

## Viewpoint

# Cones and consequences: the false dichotomy of conifers vs broad-leaves has critical implications for research and modelling

## Summary

In plant science research and modelling, particularly from the northern hemisphere, the terms ‘needle-leaved’ and ‘conifer’ along with ‘broad-leaved’ and ‘angiosperm’ are often used synonymously, creating the false dichotomy that conifers are needle-leaved and angiosperms are broad-leaved. While these equivalences may be largely correct in the temperate northern hemisphere, they do not hold true in equatorial and southern hemisphere forests. Confounding needle-leaved conifers and broad-leaved angiosperms presents significant issues in empirical research and modelling. Here, we highlight the likely origins and impacts of misusing conifer-related terminology, the misinterpretation that ensues and its implications. We identify the issue of a focus on Pinaceae and coin the term ‘Pinaceae panacea’ to describe this. We provide recommendations for future research: from standardising the use of definitions to shifting away from using Pinaceae as a model group for all conifers.

## The problem

In plant science and modelling, the use of the binary ‘conifers’ vs ‘broad-leaves’ to categorise tree species, forests and define plant functional types is alarmingly common. At the root of this is the direct comparison of a morphological term, ‘broad-leaves’ and a taxonomic term, ‘conifer’. With ‘conifer’ often used synonymously and interchangeably with ‘needle-leaved’, this dichotomy implies that conifers and broad-leaved are antonyms, negating the global diversity in leaf shape across both conifer and angiosperm trees. The incorrect equation of needle-leaved and conifer, along with broad-leaved and angiosperm sets up a false dichotomy which has cascading negative implications. This starts with negating the diverse array of leaf morphologies displayed by conifer and angiosperm species. These categories, or derivations of these, are used in many scientific publications including empirical research, global models and predictions. The misuse of terms and subsequent

miscategorisation of trees therefore affects our understanding of plant systems and the accuracy of our projections with implications for research, conservation and beyond.

## Definitions

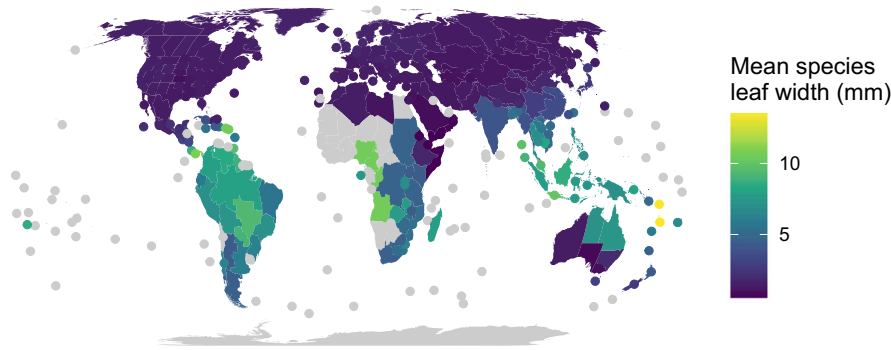
Trees, which are the focus of this paper, can be categorised as either gymnosperms or angiosperms. *Gymnosperms* are nonflowering seed plants that encompass but are not limited to conifers, cycads and ginkgos. *Conifers* are defined as plants belonging to the Coniferae, the order of woody gymnosperms comprising trees bearing cones (Oxford English Dictionary, 2023) which can exhibit many leaf widths and shapes (Fig. 1) and consist of c. 615 perennial extant species (Farjon, 2018). *Angiosperms* are the most numerous, diverse and widespread extant plant group (Kvaček *et al.*, 2020) taking many forms, from herbs to shrubs and trees, and also exhibit diverse leaf morphologies.

While there are many leaf shapes in trees, for example, awl and scale leaves, here we focus primarily on the two leaf shapes which are the basis of most misattribution of tree-related terminology and classification: *needle-leaf* refers to a narrow leaf form, sometimes also termed ‘acicular’. While more common in conifers, this leaf shape is also present in angiosperms, notably in, but not limited to, Proteaceae (e.g. *Hakea lissosperma*, *Orites acicularis*, *Grevillea rosmarinifolia*; Fig. 1) with species occurring in dry climates across Eurasia and Africa. *Broad-leaf* encompasses all leaves that possess a large surface area. Many angiosperms have broad-leaves, a character which has evolved to maximise light capture through photosynthesis (Biffin *et al.*, 2011) but this leaf shape is also present in conifers, for example, in many species within Podocarpaceae and Araucariaceae.

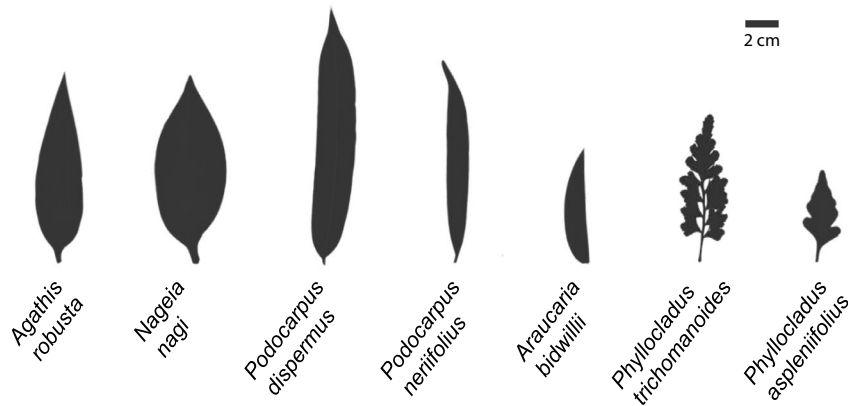
## The ‘Pinaceae Panacea’

One of the key advantages of using conifers as an ecological study group is that they are near-globally distributed, with representatives in a wide range of ecosystems (Fig. 2). However, treating ‘coniferous’ as a synonym for ‘needle-leaved’ reduces conifers to largely the northern hemisphere temperate species, many of which are members of Pinaceae (Fig. 2). The ecological dominance and relative morphological homogeneity of this group combined with the historically large proportion of scientific research from the global north (Auge *et al.*, 2024) underpins the emergence of what we term the ‘Pinaceae panacea’ (whereby Pinaceae is often used as a model group for all conifers), and the false dichotomy of ‘needle-leaved’ conifers vs ‘broad-leaved’ angiosperms. For example, foliar nitrogen records for gymnosperms in the TRY database (Kattge *et al.*, 2020) are almost entirely (91.5%) species in Pinaceae, with just 4.3% of records belonging to Southern hemisphere species.

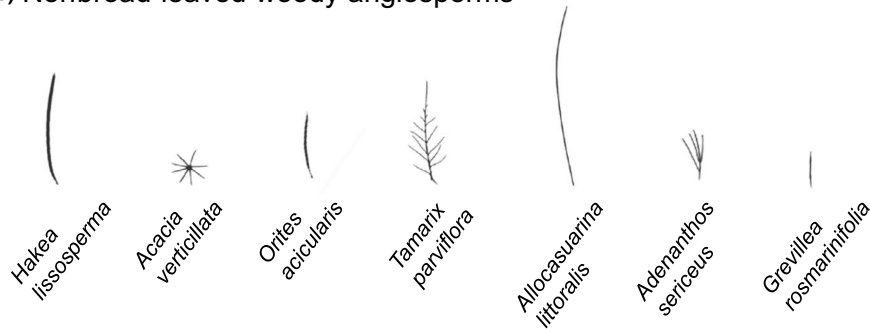
## (a) Mean leaf width in conifer species



## (b) Broad-leaved conifers



## (c) Nonbroad-leaved woody angiosperms

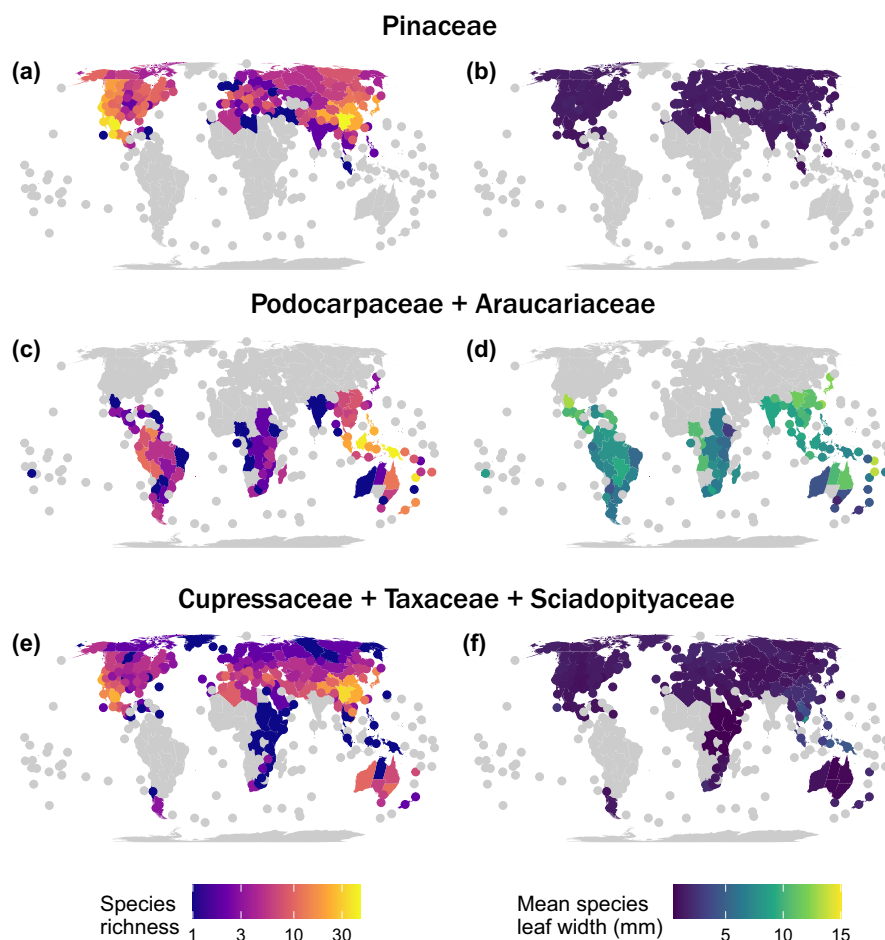


**Fig. 1** Global distribution of conifer leaf widths and silhouettes of both broad-leaved conifers and nonbroad-leaved woody angiosperms. (a) Geographic distribution of conifer leaf width. The colour gradient shows the mean leaf width (mm) of native conifer species, mapped at 'botanical country' resolution (Level 3 of the World Geographic Scheme for Recording Plant Distributions; Brummitt, 2001). (b) Leaf scans of broad-leaved conifers and (c) nonbroad-leaved woody angiosperms; leaves in (b, c) are scans taken from fresh material. Bar, 2 cm.

In northern temperate and boreal systems, evergreen, needle-leaved conifers generally dominate high latitudes and elevations, whereas broad-leaved, deciduous angiosperms occupy lower latitudes and elevations (Sprugel, 1989). However, this pattern does not hold true for global plant diversity. In tropical ecosystems, home to over half of all conifer species (52.5% native to the tropics and subtropics; from the World Checklist of Vascular Plants; Govaerts *et al.*, 2021), the morphological and ecological differences between conifers and angiosperms are less apparent. Conifers in these systems tend to be members of the 'southern conifers' (Podocarpaceae, Araucariaceae, Callitroideae, Fig. 2), separated from the characteristic northern lineages (including Pinaceae) by over 60 million years of evolutionary and ecological isolation (Leslie *et al.*, 2012).

The evolution of the major northern hemisphere clades Pinaceae and Cupressoideae (Cupressaceae) has been driven primarily by

temperature; these clades include many species with extreme resistance to cold (Strimbeck & Schaberg, 2009) and more recent evolutionary radiations (Forest *et al.*, 2018). These clades both feature trees which share many physical characteristics, with slim leaves that can be needle-like (Pinaceae), thin and flattened (e.g. *Larix*-larch and *Pseudotsuga*-Douglas fir) or scale-like and tightly appressed to the stem (e.g. *Juniperus*, *Sequoia*). By contrast, the southern conifer clades (Podocarpaceae, Araucariaceae and Callitroideae) tend to have much older lineages (Forest *et al.*, 2018) and display higher variation in leaf form, from scale-like and appressed (e.g. *Microcachrys*, *Callitris*) to awl-like (e.g. *Araucaria*) and even broad and multi-veined (e.g. *Nageia*, *Agathis*, *Phyllocladus*) (Fig. 1). Water, rather than temperature, has been the primary long-term ecological constraint for these southern lineages (Leslie *et al.*, 2012; Brodribb *et al.*, 2014; Brown *et al.*, 2021). These hemisphere-scale differences are apparent even



**Fig. 2** The relationships between hemisphere, clade and leaf morphology for the major extant conifer clades. Species richness (a, c, e) of each of the three major conifer clades (from Leslie *et al.*, 2012), mapped to botanical countries and distribution of mean leaf width (b, d, f) partitioned by clade.

within genera, with *Pinus krempfii*, the only species of Pinaceae that occurs in the southern hemisphere, featuring wide, flattened leaves that are functionally more similar to those of podocarps than other *Pinus* species (Brodribb & Feild, 2008).

We note that the tendency to use the temperate northern hemisphere as a proxy for global biodiversity is not unique to conifers; latitudinal biases and shortfalls in plant science are well documented, from foundational taxonomic knowledge (Freeman & Pennell, 2021) to species' distributions (Diniz Filho *et al.*, 2023), traits (Maitner *et al.*, 2023) and other data (e.g. genome size; table S4 in Soto Gomez *et al.*, 2024). These biases are further compounded by differences in digitisation and availability of data (e.g. Ronquillo *et al.*, 2023) and access to herbarium specimens due to their physical locations (Park *et al.*, 2023). While addressing these shortfalls directly will require sustained, targeted collection and digitisation efforts, imprecise use of language further reinforces and amplifies biases towards temperate, northern hemisphere science.

### Implications: empirical research

Empirical research, based on experiments and observation, produces fundamental and foundational information on plants at the cellular, organismic, population and ecosystem scales. This knowledge informs conservation and modelling. However, it is not

uncommon to see empirical research in trees using, or based on, the false dichotomy of conifers vs broad-leaves (i.e. Bachofen *et al.*, 2024; Li *et al.*, 2024; Shi *et al.*, 2024). In many studies, conifer vs broad-leaf terminology is prevalent in the study context (i.e. introduction) and is used to build aims and hypotheses which inform the conclusions and new research perspectives, perpetuating the incorrect use of these terms in future research.

Research papers from across diverse topics frame hypotheses around comparing broad-leaves (sometimes referred to as hardwood) vs coniferous (referred to as softwood) forests (Seiwa *et al.*, 2021; Morikawa *et al.*, 2022). The subjects of these papers include but are not limited to responses to environmental changes (Zhang *et al.*, 2020; Q. Liu *et al.*, 2023), carbon flux and allocation (Oulehle *et al.*, 2018; Rog *et al.*, 2024), the impact of forest type on run-off (Swank & Douglass, 1974; Komatsu *et al.*, 2011), soil pollution (Steinparzer *et al.*, 2023), soil invertebrates and soil fertility (J. Liu *et al.*, 2023), vertebrates (Mittelman *et al.*, 2024) and forest evapotranspiration (Komatsu *et al.*, 2007). While the needle-leaved conifer and broad-leaved angiosperm forest dichotomy does exist, particularly in the northern hemisphere, when the study focal region is not clearly stated and the limitations of the conclusions are not acknowledged, these studies perpetuate the northern hemisphere centric concept of a binary in forest types, negating global tree and forest diversity.

Importantly, a continued focus on solely coniferous needle-leaved and angiosperm broad-leaved forests, without the acknowledgement of alternatives, leads to a widening gap in our knowledge of important alternative forest systems. This results in a negation of the tropics, where many broad-leaved conifers reside (Govaerts *et al.*, 2021). The tropics are not only home to a large proportion of terrestrial biodiversity but are also identified as being particularly vulnerable to climate and land-use change (Newbold *et al.*, 2015). Forests dominated by needle-leaved angiosperms such as the *Allocasuarina* forests of Australia and southeast Asia (Chonglu *et al.*, 2005; Broadhurst, 2012) are also neglected under a binary view of forest types. With the information produced by empirical research playing a fundamental role in our global understanding of tree and forest function and dysfunction, considering only two of the wide and varying forest types (i.e. the Food and Agriculture Organization reported 20 forest types, FAO & UNEP, 2020) leads to a misunderstanding of forest responses to biotic and abiotic stressors.

### Implications: plant functional types and global modelling

Inaccurate use of conifer-related terminology or using temperate northern species as a proxy for conifer diversity also has significant implications for global-scale modelling. Characterising and quantifying plant function is crucial for understanding how ecosystems work and therefore for better predictions of future changes. To describe ecosystem complexity, plant species are often categorised according to their functional traits into plant functional types (PFTs; Díaz *et al.*, 2016; Bongers *et al.*, 2021). These PFTs are used in land surface modelling, biodiversity characterisations and trait-based estimations of the distribution of vegetation types. Including PFTs increases the predictive power of estimations (Dechant *et al.*, 2024); however, PFTs are found to be most accurate in comparatively low diversity areas such as Europe and less precise in more complex systems with higher diversity (Peaucelle *et al.*, 2017). The groupings represented in PFTs are not fixed categories, and the species they benchmark can vary depending on the available data or the purpose of the study (Dechant *et al.*, 2024).

Plants are most commonly classified based on a combination of growth form, leaf type and leaf phenology (i.e. evergreen needle-leaf tree: Ma *et al.*, 2023; Dechant *et al.*, 2024; Hasler *et al.*, 2024). Databases such as TRY (Kattge *et al.*, 2020) or the Tallo dataset (Jucker *et al.*, 2022) include categories that allow accurate classification of leaf types with terms, such as growth form, leaf type, leaf phenology, woodiness, phylogenetic group. Using leaf characteristics and taxonomy, PFTs can be assigned easily without employing the conifer vs broad-leaf dichotomy, which can lead to miscategorisations of tree and forest types.

The most controversial use of PFTs in trees generally occurs in two scenarios: (1) when regional characteristics are upscaled to the global level, such as in generalisations of plant strategies; or (2) when PFTs include 'conifer' or 'broad-leaf' categories that are not underpinned by accurate taxonomic or leaf morphological definitions.

Conifers in the northern hemisphere are often described as early successional species, having fast growth rates and high fecundity when resources are abundant, using mainly Pinaceae as a reference. By contrast, 'broad-leaves' (referring to angiosperms) are often presented with the opposite traits (Westoby & Wright, 2006; Chave *et al.*, 2009). However, these generalisations are largely only true when considering northern hemisphere temperate forests, with global conifers encompassing a diverse array of ecological strategies (Biffin *et al.*, 2011). This becomes an issue when global studies utilise research with a regional focus to support their statements. An example of this is illustrated in a study that maps leaf form and habit at a global scale (Ma *et al.*, 2023). The authors base the idea that broad-leaved and needle-leaved trees have contrasting water use strategies on a study focussed solely on boreal systems (Augusto *et al.*, 2015), and likewise, the idea that needle-leaved species have lower photosynthetic rates than their broad-leaved counterparts is based on a study focused solely on evergreen conifers and angiosperms in productive habitats (Lusk *et al.*, 2003). In other cases, the existence of broad-leaved gymnosperms is omitted in global studies (Yang *et al.*, 2024), possibly due to a dearth of sampled data for broad-leaved gymnosperms, influenced by the effects of the 'Pinaceae Panacea'.

Direct misuse of conifer-related terminology in defining PFTs also results in miscategorisation. A common source of confusion derives from Olson *et al.* (2001), with almost 6000 citations, which defines ecoregions. Some of the categories in this framework are limiting, for example, 'tropical and subtropical conifer forests' and 'tropical and subtropical dry/moist broad-leaved forests'. This enhances and perpetuates the conifer/broad-leaf dichotomy and precludes the inclusion of the many broad-leaved conifers of the southern hemisphere. Adopting these categories for defining PFTs in subsequent research has led to sustained use of these misleading groupings. Of the 647 gymnosperm species with at least one trait measurement in the TRY database (Kattge *et al.*, 2020), only 50.7% are categorised as needle-leaved. If treating all conifers as needle-leaved, and all angiosperms as broad-leaved, the ecological significance of leaf morphology is likely to be obscured by the mis-categorisation of nearly half of all conifer species in the database. Examples of this erroneous categorisation can be found in some of an author's own work (Vallicrosa *et al.*, 2022a,b) and in other examples that followed a similar approach (Bouchard *et al.*, 2024; Mo *et al.*, 2024; Sarneel *et al.*, 2024).

The recent examples mentioned above (all published within the last 3 years) demonstrate the prevailing widespread misattribution of terminology for tree classification in modelling that underpins important global studies and predictions. Such miscategorisations are especially concerning since they are repeatedly reviewed and published in high-impact journals. Miscategorising trees systematically neglects a significant portion of global plant diversity and perpetrates the historical under sampling of the global south (Auge *et al.*, 2024).

### Recommendations

We outline some practical recommendations to minimise miscategorisation and misinterpretation in our collective efforts



as a research community to categorise trees and predict their responses in a changing climate.

### Avoid the false 'conifer', 'broad-leaf' dichotomy

Using 'conifer' and 'broad-leaf' as distinct categories in global studies is misleading. 'Conifers' and 'broad-leaves' are only distinct categories in specific regions of the globe, while this dichotomy does not hold in many others. By strictly using a combination of growth form, leaf type (considering the various morphologies such as awl-shaped, scale, etc.) and leaf phenology, we can safely upscale our results to a broader scale.

### Stop using Pinaceae as the sole model group for conifers

Despite being one of the most studied families among gymnosperms, Pinaceae is not representative of all conifers. Where possible, including reference to the diversity contained within conifers from other families is desired and strongly encouraged. If the desired information about other conifer families is unavailable, we suggest discussing the lack of information for these less studied families and encouraging further research.

### Separate taxonomic and morphological terms and contextualise your study

Morphological and taxonomic terms should never be used interchangeably, especially in global studies. When categorising forests and trees, we suggest using both the taxonomic (angiosperm vs gymnosperms) and morphological (broad-leaved vs needle-leaved) categorisations used in the TRY database (Kattge *et al.*, 2020). For more localised studies, where 'conifer' can be synonymous with 'needle-leaved', we recommend clearly contextualising statements.

### Careful selection of references as an author and a reviewer

Both when writing and reviewing work, care should be taken when selecting references to ensure that previous misuse of conifer-related categorisations and terminology is not perpetuated. More specifically, definitions of tree or forest types that only apply to northern hemisphere systems should not be used to make inferences about conifers or angiosperms at a global scale.

## Conclusion

Classification of conifers as solely needle-leaved and angiosperms as broad-leaved is incorrect and misrepresents the global diversity of trees. This has consequences not only for reducing the visibility of tree diversity with implications for conservation but also for empirical research, describing global flora and predicting future patterns using PFTs. We by no means intend to disregard the validity of the research contained within the papers that we cite, but rather to identify the potential or realised impacts of using this common dichotomy incorrectly, arguing that misuse of terminology in classifying trees can have

severe consequences for the study of ecosystems and the accuracy of predictions about the future of our forests. However, we believe that by acknowledging this issue and following the recommendations outlined above, we can collectively undertake research and build predictive models that are accurate and representative, underpinned by clear, considered and well-defined terminology.

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## Competing interests

None declared.

## Author contributions

KMJ and HV conceived the Viewpoint, wrote the initial draft and contributed equally to the manuscript. MJMB and KIB provided data and created visuals. All authors contributed ideas and wrote the final manuscript.

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## References

- Augé G, Sunil RS, Ingle RA, Rahul PV, Mutwil M, Estevez JM. 2024. Current challenges for plant biology research in the Global South. *New Phytologist* 244: 1168–1174.
- Augusto L, De Schrijver A, Vesterdal L, Smolander A, Prescott C, Ranger J. 2015. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. *Biological Reviews* 90: 444–466.
- Bachofen C, Tumber-Dávila SJ, Mackay DS, McDowell NG, Carminati A, Klein T, Stocker BD, Mencuccini M, Grossiord C. 2024. Tree water uptake patterns across the globe. *New Phytologist* 242: 1891–1910.
- Biffin E, Brodribb TJ, Hill RS, Thomas P, Lowe AJ. 2011. Leaf evolution in Southern Hemisphere conifers tracks the angiosperm ecological radiation. *Proceedings of the Royal Society B: Biological Sciences* 279: 341–348.
- Bongers FJ, Schmid B, Bruehlheide H, Bongers F, Li S, von Oheimb G, Li Y, Cheng A, Ma K, Liu X. 2021. Functional diversity effects on productivity increase with age in a forest biodiversity experiment. *Nature Ecology & Evolution* 5: 1594–1603.
- Bouchard E, Searle EB, Drapeau P, Liang J, Gamarra JGP, Abegg M, Alberti G, Zambrano AA, Alvarez-Davila E, Alves LF *et al.* 2024. Global patterns and environmental drivers of forest functional composition. *Global Ecology and Biogeography* 33: 303–324.
- Broadhurst LM. 2012. Genetic diversity and population genetic structure in fragmented *Allocasuarina verticillata* (Allocasuarinaceae) – implications for restoration. *Australian Journal of Botany* 59: 770–780.
- Brodribb TJ, Feild TS. 2008. Evolutionary significance of a flat-leaved *Pinus* in Vietnamese rainforest. *New Phytologist* 178: 201–209.
- Brodribb TJ, McAdam SA, Jordan GJ, Martins SC. 2014. Conifer species adapt to low-rainfall climates by following one of two divergent pathways. *Proceedings of the National Academy of Sciences, USA* 111: 14489–14493.
- Brown MJM, Brodribb TJ, Jordan GJ. 2021. No-analogue associations in the fossil record of southern conifers reveal conservatism in precipitation, but not temperature axes. *Global Ecology and Biogeography* 30: 2455–2466.
- Brummitt RK. 2001. *World geographic scheme for recording plant distributions*, 2<sup>nd</sup> edn. Pittsburgh, PA, USA: Hunt Institute for Botanical Documentation, Carnegie Mellon University.
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.
- Chonglu Z, Jiayu B, Yong Z. 2005. Introduction and conservation of casuarina trees in China. *Forest Research* 18: 345–350.
- Dechant B, Kattge J, Pavlick R, Schneider FD, Sabatini FM, Moreno-Martínez Á, Butler EE, van Bodegom PM, Vallicrosa H, Kattenborn T *et al.* 2024. Intercomparison of global foliar trait maps reveals fundamental differences and limitations of upscaling approaches. *Remote Sensing of Environment* 311: 114–276.
- Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC *et al.* 2016. The global spectrum of plant form and function. *Nature* 529: 167–171.
- Diniz Filho JAF, Jardim L, Guedes JJ, Meyer L, Stropp J, Frateles LEF, Pinto RB, Lohmann LG, Tessarolo G, de Carvalho CJB *et al.* 2023. Macroecological links between the Linnean, Wallacean, and Darwinian shortfalls. *Frontiers of Biogeography* 15: e59566.
- FAO, UNEP. 2020. *The State of the World's Forests (SOFO)*. doi: [10.4060/ca8642en](https://doi.org/10.4060/ca8642en).
- Farjon A. 2018. The Kew review: conifers of the world. *Kew Bulletin* 73: 8.
- Forest F, Moat J, Baloch E, Brummitt NA, Bachman SP, Ickert-Bond S, Hollingsworth PM, Liston A, Little DP, Mathews S *et al.* 2018. Gymnosperms on the EDGE. *Scientific Reports* 8: 6053.
- Freeman BG, Pennell MW. 2021. The latitudinal taxonomy gradient. *Trends in Ecology & Evolution* 36: 778–786.
- Govaerts R, Nic Lughadha E, Black N, Turner R, Paton A. 2021. The World Checklist of Vascular Plants, a continuously updated resource for exploring global plant diversity. *Scientific Data* 8: 215.
- Hasler N, Williams CA, Denney VC, Ellis PW, Shrestha S, Terasaki Hart DE, Wolff NH, Crowther TW, Werden LK, Cook-Patton S. 2024. Accounting for albedo change to identify climate-positive tree cover restoration. *Nature Communications* 15: 2275.
- Jucker T, Fischer FJ, Chave J, Coomes DA, Caspersen J, Ali A, Loubota Panzou GJ, Feldpausch TR, Falster D, Usoltsev VA *et al.* 2022. Tallo: a global tree allometry and crown architecture database. *Global Change Biology* 28: 5254–5268.
- Kattge J, Bönsch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala T, Abedi M *et al.* 2020. TRY plant trait database – enhanced coverage and open access. *Global Change Biology* 26: 119–188.
- Komatsu H, Kume T, Otsuki K. 2011. Increasing annual runoff – broadleaf or coniferous forests? *Hydrological Processes* 25: 302–318.
- Komatsu H, Tanaka M, Kume T. 2007. Do coniferous forests evaporate more water than broad-leaved forests in Japan? *Journal of Hydrology* 336: 361–375.
- Kvaček J, Coiffard C, Gandolfo M, Herman AB, Legrand J, Mendes MM, Nishida H, Ge S, Wang H. 2020. When and why nature gained angiosperms. In: Martinetto E, Tschopp E, Gastaldo RA, eds. *Nature through time*. Cham, Switzerland: Springer, 129–158.
- Leslie AB, Beaulieu JM, Rai HS, Crane PR, Donoghue MJ, Mathews S. 2012. Hemisphere-scale differences in conifer evolutionary dynamics. *Proceedings of the National Academy of Sciences, USA* 109: 16217–16221.
- Li J, Xie Y, Camarero JJ, Gazol A, de González Andrés E, Ying L, Shen Z. 2024. Optimistic growth of marginal region plantations under climate warming: assessing divergent drought resilience. *Global Change Biology* 30: e17459.
- Liu J, Wang X, Kou Y, Zhao W, Liu Q. 2023. Differences in the effects of broadleaf and coniferous trees on soil nematode communities and soil fertility across successional stages. *Plant and Soil* 485: 197–212.
- Liu Q, Song M, Kou L, Li Q, Wang H. 2023. Contrasting effects of nitrogen and phosphorus additions on nitrogen competition between coniferous and broadleaf seedlings. *Science of the Total Environment* 861: 160661.
- Lusk CH, Wright I, Reich PB. 2003. Photosynthetic differences contribute to competitive advantage of evergreen angiosperm trees over evergreen conifers in productive habitats. *New Phytologist* 160: 329–336.
- Ma H, Crowther TW, Mo L, Maynard DS, Renner SS, Van den Hoogen J, Zou Y, Liang J, de-Miguel S, Nabuurs GJ *et al.* 2023. The global biogeography of tree leaf form and habit. *Nature Plants* 9: 1795–1809.
- Maitner B, Gallagher R, Svenning JC, Tietje M, Wenk EH, Eiserhardt WL. 2023. A global assessment of the Raunkiaerian shortfall in plants: geographic biases in our knowledge of plant traits. *New Phytologist* 240: 1345–1354.
- Mittelman P, Appleby SM, Balkenhol N. 2024. Forest composition shapes seed-rodent interactions in a gradient of broadleaves and conifers. *Journal of Applied Ecology* 61: 1944–1954.
- Mo L, Crowther TW, Maynard DS, van der Hoogen J, Ma H, Bialic-Murphy L, Liang J, de-Miguel S, Nabuurs GJ, Reich P *et al.* 2024. The global distribution and drivers of wood density and their impact on forest carbon stocks. *Nature Ecology & Evolution* 8: 2195–2212.
- Morikawa Y, Hayashi S, Negishi Y, Masuda C, Watanabe M, Watanabe K, Masaka K, Matsuo A, Suzuki M, Tada C *et al.* 2022. Relationship between the vertical distribution of fine roots and residual soil nitrogen along a gradient of hardwood mixture in a conifer plantation. *New Phytologist* 235: 993–1004.
- Newbold T, Hudson L, Hill S, Contu S, Lysenko I, Senior RA, Börger L, Bennett DJ, Choimes A, Collen B *et al.* 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520: 45–50.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC *et al.* 2001. Terrestrial ecoregions of the World: a new map of life on Earth. *Bioscience* 51: 933–938.
- Oulehle F, Tahovská K, Chuman T, Evans CD, Hruška J, Růžek M, Bárta J. 2018. Comparison of the impacts of acid and nitrogen additions on carbon fluxes in European conifer and broadleaf forests. *Environmental Pollution* 238: 884–893.
- Oxford English Dictionary. 2023. s.v. “conifer (n.)”. doi: [10.1093/OED/4171658952](https://doi.org/10.1093/OED/4171658952).

- Park DS, Feng X, Akiyama S, Ardiyani M, Avendaño N, Barina Z, Bärtschi B, Belgrano M, Betancur J, Bijmoer R *et al.* 2023. The colonial legacy of herbaria. *Nature Human Behaviour* 7: 1059–1068.
- Peaucelle M, Bellassen V, Ciais P, Peñuelas J, Viovy N. 2017. A new approach to optimal discretization of plant functional types in a process-based ecosystem model with forest management: a case study for temperate conifers. *Global Ecology and Biogeography* 26: 486–499.
- Rog I, Hilman B, Fox H, Yalin D, Qubaja R, Klein T. 2024. Increased belowground tree carbon allocation in a mature mixed forest in a dry versus a wet year. *Global Change Biology* 30: e17172.
- Ronquillo C, Stropp J, Medina NG, Hortal J. 2023. Exploring the impact of data curation criteria on the observed geographical distribution of mosses. *Ecology and Evolution* 13: e10786.
- Sarneel JM, Hefting MM, Sandén T, van den Hoogen J, Routh D, Adhikari BS, Alatalo JM, Aleksanyan A, Althuizen IHJ, Alsafran MHSA *et al.* 2024. Reading tea leaves worldwide: decoupled drivers of initial litter decomposition mass-loss rate and stabilization. *Ecology Letters* 27: e14415.
- Seiwa K, Kunii D, Masaka K, Hayashi S, Tada C. 2021. Hardwood mixture enhances soil water infiltration in a conifer plantation. *Forest Ecology and Management* 498: 119508.
- Shi Z, Meng Q, Luo Y, Zhang M, Han W. 2024. Broadleaf trees switch from phosphorus to nitrogen limitation at lower latitudes than conifers. *Science of the Total Environment* 914: 169924.
- Soto Gomez M, Brown MJM, Pironon S, Bureš P, Verde Arregoitia LD, Veselý P, Elliott TL, Zedek F, Pellicer J, Forest F *et al.* 2024. Genome size is positively correlated with extinction risk in herbaceous angiosperms. *New Phytologist* 243: 2470–2485.
- Sprugel DG. 1989. The relationship of evergreenness, crown architecture, and leaf size. *The American Naturalist* 133: 465–479.
- Steinparzer M, Schaubmayr J, Godbold DL, Rewald B. 2023. Particulate matter accumulation by tree foliage is driven by leaf habit types, urbanization- and pollution levels. *Environmental Pollution* 335: 122289.
- Strimbeck G, Schaberg P. 2009. Going to extremes: low-temperature tolerance and acclimation in temperate and boreal conifers. In: Gusta L, Wisniewski M, Tanino K, eds. *Plant cold hardiness: from the laboratory to the field*. Oxfordshire, UK: CABI, 226–239.
- Swank WT, Douglass JE. 1974. Streamflow greatly reduced by converting deciduous hardwood stands to pine. *Science* 185: 857–859.
- Vallicrosa H, Sardans J, Maspons J, Peñuelas J. 2022a. Global distribution and drivers of forest biome foliar nitrogen to phosphorus ratios (N:P). *Global Ecology and Biogeography* 31: 861–871.
- Vallicrosa H, Sardans J, Maspons J, Zuccarini P, Fernández-Martínez M, Bauters M, Goll DS, Ciais P, Obersteiner M, Janssens IA *et al.* 2022b. Global maps and factors driving forest foliar elemental composition: the importance of evolutionary legacy. *New Phytologist* 233: 169–181.
- Westoby M, Wright IJ. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution* 21: 261–268.
- Yang H, Wang S, Son R, Lee H, Benson V, Zhang W, Zhang Y, Zhang Y, Kattge J, Boenisch G *et al.* 2024. Global patterns of tree wood density. *Global Change Biology* 30: e17224.
- Zhang YL, Moser B, Li MH, Wohlgemuth T, Lei JP, Bachofen C. 2020. Contrasting leaf trait responses of conifer and broadleaved seedlings to altered resource availability are linked to resource strategies. *Plants* 9: 621.

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