

The Global Woody Surface: A Planetary Interface for Biodiversity, Ecosystem Function, and Climate

Jonathan Gewirtzman¹

¹Yale School of the Environment, Yale University, New Haven, CT, USA

*Corresponding author: jonathan.gewirtzman@yale.edu

This paper is a non-peer reviewed preprint submitted to EarthArXiv.

Recent quantification reveals that global aboveground woody surface area of forests spans approximately 143 (± 59) million km²—a magnitude equivalent to Earth's entire terrestrial surface area of 149 million km² (1). This complex network of bark, stems, and branches represents a "third dimension" of Earth's ecosystems, a dynamic planetary interface that expands and contracts with forest cover and disturbance. These woody surfaces add vertical expanse and complexity to ecological surface area that scale with vegetation structure rather than geographic extent, and unlike the terrestrial land surface, woody surface area can be dramatically increased or reduced by human activity and management decisions.

Emerging evidence reveals the substantial biogeochemical significance of this interface (Figure 1). Woody surfaces mediate massive fluxes of climatically important compounds. Stem respiration alone transfers 27.4 ± 5.9 PgC annually to the atmosphere, a carbon flux nearly three times larger than global fossil fuel emissions (2, 3). Simultaneously, tree stems can function as atmospheric methane sinks, potentially removing 24.6–49.9 Tg of methane yearly through specialized bark-dwelling microbial communities, a flux comparable to the global soil methane sink (~ 30 TgCH₄ yr⁻¹) and approaching the magnitude of methane emissions from the entire natural gas sector (1, 4). These processes operate at magnitudes that rival major components of Earth's carbon cycle, yet remain poorly integrated into current modeling frameworks.

This oversight reflects both historical research priorities and methodological constraints. Forest science emphasized timber volume over surface area, climate research focused on photosynthetic surfaces and soil carbon, and most woody surface area exists in forest canopies beyond the reach of ground-based measurement approaches. However, advances in remote sensing technologies—including terrestrial laser scanning, airborne LiDAR, and the spaceborne GEDI mission—are revealing the importance of forest structural complexity for ecosystem dynamics and enabling unprecedented analysis of three-dimensional surfaces at multiple scales (5). Accumulating evidence indicates that woody surfaces perform ecological functions with considerable implications for understanding forest contributions to forest structure and health, global biogeochemical cycles, and planetary climate.

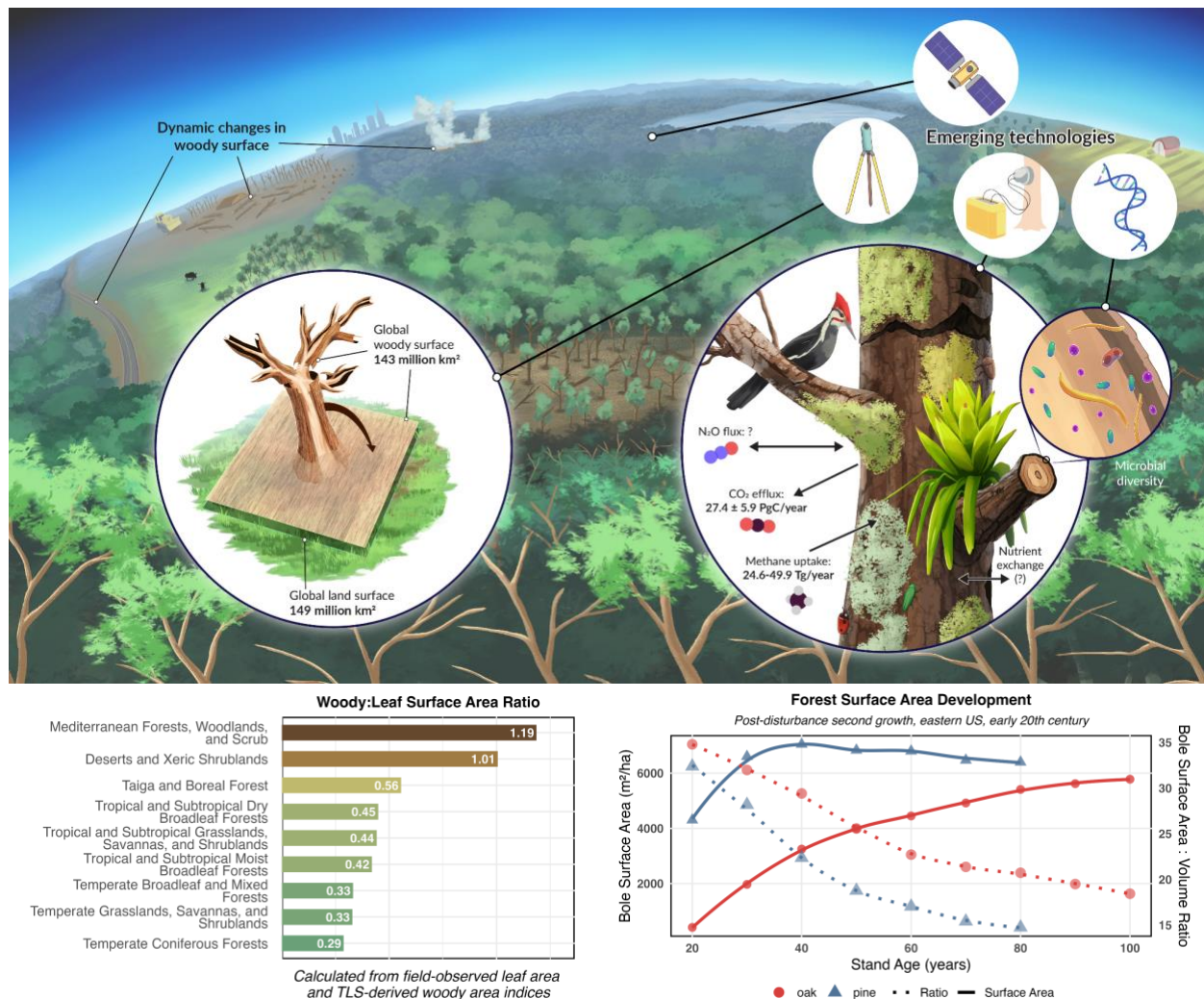


Figure 1. Woody surfaces constitute a massive, dynamic planetary interface with unexplored ecological and environmental significance. *Top:* conceptual diagram showing global aboveground woody surface area (nearly equal to Earth's terrestrial land surface; left inset), yet remains largely unaccounted for in Earth system models. This three-dimensional interface mediates substantial atmospheric exchanges of compounds including greenhouse gases, and numerous others that remain unquantified, as well as hosting biodiversity across the domains of life (right inset). The planetary woody interface scales dynamically with forest cover, expanding and contracting with deforestation and restoration. Emerging technologies (small insets) enable systematic investigation of this previously inaccessible interface across scales from microbial communities to global monitoring [© Elena Hartley www.elabarts.com].

Bottom left: Woody surface-to-leaf surface area ratios across forest biomes, calculated from field measurements of leaf area index (two-sided LAI for like comparison; data from (6, 7)) combined with woody surface area estimates (data from (1)), showing 4-fold variation across biomes. **Bottom right:** Bole (stem) surface area development and surface area:volume ratios over 8 decades of forest stand growth for oak and pine stands across the eastern United States (derived from 1920s-1930s USDA Forest Service growth and yield tables; derived by (8)), showing divergent trajectories between forest types and demonstrating the temporal dynamism of woody surface area.

Environmental and Ecological Functions of Woody Surfaces

Tree stems and branches serve as active sites for the exchange of climatically important gases. While trees have increasingly been recognized as methane sources in wetland and some upland environments, recent studies demonstrate that stems in upland tropical, temperate, and boreal forests may also act as net atmospheric methane sinks (1). This uptake occurs primarily above two meters from the forest floor, mediated by methanotrophic bacteria that can constitute up to 25% of microbial communities on certain tree species (9). Given methane's 20-year global warming potential of 84 times that of CO₂, this process represents a previously unquantified climate service that could substantially alter forest climate valuations.

Woody surfaces also contribute substantially to forest carbon budgets through stem respiration. This flux involves complex internal dynamics of production, transport, refixation, and consumption that vary spatially across tree structures—including specialized exchange sites such as lenticels—and temporally with growth, environmental conditions, and tissue damage (10, 11). These exchanges are neither static nor uniform, exhibiting considerable variation with height, species, and environmental conditions.

In addition to carbon and methane, woody surfaces facilitate exchange of hydrogen, carbon monoxide, volatile organic compounds, and other trace gases, while potentially serving as sites for nutrient uptake and various biogeochemical transformations (12). Emerging understanding suggests that aboveground nutrient absorption can be a quantitatively important pathway for forest nutrition (13), and woody surfaces have demonstrated but unquantified capacity for direct uptake of nitrogen, phosphorus, and potassium (14). The structure and biology of tree woody surfaces also make them interceptors of air pollutants, a trait that can be exploited for air quality management in certain settings (15).

The microbial communities inhabiting woody surfaces—termed the "caulosphere"—constitute biogeochemical hotspots with distinct taxonomic and functional characteristics. Recent work has identified specialized bacterial groups that actively mediate cycling of hydrogen and carbon monoxide under aerobic conditions (12). These surface-associated communities complement the diverse endophytic microbiomes within woody tissues, where an average tree harbors approximately one trillion prokaryotic cells in its aboveground woody components alone (16), with these microbiomes demonstrating capacity for greenhouse gas emission and nitrogen fixation (17). This vast microbial ecosystem transforms trees into holobionts—integrated biological units composed of the plant and its microbiota—with caulosphere communities showing sensitivity to environmental change that makes documenting this biodiversity urgent.

Beyond microbes, woody surfaces support diverse epiphytic plant communities and provide critical habitat for arboreal animals for nesting and foraging. Surface properties—including bark texture, chemistry, and shedding patterns—strongly influence community assembly and the diversity and abundance of trunk-associated biota across all domains of life. While research has traditionally examined the ecology of some lichens, mosses, higher plants, animals, and microbes in isolation, understanding the cross-kingdom community and ecosystem ecology of these surfaces—and their function as integrated ecological units in their own right—represents a major frontier for biodiversity science (18).

The Scale and Measurement Challenge

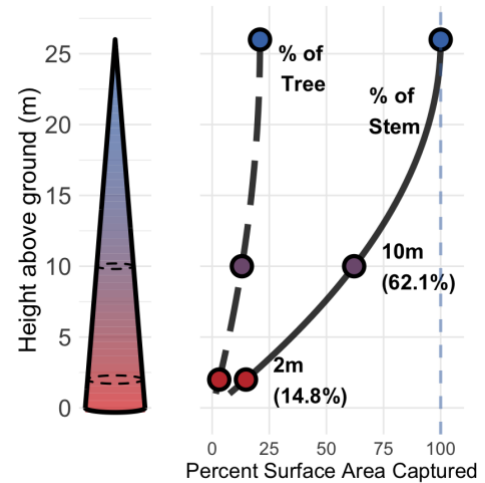
Woody surfaces have received disproportionately limited attention compared to leaf surfaces. Leaf area index (LAI)—the total one-sided area of leaf tissue per unit ground surface area—is one of the most widely measured vegetation parameters, capturing leaves' roles in photosynthesis, transpiration, gas exchange regulation, foliar uptake of water and nitrogen, volatile organic compound emissions, and pollutant interception. While LAI is a core parameter in Earth system models, woody surface area remains largely unaccounted for, despite providing complementary but distinct ecological functions as persistent exchange surfaces that remain active even when leaves are absent seasonally in deciduous systems. Moreover, the balance of leaf to woody surface area varies across Earth's biomes (*Figure 1, bottom left*), a fact recognized in the mensuration of leaf area indices, but overlooked for its potential impact of ecosystem structure and services such as habitat provision.

A foundational study by Whittaker and Woodwell (19) found several square meters of plant surface occur above each square meter of ground surface in temperate forests, including 0.3–0.6 m² of stem bark, 1.2–2.2 m² of branch bark, and 3.0–6.0 m² of leaves. Importantly, they found branch bark surface increases more rapidly than leaf surface with increasing tree size, indicating shifts in surface proportions with forest development. Surface area remains poorly understood as a forest property; while self-thinning laws govern stand development, it remains unknown how surface area varies through succession, given that surface area does not directly scale with volume (20, 21). Different tree architectures and assemblages can lead to differing surface area magnitudes for different forest types, stand histories and ages (*Figure 1, bottom right*).

The spatial distribution and accessibility of woody surfaces present fundamental measurement challenges. Traditional ground-based studies typically sample only roughly the lower two meters of tree stems that an average person can reach from the ground, creating severe sampling bias. For an average temperate forest tree, the surface below breast height (1.37 m) may be 2% or less of the total tree woody surface (*Table 1*). This sampling limitation is compounded by the extreme spatial non-uniformity of woody surface processes, where biogeochemical hotspots may be distributed throughout the three-dimensional canopy structure. Methane uptake, for example, is thought to occur primarily above two meters from the forest floor, suggesting traditional sampling limitations potentially misrepresent forest-scale biogeochemical processes and limit our understanding of surface-atmosphere interactions.

Table 1: Woody surface coverage below different sampling heights on a 26-meter tall tree with 40 cm diameter at breast height (DBH). Surface areas calculated as truncated cone lateral surface area, with linear stem taper from DBH to tree apex. Total tree surface area includes estimated branch surface area using allometric relationships from Whittaker & Woodwell (1967). Total stem surface area: 17.25 m² | Total tree surface area (with branches): 82.4 m².

Sampling height	Stem surface area below height	% of total stem surface	% of total tree woody surface
2 m	2.55 m ²	14.8%	3.1%
10 m	10.72 m ²	62.1%	13.0%
26 m (full height)	17.25 m ²	100%	20.9%



Surface area quantification itself presents conceptual challenges analogous to the coastline paradox—measured area increases substantially with measurement resolution due to bark texture, crevices, and three-dimensional complexity. While simple geometric projections may suffice for scaling many ecosystem-atmosphere exchanges, finer-scale fractal surface features may be critical for stemflow regulation, habitat provision for animals and fungi, and pathogen ingress sites.

Advances in remote sensing technologies are transforming measurement capabilities. Terrestrial laser scanning provides millimeter-level structural detail enabling rapid surface area quantification across forest stands. Airborne and spaceborne LiDAR systems, including the GEDI mission, offer unprecedented ability to assess three-dimensional forest structure at landscape to global scales. These technologies enable systematic investigation of woody surface ecology across the full vertical profile of forest canopies (22, 23), and its importance for forest processes and productivity (24).

Climate Policy Implications

The woody surface interface scales dynamically with forest cover, creating feedbacks between forest structure and biogeochemical function that current policy frameworks do not capture. Forest carbon markets focus primarily on biomass and soil carbon, missing complementary services like atmospheric methane removal that may add 10% to forest climate benefits (1). With hundreds of millions hectares of potential tropical forest expansion projected (25), strategic species selection and management could optimize multiple trace gas exchanges rather than carbon storage alone.

This contributes to significant unknowns in climate accounting, where forest structure and processes—not just area or volume—may determine atmospheric services in ways we don't fully understand. Without understanding how woody surfaces respond to management practices,

disturbance regimes, and environmental change, forest climate contributions could vary in ways not predicted by existing models or valuation systems.

Research Priorities

Advancing woody surface science requires targeted research investments across multiple scales. Laboratory studies must characterize the environmental controls on microbial community assembly and gas exchange rates, including moisture thresholds, nutrient limitations, and succession dynamics that determine surface biogeochemical activity. Field research should prioritize developing or utilizing canopy-access methods for direct flux measurements, given that traditional ground-based approaches may capture only a small percentage of total tree woody surface area (*Table 1*).

At ecosystem scales, remote sensing integration with process models represents the path forward for global quantification and monitoring. The cross-kingdom ecology of woody surfaces—linking microbial, plant, and animal communities—remains unexplored despite representing a major component of forest biodiversity that could inform management strategies. Documenting this diversity is particularly urgent in the face of global change that could alter or eliminate countless yet unknown species.

The integration of woody surface processes into Earth system models represents a key challenge requiring new parameterizations and measurement approaches. Model development should focus on parameterizing woody surface area as a dynamic vegetation property, analogous to leaf area index, enabling predictions of how changing forest structure affects atmospheric chemistry under future climate scenarios.

Key research priorities include developing standardized protocols for woody surface area quantification across species and ecosystems, including clear definitions of surface area compartments; clarifying linkages between surface structure, microbial communities, and biogeochemical processes; leveraging remote sensing technologies to estimate global woody surface area and monitor spatiotemporal dynamics; improving field measurement techniques for quantifying gas exchange within upper canopies; and expanding vegetation models to incorporate woody surface exchanges alongside existing leaf- and soil-based frameworks.

Realizing this potential requires rapid advancement in woody surface science, from fundamental understanding of microbial processes to landscape-scale modeling of gas exchange. Integration of woody surface processes into climate science, forest management, and conservation planning represents both a scientific imperative and a practical necessity for effective climate policy.

References

1. V. Gauci, S. R. Pangala, A. Shenkin, J. Barba, D. Bastviken, V. Figueiredo, C. Gomez, A. Enrich-Prast, E. Sayer, T. Stauffer, B. Welch, D. Elias, N. McNamara, M. Allen, Y. Malhi, Global atmospheric methane uptake by upland tree woody surfaces. *Nature* **631**, 796–800 (2024).
2. H. Zhang, H. Wang, I. J. Wright, I. C. Prentice, S. P. Harrison, N. G. Smith, A. C. Westerband, L. Rowland, L. Plavcová, H. Morris, P. B. Reich, S. Jansen, T. Keenan, N. B. Nguyen, Thermal acclimation of stem respiration implies a weaker carbon-climate feedback. *Science* **388**, 984–988 (2025).
3. P. Friedlingstein, M. O’Sullivan, M. W. Jones, R. M. Andrew, J. Hauck, P. Landschützer, C. Le Quéré, H. Li, I. T. Lujikx, A. Olsen, G. P. Peters, W. Peters, J. Pongratz, C. Schwingshackl, S. Sitch, J. G. Canadell, P. Ciais, R. B. Jackson, S. R. Alin, A. Arneth, V. Arora, N. R. Bates, M. Becker, N. Bellouin, C. F. Berghoff, H. C. Bittig, L. Bopp, P. Cadule, K. Campbell, M. A. Chamberlain, N. Chandra, F. Chevallier, L. P. Chini, T. Colligan, J. Decayeux, L. M. Djutchouang, X. Dou, C. Duran Rojas, K. Enyo, W. Evans, A. R. Fay, R. A. Feely, D. J. Ford, A. Foster, T. Gasser, M. Gehlen, T. Gkritzalis, G. Grassi, L. Gregor, N. Gruber, Ö. Gürses, I. Harris, M. Hefner, J. Heinke, G. C. Hurtt, Y. Iida, T. Ilyina, A. R. Jacobson, A. K. Jain, T. Jarníková, A. Jersild, F. Jiang, Z. Jin, E. Kato, R. F. Keeling, K. Klein Goldewijk, J. Knauer, J. I. Korsbakken, X. Lan, S. K. Lauvset, N. Lefèvre, Z. Liu, J. Liu, L. Ma, S. Maksyutov, G. Marland, N. Mayot, P. C. McGuire, N. Metzl, N. M. Monacci, E. J. Morgan, S.-I. Nakaoka, C. Neill, Y. Niwa, T. Nützel, L. Olivier, T. Ono, P. I. Palmer, D. Pierrot, Z. Qin, L. Resplandy, A. Roobaert, T. M. Rosan, C. Rödenbeck, J. Schwinger, T. L. Smallman, S. M. Smith, R. Sospedra-Alfonso, T. Steinhoff, Q. Sun, A. J. Sutton, R. Séférian, S. Takao, H. Tatebe, H. Tian, B. Tilbrook, O. Torres, E. Tourigny, H. Tsujino, F. Tubiello, G. van der Werf, R. Wanninkhof, X. Wang, D. Yang, X. Yang, Z. Yu, W. Yuan, X. Yue, S. Zaehle, N. Zeng, J. Zeng, Global carbon budget 2024. *Earth Syst. Sci. Data* **17**, 965–1039 (2025).
4. M. Saunio, A. Martinez, B. Poulter, Z. Zhang, P. A. Raymond, P. Regnier, J. G. Canadell, R. B. Jackson, P. K. Patra, P. Bousquet, P. Ciais, E. J. Dlugokencky, X. Lan, G. H. Allen, D. Bastviken, D. J. Beerling, D. A. Belikov, D. R. Blake, S. Castaldi, M. Crippa, B. R. Deemer, F. Dennison, G. Etiope, N. Gedney, L. Höglund-Isaksson, M. A. Holgersson, P. O. Hopcroft, G. Hugelius, A. Ito, A. K. Jain, R. Janardanan, M. S. Johnson, T. Kleinen, P. B. Krummel, R. Lauerwald, T. Li, X. Liu, K. C. McDonald, J. R. Melton, J. Mühle, J. Müller, F. Murguía-Flores, Y. Niwa, S. Noce, S. Pan, R. J. Parker, C. Peng, M. Ramonet, W. J. Riley, G. Rocher-Ros, J. A. Rosentreter, M. Sasakawa, A. Segers, S. J. Smith, E. H. Stanley, J. Thanwerdas, H. Tian, A. Tsuruta, F. N. Tubiello, T. S. Weber, G. R. van der Werf, D. E. J. Worthy, Y. Xi, Y. Yoshida, W. Zhang, B. Zheng, Q. Zhu, Q. Zhu, Q. Zhuang, Global methane budget 2000–2020. *Earth Syst. Sci. Data* **17**, 1873–1958 (2025).
5. T. de Conto, J. Armston, R. Dubayah, Characterizing the structural complexity of the Earth’s forests with spaceborne lidar. *Nat. Commun.* **15**, 8116 (2024).
6. G. P. Asner, J. M. O. Scurlock, J. A. Hicke, Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Glob. Ecol. Biogeogr.* **12**, 191–205 (2003).
7. A. Iio, K. Hikosaka, N. P. R. Anten, Y. Nakagawa, A. Ito, Global dependence of field-observed leaf area index in woody species on climate: a systematic review: Global dependence of leaf area index on climate. *Glob. Ecol. Biogeogr.* **23**, 274–285 (2014).
8. S. G. Boyce, The Use of Bole Surface in the Estimation of Woodland Production. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **271**, 139–148 (1975).
9. L. C. Jeffrey, D. T. Maher, E. Chiri, P. M. Leung, P. A. Nauer, S. K. Arndt, D. R. Tait, C. Greening, S. G. Johnston, Bark-dwelling methanotrophic bacteria decrease methane emissions from trees. *Nat. Commun.* **12**, 2127 (2021).
10. R. O. Teskey, A. Saveyn, K. Steppe, M. A. McGuire, Origin, fate and significance of CO₂ in tree stems. *New Phytol.* **177**, 17–32 (2008).
11. A. S. Gorgolewski, J. Vantellingen, J. P. Caspersen, S. C. Thomas, Overlooked sources of methane emissions from trees: branches and wounds. *Can. J. For. Res.* **52**, 1165–1175 (2022).

12. P. M. Leung, L. C. Jeffrey, S. K. Bay, P. Gomez-Alvarez, M. Hall, S. G. Johnston, J. Dittmann, T. Jirapanjawat, T. F. Hutchinson, N. V. Coleman, X. Dong, E. Deschaseaux, D. T. Maher, C. Greening, Wetland tree barks are dynamic hotspots for microbial trace gas cycling, *bioRxiv* (2024)p. 2024.07.02.601631.
13. X. Li, C. Zhang, B. Zhang, L. Jiang, S. Tang, C. Sun, Y. Bai, Y. Wang, Y. Shi, L. Ma, W. Zhang, Q. Ye, J. Yan, K. Wang, J. Fu, W. Du, D. Ha, Y. Ju, S. Wan, L. Hong, Y. Fang, E. Siemann, Y. Luo, P. B. Reich, S. Fu, Underappreciated role of canopy nitrogen deposition for forest productivity. *Proc. Natl. Acad. Sci. U. S. A.* **122**, e2508925122 (2025).
14. H. B. Tukey, R. L. Ticknor, O. N. Hinsvark, S. H. Wittwer, Absorption of nutrients by stems and branches of woody plants. *Science* **116**, 167–168 (1952).
15. T. E. Barrett, A. G. Ponette-González, J. E. Rindy, K. C. Weathers, Wet deposition of black carbon: A synthesis. *Atmos. Environ.* (1994) **213**, 558–567 (2019).
16. W. Arnold, J. Gewirtzman, P. A. Raymond, M. C. Duguid, C. R. Brodersen, C. Brown, N. Norbraten, Q. T. V. Wood, M. A. Bradford, J. Peccia, A diverse and distinct microbiome inside living trees. *Nature*, 1–10 (2025).
17. S. L. Doty, A. W. Sher, N. D. Fleck, M. Khorasani, R. E. Bumgarner, Z. Khan, A. W. K. Ko, S.-H. Kim, T. H. DeLuca, Variable nitrogen fixation in wild *Populus*. *PLoS One* **11**, e0155979 (2016).
18. M. E. Spicer, C. L. Woods, A case for studying biotic interactions in epiphyte ecology and evolution. *Perspect. Plant Ecol. Evol. Syst.* **54**, 125658 (2022).
19. R. H. Whittaker, G. M. Woodwell, Dimension and Production Relations of Trees and Shrubs in the Brookhaven Forest, New York. *J. Ecol.* **56**, 1–25 (1968).
20. A. Inoue, T. Nishizono, Conservation rule of stem surface area: a hypothesis. *Eur. J. For. Res.* **134**, 599–608 (2015).
21. V. L. Gavrikov, “Stem Surface Area as Subject of Study” in *Stem Surface Area in Modeling of Forest Stands*, V. L. Gavrikov, Ed. (Springer International Publishing, Cham, 2017), pp. 1–13.
22. K. Calders, J. Adams, J. Armston, H. Bartholomeus, S. Bauwens, L. P. Bentley, J. Chave, F. M. Danson, M. Demol, M. Disney, R. Gaulton, S. M. Krishna Moorthy, S. R. Levick, N. Saarinen, C. Schaaf, A. Stovall, L. Terryn, P. Wilkes, H. Verbeeck, Terrestrial laser scanning in forest ecology: Expanding the horizon. *Remote Sens. Environ.* **251**, 112102 (2020).
23. J. W. Atkins, P. Bhatt, L. Carrasco, E. Francis, J. E. Garabedian, C. R. Hakkenberg, B. S. Hardiman, J. Jung, A. Koirala, E. A. LaRue, S. Oh, G. Shao, G. Shao, H. H. Shugart, A. Spiers, A. E. L. Stovall, T. D. Surasinghe, X. Tai, L. Zhai, T. Zhang, K. Krause, Integrating forest structural diversity measurement into ecological research. *Ecosphere* **14**, e4633 (2023).
24. X. Liu, Y. Feng, T. Hu, Y. Luo, X. Zhao, J. Wu, E. E. Maeda, W. Ju, L. Liu, Q. Guo, Y. Su, Enhancing ecosystem productivity and stability with increasing canopy structural complexity in global forests. *Sci. Adv.* **10**, ead11947 (2024).
25. F. Hua, L. A. Bruijnzeel, P. Meli, P. A. Martin, J. Zhang, S. Nakagawa, X. Miao, W. Wang, C. McEvoy, J. L. Peña-Arancibia, P. H. S. Brancalion, P. Smith, D. P. Edwards, A. Balmford, The biodiversity and ecosystem service contributions and trade-offs of forest restoration approaches. *Science* **376**, 839–844 (2022).

Acknowledgements: I thank Vincent Gauci, Mark Bradford, Peter Raymond, Jackie Matthes, Luke Jeffrey, Atticus Stovall, Josep Barba, and Kathleen Savage for valuable discussions that helped shape the ideas presented in this perspective. Thank you to Elena Hartley for the design of the illustration in Figure 1.

Data and Code Availability: LAI data processing and surface area integration workflows are available at https://github.com/jgewirtzman/lai_wai under MIT license. Source datasets are from Asner et al. (2003) [ORNL DAAC], Iio et al. (2014), and Gauci et al. (2024).

Funding: J.G. was supported by the NSF Graduate Research Fellowship Program and the Yale Institute for Biospheric Studies.

Competing Interests: The author declares no competing interests.