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Compositional breakpoints of freshwater plant communities across continents

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ABSTRACT

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Unravelling patterns and mechanisms of biogeographical transitions is crucial if we are to understand compositional gradients at large spatial extents, but no studies have thus far examined breakpoints in community composition of freshwater plants across continents. Using a dataset of almost 500 observations of lake plant community composition from six continents, we examined, for the first time, if such breakpoints in geographical space exist for freshwater plants and how well a suite of ecological factors (including climatic and local environmental variables) can explain transitions in community composition from the subtropics to the poles. Our combination of multivariate regression tree (MRT) analysis and *k*-means partitioning suggests that the most abrupt breakpoint exists between temperate to boreal regions on the one hand and freshwater plant communities harbouring mainly subtropical or Mediterranean assemblages on the other. The spatially structured variation in current climatic conditions is the most likely candidate for controlling these latitudinal patterns, although one cannot rule out joint effects of eco-evolutionary constraints in the harsher high-latitude environments and post-glacial migration lags after Pleistocene Ice Ages. Overall, our study supports the foundations of global regionalisation for freshwater plants and anticipates further biogeographical research on freshwater plant communities once datasets have been harmonised for conducting large-scale spatial analyses.

Key words: aquatic macrophytes, biogeography, latitudinal patterns, regionalisation

RESUMEN

Puntos de inflexión en los gradientes de composición de las comunidades de plantas acuáticas de diferentes continentes

Desentrañar los patrones y mecanismos que subyacen a las transiciones biogeográficas es un requisito fundamental a la hora de comprender los gradientes de composición de las comunidades ecológicas a grandes extensiones espaciales, si bien ningún estudio ha examinado explícitamente estos puntos de inflexión para comunidades de plantas acuáticas de diferentes continentes. Utilizando una completa base de datos que condensa un total de casi 500 observaciones individuales sobre las comunidades florísticas lacustres de seis continentes, este trabajo pretende delinear las transiciones biogeográficas en plantas acuáticas a escala global, así como valorar el papel que desempeñan diversos mecanismos ecológicos (a saber, las condiciones climáticas y las características locales del hábitat) sobre estos puntos de inflexión en el espacio geográfico comprendido entre las latitudes subtropicales y los polos. Nuestros resultados obtenidos mediante la ejecución simultánea de árboles de regresión multivariante (MRT) y algoritmos de agrupación por k-*medias demuestran la existencia de un punto de inflexión entre las regiones templadas y boreales y los lagos localizados en las bandas subtropicales y en las inmediaciones del Mediterráneo. La estructura espacial que subyace a la distribución de los condicionantes climáticos en nuestro planeta parece ser el principal mecanismo de control de dichas transiciones biogeográficas, si bien estos patrones latitudinales también podrían explicarse en base a constricciones eco-evolutivas en las regiones más septentrionales y a la colonización diferencial de los territorios norteños antaño cubiertos por el hielo durante el Último Máximo Glacial. En síntesis, nuestro estudio proporciona una base teórica preliminar para futuras investigaciones encaminadas a delimitar las unidades geográficas de los principales componentes de la flora acuática contemporánea y también anticipa un creciente interés por los estudios de carácter fitogeográfico en las aguas continentales, si bien los análisis venideros deberán prestar especial atención a la armonización de datos biológicos potencialmente heterogéneos en naturaleza y con orígenes dispares.*

Palabras clave: *biogeografía, macrófitos acuáticos, patrones latitudinales, regionalización*

INTRODUCTION

Freshwater plants are a widely distributed group of photosynthetic organisms that play essential functional roles in freshwaters (Carpenter & Lodge, 1986, Chambers et al., 2008, Moi et al., 2022). For instance, together with microalgae, freshwater plants are responsible for the primary production of continental waters (Krause-Jensen & Sand-Jensen, 1998) and are an important food source for many other organisms (Carpenter & Lodge, 1986). Freshwater plants also act as ecosystem engineers by providing habitats and shelter to a variety of organisms (van Donk & van de Bund, 2002) and modulate the diversity and compositional variation of other aquatic animal communities (García-Girón et al., 2020a). Since freshwater plants are taxonomically and ecolo-

gically well known, and occur in almost all freshwater ecosystems worldwide, a better understanding of the patterns and mechanisms affecting their distributions at global and continental extents would be valuable from both basic and applied perspectives (Alahuhta et al., 2021, Iversen et al., 2022, Lind et al., 2022).

Explanations for biogeographical patterns of freshwater organisms when the focus is on local communities are still elusive. This is partly due to the lack of comparable regional survey data over large geographical areas. This is unfortunate because better knowledge of species diversity and distributions at large spatial extents, such as continents, is intimately related to understanding and predicting ecosystem functioning and resilience (e.g., Pessarrodona et al., 2019). This knowledge is also critical for delineating areas for sustainable management and conservation (Bailey, 2010, Vilmi et al., 2017). Explaining and testing hypotheses related to compositional gradients across continents require comparative analyses of multiple datasets, which rarely exist. In consequence, it is still difficult to draw comprehensive conclusions about the existence of breakpoints in community composition as well as the role of climatic gradients (e.g., temperature and precipitation) and local environmental features (e.g., mineral content and nutrients) on these biogeographical transitions in freshwater plants. These empirical exercises would not only provide insightful information about eco-evolutionary constraints and physiological trade-offs associated with important ecological gradients, but also offer a means of testing the very foundations of global regionalisation for freshwater plants (Alahuhta & García-Girón, 2022).

While a relatively large number of studies have examined variation in freshwater plant richness and diversity across large spatial extents (e.g., Murphy et al., 2019, Alahuhta et al., 2020, García-Girón et al., 2020b, 2021), virtually no studies have yet examined compositional breakpoints (*sensu* Heino & Alahuhta, 2015) based on high-resolution resolution data (e.g., a local community from an individual lake) worldwide. Simultaneous comparison of multiple study regions from different continents and environmental settings should, however, lead to a better understanding of such breakpoints in geographical space, helping to elucidate whether marked thresholds in community composition are moulded predictably by a set of ecological factors. Here, we test if global compositional breakpoints exist for freshwater plants using a standardised fine-grained database of individual lakes across 16 regions from six continents. More specifically, we addressed the following question: What are the contributions of climatic and local environmental variables to compositional gradients in freshwater plant communities across continents, if such biogeographical transitions exist? Similar to what has been found for different groups of New World vertebrates (Castro-Insua et al., 2016) and Fennoscandian beetles (Heino & Alahuhta, 2015), we hypothesised that the existence of compositional breakpoints in freshwater plant communities would be mediated by spatially structured variation in current climatic conditions from the subtropics to the poles.

METHODS

Our study was based on local community data of lake plants compiled for 16 regions (ca., 30 different lakes within each region) with variable sizes from around the world (Fig. 1) and covering all major continents inhabitable for freshwater plants (see Chambers et al., 2008). The species presence-only observations (i.e., species × sites matrix) were obtained from field surveys using broadly the same methods within each study region, including submerged (e.g., elodeids), floating-leaved, free-floating (e.g., lemnids), and emergent forms (Cook, 1999). This dataset is one of the world's few available repositories of local freshwater plant communities across continents and has already been described in detail to investigate the global variation of beta diversity (Alahuhta et al., 2017, García-Girón et al., 2020b) and community-environment relationships (Alahuhta et al., 2018, García-Girón et al., 2020c). Local environmental variables consisted of lake area (km^2), Secchi depth (m), and water total phosphorus concentration (µg/l). Local variables were surveyed and determined following similar methods within each study region (see Alahuhta et al., 2017, 2018 and García-Girón et al., 2020b, 2020c for details). Climate variables included atmos-

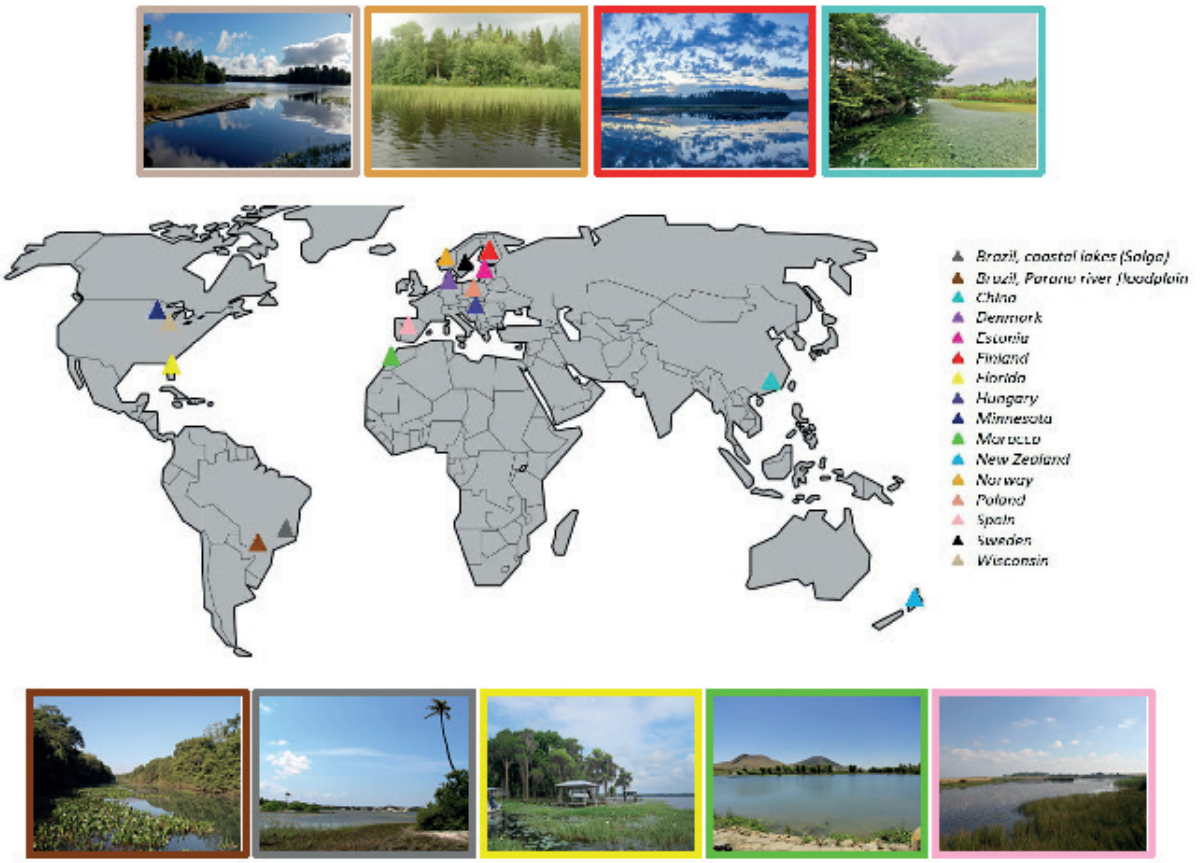

Figure 1. Study regions are indicated as coloured triangles with photographs of some representative study lakes in (from left to right) the Laurentian Mixed Forest Province of Wisconsin (USA), Norway, Finland, China, the Upper Paraná River floodplain, the Brazilian eastern coast, Florida, Morocco, and Spain (see Alahuhta et al., 2017, 2018 and García-Girón et al., 2020b, 2020c for details). Photographs are courtesy of (from left to right): Laura Sass, Håkan Sansten, Jun Xu, Roger P. Mormul, Sarian Kosten, Mark V. Hoyer, Laila Rhazi, and Jorge García-Girón. *Se indican las regiones estudiadas con triángulos de colores y anexas al mapa algunas fotografías de lagos representativos en (de izquierda a derecha) los Bosques Mixtos de la Provincia Laurentina en Wisconsin (EE. UU.), Noruega, Finlandia, China, la llanura aluvial del Río Paraná, la costa este de Brasil, Florida, Marruecos y España (consultar Alahuhta et al., 2017, 2018 y García-Girón et al., 2020b, 2020c para detalles adicionales). Las fotografías aquí expuestas son cortesía de (de izquierda a derecha) Laura Sass, Håkan Sansten, Jun Xu, Roger P. Mormul, Sarian Kosten, Mark V. Hoyer, Laila Rhazi y Jorge García-Girón.*

pheric annual mean temperature (°C), atmospheric annual temperature range (°C), and annual precipitation (mm) defined for each study lake based on 30 years average values (1-km resolution data) obtained from WorldClim (Hijmans et al., 2005).

We examined breakpoints of community variation along climatic and local environmental gradients using multivariate regression tree analysis (MRT, De'ath, 2002). MRT forms clusters of species and sites (i.e., individual lakes) modelled from species and environmental relationships by the repeated splitting of the data, minimising the dissimilarity of local communities within clusters and the within-group sums of squares (Borcard et al., 2011). This method retains a solution with the greatest predictive power and can handle situations where community-environment relationships are non-linear (Legendre & Legendre, 2012). We applied MRT based on Euclidean distance of χ^2-transformed multivariate species data (i.e., response variables) and climatic and local environmental variables as explanatory variables. We also ran trial analyses with latitude and longitude included among the predictor variables to

account for potential effects of dispersal barriers across regions (Heino & Alahuhta, 2015). Our results, however, remained largely the same when latitude and longitude were forced into the set of constraining variables, and their inclusion did not increase the explanatory power of the MRTs. Thus, for simplicity, we focused only on findings based on the remaining climatic and local environmental variable alone. The final MRT model with the minimum cross-validated error (CV Error) was selected as the 'best' tree after 10 000 cross-validations.

The MRT was based on pooled community composition data where freshwater plant survey methods were not strictly identical (although still comparable) among the regions. However, all the survey methods used have similar features for which they all should be considered as transect surveys, following the suggestions of Kolada et al. (2009). MRTs are robust enough to describe and explore complex relationships between potentially imbalanced, but still comparable local community composition data (De'ath, 2002). We then used a combination of *k*-means partitioning and χ^2 tests to assess the robustness of the MRT results (Heino & Alahuhta, 2015). *K*-means partitioning clustered the study sites based on the number of groups corresponding to those from the MRT at the first node and the number of final MRT leaves. Finally, we compared the matches between the MRT and *k*-means clusters using χ^2 tests (Borcard et al., 2011). MRTs were computed using the R library *MVPART-wrap* (Ouellette & Legendre, 2014), whereas *k*-means clustering and χ^2 tests were performed with R packages *Rcmdr* (Fox et al., 2022) and *coin* (Hothorn et al., 2021), respectively.

RESULTS

The MRT analysis showed that temperature variables were most clearly associated with compositional breakpoints of freshwater plant communities across the world (Fig. 2). Mean temperature was associated with the strongest community breakpoint, accounting for 8.7 % of the variation in species composition, followed by temperature range (6.8 %) and total phosphorus (ca., 1–2 %). In the first drop, lakes were split by a mean annual temperature of 9.1 °C. On the left were relatively warm regions ranging between > 40° S and 40° N, whereas on the right-hand side of the plot were rather cold regions from the northern temperate realms. Interestingly, geographical patterns in the location of the thresholds in species composition along the latitudinal gradient remained largely the same considering the terminal MRT leaves (Fig. 2). χ^2 tests found a statistically significant relationship between MRT results and *k*-means clustering (MRT first node, $\chi^2 = 148.7$ and p-value < 0.001; MRT final leaves,$\chi^2 = 113.6$ and p-value < 0.001), supporting the robustness of such biogeographical transitions in our regression trees.

DISCUSSION

Similar to what has been found for several groups of New World vertebrates (Castro-Insua et al., 2016) and Fennoscandian beetles (Heino & Alahuhta, 2015), our findings supported the notion that compositional breakpoints in freshwater plants are driven by the spatially structured variation in current climatic conditions across the world. Perhaps more importantly, our results extend the views of previous biogeographical studies of freshwater plants (e.g., Chappuis et al., 2012, Murphy et al., 2019, Alahuhta et al., 2020, Lobato-de Magalhães et al., 2021) and support the foundations of global regionalisation for these organisms (see Alahuhta & García-Girón, 2022 for a tentative example on freshwater floras of Greenland, continental Canada and the USA). This reasoning is intuitive given that a biogeographical transition exists between temperate to boreal regions occurring north of 40° N and communities harbouring mainly subtropical and southernmost Mediterranean species between > 40° S and 40° N (Fig. 2).

Local environmental variables are alone unlikely to account for breakpoints in community composition across continents (Heino, 2011). Instead, climatic conditions are a more likely candidate for controlling these latitudinal patterns. The spatially structured variation in mean annual temperature and temperature range is thought to be of paramount importance for terrestrial (e.g., Kreft & Jetz, 2007) and freshwater (e.g., Alahuhta et al.,

2021) plants. This is because average temperature and its seasonal variability affect dormancy, turion formation, seed germination, and seasonal growth rate (Lacoul & Freedman, 2006), potentially affecting their geographical distributions. This observation agrees with the empirical results presented here, suggesting that climatic factors may act universally across terrestrial and freshwater plants, at least when it comes to large-scale compositional breakpoints in geographical space (e.g., Hawkins et al., 2003, Whittaker et al., 2007). In practice, although we could not provide direct tests of these changes, we can tentatively suggest that current trends of climate warming are likely to modify freshwater plant ranges worldwide (cf. García-Girón et al., 2021; Lind et al., 2022), and consequently dissociate biogeographical transitions through climate-driven shifts across continents (e.g., Dobrowski et al., 2021).

Alternatively, the major compositional break-

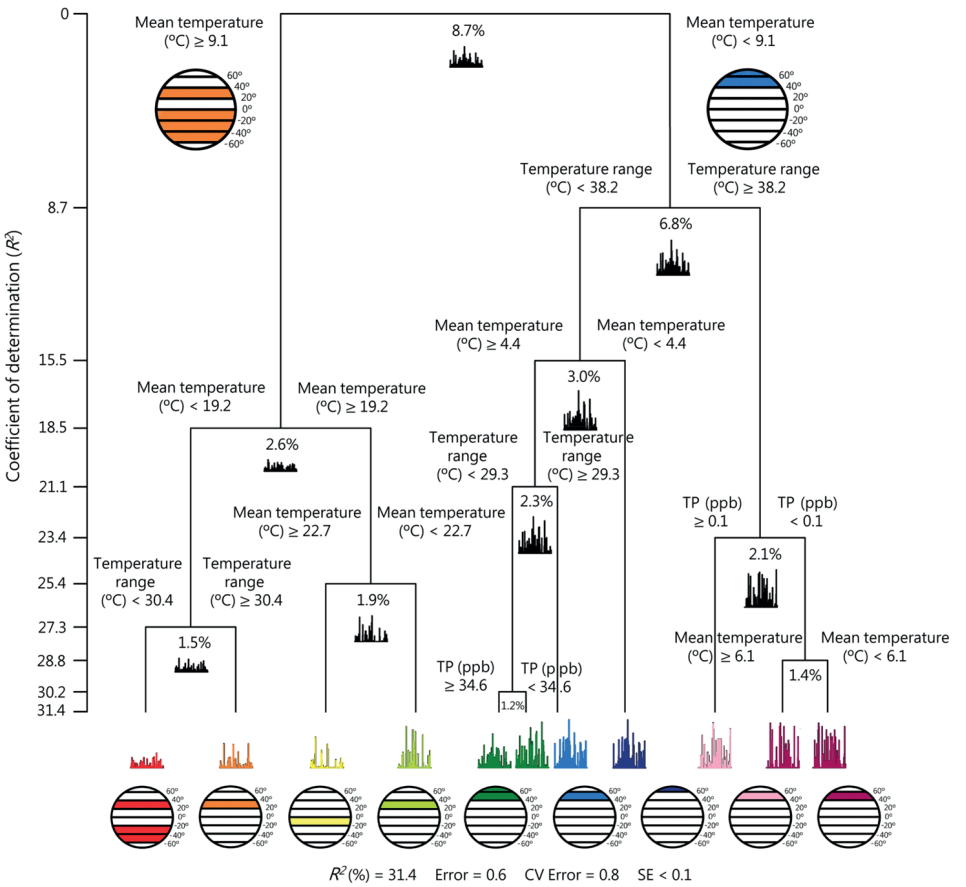

Figure 2. Multivariate regression tree (MRT) for freshwater plants using data from almost 500 lakes across the world. This is the `best´ tree with minimum cross-validated error. Histograms under each node indicate the distribution of multiple subsets of plant species within site groups. Insets are the main geographical regions of the Earth's surface for each site group. Colour chart for major latitudinal bands follows that for histograms. The statistics at the bottom of the plot are: the coefficient of determination (%, R^2), the residual error (Error), the cross-validated error (CV Error), and the standard error (SE). *Árbol de regresión multivariante para las comunidades de plantas acuáticas de un total de casi 500 lagos distribuidos en diferentes partes del mundo. Se incluye el resultado con menor error por validación cruzada. Los histogramas localizados bajo los nodos del árbol indican la distribución de múltiples subconjuntos de especies dentro de cada grupo. También se incluyen las bandas latitudinales ocupadas por los lagos de cada grupo utilizando una escala de color consistente con los ya citados histogramas. Los valores estadísticos del gráfico son los siguientes: coeficiente de determinación (%, R^2), error residual (Error), error de validación cruzada (CV Error) y error estándar (SE).*

points found here between temperate/boreal *vs.* subtropical/southern Mediterranean regions (Fig. 2) could also reflect eco-evolutionary constraints linked to withstanding colder conditions (e.g., harsh winter conditions and sediment freezing) and shorter development periods for freshwater plants at increasingly higher latitudes. This explanation is consistent with trait-dependent adaptations to high-latitude environments and differential selection for sets of more generalist species in northern regions (Heino et al., 2009). Late Quaternary climate change may also have imprinted biogeographical transitions between the harsher north and the more benign south. Freshwater plants were eliminated at high latitudes during the Pleistocene Ice Ages, and these regions have been gradually recolonised after the retreat of the ice sheets (Sawada et al., 2003). The biogeographical transition towards northern areas may, indeed, indicate that northernmost biomes might not have had enough time to become recolonised by some species following the onset of the most recent interglacial period (Dehling et al., 2010), particularly some rare and potentially more specialist ones (García-Girón et al., 2021). However, the degree to which freshwater plant distributions agree with this hypothesis is still open to intense debate (e.g., Alahuhta et al., 2020, Murphy et al., 2020, García-Girón et al., 2021). Whatever the case, the relatively low coefficients of determination ($R^2 \sim 30$ %) from our MRT models, although still ecologically meaningful, emphasise that some ecogeographical mechanisms beyond those measured in our study likely contributed to compositional gradients of freshwater plants across continents. For example, alkalinity (Iversen et al., 2019) and water availability (Chappuis et al., 2012) have been found to strongly drive distributions and community composition of freshwater plants at different spatial scales, although consistent community-environment relationships seem to be the exception rather than the rule at sub-continental extents (García-Girón et al., 2020c). On the other hand, overseas dispersal of propagules by migratory birds is also known to lead to either range expansion or shifts (Viana et al., 2016), and therefore has also the potential to help explain freshwater plant species distributions (Reynolds et al., 2015; Green et al., 2016).

The general lack of statistical power (see Alahuhta et al., 2021) does not compromise the validity of our findings. Instead, it should provide yet another incentive to join efforts in an attempt to understand the causal mechanisms and factors underlying freshwater plant distributions. For instance, seemingly simple tasks such as compiling comprehensive multi-trait inventories of the world's freshwater plant species proved daunting (Iversen et al., 2022), and even obtaining fine-grained observational data of local communities across continents has been a challenge (Alahuhta et al., 2017). Hopefully, there will be an increase in the quality and quantity of standardised field surveys beyond botanical research perspectives (especially in geographically less-studied regions of Africa, eastern Europe, southern Asia, and Australasia) that should allow further evaluations of biogeographical rules in freshwater plants. These future exercises should pay special attention to harmonisation of potentially heterogeneous datasets to be analysable in the same research context and include local community samples (i.e., presence-only or abundance-based records) from strictly comparable field surveys across different spatial levels of interest (Pan et al., 2023). For the moment, we hope that our findings here will contribute to ongoing discussions in freshwater plant research by showing that large-scale biogeographical transitions exist for these organisms and that such breakpoints may be formed by either curent climatic conditions, eco-evolutionary constraints in the harsher high-latitude environments, post-glacial migration lags, or (more likely) their combined effects on species potential ranges.

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DATA AVAILABILITY STATEMENT

The datasets are from state or national administration, where they can be obtained by request (see Alahuhta et al., 2017, 2018 and García-Girón et al., 2020b, 2020c for details).

CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

Jorge García-Girón: Conceptualisation, Data curation, Formal analysis, Methodology, Investigation, Writing - original draft, Writing - review & editing, Visualisation. **Jani Heino:** Writing - original draft, Writing - review & editing, Supervision, Validation. **Janne Alahuhta:** Conceptualisation, Writing - original draft, Writing - review & editing, Supervision, Validation. **All authors:** Funding acquisition, Resources, Supervision, Validation.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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