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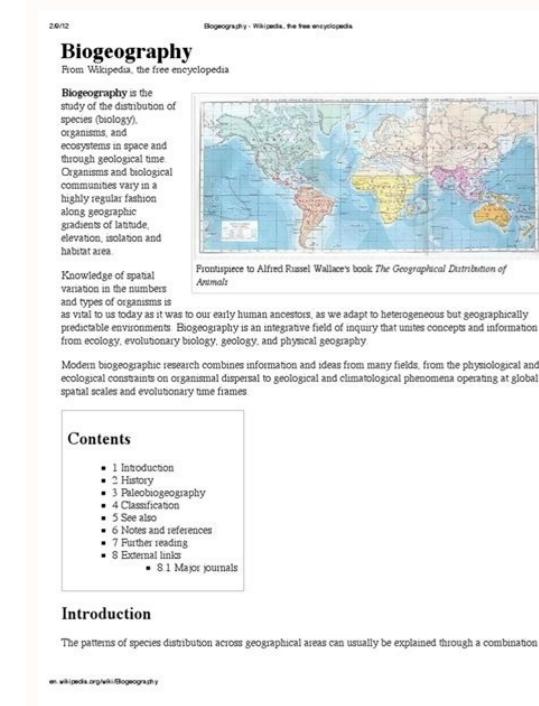


Figure 5d), revealing that this data analysis scheme is highly sensitive to receptor interaction. The $V(\overline{R_r^2})$ value of the correlated Qdot585-EGF-EGFRs is considerably lower in A431 cells, attributable to highly effective receptor-lipid and receptor-receptor interactions in A431 cells Turkcan et al. (2013). To inspect the nature of interactions and the relevance to receptor-induced lipid ordering, we again took advantages of the drug effects with nystatin and M β CD. Figure 6b and c display the MSD histograms of the correlated Qdot585-EGF-EGFRs. Pretreatment of HeLa cells with M β CD shifts the MSD profile of liganded EGFRs to the side of higher diffusion constant. M β CD treatment also broadens the MSD profile of liganded EGFRs in A431 cells. The $V(\overline{R_r^2})$ - $\overline{R_r^2}$ plots for the three cell lines pretreated with nystatin are presented in Figure 6(e). Correlated Qdot585-EGF-EGFRs appear to experience a weaker interaction in the nystatin-treated A431 cells, as evidenced by an increased $V(\overline{R_r^2})$ value. This observation may be explained with less stable lipid domain due to lower amount of cholesterol, resulting in larger variance of diffusing step size of the correlated receptors. By contrast, the effective interaction becomes stronger in nystatin-treated MCF-12A cells, suggesting the effect of cholesterol-mediated interaction is opposite to that of receptor-lipid interaction. The $V(\overline{R_r^2})$ of correlated Qdot585-EGF-EGFR in A431 increases by two orders of magnitude from 10^{-2} of native cells to 1 of M β CD treated cells. Noteworthy, the $V(\overline{R_r^2})$ value can be increased to higher than 10 in M β CD treated HeLa and MCF-12A cells, revealing that a deterministic dimerization interaction will dominate after membrane cholesterol is depleted. These observation results exhibit the vital role of membrane cholesterol in mediating the interaction between liganded receptors in the three cell lines under study.

4 Discussion

A receptor protein can induce order in the surrounding lipids through the receptor-lipid interaction Gómez-Llobregat et al. (2013). The degree of induced lipid order is determined by the effects of receptor-lipid interaction and the amount of cholesterol in the plasma membrane. Recent molecular dynamics (MD) simulations of human receptor tyrosine kinases in various lipid bilayers revealed that the predominant drivers of the receptor-induced lipid ordering domains may originate from electrostatic interactions between the anionic lipids and clustering basic residues in the juxtamembrane starting region of receptors "Hedger et al. (2015). Lipid domains had been predicted to exist in multicomponent membranes and experimentally observed on artificial membranes. For example, thermal fluctuations on a multicomponent membrane can produce inhomogeneities of lipid phases because the order parameters of lipid systems depend not only on the lipid composition but also on the compositional difference of two lipid leaves Shlomovitz et al. (2014). Coupling between inner and outer leaves of an asymmetric lipid bilayer could also produce



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