops, where modifications influence the expression of their own modifying enzymes, also deserves further study, as such loops could stabilize or destabilize dormancy states at cellular level (Deritei, Rozum, Ravasz Regan, & Albert, 2019; J. Wu et al., 2023; Yeo et al., 2018). Finally, the therapeutic implications of modulating RNA modifications in dormant cells remain largely unexplored. In cancer, targeting the epitranscriptome could potentially force dormant cells into reactivation and subsequent vulnerability to therapy (Tamamouna, Pavlou, Neophytou, Papageorgis, & Costeas, 2022). In agriculture, manipulating RNA modification patterns in seeds might offer strategies for improving crop resilience or germination control (Lieberman-Lazarovich, Kaiserli, Bucher, & Mladenov, 2022).

In summary, the field stands at a pivotal point, with enough foundational evidence to justify a central role for RNA modifications in dormancy, yet with ample opportunity for discovery. Future work will benefit from multidisciplinary approaches that combine molecular biology, systems-level analysis, and evolutionary perspectives to unravel the full significance of the epitranscriptome in the logic of cellular dormancy.

Box 1 | Key concepts referred in this article
Dormancy: A reversible, energy-conserving state in which cells or organisms halt growth and division to

survive adverse conditions.

Epitranscriptomics: The study of chemical modifications on RNA molecules that influence their function, stability, and translation without altering nucleotide sequences.

m6A (N6-methyladenosine): The most abundant internal mRNA modification in eukaryotes, regulating RNA metabolism through reader, writer, and eraser proteins.

RNA writers: Enzymes (e.g., METTL3/METTL14) that install chemical modifications onto RNA, setting the stage for downstream regulatory effects.

RNA erasers: Demethylases (e.g., FTO, ALKBH5) that remove RNA modifications, enabling reversibility and dynamic regulation.

RNA readers: Proteins that recognize specific RNA modifications and mediate effects on stability, localization, or translation.

Cellular quiescence: A non-proliferative, reversible state often observed in stem cells and associated with dormancy.

mRNA stability: The resistance of transcripts to degradation, influenced by sequence elements and post-transcriptional modifications.

Translation control: Regulation of protein synthesis from mRNA, often through modifications or binding proteins that affect ribosome recruitment.

Stress granules: Cytoplasmic aggregates of stalled translation initiation complexes that store mRNAs during stress or dormancy.

P-bodies: Cytoplasmic sites for mRNA decay and storage, often active during translational repression in dormancy.

Bet-hedging: An evolutionary strategy where phenotypic variability increases survival under fluctuating or unpredictable environments.

Cap-independent translation: A mechanism of translation initiation not requiring the 5' cap, often employed during stress or dormancy.

Phase separation: The formation of membraneless compartments (e.g., stress granules) through physicochemical interactions among proteins and RNAs.

Pseudouridine (Ψ): A common RNA modification that can alter RNA structure and translation, present in tRNAs, rRNAs, and some mRNAs.

m5C (5-methylcytosine): A modification that can influence RNA export, localization, and stability, though its role in dormancy is still emerging.

Transcriptomic plasticity: The ability of a cell to rapidly alter its RNA expression and regulatory landscape in response to environmental changes.

Dormancy entry signals: Environmental or endogenous cues (e.g., hypoxia, nutrient deprivation) that initiate transition into a dormant state.

Reactivation cues: External or internal triggers that prompt exit from dormancy and resumption of cellular activity.

535

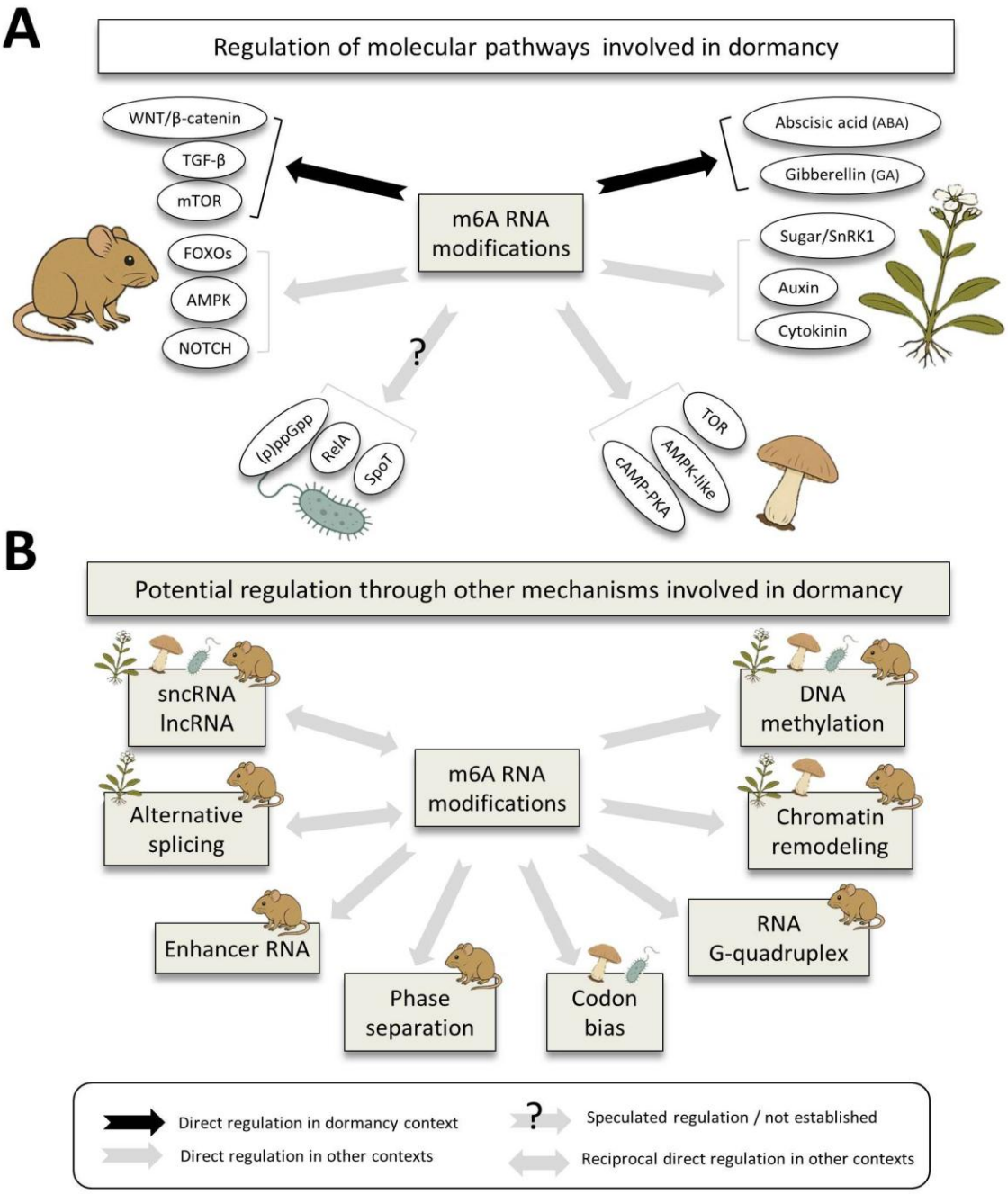

Figure 1. Potential involvements of m6A RNA modification in dormancy related molecular mechanisms. (**A**) Signaling pathways involved in different types of dormancy state across living organisms, and their regulatory connections with m6A RNA modification. (**B**) Potential regulatory effects of m6A RNA modification on dormancy via other mechanisms known to contribute to this process. The mouse, plant, fungus, and bacterium icons above each mechanism indicate the existing evidence for that mechanism's involvement in dormancy in animals, plants, fungi, and bacteria, respectively.

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Authors' contributions

E.P.A. conceived the study, drafted the manuscript and designed the figure.

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1202