Changes in biodiversity impact atmospheric chemistry through plant volatiles and particles

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Abstract

Climate extremes in tandem with biodiversity change affect emissions of biogenic volatile organic compounds (BVOCs) from plants and, as a result, the formation of biogenic secondary organic aerosols (BSOA). The resulting BSOA can have a wide variety of impacts, such as on Earth's radiative balance and cloud formation. However, it is unclear to what extent changes in BVOC emissions and BSOA formation are related to biodiversity. Here we present a conceptual framework of the relationships between biodiversity and BVOC emissions based on our current mechanistic understanding and existing knowledge. We tested parts of this framework using a tree diversity experiment as a case-study. We find that the amount of BVOCs in most cases decreases with biodiversity, implying that tree mixtures produce less than expected BVOC compared to tree monocultures. However, some BSOA compounds increased and some decreased relative to what is expected from monocultures. Based on these mixed results, we recommend further field measurements on the patterns of BVOC emission and BSOA formation across biodiversity gradients to improve our understanding and accuracy of the amounts of the compounds emitted. Future studies need a multidisciplinary approach to open a new research nexus where the fields of climate science, biology and atmospheric chemistry interact.

Keywords: Biodiversity, biogenic aerosol, biosphere-atmosphere interactions, biotic and abiotic stress, BVOC emissions, climate change

1. Introduction

Biosphere and atmosphere are tightly interconnected (McPherson, 2007; Steiner, 2020), making the understanding of their interactions critically important as human life depends on them (Mahecha et al., 2022; Pörtner et al., 2021). On the one hand, a suite of atmospheric drivers can affect the biosphere in different ways (Steiner, 2020), including detrimental impacts of rising temperatures on ecosystem integrity and biodiversity (Pecl et al., 2017). On the other hand, the biosphere can exert feedbacks to the atmosphere, e.g. by releasing various **biogenic volatile organic compounds** (BVOCs) through plants (Arneth et al., 2010; Yáñez-Serrano et al., 2020) or soil (Werner et al. 2021). Following their emission, the atmospheric oxidation of plant-emitted BVOCs leads to gas-phase products which can either partition with already existing particles or form new ones (Ehn et al., 2014), resulting in **biogenic secondary organic aerosols** (BSOA; Hallquist et al., 2009). BSOA are particularly important particles for the radiative balance of the Earth (Petäjä et al., 2022). Importantly, climate extremes as well as biodiversity change affect emissions of BVOCs from plants (Kleist et al., 2012; Werner et al., 2021) and, consequently, BSOA formation (Paasonen et al., 2013). However, studies using concerted measurements of BVOCs and BSOA along diversity gradients of emitting plant species are largely missing (but see Wang et al., 2018). This lack of knowledge is particularly worrying given that human activities have traditionally favoured monoculture plantations (Messier et al., 2022), and scientific guidance is urgently needed for major reforestation efforts, especially in the light of current global climate change (Eisenhauer et al., 2022).

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 (Joutsensaari et al., 2015; Kigathi et al., 2019). These BVOCs are produced primarily via the leaf surface as a result of metabolic processes and as a reaction to **abiotic** and **biotic stress** (Niinemets, 2010; Peñuelas & Staudt, 2010). Plant-released BVOCs determine important biotic interactions such as intra- and interspecific communication (Heil & Karban, 2010) as well as herbivore and pathogen defences (Dicke & Baldwin, 2010). BVOCs can also protect plants against abiotic stress such as heat, drought, and high radiation (Loreto & Schnitzler, 2010; Peñuelas & Staudt, 2010).

In the forest, individual trees are not isolated but compete with their con- and heterospecific neighbours for resources, such as light, water, and nutrients (Trogisch et al., 2021). Resource availability directly affects eco-physiological processes such as photosynthetic rates (Ellsworth et al., 2022; Liang et al., 2020; Wright et al., 2004) and thus

allocation to growth and potential interaction strength. In monocultures or low diverse forest stands, neighbouring 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 (Schuldt et al., 2019) or rooting depth (Barry et al., 2019; Loreau et al., 2001), often leading to higher stand productivity (Chen et al., 2020) and leaf area index (Peng et al., 2017). Likewise, forests with diverse leaf chemical traits can enhance soil nutrient availability through diverse plant inputs (leaf and root litterfall) and soil microbial communities and activities (Prada-Salcedo et al., 2021; Sanaei et al., 2022), thereby increasing forest stand productivity. As **forest biomass production** and BVOC emissions are highly correlated (Cao et al., 2022; Tang et al., 2018), diverse forests should thus emit higher amounts of BVOC (Figure 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 uses (Loreau et al., 2001) and microclimate amelioration, particularly in dry seasons (Schwendenmann et al., 2015). In addition, complexity in the vertical and horizontal stratification of diverse stands can relieve thermal stresses (Pires et al., 2018) and alleviate the risks of drought stress (Thurm et al., 2016). Indeed, decreasing heat and drought stress in mixed communities is likely to result in lower leaf temperature, which could result in lower BVOC emissions (Morfopoulos et al., 2022; Simin et al., 2021). 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 (Figure 1, Hypothesis 2).

Second, more diverse plant communities show decreased per capita herbivory damage and pathogen infection (Barnes et al., 2022; Rutten et al., 2021). Although multi-plant diets may be beneficial for different herbivores *per se* (Rapport, 1980; Unsicker et al., 2008), 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” (Barnes et al., 2022; Root, 1973). Furthermore, the heterogeneity of plant nutritive traits in diverse stands suppresses herbivore abundance, resulting in declining herbivore performance (Wetzel et al., 2016), likely due to non-host species reducing the accessibility of host species (Feeny, 1970). Overall, reduced biotic stress through herbivores

and pathogens in mixtures should reduce the amount of BVOC emissions (Figure 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 (e.g. Randlkofer et al., 2010).

Once entering the atmosphere, plant-derived VOCs react quickly with ambient hydroxyl radicals (OH), Ozone (O_3), and nitrogen trioxide radicals (NO_3) to build up low-volatility BVOCs, acting as a substantial source for BSOA production (Atkinson & Arey, 2003; Ziemann & Atkinson, 2012). When BSOA compounds are large enough, they can act as **cloud condensation nuclei** (CCN), which play a critical role in physicochemical processes of the climate (Laothawornkitkul et al., 2009). However, the conversion of BVOC to BSOA is strongly determined by air temperature, the rate and lifetime of emitted BVOCs and their reaction rates with the above-mentioned oxidants (Atkinson & Arey, 2003; Guenther, 2013). High BVOC emissions, e.g. due to rising temperature, increase BSOA formation which in turn leads to surface cooling due to the effect of BSOA on radiation and reflectivity of clouds (Paasonen et al., 2013; Petäjä et al., 2022). Recent findings suggest that biotic and abiotic stress-induced BVOC emissions even accelerate climate-relevant BSOA formation (Holopainen et al., 2022; Joutsensaari et al., 2015; Zhao et al., 2017). Collectively, by doing so, BSOA impact local climate either directly by perturbing incoming solar radiation paths (Charlson et al., 1992), or indirectly by influencing the microphysical properties of clouds (Haywood & Boucher, 2000).

Our mechanistic understanding and existing knowledge suggest that increasing biodiversity could predictably influence the amount of BVOCs 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 (Figure 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 (Eisenhauer & Weigelt, 2021). Accordingly, in this Opinion paper, we highlight the need for interdisciplinary work at the interface between the biosphere and the atmosphere to better understand the reciprocal effects of biodiversity and climate change (Mahecha et al., 2022). 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 a tree diversity experiment. Here, we simultaneously measured the magnitude and variability

of BVOC and BSOA compounds in ten plots differing in tree diversity at the MyDiv site in Germany (Ferlian et al., 2018). Given the existing literature, we hypothesize that tree diversity, depending on plant biomass productivity and abiotic and biotic stress patterns in monocultures and mixtures, could either promote (H1) or reduce (H2 and H3) BVOC emissions (Figure 1).

BOX 1 | Glossary:

Abiotic stress refers to the negative effects of non-living organisms (or environmental drivers) such as heat, drought, and light on the metabolites, physiology, growth, and productivity of plants.

Biogenic secondary organic aerosols (BSOA) consist of fine particulate matter ($PM_{2.5}$) produced by the reaction of BVOC with ambient oxidants hydroxyl radical (OH), ozone (O_3), or nitrate radical (NO_3) (Tröstl et al., 2016).

Biogenic volatile organic compounds (BVOCs) are the largest group of biogenic organic compounds that are emitted from biogenic sources such as plant vegetation, comprising hemiterpenes (isoprene), monoterpenes, sesquiterpenes, homoterpenes, as well as diterpenes (Laothawornkitkul et al., 2009).

Biotic stress refers to the adverse mechanical effects of living organisms such as herbivores and pathogens on plants' metabolites, physiology, growth, and productivity.

Cloud condensation nuclei (CCN) are newly built-up particles including ones from BSOA, that are 50 nm in size or larger and can facilitate the formation of cloud droplets (Kerminen et al., 2012).

Forest biomass production is a measure of forest stand productivity and shows the accumulation of above-ground biomass over time.

Monoterpenes are the main components of BVOC with a carbon chain twice as long ($C_{10}H_{16}$), are emitted from many plants as well as soil with high oxidation rate in the atmosphere (Byron et al., 2022).

Tree diversity is a measure that is mostly used for describing the number of tree species or genotypes within a particular area (e.g., site or plot). Based on different functional traits and their phylogenetic distance, tree diversity may also describe the functional and phylogenetic diversity, respectively, of a site, plot, or region. Furthermore, at larger spatial scales, tree diversity may describe the dissimilarity in community composition of different stands (β-diversity) or the diversity of different landscapes. In this paper and case study, we refer to the number of tree species per plot or stand.

2. BOX 2 | Case study:

2.1. Material and 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 (Ferlian et al., 2018), between September 21 and October 13, 2021 (13 days in total). 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 and BSOA were simultaneously collected for four hours offline method (10:00 AM to 2:00 PM) using custom-built samplers installed at the top of the canopy of each plot (plot-level measurement; for more detail about custom-built samplers, see the supplementary information). As such, BVOCs were collected using Tenax and Carbotrap absorbent cartridges and were then analysed by gas chromatography mass spectrometry (GC/MS). BSOA compounds were captured on quartz filters based on the Gillian 12 pump /PEM monitor low volume sampling system and were then analysed by Orbitrap ultrahigh-performance liquid chromatography mass spectrometry.

We then calculated the relative difference in monoculture vs. mixture plots with:

$$\text{Mixture compound}_{\text{expected}} = \frac{\sum \text{Monoculture compound}_{\text{observed}}}{\text{Species richness}}$$

After that, we compared the ratio of mean differences between monoculture and mixture using the observed and expected values of each BVOC or BSOA compound to see whether there was an additive effect of tree diversity on BVOC emission or BSOA formation. Positive values indicate that the mixture produced a greater amount of compounds than expected based on the monoculture data, and vice versa.

2.2. Results and discussion

On average, nine different BVOCs (monoterpene) and fifteen BSOA compounds were quantified from the investigated plots. The relative difference in monoculture and mixture showed that increasing tree diversity significantly decreased the overall concentration of BVOCs (Figure 2; $p < 0.01$), indicating that the effects were non-additive (less than expected from monocultures). However, there were no significant differences in BVOC emissions among tree species (except for some compounds, Figure S1c,i). Our results support

hypotheses H2 and H3 that differences in biotic and abiotic stress patterns in monocultures and mixtures affect BVOC emissions. These results reinforce the general notion that the concentration of the emitted BVOCs might be dependent on the relative dominance of biotic and abiotic stresses (Holopainen & Gershenzon, 2010). For BSOA, 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 (Figure 3; $p = 0.46$), the same overall pattern was found for the observed BSOA compounds (Figure S2) This 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 pattern coupled to the measured BVOC. However, in certain cases, a local linkage was observed, cf. Figure S3. 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 (Holopainen et al., 2022; Joutsensaari et al., 2015; Zhao et al., 2017). The complex formation patterns of BSOA reflect that oxidation products are dependent not only on biotic and abiotic stress but also on the source precursor and atmospheric oxidants (Atkinson & Arey, 2003; Guenther, 2013). Finally, it should be noted that since we only measured four broad-leaved tree species planted as monocultures and mixtures, any generalization would be premature at this point in time. Thus, we acknowledge that testing our hypothesis will necessitate further experimental work to improve our understanding of how the magnitude and composition of BVOC and BSOA will change across tree diversity gradients.

3. Conclusions and research perspectives

Climate change and biodiversity are inseparably interdependent and reciprocally reinforcing (Mahecha et al., 2022; Pörtner et al., 2021). Forests, as well-known diverse ecosystems, have a significant impact on climate change while also providing essential services to humans (Bonan, 2008). The amplified climate warming profoundly increases the probability of extreme events such as drought and heat waves (IPCC, 2013). These climate extremes, which are expected to continue over the forthcoming century (Fischer et al., 2021), will likely accelerate forest biodiversity loss, change forest composition, and diminish the associated productivity (Mahecha et al., 2022). While forests will be subjected to more stress caused by climate extremes, diverse forests, which consist of a mixture of drought- and heat-tolerant species, offset climate change effects (Schnabel et al., 2022). In addition, BVOCs emitted by

forests are highly temperature-dependent; 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% (Peñuelas & Llusià, 2003). Meanwhile, this rising temperature, combined with climate extremes, would increase tree mortality globally (Hartmann et al., 2022), resulting in detrimental impacts on forest biodiversity and functioning. Furthermore, since climate warming is advantageous for herbivores and pathogens, the risk of herbivores and pathogens affecting biodiversity would increase as a result of continued climate change (Jactel et al., 2019). The resultant increase in herbivores and pathogens would trigger an increase in BVOC emissions (Huang et al., 2018; Tiiva et al., 2018). In addition, climate extremes could also affect the availability and magnitude of the ambient oxidants such as O_3, and NO_3 (Arneth et al., 2010), which are key to the oxidation of BVOCs and also determine the rate and composition of the oxidation product (Ehn et al., 2014). Thus, changes in the quality and quantity of BVOC emissions due to the above-mentioned factors could potentially affect the size and composition of BSOA (Sporre et al., 2019; Yli-Juuti et al., 2021; Zhao et al., 2017). The resulting BSOA, depending on their properties, may scatter or absorb radiation and thus control the radiative balance of the earth (Carslaw et al., 2010). While scattering BSOA can cool the earth by facilitating the formation of clouds, absorbing BSOA inhibits cloud formation and thus warms the earth (Charlson et al., 1992). Given the significant changes in biodiversity and climate caused primarily by human activities, linking atmospheric and biological measurements is crucial for understanding atmosphere-biosphere feedbacks. However, to what extent changes in atmospheric chemistry and climate change are related to biodiversity is largely unknown. 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. In addition, we need local and regional-scale models, combined with field and chamber measurements, to improve our understanding of biosphere-atmosphere interactions. A multidisciplinary approach at the biosphere-atmosphere interface would extend our understanding of the reciprocal effects of biodiversity and climate change (Mahecha et al., 2022) 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.

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Conflict of interest

The authors declare no conflict of interest.

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Figure captions

Figure 1. The figure outlines the processes and mechanisms (a) as well as hypotheses (b) 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 red and blue lines, respectively. The hypothesized positive relationships between BVOC emissions and BSOA formation is indicated in black.

Figure 2. A forest plot summarizing the results of the ratio of mean differences between monoculture and mixture for changes in BVOCs as a result of diversity change. The squares' sizes and widths represent each compound's weight, while the diamond (red colour) represents the overall effect estimate of the meta-analysis. Effect sizes were calculated using log response-ratios. The horizontal lines of the squares show 95% confidence intervals (CI). *p*-values are given for each compound and for the overall effect.

Figure 3. A forest plot summarizing the results of the ratio of mean differences between monoculture and mixture for changes in BSOA compounds as a result of diversity change. The squares' sizes and widths represent each compound's weight, while the diamond (red colour) represents the overall effect estimate of the meta-analysis. Effect sizes were calculated using log response-ratios. The horizontal lines of the squares show 95% confidence intervals (CI). *p*-values are given for each compound and for the overall effect. Abbreviations: DTAA, Diaterpenylic acid acetate; MBTCA, 3-methyl-1,2,3-butanetricarboxylic acid.

Figure 1.

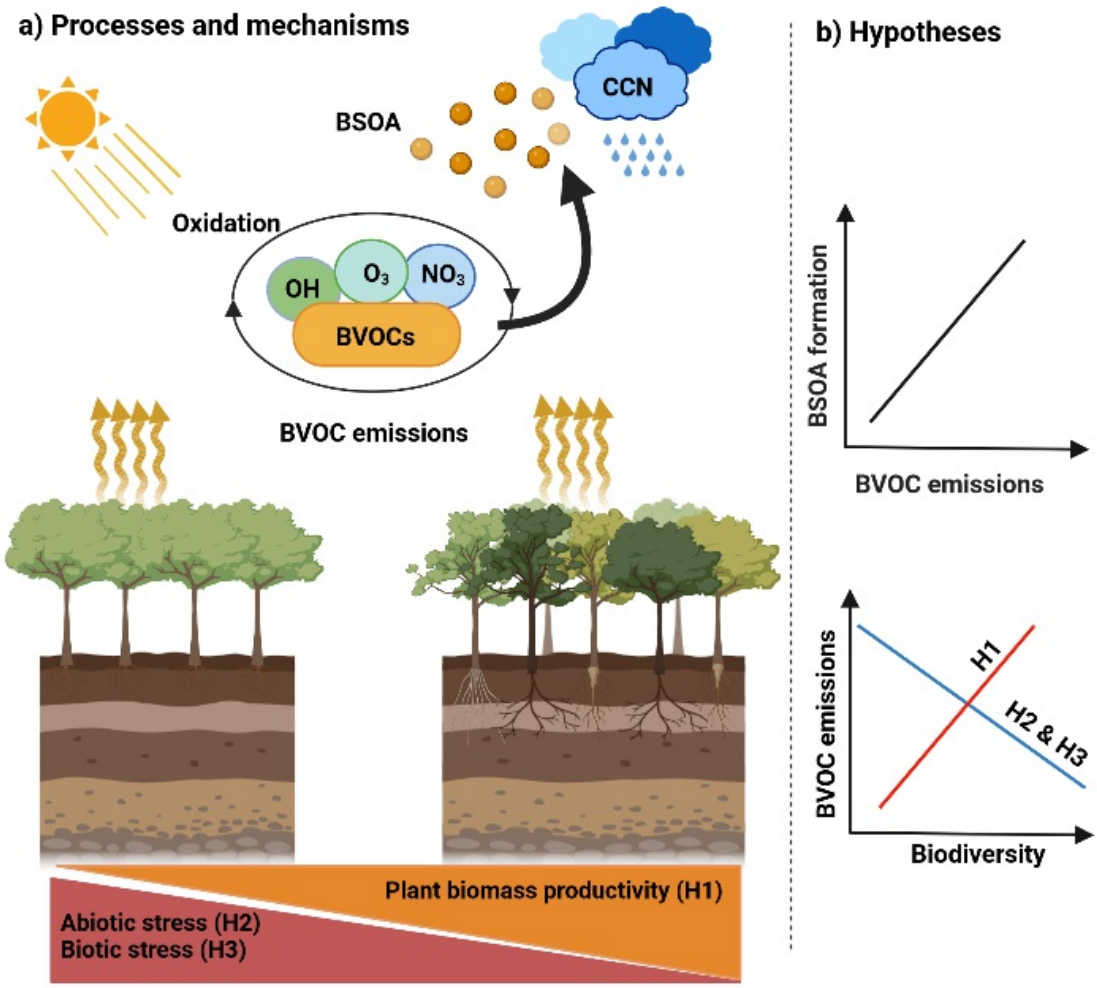

a) Processes and mechanisms
CCN
BSOA
Oxidation
OH
O3
NO3
BVOCs
BVOC emissions
Plant biomass productivity (H1)
Abiotic stress (H2)
Biotic stress (H3)
b) Hypotheses
BSOA formation
BVOC emissions
BVOC emissions
H1
H2 & H3
Biodiversity

Figure 2.

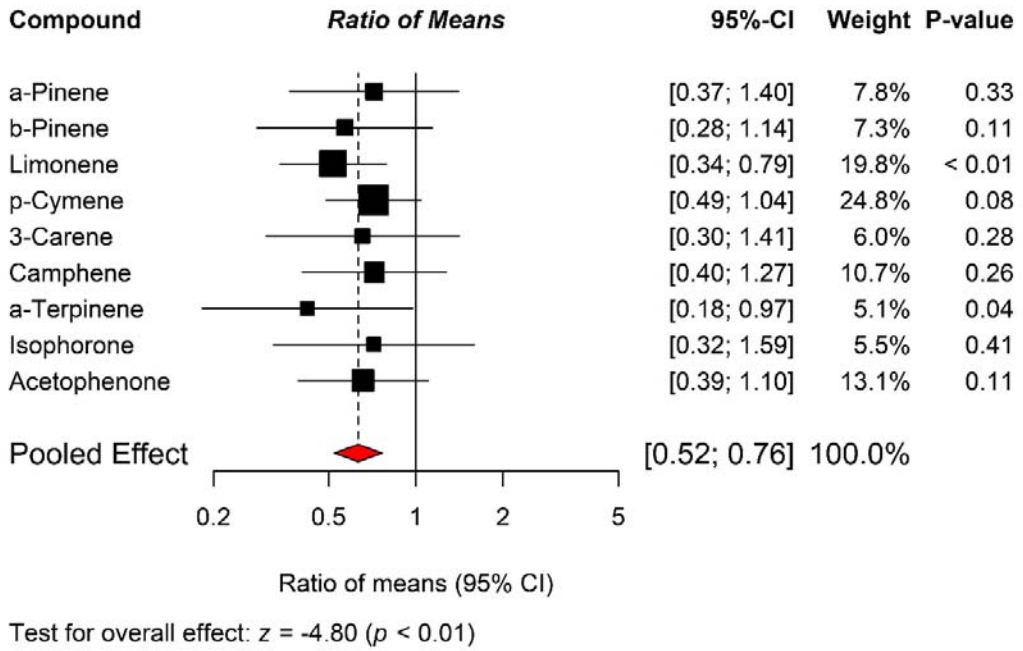
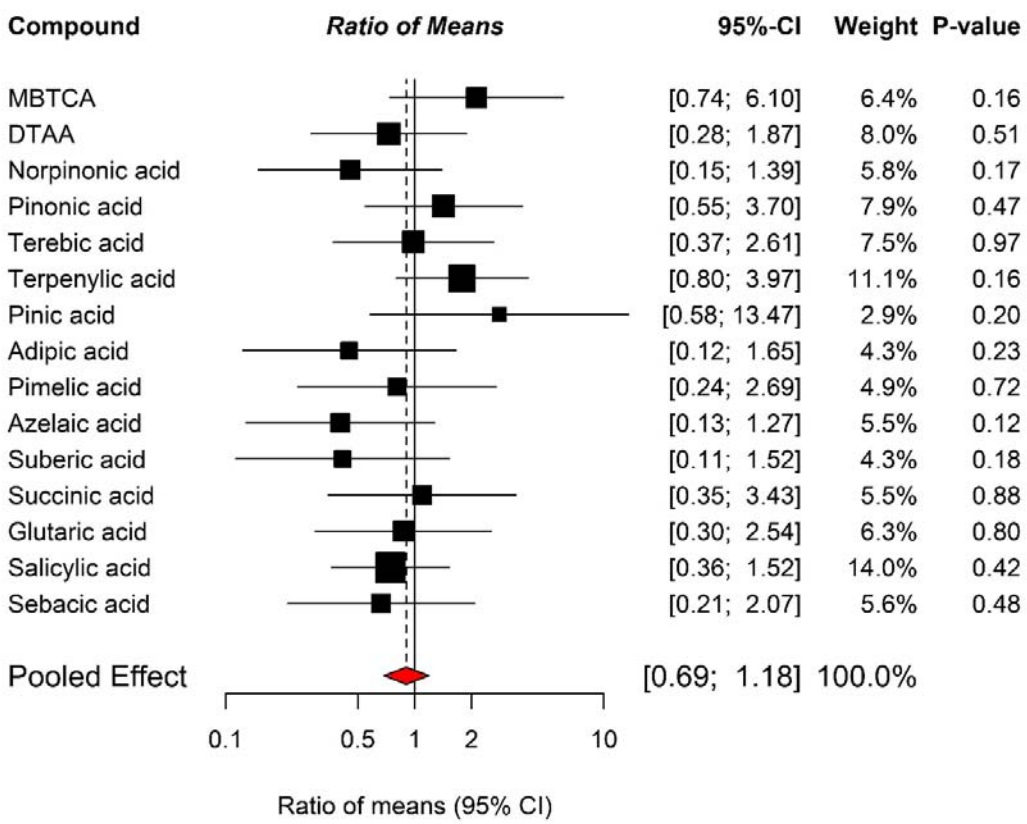

Compound
Ratio of Means
95%-CI
Weight
P-value
a-Pinene [0.37; 1.40] 7.8% 0.33
b-Pinene [0.28; 1.14] 7.3% 0.11
Limonene [0.34; 0.79] 19.8% < 0.01
p-Cymene [0.49; 1.04] 24.8% 0.08
3-Carene [0.30; 1.41] 6.0% 0.28
Camphene [0.40; 1.27] 10.7% 0.26
a-Terpinene [0.18; 0.97] 5.1% 0.04
Isophorone [0.32; 1.59] 5.5% 0.41
Acetophenone [0.39; 1.10] 13.1% 0.11
Pooled Effect [0.52; 0.76] 100.0%
0.2
0.5
1
2
5
Ratio of means (95% CI)
Test for overall effect: z = -4.80 (p < 0.01)

Figure 3.



Test for overall effect: z = -0.75 (p = 0.46)

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