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Membrane-Anchored Mobile Tethers Modulate Condensate Wetting, Localization, and Migration

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Biomolecular condensates frequently rely on membrane interactions for recruitment, localization, and biochemical substrates. Many of these interactions are mediated by membrane-anchored molecules such as proteins or specific lipids, which we refer to as "mobile tethers" since they can typically diffuse within the membrane while still interacting with the condensate. The presence of mobile tethers creates a surface with dynamic and spatially inhomogeneous wetting properties that are typically overlooked by traditional wetting theories. Here, we propose a general theoretical framework to study how mobile tethers impact both equilibrium and dynamic properties of condensate wetting. We show that a favorable tether-condensate interaction leads to tether enrichment at the condensate-membrane interface, which modifies the equilibrium condensate–membrane surface tension and contact angle. Increasing tether abundance on the membrane can drive transitions between wetting regimes, with only a modest tether density and binding energy required for biologically relevant scenarios. Furthermore, tethers modulate how condensates react to complex membrane geometries. By helping condensates coat membranes, mobile tethers can facilitate condensate localization to junctions of membrane structures, such as the reticulated membranes inside the algal pyrenoid. Both tether abundance and mobility affect how droplets interact with complex membrane geometries, such as droplet migration along membrane tubules of varying radii. These results provide a framework to study the implications of tether-mediated condensate-membrane interactions for cellular organization and function.

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I. INTRODUCTION

Biomolecular condensates—intracellular compartments formed via phase separation—are essential for diverse biological processes, including gene regulation, metabolism, and cell signaling [1,2]. In many instances, proper condensate function relies on interactions with membranes [3–9]. These membrane interactions can spatially organize condensates, concentrate interaction partners, and facilitate access to reactants. The algal pyrenoid exemplifies this interplay [10]: condensates enriched with the CO_2-fixing enzyme Rubisco form around traversing membranes that supply CO_2 to enhance photosynthetic efficiency. Conversely, condensates can also facilitate membrane processes such as transport, signaling, force generation, and structural remodeling. For example, focal adhesion kinase forms condensates on the cytoplasmic membrane, binding to lipids at sites where focal adhesions assemble, thereby regulating cell motility [11]. Similarly, B-cell activation involves condensation on the plasma membrane that is essential for downstream signaling [12]. More broadly, unraveling the dynamic relationship between condensates and membranes is proving to be essential for understanding intracellular organization and function.

In many cases, membrane-associated condensates do not directly wet membranes. Instead, they adhere to membrane surfaces via tethering molecules, such as proteins or specific lipids, that are anchored to the membrane. In the pyrenoid of the model alga *Chlamydomonas reinhardtii*, for example, pyrenoid-traversing membranes feature tethers like RBMP1, RBMP2, and SAGA1, which directly bind to Rubisco [13,14]. These tether proteins are essential for the assembly of the pyrenoid condensate around traversing membrane tubules, a structure that is crucial for the pyrenoid's function in CO_2 fixation. In this case and others, elucidating how tethers mediate condensate-membrane interactions is key to understanding the structure and function of membrane-associated condensates.

A key characteristic of these tether molecules is their ability to diffuse laterally within the membrane. As the condensate wets the membrane, the tethers can dynamically redistribute,

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enriching at the condensate-membrane interface due to favorable interactions with the condensate. This creates a surface with dynamic and spatially inhomogeneous wetting properties, which can affect both the equilibrium and the dynamic aspects of condensate wetting. These effects are typically overlooked by traditional wetting theories, which often assume static surface properties [15,16], or theories of soft wetting, where the dynamics comes from substrate deformation [17]. Here, motivated by both biological significance and theoretical interest, we seek to address the general question of how mobile tethers affect the condensate-membrane interaction and wetting.

In this work, we present a general theoretical framework that describes the coupled dynamics of condensates and mobile tethers. We find that mobile tethers enrich in the condensate-membrane interface, thereby reducing the surface tension with the membrane and modifying the equilibrium contact angle. By tuning the expression level of attractive tethers, cells can drive transitions from nonwetting to partial or complete wetting. The per-tether binding energy required for such wetting transitions is estimated to be modest (only a few $k_\mathrm{B}T$) for typical values of tether density and condensate surface tension. Furthermore, mobile tethers facilitate condensate localization to intersecting membrane structures, such as the reticulated membranes inside the pyrenoid. Finally, both tether abundance and mobility affect droplet migration on spatially varying membrane structures such as tapering tubules. Overall, our framework provides tools for understanding the role of tether-mediated condensate-membrane interactions in cellular organization and function.

II. RESULTS

A. A general theoretical framework for tether-mediated wetting

We study a general theory that describes the densities of tethers and condensates with fields ψ (defined on the membrane) and ϕ (defined in the bulk), respectively. A high (low) value of ϕ corresponds to a condensate dense (dilute) phase. The interactions are captured by a total free energy:

$$\beta F = c_{\psi,0}\int \mathrm{d}A\left[f_\psi(\psi)+\frac{\lambda_\psi}{2}(\nabla\psi)^2 - E(\psi,\phi|_\mathrm{surf})\right] + c_{\phi,0}\int \mathrm{d}V\left[f_\phi(\phi)+\frac{\lambda_\phi}{2}(\nabla\phi)^2\right], \tag{1}$$

where the first integral is over the membrane area, and the second integral is over the bulk volume. Energy is measured in units of $\beta^{-1}=k_\mathrm{B}T$. $c_{\psi,0}$ and $c_{\phi,0}$ are reference concentrations for the tether and condensate so that the free-energy densities are nondimensionalized: $E(\psi,\phi|_\mathrm{surf})$ captures both condensate-tether and condensate-membrane interactions; $f_\psi(\psi)$ and $f_\phi(\phi)$ are the free-energy densities of tethers and condensates, respectively; and λ_ψ and λ_ϕ are constants associated with interface energies. Without loss of generality, we consider the nondimensionalized system, setting $c_{\psi,0}k_\mathrm{B}T=1$ and $c_{\phi,0}k_\mathrm{B}T=1$ by rescaling the unit of length by $l_0=c_{\psi,0}/c_{\phi,0}$ and energy by $E_0=c_{\phi,0}k_\mathrm{B}Tl_0^3$ (see Sec. I A of the Supplemental Material [18] for details). The model encompasses a large class of systems and interactions by allowing the free-energy densities $f_\psi(\psi)$ and $f_\phi(\phi)$ and the interaction energy $E(\psi,\phi|_\mathrm{surf})$ to take any reasonable form.

By minimizing the free energy in Eq. (1), we obtain the equilibrium concentration profile, from which the contact angle θ can be measured [Figs. 1(a) and 1(b)]. To study the dynamics of wetting, we can further prescribe conserved (model B) dynamics [23]:

$$\partial_t\psi=\nabla\cdot(M_\psi\nabla\mu_\psi),\quad \partial_t\phi=\nabla\cdot(M_\phi\nabla\mu_\phi), \tag{2}$$

where M_ψ and M_ϕ are mobility coefficients, and $\mu_\psi=\delta F/\delta\psi$ and $\mu_\phi=\delta F/\delta\phi$ are the dimensionless chemical potentials of the tethers (ψ) and the condensate (ϕ), respectively. We rescale time by $t_0=l_0^2/(M_\phi E_0)$ such that $M_\phi=1$. The model B approach describes overdamped diffusive relaxation of the condensate and tether fields and does not include hydrodynamic momentum transport, which would require model H [23].

To illustrate the physical picture, we study a minimal model for interrogating how mobile tethers affect condensate wetting. We consider a linear interaction energy, $E(\psi,\phi)=(h_0+h_1\psi)\phi$, where h_0 and h_1 describe condensate-membrane and condensate-tether interactions, respectively. $h_1>0$ represents an attractive condensate-tether interaction, while the bare membrane could be either repelling ($h_0<0$) or attracting ($h_0>0$) for the condensate. We use Flory-Huggins free energies for self-energies $f_\xi(\xi)=\xi\ln\xi+(1-\xi)\ln(1-\xi)+\chi_\xi\xi(1-\xi)$, with $\xi\in\{\psi,\phi\}$ representing the area or volume fraction of tether or condensate, respectively [24]. The first two terms represent the entropy of mixing, while the parameter χ_ξ quantifies the effective interaction bias between components: positive χ_ξ corresponds to unfavorable mixing and promotes phase separation. In the limit $\chi_\psi=0$ (purely entropic limit for tethers), the self-organization of tethers in the membrane is energetically neutral and driven purely by entropy.

Regarding how tether mobility affects condensate behavior, we find that the physical picture that emerges from the minimal model persists over a broad range of physically motivated parameter choices and modeling details, such as condensate free-energy density, tether-tether interaction, or tether-condensate interaction strength (see Sec. I C of the Supplemental Material [18]). It is also straightforward to extend the model to describe multicomponent condensates and/or tethers, as well as more complex interactions.

B. Mobile tethers control equilibrium wetting properties

In classical wetting theory, the contact angle θ of a droplet on a surface is determined by force balance at the three-phase junction through the Young-Dupré equation [15], which relates θ to the difference of surface tensions [Fig. 1(a)]. In the presence of mobile tethers, favorable tether-condensate interactions enrich tethers within a wetting condensate [Fig. 1(a)], thereby creating a surface with inhomogeneous wetting properties, which in turn modifies the surface tensions and the contact angle.

Condensate phase separation creates dense and dilute phases in the bulk, with binodal concentrations ϕ_den and ϕ_dil (as measured in volume fractions), respectively. The concentration difference $\Delta\phi=\phi_\mathrm{den}-\phi_\mathrm{dil}$ drives the attraction of

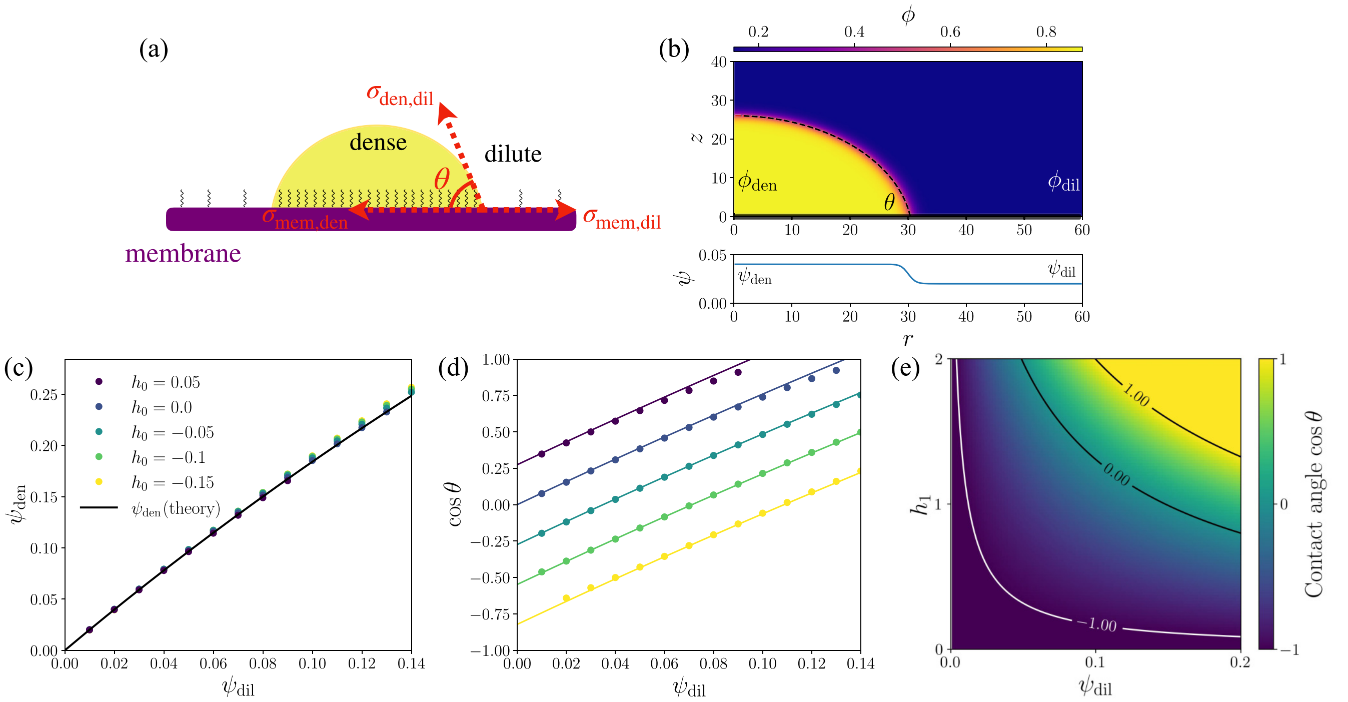

FIG. 1. Mobile-tether-mediated condensate wetting of membranes. (a) Illustration of a biomolecular condensate (yellow) interacting with mobile tether molecules (black) to wet a membrane (purple). The interaction creates a localized enrichment of tethers around the condensate, surrounded by a lower background concentration of tethers. mem, den, and dil represent membrane, dense phase, and dilute phase, respectively. The contact angle θ is determined by force balance at the three-phase junction: $\sigma_{\text{den,dil}}\cos\theta = \sigma_{\text{mem,dil}} - \sigma_{\text{mem,den}}$, where the σ's are surface tensions. (b) A typical equilibrium concentration profile obtained from numerical simulations. The condensate field ϕ (top) and the tether field ψ (bottom) are plotted in cylindrical coordinates (r, z) with axial symmetry. The thick black line indicates the flat membrane at $z = 0$. The black dashed curve is a spherical cap fit to the condensate surface contour. (c) Condensate-enriched tether concentration ψ_{den} increases with bulk tether concentration ψ_{dil}, for different condensate-membrane interactions h_0, consistent with theory [solid curve, Eq. (4)]. (d) Contact angle $\cos\theta$ as a function of tether concentration ψ_{dil} for different values of h_0 [see legend in panel (c)] agrees well with theory [solid curves, Eq. (5)]. (e) $\cos\theta$ [Eq. (5)] as a function of condensate-tether interaction h_1 and tether concentration ψ_{dil} for $h_0 = -0.2$. Contours for $\cos\theta = \pm 1$ represent wetting transitions to complete and no wetting, respectively. In all simulations, ψ has a Dirichlet boundary condition while ϕ has a no-flux boundary condition. Tethers are purely entropic ($\chi_\psi = 0$); see Fig. S1 [18] for simulations with $\chi_\psi \neq 0$. For panels (b)–(d), tether-condensate interaction strength is $h_1 = 1$; see Fig. S2 [18] for other values of h_1. Other parameters are $\chi_\phi = 2.5$, $\lambda_\phi = 1$, $\lambda_\psi = 0$; $\psi_{\text{dil}} = 0.02$ and $h_0 = 0$ for panel (b); and $h_0 = -0.2$ for panel (e).

tethers to the condensate, resulting in a tether area fraction, ψ_{den}, in contact with the dense phase, which is higher than that in contact with the dilute phase ψ_{dil} [Fig. 1(b)]. This partition of tethers reaches equilibrium when chemical potentials are balanced: $\mu_\psi(\psi_{\text{den}}, \phi_{\text{den}}) = \mu_\psi(\psi_{\text{dil}}, \phi_{\text{dil}})$, which leads to

$$\ln\frac{\psi_{\text{den}}}{1-\psi_{\text{den}}} = \ln\frac{\psi_{\text{dil}}}{1-\psi_{\text{dil}}} + h_1\Delta\phi + 2\chi_\psi(\psi_{\text{den}} - \psi_{\text{dil}}), \tag{3}$$

where we have approximated the condensate concentrations at the surface with the bulk binodal concentrations (see Sec. I B of the Supplemental Material [18] for details). Equation (3) is accurate to first order in the interaction energy $O(h_0, h_1)$. If the tethers mix in the membrane purely entropically ($\chi_\psi = 0$), ψ_{den} can be solved analytically:

$$\psi_{\text{den}} = \frac{\psi_{\text{dil}} e^{h_1\Delta\phi}}{1 + \psi_{\text{dil}}(e^{h_1\Delta\phi} - 1)}, \tag{4}$$

which can be viewed as Langmuir adsorption of tethers by the condensate [25]. Equation (4) agrees well with numerical simulations across a wide range of ψ_{dil}, for both repelling ($h_0 < 0$) and attracting ($h_0 > 0$) interactions between the bare membrane and the condensate [Fig. 1(c)].

The presence of attractive tethers reduces both surface tensions $\sigma_{\text{mem,den}}$ and $\sigma_{\text{mem,dil}}$. However, the decrease in $\sigma_{\text{mem,den}}$ is more substantial due to tether enrichment in the condensate ($\psi_{\text{den}} > \psi_{\text{dil}}$). This, in turn, modifies the contact angle θ, which is determined by force balance at the three-phase junction: $\sigma_{\text{den,dil}}\cos\theta = \sigma_{\text{mem,dil}} - \sigma_{\text{mem,den}}$. To the leading order in $O(h_0, h_1)$, the modified contact angle is (see Sec. I B of the Supplemental Material [18] for details)

$$\cos\theta = \frac{\sigma_{\text{mem,dil}} - \sigma_{\text{mem,den}}}{\sigma_{\text{den,dil}}} = \frac{\Delta\sigma_0 + \Delta\sigma_1}{\sigma_{\text{den,dil}}}, \tag{5}$$

where $\Delta\sigma_0 = h_0\Delta\phi$ is the surface tension difference in the absence of tethers, and $\Delta\sigma_1 = \ln\frac{1-\psi_{\text{dil}}}{1-\psi_{\text{den}}} - \chi_\psi(\psi_{\text{den}}^2 - \psi_{\text{dil}}^2)$ is the additional surface tension difference due to mobile tethers. In the purely entropic limit for tethers ($\chi_\psi = 0$), $\Delta\sigma_1$ simplifies to

$$\Delta\sigma_1 = \ln[1 + \psi_{\text{dil}}(e^{h_1\Delta\phi} - 1)], \tag{6}$$

which increases monotonically with tether abundance ψ_{dil} and tether-condensate interaction h_1. Indeed, numerical simulations find the contact angle in simulations to be in excellent agreement with Eq. (5) [Fig. 1(d), solid curves]. Thus, an attractive interaction due to mobile tethers can substantially modulate wetting over a wide range of contact angles.

Wetting transitions occur at $\cos\theta = 1$, when a droplet completely wets a membrane, and at $\cos\theta = -1$, when a droplet detaches from a membrane (nonwetting). Tethers can induce transitions between these wetting regimes. This can be simply illustrated in the limit of purely entropic tethers ($\chi_\psi = 0$): For a repelling membrane that is initially in the nonwetting regime ($h_0 < -\sigma_{\mathrm{den,dil}}/\Delta\phi$), both partial wetting [$\cos\theta \in (-1, 1)$] and complete wetting ($\cos\theta = 1$) regimes can be achieved via a high enough density of attractive tethers [Fig. 1(e)]. To reach complete wetting, the required critical density of tethers is $\psi^\star_{\mathrm{dil}} = \frac{e^{\sigma_{\mathrm{den,dil}} - h_0\Delta\phi} - 1}{e^{h_1\Delta\phi} - 1}$, which must stay below 1 since ψ is defined in terms of area fraction. Since $\psi^\star_{\mathrm{dil}}$ vanishes in the limit of large h_1, a finite density of tethers is sufficient to access all three wetting regimes as long as the tether-condensate attraction is strong enough.

For the sake of analytical tractability, our comparison of theoretical expressions to numerical simulations (Fig. 1) has primarily focused on purely entropic mobile tethers ($\chi_\psi = 0$). However, our theory can also describe tethers with a nonzero energetic cost of mixing ($\chi_\psi \neq 0$) and incorporate alternative forms of condensate free energies $f_\phi(\phi)$. These generalizations conform with the same physical picture, with excellent quantitative agreement between theory and simulations (see Sec. I C of the Supplemental Material [18]).

For real tether molecules, how much binding energy is required to significantly affect wetting properties? Typically, the membrane would be slightly repulsive for polymer condensates because being close to a membrane reduces the conformational entropy of polymers, leading to an estimated $\Delta\sigma_0 \approx -10^{-1}\ k_{\mathrm{B}}T/\mathrm{nm}^2$ [26]. In aqueous buffer, biomolecular condensate surface tensions are typically of the same order, $\sigma_{\mathrm{den,dil}} \approx 10^{-1}\ k_{\mathrm{B}}T/\mathrm{nm}^2$ [27]. Thus, to drive wetting, tethers must reduce surface tension by the same order, $\Delta\sigma_1 \approx 10^{-1}\ k_{\mathrm{B}}T/\mathrm{nm}^2$. A typical tether density of $n \approx 10^{-2}\ \mathrm{nm}^{-2}$ [28] yields a required binding energy of $\epsilon \approx O(1)\ k_{\mathrm{B}}T$ (see Sec. II of the Supplemental Material [18] for details). Despite being a rough estimate, these calculations show that a modest per-tether binding energy (a few $k_{\mathrm{B}}T$) is sufficient to drive wetting transitions. Therefore, cells can potentially regulate condensate wetting by tuning the expression level of tether molecules.

C. Mobile tethers facilitate condensate localization dynamics

Thus far, we have focused on equilibrium morphologies. How might mobile tethers affect the dynamics of condensate formation and localization? In the alga *C. reinhardtii*, for example, the pyrenoid condensate dissolves and reforms every cell division [29], and the new pyrenoid centers around a reticulated region where many membrane tubules meet. Since the reticulated region has a high membrane area per volume, it might therefore be able to enrich tethers more effectively than other regions of the tubule. Hence, we hypothesize that mobile tethers may facilitate condensate localization by enrichment in the reticulated region.

To simply illustrate this mechanism, we study a two-dimensional system which is bounded by membranes on the left and bottom sides and closed (by no-flux boundary conditions) on the other two (Fig. 2). The bottom-left corner is most favorable for the condensate since it can interact there with the largest amount of membrane area (and therefore tethers), analogous to the reticulated region in the pyrenoid. We envision that the condensate can form near the membrane via either heterogeneous nucleation or recruitment by membrane proteins. Thus, initially in simulations, the condensate coats part of the membrane, and its bulk concentration is between binodal and spinodal concentrations. We then simulate the model to study how tether mobility affects condensate localization dynamics.

If tethers have a high mobility ($M_\psi = 1$), they quickly enrich in the condensate and help it localize to the corner [Fig. 2(a)]. In contrast, if the tether mobility is low ($M_\psi = 0.1$), the condensate first breaks up into smaller droplets and only slowly relocalizes to the corner through a coarsening process [Fig. 2(b)]. In both cases, the coarsening is purely due to diffusive flux of the condensate (Ostwald ripening). Even though both cases reach the same equilibrium state, the latter process is much slower [Fig. 2(d)]. If the tethers are completely immobile ($M_\psi = 0$, which is equivalent to a homogeneous membrane without tethers), the condensate still localizes to the membrane junction, although the equilibrium state is slightly different due to a different contact angle [Fig. 2(c), inset]. The localization dynamics are comparable to those of the low-tether-mobility system and much slower than those of the high-tether-mobility one [Figs. 2(c) and 2(d)]. Thus, by helping the condensate to optimize its membrane contacts, mobile tethers can facilitate coarsening and localization with respect to membrane structures.

D. Tether abundance and mobility affect condensate migration on tubules

Our theoretical framework enables the study of mobile-tether-mediated wetting of a myriad of possible membrane structures, including tubes, sheets, and cristae. Membrane morphology can also vary in space: For example, membrane structures in the pyrenoid condensate in *C. reinhardtii* transition from flat sheets to cylindrical tubules to even narrower contorted tubules as they traverse the condensate [13]. As droplets wet such spatially varying structures, they may be impelled to migrate along the surface to minimize the overall energy [30]. As highlighted in the example above, the presence of mobile tethers could modulate or amplify the effects of membrane geometry on condensate behavior, such as condensate migration.

To illustrate such geometric effects, we consider the dynamics of a condensate that wets a membrane tubule of varying radius. Such structures can be found in the pyrenoid, where the traversing tubules narrow as they go inside the condensate [31]. Here we consider a (truncated) cone geometry where the tubule radius varies linearly along its long axis [Fig. 3(a), black line], although the theoretical arguments are general for other geometries as well.

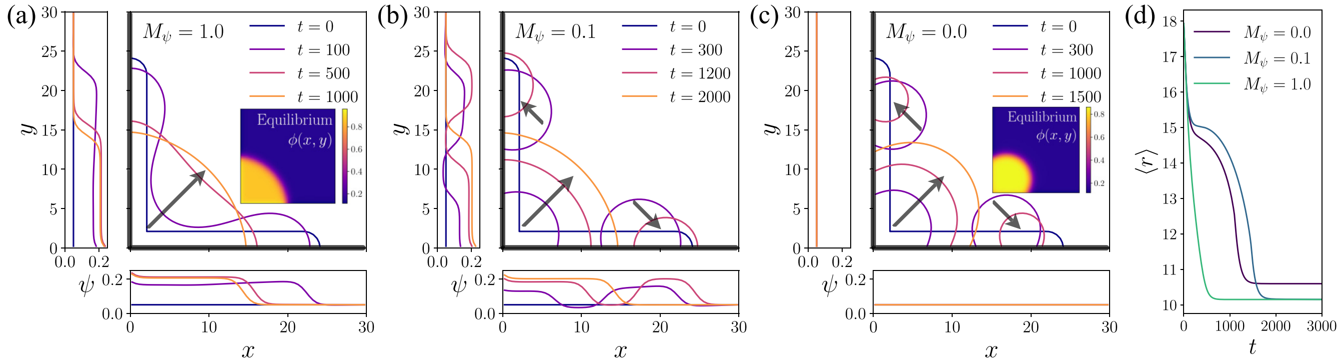

FIG. 2. Mobile tethers facilitate dynamic condensate relocalization. (a)–(c) Dynamics of condensate localization for tether mobility $M_\psi = 1.0$ (a), $M_\psi = 0.1$ (b), and $M_\psi = 0.0$ (c). The simulation domain is a two-dimensional system (x, y) with membranes on the left and bottom boundaries (indicated by thick black lines). Different colors indicate concentration profiles at different times (legend), with the condensate ϕ represented by interface contours and the tether density ψ shown in the left and bottom insets. Insets in panels (a) and (c) show the final equilibrium profile for $\phi(x, y)$. Black arrows indicate the time evolution of the interface contours to guide the eye. The tether density at the boundaries is $\psi_{\text{dil}} = 0.05$. The overall $\langle\phi\rangle$ is conserved due to no-flux boundary conditions. (d) Condensate location as quantified by the average distance from the bottom-left corner $\langle r\rangle = \int \delta\phi(x, y)\sqrt{x^2 + y^2}\mathrm{d}x\mathrm{d}y / \int \delta\phi(x, y)\mathrm{d}x\mathrm{d}y$, where $\delta\phi = \phi - \phi_{\text{dil}}$. See the Supplemental Material [18] for details and simulation videos.

When the tubule is thin (compared to $V^{1/3}$, where V is the droplet volume), the droplet can adopt an axisymmetric barrel-like shape that wraps around the tubule. By contrast, the droplet can also wet only one side of the tubule and adopt an asymmetric clamshell-like shape when the tubule is thick [32–35]. Here, we focus on the former case, where the droplet is able to wrap around the tubule [Fig. 3(a)].

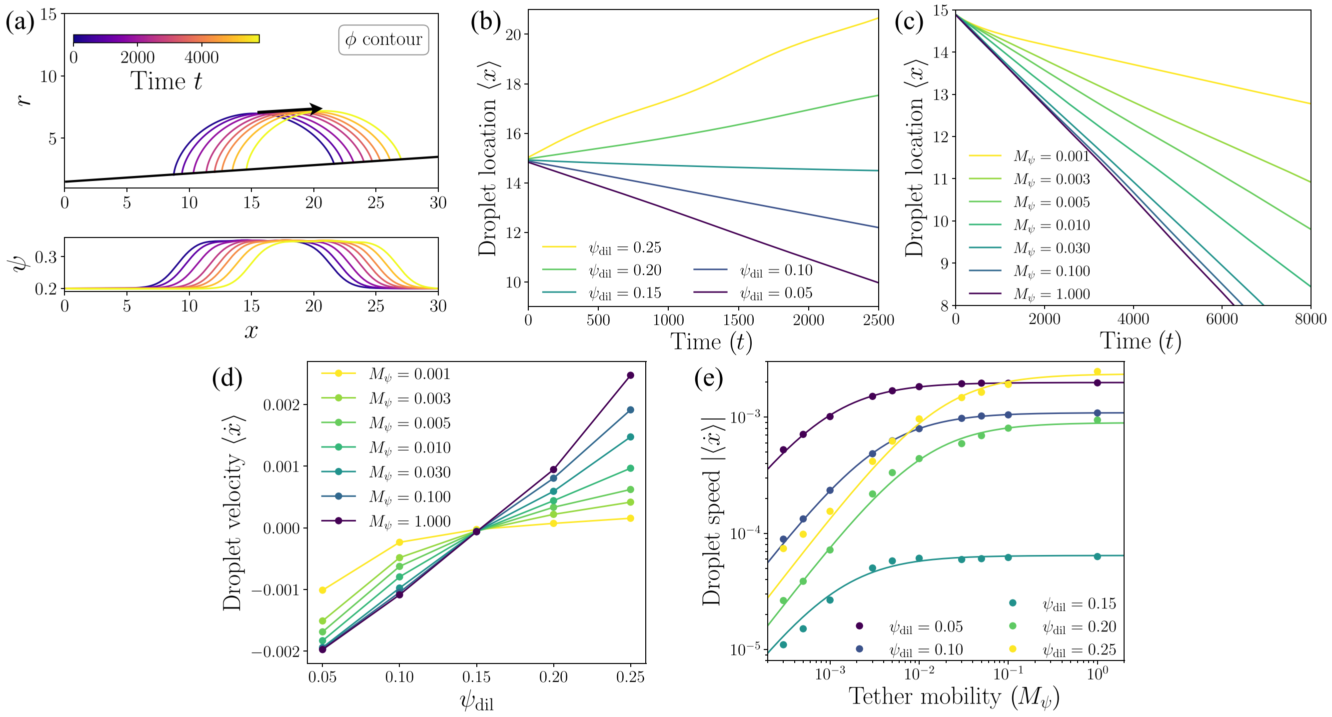

FIG. 3. Mobile tethers affect condensate migration on a tubule of varying radius. Here, we consider a (truncated) cone geometry where the tubule radius varies linearly along its long axis, although similar results hold for other geometries as well. (a) Time course of the condensate ϕ (top contours) and tether ψ (bottom) densities on a tubule of varying radius, in cylindrical coordinates (r, x) where x runs along the central axis of the tubule. Curves of different colors represent different times (inset legend), with the arrow indicating the direction of migration. The black line indicates the tubule surface. (b) and (c) Condensate location as quantified by the average position $\langle x\rangle$ for different tether concentrations ψ_{dil} for $M_\psi = 1.0$ (b) and different tether mobilities M_ψ for $\psi_{\text{dil}} = 0.10$ (c). (d) Migration velocity $\langle\dot{x}\rangle \equiv \frac{\mathrm{d}\langle x\rangle}{\mathrm{d}t}$ as a function of ψ_{dil} for different values of M_ψ. (e) Migration speed $|\langle\dot{x}\rangle|$ as a function of M_ψ for different concentrations of ψ_{dil}. Solid curves are fits to $|\langle\dot{x}\rangle| = (f_\phi + f_\psi/M_\psi)^{-1}$, with f_ϕ and f_ψ being fitting parameters. See the Supplemental Material [18] for details and parameters.

We expect such an axisymmetric droplet to migrate along the tubule, moving down the gradient of free energy until reaching a minimum-energy equilibrium position. The equilibrium location will depend on the contact angle θ, where a smaller θ (more wetting) favors regions of larger radius, and vice versa. By approximating the cross section of the barrel-shaped droplet as circular (see Sec. III of the Supplemental Material [18] for numerical justification), we find that the droplet always moves to the smallest radius for $\theta > \pi/2$, while for $\theta < \pi/2$ the droplet prefers a finite radius that scales as $r \sim V^{1/3} \cot\theta$ (see Sec. III of the Supplemental Material [18] for details). We note, however, that if $r/V^{1/3}$ is too large, the axisymmetric barrel becomes unstable and the droplet moves to wet only one side of the cylinder (clamshell shape) [32,35]. Nevertheless, for a droplet initialized on a relatively thin tubule, the contact angle θ dictates whether it initially moves to a small radius or a large radius.

Since the contact angle θ can be modulated by the tether abundance ψ_{dil} [Eq. (5), Fig. 1(d)], we expect that ψ_{dil} can affect the equilibrium location of the droplet on the tubule. Specifically, increasing the tether abundance ψ_{dil} decreases θ [Fig. 1(d)], thereby shifting the equilibrium location to a larger radius. Indeed, when we initialize a droplet at a particular location on the tubule, it migrates towards a small radius when ψ_{dil} is low (large θ), but towards a large radius when ψ_{dil} is high (small θ) [Fig. 3(b)]. Increasing tether mobility M_ψ leads to faster migration [Fig. 3(c)], while a very small M_ψ can lead to self-trapping, pinning the droplet and arresting migration.

These results suggest that tether abundance and mobility affect different aspects of droplet migration on spatially varying membrane structures: Tuning the tether abundance ψ_{dil} can modulate the total force on the droplet and control its preferred localization on the tubule, while tuning the tether mobility M_ψ can control droplet migration speed [Fig. 3(d)]. In the overdamped limit, the driving force due to the free-energy gradient (or equivalently, surface tension forces) is balanced by viscous drag from both the condensate and the tethers. Here, the drag is controlled by the mobility coefficients M_ϕ and M_ψ. Thus, the droplet velocity is given by

$$-\frac{\partial E}{\partial x} = \gamma_{\text{drag}}\dot{x} = \left(\gamma_\phi M_\phi^{-1} + \gamma_\psi M_\psi^{-1}\right)\dot{x}, \tag{7}$$

where the driving force $F_{\text{drive}} = -\partial_x E(x)$ is along the long axis of the tubule, where $E(x)$ is the total energy for the droplet at position x. The precise form of $E(x)$ is not needed for the analysis below, although it can be estimated by $E(V, r)$, which is the energy of a droplet of volume V wetting a tubule of local radius $r(x)$ (see Sec. III A of the Supplemental Material [18]). $\gamma_\phi M_\phi^{-1}$ and $\gamma_\psi M_\psi^{-1}$ represent the drag arising from diffusive transport of the condensate and the tethers, respectively (see Sec. III B of the Supplemental Material [18] for detailed derivation). Thus, droplet speed depends on tether mobility via an inverse linear relationship, $|\dot{x}| = (f_\phi + f_\psi/M_\psi)^{-1}$, with $f_\phi = \gamma_\phi M_\phi^{-1}/|\partial_x E|$ and $f_\psi = \gamma_\psi/|\partial_x E|$. This relation between $|\dot{x}|$ and M_ψ is in good agreement with numerical simulations [Fig. 3(e), with f_ψ and f_ϕ as fitting parameters]. The ratio of coefficients $f_\psi/f_\phi = M_\phi\gamma_\psi/\gamma_\phi$ depends on tether concentrations ψ_{dil} and ψ_{den}. We estimate this ratio to be proportional to $\psi_{\text{dil}}(\psi_{\text{den}} - \psi_{\text{dil}})$, which is confirmed numerically by fitting $|\dot{x}|$ to obtain f_ψ and f_ϕ (see Sec. III B of the Supplemental Material [18] for details). In other words, tethers can slow down droplet migration if they cannot redistribute quickly enough to maintain an energetically favorable wetting configuration as the droplet moves. In the limit of immobile tethers ($M_\psi \to 0$), the droplet becomes trapped in place.

Taken together, our results show that mobile tethers provide a mechanism to control how condensates respond to membrane geometry by modulating both the condensate's favorable location and its migration speed.

III. DISCUSSION

Membrane proteins and specialized lipids play an important role in regulating membrane functions, including their interaction with biomolecular condensates. However, the mobility of tethering molecules within the membrane has been largely overlooked in previous studies of condensate wetting. Here, we develop a general theoretical framework for mobile-tether-mediated wetting and show that tethering molecules can substantially modulate both equilibrium and dynamical aspects of condensate wetting, including migration and localization. These results suggest potential mechanisms for cells to regulate condensate formation and organization via the expression of mobile tethering molecules.

Our theory is relevant for a wide range of biological systems, including the algal pyrenoid [13,14,36], focal adhesion proteins [37,38], T-cell activation [39], actin assembly [40], and potentially the organization of ER exit sites [41–43]. Since a modest tether density and per-tether binding energy (a few $k_{\text{B}}T$) would be sufficient to substantially affect wetting properties, it is plausible for cells to regulate a wide range of condensates via mobile tethering molecules. Experimentally perturbing tethering molecules in cells will provide valuable insights into their importance for these structures.

Besides providing insights into *in vivo* structures and functions, our framework also makes quantitative predictions that can be tested *in vitro*. One direct test would be to place fluorescently tagged tethering molecules in supported lipid bilayers and track the tether concentrations ψ_{dil} and ψ_{den} as the membrane is wetted by a condensate that is attracted to the tether molecule. Repeating such experiments at different tether concentrations ψ_{dil} would enable a quantitative test for the tether enrichment predicted by theory [Eq. (4) and Fig. 1(c)]. In addition, the contact angle can potentially be measured by confocal imaging and compared with theory [Eq. (5) and Fig. 1(d)].

While this work focuses on tether-mediated wetting of a fixed membrane, our framework can be extended to include effects such as membrane deformation [44–46] and active processes [47], such as post-translational modification upon wetting. An important extension is to take hydrodynamic coupling into account [48–50], for instance, by using model H [23] to describe condensate and tether dynamics. Another potential direction is to study the role of tethers in the prewetting regime, where a thin surface phase could emerge at concentrations below the binodal for bulk phase separation [51–54]. Going beyond deterministic field theories, it will be interesting to study how mobile tethers affect rare events such as nucleation [55]. In a biological context, it will also be interesting to study how tether-mediated wetting affects downstream signaling, which is often a nonequilibrium process [39,40,56–58]. It may also be rewarding to explore how tethers affect the way condensates navigate membrane structures with complex geometries, such as endoplasmic reticulum (connected sheets), mitochondria (cristae), and endosomes (tubulovesicular structures). Overall, our framework paves the way for the study of how mobile-tether-mediated interactions affect condensate morphology, dynamics, and function.

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DATA AVAILABILITY

The data that support the findings of this article are openly available [59].

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Supplemental Material: Membrane-anchored mobile tethers modulate condensate wetting, localization, and migration

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CONTENTS

I. THEORETICAL FRAMEWORK

A. Model

As discussed in the main text, we consider a system where (three-dimensional) biomolecular condensates can interact with a (two-dimensional) membrane. The total free energy reads:

$$\beta F = c_{\psi,0} \int \mathrm{d}A \left[f_\psi(\psi) + \frac{\lambda_\psi}{2}(\nabla\psi)^2 - E(\psi, \phi|_{\mathrm{surf}}) \right] + c_{\phi,0} \int \mathrm{d}V \left[f_\phi(\phi) + \frac{\lambda_\phi}{2}(\nabla\phi)^2 \right], \tag{S1}$$

where ϕ is the condensate density field and ψ is the tether density field. The first integral is over the membrane area, while the second integral is over the bulk volume. $f_\phi(\phi)$ and $f_\psi(\psi)$ are the free-energy densities of the condensate and tethers, respectively; $E(\psi, \phi|_{\mathrm{surf}})$ describes the interaction energy between the condensate and the tether/membrane, with $\phi|_{\mathrm{surf}}$ denoting the condensate density at the membrane surface. λ_ψ and λ_ϕ are related to the line/surface tensions. The free energy is measured in units of $\beta^{-1} = k_{\mathrm{B}}T$. While the model can be used to describe a large class of systems by allowing the free-energy densities $f_\phi(\phi)$ and $f_\psi(\psi)$ and the interaction energy $E(\psi, \phi|_{\mathrm{surf}})$ to take different forms, we will focus on a minimal model to illustrate the essential physical picture.

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The tether and condensate fields evolve following gradient (model-B) dynamics that minimize the free energy [1]:

$$\partial_t\psi = \nabla\cdot(M_\psi\nabla\mu_\psi),\quad \partial_t\phi = \nabla\cdot(M_\phi\nabla\mu_\phi), \tag{S2}$$

where M_ψ and M_ϕ are mobility coefficients, while $\mu_\psi = \delta F/\delta\psi$ and $\mu_\phi = \delta F/\delta\phi$ are the chemical potentials of the tethers and condensate, respectively. The condensate obeys no-flux boundary condition at the membrane surface:

$$\hat{n}\cdot\nabla\mu_\phi = 0, \tag{S3}$$

where $\hat{n}$ is the unit normal vector pointing out of the membrane. Additionally, the bulk-surface interaction gives the following wetting boundary condition:

$$\lambda_\phi\hat{n}\cdot\nabla\phi|_{\mathrm{surf}} = -\partial_\phi E(\psi,\phi|_{\mathrm{surf}})\cdot\frac{c_{\psi,0}}{c_{\phi,0}}, \tag{S4}$$

which reflects a local change in condensate concentration near the membrane surface due to the condensate's interaction with the membrane and tethers. Briefly, this can be derived by taking the variation of the total free energy and collecting terms that involve the condensate concentration at the surface, $\phi|_{\mathrm{surf}}$:

$$\beta\delta F \sim -c_{\psi,0}\int \mathrm{d}A\,\partial_\phi E(\psi,\phi|_{\mathrm{surf}})\delta\phi|_{\mathrm{surf}} + c_{\phi,0}\int \mathrm{d}V\,\left[f_\phi'(\phi)\delta\phi + \lambda_\phi\nabla\phi\cdot\nabla\delta\phi\right] + \cdots, \tag{S5}$$

$$\sim -c_{\psi,0}\int \mathrm{d}A\,\partial_\phi E(\psi,\phi|_{\mathrm{surf}})\delta\phi|_{\mathrm{surf}} - c_{\phi,0}\int \mathrm{d}A\,\lambda_\phi\hat{n}\cdot\nabla\phi|_{\mathrm{surf}}\delta\phi|_{\mathrm{surf}} + \cdots, \tag{S6}$$

where $\cdots$ contains terms that do not involve $\delta\phi|_{\mathrm{surf}}$. The second line is obtained by integrating the $\nabla\phi\cdot\nabla\delta\phi$ term by parts and lumping the volume integral term into $\cdots$ since they do not involve $\delta\phi|_{\mathrm{surf}}$. The minus sign is because the normal vector $\hat{n}$ is defined to point out of the membrane/into the condensate. Setting the coefficient of $\delta\phi|_{\mathrm{surf}}$ to zero gives the wetting boundary condition Eq. (S4).

Without loss of generality, we perform the following non-dimensionalization: length is rescaled by l_0, time is rescaled by t_0, and energy is rescaled by E_0. The non-dimensionalized free energy reads:

$$\tilde{F} = \frac{F}{E_0} = \frac{k_{\mathrm{B}}Tl_0^2c_{\psi,0}}{E_0}\int \mathrm{d}\tilde{A}\left[f_\psi(\psi) + \frac{\tilde{\lambda}_\psi}{2}\left(\tilde{\nabla}\psi\right)^2 - E(\psi,\phi|_{\mathrm{surf}})\right] + \frac{k_{\mathrm{B}}Tl_0^3c_{\phi,0}}{E_0}\int \mathrm{d}\tilde{V}\left[f_\phi(\phi) + \frac{\tilde{\lambda}_\phi}{2}(\tilde{\nabla}\phi)^2\right], \tag{S7}$$

where $\tilde{\nabla} = \partial_{\tilde{x}} = l_0\nabla$, $\tilde{\lambda}_* = \lambda_*/l_0^2$, with $* \in \{\phi,\psi\}$. f and E do not need to be rescaled because they already represent the per-concentration energy densities. The non-dimensionalized dynamical equations read:

$$\partial_{\tilde{t}}\psi = \tilde{\nabla}\cdot\left(\tilde{M}_\psi\tilde{\nabla}\tilde{\mu}_\psi\right),\quad \partial_{\tilde{t}}\phi = \tilde{\nabla}\cdot\left(\tilde{M}_\phi\tilde{\nabla}\tilde{\mu}_\phi\right), \tag{S8}$$

where $\tilde{M}_* = M_*t_0E_0/l_0^2$ with $* \in \{\phi,\psi\}$ is the non-dimensionalized mobility coefficient, and $\tilde{\mu}_* = \partial_*\tilde{F}$ is the non-dimensionalized chemical potential. The wetting boundary condition is also non-dimensionalized:

$$\tilde{\lambda}_\phi\hat{n}\cdot\tilde{\nabla}\phi|_{\mathrm{surf}} = -\partial_\phi E(\psi,\phi|_{\mathrm{surf}})\cdot\frac{c_{\psi,0}}{c_{\phi,0}l_0}. \tag{S9}$$

Without loss of generality, we consider the following non-dimensionalization:

$$l_0 = c_{\psi,0}/c_{\phi,0},\quad E_0 = c_{\phi,0}k_{\mathrm{B}}Tl_0^3,\quad t_0 = l_0^2/(M_\phi E_0). \tag{S10}$$

The first two conditions remove the coefficients in total free energy: $\frac{k_{\mathrm{B}}Tl_0^2c_{\psi,0}}{E_0} = 1$ and $\frac{k_{\mathrm{B}}Tl_0^3c_{\phi,0}}{E_0} = 1$; the coefficient in the wetting boundary condition is also removed: $\frac{c_{\psi,0}}{c_{\phi,0}l_0} = 1$. The last condition sets the rescaled condensate mobility $\tilde{M}_\phi = 1$.

To summarize the non-dimensionalized system, omitting the ˜ notation for the sake of simplicity:

$$F = \int \mathrm{d}A\left[f_\psi(\psi) + \frac{\lambda_\psi}{2}(\nabla\psi)^2 - E(\psi,\phi|_{\mathrm{surf}})\right] + \int \mathrm{d}V\left[f_\phi(\phi) + \frac{\lambda_\phi}{2}(\nabla\phi)^2\right], \tag{S11}$$

$$\partial_t\psi = \nabla\cdot(M_\psi\nabla\mu_\psi),\quad \partial_t\phi = \nabla^2\mu_\phi, \tag{S12}$$

$$\lambda_\phi\hat{n}\cdot\nabla\phi|_{\mathrm{surf}} = -\partial_\phi E(\psi,\phi|_{\mathrm{surf}}),\quad \hat{n}\cdot\nabla\mu_\phi = 0. \tag{S13}$$

Eqs. (S11), (S12), and (S13) are the non-dimensionalized system that we will study hereafter (and for most of the main text). The only place where we need to explicitly consider dimensionality is for estimating the energy scales for real tethers (see the last paragraph of Section II.B in the main text, and Section II in the Supplementary Material).

B. Derivation for tether-mediated enrichment and wetting

For the sake of simplicity, we use Flory-Huggins free-energy densities for both the condensate and the tethers

$$f_\psi(\psi) = \psi \ln \psi + (1-\psi)\ln(1-\psi) + \chi_\psi \psi(1-\psi), \tag{S14}$$

$$f_\phi(\phi) = \phi \ln \phi + (1-\phi)\ln(1-\phi) + \chi_\phi \phi(1-\phi), \tag{S15}$$

with ψ and ϕ denoting the area or volume fraction of tether and condensate, respectively. χ_ψ and χ_ϕ are the Flory-Huggins interaction parameters for the tether and the condensate, respectively.

We further assume a linear interaction energy (non-dimensionalized in the same way as f_ψ)

$$E(\psi,\phi) = (h_0 + h_1\psi)\phi, \tag{S16}$$

where h_0 and h_1 describe condensate-membrane and condensate-tether interactions, respectively. The chemical potentials are given by:

$$\mu_\psi = \frac{\delta F}{\delta \psi} = \ln\frac{\psi}{1-\psi} + \chi_\psi(1-2\psi) - \lambda_\psi \nabla^2\psi - h_1\phi|_{z=0}, \tag{S17}$$

$$\mu_\phi = \frac{\delta F}{\delta \phi} = \ln\frac{\phi}{1-\phi} + \chi_\phi(1-2\phi) - \lambda_\phi \nabla^2\phi, \tag{S18}$$

where z is the perpendicular distance from the membrane, with $z=0$ indicating the membrane surface.

a. Tether enrichment. Let ϕ_{den} and ϕ_{dil} denote condensate densities in the dense phase and the dilute phase, respectively. The corresponding tether densities in the dense and dilute phases are denoted as ψ_{den} and ψ_{dil}. The tether chemical potential is balanced between these two homogeneous phases:

$$\mu_\psi(\psi_{\mathrm{den}}, \phi_{\mathrm{den}}) = \mu_\psi(\psi_{\mathrm{dil}}, \phi_{\mathrm{dil}}) \tag{S19}$$

$$\Rightarrow \quad \ln\frac{\psi_{\mathrm{den}}}{1-\psi_{\mathrm{den}}} - h_1\phi_{\mathrm{den}}|_{z=0} - 2\chi_\psi\psi_{\mathrm{den}} = \ln\frac{\psi_{\mathrm{dil}}}{1-\psi_{\mathrm{dil}}} - h_1\phi_{\mathrm{dil}}|_{z=0} - 2\chi_\psi\psi_{\mathrm{dil}}. \tag{S20}$$

Approximating the surface density $\phi|_{z=0}$ with the bulk binodal values[1], we have [Eq. (3) in the main text]:

$$\ln\frac{\psi_{\mathrm{den}}}{1-\psi_{\mathrm{den}}} = \ln\frac{\psi_{\mathrm{dil}}}{1-\psi_{\mathrm{dil}}} + h_1\Delta\phi + 2\chi_\psi(\psi_{\mathrm{den}} - \psi_{\mathrm{dil}}), \tag{S21}$$

where $\Delta\phi = \phi_{\mathrm{den}}|_{z=0} - \phi_{\mathrm{dil}}|_{z=0} \approx \phi_{\mathrm{den}} - \phi_{\mathrm{dil}}$ is the difference between binodal concentrations.

In the limit of purely entropic tethers ($\chi_\psi = 0$), ψ_{den} can be solved for analytically:

$$\psi_{\mathrm{den}} = \frac{\psi_{\mathrm{dil}} e^{h_1\Delta\phi}}{1 + \psi_{\mathrm{dil}}(e^{h_1\Delta\phi} - 1)}, \tag{S22}$$

which is Eq. (4) in the main text. For $\chi_\psi \neq 0$, ψ_{den} can be solved for numerically. These results describe tether enrichment in the condensate during its wetting.

b. Wetting properties. The contact angle θ is given by force balance at the three-phase junction:

$$\sigma_{\mathrm{den,dil}} \cos\theta = \sigma_{\mathrm{mem,dil}} - \sigma_{\mathrm{mem,den}} \equiv \Delta\sigma, \tag{S23}$$

where the σs represent surface tensions. $\sigma_{\mathrm{den,dil}}$ is the surface tension between the dense and dilute phases in 3D and is independent of the tether concentration. The surface tension with the membrane is $\sigma_{\mathrm{mem},*}$, with $* \in \{\mathrm{den}, \mathrm{dil}\}$ denoting the dense or dilute phase, respectively. They are given by computing the excess free energy per unit area:

$$\sigma_{\mathrm{mem},*} = f_\psi(\psi_*) - E(\psi_*, \phi_*|_{z=0}) - \mu_\psi(\psi_*, \phi_*|_{z=0})\psi_* + \Delta f_{\mathrm{excess}}(\psi_*, \phi_*) \equiv \tilde{\sigma}_{s*} + \Delta f_{\mathrm{excess}}(\psi_*, \phi_*), \tag{S24}$$

with $* \in \{\mathrm{den}, \mathrm{dil}\}$. $\mu_\psi(\psi_*, \phi_*|_{z=0}) = \ln\frac{\psi_*}{1-\psi_*} + \chi_\psi(1-2\psi_*) - h_1\phi_*|_{z=0}$ is the tether chemical potential. $\Delta f_{\mathrm{excess}}(\psi_*, \phi_*)$ is defined below and will prove to be higher order in h_0 and h_1. We define $\tilde{\sigma}_{\mathrm{mem},*}$ to be the sum of the first three

---

[1] The correction due to this approximation is $\mathcal{O}(h_0^2, h_1^2)$, which, as shown below, is a higher-order term.

terms, which is given by

$$\begin{aligned}\tilde{\sigma}_{\mathrm{mem},*} =& f_\psi(\psi_*) - E(\psi_*, \phi_*|_{z=0}) - \mu_\psi(\psi_*, \phi_*|_{z=0})\psi_* \\ =& \psi_* \ln \psi_* + (1-\psi_*)\ln(1-\psi_*) + \chi_\psi \psi_*(1-\psi_*) - (h_0 + h_1\psi_*)\phi_* - \psi_* \left(\ln \frac{\psi_*}{1-\psi_*} + \chi_\psi(1-2\psi_*) - h_1\phi_* \right) \\ =& \ln(1-\psi_*) + \chi_\psi \psi_*^2 - h_0\phi_*. \end{aligned} \tag{S25}$$

The surface tension difference due to these terms reads

$$\Delta\tilde{\sigma} \equiv \tilde{\sigma}_{\mathrm{mem,dil}} - \tilde{\sigma}_{\mathrm{mem,den}} = h_0(\phi_{\mathrm{den}} - \phi_{\mathrm{dil}}) + \ln \frac{1-\psi_{\mathrm{dil}}}{1-\psi_{\mathrm{den}}} - \chi_\psi(\psi_{\mathrm{den}}^2 - \psi_{\mathrm{dil}}^2) \equiv \Delta\sigma_0 + \Delta\sigma_1, \tag{S26}$$

where $\Delta\sigma_0 = h_0(\phi_{\mathrm{den}} - \phi_{\mathrm{dil}}) = h_0\Delta\phi$ is the surface tension difference in the absence of tethers, and $\Delta\sigma_1 = \ln \frac{1-\psi_{\mathrm{dil}}}{1-\psi_{\mathrm{den}}} - \chi_\psi(\psi_{\mathrm{den}}^2 - \psi_{\mathrm{dil}}^2)$ is the additional surface tension difference due to mobile tethers. Note that to the leading order, we have $\Delta\tilde{\sigma} = \mathcal{O}(h_0, h_1)$.

$\Delta f_{\mathrm{excess}}(\psi_*, \phi_*|_{z=0})$ is the excess free-energy density due to a boundary layer of condensate at the membrane surface. Let $\hat{\phi}_*(z)$ denote the condensate concentration at distance z from the membrane in the dense ($* = \mathrm{den}$) and dilute ($* = \mathrm{dil}$) phases. Near the membrane, $\hat{\phi}_*(z)$ deviate from the binodal concentrations ϕ_*, leading to excess free energy per surface area:

$$\Delta f_{\mathrm{excess}}(\psi_*, \phi_*) = \int \mathrm{d}z_1 \left[g_\phi(\hat{\phi}_*(z_1)) + \frac{\lambda_\phi}{2}(\partial_z \hat{\phi}_*(z_1))^2 - g_\phi(\phi_*) \right], \tag{S27}$$

where ϕ_* denotes the binodal concentration, and $g_\phi(\phi) = f_\phi(\phi) - \mu_\phi \phi$ is the Gibbs free energy of the condensate. The concentration profile $\hat{\phi}_*(z_1)$ is the solution to the following boundary value problem:

$$\partial_z \mu_{\hat{\phi}}(z) = 0, \quad z > 0, \tag{S28}$$

$$\lambda_\phi \partial_z \hat{\phi}_*(z) = -(h_0 + h_1\psi_*), \quad z = 0, \tag{S29}$$

$$\lim_{z\to\infty} \hat{\phi}_*(z) = \phi_*. \tag{S30}$$

In practice, we find that the excess free energy density is negligible compared to the other terms. This can be explained by the following scaling argument: To the leading order in $\delta\phi_*(z) = \hat{\phi}_*(z) - \phi_*$, the excess free energy is

$$\Delta f_{\mathrm{excess}} \sim \frac{\Delta z}{2} \cdot \left[\lambda_\phi \delta\phi_*'(z)^2 + g''(\phi)\delta\phi_*(z)^2 \right] = \mathcal{O}(\delta\phi_*^2), \tag{S31}$$

where Δz is the boundary layer thickness, and we have used $g'(\phi) = 0$ at the binodal concentration. From the wetting condition [Eq. (S29)], we find $\delta\phi_* = \mathcal{O}(h_0, h_1)$. Hence, the excess free energy becomes quadratic in the interaction parameters:

$$\Delta f_{\mathrm{excess}} = \mathcal{O}\big(h_0^2, h_1^2\big), \tag{S32}$$

which is a higher-order term compared to $\Delta\tilde{\sigma}$.

In summary, to the leading order of $\mathcal{O}(h_0, h_1)$, the contact angle is given by

$$\cos\theta = \frac{\sigma_{\mathrm{mem,dil}} - \sigma_{\mathrm{mem,den}}}{\sigma_{\mathrm{den,dil}}} \approx \frac{\Delta\tilde{\sigma}}{\sigma_{\mathrm{den,dil}}} = \frac{\Delta\sigma_0 + \Delta\sigma_1}{\sigma_{\mathrm{den,dil}}}, \tag{S33}$$

where $\Delta\sigma_0 = h_0(\phi_{\mathrm{den}} - \phi_{\mathrm{dil}}) = h_0\Delta\phi$ is the surface tension difference in the absence of tethers, and $\Delta\sigma_1 = \ln \frac{1-\psi_{\mathrm{dil}}}{1-\psi_{\mathrm{den}}} - \chi_\psi(\psi_{\mathrm{den}}^2 - \psi_{\mathrm{dil}}^2)$ is the additional surface tension difference due to mobile tethers. This produces Eq. (5) in the main text.

c. Wetting with purely entropic tethers. In the limit of purely entropic tethers ($\chi_\psi = 0$), we can substitute ψ_{den} with Eq. (S22) to get a simplified expression for $\Delta\sigma_1$:

$$\Delta\sigma_1 = \ln\left[1 + \psi_{\mathrm{dil}}(e^{h_1\Delta\phi} - 1)\right], \tag{S34}$$

which produces Eq. (6) in the main text. The contact angle simplifies to

$$\cos\theta = \frac{h_0(\phi_{\mathrm{den}} - \phi_{\mathrm{dil}}) + \ln\left[1 + \psi_{\mathrm{dil}}(e^{h_1\Delta\phi} - 1)\right]}{\sigma_{\mathrm{den,dil}}}. \tag{S35}$$

To achieve complete wetting ($\cos\theta = 1$), the critical tether density $\psi_{\mathrm{dil}}^\star$ is given by

$$\sigma_{\mathrm{den,dil}} = h_0\Delta\phi + \ln\left[1 + \psi_{\mathrm{dil}}^\star(e^{h_1\Delta\phi} - 1)\right] \Rightarrow \psi_{\mathrm{dil}}^\star = \frac{e^{\sigma_{\mathrm{den,dil}} - h_0\Delta\phi} - 1}{e^{h_1\Delta\phi} - 1}. \tag{S36}$$

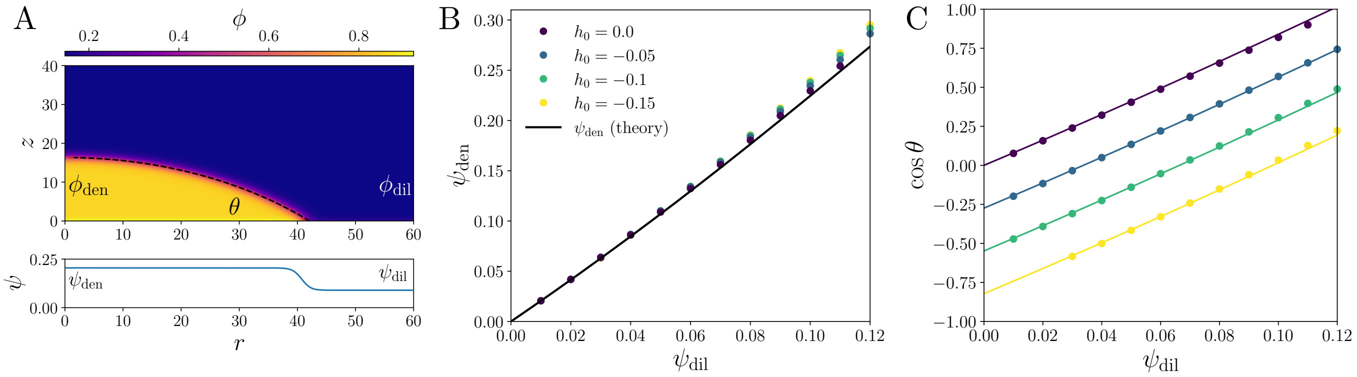

FIG. S1. Condensate wetting of membranes mediated by mobile tethers with $\chi_\psi = 1$ and $\lambda_\psi = 1$; all the other parameters are identical to Fig. 1 in the main text. (A) A typical equilibrium concentration profile obtained from numerical simulations. The condensate field ϕ (top) and tether field ψ (bottom) are plotted in cylindrical coordinates (r, z) with axial symmetry. The membrane is flat at $z = 0$. The black dashed curve is a spherical cap fit to the condensate surface contour. Parameters: $h_0 = 0$, $\psi_{\rm dil} = 0.09$. (B) Condensate-enriched tether concentration $\psi_{\rm den}$ increases with bulk tether concentration $\psi_{\rm dil}$, for different condensate-membrane interactions h_0, consistent with theory [solid curve, by numerically solving Eq. (S21) for $\psi_{\rm den}$]. (C) Contact angle $\cos\theta$ as a function of tether concentration $\psi_{\rm dil}$ for different h_0 (see legend in B) agrees well with theory [solid curves, Eq. (S33)].

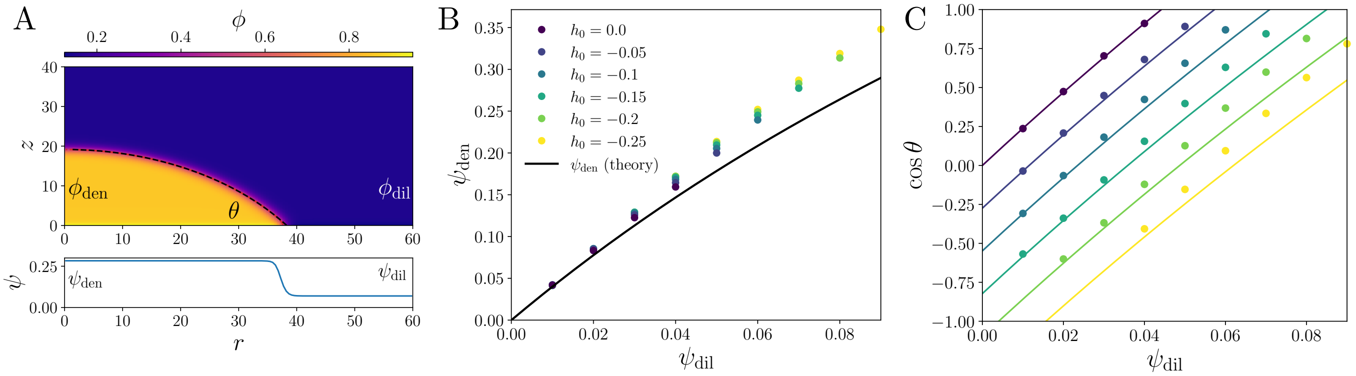

FIG. S2. Tether-mediated condensate wetting with a stronger tether-condensate interaction strength ($h_1 = 2.0$; all the other parameters are identical to Fig. 1 in the main text). (A) A typical equilibrium concentration profile obtained from numerical simulations (see Fig. S1A caption for a detailed description) for $h_0 = -0.2$ and $\psi_{\rm dil} = 0.07$. (B) Condensate-enriched tether concentration $\psi_{\rm den}$ increases with bulk tether concentration $\psi_{\rm dil}$, for different condensate-membrane interactions h_0, compared with theory [solid curve, Eq. (S22)]. (C) Contact angle $\cos\theta$ as a function of tether concentration $\psi_{\rm dil}$ for different h_0 (see legend in B) agrees well with theory [solid curves, Eq. (S35)]. Note that since the theory is only to the leading order $\mathcal{O}(h_0, h_1)$, it becomes less accurate at large h and $\psi_{\rm dil}$.

C. Generality of the results: Additional numerical simulations

Fig. 1 in the main text demonstrates good agreement between theory and numerical simulation of the full model. To illustrate the physical picture, it focuses on the simplest case of Flory-Huggins free energy, purely entropic tethers ($\chi_\psi = 0$ and $\lambda_\psi = 0$), and tether-condensate interaction strength $h_1 = 1$. Here, we demonstrate that our results are general and not sensitive to the specific choices of parameters or functional forms of the free energy.

1. *Allowing $\chi_\psi \neq 0$ for tethers*

In the main text, we focus on the case of purely entropic tethers ($\chi_\psi = 0$) to take advantage of analytical tractability [Eqs. (S22) and (S35)] to illustrate the physical picture. However, our analysis is also valid for $\chi_\psi \neq 0$, which describes an energetic cost of mixing in the membrane. The only difference is that the tether enrichment and contact angle need to be determined numerically from Eqs. (S21) and (S33), respectively. Fig. S1 shows the comparison for $\chi_\psi = 1.0$

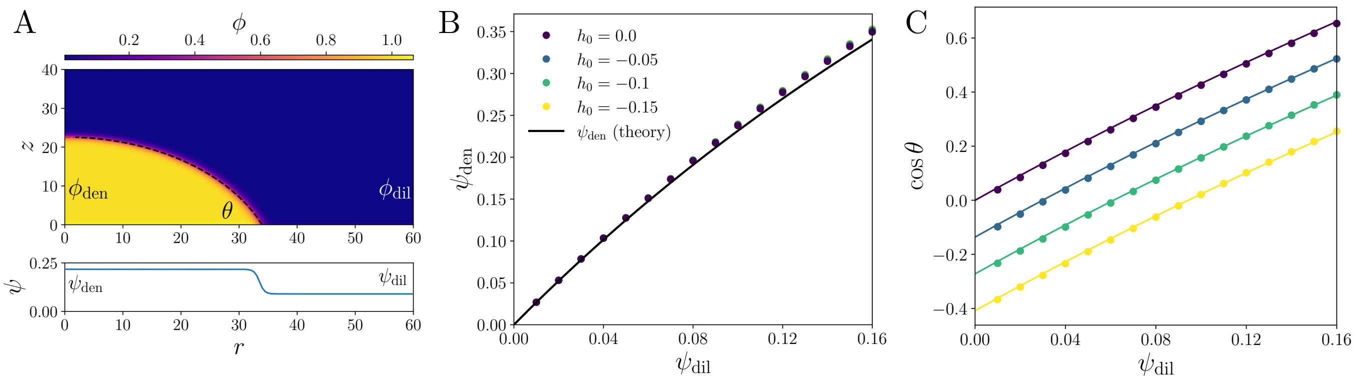

FIG. S3. Tether-mediated condensate wetting with a ϕ^4 free energy density for the condensate [Eq. (S37)]. $\chi_\psi = 2.5$ and all the other parameters are identical to Fig. 1 in the main text. (A) A typical equilibrium concentration profile obtained from numerical simulations (see Fig. S1A caption for a detailed description) for $h_0 = 0$ and $\psi_{\rm dil} = 0.09$. (B) Condensate-enriched tether concentration $\psi_{\rm den}$ increases with bulk tether concentration $\psi_{\rm dil}$, for different condensate-membrane interactions h_0, compared with theory [solid curve, Eq. (S22)]. (C) Contact angle $\cos\theta$ as a function of tether concentration $\psi_{\rm dil}$ for different h_0 (see legend in B) agrees well with theory [solid curves, Eq. (S35)].

and $\lambda_\psi = 1.0$. The theory accurately captures tether enrichment (Fig. S1B) and contact angle (Fig. S1C) for a wide range of h_0 and $\psi_{\rm dil}$.

2. *Varying the tether-condensate interaction strength h_1.*

As mentioned above, our main results [Eqs. (S22) and (S35)] are derived to the leading order of $\mathcal{O}(h_0, h_1)$. This allowed us to approximate the difference in surface concentration with the difference between binodal concentrations, i.e. $\Delta\phi = \phi_{\rm den}|_{z=0} - \phi_{\rm dil}|_{z=0} \approx \phi_{\rm den} - \phi_{\rm dil}$ and to neglect $\Delta f_{\rm excess}$ when computing the surface tension difference $\Delta\sigma$. As the tether-condensate interaction strength h_1 increases, we expect a thin boundary layer to form near the membrane where the condensate is enriched compared to the bulk, with the level of enrichment differing between dense and dilute phases. This effect leads to an $\mathcal{O}(h_0^2, h_1^2)$ correction to our theory.

Fig. S2 shows the comparison between theory and simulation for $h_1 = 2.0$. As expected, increasing h_1 did not change the qualitative behavior of $\psi_{\rm den}$ and $\cos\theta$, but the quantitative agreement is less satisfactory compared to Fig. 1 in the main text ($h_1 = 1.0$).

3. *Varying the form of the free energy*

The analytical results [Eqs. (S22) and (S35)] are general and do not require assuming any functional form for the condensate free energy $f_\phi(\phi)$, which was not used in the derivation in Section I.B. To demonstrate this, we use a ϕ^4 double-well free-energy density for the condensate:

$$f_\phi(\phi) = \chi_\phi \phi^2 (1-\phi)^2, \tag{S37}$$

with tethers still described by a Flory-Huggins free energy. Our analytical results [Eqs. (S22) and (S35)] still hold, with the binodal concentrations $\phi_{\rm dil}$ and $\phi_{\rm den}$ obtained from a Maxwell common tangent construction of $f_\phi(\phi)$. Fig. S3 shows excellent agreement between theory and simulation.

II. ESTIMATING THE TETHER BINDING ENERGY REQUIRED TO DRIVE WETTING TRANSITION

Here, we estimate the value of $\Delta\sigma_0$, which is the dilute/dense phase surface tension difference due to the condensate-membrane interaction. Typically, a membrane would be slightly repulsive for a polymer condensate because being close to the membrane reduces the conformational entropy of the polymers. Thus, we can estimate the magnitude of this effect by considering polymer "blobs" close to the membrane. Each "blob" would contribute $1 k_{\rm B}T$, and the number of polymer “blobs” per unit area could be estimated by $1/R_g^2$ with R_g being the radius of gyration. For an intrinsically disordered protein (IDP) of length ~ 100 a.a., we estimate $R_g \sim 3\text{nm}$ [2], and therefore $1/R_g^2 \sim \mathcal{O}(10^{-1})\text{nm}^2$. Thus, the surface tension due to entropic repulsion is of the order $\Delta\sigma_0 \sim -\mathcal{O}(10^{-1})k_\text{B}T/\text{nm}^2$.

On the other hand, previous micropipette aspiration found that the typical biopolymer condensate surface tension $\sigma_\text{den,dil}$ is at most $\mathcal{O}(1)\text{mN/m}$, or equivalently $\mathcal{O}(10^{-1})k_\text{B}T/\text{nm}^2$ [3]. Thus, to achieve complete wetting, the additional surface tension difference due to tethers must also reach $\Delta\sigma_1 = \sigma_\text{den,dil} - \Delta\sigma_0 \sim \mathcal{O}(10^{-1})k_\text{B}T/\text{nm}^2$.

To estimate the corresponding binding energy relevant for real tethers, we recall that during non-dimensionalization, the surface tension was renormalized by $\frac{E_0}{l_0^2} = c_{\psi,0}k_\text{B}T$, with a close-packed tether density set by $c_{\psi,0}$. Thus, in the limit of dilute tethers $\psi_\text{dil} = n/c_{\psi,0} \ll 1$, where n is the (dimensional) tether density in contact with the dilute phase, we have

$$\frac{\Delta\sigma_1}{k_\text{B}T} = c_{\psi,0}\ln\left[1+\psi_\text{dil}(e^{h_1\Delta\phi}-1)\right] \approx c_{\psi,0}\psi_\text{dil}(e^{h_1\Delta\phi}-1) = n(e^{\epsilon}-1), \tag{S38}$$

where $n \sim 10^{-2}\text{nm}^2$ [4] is the dimensional tether number density, and $\epsilon = h_1\Delta\phi$ is the energy reduction per tether when inside the condensate, measured in units of $k_\text{B}T$. This leads to

$$\epsilon = \ln\left(1+\frac{\Delta\sigma_1}{c_\text{g}k_\text{B}T}\right) \sim \ln\left[1+\mathcal{O}(10)\right] \sim \mathcal{O}(1)\ (k_\text{B}T), \tag{S39}$$

which suggests that a binding energy of a few $k_\text{B}T$ per tether is sufficient to modulate equilibrium condensate-membrane wetting properties.

III. DROPLET MIGRATION ON A TUBULE OF VARYING RADIUS

A. Equilibrium position of a droplet

In this section, we consider the free energy of a droplet as it wets a membrane tubule in an axisymmetric configuration that wraps around the tubule. If the radius of the tubule is slow-varying compared to the droplet size, we can approximate the tubule locally as a cylinder of radius r (Fig. S4A). Thus, the free energy of the droplet $E(V,r)$ is determined by its volume V and the local tubule radius r.

The droplet adopts a barrel-shaped constant-mean-curvature surface when wetting the cylinder [5]. For analytical tractability and motivated by our numerical simulations (Fig. S4B), we approximate the cross-section profile as a circular cap (Fig. S4A). The radius R is determined by constraining the volume of the droplet:

$$V(R,r,\cos\theta) = \frac{1}{6}\pi R^2(12\theta r - 6r\sin 2\theta + 9R\sin\theta + R\sin 3\theta - 12\theta R\cos\theta), \tag{S40}$$

where θ is the contact angle. The total surface free energy is given by

$$\begin{aligned} E(R,r,\cos\theta) &= A_\text{mem,den}\sigma_\text{mem,den} + A_\text{mem,dil}\sigma_\text{mem,dil} + A_\text{den,dil}\sigma_\text{den,dil} && \text{(S41)}\\ &= (A_0 - A_\text{mem,den})\sigma_\text{mem,dil} + A_\text{mem,den}\sigma_\text{mem,den} + A_\text{den,dil}\sigma_\text{den,dil} && \text{(S42)}\\ &= E_0 + A_\text{mem,den}(\sigma_\text{mem,den} - \sigma_\text{mem,dil}) + A_\text{den,dil}\sigma_\text{den,dil} && \text{(S43)}\\ &= E_0 + \sigma_\text{den,dil}(A_\text{den,dil} - A_\text{mem,den}\cos\theta), && \text{(S44)} \end{aligned}$$

where A_0 is the total membrane area, $E_0 = A_0\sigma_\text{mem,dil}$, and $A_\text{mem,den}$, $A_\text{mem,dil}$, and $A_\text{den,dil}$ are the areas of the membrane-condensate, membrane-solvent, and condensate-solvent interfaces, respectively. The last line follows from the force balance at the three-phase junction [Eq. (S23)]. Applying our droplet shape ansatz, we have

$$E(R,r,\cos\theta) = 4\pi R(\theta r - \cos\theta(r\sin\theta + \theta R) + R\sin\theta). \tag{S45}$$

The equilibrium position of the droplet is determined by the r_eq that minimizes the free energy $E(V,r)$ for a fixed droplet volume V. The constrained optimization problem can be solved by introducing a Lagrange multiplier λ:

$$\mathcal{L}(R,r,\cos\theta,\lambda) = E(R,r,\cos\theta) - \lambda(V(R,r,\cos\theta) - V_0). \tag{S46}$$

The optimum is given by

$$\frac{\partial\mathcal{L}}{\partial R} = 0, \quad \frac{\partial\mathcal{L}}{\partial r} = 0, \quad V(R,r,\cos\theta) = V_0. \tag{S47}$$

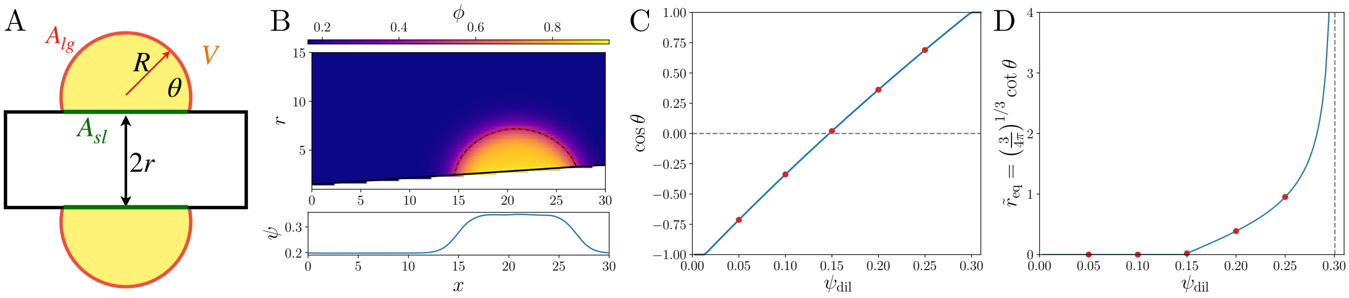

FIG. S4. Equilibrium position of a droplet on a tubule of varying radius. (A) Illustration of the ansatz used for computing the free energy of a droplet of volume V wetting a cylinder of radius r with contact angle θ. This is a cross-sectional view where the droplet assumes a circular cap shape with radius R. (B) Snapshot of the condensate profile ϕ (top) and tether profile ψ (bottom) for a droplet migrating on a tubule (membrane indicated by the black line) obtained from numerical simulation. The red dashed curve shows that a circular fit is in good agreement with the interface contour (black dashed curve). (C) Contact angle $\cos\theta$ as a function of tether density $\psi_{\rm dil}$. (D) Normalized equilibrium tubule radius $\tilde{r}_{\rm eq} \equiv r_{\rm eq}/V^{1/3}$ as a function of tether density $\psi_{\rm dil}$. In (C) and (D), blue curves are theoretical predictions [Eq. (S33)] and [Eq. (S49)]), and red data points simply indicate the theoretical predictions evaluated at the $\psi_{\rm dil}$ values used in Fig. 3 in the main text. In (D), the vertical dashed line indicates $\tilde{r}_{\rm eq} \to +\infty$ as $\theta \to 0$. Parameters: $h_0 = -0.2$, $h_1 = 1$, $\chi_\phi = 2.5$, $\lambda_\phi = 1$, $\chi_\psi = 0$, $\lambda_\psi = 0$. For (B), $\psi_{\rm dil} = 0.20$ and mobilities $M_\phi = 1.0$ and $M_\psi = 1.0$.

The solutions are:

$$\tilde{r} \equiv r/V^{1/3} = \left(\frac{3}{4\pi}\right)^{1/3} \cot\theta, \quad \tilde{R} \equiv R/V^{1/3} = \tilde{r}/\cos\theta = \left(\frac{3}{4\pi}\right)^{1/3} \csc\theta, \quad \lambda = \frac{2}{R}. \tag{S48}$$

Since the radius r must be positive, this solution is only physical for $\theta \in (0, \pi/2)$. For $\theta \in (\pi/2, \pi)$, the surface energy increases monotonically with r, and the droplet would prefer to reside at the smallest radius possible. Putting these results together, we arrive at the equilibrium radius of the tubule where the droplet prefers to locate:

$$r_{\rm eq} = \begin{cases} V^{1/3}\left(\frac{3}{4\pi}\right)^{1/3} \cot\theta, & \theta \in (0, \pi/2), \\ 0, & \theta \in (\pi/2, \pi). \end{cases} \tag{S49}$$

Hence, tuning tether abundance $\psi_{\rm dil}$ (and thus the contact angle θ) can control the equilibrium position of the droplet on a tubule of varying radius (Fig. S4C,D). Theoretical predictions for the $\psi_{\rm dil}$ values used in Fig. 3 in the main text are indicated by red data points: for $\psi_{\rm dil} = 0.05, 0.10$, the droplet moves to the left to decrease r; for $\psi_{\rm dil} = 0.15, 0.20, 0.25$, the droplet moves to the right to increase r.

B. Droplet migration velocity

As a droplet migrates on a tubule, its velocity $\dot{x}$ is determined by the balance between the driving force due to the surface energy gradient and the drag force:

$$F_{\rm drive} = -\frac{\partial E}{\partial x} = \gamma_{\rm drag}\dot{x} = (\gamma_\phi M_\phi^{-1} + \gamma_\psi M_\psi^{-1})\dot{x} = F_{\rm drag}, \tag{S50}$$

where $\gamma_{\rm drag}$ is the drag coefficient, which, as shown below, will be inversely proportional to the mobility coefficients M_ϕ and M_ψ of the condensate and tethers, respectively. γ_ϕ and γ_ψ are constants that depend on the concentration profile of the condensate and tethers, respectively, which will be derived below.

As derived in the previous section $E(V, r)$ depends on both the droplet volume V and the local tubule radius r, which gives the driving force $F_{\rm drive} = -\frac{\partial E}{\partial x} = -\frac{\partial E}{\partial r}\frac{\partial r}{\partial x}$. The velocity $\dot{x}$ depends on M_ψ via an inverse linear relation:

$$\dot{x} = \left(f_\phi + f_\psi M_\psi^{-1}\right)^{-1}, \tag{S51}$$

where

$$f_\phi = \frac{\gamma_\phi}{M_\phi} \cdot \left(-\frac{\partial E}{\partial r}\frac{\partial r}{\partial x}\right), \quad f_\psi = \gamma_\psi \cdot \left(-\frac{\partial E}{\partial r}\frac{\partial r}{\partial x}\right). \tag{S52}$$

Estimating f_ϕ and f_ψ requires computing the drag coefficients γ_ϕ and γ_ψ, which we turn to next.

The drag coefficient is determined from the total dissipation:

$$P = \gamma \dot{x}^2 = \int \mathrm{d}V \, \frac{\left|\vec{J}_\phi\right|^2}{M_\phi} + \int \mathrm{d}A \, \frac{\left|\vec{J}_\psi\right|^2}{M_\psi} = \int \mathrm{d}V \, M_\phi |\nabla \mu_\phi|^2 + \int \mathrm{d}A \, M_\psi |\nabla \mu_\psi|^2, \tag{S53}$$

where $\vec{J}_\phi = -M_\phi \nabla \mu_\phi$ and $\vec{J}_\psi = -M_\psi \nabla \mu_\psi$ are the fluxes of the condensate and tethers, respectively. Further integrating by parts, we have

$$P = -\int \mathrm{d}V \, M_\phi \mu_\phi \nabla^2 \mu_\phi - \int \mathrm{d}A \, M_\psi \mu_\psi \nabla^2 \mu_\psi. \tag{S54}$$

For a traveling wave solution, we have $\partial_t \phi = -\dot{x}\partial_x \phi$ and $\partial_t \psi = -\dot{x}\partial_x \psi$. Thus, their (model B) dynamics satisfy

$$\partial_t \psi = -\dot{x}\partial_x \psi = M_\psi \nabla^2 \mu_\psi, \quad \partial_t \phi = -\dot{x}\partial_x \phi = M_\phi \nabla^2 \mu_\phi. \tag{S55}$$

$\mu_{\phi,\psi}$ are solutions to Poisson equations with source terms $-\dot{x}\partial_x \phi / M_\phi$ and $-\dot{x}\partial_x \psi / M_\psi$, respectively. We can rescale the chemical potentials by the strength of the source:

$$\mu_\phi = \frac{\dot{x}}{M_\phi} \tilde{\mu}_\phi, \quad \mu_\psi = \frac{\dot{x}}{M_\psi} \tilde{\mu}_\psi, \tag{S56}$$

where $\tilde{\mu}_\phi$ and $\tilde{\mu}_\psi$ are solutions to the Poisson equations with unit source terms:

$$\nabla^2 \tilde{\mu}_\phi = -\partial_x \phi, \quad \nabla^2 \tilde{\mu}_\psi = -\partial_x \psi. \tag{S57}$$

Substituting these back into the expression for P, we have

$$P = -\int \mathrm{d}V \, \dot{x}^2 M_\phi^{-1} \tilde{\mu}_\phi \nabla^2 \tilde{\mu}_\phi - \int \mathrm{d}A \, \dot{x}^2 M_\psi^{-1} \tilde{\mu}_\psi \nabla^2 \tilde{\mu}_\psi, \tag{S58}$$

$$= \dot{x}^2 \left(\int \mathrm{d}V \, M_\phi^{-1} \tilde{\mu}_\phi \partial_x \phi + \int \mathrm{d}A \, M_\psi^{-1} \tilde{\mu}_\psi \partial_x \psi \right) = \gamma_{\mathrm{drag}} \dot{x}^2, \tag{S59}$$

which gives the coefficients

$$\gamma_\phi = \int \mathrm{d}V \, \tilde{\mu}_\phi \partial_x \phi = \int \mathrm{d}V \, (-\partial_x \tilde{\mu}_\phi) \phi, \tag{S60}$$

$$\gamma_\psi = \int \mathrm{d}A \, \tilde{\mu}_\psi \partial_x \psi = \int \mathrm{d}A \, (-\partial_x \tilde{\mu}_\psi) \psi. \tag{S61}$$

Since the chemical potential gradients $-\partial_x \tilde{\mu}_{\phi,\psi}$ are non-zero only at the interface region, we estimate that $\gamma_{\phi,\psi}$ are proportional to the interface area/length as well as to the concentrations:

$$\gamma_\phi \sim A_{\mathrm{den,dil}} \cdot \frac{\Delta\phi}{\lambda_\phi} \phi_{\mathrm{den}}, \quad \gamma_\psi \sim L_{\mathrm{mem,den,dil}} \cdot \frac{\Delta\psi}{\lambda_\psi} \psi_{\mathrm{den}}, \tag{S62}$$

where $\Delta\phi$ and $\Delta\psi$ are the concentration differences across the interface, λ_ϕ and λ_ψ are the interface thicknesses, $A_{\mathrm{den,dil}}$ is the area of the condensate-solvent interface, and $L_{\mathrm{mem,den,dil}}$ is the length of the three-phase contact line.

Assuming that the geometry and the condensate concentrations difference $\Delta\phi$ remain approximately unchanged with varying M_ψ (which is valid for the simulations in Fig. 3E), the main effect of changing tether abundance ψ_{dil} should be due to the ψ dependence in γ_ψ. Thus, we estimate:

$$\frac{f_\psi}{f_\phi} = M_\phi \frac{\gamma_\psi}{\gamma_\phi} \propto (\psi_{\mathrm{den}} - \psi_{\mathrm{dil}}) \psi_{\mathrm{dil}}. \tag{S63}$$

This is consistent with our numerical results (Fig. S5), where we find a linear relation between f_ψ/f_ϕ and $(\psi_{\mathrm{den}} - \psi_{\mathrm{dil}})\psi_{\mathrm{dil}}$.

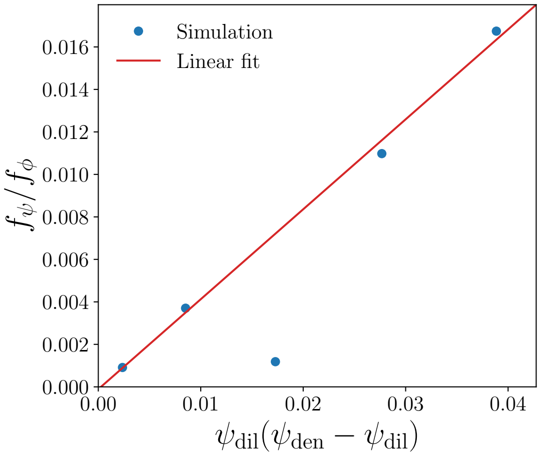

FIG. S5. Proportionality between f_ψ/f_ϕ and $(\psi_{\rm den}-\psi_{\rm dil})\psi_{\rm dil}$ [Eq. (S63)]. Blue circles are numerical results obtained from simulations in Fig. 3E, and the red line is a linear fit excluding the point at $\psi_{\rm dil}=0.15$, for which the droplet velocity is too small for an accurate estimate of the drag coefficients.

IV. DETAILS OF NUMERICAL SIMULATIONS

To solve the governing equations [Eqs. (S11), (S12), and (S13)] for the condensate and tethers, we use a finite-volume numerical scheme [6] with first-order forward Euler time-stepping for time evolution. The condensate field ϕ obeys no-flux boundary conditions at all boundaries in addition to wetting boundary conditions at membrane interfaces. The tether field ψ obeys Dirichlet boundary conditions with fixed bulk tether concentration $\psi_{\rm dil}$. The wetting boundary condition is prescribed using the ghost point method, where the ϕ value at each ghost point is interpolated from the two nearest interior points that are not collinear with the ghost point. The volumes near the boundary are treated with the cut-cell method. The implementation of cut-cell and ghost point methods was simplified from previous work [7–9].

For Fig. 1 (and Figs. S1, S2, and S3), the simulation is performed in cylindrical coordinates, with spatial discretization $r_n=\frac{nr_{\rm max}}{N}$, $z_m=\frac{mz_{\rm max}}{M}$, where $r_{\rm max}=60$ and $z_{\rm max}=40$ set the system size and $N=M=128$ set the spatial resolution. The simulation is run until the system reaches its equilibrium state. The contact angle is measured by fitting the contour to a spherical cap $R^2=r^2+(z-z_0)^2$, which gives $\cos\theta=-z_0/R_0$. $\sigma_{\rm den,dil}$ is evaluated from the phase field simulations by integrating the excess free energy density across a flat interface. The parameters for Fig. 1 are: $\chi_\phi=2.5$, $\lambda_\phi=1$, $\chi_\psi=0$, $\lambda_\psi=0$; $h_1=1$ for (B)–(D); $\psi_{\rm dil}=0.02$ and $h_0=0$ for (B); $h_0=-0.2$ for (E).

For Fig. 2, the simulation was performed in 2D planar coordinates, with spatial discretization $x_n=\frac{nx_{\rm max}}{N}$, $y_m=\frac{my_{\rm max}}{M}$ with $x_{\rm max}=y_{\rm max}=30$ and $N=M=64$. The parameters are: $h_0=-0.2$, $h_1=2$, $\chi_\phi=2.5$, $\lambda_\phi=1$, $\chi_\psi=0$, $\lambda_\psi=0$. Tether concentration is fixed at the boundary by Dirichlet boundary condition $\psi_{\rm dil}=0.05$. The videos for the dynamics are available as supplemental videos (`si_movie_1_M1.0.mp4` for $M_\psi=1.0$ and `si_movie_2_M0.1.mp4` for $M_\psi=0.1$).

To quantify how fast the droplet reaches its equilibrium configuration at the lower-left corner where the two membranes meet, we defined an average distance $\langle r\rangle=\int\delta\phi(x,y)\sqrt{x^2+y^2}\,{\rm d}x\,{\rm d}y\,/\int\delta\phi(x,y)\,{\rm d}x\,{\rm d}y$, where $\delta\phi=\phi-\phi_g$ is the condensate concentration subtracted by the dilute phase.

For Fig. 3 (and Figs. S4 and S5), the simulation was performed in cylindrical coordinates (r,x), where the x-axis runs along the center of the tubule. The tubule radius is given by $R(x)=R_0+R_1x$, with $R_0=1.5$ and $R_1=1/15$. Spatial discretization is given by $r_n=r_0+\frac{nr_{\rm max}}{N}$, $x_m=\frac{mx_{\rm max}}{M}$, where $r_0=1.0$, $r_{\rm max}=15$ and $x_{\rm max}=30$ set the system size and $N=64$ and $M=128$ set the spatial resolution. The equations are only evolved in grid points inside the domain $[r>R(x)]$ with wetting boundary conditions implemented by ghost points. The average position $\langle x\rangle$ is computed from the volume inside the contour $\phi>(\phi_{\rm den}+\phi_{\rm dil})/2$. Tether concentration is fixed at the boundary by Dirichlet boundary condition at the right boundary $(x=x_{\rm max})$. The parameters are: $h_0=-0.2$, $h_1=1$, $\chi_\phi=2.5$, $\lambda_\phi=1$, $\chi_\psi=0$, $\lambda_\psi=0$. For Fig. 3A, $\psi_{\rm dil}=0.20$ and $M_\psi=1.0$; for Fig. 3B, $M_\psi=1.0$; for Fig. 3C, $\psi_{\rm dil}=0.10$.

The simulations are performed in Python, with codes available at `https://github.com/qiweiyuu/tether`.

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