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Changes in biodiversity impact atmospheric chemistry and climate through plant volatiles and particles

Anvar Sanaei[1✉], Hartmut Herrmann[2], Loreen Alshaabi[2], Jan Beck[2], Olga Ferlian[1,3], Khanneh Wadinga Fomba[2], Sylvia Haferkorn[2], Manuela van Pinxteren[2], Johannes Quaas[3,4], Julius Quosh[1,3], René Rabe[2], Christian Wirth[1,3], Nico Eisenhauer[1,3] & Alexandra Weigelt[1,3]

Climate extremes in tandem with biodiversity change affect plant emissions of biogenic volatile organic compounds, as a result, the formation of biogenic secondary organic aerosols. The resulting biogenic secondary organic aerosols can have a wide variety of impacts, such as on Earth's radiative balance or cloud- and precipitation formation. However, at present, it is unclear how changing biodiversity will lead to changes in biogenic volatile organic compound emissions, biogenic secondary organic aerosols and their corresponding effects. We present a conceptual framework of the relationships between biodiversity and biogenic volatile organic compound emissions based on our current mechanistic understanding and combining knowledge from the fields of biology and atmospheric chemistry. Parts of this framework are tested in a case study using a tree diversity experiment. The relative differences in tree monocultures and mixtures show that the overall concentration of biogenic volatile organic compounds decreases with increasing biodiversity, but results for biogenic secondary organic aerosols are mixed and overall non-significant. A deeper understanding of how changing biodiversity influences biogenic organic compound emissions and biogenic secondary organic aerosol formation requires in-depth investigations of microclimate conditions, accurate monitoring of above- and below-ground biotic and abiotic stress, and manipulating stress conditions across long-term biodiversity experiments.

[1] Institute of Biology, Leipzig University, 04103 Leipzig, Germany. [2] Leibniz Institute for Tropospheric Research (TROPOS), Atmospheric Chemistry Department (ACD), 04318 Leipzig, Germany. [3] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany. [4] Institute for Meteorology, Leipzig University, 04103 Leipzig, Germany. ✉email: anvar.sanaei@uni-leipzig.de

Biosphere and atmosphere are tightly interconnected[1,2], making the understanding of their interactions critically important as human life depends on them[3,4]. On the one hand, a suite of atmospheric drivers can affect the biosphere in different ways[2], including detrimental impacts of rising temperatures on ecosystem integrity and biodiversity[5]. On the other hand, the biosphere can exert feedbacks to the atmosphere, e.g. by releasing various biogenic volatile organic compounds (BVOCs) through plants[6,7] or soil[8]. Following their emission, the atmospheric oxidation of plant-emitted BVOCs leads to gas-phase products, which can either condense on already existing particles or form new ones[9], resulting in biogenic secondary organic aerosols (BSOA)[10], which are important particles for the radiative balance of the Earth[11]. Climate extremes as well as biodiversity change affect emissions of BVOCs from plants[8,12] and, consequently, BSOA formation[13]. However, studies using concerted measurements of BVOCs and BSOA along diversity gradients of emitting plant species are largely missing[14]. This lack of knowledge is particularly worrying given that human activities have traditionally favored monoculture plantations[15], and scientific guidance is urgently needed for major reforestation efforts, especially in the light of current global climate change[16].

Tree species release a large variety of hydrocarbons, especially isoprene for deciduous trees and monoterpenes for coniferous trees. However, the composition and magnitude of emitted BVOCs are highly species-specific[17,18]. These BVOCs are produced primarily via the leaf surface as a result of metabolic processes and as a reaction to abiotic and biotic stress[19,20]. Plant-released BVOCs determine important biotic interactions such as intra- and interspecific communication[21] as well as herbivore and pathogen defences[22]. BVOCs can also protect plants against abiotic stress such as heat, drought, and high radiation[20,23].

In the forest, individual trees are not isolated but compete with their con- and heterospecific neighbors for resources, such as light, water, and nutrients[24]. Resource availability directly affects eco-physiological processes such as photosynthetic rates[25–27] and thus allocation to growth and potential interaction strength. In monocultures or low diverse forest stands, neighboring trees share largely identical ecological niches and thus strongly compete for available resources. In contrast, mixed forests enable resource partitioning, e.g. via differences in tree architecture[28] or rooting depth[29,30], often leading to higher stand productivity[31] and leaf area index[32]. Likewise, forests with diverse leaf chemical traits can enhance soil nutrient availability through diverse plant inputs of leaf and root litter and through soil microbial communities and activities[33,34], thereby increasing forest stand productivity. As forest biomass production and BVOC emissions are highly correlated[35,36], diverse forests should thus emit higher amounts of BVOC (Fig. 1, Hypothesis 1).

Yet, there are at least two counteracting mechanisms which should lead to decreased BVOC emissions with increasing tree diversity. First, more diverse plant communities increase facilitation and thereby might mitigate abiotic stress. It has been shown that functionally diverse plant communities can increase water use efficiencies through variation in root architecture as a result of spatiotemporal complementary resource use[29] and microclimate amelioration, particularly in dry seasons[37]. In addition, complexity in the vertical and horizontal stratification of diverse stands can relieve thermal stresses[38,39] and alleviate the risks of drought stress[40]. Indeed, decreasing heat and drought stress in mixed communities is likely to result in lower leaf temperature, which could result in lower BVOC emissions[18,41]. Given that abiotic stress, but particularly heat and drought are known to be important drivers of BVOC emissions, we hypothesize a decrease in BVOC concentrations in mixtures where abiotic facilitation mediates abiotic stress reduction (Fig. 1, Hypothesis 2).

Second, more diverse plant communities show decreased per capita herbivory damage and pathogen infection[42,43]. Although multi-plant diets may be beneficial for different herbivores per se[44,45], plant natural enemies are also more abundant in more diverse plant communities, which could reduce herbivory pressures as well as insect outbreaks (top-down regulation), as supposed by the "enemies hypothesis"[43,46]. Furthermore, the heterogeneity of plant nutritive traits in diverse stands suppresses herbivore abundance, resulting in declining herbivore performance[47], likely due to non-host species reducing the accessibility of host species[48]. Overall, reduced biotic stress through herbivores and pathogens in mixtures should reduce the amount of BVOC emissions (Fig. 1, Hypothesis 3) but might increase the diversity of emitted compounds. However, irrespective of the change in the amount of BVOC emissions with increasing tree diversity – which might increase or decrease depending on the primary mechanism – we would expect that the diversity of emitted compounds increases in mixed forests given that BVOC emissions are known to be highly species-specific[49].

Once entering the atmosphere, plant-derived VOCs react quickly with ambient hydroxyl radicals (OH), Ozone (O_3), and nitrate radicals (NO_3) resulting in the formation of BVOC oxidation products that are more oxidized than the compounds originally emitted. These compounds, including highly oxygenated molecules (HOMs) or, as more recently called, oxygenated organic molecules (OOMs)[50,51], have lower vapor pressures and better water solubility and can hence contribute to BSOA as atmospheric particles[52]. Changing BSOA fractions in organic particle composition could have different effects. First, it could influence radiative effects of the particles themselves ('direct effect') and hence couple to climate. Secondly, such compositional changes could influence the particles' ability and effectiveness to act as cloud condensation nuclei (CCN), thus influencing cloud formation with all its respective consequences for radiation through aerosol-cloud interactions ('indirect effects') that also affect precipitation formation rates[53–55]. However, the conversion of BVOC to BSOA is strongly determined by the local atmospheric composition and oxidation regime, temperature, the kinetics and mechanism of the emitted BVOCs and their respective reactions in the gas phase including their phase transfer characteristics and their particle-phase chemistry[56–58]. High BVOC emissions, e.g. due to rising temperature, increase BSOA formation which, to some extent, could trigger a heating by direct particle absorption but it could also lead to a cooling due to the effect of BSOA on cloud formation and reflectivity of clouds[11,13]. Recent findings suggest that biotic and abiotic stress-induced BVOC emissions even accelerate climate-relevant BSOA formation[59–61].

Our mechanistic understanding and existing knowledge suggest that increasing biodiversity could predictably influence the amount of BVOC released. So far, studies have primarily focused on single tree species though, with no studies available at the time using concerted measurements of BVOCs and BSOA in tree stands or along experimental or natural tree diversity gradients (Fig. 1). We argue that this is a critical knowledge gap, as BVOC composition has been recognized as a powerful stress indicator and an important feedback mechanism of climate change[62]. Addressing this knowledge gap is relevant to understand the causal connections between biodiversity and climate change and to overcome these coupled crises as two of the most urgent challenges facing humanity[3]. To support our claim that biodiversity might play a significant role in this context and to inspire future research, we present the first data from a case study in the

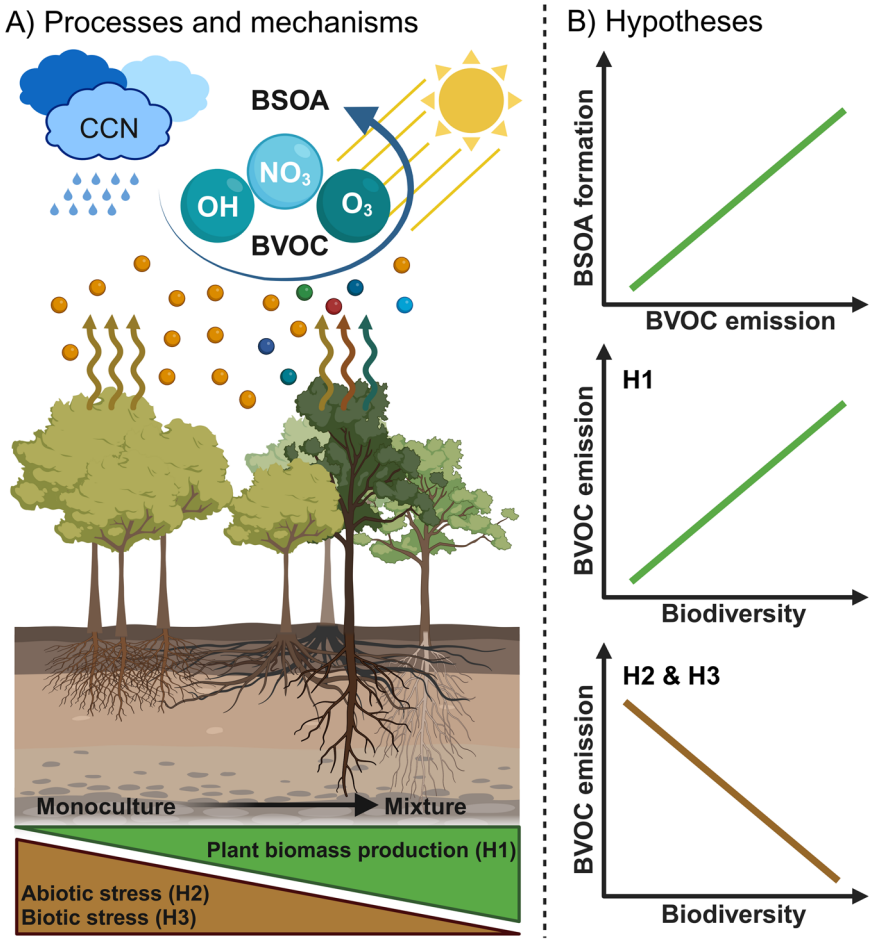

Fig. 1 Scheme showing basic processes and mechanisms related to biodiversity, biogenic volatile organic compounds and biogenic secondary organic aerosols. The figure outlines (**A**) the processes and mechanisms, and (**B**) the general hypotheses related to biogenic volatile organic compound (BVOC) emissions across biodiversity gradients (monoculture vs. mixtures), biogenic secondary organic aerosol (BSOA), and cloud condensation nuclei (CCN) formation. The hypothesized positive and negative relationships between BVOC emissions and biodiversity are represented by the green (the first hypothesis; H1) and brown (the second and third hypotheses; H2 and H3) lines, respectively. The hypothesized positive relationship between BVOC emissions and BSOA formation is indicated in green. The figure was created with BioRender.com.

MyDiv tree diversity experiment site in Germany[63]. Here, we simultaneously measured the magnitude and variability of BVOC and BSOA compounds in ten plots differing in tree diversity. Using this case study, we aim to put forward the link between biodiversity and BVOC/BSOA and provide a first test of principle in support of the conceptual framework. Our results show that the amount of BVOCs tends to decrease with biodiversity in most cases, while mixed results were found for BSOA compounds. Our findings highlight the need for multidisciplinary work at the interface between the biosphere and the atmosphere to better understand the reciprocal effects of biodiversity and climate change[4].

Results and discussion

BVOC emissions across biodiversity. We quantified nine different BVOCs from the investigated plots in the MyDiv experiment, i.e. α-pinene, camphene, β-pinene, 3-carene, p-cymene, limonene, α-terpinene, isophorone, and acetophenone. Our results show that most of the observed BVOC compounds were not significantly different between the individual tree species in single-species plantations (hereafter monocultures) and their corresponding multiple-species plantations (hereafter mixtures), with some notable exceptions (Fig. 2). In particular, we find some significant differences in the emission of limonene and acetophenone (ANOVA: $p = 0.01$ and $p < 0.01$, respectively; Fig. 2A, I) which was higher in monoculture plots, particularly in *Sorbus aucuparia* L. (Fig. 2A, I), highlighting the species-specific dependency of BVOC emission rates[17,18].

The comparison between the observed and expected amounts of each BVOC compound in mixture plots (two- and four-species mixtures) shows that there were no significant differences; however, we found a few exceptions (Fig. 3). In four-species mixtures, some BVOC compounds differed significantly between the observed and expected amounts (Fig. 3). As such, the observed amounts of limonene and acetophenone were significantly lower than the expected values (t-test: $p = 0.04$ and $p < 0.01$, respectively; Fig. 3C, I). This indicates that four-species mixtures produced lower amounts of limonene and acetophenone than expected.

The relative differences in monocultures and mixtures based on standardized mean difference analysis across diversity levels show that increasing tree diversity significantly decreased the overall concentration of BVOCs (the overall standardized mean difference: $p < 0.01$, Fig. 4). Particularly, the relative differences in the means of observed and expected amounts of limonene were significant (the standardized mean difference: $p < 0.01$, Fig. 4), and β-pinene, p-cymene, α-terpinene and acetophenone were marginally significant (the standardized mean difference:

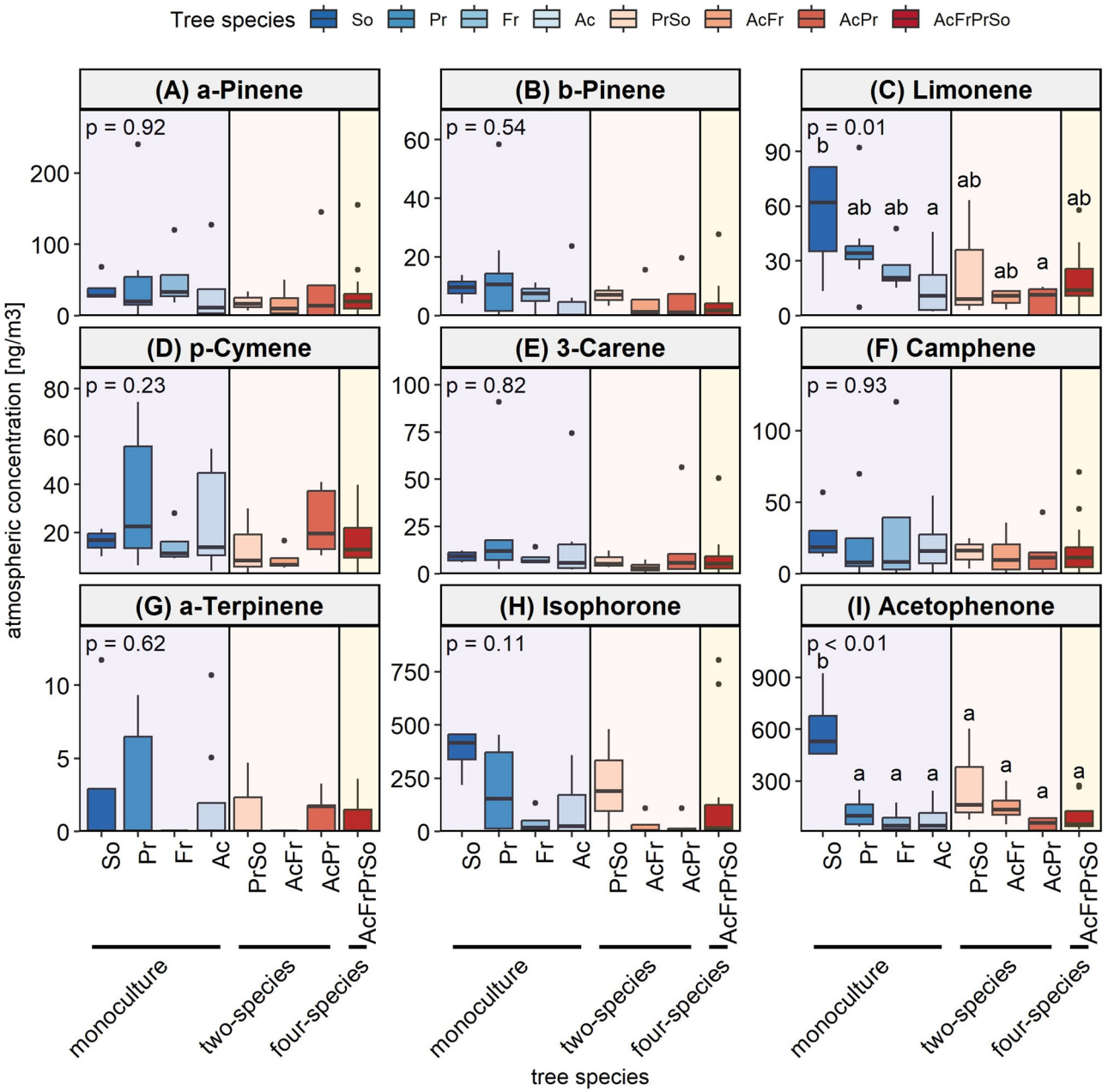

Fig. 2 Differences in observed biogenic volatile organic compounds across individual tree species and mixtures. Changes in observed emitted biogenic volatile organic for (**A**) α-Pinene, **B** β-Pinene, **C** Limonene, **D** p-Cymene, **E** 3-Carene, **F** Camphene, **G** α-Terpinene, **H** Isophorone, and **I** Acetophenone across individual tree species and mixtures. Boxes indicate interquartile ranges (bottom and top parts of the box), and median lines (horizontal lines within boxes) and whiskers indicate the minimum and maximum of the measurement. *p*-values are shown. Different letters above boxes represent significant differences among tree species ($p < 0.05$; Tukey's test). Abbreviations: So = *Sorbus aucuparia* L., Pr *Prunus avium* (L.) L., Fr *Fraxinus excelsior* L., Ac *Acer pseudoplatanus* L.

$p = 0.09$, $p = 0.08$ and $p = 0.06$, respectively; Fig. 4), meaning that mixtures produced significantly less than expected amounts of these compounds compared to monocultures. The relative differences in monoculture and mixtures for two-and four-species mixtures also showed the same decreasing trend of BVOC emissions with increasing tree diversity and were significant (the standardized mean difference, $p < 0.01$, Supplementary Fig. 1). As such, the relative differences in the means of observed and expected amounts of limonene were significant in two-and four-species mixtures (the standardized mean difference: $p = 0.05$ and $p = 0.03$, Supplementary Fig. 1), while acetophenone and α-terpinene showed strong and marginal significance in four-species mixtures, respectively (the standardized mean difference: $p < 0.01$ and $p = 0.09$, respectively; Supplementary Fig. 1B). The overall results indicate that tree diversity significantly reduced BVOC emissions, supporting our second and third hypotheses (H2 and H3). Concurrently, although most of the BVOC compounds' bivariate regression relationships with annual wood productivity were not significant (Supplementary Fig. 2), three of the BVOC compounds — namely limonene, isophorone and acetophenone — showed significant negative associations with annual wood productivity (Supplementary Fig. 2C, H, I), inconsistent with our first hypothesis of biomass production (H1).

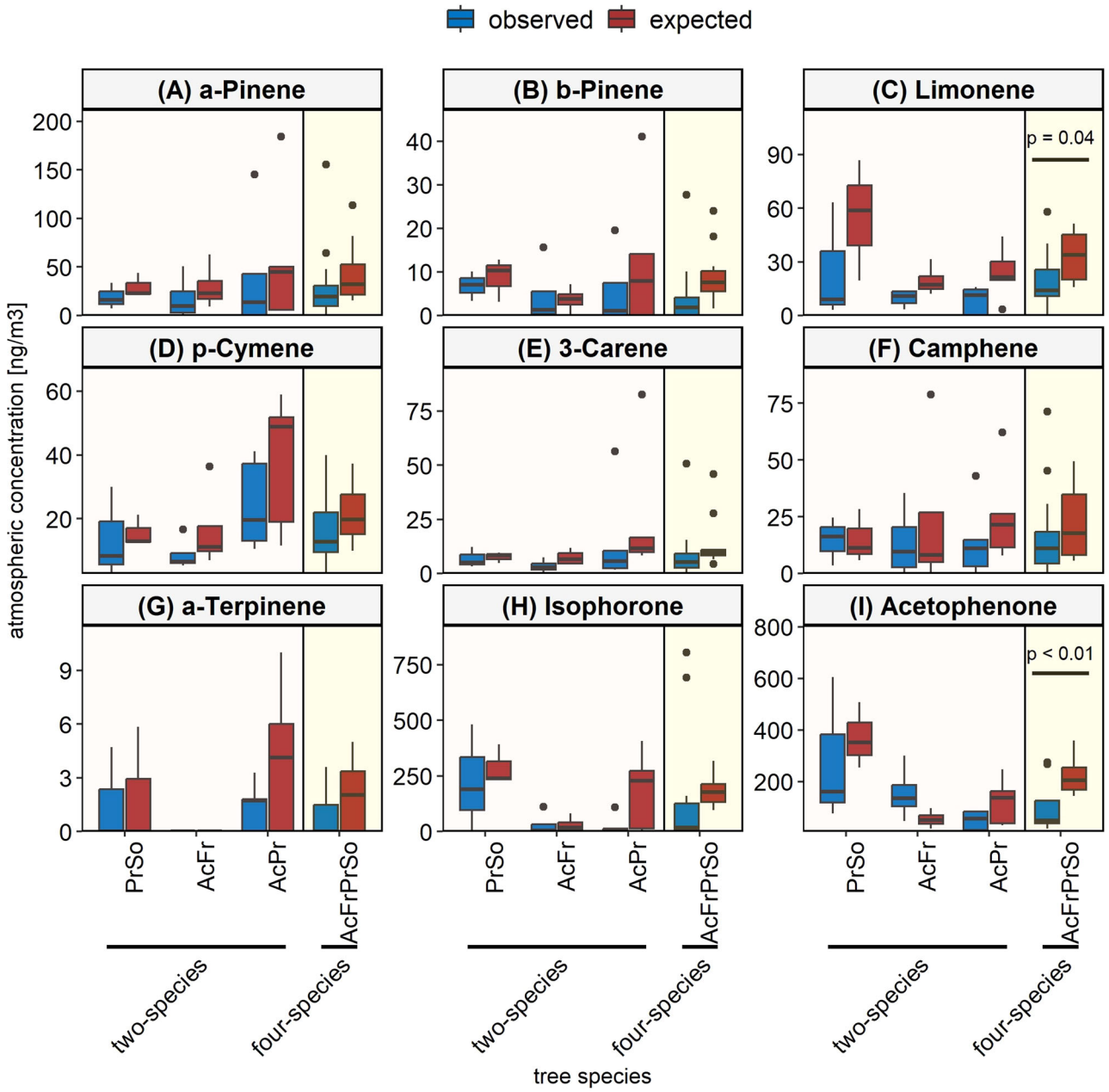

Fig. 3 Differences in observed and expected biogenic volatile organic compounds across tree mixtures. Changes in observed and expected biogenic volatile organic for (**A**) α-Pinene, **B** β-Pinene, **C** Limonene, **D** p-Cymene, **E** 3-Carene, **F** Camphene, **G** α-Terpinene, **H** Isophorone, and **I** Acetophenone across tree mixtures (two- and four-species mixtures). Boxes indicate interquartile ranges (bottom and top parts of the box), and median lines (horizontal lines within boxes) and whiskers indicate the minimum and maximum of the measurement. *p*-values are shown (t-test). Abbreviations: So *Sorbus aucuparia* L., Pr *Prunus avium* (L.) L., Fr *Fraxinus excelsior* L., Ac *Acer pseudoplatanus* L.

Consistent with our second hypothesis of abiotic stress amelioration (H2), the decline in BVOC emissions with increasing biodiversity could partly be due to a reduced competition for resources (e.g., light and water) because the emission of BVOCs acts as a defence strategy during plant competition[64]. Besides, mixed plots can alleviate thermal and water stress[37,38] through spatial and structural complexity of canopy cover[37] and also differences in rooting depth [37]or leaf phenology, which has been shown to have an effect on photosynthetic seasonality[65]. In this context, microclimate buffering is important, as at a global scale, an increase of 2–3 °C in the mean global temperature due to global warming has been shown to increase global BVOC emissions by 30–45%[66]. Decreasing BVOC emissions with increasing biodiversity also supports our third hypothesis of reduced biotic stress (H3), and can be explained by multiple mechanisms: First, a higher percentage of leaf area eaten by herbivores, which may occur in monoculture due to a higher probability of herbivores[43], can increase BVOC emissions[67]. Second, increasing plant diversity decreases herbivore per capita effects on plants while simultaneously benefiting predators[42,43]. Third, heterogeneity in plant defense strategies in highly diverse communities reduces herbivore performance[68]. Fourth, plant-herbivore interactions also highly depend on the heterogeneity of available nutrients. For instance, herbivore abundance and performance decrease with plant nutrient variability[46,47], indicating that diverse stands are

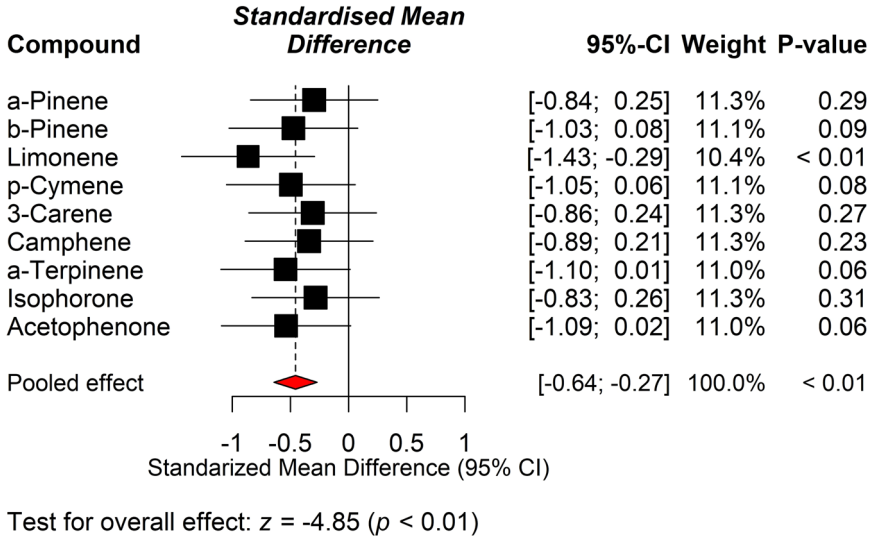

Fig. 4 The relative differences in the means of biogenic volatile organic compounds. A forest plot summarizing the results of the standardized mean difference between monocultures and mixtures for changes in biogenic volatile organic compounds as a result of diversity change. The squares' sizes and widths represent each compound's weight, while the diamond (red color) represents the overall effect estimate of the analysis. Effect sizes were calculated using the standardized mean difference. The horizontal lines of the squares show 95% confidence intervals (CI). *p*-values are given for each compound and for the overall effect.

expected to have reduced herbivory damage[69], resulting in lower BVOC emissions. Altogether, biotic and abiotic patterns may result in lower emission rates of BVOC in mixtures compared to monocultures, stressing the potential importance of both, biotic and abiotic factors on BVOC emissions[23,70], yet further experiments are urgently needed to properly test these hypotheses.

BSOA formation across biodiversity. We quantified a total of fifteen BSOA compounds on the investigated plots throughout the 2021 sampling period. These analytes were diaterpenylic acid acetate [DTAA], 3-methyl-1,2,3-butanetricarboxylic acid [MBTCA], norpinonic acid, pinonic acid, terebic acid, terpenylic acid, pinic acid, adipic acid, pimelic acid, azelaic acid, suberic acid, succinic acid, glutaric acid, salicylic acid, and sebacic acid. Although the observed BSOA compounds did not significantly differ between individual tree species and their corresponding mixtures (Fig. 5), succinic and sebacic acid were tendentially higher in monoculture compared to mixture plots (Fig. 5L, O); by contrast, pinonic and terebic acid were tendentially higher in mixture plots compared to monoculture plots (Fig. 5D, E).

While we found no significant differences between observed and expected amounts in BSOA compounds, individual mixtures produced tendentially more or less BSOA compounds than expected. In particular, a mixture of *Acer pseudoplatanus* L. and *Fraxinus excelsior* L. and also a mixture of *Prunus avium* (L.) L. and *Sorbus aucuparia* L. produced a larger than expected amount of norpinonic acid (Fig. 6C). Similarly, the mixture of *Acer pseudoplatanus* L. and *Fraxinus excelsior* L. produced a larger than expected amount of glutaric acid (Fig. 6M).

Concurrently, the relative differences analysis shows that different compounds responded differently to increasing tree diversity, showing that some BSOA compounds (like 3-methyl-1,2,3-butanetricarboxylic acid [MBTCA], pinonic acid, pinic acid, and terpenylic acid) increase relative to what is expected from monocultures but others (like norpinonic acid, adipic acid, suberic acid, and azelaic acid) decrease; however, the overall results were mixed and non-significant (the standardized mean difference: $p = 0.26$, Fig. 7). Although the relative differences analysis pattern in two-species and four-species mixtures revealed mixed results, the overall results were significant for two-species mixtures (the standardized mean difference: $p = 0.05$, Supplementary Fig. 3A), but non-significant for four-species mixtures (the standardized mean difference: $p = 0.89$, Supplementary Fig. 3B).

The mixed results might be due to the influence of regional air masses, as the atmospheric conversions from BVOC to BSOA require some time corresponding to spatial spread and thus preventing the identification of a local BSOA occurrence patterns coupled to the measured BVOC. Although we correlated atmospheric radicals and α-pinene with BSOA compounds across tree diversity gradients, we were unable to find significant associations for most of the BSOA compounds due to the small number of measured plots, resulting in low statistical power. However, we did find significant associations in some cases, for example, between norpinonic acid and the products (Supplementary Fig. 4). Although our knowledge about biodiversity effects on BSOA formation is limited, it seems likely that biotic and abiotic stresses also matter indirectly for BSOA formation[59–61]. For instance, using a compact chamber, temperature dependence of BSOA formation from α- pinene has been reported[71], which might partly be related to physical or abiotic differentiation in mixtures versus monocultures. Earlier studies observed a higher formation rate of OH radicals in humid conditions[72], which may increase the formation of some BSOA compounds even if BVOCs are low. In addition, the complex formation patterns of BSOA reflect the potential that source precursor and atmospheric oxidants can also matter for oxidation products[56,57]. Specifically, the differential response of BSOA compounds to diversity gradients could partly be explained by the difference in the gas-phase mechanisms related to the oxidation of α- and β-pinene[73,74]. For example, MBTCA, which is formed from the oxidation (OH radical) of α-pinene, is a stronger functionalized compound than pinic and pinonic acid[75]. It is obvious that local climate variability could affect the availability and magnitude of ambient oxidants such as O_3, and NO_3[6], which are key to the oxidation of BVOCs and also determine the rate and composition of the oxidation products[9,76]. Thus, changes in the quality and quantity of BVOC emissions due to biotic and abiotic factors and also oxidant concentrations could potentially

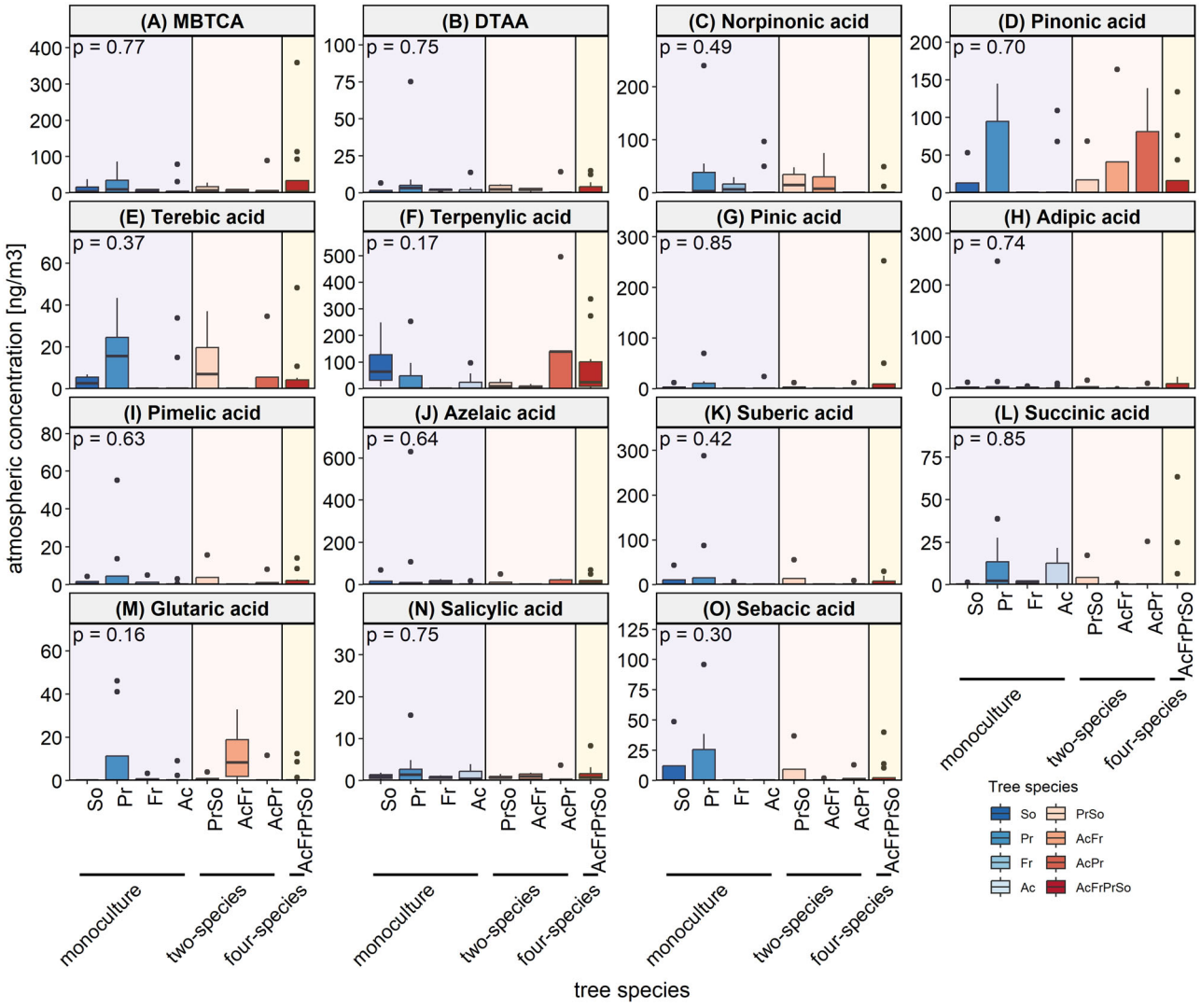

Fig. 5 Differences in observed biogenic secondary organic aerosols across individual tree species and mixtures. Changes in biogenic secondary organic aerosol for each (**A**) MBTCA, **B** DTAA, **C** Norpinonic acid, **D** Pinonic acid, **E** Terebic acid, **F** Terpenylic acid, **G** Pinic acid, **H** Adipic acid, **I** Pimelic acid, **J** Azelaic acid, **K** Suberic acid, **L** Succinic acid, **M** Glutaric acid, **N** Salicylic acid, and **O** Sebacic acid across individual tree species and mixtures. Boxes indicate interquartile ranges (bottom and top parts of the box), and median lines (horizontal lines within boxes) and whiskers indicate the minimum and maximum of the measurement. *p*-values are shown. Abbreviations: So *Sorbus aucuparia* L., Pr *Prunus avium* (L.) L., Fr *Fraxinus excelsior* L., Ac *Acer pseudoplatanus* L., MBTCA 3-methyl-1,2,3-butanetricarboxylic acid and DTAA diaterpenylic acid acetate.

affect the size and composition of BSOA[61,77–79]. The resulting BSOA, depending on their properties, may scatter or absorb radiation and thus control the radiative balance of the earth[80]. Larger BSOA concentrations lead to larger cloud droplet number concentrations, implying less sunlight reaching the ground[81–83]. This effect leads to less sunlight over boreal forests[11,84,85]. At larger droplet concentrations, in turn, the precipitation formation rate in low clouds is reduced[86,87], with potential implications for further change in surface solar radiation but also precipitation characteristics. Overall, we acknowledge that testing our hypothesis needs further experimental work to improve our understanding of how the magnitude and composition of BVOC and BSOA will change across tree diversity gradients.

Conclusions and research perspectives. In light of significant human-induced changes in biodiversity and climate, the link between atmospheric and biological measurements is crucial to improve our understanding of atmosphere-biosphere feedbacks. However, to what extent changes in atmospheric chemistry and climate change are related to biodiversity is largely unknown. Here we show that the general relationship between biodiversity and BVOC emissions works in principle. The aim of this study is not to properly test our hypotheses, but rather to put forward the relationship between biodiversity and BVOC or BSOA. So, with this first and limited dataset any modeling and generalization would be premature. Based on our mixed results, we argue, that measuring BVOC emissions and BSOA formation across biodiversity gradients alone is not enough to fully understand their magnitude and composition. A deeper understanding requires in-depth investigations of microclimate conditions, above- and below-ground herbivores and pathogens, soil microbial communities, accurate monitoring of biotic and abiotic stress, and manipulating biotic and abiotic stress across long-term biodiversity experiments. Another important component that needs to be considered is the seasonality of photosynthetic activity, as we know it changes with leaf phenology[65]. In addition, we need local and regional-scale models, combined with field and chamber

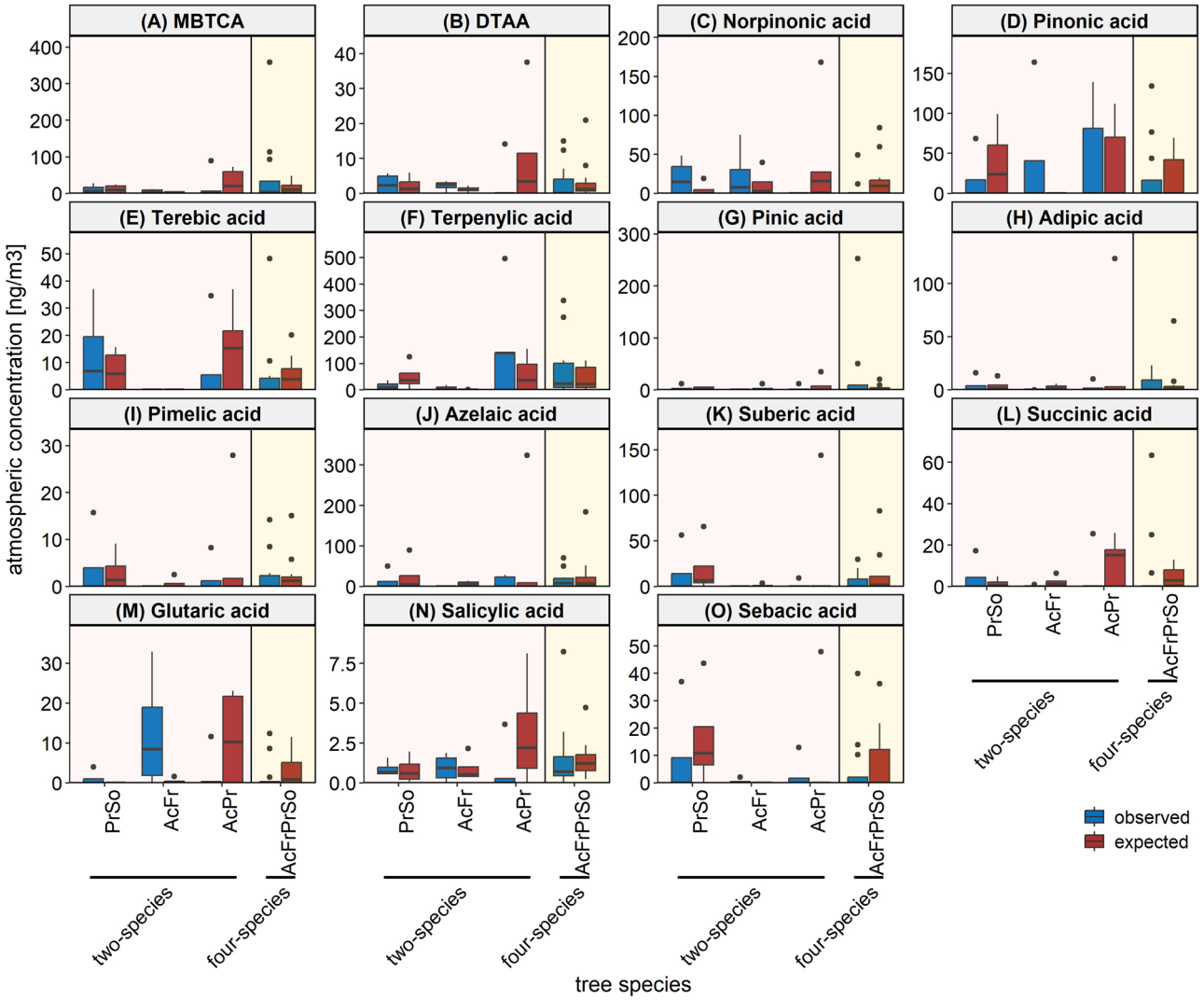

Fig. 6 Differences in observed and expected biogenic secondary organic aerosols across tree mixtures. Changes in observed and expected biogenic secondary organic aerosol for each (**A**) MBTCA, **B** DTAA, **C** Norpinonic acid, **D** Pinonic acid, **E** Terebic acid, **F** Terpenylic acid, **G** Pinic acid, **H** Adipic acid, **I** Pimelic acid, **J** Azelaic acid, **K** Suberic acid, **L** Succinic acid, **M** Glutaric acid, **N** Salicylic acid, and (**O**) Sebacic acid across tree mixtures (two- and four-species mixtures). Boxes indicate interquartile ranges (bottom and top parts of the box), and median lines (horizontal lines within boxes) and whiskers indicate the minimum and maximum of the measurement. Abbreviations: So *Sorbus aucuparia* L., Pr *Prunus avium* (L.) L., Ac *Acer pseudoplatanus* L., Fr *Fraxinus excelsior* L., Ac *Acer pseudoplatanus* L., MBTCA 3-methyl-1,2,3-butanetricarboxylic acid and DTAA diaterpenylic acid acetate.

measurements, to improve our understanding of biosphere-atmosphere interactions. These experimental platforms along with the expertise exist in each of the separate disciplines. Therefore, a multidisciplinary approach at the biosphere-atmosphere interface would extend our understanding of the reciprocal effects of biodiversity and climate change[4] and help to unravel the extent to which emissions of isoprenoids and aerosol formation are related to biodiversity. This will open a new area of research where the fields of biology, climate science, and atmospheric chemistry may interact.

Methods

We tested the effect of tree diversity on BVOC emission and BSOA formation by varying tree species richness, including monocultures, two- and four-species mixtures at the MyDiv experimental site located in Saxony-Anhalt, Germany[63], between September 21 and October 13, 2021 (13 days in total). The MyDiv experiment comprises eighty 11 ×11 m plots that are located 2 m apart. We used ten of these plots in our case study. The monoculture plots consisted of *Acer pseudoplatanus* L., *Fraxinus excelsior* L., *Prunus avium* (L.) L., and *Sorbus aucuparia* L. The two-species mixture plots consisted of three sets: a mixture of *A. pseudoplatanus* and *F. excelsior*; a mixture of *A. pseudoplatanus* and *P. avium*; and a mixture of *P. avium* and *S. aucuparia*. The four-species mixture plot consisted of all four species. Two monoculture plots, one two-species mixture plot, and one four-species mixture plot were sampled per day for at least four consecutive days (except rainy days). BVOC emissions and BSOA compounds were captured simultaneously using samplers installed in the upper layer of the canopy of each plot. The aluminum sampling box was custom-made and equipped with gas phase (for BVOC) and particulate matter (for BSOA) sampling systems. The gas phase sampling system consisted of a 2-cm-diameter tube with a glass-fritted disc to prevent insect intrusion. The tube was connected to Carbotrap 300 and Tenax cartridges (Supelco, Bad Homburg, Germany) and a GilAir Plus pump (Sensidyne, USA) operating at 150 ml/min using flexible PVC

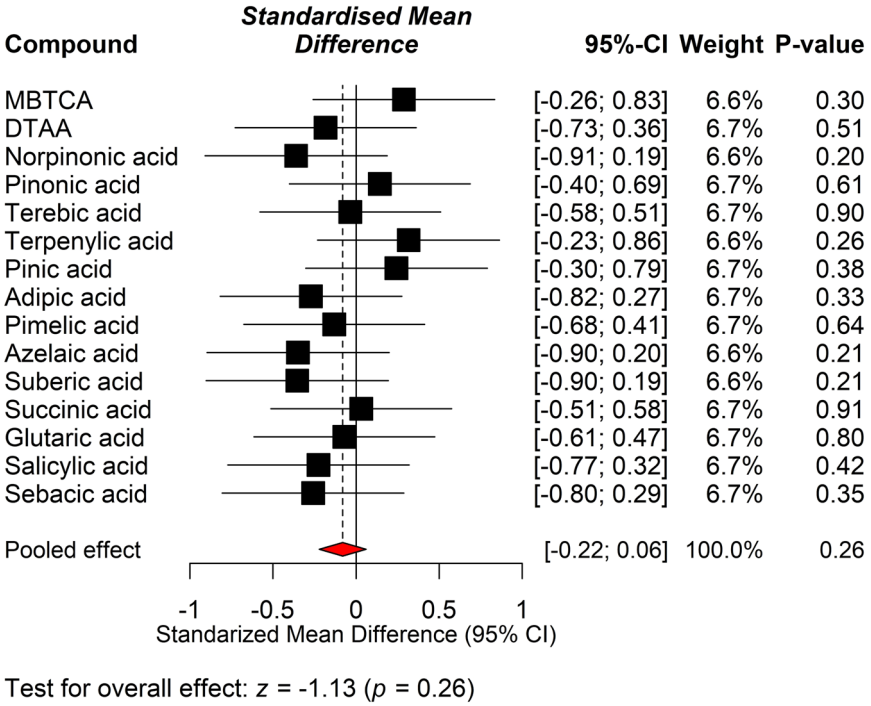

Fig. 7 The relative differences in the means of biogenic secondary organic aerosols. A forest plot summarizing the results of the standardized mean differences between monocultures and mixtures for changes in biogenic secondary organic aerosols as a result of diversity change. The squares' sizes and widths represent each compound's weight, while the diamond (red color) represents the overall effect estimate of the analysis. Effect sizes were calculated using the standardized mean diffrenece. The horizontal lines of the squares show 95% confidence intervals (CI). *p*-values are given for each compound and for the overall effect. Abbreviations: MBTCA 3-methyl-1,2,3-butanetricarboxylic acid, DTAA Diaterpenylic acid acetate.

tubes. The particulate matter (PM) system consisted of a PM10 PEM impactor (SKC, USA) inlet connected to a Gillian 12 pump (Sysidyne, USA) operating at 10 l/min. We used an off-line method, where the applied adsorbent cartridges for capturing BVOC and quartz filters for capturing BSOA lasted for four hours (10:00 AM to 2:00 PM). After four hours of sampling, the cartridges and filters were transferred to the laboratory for further analysis. The tubes were immediately sealed, stored at 4 °C, and measured within 3–5 days. All filters were brought to storage at −18 °C in light-protected containers. Field blanks were taken and values were usually below 10% of the value of the ambient concentration. Before sampling in the field, every filter was preheated at 105 °C for 24 h and each tube was conditioned at 220 °C to avoid any contamination. We have tried to assess background levels of BSOA to discriminate the production from the plots from the local background. Unfortunately, the deployed Digitel high volume sampler at the background station had sampling characteristics not identical to those of the plot-deployed measurement boxes.

Quantification of BVOC compounds trapped in adsorbent cartridges was then conducted by gas chromatography mass spectrometry (GC/MS, Agilent, Waldbronn, Germany) combined with thermodesorption (Perkin Elmer, Rodgau, Germany). To do so, the BVOCs were first desorbed from the cartridges with a heating rate of 7 °C/min and a flow rate of 50 ml/min to a final temperature of 220 °C. Then the BVOCs were cryofocused at −30 °C on a cooling trap. The trap was heated to 220 °C (hold time: 3 min) with 1 ml/min and the BVOCs were transferred to the Zebron ZB-5ms (30 m; 0,25 mm; 0,25 µm) capillary column. The initial temperature of the column was 35 °C (hold time: 5 min) and then increased stepwise to 120 °C (ramp: 5 °C/min) and finally to 320 °C (ramp: 20 °C/min) and hold for 12 min. Finally, the observed BVOCs were identified using known calibration standards. For external calibration, a methanolic solution mix of the standard compounds was injected to an empty glass tube that was connected to the calibration tube filled with Tenax material. Under gentle heating and with nitrogen as a carrier gas, the methanolic solution was evaporated and the compounds were transferred to the calibration tube. Six calibration levels were prepared with concentrations between 0.5 and 20 ng per tube. Each calibration level was measured three times and the relative standard deviation was usually between 2 and 10%. Detection limits at S/N ≥ 3 (signal to noise ratio) ranged close to the lowest calibration level. Before and after each sample batch, a calibration was performed and after each 6–10th sample a calibration tube with limonene was measured as standard control. In addition, blank tubes (tubes that were not probed) were measured before each sample batch to check for contaminations. As a result of this, the following compounds were identified: α-pinene, β-pinene, camphene, 3-carene, p-cymene, limonene, α-terpinene, isophorone, and acetophenone.

To analyze BSOA constituents every filter was cut into small pieces and transferred to an extraction vial. 1.0 mL of a water acetonitrile mixture (1:1) was used as an extraction solvent. All samples were shaken for 30 min at 1000 min^{-1} and then transferred into vials with a syringe filter (pore size: 0.2 µm, wwPTFE membrane). The analysis of the extracts was done with ultrahigh-performance LC system equipped with a C_{18} column (Acquity HSST3, 1.8 mm, 2.1 × 100 mm, Waters). The eluents were ultrapure water with 0.1% formic acid (eluent A) and acetonitrile with 0.1% formic acid (eluent B). With a flow rate of 0.3 mL min^{-1}, the following gradient was used: 5% B at 0 min, 5% B at 1.0 min, 100% B at 16.0 min, 100% B at 18.0 min, 5% B at 18.1 min, 5% B at 21.0 min. The LC effluent was connected to a high resolution Orbitrap mass spectrometer (Q Exactive Plus, Thermo Fisher Scientific) equipped with an ESI source operated in the negative mode (3.5 kV). Each sample was measured three times in full scan mode (m/z 50–750, R = 70k at m/z 200). After every tenth

sample, a water blank and a quality control standard at medium concentration were measured alternately to evaluate possible carry-over and system stability. Finally, the following BSOA compounds were quantified via an external calibration in the range 0.024-400 μg L^{-1}: diaterpenylic acid acetate [DTAA], 3-methyl-1,2,3-butanetricarboxylic acid [MBTCA], norpinonic acid, pinonic acid, terebic acid, terpenylic acid, pinic acid, adipic acid, pimelic acid, azelaic acid, suberic acid, succinic acid, glutaric acid, salicylic acid, and sebacic acid. By measuring a dilution series, limit of detection (LOD) at S/N ≥ 3 was determined.

In addition to gas and particle phase measurements, local meteorological parameters i.e., air temperature, humidity, air pressure, wind speed and direction, precipitation, and ultraviolet radiation were measured at the top of the canopy of each plot. The overall variation of meteorological parameters are shown in Supplementary Figs. 5 and 6. For NO_3 and ozone, the overall concentration was measured (Supplementary Fig. 7). With tree height and stem diameter, we calculated wood volume for each plot for the beginning of the growing period (2015) and also measurement time (2021)[88]. Accordingly, we calculated annual wood productivity by deducting 2021 wood volume data for each plot from the beginning of the growing period using the MyDiv inventory data[89,90]. More details about the quantification of wood volume and annual wood productivity can be found in the current study[88].

We first compared the amounts of observed emitted BVOC and BSOA compounds across biodiversity gradients using a one-way analysis of variance (ANOVA) test, and where the ANOVA test was significant, we used Tukey's HSD for pairwise multiple comparisons. Due to the highly reactive nature of α- and β-pinene with atmospheric oxidants such as ozone and OH radical[91,92], we performed the Pearson's correlation coefficients between the products (reacted between α- and β-pinene and ozone and ultraviolet radiation) and the observed BSOA compounds. We analyzed the correlation coefficients separately for each measurement week to account for weekly changes of abiotic conditions.

Next, we calculated the expected amount of each BVOC or BSOA compound in the mixture from their respective amounts of observed compounds in monoculture based on the species richness of the mixture plot:

$$\text{Expected amount of compounds in mixture plot} = \frac{\sum \text{Observed amount of compound in monoculture}}{\text{Plot species richness}}$$

We then compared the observed and expected amounts of each BVOC or BSOA compound using a two-sample t-test.

After that, we used a commonly known Cohen's d effect size[93], the standardized mean difference (SMD), to quantify the magnitude and direction of the biodiversity effects on BVOC emission or BSOA formation in monocultures and mixtures. For this, we calculated the SMD for each BVOC compound or BSOA formation and their overall differences between monoculture and mixture using the observed and expected values of each BVOC or BSOA compound[94] to see the differences in BVOC emission or BSOA formation between monoculture and mixtures.

$$\text{SMD} = \frac{\text{Mean}_{\text{observed}} - \text{Mean}_{\text{expected}}}{\sqrt{(\text{standard deviation}^2_{\text{observed}} + \text{standard deviation}^2_{\text{expected}})/2}}$$

This measure calculates the effect size for each BVOC or BSOA compound, and also for the overall by combining the observed and expected values of all quantified BVOC or BSOA compounds. This approach also assigns a weight to each SMD using the inverse of the variance [94] (within-compound variance), which requires the mean, standard deviation as well as the number of observations[94] for the observed and expected compounds. To infer how tree diversity levels contribute to BVOC emission or BSOA formation, we performed three separate SMD analyses for BVOC or BSOA compounds for the overall mixtures (a combination of two-and four-species mixtures), two-species mixtures, and four-species mixtures. We finally visualized the results using a forest plot, which shows the effect size of each individual BVOC or BSOA compound and the overall estimates. As such, positive values indicate that the mixture produced a higher amount of compounds than expected based on the monoculture data, and vice versa. All analyses were done using the R v.4.1.3 platform[95].

Data availability

Data generated during the study are available on the MyDiv experiment database (https://doi.org/10.25829/GJ9X-EZ41).

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Author contributions

A.W., H.H., N.E., Jo.Q. and C.W. conceived the ideas. L.A., J.B., H.W.F., O.F., Ju.Q., M.v.P. and R.R. collected the data. L.A., J.B., H.W.F., H.H., S.H. and M.v.P. coordinated associated lab measurements. A.S. analyzed the data and wrote the first draft of the manuscript. N.E., H.H., Jo.Q., A.W. and C.W. contributed to the writing via multiple rounds of revision. All authors contributed critically to the drafts and gave final approval for publication.

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The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Anvar Sanaei.

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