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ORIGINAL ARTICLE

Tropical wood stores substantial amounts of nutrients, but we have limited understanding why

Marijn Bauters[1,2,3] | Oriol Grau[4,5] | Sebastian Doetterl[6] | Katherine D. Heineman[7,8] | James W. Dalling[9,10] | Cecilia M. Prada[9] | Marco Griepentrog[6,11] | Yadvinder Malhi[12] | Terhi Riutta[12] | Marina Scalon[12,13] | Takeshi Inagawa[12] | Noreen Majalap[14] | Hans Beeckman[15] | Jan Van den Bulcke[16] | Michael P. Perring[17,18,19] | Aurélie Dourdain[20] | Bruno Hérault[21,22,23] | Pieter Vermeir[24] | Isaac A. Makelele[1] | Pere R. Fernández[4,5] | Jordi Sardans[4,5] | Josep Peñuelas[4,5] | Ivan A. Janssens[3]

[1]Isotope Bioscience Laboratory – ISOFYS, Department of Green Chemistry and Technology, Faculty of Bioscience Engineering, Ghent University, Gent, Belgium

[2]Computational and Applied Vegetation Ecology – CAVElab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Gent, Belgium

[3]Research Group of Plants and Ecosystems (PLECO), Department of Biology, University of Antwerp, Wilrijk, Belgium

[4]CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra, Catalonia, Spain

[5]CREAF, Cerdanyola, Catalonia, Spain

[6]Soil Resources, Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland

[7]Center for Plant Conservation, Escondido, California, USA

[8]San Diego Zoo Institute for Conservation Research, Escondido, California, USA

[9]Department of Plant Biology and Program for Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana, Illinois, USA

[10]Smithsonian Tropical Research Institute, Balboa, Ancon, Panama

[11]Biogeoscience, Department of Earth Sciences, ETH Zurich, Zurich, Switzerland

[12]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

[13]Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal do Paraná, Curitiba, Brazil

[14]Sabah Forestry Department, Forest Research Centre, Sabah, Malaysia

[15]Royal Museum for Central Africa, Tervuren, Belgium

[16]UGent-Woodlab - Laboratory of Wood Technology, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Gent, Belgium

[17]Forest & Nature Lab, Department of Environment, Ghent University, Melle-Gontrode, Belgium

[18]Ecosystem Restoration and Intervention Ecology Research Group, School of Biological Sciences, The University of Western Australia, Crawley, Western Australia, Australia

[19]UKCEH (UK Centre for Ecology & Hydrology), Environment Centre Wales, Bangor, Gwynedd, UK

[20]CIRAD, UMR Ecologie des Forêts de Guyane, Kourou, French Guiana, France

[21]CIRAD, UPR Forêts et Sociétés, Yamoussoukro, Côte d'Ivoire

[22]Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France

[23]Institut National Polytechnique Félix Houphouët-Boigny, INP-HB, Yamoussoukro, Côte d'Ivoire

[24]Laboratory for Chemical Analyses – LCA, Department of Green Chemistry and Technology, Ghent University, Ghent, Belgium

Correspondence
Marijn Bauters, Isotope Bioscience Laboratory – ISOFYS, Department of Green Chemistry and Technology, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, 9000 Gent, Belgium.
Email: Marijn.Bauters@UGent.be

Abstract

Rock-derived nutrients such as calcium (Ca), magnesium (Mg), phosphorus (P), and potassium (K) are essential plant resources, yet depleted in highly weathered tropical soils, leading to nutrient limitation of productivity or other ecosystem processes. Despite

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this, substantial amounts of rock-derived nutrients occur within wood, which raises questions about the role that wood nutrients play in the ecology of tropical forests. Using data from forests across the tropics, we quantify wood nutrient stocks at individual tree and ecosystem levels. At the ecosystem level, we show that tropical wood can store substantial amounts of rock-derived nutrients. Furthermore, on a tree level, tree species vary widely in woody nutrient concentrations. These observations raise important questions as to the biogeochemical or ecological drivers that lead to this variability, as well as the role that woody tissue plays in the buffering and cycling of nutrients. We offer some potential explanations and direction for future research to explore this under-appreciated but sizable store of inorganic nutrients in tropical biomass.

KEYWORDS
biogeochemistry, calcium, magnesium, nutrient budget, nutrients, phosphorus, potassium, wood

1 | INTRODUCTION

Carbon assimilation in plants is sustained by a range of nutrients that can be allocated to short-lived organs (leaves, fine roots) or long-lived woody tissues (stems, branches, boles, coarse roots) (Kaspari et al., 2008). Although nitrogen (N) limits plant growth in many ecosystems, it is a virtually infinite resource that can be imported from the atmosphere into a plant-available form via biological fixation, lightning and atmospheric deposition (Vitousek & Howarth, 1991). Contrastingly, so-called rock-derived nutrients such as phosphorus (P), magnesium (Mg), calcium (Ca), and potassium (K), are supplied by weathering of soil parent material before they begin cycling within the biosphere. However, as the soil substrate ages and weatherable minerals decline, these nutrients become increasingly depleted through long-term leaching processes (Landeweert et al., 2001; Vitousek et al., 2010; Vitousek & Sanford, 1986; Walker & Syers, 1976), increasing the importance of nutrient recycling within the biosphere. As such, old-growth forests on strongly weathered soils increasingly depend on atmospheric inputs of P and cations, rather than on in-situ soil weathering inputs (Chadwick et al., 1999; Hedin et al., 2003). Further, an efficient recycling of these nutrients in the soil-plant continuum reduces leaching losses and enables tropical ecosystems to grow on old, nutrient-depleted soils (Vitousek, 1982, 1984).

In view of the efficient recycling of these resources, research has mainly focused on the exchange of nutrients between soil and short-lived tissues such as leaves and fine roots. In contrast, wood represents a long-term, slow-turnover pool of carbon with obvious relevance for the global carbon cycle (Martin et al., 2018). The importance of nutrient storage in tropical woody tissues for forest biogeochemistry has been recognized (Klinge et al., 1984; Vitousek & Sanford, 1986), but apart from some nutrient budgeting studies (Bond, 2010; Klinge et al., 2016) little is known on the role of wood in the biogeochemical cycles of tropical forests. In theory, nutrient storage in woody tissues could be quantitatively important as an ecosystem-scale nutrient pool in many tropical forests, as these forests exhibit high aboveground standing biomass stocks paired with low rock-derived nutrient concentrations in the strongly weathered soils (Grau et al., 2017). Additionally, although wood nutrient concentrations exhibit marked variation at the global scale (Meerts, 2002), we still know little about what drives this variability (Heineman et al., 2016); is this mainly driven by site fertility, or is wood nutrient storage tied to a species-specific strategy, and hence rooted in an ecological strategy to thrive in nutrient-poor environments?

Here, we bring together several datasets of woody nutrient concentrations from different tropical forests spanning three continents. The dataset allows us to explore two questions: (1) is woody nutrient storage quantitatively important on an ecosystem scale across tropical forests, and (2) how is variability in wood nutrient storage constrained across hundreds of tropical trees, growing on different soils. To address these research questions, we calculated woody nutrient stocks, using biomass estimation methods together with measurements of nutrient concentrations in wood, and compare those to what nutrients are stored in the soil. Additionally, we used repeated biomass inventories to quantify the annual flux of nutrients going in the wood, to compare this to the order of magnitude of nutrients being deposited on an annual basis. We preferentially use heartwood concentrations in our estimations, where available, to conservatively estimate the nutrients that are long-term stored in woody tissue, leaving out potential nutrient resorption from sapwood when transitioning into heartwood (Heineman et al., 2016). Additionally, we use the combined dataset to show that variability on a tree-level (rather than on ecosystem-level) is constrained by both edaphic factors and tree family and species information.

As acknowledged in the material and methods section, the combined dataset has not been gathered in a fully consistent way, and we had to make assumptions and accept uncertainties in analyzing the data. However, our main intent here is to build further on the exploration of the two research questions, and stimulate future research on the questions that are raised by these observations. These

observations conservatively suggest that there are important but poorly understood biogeochemical and ecological processes underlying nutrient allocation to wood.

2 | MATERIAL AND METHODS

The data used in this study have been collected in different projects in the several study areas (Table 1, Table S1), with different types of data available for the separate study sites.

2.1 | Study sites and inventory

An overview of the study sites is given in Table 1 and Table S1. For Borneo, the research was conducted in the sites described by Riutta et al. (2018): these are one hectare plots that were inventoried following the RAINFOR protocol. Plots were either impacted by logging (SAFE-project plots; SAF), or old-growth from the Danum Valley (DAN) or Maliau Basin Conservation area (MLA). In the Democratic Republic of Congo, the study was carried out in a lowland forest chronosequence forest in Yoko, roughly 30 km south of Kisangani. Vegetation at the study site is classified as semi-deciduous rain forest, and the climate falls within the Af-type (tropical rain forest climate; Bauters et al., 2019). The forest was inventoried following the RAINFOR protocol (Malhi et al., 2002), in plots of 40 by 40 m in 5 stages (i.e., 5-year-old forest, 12-year-old forest, 20-year-old forest, 60-year-old forest, and old-growth forest), with plots installed in triplicate in every stage. In Panama, we sampled woody tissue in the Fortuna Forest Reserve (19 500 ha) and the adjacent Palo Seco Forest Protectorate (125,000 ha), henceforth Fortuna, in western Panama. This region encompasses old-growth, lower montane forest, ranging between 700 and 1500 m above sea level. Inventories were carried out as described in Heineman et al. (2016) and Condit et al. (2013). In French Guiana, the study was conducted in the Paracou research station (Gourlet-Fleury et al., 2004). Study plots at the Paracou site are located on schist soils with veins of pegmatite along a Precambrian metamorphic formation called the Bonidoro series (Epron et al., 2006). Finally, Brazilian sites were composed of old-growth lowland Amazon forest, montane Atlantic forest and Cerradão forest, which is transitional forest between wet and dry tropical forest.

2.2 | Wood sample collection, preparation, and analysis

In Borneo, 420 woody tissue samples were collected from bark, sapwood, heartwood, the top of the trunk and branches. Tree components were sampled in August 2015. Thirty trees ≥10 cm diameter at breast height (DBH), which consisted of 10 tree species with three replicates were selected in the study site. Sampled trees had no visible damage (e.g., no insect damage, chlorotic leaves and bent stems). All measurements (the number of branches, and diameters and length of all sampled locations) were conducted using a measuring tape within hours after the sampled trees were felled. Directly following felling, sampled woody components were cut using a chainsaw. Within each tree, the tree stem was sampled just below the breast height at 1.3 m off the ground. The samples were brought to the chemistry laboratory, Forest Research Centre in Seplilok, Sabah, Malaysia. Samples were partitioned to three sections: bark, sapwood and heartwood. The collected trunk disk was divided into sapwood and heartwood based on a distinguishable color difference after mechanical sanding. If there was no clear color difference, the corner of the disk was used as a sapwood sample and the wood around the pith as a heartwood sample. First, all samples were oven-dried at 50

TABLE 1 Concise overview of the study sites and the data available from the different sites. A more elaborate overview can be found in Table S1

Site	Forest type	Sites	Data available
Borneo	Lowland forest	Old-growth + logging gradient	Wood nutrient concentrations Two censuses Soil nutrient data
Congo	Lowland forest	Old-growth + successional gradient	Wood nutrient concentrations Two censuses Leaf trait data Soil nutrient data
Guiana	Lowland forest	Old-growth	Wood nutrient concentrations Two censuses Soil nutrient data
Panama	Lower montane forest	Old-growth on a P gradient	Wood nutrient concentrations Two censuses Soil nutrient data
Brazil—Amazon	Lowland tropical forest	Old-growth forest	Wood nutrient concentrations
Brazil—Atlantic	Montane forest	Old-growth forest	Wood nutrient concentrations
Brazil—Cerradão	Transitional forest	Old-growth forest	Wood nutrient concentrations

°C to constant weight for five days, and were then ground with a Thomas Wiley Mill to pass through a 100-mesh (212-μm) sieve. Each sample was digested following the sulfuric acid-hydrogen peroxide-lithium sulfate digest procedure. Phosphorus in the digest was determined using the molybdenum-blue method and read at 880 nm on a spectrophotometer (HITACHI UV-VIS, Tokyo, Japan), while K, Ca, and Mg contents were measured on an atomic absorption spectrometer (GBC Scientific Equipment, Victoria, Australia).

In Congo, 211 individual trees, covering 93 species, were cored at breast height (1.3 m) on two opposite sides of the tree until the center of the stem and wood cores were air-dried. Subsequently, we discarded the outer 20% of the wood cores to target analysis of the long-term storage of nutrients in the heartwood. The wood samples were first ground and then homogenized and subsequently all samples were dry-ashed at 550°C for 5.5 h; the ash was dissolved in 2 M HCl solution and filtered through a P-free filter. The aliquots were then analyzed for P, Ca, K, and Mg by inductively coupled plasma atomic emission spectroscopy (ICP AES, IRIS interpid II XSP, Thermo scientific, USA). Sampling was done outside of the monitoring plots so as not to affect the natural dynamics of the individuals in the plots, but always in the border zone around the plot for the respective species or individuals.

In Panama, the sampling design is well described by Heineman et al. (2016). In short, wood core samples were extracted from 301 individual trees from 76 species at Fortuna. In all plots, we sampled 7–22 woody species with the greatest basal area in each plot. We cored three trees >10 cm DBH per species using a 4.3-mm Haglöf increment borer. Cores were taken at breast height (1.3 m) to a depth of half the DBH of the tree. Trees at Fortuna were cored outside permanent forest plots, but within 100 m of the plot boundary in February 2011. A mini- Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) was used to grind wood core samples in 5 cm segments to account for possible radial differences in wood attributes. To prepare wood and leaf material for Ca K, Mg, and P analysis, samples were dry-ashed at 550°C for 1 h and the ash dissolved in 1 M HNO3. Base cations for all samples and P in tissues collected at Fortuna were measured using inductively coupled plasma-optical emission spectrometry (ICP-OES) on an Optima 2000 DV (Perkin Elmer, Waltham, MA, USA). A subset of Fortuna wood samples with P concentrations below the ICP-OES detection limit were analyzed for P via automated molybdate colorimetry using the Lachat Quickchem 8500 (Hach Ltd, Loveland, CO, USA). For samples above the detection limit of the ICP analyzed on both instruments, P measurements by spectrometry and colorimetry were closely correlated ($R^2 = .95$, $N = 10$) with an intercept that did not significantly differ from zero. We included certified reference samples (NIST 1515, apple leaves) and internal laboratory control standards in all analyses.

In French Guiana, we cored a total of 117 individual trees, covering 10 species, using a 4.3-mm borer and took cores at breast height (1.3 m) to a depth of half the DBH of the tree. When possible, we selected trees within the 20–30 cm DBH range and as similar as possible between them. If this was not possible to sample trees of 20–30 cm DBH for a given species (e.g., species with small max DBH such as *Oxandra asbeckii* (Pulle) R.E.Fr.), then we sampled other sizes (e.g., 10–20 cm DBH), as close as possible to the range used for the other species. We took one wood core from each adult tree, which was completely ground. For the determination of P, Ca, Mg, K and other micronutrients, the samples were oven-dried at 70°C during 48 h and ground, pulverized and homogenized in a ball mill (Retsch, Germany). 0.25 g of each wood sample was digested with 5 ml of HNO3 (Merck) in a microwave model UltraWavem (Milestone, Sorisole, Italy). This process created a solution that was analyzed with an Inducted Coupled Plasma Mass Spectrometry model 7500ce (Agilent).

For Brazilian sites, we sampled 3–5 individuals from species representing ca. 80% of the community basal area. Cerradão (35 individual trees covering seven species in each site) sites were located in the Bacaba Municipal Park (14°42′22″ S, 52°21′07″ W), Nova Xavantina, Mato Grosso State. Amazon forest site (45 individual tree covering 15 species) was located in the Floresta Nacional do Tapajós (4°04′74″ S, 54°93′28″ W), Belterra, Pará State. Atlantic forest site (87 individual tree covering 29 species) was located in the Parque Estadual Serra do Mar (23°33′51″ S, 45°14′59″ W), Sao Paulo State. Wood core samples were collected at breast height (DBH ≈ 1.30 m), using a 4.3-mm Haglöf increment borer to a depth of half the DBH of the tree. After being oven-dried at 70°C until constant weight, dried samples were sent to Laboratório de Análises de Viçosa-MG, for nutrient concentration analyses. N and P (g/kg) were determined by Kjedahl digestion and UV-Vis spectroscopy, respectively, and the other nutrients (Ca, Mg, and K, g/kg) were determined by atomic absorption spectrometry.

2.3 | Soil sample collection and analysis

For Borneo, we sampled five separate soil layers (0–10, 10–20, 20–30, 30–50, and 50–100 cm) by digging three soil pits per plot and compositing one sample per layer based on the three pits. Samples were measured with ICP-OES after extraction with "aqua regia" ($HCl:HNO_3$, 3:1, v:v). Additionally, soil bulk density values were determined for 6 different soil layers until one meter depth per plot (0–5, 5–10, 10–20, 20–30, 30–50, and 50–100 cm). For Congo, we sampled five separate soil layers (0–10, 10–20, 20–30, 30–50, and 50–100 cm) by digging three soil pits per plot and compositing one sample per layer based on the three pits. Additionally, samples for bulk density analysis were taking at all increment layers in the same pits. Samples were measured with ICP-OES after extraction with "aqua regia" ($HCl:HNO_3$, 3:1, v:v). In Panama, soil samples were taken in three layers until 50 cm depth (0–10, 10–20, and 20–50 cm) from 13 locations in each 1-ha plot during the wet season. We analyzed total soil Ca, K, Mg concentrations in 2014 using archived soils stored in the Smithsonian Tropical Research Institute Soil Analysis Lab that were collected from the Fortuna plots between 2003–2008. For each plot, we analyzed one sample for each of three soil depths (0–10, 10–20, 20–50 cm). Each soil sample was created by bulking, and homogenizing 50 mg across five locations in the plot.

We digested 200 mg from each ground, dried soil sample in 50 ml of 1 M nitric acid overnight. We determined elemental concentrations of digests using the ICP-OES in the STRI Soils Lab. We used the "Montana" soil standard (NIST SRM 2710a) as a reference material. In French Guiana, a pooled soil sample was collected around the base of each of the sampled individuals, to a depth of 10 cm with a soil corer (after removing the upper layer of litter). For the determination of P, Ca, Mg, K, and other micronutrients, the samples were oven-dried at 70°C during 48 h and ground, pulverized, and homogenized in a ball mill (Retsch, Germany). 0.1 g of each sample were digested with HNO_3, HF, and HCl (Merck) in a microwave model UltraWavem (Milestone, Sorisole, Italy). This process created a solution that was analyzed with an Inducted Coupled Plasma Mass Spectrometry model 7500 ce (Agilent). Reference materials were used during this analysis: NIST 2711a, Montana Soil, and CRM005, Sewage Amended Soil. For French Guiana, we had no bulk density measurements of the sample plots, but used an average bulk density measurement from 360 measurements at nearby plots at the Paracou station. For the other sites, bulk density was always determined by drying a known volume of soil at 105°C.

2.4 | Trait data—Congo

Specific leaf area (SLA) is a key leaf trait, which co-varies with leaf photosynthesis performance, and leaf N content (LNC) (Reich, 2014; Wright et al., 2004) all of which are correlated with primary production, carbon and nutrient cycling, and litter decomposition (Reich, 2014). Wood density (WD) is often used as a key trait for growth rates and turnover rates of the wood (Chave et al., 2009). Leaf samples were collected in Congo from the species that were sampled for wood nutrients. For the selected species, leaf samples were collected from at least three individuals. Leaf traits were measured on mature and fully sunlit leaves collected following internationally accepted protocols (Perez-Harguindeguy et al., 2013) with the help of tree climbers. Leaf area was measured directly after the sampling, that is, on the same day, in our field lab and in <4 days they were oven-dried at 80°C for 48 h, weighed again, and prepared for future chemical analyses. Leaf area was measured by the Easy Leaf Area (ELA) App for android (Easlon & Bloom, 2014). We then calculated SLA per tree individual by dividing the total leaf area by total leaf dry mass. Leaf samples were further analyzed for LNC using an elemental analyzer (ANCA-SL, SerCon, UK), interfaced with an isotope ratio mass spectrometer (IRMS) (20–22, SerCon, UK). For WD determination, two wood cores were sampled from the opposite sides of individual trees at the point of DBH measurement and collected from all the inventoried species, outside of the permanent monitoring plots (Chave, 2006). The wood cores were first measured for green volume by the water displacement method (WDM) method, subsequently oven-dried for 48 h at 105°C, and weighed again to get the oven-dry mass. Subsequently, wood density was calculated as the ratio of wood oven-dried mass by the mass of water displaced by the wood sample.

2.5 | Data and statistical analysis

We calculated biomass for all inventoried plots for several census years (Table S1), using the BIOMASS package in R (Réjou-Méchain et al., 2017), and stock calculations were done using the most recent census year. The BIOMASS package uses DBH, tree height, and wood density information to calculate aboveground biomass, using the pantropical equations as developed by Chave et al. (2014). Annual wood nutrient uptake was calculated based on stock differences between two censuses. We calculated species-specific nutrient contents of the wood for all sampled species. For the nutrient stock estimates in the wood, we multiplied the species-average nutrient contents with the biomass of the respective species in the plot. If species-specific nutrient information was absent for certain species, we multiplied the biomass of those individuals with the average nutrient concentration of that region, in order not to skew the plot-data. Plot-level stocks were obtained by summing up the individual tree nutrient stocks and were standardized to Mg ha^{-1}. Except for the specific analysis on intra-individual variability in wood nutrient content (Table S2), we used heartwood samples where possible for the calculations and analysis. For soil nutrient stocks, we used the maximum available data per region, being the layer-specific bulk density and nutrient content in the different plots to calculate soil nutrient stocks until one meter depth. If layer-specific information was only available until a certain depth, we used the deepest soil layer values to extrapolate, for both nutrient content, and soil bulk density values. All soil nutrient stocks were expressed as Mg/ha.

For the decomposition of variance in wood nutrient concentrations across the dataset into intra-region, intra-family, and intra-species variance, we first fitted a random effects model with nested random effects, that is, plant species nested in plant family, and plant family nested in region. We subsequently extracted the variance that was estimated to be associated with the different nesting levels and considered it to be the “structural variation” with the respective level. For this decomposition of variance, we used the Bayesian multilevel model package “brms” (Bürkner, 2018), with weakly informed Gaussian prior distributions for all effects. After fitting, the estimates of variance were extracted via the posterior distributions of the random error terms. For interrelations between wood nutrient concentrations (Table S4), and correlations between wood nutrient concentrations and traits (Table S3), we used the Congo dataset along with a local trait dataset of the selected species.

2.6 | Uncertainties and assumptions in the analyses

This study opportunistically brings together data from different study areas in the tropics. In compiling the database, we had to deal with several inconsistencies. We acknowledge below how these inconsistencies might affect the analyses presented in the paper.

In the analyses of wood nutrient contents, we only used wood nutrient concentrations of the inner part of the wood cores, that is, the heartwood where possible. This was done for two reasons:

(1) we simply lack the sapwood nutrient concentrations for the whole database, and (2) an additional analysis on the variability of nutrients in different woody tissue types showed that heartwood consistently has lower nutrient concentrations than bark and lower P and K concentration than sapwood (Table S2). We assume that if there could be wood nutrient resorption, than plants would re-translocate this from the "youngest" tissue, that is the sapwood, as it transitions into heartwood, as also shown by Heineman et al. (2016). Hence, in trying to estimate the long-term storage of nutrients, the most conservative would be to use heartwood nutrient concentrations, because there might be a resorption flux from the sapwood. However, we do acknowledge that including sapwood in the wood nutrient stock quantification, along with other woody tissues, might considerable change the estimated wood nutrient. As we have no experimental setup (yet, one of the goals of this piece is also to stimulate further research and such setups) to determine the resorption from those tissues, we made this assumption. Additionally, the dataset also includes data of whole wood core nutrients (from Brazil, French Guiana, and Panama). While we acknowledge that this might potentially impact the reported estimates here, sapwood nutrient concentrations are known to be positively correlated to heartwood nutrient concentrations (Meerts, 2002), as again confirmed (only for wood nitrogen) later (Martin et al., 2014). Mainly for P and K, there seems to be a lower heartwood vs sapwood nutrient concentration, while for Ca and Mg minor differences between heart- and sapwood have been reported (Heineman et al., 2016; Meerts et al., 2002). This means that for sites where not only heartwood, but whole wood cores were sampled, we potentially overestimate the storage of P and K in the wood, which should be kept in mind while interpreting these results.

For Congo, we had wood nutrient data for almost all species, while for the other sites only a selection of species was sampled. In this case, as described in the methods, we used region-averaged nutrient concentrations to appoint nutrient concentrations to the non-sampled species. We acknowledge that these extrapolations and assumptions could change the estimations, and the data and discussion we present should be interpreted with this in mind. It is notable that the sites where we have the most complete sampling of species in plots (i.e., Congo) clearly demonstrate the importance of wood nutrient storage, emphasizing the need to expand sampling campaigns across species and regions. Our overarching aim is not to provide a precise estimate of wood storage in different tropical systems but to highlight the need to consider woody tissue nutrients in tropical forest ecosystem biogeochemical assessments, given their potential importance.

Finally, soil nutrient extraction methods across sites differ, likely also in their efficiency of extracting total soil P and cations, and results must hence be interpreted accordingly. Classic "total" soil digestions use HF for extracting (Gaudino et al., 2007), but HF is notoriously hazardous to work with, which is why many labs use extraction methods with aqua regia, without HF. This "light" extraction is likely to not extract the entire "total" soil nutrient pool. In this study, only the Guiana soil samples were extracted using HF, while for other sites, "light" protocols were used. We hence caution against interpreting the other soil pools as being the actual "total" soil pools, although in literature aqua regia digestions are commonly referred to as "total" soil nutrients.

3 | RESULTS

The estimated wood nutrient stocks in undisturbed old-growth forests at the different sites varied widely for all elements (Table S5). For Ca, this varied from 0.49 ± 0.18 (arithmetic mean ± standard deviation) in Panama to 1.08 ± 0.13 Mg/ha in Guiana. Wood K stocks ranged from 0.52 ± 0.18 in Panama to 0.83 ± 0.09 Mg/ha in Congo, while for Mg we found 0.15 ± 0.07 in Panama to 0.31 ± 0.04 Mg/ha in Guiana. Finally, wood P stocks were the lowest in Borneo, with 0.02 ± 0.01 Mg/ha, while the Congo forest plots amounted to 0.08 ± 0.02 Mg/ha. The flux of nutrients sequestered in the wood, as estimated from the annual woody increment combined with the wood nutrient concentrations averaged at 12.8 kg Ca/ha/yr, 7.9 kg K/ha/yr, 4.1 kg Mg/ha/yr and 0.5 kg P/ha/yr across all sites, including the younger forest plots in Congo and selectively logged plots in Borneo. The ratio of total nutrients stored in the wood versus the nutrient stocks in the wood and upper meter of soil ranged from 0.2% for Mg in Borneo to 89% for Ca in a plot in Borneo; representing the minimum and maximum over the entire undisturbed old-growth plot set (Figure 1). A more complete scanning of element stocks in woody tissue in Guiana confirmed the potential importance of Ca stocks in wood, showing 28% of the total ecosystem stock (i.e., here the wood and upper meter of soil) was stored in the wood, and further showed that wood also stores important micronutrients such as molybdenum (5.6%) and manganese (5.5%) (Figure 2). Site-level average nutrient concentrations ranged from 1529 to 2708 ppm for Ca, 1554 to 2336 ppm for K, 443 to 766 ppm for Mg and 54 to 115 ppm for P, but with individual wood nutrient concentrations varying much more. As such, individual tree maximum nutrient concentrations over the entire dataset amounted to 16280 ppm for Ca, 12223 ppm for K, 3205 ppm for Mg and 1490 ppm for P (Figure 3). Finally, our decomposition of variance revealed that species-level information explained as much as 35% of the variability in wood P concentration, while for Mg this was only 8%. Family-level taxonomic information constrained most variability (29%) in the concentration of Mg in wood, while it was only 14% of variation in wood P concentration. Region was most important for Mg (35%) and less so for P (23%) (Figure 3).

4 | DISCUSSION

4.1 | On an ecosystem-level: wood stores substantial amounts of rock-derived nutrients

We find that woody biomass can take up and store substantial amounts of rock-derived nutrients across the tropics, exemplified here with data from old-growth forest stands from Borneo, Congo,

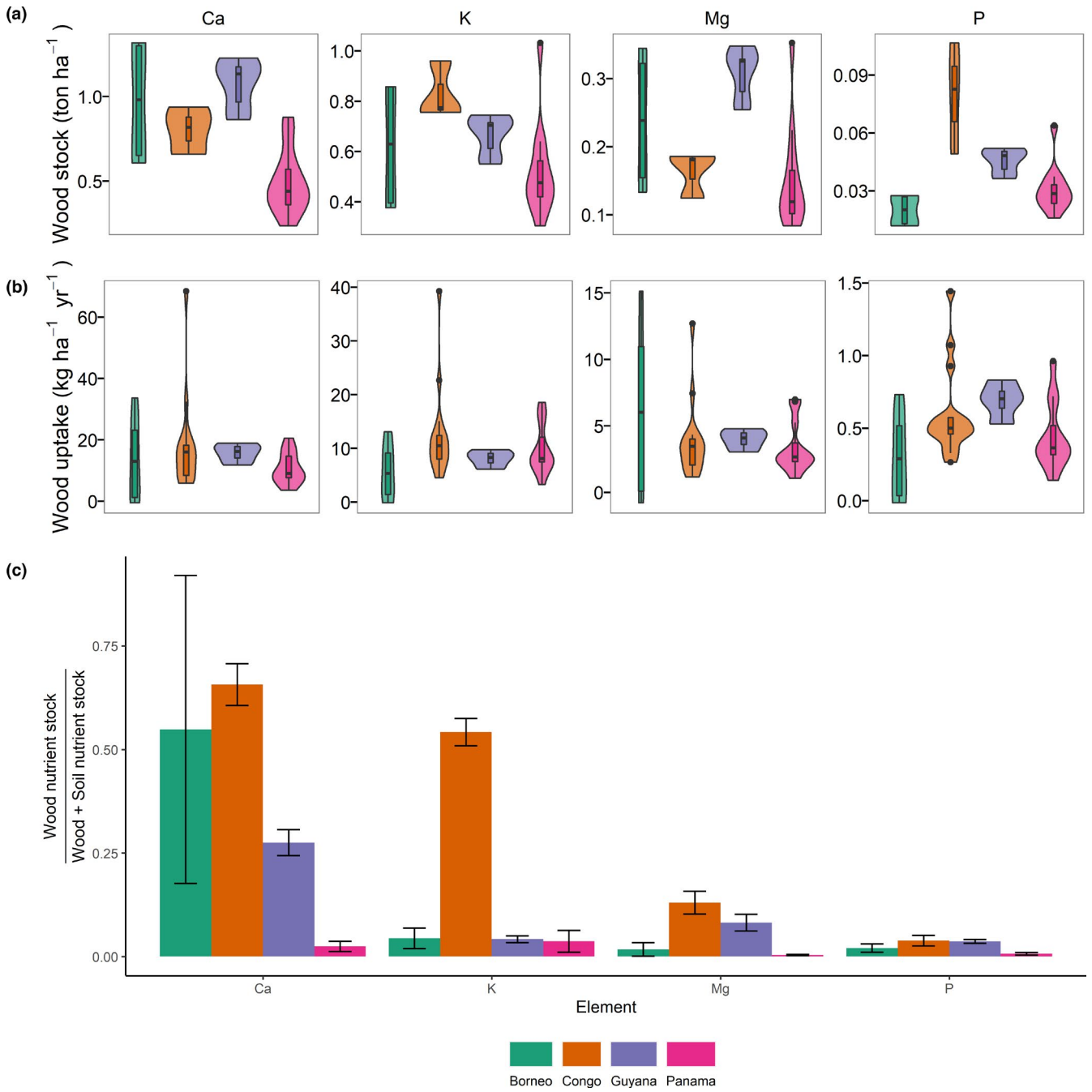

FIGURE 1 (a) Wood nutrient stocks in undisturbed old-growth forests across the tropics (excluding disturbed plots in Borneo and secondary forests in Congo).; (b) Annual uptake of nutrients by wood in varying forest types across the tropics (including disturbed forest plots in Borneo and secondary forests in Congo); (c) Woody biomass fraction of the total nutrient stock (in wood and the upper meter of soil) for tropical forests of Borneo, Congo, French Guiana and Panama (excluding disturbed plots in Borneo and secondary forests in Congo). For the calculation of the fraction of nutrients stored in the woody biomass, different digestion techniques were used for the soil total nutrient analysis across sites, hence these fractions need to be interpreted with caution

French Guiana and Panama (Figure 1a). On sites with relatively low soil nutrient concentrations, rock-derived nutrients in wood represent a larger proportion of the total ecosystem nutrient stock than in systems on richer soils (Table S5, Figure 2). Combining growth data of permanent sampling plots with the wood nutrient data, we find that the annual flow of nutrients into the wood pool is substantial: of similar magnitude to the typical rates of atmospheric deposition in tropical forest ecosystems. For P, for example, 0.5–1 kg/ha/yr wood uptake (Guiana; Figure 1b) is close to the average net deposition of 1.1 kg P/ha/yr that is assumed for tropical forests in vegetation models (Wang et al., 2018). The same is true for the annual uptake of Ca, K, and Mg by wood (Figure 1) and measured net deposition rates in French Guiana (respectively for wood uptake and deposition Ca: 19 vs. 34.1 kg/ha/yr; K: 9 vs. 14 kg/ha/yr; Mg: 4.5 vs. 7.1 kg/ha/yr;

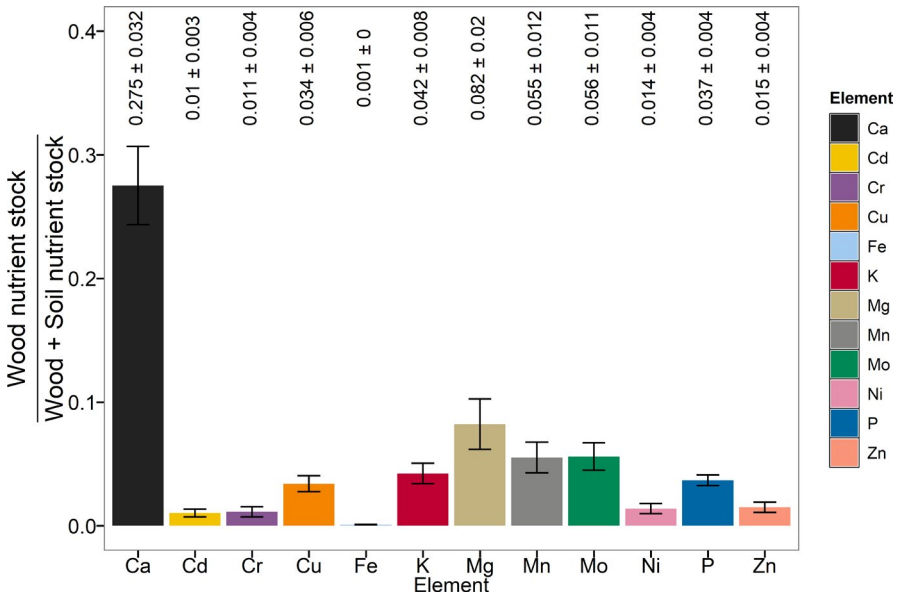

FIGURE 2 More complete analysis of elements in the woody tissue of Guiana's tropical forest. Bars indicate the plot averages of woody biomass fraction of the total nutrient stock (in wood and the upper meter of soil, with total soil nutrients), with standard deviation across the plots ($N = 6$)

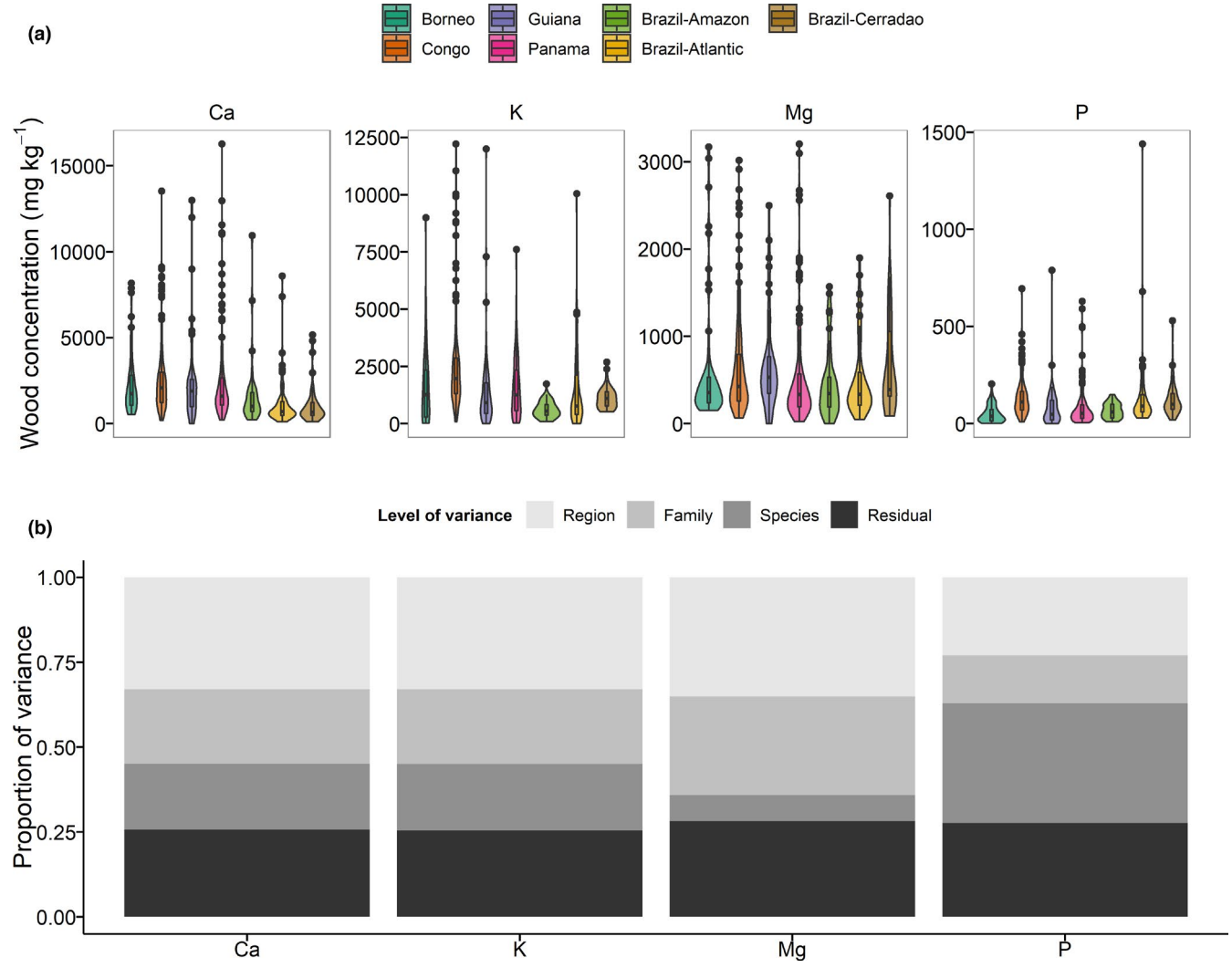

FIGURE 3 (a) Variability of nutrient concentration within and between forest types across the tropics (b) Relative structural variance for nutrients explained by region, plant family, species or unexplained variance (residual) across all samples in the dataset

Van Langenhove et al., 2020). Noting that yearly nutrient accrual in wood can be similar to net depositional inputs shows that allocation of nutrients to woody tissues should not be ignored for tropical forest biogeochemistry.

Our wood stock and uptake estimates are conservative being based as much as possible on heartwood nutrient concentrations, and given that heartwood consistently has lower nutrient concentrations than bark and lower P and K concentration than sapwood (Table S2; Heineman et al., 2016; Meerts, 2002). Further analysis of the lowland forests of French Guiana indicates that wood storage might also be important for other essential micronutrients such as molybdenum, manganese and copper (Figure 2), extending our call for more "dedicated" biogeochemical research on wood nutrient allocation to other elements.

4.2 | On a plant-level: considerable variability in plant-level woody nutrient storage

Although wood nutrient concentrations exhibit marked variation at the global scale (Meerts, 2002), we still know little about what drives this variability (Heineman et al., 2016). For tropical forests, our dataset shows that variation in wood nutrient concentration is considerable (Figure 3a). Furthermore, variation in wood nutrient concentrations across our dataset was predominantly constrained by site-level characteristics for Ca, K and Mg, but determined at the plant species level for P (Figure 3b), suggesting a difference in drivers and mechanisms controlling uptake and allocation of these nutrients in wood. Consequently, variation in wood P storage appears to be linked to a dimension of evolutionary adaptation and ecological variation among species, while wood Ca, Mg and K appear to be defined by the abiotic environment. However, in trying to link wood P to known ecological trade-offs in leaf and wood economics (Chave et al., 2009; Wright et al., 2004), we did not find a discernible link between leaf or wood economics and wood P concentration (Table S3). On the other hand, wood P, Ca, Mg and K concentrations seem to be inter-correlated (Table S4), meaning that high wood P species are also likely to store more Ca, Mg and K in their wood. Indeed, a spectrum in wood nutrient concentration exists, whether or not it is linked to life-history trade-offs.

4.3 | Seeing the wood for the trees

By using our pantropical dataset, we show that the magnitude of ecosystem-level wood nutrient storage, and the variability in wood nutrient concentrations among species, are substantial. Both observations indicate that wood nutrient storage involves important processes in tropical forest biogeochemistry and ecology. In particular, the substantial storage of nutrients in woody tissue (Figure 1) raises an apparent paradox. Tropical forests are considered limited by at least P, and possibly also by other rock-derived nutrients (Turner et al., 2018; Wright, 2019). Several of the mechanisms by which tropical plants meet their P demand come at quite a high carbon cost (e.g., scavenging or mining via mycorrhizal symbiosis; Lambers et al., 2008), yet trees seem to store substantial amounts of P in their wood, where they have little physiological value in comparison with short-term demands of leaf, flower, fruit, and seed production. Furthermore, the ecological role of variation in wood nutrient concentrations remains unclear. Is maximizing wood nutrient concentrations an ecological strategy to minimize the risk of nutrient losses from the ecosystem by leaching or erosion and/or an unconstrained and inefficient use of nutrients? Do certain species accumulate these nutrients in wood to outcompete neighboring trees in the uptake of limiting nutrients? Whether nutrients can be resorbed and reused from the heartwood remains largely unknown, which highlights the limited understanding of the mechanisms at play. The contrasting nutrient concentrations we observe across tissue types (for Borneo; Table S2) are consistent with the observations of Heineman et al. (2016), who reported radial decreases in wood nutrients on bark-to-pith gradients. This suggests that nutrients are partly resorbed when transitioning from sap- to heartwood, which—in turn—points to a physiological control over wood nutrients. As such, trees could benefit in the longer term by conserving nutrients in woody tissues, even if only by withholding those nutrients from their neighbors.

As a consequence of our limited understanding on nutrient reallocation from wood, part of the tropical forest biogeochemistry research today is not taking into account the woody pool as a potential sink or source for nutrients. For example, wood storage could help explain the lack of consistency in fertilization experiments across the tropics (Wright, 2019; Wright et al., 2011), since it introduces plasticity in the tree-level response to altered soil nutrients and an extra overlooked sink and source of nutrients.

5 | CONCLUSION

In conclusion, our data show that potentially substantial amounts of rock-derived nutrients are stored in woody tissues, contributing to the long-term retention of these nutrients in tropical forests. This process likely contributes to the ability of tropical forests to establish and maintain high productivity and biomass stocks on soils depleted of rock-derived nutrients. The magnitude of the measured wood nutrient stocks and annual uptake indicates the importance of consistently including wood nutrients in forest biogeochemistry studies (e.g., on controls of nutrient limitation) and management of tropical forests under global change. Furthermore, despite our additional considerations on strong variation in soil versus wood nutrient storage and the evolutionary role of nutrient storage in wood, questions on the ecological strategy behind variation in wood nutrient storage remain unresolved. Indeed, the role of wood in nutrient cycling has been largely ignored since research in the 1980s. It is time to see the wood for the trees.

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AUTHOR CONTRIBUTIONS

M.B and I.A.J. conceived the idea and coordinated the data compilations. M.B. analyzed the data. M.B. and I.M. collected field data in Congo, O.G., A.D., B.H., J.S, J.P. and I.A.J. collected field data in French Guiana. K.D.H., J.W.D., B.L.T. and C.M.P. collected field data in Panama. Y.M., T.R., M.S., T.I. and N.M. collected field data in Borneo. M.B., P.V., P.R.F., T.I. and K.D.H. analyzed the wood samples. S.D., M.G. and P.R.F. analyzed the soil samples. M.B. wrote the paper, all co-authors discussed the results, gave suggestions for further analyses and commented on the manuscript.

DATA AVAILABILITY STATEMENT

The data underlying nutrient stocks presented in the figures are available in the supplementary information accompanying this paper. Raw data on wood nutrient concentrations can be made available upon request with the corresponding author.

ORCID

Marijn Bauters https://orcid.org/0000-0003-0978-6639
James W. Dalling https://orcid.org/0000-0002-6488-9895
Yadvinder Malhi https://orcid.org/0000-0002-3503-4783
Marina Scalon https://orcid.org/0000-0003-2069-8226
Takeshi Inagawa https://orcid.org/0000-0001-8446-0423
Jan Van den Bulcke https://orcid.org/0000-0003-2939-5408
Michael P. Perring https://orcid.org/0000-0001-8553-4893
Bruno Hérault https://orcid.org/0000-0002-6950-7286
Josep Peñuelas https://orcid.org/0000-0002-7215-0150

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