



Discussion

Moving ecological tree-ring big data forwards: Limitations, data integration, and multidisciplinary

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ABSTRACT

In recent years, tree-ring databases have emerged as a remarkable resource for ecological research, allowing us to address ecological questions at unprecedented temporal and spatial scales. However, concerns regarding big tree-ring data limitations and risks have also surfaced, leading to questions about their potential to be representative of long-term forest responses. Here, we highlight three paths of action to improve on tree-ring databases in ecology: 1) Implementing consistent bias analyses in large dendroecological databases and promoting community-driven data to address data limitations, 2) Encouraging the integration of tree-ring data with other ecological datasets, and 3) Promoting theory-driven, mechanistic dendroecological research. These issues are increasingly important for tackling pressing cross-disciplinary research questions. Finally, although we focus here on tree ring databases, these points apply broadly across many aggregative databases in ecology.

1. Introduction

The potential of large tree-ring databases to enrich ecological and climatological research with a long-term perspective has garnered increasing attention (e.g. Babst et al., 2018; Jeong et al., 2021). There has been a notable surge in studies using these databases to address fundamental ecological and conservation questions (e.g. Babst et al., 2019; Klesse et al., 2023; Li et al., 2023; Mu et al., 2023). These studies are possible thanks to the vast spatial and temporal coverage of publicly available tree-ring datasets – a reflection of the continued commitment of the tree-ring community to contribute and support open global data (Guiterman et al., 2024). However, alongside these promising developments, concerns have also arisen regarding limitations of tree ring data and which caveats should be applied to their interpretation (Zhao et al., 2018; Klesse et al., 2018; Pearl et al., 2020). Some of these

concerns are not surprising, given that the intent of most collections in tree-ring databases, historically speaking, was to reconstruct climate. As such, they were limited in their choice of geographic locations and species to those most suitable for climatic reconstructions. On many occasions, this translated into relatively small sample sizes per location and specific selection of sites and trees with the strongest climate signal. These decisions can limit ecological inference from these data, especially when sampling is limited to canopy-dominant trees (Nehrbass-Ahles et al., 2014, Klesse et al., 2018, but see Williams et al., 2013 to illustrate the ecological value of these analyses, even using currently available data). We do not mean to condemn or criticize contributors of tree ring data or the maintainers of these incredibly valuable data resources. Quite the contrary: the initial efforts in data sharing at global scales during the 1970s were groundbreaking. Now, as we move into the current crisis of global change, a widespread, open discussion of these

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important issues could increase the value of these databases and amplify their use in ecological research.

The primary data set for accessing tree growth across the globe is the International Tree Ring Data Bank (ITRDB), a publicly available and maintained set of more than 6000 individual sites containing over 9000 raw data files, widely used in dendrochronological and climatological research (Guiterman et al., 2024). From an ecological perspective, ITRDB collections are known to poorly represent global forest ecosystems (Zhao et al., 2018), purposely show heightened climate sensitivity compared with average forests (Klesse et al., 2018), and have inconsistent sample replication over time, which could obscure climate change trends (Babst et al., 2019). Additionally, sites in the ITRDB generally lack ecologically important metadata (most ITRDB sites include only basic location information and coordinates, and tree-ring width measurements). Some solutions have been proposed, such as priority sampling metrics (Zhao et al., 2018), integrating tree-ring with earth observation and forest inventory data to improve sampling (Babst et al., 2018; Heilman et al., 2022), and implementing more mechanistic or generative models that address the complex structure and drivers of secondary growth (e.g., climatic and non-climatic factors (Schofield et al., 2016) and their interactions (Rollinson et al., 2016)). However, wide-scale adoption of these approaches is still in early stages, leaving these issues still largely unaddressed. Here, we call for a coordinated and fresh look at sample design, data collection and data sharing practices in

tree-ring ecology to continue improving what is a remarkable resource for long-term ecological research.

2. The need for proactive, community-driven improvements

To move forward in creating useful, representative tree-ring datasets for ecology, we believe that increased coordination, collaboration, and transparency will be key, rather than continuing to rely solely on individual action. Specifically, this should happen through a combination of community-driven initiatives (which involve simple things like universal column headers and order for databases, and integrating bias analysis in existing databases), and top-down action (such as funding agency requirements, focused funding for international collaboration and data curation, and improving personal incentives for data collectors to make their data openly available).

These issues are hardly unique to dendrochronology – they are common to most aggregated databases. The widespread nature of such issues has motivated a movement towards better scientific data practices, based on the ‘FAIR’ data principles (Findability, Accessibility, Interoperability, and Reusability) (Wilkinson et al., 2016). Implementing these ideas in tree-ring research may help to develop proactive, community-driven guidelines that encourage greater coordination among dendroecologists and improved communication across fields. Here, we discuss three key paths of actions that we believe can be

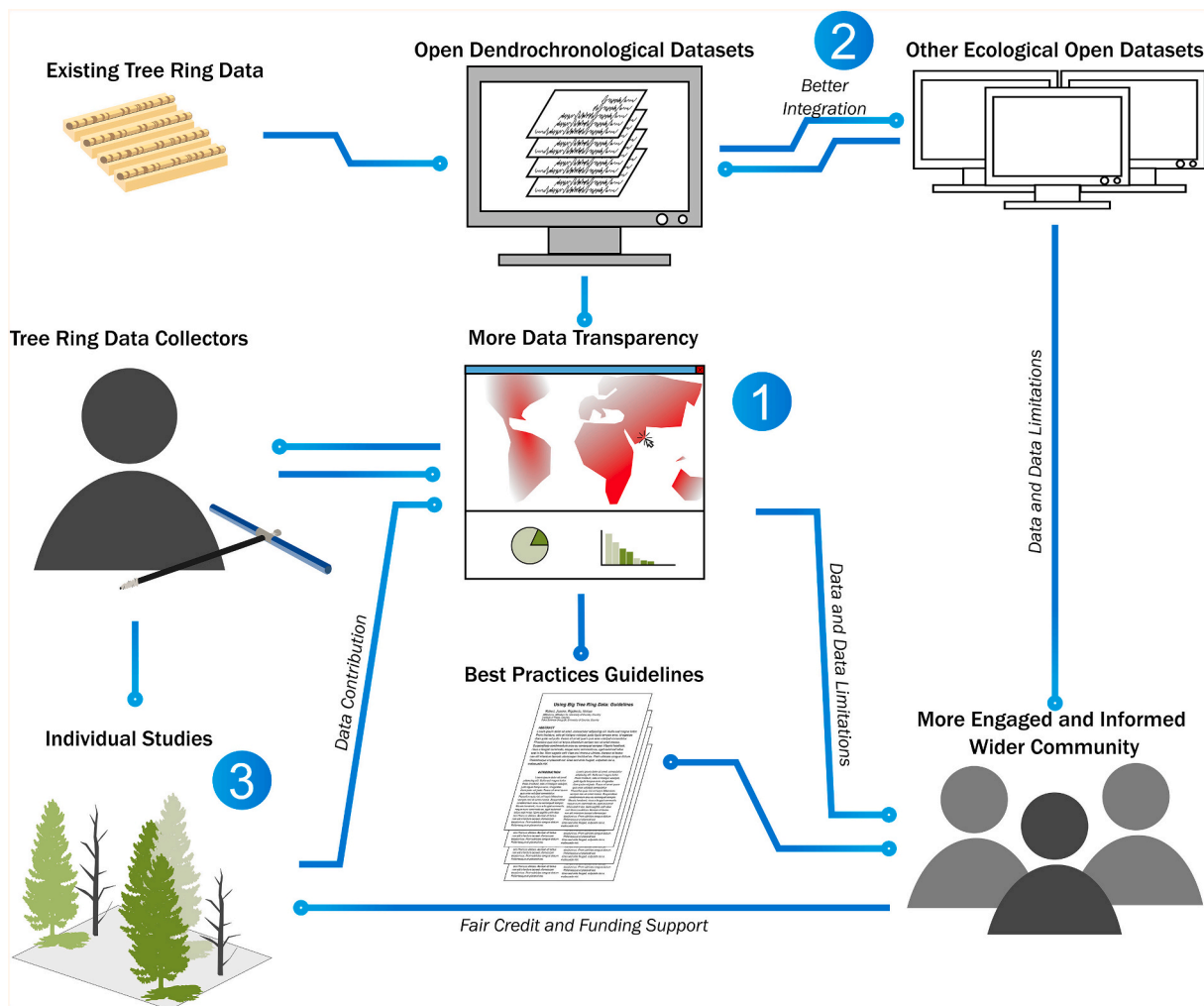


Fig. 1. Schematic representation of a better data integration in large tree-ring data bases, focused on better coordination, information, and transparency. The numbered labels identify the target of each of the three main actions proposed in this work. 1) Implementing bias analyses and address data limitations, 2) Encouraging better data integration, and 3) Promoting theory-driven, mechanistic dendroecological research including physiology and ecology alongside climate.

implemented in a relatively short time span to enhance tree-ring ecological data, mitigate known limitations, and, by doing so, benefit both tree-ring and broader ecological communities (Fig. 1).

2.1. Implementing bias analyses in large dendroecological databases and promoting community-driven data to address data limitations

The booming use of large tree-ring data for macroecological analyses mirrors aspects of citizen or community science. Early community science promised to simultaneously engage the public, boost replication over traditional data and reduce costs, greatly expanding the horizons of ecological research. The subsequent process of validating citizen-gathered data and understanding what citizen science can (and cannot) contribute to mainstream science has been important for growth of this subdiscipline and its integration into mainstream ecology (Burgess et al., 2017; Parrish et al., 2018). Large scale citizen science and crowdsourcing programs (such as eBird, iNaturalist, and the National Phenology Network, to name a few) have shown the advantage of promoting and embracing efforts to scrutinize and improve data quality transparently (e.g. (Kelling et al., 2015, Campbell et al., 2023)) and should inspire similar examination in tree ring ecology. This process has also shown that even substantially increasing replication, the path seemingly taken by most large ecological databases, cannot, by itself, address issues related to representativity and spatial and taxonomical coverage (Daru and Rodriguez, 2023), suggesting a need for more intentional, proactive approaches.

Dendroecology now faces similar challenges: aggregated datasets of long-term tree-ring data have grown to impressive scale, but issues regarding representativity and coverage have persisted. Without better coordination and transparency, sampling design and species targeting are likely to continue prioritizing certain taxa (e.g. conifers) and geographic regions (e.g. temperate or mountain forests subjected to temperature or moisture limitations) that are easier to process, access, and/or are known to provide stronger climate signals. While these criteria may provide datasets well suited to climate reconstructions, such data are likely not equally representative to the ecology of forested ecosystems (Rollinson et al., 2021). As a consequence, large tree-ring databases (including the ITRDB) have currently a limited ability to address ecological questions. For example, using the ITRDB to study trees other than dominant canopy ones, estimating potential changes in species compositions or dominance, investigating poorly sampled areas such as tropical and subtropical forests, or exploring overall growth responses to higher carbon availability (increasing CO₂), would all offer unrepresentative results that may lead to erroneous interpretation or conservation actions.

Another issue tree ring databases face is buy-in from the community – many ecologically-based tree ring studies do not submit their data to these databases. The question then is, why has data sharing not grown at the same pace as dendrochronology has expanded (Babst et al., 2017)? First, it is necessary to acknowledge the commitment to open data of the pioneers of modern dendrochronology in the 1970s and 1980s, such as H. Fritts, F.R. Schweingruber, E.R. Cook, or D. Stahle, who are still among the top contributors to the ITRDB. These personal efforts boosted the early development of the dataset but have not been matched since. The increasingly competitive academic market, together with the lack of norms for fairly crediting data contributors, and the more widespread ability to perform large data analyses, may contribute to the hesitation of researchers to share their original data. It is also important to acknowledge the role of cultural differences in this regard. Data sharing and open data practices are not universal, and in many geographic regions data that are rarely contributed to open repositories. For example, Su et al. (2024) aimed to explore forest population dynamics in southern China but found only 12 available chronologies in the ITRDB. However, they were able to expand this number by 100 locations through extracting chronologies from the literature (both Chinese and internationally published research, which were not made openly available

elsewhere). At that time, more than 90 % of the existing (and on many occasions publicly funded) data in this particular region was neither available nor listed as potentially accessible anywhere. This problem occurs in many regions worldwide. Greater consistency and enforcement of open access rules by funding agencies are needed, to reduce redundancy and make sure that publicly funded data are efficiently and widely used via promoting open data policies and FAIR practices (e.g., Wilkinson et al., 2016; Fredston and Lowndes, 2024). Additionally, dedicating funds to actively gather and archive publicly funded data, as well as giving fair credit and recognition to data collectors (professionally and scientifically, for example by making data papers a more highly valued academic merit), are fundamental components of the future of scientific big data (Wood-Charlson et al., 2022). Nonetheless, while maybe not matching the growing trend of dendroecology as a field, contributions to the ITRDB have increased in recent years, giving clear reasons for optimism. Since 2002, when the year of contribution started to be documented, the ITRDB averages 186 studies/year. Since 2019, the average is 264, and 2023 saw 331 new datasets contributed.

We believe analyses aiming to detect and communicate data bias are a powerful yet underused tool that can address both issues, allowing the field to identify and prioritize sampling of underrepresented conditions and taxa, and then guiding community efforts towards building increasingly representative datasets (Zhao et al., 2018). Currently, researchers upload data associated with their studies to larger databases without much consideration to the larger-scale needs and limitations in the database. This lack of database-wide consistency and context also affects those who wish to access and use the data for their analyses, who may well not be aware of the traditions and limitations in the field. Bias analyses approaches can recognize and incentivize the contribution of critically missing data, motivating researchers to pursue, and funders to fund, its acquisition and promote greater availability. Incorporating bias and representativity metrics, so they are easily available and displayed across the databases' portal will improve interpretation and contextualization of results from these data, and provide clear guidelines to promote future representative data collection.

2.2. Encouraging the integration of tree-ring data with other ecological datasets

Tree-ring data are not well-integrated within most ecological data networks, despite the potential insights that such integration would bring (Babst et al., 2017). For example, building connections between functional traits regulating resource acquisition, stress tolerance, and competitive ability (especially foliar traits) with growth data from the ITRDB would help form a more complete picture of growth efficiency and environmental responsiveness. Unfortunately, trait databases (e.g. TRY, Kattge et al., 2020) are seldom linked to annual tree-ring data. Instances in which tree ring data are integrated with other types of ecological data have led to substantial advancements. For instance, within paleoecological networks, tree ring data are sometimes combined with other proxy reconstruction data such as ice cores, fossil, or pollen records. Similarly, in LTER datasets (<https://lternet.edu/using-lter-data/>), associated dendrochronological data are often available and used jointly with many other data proxies (e.g. D'Orangeville et al., 2022). These examples remain the exception rather than the rule, and, large tree-ring databases also rarely accommodate data collected following typical ecological sampling (such as forest structure and composition or tree size), meaning that very little tree-ring data collected in this way have been integrated into ITRDB despite the potential such additional information would provide for a more robust ecological forecasting of tree growth (Heilman et al., 2022) and other applications.

Understanding early tree ring research may provide helpful historical context for the origin of today's databases. Early research on regional and global climate histories in tree-ring research started in the 1960s and 1970s. The development of the ITRDB started in the 1970s and,

today, is a five-decade testament to how data sharing can enhance a broad research community. During the 1960s and 1970s, landscape ecology was taking center stage. It was not likely until a decade or two later until regional and global scale ecological studies began moving onto that stage. Remote sensing and satellites did much to grow this field, and only in the last decade or so did dendroecological studies become prominent at subcontinental and larger scales (other than a few early pioneering studies e.g. Brubaker, 1980, Johnson et al., 1988, Swetnam and Betancourt, 1990, Villalba et al., 2001, Graumlich, 1993).

In fact, non-ring-width dendroecological data have also struggled to be integrated in the currently rigid structure of large tree-ring databases, prompting the emergence of alternative, case-specific databases, such as IMPD (<https://www.ncei.noaa.gov/products/paleoclimatology/fire-history>), which include fire scar chronologies among its data, or DEN (Rayback et al., 2020) for dendroecological plots, mostly in the Northeastern US. These great initiatives show that it is certainly feasible to incorporate a richer and more complex metadata into ITRDB's dataset. Whether it is better to expand the ITRDB to incorporate more data types or build more case-specific databases for different types of proxies is unclear. Case-specific databases can be more targeted and tailored to the specific needs of the field, but they also run the risk of being hard to find and thus underused by the broader community. Regardless, updating and expanding current widely used databases to better incorporate additional types of data should be a priority if we are to increase their use. In fact, the ITRDB has made remarkable progress in the last years on many of the most pressing issues identified by the community, such as assigning DOI, data verification, accessibility, and error correction (Manzanedo and Pederson, 2019; Guiterman et al., 2024). This work needs to continue and expand. Improving data structures to accommodate the valuable diversity of data that the tree-ring community produces and expand the associated metadata to more modern standards to improve data quality, diversity, and accessibility.

A knowledge gap that hampers the access to and widespread use of open tree-ring data by non-tree-ring experts is the scarcity of information on how to use (and not misuse) tree-ring big data. To provide one example, many ITRDB studies aimed at reconstructing climate, sampled 20–40 large, old, and canopy-dominant trees, living under low or no competition in marginal conditions, with target trees usually non-randomly selected over a large area (discussed in Carrer, 2011), and usually taking multiple (frequently two) samples per tree. This sampling strategy is so widespread that it is not even always explicitly stated. In addition, ITRDB does not include any information regarding sampling, nor does it provide GPS coordinates per tree, but a general location per site. Naming schemes to signal samples from the same tree are also not always consistent, especially for older collections, which makes it difficult for anyone to assess whether two growth series are from the same tree or not. All of this is unlikely to be known by any non-tree-ring expert accessing and using the data. Linking tree growth with large satellite products (e.g. soil, temperature, slope, or topographical products) without considering this local variability, pseudoreplication, and lack of general representativity can lead to erroneous conclusions.

Increasing tree ring data accessibility will help foster multidisciplinary ecological research, but doing so without providing guidelines and best-practices in tree-ring big data is likely to affect results, and thus dendroecology's credibility as a whole. Of course, directly involving tree-ring experts in multidisciplinary teams offers one means to address this, but since this is not always feasible, we believe the broader community would greatly benefit from the creation of user-friendly guidelines to help with key aspects of using and interpreting big tree-ring data. These guidelines may take the form of openly available concise papers or reports and cover aspects such as historical sampling design, individual tree targeting, core selection and discarding practices, consequences of detrending and chronology building, limitations and advances in tropical dendrochronology, and interpretation of new tree-ring metrics (e.g. Frank et al., 2022, Andreu-Hayles et al., 2023, Druckenbrod et al., 2024). The combination of these easily accessible

information with increased transparency of data bias and representativity can ensure a better use of big open tree ring data.

2.3. Promoting theory-driven and mechanistic dendroecological approaches

In addition to addressing data limitations and enhancing integration, we emphasize the importance of theory-driven and mechanistic approaches in dendroecological research. While we should strive to improve the available data, this should not stop us from continuing to improve the methods to address the unbalanced and inherently complex structure that are likely to always exist in big ecological data. Understanding *why* we see the climatic and ecological patterns in tree rings may require a deeper exploration of the physiological underpinnings of wood structure and growth, and measurements at a scale below the ring-level. Likewise, core collections hold a mostly untapped record of inter-annual variation in hydraulic parameters and investment in ray parenchyma that could unravel the impact of climate on feedback relationships between wood structure and tree performance.

Dendrochronology's history, with its early focus on climatic reconstruction and cross-dating assistance, has led to legacies in both the methodological approaches applied and the types of questions asked. For example, many dendroecological studies use correlative rather than mechanistic approaches for quantifying growth patterns of interest, focus on pooled signals (e.g. site averages) rather than explicitly quantifying variation among populations and individuals, and often employ a highly selective sampling strategy focused on maximizing tree-to-tree agreement and climatic signal (but see e.g. Carrer, 2011 and Perret et al., 2024). Studies focusing on climate-growth correlations can greatly benefit from incorporating broad ecological theories (e.g. diversity-productivity, fundamental-realized niches, coexistence theory). Similarly, tree traits could benefit from involving long-term perspective through the use of tree-ring-based traits (e.g. Housset et al., 2018). Quantifying climate-growth relationships in this time of climate change continues to be an important goal. However, ecological tree-ring studies will benefit from a more robust framework for hypothesis testing and the development of predictive models, building upon existing theoretical frameworks in ecology, physiology, and dendrochronology.

Continuous reevaluation of methodological approaches in tree-ring sciences will ensure their suitability for ecological investigations. Sampling trees across life stages and canopy positions (e.g., Ettinger and HilleRisLambers, 2013), and developing standardization models that do not remove biotic processes and disturbances (e.g. Rollinson et al., 2016), are great starting points to achieve a more ecological framework for tree-ring based studies. Another point perhaps not frequently discussed is the practice of discarding samples due to weaker agreement with overall chronologies. While this approach may be well-suited when the goal is reconstructing past climates (Fritts, 1976), it does not seem appropriate for many ecological investigations. For example, understanding the growth of an entire population of trees, rather than a small subset of large open-grown trees in harsh conditions or canopy trees, will give a greater insight into the ecology of whole forests (Pederson et al., 2017).

Expanding our understanding of the physiological processes governing xylogenesis (the process of radial wood production by the cambium), growth allocation, and their links to other plant traits and processes, will also strengthen our ability to mechanistically relate tree-ring widths to abiotic factors and biotic interactions. In this sense, xylogenesis is crucial to integrate into our understanding the significance of ring-level variation. Xylogenesis requires positive internal water pressure (turgor) for living cambial cells to expand and divide. When water availability is low, biophysical limitations on cell growth are reached when turgor levels are insufficient to breach the yield-threshold for cell wall division and expansion (Cosgrove et al., 1984; Cosgrove, 2005) and growth ceases throughout the tree (Peters et al., 2021). The mechanisms of climate-driven growth cessation or alteration

are a growing area of research and deepening our understanding will facilitate linking climate, carbohydrate storage, legacy effects, and tree growth in a cohesive framework.

We would be remiss not to shortly mention some of the most exciting advancements in tree-ring ecology in recent years particularly the remarkable development of tropical and subtropical ecology (e.g. Quesada-Román et al., 2022; Zuidema et al., 2022), the expansion of proxies further than the traditional width-related ones, such as high-resolution isotopic composition (e.g. van der Sleen et al., 2017; Vitali et al., 2021), advancements in multiproxy approaches to improve forecasting (e.g. Heilman et al., 2022), intra-annual growth metrics from microcores (e.g. Rademacher et al., 2022), moving towards studying individual tree responses within plots (e.g. Trouillier et al., 2018), and microCT scanning approaches for high-resolution physiology (Van den Bulcke et al., 2014), all highlight the incredible promise to deepen our understanding of tree ecology across scales and ecosystems worldwide offered by dendroecology.

3. Conclusions

As large dendroecological datasets expand and become more accessible, the time is ripe for proactive measures to promote their integration into mainstream ecology and address some of their longer standing issues. We have highlighted here three main lines of actions that focus on communication, integration and mechanistic research. These can be summarized in these direct actions:

- Increase transparency and information on available tree ring data and sampling biases, including using bias analyses to optimize new data collection.
- Promote contributing and maintaining open data more positively in career development and funding decisions, especially for those whose research contributes critically missing data.
- Continue to modernize and consolidate large tree ring databases, incorporating the knowledge gained from many successful ongoing initiatives in the field.
- Continue and expand funding and support to tree ring repositories and data collectors to allow them to host more and more diverse tree ring data.
- Produce easily accessible guidelines on best practices (and pitfalls) of using big tree ring data to promote its correct, wider use. Continuous re-evaluation of these practices when applied to ecological questions is also paramount.
- Promote mechanistic approaches and ecological theory-driven approaches as a central part of dendrochronology.

By focusing on these issues, we can start to unlock the full potential of tree-ring data, as a central pillar of long-term ecology.

CRediT authorship contribution statement

Rubén D. Manzanedo: Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Alana R.O. Chin:** Writing – review & editing, Conceptualization. **Ailene K. Ettinger:** Writing – review & editing, Conceptualization. **Neil Pederson:** Writing – review & editing, Conceptualization. **Kavya Pradhan:** Writing – review & editing, Conceptualization. **Christopher H. Guiterman:** Writing – review & editing, Conceptualization. **Jiajia Su:** Writing – review & editing. **Frederik Baumgarten:** Writing – review & editing, Conceptualization. **Janneke Hille Ris Lambers:** Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

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Data availability

No data was used for the research described in the article.

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