

<https://doi.org/10.1038/s44458-026-00070-6>

Lytic polysaccharide monooxygenases as global carbon cycle regulators and a lever to the bioeconomy



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Cellulose, hemicellulose, and chitin are Earth's most abundant biopolymers, yet their crystalline structure makes them highly recalcitrant, creating a bottleneck in the global carbon cycle and the bioeconomy. For decades, polysaccharide degradation strategies focussed exclusively on hydrolytic enzymes. This perspective synthesises breakthroughs, highlighting the discovery of lytic polysaccharide monooxygenases and providing a comprehensive framework to evaluate their global function. We chart the scientific evolution of these enzymes into powerful, context-dependent hydrogen peroxide-driven peroxygenases using an oxidative mechanism to disrupt crystalline surfaces. We argue this synergistic oxidative-hydrolytic strategy is nature's primary solution to the polysaccharide challenge. We propose two hypotheses: first, that lytic polysaccharide monooxygenases are critical gatekeepers of the carbon cycle in terrestrial and marine ecosystems; and second, that their oxidative chemistry can be engineered for broad frontiers, including advanced biorefineries and synthetic polymer degradation. Embracing this oxidative paradigm is essential for ecological understanding and architecting a circular economy.

Cellulose, hemicellulose, and chitin represent the planet's primary investment in structural biopolymers, collectively accounting for over 100 gigatons of carbon annually^{1,2}. This vast reservoir of polysaccharides can be conceptualised as the dark matter of the biosphere: An immense, yet largely inaccessible, repository of stored energy and fixed carbon that fundamentally governs the tempo of global carbon cycling³. Cellulose, the primary structural component of plant cell walls, is the most abundant organic polymer on Earth, closely followed by hemicelluloses, such as xylan, and chitin, the nitrogen-containing analogue found in fungal cell walls and arthropod exoskeletons, is a close second^{4,5}. The sheer scale of this biological infrastructure is staggering, yet its contribution to active metabolic pathways is profoundly limited by its inherent stability. This stability forms a critical bottleneck in natural ecosystems and presents a formidable challenge to the development of a sustainable bioeconomy.

The primary obstacle to unlocking this enormous resource lies in the crystalline nature of these polysaccharides. Individual glucan, xylan, or N-acetylglucosamine chains are assembled with remarkable precision into tightly packed, hydrogen-bonded microfibrils, creating a quasi-crystalline structure that is highly resistant to enzymatic or chemical attack^{6,7}. This recalcitrance is a defining feature of structural polysaccharides, ensuring the physical integrity of organisms from the smallest fungi to the largest trees.

However, it also means that the vast majority of carbon fixed within these polymers is effectively sequestered, slowing its return to the atmosphere and limiting the efficiency of biogeochemical cycles⁸. For decades, the prevailing paradigm for overcoming this barrier, both in nature and in industrial settings, has been centred exclusively on hydrolysis – the enzymatic or acidic cleavage of glycosidic bonds to release soluble sugars⁹. This approach has defined the field of carbohydrate chemistry and biotechnology, driving research into cellulases and chitinases as the sole molecular tools for polysaccharide degradation. However, historical accounts, such as the C1–Cx hypothesis by Reese et al. in the 1950s¹⁰ and later oxidative observations by Eriksson et al.¹¹, already hinted that hydrolysis alone could not explain the rapid degradation of crystalline substrates observed in nature.

This hydrolytic-centric view is now clearly evolving. While hydrolytic enzymes are undeniably crucial, a growing body of evidence suggests they do not act alone. The discovery and characterisation of lytic polysaccharide monooxygenases (LPMOs) have revealed an oxidative strategy for cleaving crystalline polysaccharides, a finding that has fundamentally reshaped our understanding of carbon cycling and enzymatic processing^{12,13}. These powerful copper-dependent enzymes work on the crystalline surface, introducing chain breaks that disrupt the structure and create new access points for canonical hydrolytic enzymes, acting in synergy to deconstruct

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what was once considered an impregnable barrier¹⁴. This paradigm shift raises a critical question: if nature's primary strategy for degrading its most stubborn polymers is a synergistic combination of oxidative and hydrolytic attack, why has the field of biotechnology remained so focused on hydrolysis alone? This article will explore the co-evolution of these two digestive strategies, charting the scientific journey from the initial discovery of oxidative activity to the modern, systems-level understanding of enzymatic synergy. We will argue that embracing this oxidative-hydrolytic paradigm is not merely an academic curiosity but a necessary step to finally address the planet's polysaccharide problem and unlock the full potential of its most abundant biopolymers across mechanism, ecology, and technology.

The oxidative power: recent advances in biochemistry

For much of modern biochemistry, the degradation of crystalline polysaccharides was viewed through a single lens: hydrolysis. The scientific consensus held that the only way to depolymerise cellulose and chitin was to deploy an arsenal of hydrolytic enzymes, cellulases and chitinases, that use water to cleave the glycosidic bonds holding the polymer chains together⁹. This dogma defined decades of research, but it failed to fully explain the remarkable efficiency of microbial systems, particularly fungi, in breaking down the planet's most recalcitrant biomass. The conceptual breakthrough arrived in the early 2000s. While patent literature hinted at hydrolase-boosting activity¹⁵, the scientific mechanism was crystallised in 2010 with the characterisation of a new class of enzymes, initially named GH61s and CBM33s, which were found to dramatically boost the activity of cellulases¹². This discovery marked a fundamental revolution, overturning the hydrolysis-only paradigm. Subsequent work by Forsberg et al. confirmed this oxidative mechanism on cellulose¹⁶, and Quinlan et al. identified copper as the essential active site metal¹⁷. These enzymes, now known as lytic

polysaccharide monooxygenases, did not break bonds in the traditional sense; instead, they performed a far more subtle and powerful function. Using a copper-containing active site, they launch an oxidative attack directly on the flat, crystalline surfaces of the polysaccharide. This action does not release sugars but rather introduces chain breaks, creating new entry points for processive hydrolases. The paradigm shifted from one of brute-force bond breaking to a sophisticated strategy of oxidatively picking the locks on a seemingly impenetrable crystalline structure¹⁴.

This discovery alone was transformative, but the revolution was not yet complete. The initial classification of these enzymes as monooxygenases was based on the logical assumption that they utilised molecular oxygen (O_2) as a co-substrate to oxidise the polysaccharide. However, a second, even more profound paradigm shift was on the horizon, questioning the very chemistry at the heart of the LPMO mechanism. In 2017, a pivotal study demonstrated that LPMOs are not monooxygenases but are, in fact, powerful and highly specific peroxygenases¹⁸. This research revealed that the true co-substrate can be hydrogen peroxide (H_2O_2), a common metabolic byproduct in the microbial world. While LPMOs can react with O_2 or H_2O_2 , recent kinetic data suggest the peroxygenase pathway prevails in many contexts, leading some in the field to suggest renaming these enzymes to reflect this dominant catalytic activity¹⁹. This finding was not merely a technical adjustment; it fundamentally altered our understanding of how these enzymes function in their natural environments. It explained how LPMOs could be so effective in the often oxygen-limited conditions found in soil, compost, and biomass aggregates, where even low fluxes of H_2O_2 produced by microbial cross-feeding can sustain activity. The kinetic advantages and unique inactivation risks of the two competing pathways are summarised in Fig. 1.

The peroxygenase pivot reframes the enzyme's action as a form of highly controlled, molecular-level bleaching. Nature, it turns out, has

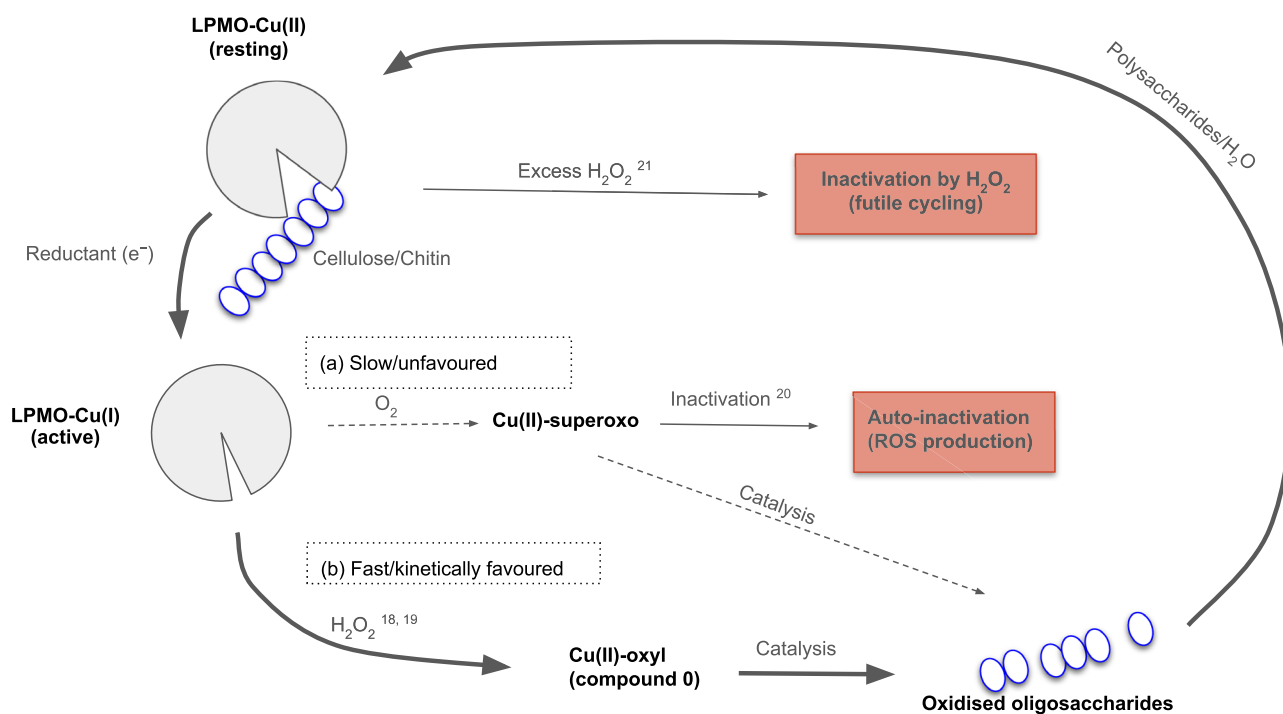


Fig. 1 | Comparative catalytic cycles of lytic polysaccharide monooxygenases illustrating the molecular oxygen and hydrogen peroxide pathways. The catalytic cycle begins with the lytic polysaccharide monooxygenase in its resting state, labelled as LPMO-Cu(II), bound to the polysaccharide substrate (P-S). Activation requires the reduction of Cu(II) to the active Cu(I) state by an external reductant (e^-). Two divergent pathways are indicated by labelled arrows. Path A represents the O_2 monooxygenase route. The LPMO-Cu(I) reacts with molecular oxygen to form an unstable intermediate, labelled as Cu(II)-Superoxo. This pathway is kinetically slow/unfavoured due to the low rate of O_2 reduction. It is prone to auto-inactivation due to

the leakage and formation of damaging reactive oxygen species (ROS)²⁰. Path B represents the fast, kinetically favoured H_2O_2 peroxygenase route through a highly reactive Cu(II)-oxyl intermediate, which dominates under optimal conditions^{18,19}. In both pathways, the reactive intermediate abstracts a hydrogen atom from the polysaccharide substrate, leading to polysaccharide substrate cleavage and the release of oxidised oligosaccharides. However, the H_2O_2 route is susceptible to rapid inactivation by H_2O_2 (futile cycling)²¹ if the H_2O_2 concentration is not tightly controlled. The successful cycle returns the enzyme to the LPMO-Cu(II) resting state.

evolved a mechanism to wield the potent oxidative power of H_2O_2 with surgical precision, targeting it to a single glycosidic bond on a vast crystalline surface without causing collateral damage²⁰. It is important to note that this reactivity is context-dependent; the availability of reductants, substrates, and light can influence whether the O_2 or H_2O_2 route dominates²¹. This insight is a crucial point of novelty and contention that makes the study of LPMOs so timely. It connects the degradation of the world's most abundant biopolymers directly to the redox state of the local environment and the metabolic activity of the entire microbial community, which collectively generates the H_2O_2 fuel²². Understanding this intricate H_2O_2 -driven catalytic cycle is now at the forefront of carbohydrate biochemistry and has profound implications for both ecological modelling and industrial biotechnology.

LPMOs as global carbon cycle regulators

The paradigm shift recognising LPMOs as H_2O_2 -driven catalysts compels us to look beyond their biochemical mechanism and consider their profound ecological implications. The sheer abundance of their substrates makes their activity inherently relevant at a planetary scale. Here, we propose the core hypothesis that LPMO activity represents a critical, and often rate-limiting, step in global carbon turnover. While direct environmental quantification is still emerging, genomic data support this ubiquity; lignocellulose-degrading fungi often carry a remarkably high number of lpmo genes, more than 60 in some species, suggesting immense evolutionary pressure to maintain these oxidative tools²³. These enzymes are not merely passive participants in decay; they are active regulators of carbon flux in forests, soils, and oceans, directly influencing the balance between CO_2 sequestration and release. By controlling the initial breach of the biosphere's most resilient carbon reservoirs, LPMOs function as gatekeepers for a substantial portion of the global carbon cycle.

This hypothesis forces us to connect the LPMO function to major, unresolved questions in ecosystem science. In terrestrial environments, the decomposition of lignocellulose is the primary bottleneck controlling the return of fixed carbon to the atmosphere. The activity of soil microbes, particularly fungi, dictates the fate of this carbon: either rapid release as CO_2 or stabilisation into soil organic matter (SOM), the largest terrestrial carbon pool^{24,25}. We posit that the prevalence and catalytic efficiency of LPMOs are a key determinant of this partitioning. Alongside other cell-wall loosening factors like expansins and swollenins²⁶, LPMOs govern the entry of plant-derived carbon into microbial food webs, thereby influencing the rate of soil organic matter formation and the long-term carbon storage capacity of soils²⁷.

This environmental partitioning is fundamentally driven by a sophisticated oxidative suite rather than a single enzymatic event. While the mechanistic focus of this synthesis remains on LPMOs, these enzymes function as part of a broader, integrated network of peroxygenases and copper-radical oxidases. Collectively, this ensemble regulates cellular redox homeostasis while providing the high-energy oxidative power necessary to deconstruct complex biomass. Situating LPMO activity within this wider synergistic framework provides the necessary perspective for understanding how microbial communities exert fine-tuned redox control over global carbon turnover, regardless of the biome.

This regulatory logic extends to the marine biosphere, where the role of LPMOs may be equally critical in the marine biosphere. The ocean's biological carbon pump is a primary driver of global carbon sequestration, transporting vast quantities of particulate organic carbon (POC) from the surface to the deep ocean in the form of marine snow²⁸. This sinking biomass, rich in both cellulose from phytoplankton and chitin from zooplankton and fungi, is a crucial food source for deep-sea ecosystems. The efficiency of the biological pump, and thus its impact on atmospheric CO_2 —depends directly on the rate at which this particulate organic carbon is remineralised by microbes during its descent²⁹. The discovery of LPMOs in diverse marine bacteria suggests they are key players in the degradation of this resilient, particle-associated carbon^{30,31}. The H_2O_2 -dependent nature of LPMOs is particularly intriguing in this context, as reactive oxygen species are known to be produced photochemically and biologically in the marine

environment, which points to a complex interplay between light, metabolism, and carbon cycling.

Elevating this perspective to a planetary scale, the environmental sensitivity of LPMOs suggests they may be part of an unquantified feedback loop in the Earth's climate system. LPMO catalysis is exquisitely dependent on local redox conditions, the availability of H_2O_2 , and the presence of electron donors, all of which are shaped by the metabolic state of the microbial community and influenced by external factors³². Could changes in temperature, ocean acidification, or the influx of pollutants like metal elements, which can interfere with the enzyme's copper active site, systematically alter LPMO activity on a global scale? If so, this would represent a direct feedback mechanism where climate change alters the fundamental rate of polysaccharide decay, thereby impacting atmospheric CO_2 concentrations in ways not currently captured by Earth system models. Viewing LPMOs as global carbon cycle regulators transforms them from objects of biochemical curiosity into essential variables for understanding and predicting our planet's future.

Harnessing the engine, architecting a circular bioeconomy

The recognition of LPMOs as H_2O_2 -driven engines of polysaccharide deconstruction is more than a fundamental scientific insight; it is a blueprint for technological innovation. By understanding and harnessing this oxidative power, we can architect a truly circular bioeconomy, moving beyond incremental improvements to reimagine how we produce materials, chemicals and energy. This vision extends from revolutionising the use of biomass to confronting the global challenge of plastic pollution.

Beyond biofuels, the biorefinery reimaged

For decades, the concept of the biorefinery has been largely synonymous with the production of liquid biofuels, a model hampered by high processing costs and economic reliance on a single, low-value product. The primary bottleneck has always been the recalcitrance of crystalline cellulose, which necessitates harsh, energy-intensive pretreatments and massive doses of hydrolytic enzymes. LPMOs fundamentally change this equation. By integrating H_2O_2 -driven LPMO activity into industrial processes, we can unlock biomass deconstruction with enhanced efficiency and under milder conditions²⁶. While enzyme production costs remain a consideration, the dramatic reduction in total protein loading and processing time offered by optimised LPMO systems presents a viable path to cost parity. This enables a paradigm shift from a simple fuel-focused model to a true, multi-product biorefinery.

In this reimaged biorefinery, LPMOs act as the master key, granting access to the cellulosic fraction not just for fermentation into ethanol, but for conversion into a portfolio of high-value products. For instance, the controlled action of LPMOs can be used to produce tailored nanocellulose materials with unique properties for applications in composites, biomedical devices, and advanced manufacturing³³. Furthermore, by efficiently separating cellulose from lignin and hemicellulose, LPMOs would facilitate the valorisation of all biomass fractions. Industrial demonstrations have already shown that controlled H_2O_2 delivery strategies markedly improve saccharification yields in commercial cocktails²². Lignin, no longer a waste product, has the potential to be converted into aromatic platform chemicals, carbon fibres, and biodegradable polymers, while hemicellulose sugars can be channelled into the production of speciality chemicals and bioplastics^{34,35}. This integrated approach, enabled by oxidative enzymology, transforms biomass from a crude fuel source into a renewable feedstock for a sustainable chemical industry, finally making the biorefinery economically viable and environmentally transformative.

An oxidative route to plastic deconstruction?

Perhaps the most profound implication of the current understanding of LPMOs lies in a domain far beyond the natural carbon cycle: the deconstruction of synthetic polymers. The global crisis of plastic pollution stems from the same chemical principle that makes cellulose so robust, the stability of its polymer chains. We propose the hypothesis that the fundamental

chemistry of LPMOs, the ability to activate C–H bonds on the surface of recalcitrant polymers, is not exclusively limited to polysaccharides. This opens a revolutionary possibility: using nature's oxidative toolkit to attack the world's most persistent artificial materials.

This concept, while speculative, is grounded in emerging evidence. Recent breakthroughs in protein engineering have demonstrated that the substrate-binding surfaces of LPMOs can be redesigned to promote interaction with non-native polymers. Burgeoning reports from 2024 and 2025 have shown that engineered LPMO variants can bind to and even perform limited oxidative modifications on biodegradable polyesters like polyhydroxyalkanoates (PHA)³⁶. However, caution is warranted regarding recalcitrant plastics like polyethylene terephthalate (PET). While directed evolution suggests LPMOs can bind PET structures, recent studies indicate that observed enhancements may be due to non-catalytic synergistic effects, such as surface disruption enhancing PETase access, rather than direct oxidative cleavage of the polymer backbone³⁷.

While the application of LPMOs to synthetic polymers remains an emerging and largely indirect field of study, it represents a major, albeit currently aspirational, frontier for the bioeconomy. Regardless of the precise mechanism, oxidative or synergistic, this research represents a significant expansion of enzymatic catalysis. If the core peroxigenase mechanism can be successfully repurposed, we could develop enzymatic systems that prime the surfaces of synthetic polymers for degradation, much like they do for cellulose. Furthermore, cell-free enzymatic cascades are already being developed to couple LPMO-assisted deconstruction with downstream conversions, offering a controlled alternative to live microbial consortia. This could create pathways not just for recycling, but for the biological upcycling of plastic waste, breaking it down into its constituent monomers or other valuable chemicals. The prospect of unleashing an evolved oxidative engine, fuelled by something as simple as hydrogen peroxide, to deconstruct our most enduring pollutants represents a radical, yet plausible, strategy to address the plastic crisis and close the loop on a truly circular economy.

The path forward to unresolved questions and future directions

The journey from viewing polysaccharide degradation as a simple hydrolytic process to understanding it as a sophisticated, H₂O₂-driven oxidative assault opens up an expanded research landscape. To fully realise the potential of LPMOs, the scientific community must now address several fundamental questions and embrace ambitious future goals. The path forward requires a multi-disciplinary effort, integrating biochemistry, ecology, and synthetic biology to master the power of these remarkable enzymes.

A primary challenge lies in understanding how nature tames its own oxidative fire³⁸. The use of hydrogen peroxide, a potent and potentially destructive oxidant, raises a critical question: how do microbial cells generate, transport, and deliver H₂O₂ to an LPMO active site with precision, all while avoiding catastrophic damage to themselves? The mechanisms of this localised redox control are still largely unknown but are likely to involve intricate networks of H₂O₂-producing enzymes, specialised transporters, and electron-donating partners that form a tightly regulated oxidative connection at the biomass surface³⁹. Deciphering these pathways is not only a fundamental biological question but also a prerequisite for industrial application. Replicating this level of control in a bioreactor is the key to developing robust, efficient, and long-lasting enzymatic systems.

Simultaneously, we have barely scratched the surface of the natural diversity of LPMOs. The LPMO-ome of the planet contains a treasure trove of enzymes waiting to be discovered. Metagenomic surveys of extreme environments, from the high-pressure depths of oceanic trenches to the digestive tracts of wood-boring insects and the geothermal vents of volcanic hot springs, will undoubtedly reveal LPMOs with distinct specificities, exceptional stability, and perhaps even previously undescribed chemistries⁴⁰. Mining this genetic diversity is essential for expanding our enzymatic toolkit, providing catalysts that can function under a wide range of industrial conditions and, crucially, on an expanded repertoire of both natural and synthetic polymer substrates.

These parallel research thrusts, control and discovery, culminate in a grand challenge for the field: to design and construct a synthetic microbial consortium capable of co-processing mixed lignocellulosic biomass and post-consumer plastic waste into a single, valuable platform chemical. Such a consortium would feature specialist microbes engineered to fulfil distinct roles: one to generate and supply H₂O₂, another to secrete a bespoke toolkit of natural and evolved LPMOs targeting both cellulose and PET, and a third to metabolise the released monomers into a product like adipic acid, a precursor for nylons and polyurethanes^{41,42}. Achieving this goal would represent the ultimate triumph of the emerging oxidative paradigm. It would validate our understanding of LPMO chemistry, demonstrate mastery over cellular redox engineering, and provide a tangible, scalable solution to the twin crises of resource depletion and plastic pollution, truly architecting a circular economy for the future.

Received: 10 October 2025; Accepted: 29 March 2026;

Published online: 08 May 2026

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Acknowledgements

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors. The authors acknowledge the institutional support and resources provided by BiotechKraft AS and the Federal University of Rio de Janeiro (UFRJ).

Author contributions

Carlos H. Saraiva Garcia conceptualised the oxidative-hydrolytic framework, provided strategic oversight for the R&D narrative, jointly wrote the primary paper, and performed the final technical revisions. Maren Saraiva Garcia jointly supervised the work, contributed to the strategic positioning of the bioeconomy synthesis, and provided critical governance oversight. Ricardo Sposina Sobral Teixeira jointly wrote the primary manuscript, conducted the literature synthesis, and managed the paper revisions. All authors reviewed and approved the final version of the paper for submission.

Competing interests

The authors declare the following competing interests: C.H.S.G. and M.S.G. are founders and executives of BiotechKraft AS, a Norwegian biotech company focused on upcycling biomass. R.S.S.T. declares no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s44458-026-00070-6>.

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Peer review information *Communications Sustainability* thanks Amaranta Kahn and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Primary Handling Editors: Jiachao Peng and Nandita Basu. A peer review file is available.

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