

Amazonian biogenic volatile organic compounds under global change

Ana M. Yáñez-Serrano^{1,2} | Efstratios Bourtsoukidis³ | Eliane G. Alves⁴ |
Maite Bauwens⁵ | Trissevgeni Stavrakou⁵ | Joan Llusà^{1,2} | Iolanda Filella^{1,2} |
Alex Guenther⁶ | Jonathan Williams³ | Paulo Artaxo⁷ | Katerina Sindelarova⁸ |
Jana Doubalova^{8,9} | Jürgen Kesselmeier³ | Josep Peñuelas^{1,2}

¹CREAF, Cerdanyola del Vallès, Spain

²CSIC, Global Ecology Unit, CREA-FCSC-UAB, Cerdanyola del Vallès, Spain

³Atmospheric Chemistry and Multiphase Chemistry Departments, Max Planck Institute for Chemistry, Mainz, Germany

⁴Department of Biogeochemical Processes, Max Planck Institute for Biogeochemistry, Jena, Germany

⁵Royal Belgian Institute for Space Aeronomy, Brussels, Belgium

⁶Department of Earth System Science, University of California, Irvine, CA, USA

⁷Instituto de Física, Universidade de Sao Paulo, São Paulo, Brazil

⁸Faculty of Mathematics and Physics, Department of Atmospheric Physics, Charles University, Prague, Czechia

⁹Modelling and Assessment Department, Czech Hydrometeorological Institute, Prague, Czechia

Correspondence

Ana M. Yáñez-Serrano, CREA, E08193
Cerdanyola del Vallès, Catalonia, Spain.
Email: ayanezserrano@yahoo.es

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Abstract

Biogenic volatile organic compounds (BVOCs) play important roles at cellular, foliar, ecosystem and atmospheric levels. The Amazonian rainforest represents one of the major global sources of BVOCs, so its study is essential for understanding BVOC dynamics. It also provides insights into the role of such large and biodiverse forest ecosystem in regional and global atmospheric chemistry and climate. We review the current information on Amazonian BVOCs and identify future research priorities exploring biogenic emissions and drivers, ecological interactions, atmospheric impacts, depositional processes and modifications to BVOC dynamics due to changes in climate and land cover. A feedback loop between Amazonian BVOCs and the trends of climate and land-use changes in Amazonia is then constructed. Satellite observations and model simulation time series demonstrate the validity of the proposed loop showing a combined effect of climate change and deforestation on BVOC emission in Amazonia. A decreasing trend of isoprene during the wet season, most likely due to forest biomass loss, and an increasing trend of the sesquiterpene to isoprene ratio during the dry season suggest increasing temperature stress-induced emissions due to climate change.

KEYWORDS

air chemistry, Amazonia, biogenic volatile organic compounds, climate, depositional processes, ecological interactions, global change, land cover, land use

1 | INTRODUCTION

Biogenic volatile organic compounds (BVOCs) are emitted by vegetation, bacteria, algae, fungi and animals. Their rates of emission vary greatly in response to biotic (e.g. herbivory) and abiotic (meteorological) factors (Šimpraga et al., 2019). They have diverse roles at multiple scales, from cellular protection and defense at the foliar level, through chemical signalling at regional level, up to influencing rainfall at the ecosystems scale (Laothawornkitkul, Taylor, Paul, & Hewitt, 2009). BVOCs profoundly affect biosphere–atmosphere interactions by atmospheric reactivity, aerosol growth processes and cloud formation, and therefore radiative balance (Kulmala et al., 2013; Nölscher et al., 2016; Pöschl et al., 2010). As BVOCs are precursors of aerosols, they can impact the regional radiative forcing directly through aerosol scattering and indirectly by influencing cloud processes. Furthermore, higher cloud cover leads into increased diffuse radiation, boosting net primary productivity and thereby BVOC emissions (Rap et al., 2018). However, BVOCs can have further impacts on the radiative forcing by their influence on tropospheric ozone formation or by increasing the lifetime of methane by suppression of its major sink, the OH radical (Peñuelas & Llusà, 2003).

Vegetation is the largest source of BVOC emissions, with tropical trees responsible for ca. 80% of global terpenoid emissions and 50% of other BVOC emissions (Guenther et al., 2012). With half of the global tropical forests, Amazonia is the largest remaining pristine continental area (Andreae et al., 2015; Pöhlker et al., 2019). Amazonia stores 50% of tropical-forest carbon, plays a vital role in the global cycles of energy, water and carbon, and has the largest biodiversity in the world (Levine et al., 2016; Malhi et al., 2008; Swift et al., 1998; ter Steege et al., 2013). This dynamic system emits large quantities of chemically diverse BVOCs to the atmosphere, with implications both within and above Amazonian forest canopies. Amazonia is highly sensitive to changes in climate and land use due to its strong energy and biochemical cycling (Levine et al., 2016). It has been established that recent human action is already altering Amazonian conditions and feedbacks (Sena et al., 2018; Shrivastava et al., 2019), complicating the understanding of BVOCs in this region. In fact, BVOC emission decrease due to forest conversion to croplands in the tropics has been shown to result in a positive radiative forcing (Jia et al., 2019; Scott et al., 2018). Additionally, the impact of Amazonian BVOCs on global primary production through diffuse radiation has large implications for the global carbon balance (Rap et al., 2018). Furthermore, by participating in cloud formation processes, Amazonian BVOCs play a key role in the regional hydrological cycle, since Amazonian rainforests contribute to precipitation throughout the South American continent (Boers et al., 2017; Rocha, Da Silva, Gomes, Vergasta, & Jardine, 2018). Therefore, it is critical to understand the BVOC response to environmental stresses caused by changes in climate and land use in Amazonia, and how these changes will feedback into the Earth system (Peñuelas & Staudt, 2010).

We here review the recent advances in Amazonian BVOC research and estimate potential future BVOC dynamics using information currently available for emission processes, resulting ecological interactions and atmospheric impacts, depositional processes, and effects and feedbacks of climate and land-use change. We propose a feedback loop, which is supported by satellite observations and model simulations of BVOC fluxes, to identify research priorities in Amazonian BVOCs.

2 | ADVANCES ON BVOC SCIENTIFIC RESEARCH IN AMAZONIA

2.1 | History of measurements

Measurements of BVOCs in Amazonian ecosystems are logistically difficult due to accessibility and power constrains. Research on this topic began in the 1970s and 1980s, when tethered balloon observations demonstrated that Amazonia is a major source of BVOC emissions to the atmosphere (Crutzen et al., 1985; Greenberg & Zimmerman, 1984; Zimmerman, Greenberg, & Westberg, 1988) providing understanding into atmospheric chemistry (Grosjean, 1995). The establishment of the Large-Scale Biosphere–Atmosphere Experiment in Amazonia (LBA) provided the first large-scale estimates of isoprene emissions and oxidation products from data collected by aircraft and tower-based stations (Kesselmeier, Guenther, Hoffmann, Piedade, & Warnke, 2009). Nevertheless, understanding of the controlling processes was still scarce due to the lack of data on temporal and spatial variability and the very limited number of BVOCs species studied (Kesselmeier et al., 2009). The most commonly used prominent technique in early studies was BVOC collection in cartridges, followed by transportation of field samples to laboratories outside the Amazonia for analysis by gas chromatography. The logistical difficulties for sample transport were addressed by establishing more locations for tower-based measurements, long-term field campaigns, new sampling approaches such as the use of drones (McKinney et al., 2019), along with more advanced analytical tools such as proton-transfer-reaction mass spectrometry (Bracho-Nunez et al., 2013; Crutzen et al., 2000; Fuentes et al., 2016; Jardine, Monson, et al., 2011; Jardine, Yañez Serrano, Arneth, Abrell, Jardine, Artaxo, et al., 2011; Jardine, Yañez Serrano, Arneth, Abrell, Jardine, van Haren, et al., 2011; Jardine et al., 2014; Jardine, Jardine, et al., 2016; Karl, Guenther, Turnipseed, Artaxo, & Martin, 2009; Kesselmeier et al., 2009; Kuhn et al., 2007; Liu et al., 2016; Rinne, Guenther, Greenberg, & Harley, 2002; Williams et al., 2001; Yañez-Serrano et al., 2015), the comparative reactivity method (Nölscher et al., 2016; Pfannerstill et al., 2018; Sinha, Williams, Crowley, & Lelieveld, 2008), photoionization detector (Harley et al., 2004), semi-volatile thermal desorption aerosol gas chromatography (Yee et al., 2018) and isoprene portable monitoring system (T. Taylor, personal communication). Extensive campaigns and projects such as GoAmazon and ATTO provided integrated investigations of emissions, chemistry, transport and cloud processes

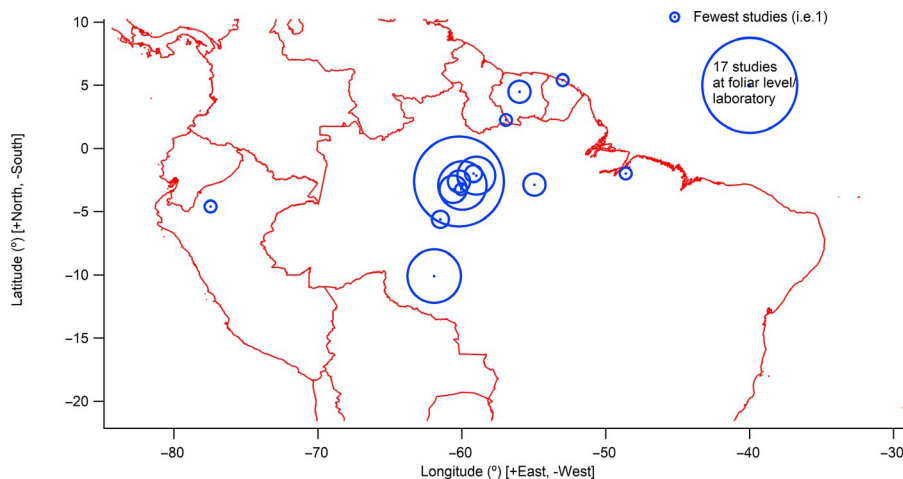


FIGURE 1 Map of Amazonia with the distribution and frequency of published biogenic volatile organic compound (BVOC) measurements. The centres of the circles represent the locations of the measurements, and the sizes of the circles represent the number of published studies of BVOCs. This graph was derived from the information of Table 1 and Supporting Information 1 [Colour figure can be viewed at wileyonlinelibrary.com]

(Andreae et al., 2015; Martin et al., 2017). Seasonality was clearly addressed (Alves et al., 2016, 2018; Nölscher et al., 2016; Yáñez-Serrano, Nölscher, et al., 2018; Yáñez-Serrano et al., 2015) and greater effort was expended towards obtaining a mechanistic understanding that was provided by foliar-level measurements under natural and controlled experiments (Alves, Harley, Gonçalves, Moura, & Jardine, 2014; Bourtsoukidis et al., 2018; Bracho-Nunez et al., 2012, 2013). Despite the increasing number of observation datasets and efforts towards addressing horizontal heterogeneity (Batista et al., 2019), comparing ecosystems remains difficult due to the spatial diversity of Amazonia (see Supporting Information 1) and the inadequate information over controlling processes. Figure 1 shows the number and location of BVOC measurements available since 1984, when the first measurements were published, showing the lack of spatial variability in the Amazonian BVOC studies to date.

2.2 | History of modelling

There are still too few observations of BVOC emissions for accurate representation of the regional variability, resulting in large uncertainty in model predictions. Initially, the BVOC emissions algorithm proposed by Guenther et al. (1995) included light- and temperature-dependent emissions of isoprene, but all other emissions were regarded as only temperature-dependent, a potentially misleading assumption (Kesselmeier & Staudt, 1999). The algorithm was updated in 1999 by a simple leaf-age activity factor to determine the dependence on meteorological conditions. The Model of Emissions of Gases and Aerosols from Nature (MEGAN) then simulated net emission rates, accounting for the losses of primary emissions (Guenther et al., 2006), with the latest update adding a longer list of compounds and their emission factors (Guenther et al., 2012; Sindelarova et al., 2014). Further BVOC emissions modelling included Organizing Carbon and Hydrology in Dynamic Ecosystem (ORCHIDEE; Messina et al., 2016) and Lund-Potsdam-Jena-General

Ecosystem Simulator (LPJ-GUESS; Acosta Navarro et al., 2014). Amazonian modelling has thus been improved, but a reliable predictive framework for emission capacities in Amazonia requires an improved mechanistic understanding of BVOC variation across plant populations and of their interactions with other living organisms and abiotic factors (Alves et al., 2018; Kuhn et al., 2004a; Salazar et al., 2018; Taylor et al., 2018).

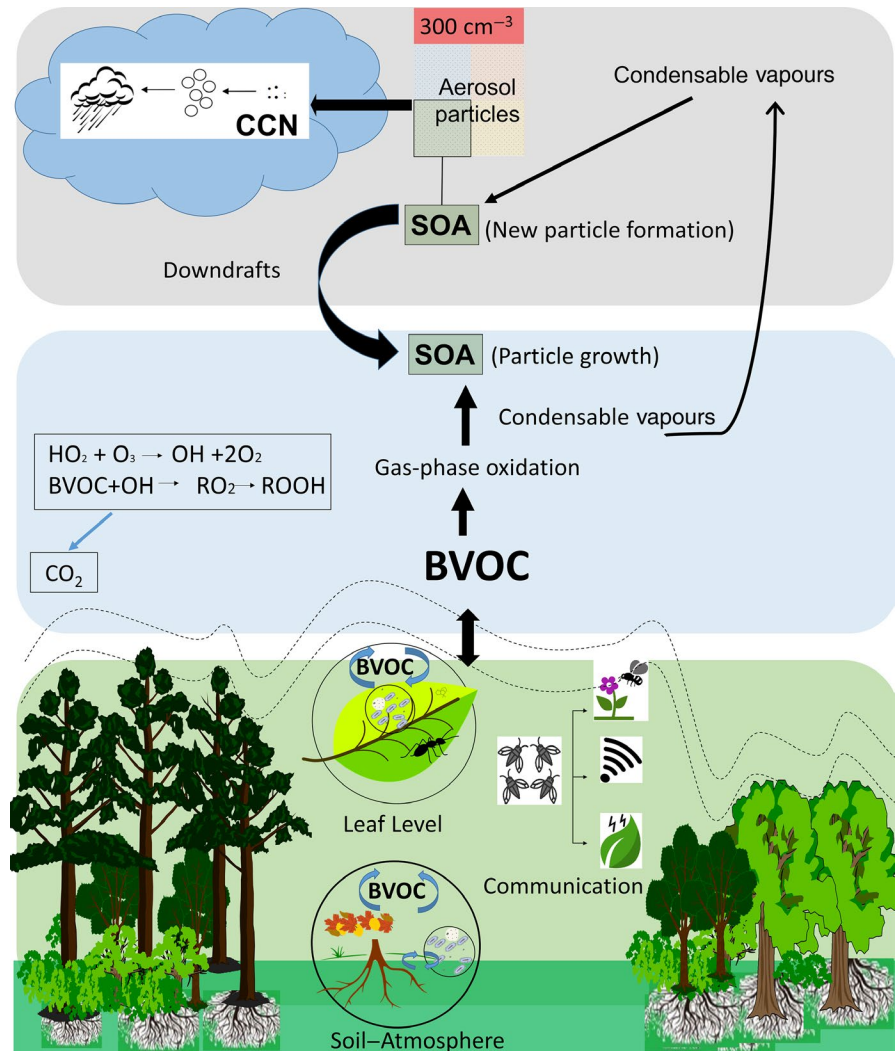
2.3 | Satellite applications

Amazonian isoprene fluxes can be derived at regional or global scales via satellite measurements (Barkley et al., 2009, 2013; Bauwens et al., 2016; Fu et al., 2019; Gu et al., 2017). This can improve our knowledge of the dynamics in scale and time. Formaldehyde is formed during the oxidation of most VOCs released in the atmosphere. It is a major intermediate product in isoprene oxidation, and therefore satellite observations of formaldehyde have been used to infer isoprene emissions at global and regional scales (Millet et al., 2008; Pamler et al., 2003; Stavrou et al., 2009). The variability of emissions estimated with these satellite data generally lies within the variability of the surface observations. Direct observations of isoprene recently acquired by the satellite-borne Cross-track Infrared Sounder (Fu et al., 2019) will open new avenues in the isoprene emission estimation from satellites. A global study using these data found a regional reduction (-2% year⁻¹) of biogenic emissions over Amazonia during the period of 2005–2013 but no plausible cause could be identified (Bauwens et al., 2016).

3 | EMISSION

The BVOCs in the Amazonian rainforest have many sources, with vegetation being the most prominent (Kesselmeier et al., 2009; Figure 2). A large variety of BVOCs are emitted from Amazonian

FIGURE 2 Schematic showing the biogenic volatile organic compound (BVOC) dynamics in a pristine Amazonian atmosphere, including sources and interactions, BVOC oxidation in the atmosphere, and subsequent aerosol production influencing cloud droplet formation and cloud dynamics. CCN, cloud condensation nuclei; SOA, secondary organic aerosol [Colour figure can be viewed at wileyonlinelibrary.com]



ecosystems. Isoprene is the most strongly emitted compound, with reported ambient mixing ratios of 0.5–15 ppb and fluxes of 0.7–12.1 mg m⁻²_{ground} hr⁻¹, although other isoprenoids have been reported such as monoterpenes (with mixing ratios typically below 1 ppb but in some cases up to 5.5 ppb, Greenberg & Zimmerman, 1984; Kesselmeier, Kuhn, et al., 2002), sesquiterpenes (SQTs; with mixing ratios up to 0.16 ppb) and even diterpenes (0.0002 ppb; Yee et al., 2018). Methanol is the second most emitted compound, with measured mixing ratios reported up to 6 ppb (Kesselmeier, Kuhn, et al., 2002; Yáñez-Serrano et al., 2015). Other oxygenated compounds have also been reported, such as acetaldehyde, acetone, methyl ethyl ketone (Bracho-Nunez et al., 2012; Rottenberger et al., 2008; Yáñez-Serrano et al., 2016), ethanol (Bracho-Nunez et al., 2012; Rottenberger et al., 2008), formaldehyde (Karl et al., 2009; Kesselmeier et al., 2000), acetic and formic acid (Jardine, Yáñez Serrano, Arneth, Abrell, Jardine, Artaxo, et al., 2011; Kuhn, Rottenberger, Biesenthal, Ammann, et al., 2002), green-leaf volatiles (GLVs; Jardine, Chambers, et al., 2015), isoprene oxidation products (including methyl vinyl ketone [MVK], methacrolein [MACR], isoprene hydroperoxide [ISOPOOH] and hydroxyacetone [Karl et al., 2009]), aromatics (Paralovo et al., 2015), sulphurous

compounds such as dimethyl sulphide (Jardine et al., 2014) as well as chlorine compounds such as methyl chloride and chloroform (Gebhardt, Colomb, Hofmann, Williams, & Lelieveld, 2008; Gregory et al., 1986; Yokouchi, Ikeda, Inuzuka, & Yukawa, 2002; Table 1; Figures 3 and 4). Additionally, the emission, and consequent atmospheric abundance is given as the sum of enantiomers due to analytical constraints, yet BVOCs are generated by enzymes and are therefore chiral. Although chemically identical, they can induce differing biological responses. Thus examining the different enantiomers would lead to a doubling of information (Williams, Yassaa, Bartenbach, & Lelieveld, 2007).

Vegetation emits BVOCs, as de novo compounds from recently photosynthesized carbon or as volatilized compounds from storage pools or resins and waxes (Kesselmeier & Staudt, 1999). These emissions may represent a substantial loss of carbon previously assimilated by photosynthesis (up to 2% of carbon fixed for tropical forests; Kesselmeier, Ciccioli, et al., 2002). Isoprene is the most common de novo biosynthesized compound, with isoprene-emitting plants found as a typical component in tropical forests (Harley et al., 2004; Šimpraga et al., 2019; Taylor et al., 2018). Further species, such as monoterpenes are also released de

TABLE 1 Isoprene ambient mixing ratios reported in the literature over Amazonian ecosystems. Data are organized by height with a line separating between within canopy mixing ratios and above canopy mixing ratios and between seasons. We considered 35 m to be the average top of the Amazonian canopy. Values reported are in ppb and as presented in the literature. They are usually means or medians. The values in parenthesis represent either SD or interquartile range when available. Where only graphical data were available we used the software Plot Digitizer to derive means and SDs. The locations are classified according to the area where the measurements were taken, namely Central Amazonia, Western Amazonia, Southwestern Amazonia, Guyana Shield and Central-east Amazonia. The techniques are GC-FID, gas chromatography flame ionization detector; GC-MS, gas chromatography mass spectrometer; IEC, ion-exchange chromatography; PTR-MS, proton transfer reaction mass spectrometer. The seasons are specified together with the exact timing of sampling: dry, dry season; D-t-W, transition from dry to wet season; wet, wet season; W-t-D, transition from wet to dry season. X stands for laboratory experiments or satellite retrievals

Site	Season	Height (m)	Isoprene (ppb)	Technique	Reference	Observations
Central Amazonia	Dry	0.05	3.13	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Dry	0.5	3.77	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Dry	1	2.77 (0.4)	GC-FID	Rasmussen and Khalil (1988)	Daytime mean (11:00–15:00, LT). Canister sampling. Near ground level
Western Amazonia	Dry	2	3.31	GC-MS	Helmig et al. (1998)	Daytime mean
Central Amazonia	Dry	4	5.35	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Dry	0–30	2.40 (1–5.24)	GC-FID	Greenberg and Zimmerman (1984)	Daytime mean. Canister sampling. Near ground to 30 m
Central Amazonia	Dry	24	19.9 (2.0)	PTR-MS	Andreae et al. (2015)	Daytime mean
Central Amazonia	Dry	24	7.62	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Dry	30	2.65 (1.39–3.38)	GC-FID	Zimmerman et al. (1988)	24 hr median. Sampling on teflon bag on tethered balloon (30 m)
Central Amazonia	Dry	38	6.13	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Dry	40	2.68 (0.9)	PTR-MS	Alves et al. (2016)	Daytime mean (10:00–14:00, LT)
Central Amazonia	Dry	40	7.94 (1.67)	PTR-MS	Wei et al. (2018)	Daytime mean
Central Amazonia	Dry	45	5 max.	GC-MS	Rinne et al. (2002)	Afternoon values. Fluxes 30°C and 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Cartridge on Disjunct Eddy Accumulation
Southwestern Amazonia	Dry	50	4.6 (2.7)	GC-FID	Aquino (2006)	Daytime mean (11:00–16:00, LT). Canister sampling
Central Amazonia	Dry	51	3.4 (1.8)	GC-FID	Kuhn et al. (2007)	Daytime mean (10:00–15:00, LT). Cartridge on Relaxed Eddy Accumulation
Central Amazonia	Dry	53	5.72	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Dry	54	7.80	PTR-MS	Rizzo, Artaxo, Karl, Guenther, and Greenberg (2010)	Maximum at noon. Disjunct Eddy Covariance
Central Amazonia	Dry	55	7.8 (3.7)	PTR-MS	Karl et al. (2007)	Daytime mean (12:00–14:00, LT). Disjunct Eddy Covariance
Southwestern Amazonia	Dry	60	4.0 (2.5)	GC-FID	Aquino (2006)	Daytime mean (11:00–16:00, LT). Canister sampling

(Continues)

TABLE 1 (Continued)

Site	Season	Height (m)	Isoprene (ppb)	Technique	Reference	Observations
Central Amazonia	Dry	79	4.81	PTR-MS	Yáñez-Serrano et al. (2015)	24 hr median. Sampling on teflon bag on tethered balloon (305 m)
Central Amazonia	Dry	305	1.73 (1.03–2.15)	GC-FID	Zimmerman et al. (1988)	Daytime mean
Western Amazonia	Dry	91–1,167	1.69	GC-MS	Helmig et al. (1998)	Daytime mean (10:00–11:30, LT). Mixed Layer Gradient
Central Amazonia	Dry	100–1,200	5.5 (2.6)	PTR-MS	Karl et al. (2007)	Daytime. Canister sampling. Aircraft flights
Central Amazonia	Dry	150–1,500	1.5 (0.75)	GC-FID	Rasmussen and Khalil (1988)	Daytime mean. Canister sampling. Flights from treetop to 2 km
Central Amazonia	Dry	35–2,000	2.27 (0.38–4.08)	GC-FID	Greenberg and Zimmerman (1984)	Daytime mean
Western Amazonia	Dry	1,481–1,554	0.16	GC-MS	Helmig et al. (1998)	Daytime mean. Canister sampling. Flights from 2 km to Tropicopause
Central Amazonia	Dry	2,000–17,000	0.19 (0.14–0.22)	GC-FID	Greenberg and Zimmerman (1984)	
Central Amazonia	Dry & D-t-W	2	1.54 (1.37)	PTR-MS	Jardine, Monson, et al. (2011)	
Central Amazonia	Dry & D-t-W	11	2.86 (1.61)	PTR-MS	Jardine, Monson, et al. (2011)	
Central Amazonia	Dry & D-t-W	17	2.86 (1.53)	PTR-MS	Jardine, Monson, et al. (2011)	
Central Amazonia	Dry & D-t-W	24	2.71 (1.37)	PTR-MS	Jardine, Monson, et al. (2011)	
Southwestern Amazonia	Dry & D-t-W	08–52	9.5 (4)	GC-FID	Kesselmeier, Kuhn, et al. (2002)	Daytime mean (11:00–18:00, LT)
Central Amazonia	Dry & D-t-W	30	2.47 (1.26)	PTR-MS	Jardine, Monson, et al. (2011)	
Central Amazonia	Dry & D-t-W	40	2.36 (1.26)	PTR-MS	Jardine, Monson, et al. (2011)	
Central Amazonia	Dry & Wet	40	2.5 (2.2)	PTR-MS	Fuentes et al. (2016)	
Central Amazonia	D-t-W	40	2.65 (1.33)	PTR-MS	Alves et al. (2016)	Daytime mean (10:00–14:00, LT)
Central Amazonia	D-t-W	40	6.76 (2.35)	PTR-MS	Wei et al. (2018)	Daytime mean
Southwestern Amazonia	D-t-W	50	3.4 (1.2)	GC-FID	Aquino (2006)	Daytime mean (11:00–16:00, LT). Canister sampling
Southwestern Amazonia	D-t-W	60	3.0 (0.5)	GC-FID	Aquino (2006)	Daytime mean (11:00–16:00, LT). Canister sampling
Central Amazonia	Wet	0	6.90	GC-MS	Kesselmeier et al. (2000)	Daytime mean (15:00, LT)
Central Amazonia	Wet	0.05	0.57	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Wet	0.5	0.57	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Wet	1	3.2 (0.9)	GC-MS	da Silva (2010)	Daytime mean (07:00–17:00, LT). Cartridge sampling
Central Amazonia	Wet	1.5	4.33 (2.02)	GC-MS	Kesselmeier et al. (2000)	Daytime mean (09:30–16:00, LT). Outside fores

(Continues)

TABLE 1 (Continued)

Site	Season	Height (m)	Isoprene (ppb)	Technique	Reference	Observations
Central Amazonia	Wet	1.5	3.01 (0.85)	GC-MS	Kesselmeier et al. (2000)	Daytime mean (09:30–16:00, LT). Inside canopy
Central Amazonia	Wet	4	0.86	PTR-MS	Yáñez-Serrano et al. (2015)	
Central-East Amazonia	Wet	8.1	0.13 (0.61)	GC-MS	Jardine, Gimenez, et al. (2016)	Night-time mean
Central-East Amazonia	Wet	8.1	8.95 (4.2)	GC-MS	Jardine, Gimenez, et al. (2016)	Daytime mean
Central Amazonia	Wet	10	4.6 (0.94)	GC-MS	da Silva (2010)	Daytime mean (07:00–17:00, LT). Cartridge sampling
Central Amazonia	Wet	20	6.17 (1.03)	GC-MS	da Silva (2010)	Daytime mean (07:00–17:00, LT). Cartridge sampling
Central Amazonia	Wet	24	2.29	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Wet	30	7.90	GC-MS	Kesselmeier et al. (2000)	Daytime mean (14:00, LT)
Central Amazonia	Wet	38	2.39	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Wet	40	1.66 (0.9)	PTR-MS	Alves et al. (2016)	Daytime mean (10:00–14:00, LT)
Central Amazonia	Wet	40	4.66 (2.21)	PTR-MS	Wei et al. (2018)	Daytime median
Central Amazonia	Wet	50	6.3 (1.32)	GC-MS	Kesselmeier et al. (2000)	Daytime mean (12:00–16:00, LT)
Southwestern Amazonia	Wet	50	4.5 (0.9)	GC-FID	Aquino (2006)	Daytime mean (11:00–16:00, LT). Canister sampling
Central Amazonia	Wet	53	1.85	PTR-MS	Yáñez-Serrano et al. (2015)	
Southwestern Amazonia	Wet	60	4.0 (1.2)	GC-FID	Aquino (2006)	Daytime mean (11:00–16:00, LT). Canister sampling
Central Amazonia	Wet	60	2.40	GC-MS/FID	Batista et al. (2019)	Mean of overall dataset. Slope forest. Cartridge sampling with drones
Central Amazonia	Wet	60	4.40	GC-MS/FID	Batista et al. (2019)	Mean of overall dataset. Plateau forest. Cartridge sampling with drones
Central Amazonia	Wet	79	1.69	PTR-MS	Yáñez-Serrano et al. (2015)	
Central Amazonia	Wet	200–500	~3	GC-MS	Kesselmeier et al. (2000)	24 hr mean. Sampling with tethered balloon
Guyana Shield	Wet	400	~2.3	GC-FID	Gregory et al. (1986)	Canister sampling
Central Amazonia	Wet	500	~3	PTR-MS	Martin et al. (2017)	During periods of clean conditions (above threshold)
Central Amazonia	Wet	200–1,000	2.86 (2.25–3.64)	GC-MS	Greenberg et al. (2004)	Daytime median and interquartiles (12:00–15:00, LT). Cartridge sampling on tethered balloon
Southwestern Amazonia	Wet	200–1,000	6.89 (2.78–7.73)	GC-MS	Greenberg et al. (2004)	Daytime median and interquartiles (12:00–15:00, LT). Cartridge sampling on tethered balloon
Central Amazonia	Wet	200–1,000	0.74 (0.6–1)	GC-MS	Greenberg et al. (2004)	Daytime median and interquartiles (12:00–15:00, LT). Cartridge sampling on tethered balloon

(Continues)

TABLE 1 (Continued)

Site	Season	Height (m)	Isoprene (ppb)	Technique	Reference	Observations
Guyana Shield	Wet	3,000	3.30	PTR-MS	Warneke et al. (2006)	
Guyana Shield	Wet	3,000	1.70	PTR-MS	Williams et al. (2001)	
Southwestern Amazonia	W-t-D	25	~4	GC-FID	Kuhn, Rottenberger, Biesenthal, Wolf, et al. (2002)	
Southwestern Amazonia	W-t-D	08–52	3.7 (0.6)	GC-FID	Kesselmeier, Kuhn, et al. (2002)	Daytime mean (11:00–18:00, LT)
Central Amazonia	W-t-D	40	4.17 (1.81)	PTR-MS	Wei et al. (2018)	Daytime mean
Southwestern Amazonia	W-t-D	50	2.1 (2.0)	GC-FID	Aquino (2006)	Daytime mean (11:00–16:00, LT). Canister sampling
Southwestern Amazonia	W-t-D	60	1.8 (1.8)	GC-FID	Aquino (2006)	Daytime mean (11:00–16:00, LT). Canister sampling
Central Amazonia	W-t-D	100	2.38 (1.16)	GC-FID	Kuhn et al. (2010)	Mean vertical profiles of isoprene and α -pinene from 8 background flights
Southwestern Amazonia	Dry	Satellite	X		Barkley et al. (2009)	
Southwestern Amazonia	Dry	Satellite	X		Bauwens et al. (2016)	
Southwestern Amazonia	Dry	Leaf level	X	GC-FID/MS	Kuhn et al. (2004b)	
Southwestern Amazonia	Dry	Leaf level	X	GC-FID/MS	Kuhn et al. (2004a)	
Southwestern Amazonia	Dry	Leaf level	X		Bracho-Nunez et al. (2012)	
Southwestern Amazonia	Dry	Leaf level	X		Bracho-Nunez et al. (2013)	
Southwestern Amazonia	Dry	Leaf level	X		Garcia et al. (2019)	
Southwestern Amazonia	Dry	Leaf level	X		Harley et al. (2004)	
Southwestern Amazonia	Dry	Leaf level	X		Jardine et al. (2013)	
Southwestern Amazonia	Dry	Leaf level	X		Jardine, Jardine, et al. (2016)	
Southwestern Amazonia	Dry	Leaf level	X		Pegoraro et al. (2005)	
Southwestern Amazonia	Dry	Leaf level	X		Taylor et al. (2019)	
Southwestern Amazonia	Dry	Leaf level	X		Taylor et al. (2018)	

Note: For a more extended table with all reported values for Amazonian ecosystems in ppb, please refer to Table 1 in Supporting Information 2. Note that in some cases fluxes in $\text{mg m}^{-2} \text{hr}^{-1}$ are reported (these cases are identified by (flux), or by an *). The compounds are presented in the following order: acetaldehyde, acetic acid, acetone, acetonitrile, acetylene, benzaldehyde, benzene, butanal, butane, butene, 1,4-cyclohexadiene, p-cymene, decanal, dichloromethane, diterpenes, dimethylsulphide, estragole, ethane, ethanol, ethylbenzene, ethylene, formaldehyde, formic acid, heptane, 1-heptene, 2-heptene, hexane, hexanol, hexene, hydrogen sulphide, hydroxyacetone (flux), isoprene (flux), isoprene (flux), linalool, methyl ethyl ketone (MEK), methanol, 2-methyl-2-butene, methyl chloroform, 2-methyl-furan, 3-methyl-furan, 6-methyl-5-heptene-2-one, methyl mecaptan, methyl iodide, total monoterpenes, total monoterpene (flux), methyl vinyl ketone and methacrolein (MVK + MACR), MVK + MACR (flux), nonanal, octane, pentanal (flux), pentane, propylene, propyne, total sesquiterpenes, total sesquiterpene (flux), styrene, sulphur dioxide, α -terpineol, toluene and m-, p- and o-xylene.

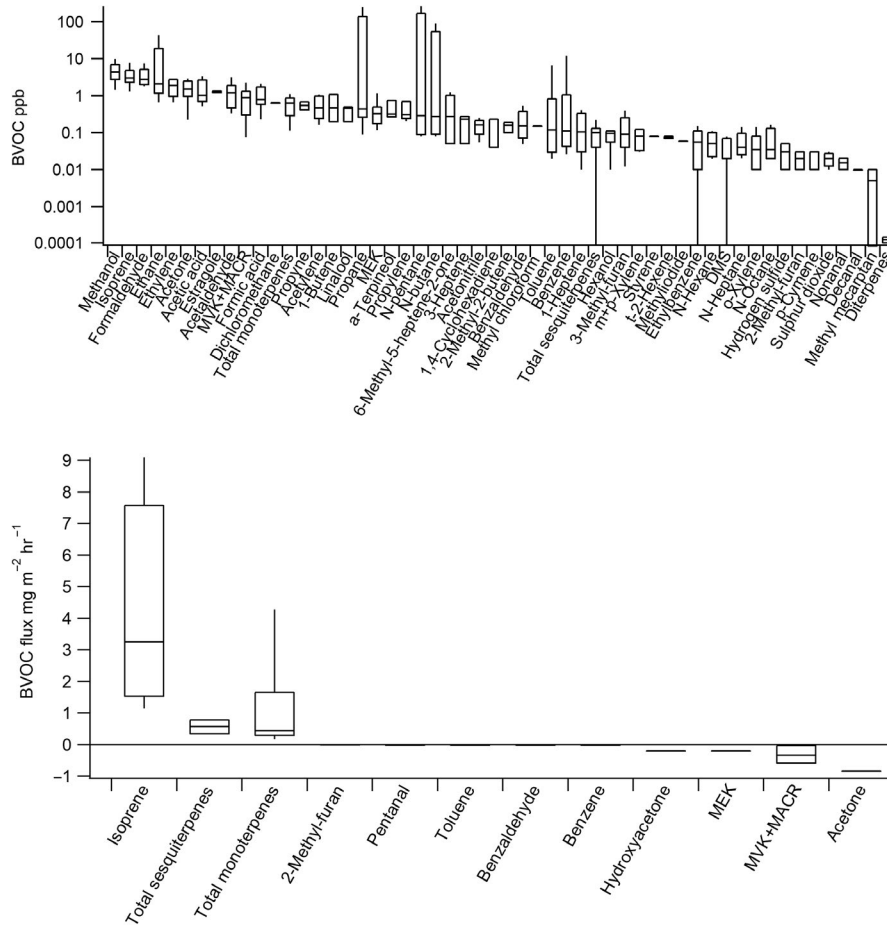


FIGURE 3 Whiskers box plot of all measured ambient concentrations (in ppb) of biogenic volatile organic compounds (BVOCs) in Amazonia to date. The ends of the box are the upper and lower quartiles showing the interquartile range, and the median is marked by a horizontal line inside the box. The whiskers are the two lines outside the box that extend to the highest and lowest observations [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 Whiskers box plot of all measured ecosystem fluxes (in $\text{mg m}^{-2} \text{hr}^{-1}$) of biogenic volatile organic compounds (BVOCs) in Amazonia to date. The ends of the box are the upper and lower quartiles showing the interquartile range, and the median is marked by a horizontal line inside the box. The whiskers are the two lines outside the box that extend to the highest and lowest observations [Colour figure can be viewed at wileyonlinelibrary.com]

novo from the leaves, glands and resin ducts (Kesselmeier & Staudt, 1999) in Amazonia (Jardine, Jardine, et al., 2015; Kuhn, Rottenberger, Biesenthal, Wolf, et al., 2002; Piva et al., 2019; Yáñez-Serrano, Nölscher, et al., 2018).

In addition to living vegetation, leaf litter is an important source of BVOCs (Greenberg et al., 2012), particularly during the start of the dry season when litterfall peaks, and decomposition is further aided by wetness with the upcoming wet season. Little is known about this BVOC source in Amazonia, but monoterpene addition to soils from leaf fall and excreted from plant resins and roots have been reported elsewhere (Delory, Delaplace, Fauconnier, & du Jardin, 2016; Marmulla & Harder, 2014), suggesting a potential, unquantified role of Amazonian ecosystems with a rapid turnover of biomass.

Soils are a poorly explored BVOC source in the Amazonian rainforest, including their microorganisms, roots and surface reactions (Tang, Schurgers, & Rinnan, 2019). SQTs have recently been found to be strongly emitted by soil bacteria (Bourtsoukidis et al., 2018), with responses to soil conditions, because microorganisms are highly spatially heterogeneous (Buscardo et al., 2018), dynamic and able to produce and consume BVOCs strongly interacting within the soil ecosystem. Also reduced sulphur compounds such as dimethyl sulphide, carbon disulphide or carbonyl sulphide can be released by soils (Bunk, Behrendt, Yi, Andreae, & Kesselmeier, 2017), including Amazonian soils (Jardine et al., 2014).

Similar to soil, microorganisms in the phyllosphere (both endo- and epiphytic) can be an important source of BVOCs. The phyllosphere contains bacteria, fungi, bryophytes and lichens and are extremely diverse in tropical forests (Roy & Banerjee, 2018). Little is known about the relationship between the phyllosphere and BVOCs, but typical colonizers of the phyllosphere can emit and metabolize BVOCs (Farré-Armengol, Filella, Llusia, & Peñuelas, 2016; Kesselmeier, Wilske, Muth, Bode, & Wolf, 1999; Rundell, Spakowicz, Narváez-Trujillo, & Strobel, 2015), therefore, the contribution of phyllospheric emissions to net ecosystem emission may be important given their abundance in rainforests (Roy & Banerjee, 2018). In addition to phyllospheric interactions, other processes at the foliar level can be a source of BVOC emissions to the atmosphere, for example, oxidation products formed interactions at the surface of leaves (Jud et al., 2016) and adsorption/desorption onto/from surfaces.

Lastly, animals are a relatively unexplored source of BVOCs in Amazonian rainforests. In particular, arthropods such as ants and termites contribute one third of the animal biomass in Amazonian upland forests, constituting several tonnes per hectare (Rinker & Lowman, 2004). Induced volatile emissions from animals, such as emissions from wood-eating termites of different social ranks (Himuro, Yokoi, & Matsuura, 2011), or emissions of formic acid from ants for defensive purposes (Brütsch, Jaffuel, Vallat, Turlings, & Chapuisat, 2017), have been reported. However, the types and

magnitudes of the emissions from Amazonian ecosystems have not been really deepened since the reports by Zimmerman, Greenberg, Wandiga, and Crutzen (1982) or Khare, Kumar, Kumari, and Srivastava (1999).

The emission rates of BVOCs from all the aforementioned sources may vary considerably as a function of driving factors. Temperature is a key driver of BVOC emissions, both for plants and soils, because it promotes enzymatic reactions in pathways of BVOC biosynthesis and their diffusion in biological tissues and soil substrates (Llusà & Peñuelas, 2000). For example, monoterpenes have been described as leaf 'thermometers', increasing in emission with temperature (Jardine et al., 2017). Emissions of SQTs and methanol are also temperature-dependent (Alves et al., 2016; Jardine, Jardine, et al., 2016; Jardine, Yáñez Serrano, Arneth, Abrell, Jardine, van Haren, et al., 2011) and isoprene has been found to protect against thermal stress in Amazonia (Garcia et al., 2019). Soil temperature is also a determinant because it increases decomposition and subsequent BVOC emission, but such processes have not been adequately addressed.

Photosynthetically active radiation and its relationship to photosynthesis are essential drivers for compounds emitted de novo, including isoprene and monoterpenes such as cis- β -ocimene (Alves et al., 2014; Harley et al., 2004; Jardine, Jardine, et al., 2015; Jardine et al., 2013, 2017; Kesselmeier & Staudt, 1999; Kuhn, Rottenberger, Biesenthal, Wolf, et al., 2002; Kuhn et al., 2004a; Llusà & Peñuelas, 2000). For example, isoprene emissions from *Hymenaea courbaril* have been strongly correlated with gross primary productivity under non-stress conditions (Kuhn et al., 2004b) and protect plants under high solar radiation conditions (Garcia et al., 2019). Rapidly changing light conditions, for example, during a sudden thunderstorm, can also induce emissions of acetaldehyde and ethanol (Holzinger, Sandoval-Soto, Rottenberger, Crutzen, & Kesselmeier, 2000). The effect of solar radiation on soils has not been well explored, but radiation would both heat the surface and decrease the water content due to evaporation, though only about one third of the radiation that arrives at the top of the canopy reaches the soil (Alves et al., 2016).

The availability of water within ecosystems affects BVOC production, whether as humidity, foliar uptake or content in soil. Drought reduces stomatal conductance, decreases intracellular CO₂ mixing ratios and as a result, increases isoprene emissions (Pegoraro, Rey, Bobich, et al., 2004), although this is dependent on the severity of drought (Niinemets, 2010; Otu-Larbi et al., 2020; Pegoraro, Rey, Greenberg, et al., 2004; Potosnak et al., 2014). GLV emission can be stimulated at high temperatures and under drought conditions (Jardine, Chambers, et al., 2015; Pfannerstill et al., 2018). The general reduction of BVOC emissions by plants due to drought depends on both changes in plant physiology and to lower foliar biomass. Emissions from Amazonian soils depend on moisture, because bacteria may become activated by water, with an emission burst after a large rainfall event and an optimal pattern of emissions, where SQT emissions are the highest under moderate levels of soil water (Bourtsoukidis et al., 2018). The soil water also affects the gas

permeability of the soil. The soil water content is therefore an essential parameter for BVOC production and release from Amazonian soils.

The atmospheric abundance of gaseous constituents is an additional regulator of BVOC emissions. The mixing ratios of BVOCs in the atmosphere, particularly of oxygenated compounds that are bidirectionally exchanged (Niinemets, Fares, Harley, & Jardine, 2014), are driven by a compensation point (i.e. a compound is emitted if the foliar concentration is higher than the ambient mixing ratios, otherwise the plant will take up the compound), as has been observed in Amazonia (Jardine, Yáñez Serrano, Arneth, Abrell, Jardine, Artaxo, et al., 2011; Kuhn, Rottenberger, Biesenthal, Ammann, et al., 2002; Rottenberger et al., 2004). The amount of oxidants in the atmosphere can induce emissions to quench oxidation (Jardine, Jardine, et al., 2015; Jardine, Monson, et al., 2011; Peñuelas & Llusà, 2001) and oxidize BVOCs generating oxidation products. Biotic and abiotic stressors at the foliar level lead to the formation of reactive oxygen species (ROS), altering plant BVOC emissions coordinated to quench the ROS (Jardine & Jardine, 2016; Sampaio Filho et al., 2018). Regional and global models currently have a module for deposition and another for emissions. For these bidirectional exchange compounds such modules must be combined. One step forward in this matter is the addition of a bidirectional exchange compound class in the MEGAN model (Guenther et al., 2012).

Increasing atmospheric CO₂ mixing ratios can affect BVOC emissions (Possell, Nicholas Hewitt, & Beerling, 2005; Wilkinson et al., 2009) directly, with higher biomass due to higher substrate availability (Lerdau, Litvak, & Monson, 1994), and thus higher foliar surface area for BVOC emission, as demonstrated for monoterpene emissions (Staudt, Joffre, Rambal, & Kesselmeier, 2001). However, no information on these processes is available for Amazonian ecosystems. These increasing CO₂ mixing ratios can also indirectly suppress the emission of compounds such as isoprene (Young, Arneth, Schurgers, Zeng, & Pyle, 2009), due to a competition of phosphoenolpyruvate (Fasbender, Yáñez-Serrano, Kreuzwieser, Dubbert, & Werner, 2018; Possell et al., 2005; Rosenstiel, Potosnak, Griffin, Fall, & Monson, 2003), which at the same time may be offset by warming and increased growth (Garcia et al., 2019; Sharkey & Monson, 2017).

Phenology, ontogeny and canopy structure play important roles in BVOC emissions in Amazonian rainforests (Alves et al., 2018; Kuhn et al., 2004b; Wei et al., 2018). The quantity of BVOCs emitted by leaves varies with the stage of maturity as a consequence of resource availability (maturity) and defensive demand (bud break and early stages; Kuhn et al., 2004b). For example, young *Vismia Guianensis* leaves emit higher quantity of methanol than mature leaves (Jardine, Jardine, et al., 2016), whereas mature leaves of *V. Guianensis* and *Eschweilera coriacea* have higher isoprene emissions than at other leaf ages (Alves et al., 2014, 2016; Jardine, Jardine, et al., 2016); and light-dependent monoterpenes are emitted exclusively during the period between bud-break and foliar maturity for *Hymenaea courbaril* (Kuhn et al., 2004b). Additionally, canopy structure plays a role in BVOC dynamics as shown with high SQT emissions in the lower canopy (Alves et al., 2016). Foliar

flushing in Central Amazonia peaks during the transition from the wet to the dry season, with a consequent peak in leaf litter and foliar turnover at the onset of the dry season (Goulden et al., 2004; Huete et al., 2006; Roberts, Nelson, Adams, & Palmer, 1998). This factor has been reported to be essential for modelling BVOC emission in Amazonia (Alves et al., 2018).

Nutrient availability is another important driver of BVOC emissions (Fernández-Martínez et al., 2018). In this regard, the role of litterfall has recently been demonstrated to be important for supplying soil with nutrients that affect microbial composition in Amazonian ecosystems (Buscardo et al., 2018), but no information is available with respect to the effect of nutrient availability on BVOC dynamics at canopy level in Amazonia.

Biotic factors such as pathogens, herbivores, herbivorous predators, pollinators and phyllospheric organisms influence the emission rates of BVOCs. Plants emit BVOCs as defensive mechanisms or for signalling within plants and ecosystems (Šimpraga et al., 2019). Alterations to these biological controls can thus affect the average BVOC emissions from plants. Little is known about the role of the phyllosphere in BVOC dynamics in the Amazonian rainforest, but some possible implications can be derived from studies elsewhere. The phyllosphere affects plant biogeography and ecosystem function, thereby affecting plant physiology. The phyllosphere reduces the amount of photosynthesis by blocking light (Huete et al., 2006), protects plants against heat (Stuntz, Simon, & Zotz, 2002), can retain water in the leaves (Coley, Kursar, & Machado, 1993; Stuntz et al., 2002), fixes nitrogen and protects plants against herbivores and abiotic stresses by the production of phytohormones and other secondary metabolites (Roy & Banerjee, 2018). The phyllosphere is also subjected to environmental conditions that can alter its role from beneficial to pathogenic. Such environmental conditions can be leaching, changes in temperature, variations in exposure to sunlight, ROS concentration (Bringel & Couée, 2015), the phyllospheric cover itself, effects of irrigation, cohabitation, foliar texture and phenology (Coley et al., 1993; Saikkonen, Faeth, Helander, & Sullivan, 1998).

Lastly, species diversity can influence the total emission of BVOCs, as has been reported for terpenoids, with substantial variation within species (Guenther, 2013). In Amazonia, an elevation gradient in isoprene emissions was attributed to the plant species distribution which differ topographically (Gu et al., 2017). The Amazonian rainforest contains a variety of ecosystems, from upland forests to flooded or seasonally flooded forests (see Supporting Information for more information). Differences in environmental conditions and adaptive strategies can be implied from differences in BVOC emission (Bracho-Nunez et al., 2012). Investigation on the effects of root anoxia on BVOC exchange is thus important for understanding the functioning of Amazonian ecosystems. Plants may react to flooding with fermentation, accompanied by emissions of ethanol and acetaldehyde to remove the large amounts of ethanol produced under root anoxia (Bracho-Nunez et al., 2012; Kreuzwieser, Schnitzler, & Steinbrecher, 1999; Rottenberger et al., 2008). The quantities and ratios of such emissions can indicate the metabolic and morphologic adaptations of flooded ecosystems (Parolin et al., 2004).

The vast amount of BVOC sources in the Amazonian rainforest (i.e. diverse species of insects, vegetation, soil and phyllosphere microorganisms) is regulated by a plethora of biotic and abiotic emission drivers (i.e. temperature, radiation, water and nutrient availability, ambient CO₂ and BVOC mixing ratios) leading to a strong seasonality (Alves et al., 2016, 2018; Barkley et al., 2009; Kesselmeier, Kuhn, et al., 2002; Kuhn et al., 2004a; Yáñez-Serrano, Nölscher, et al., 2018; Yáñez-Serrano et al., 2015). While increasing research addresses BVOC emissions over single or combined emission drivers, the large-scale biodiversity and interplay of biotic and abiotic processes remains challenging. Within such large ecosystems, ecological interactions may have an important, but poorly explored, role in regulating the BVOC emissions of the Amazon rainforest.

4 | ECOLOGICAL INTERACTIONS

Biogenic volatile organic compounds are assumed to play a strong role in ecological interactions in Amazonia (Figure 2). BVOC sources create volatile blends that can serve to identify the species of a recipient (Piva et al., 2019), allowing us to understand the nature of such communication (e.g. the identity and density of an attacking herbivore; Pinto-Zevallos, Bezerra, Souza, & Ambrogi, 2018), and can also direct the evolution of plant chemical diversity (Salazar et al., 2018).

Signalling within plants can be based on cascading signals of jasmonates, salicylates and ethylene, but also other types of BVOCs such as GLV, methanol or isoprenoids (Filella, Peñuelas, & Llusà, 2006; Matsui, 2016; Matsui, Sugimoto, Mano, Ozawa, & Takabayashi, 2012; Seco, Filella, Llusà, & Peñuelas, 2011). The function of their emission can be involved in: inducing the production of BVOCs that can downregulate floral volatiles to produce BVOCs associated with fruit ripening, inducing BVOC production for defensive purposes, or for individual plant coexistence (Kigathi, Weisser, Reichelt, Gershenson, & Unsicker, 2019; Ninkovic, Rensing, Dahlin, & Markovic, 2019). However, to our knowledge, these processes have not been investigated in Amazonia.

Another type of signalling occurs between plants and other living organisms in ecosystems for reproduction, defense, awareness of neighbouring plants and modulating adaptation and evolution (Fine, Mesones, & Coley, 2004; Laothawornkitkul et al., 2009; Salazar et al., 2018). Plants emit floral blends to attract specific pollinators to aid reproduction. As rewards for pollination they offer pollen and also resins, although the latter more rarely, as for some Amazonian *Clusia* species (Bittrich & Amaral, 1997). Guarana trees emit higher amounts of (E)- β -ocimene during night to attract nocturnal bees (Krug et al., 2018). The preferences of bees for collecting pollen from other Amazonian plant species are nevertheless still unclear (Kaminski & Absy, 2006). Furthermore, the role of phyllospheric floral bacteria has been pointed out to be of importance for BVOC emissions (Peñuelas et al., 2014), although no information is available for the Amazonian rainforest. Other types of communication associated with reproduction involve

the production of fruit odours for seed dispersal (Laothawornkitkul et al., 2009), for the seeds of a plant or of neighbouring plants (Gfeller et al., 2019), particularly in Amazonia with seed-ant mutualism (Youngsteadt, Baca, Osborne, & Schal, 2009).

Biogenic volatile organic compounds emitted for defensive purposes have characteristic blends, in both abundance and chemical diversity, are species specific (Courtois et al., 2009; Sharifi, Lee, & Ryu, 2018), serve an awareness role with neighbouring plants (De Moraes, Mescher, & Tumlinson, 2001; Kessler & Baldwin, 2001), and can affect plant chemical diversity (Salazar et al., 2018). Such interactions can also occur between aboveground plants and roots, with important implications for BVOC interactions within the soil ecosystem (Delory et al., 2016). Herbivory in tropical rainforests has been estimated to consume 12%–30% of the foliar area annually, with insects dominating foliar consumption, at 680 kg ha⁻¹ year⁻¹ (Rinker & Lowman, 2004). The role of BVOC emission in the Amazonian rainforest induced by herbivory is thus expected to be substantial but has not been characterized on regional scales.

Plants, including their roots, can emit BVOCs to attract predators of herbivores (Aartsma, Bianchi, van der Werf, Poelman, & Dicke, 2017; Sharifi et al., 2018). SQTs are good attractors of plant bodyguards (Rasmann et al., 2005) whereas isoprene repels them (Loivamäki, Mumm, Dicke, & Schnitzler, 2008). For example, the Amazonian ant *Allomerus octoarticulatus* can be attracted to damage from herbivory by its mutualistic plant *Hirtella myrmecophila* (Romero & Izzo, 2004), showing the complex interaction between plants and ants. In fact, the relationship between ants and plant size in Amazonia can shape arthropod communities (Izzo & Vasconcelos, 2005). The extent of the damage from herbivory feeds back on the defensive blends, as for cassava (Pinto-Zevallos et al., 2018), sometimes jeopardizing the plant's protection (von Dahl, Hävecker, Schlögl, & Baldwin, 2006).

Plants, microbes and animals can emit BVOCs as direct toxins, deterrents or repellents against herbivores (De Moraes et al., 2001; Kessler & Baldwin, 2001; Laothawornkitkul et al., 2009; Prestwich, 1984; Saikkonen et al., 1998; Sharifi et al., 2018). For example, Formicinae ants emit formic acid as a defensive strategy (Brütsch et al., 2017) or GLV plant emissions can prime neighbouring plants against herbivores (Engelberth, Alborn, Schmelz, & Tumlinson, 2004). Moreover, signalling can be negative, like isoprene that serves as a negative cue, informing insects where not to forage (Gershenzon, 2008; Laothawornkitkul et al., 2008).

Protection against pathogens and sealing wounds are also drivers for BVOC emissions (Laothawornkitkul et al., 2009; Ninkovic et al., 2019; Šimpraga et al., 2019). For example, the biosynthesis of natural rubber by *Hevea brasiliensis* is stimulated by wounding, releasing methyl jasmonate and ethylene (Duan et al., 2010), which is then oxidized during latex coagulation, sealing the wound (Piva et al., 2018). *Nicotiana tabacum* plants emit methyl salicylate when pathogenic infections are present, inducing the expression of defensive genes in neighbouring plants (Shulaev, Silverman, & Raskin, 1997) and phytopathogens

can turn plants into sources of carbonyl sulphide (Bloem, Haneklaus, Kesselmeier, & Schnug, 2012) rather than sinks as generally seen (Whelan et al., 2018). The role of the phyllosphere in defense against pathogens has been established for Amazonia (Azevedo, Maccheroni, Pereira, & De Araújo, 2000; de Sia et al., 2013; Gazis & Chaverri, 2015; Vaz et al., 2018), where pathogenic disease such as anthracnose can be especially important for modulating the expansion and production of guarana plantations (Bogas et al., 2015). BVOC emissions to protect against pathogens may thus be important for identifying plant diseases.

Lastly, abiotic factors driving BVOC emission can also alter ecological interactions. Amazonian plants have been shown to protect themselves against excessive heat: by emitting isoprene (Jardine, Jardine, et al., 2016) and distinct monoterpene species (Jardine et al., 2017), by oxidizing isoprene within leaf tissues and therefore releasing MVK + MACR (Jardine, Monson, et al., 2011) or by emitting GLV due to high temperatures and drought as part of induced senescence processes (Jardine, Chambers, et al., 2015). There are other abiotic factors altering ecological interactions. In Amazonia, rain can alter SQT speciation from soils (Bourtsoukidis et al., 2018). Ozone can affect plant physiology (Loreto, Pinelli, Manes, & Kollist, 2004). BVOC oxidation can disrupt plant olfactory cues (Vuorinen, Reddy, Nerg, & Holopainen, 2004). Masking of BVOCs or ovipositional stimulants induced by herbivory may affect the range of the signal (Farré-Armengol, Peñuelas, et al., 2016; Pinto, Blande, Souza, Nerg, & Holopainen, 2010). SQTs emitted by soils and vegetation have been shown to quench ozone within the canopy of an Amazonian rainforest (Bourtsoukidis et al., 2018; Jardine, Yañez Serrano, Arneith, Abrell, Jardine, van Haren, et al., 2011). Thus, the abundance of ambient ozone regulates the distance over which the ecological BVOC signals are transported (Conchou et al., 2019). In fact, given the toxicity of ozone, trees have been shown to emit reactive BVOCs to quench the ozone levels (Bourtsoukidis et al., 2012). Additionally, ozone mixing ratios increase after biomass burning and urban pollution plumes in Amazonia (Wei et al., 2019), so these processes could be important for plant fitness and ecological interactions in the future Amazonia. At last, atmospheric CO₂ increase is expected to alter ecological interactions either by increasing BVOC emissions due to higher substrate availability, decrease BVOC emissions due to BVOC synthases competition in biosynthesis, or due to a modification of the emitted compounds (Yuan, Himanen, Holopainen, Chen, & Stewart, 2009).

While the role of BVOCs in ecological interactions is widely accepted, it is currently unknown how these will regulate the cumulative BVOC release from Amazonia. Disturbing established communication links among trees and between trees and insects may have unforeseen consequences for the ecosystem and species protection from pathogens. Anthropogenic activity alters ecological interactions; therefore, the rapidly changing atmospheric conditions may be a highly important piece of the puzzle in understanding the BVOC dynamics within Amazonia.

5 | ATMOSPHERIC IMPACT

The impact of Amazonian BVOCs on atmospheric chemistry is highly dynamic, with strong diel and seasonal characteristics. The vast emissions of reactive BVOCs, in combination with high emissions of other trace gases, insolation, high temperature and humidity, and high OH concentrations make the Amazonian atmosphere a tropical photoreactor (Andreae, 2001). BVOCs emitted to the Amazonian atmosphere are rapidly oxidized by OH radicals during the day and more slowly by ozone, or by NO₃ radicals at night (Paulson & Orlando, 1996). Some of the BVOCs emitted are very reactive, such as isoprene towards OH (Nölscher et al., 2016) and SQTs towards O₃ (Jardine, Yáñez Serrano, Arneth, Abrell, Jardine, Artaxo, et al., 2011). Isoprene, in particular, can deplete tropical OH concentrations, thus indirectly affecting BVOC oxidation (Taraborrelli et al., 2012) and the lifetimes of climate relevant gases such as methane.

OH reactivity is a measurable parameter quantifying the total loss frequency of OH radicals in the atmosphere, including BVOCs and other reactive trace gases. It can be used to assess how comprehensively the reactivity of BVOCs can be accounted for in Amazonia. The difference between the calculated OH reactivity versus the observed OH reactivity indicates that there is a large portion of unexplained reactivity (OH missing reactivity) possibly due to unmeasured compounds not accounted for in the calculation of OH reactivity from the sum of the individual compounds. Missing reactivity measured at a single Amazonian rainforest location was strongly seasonal, being lower during the wet season (10 s⁻¹; missing OH reactivity of 5%–15%) and higher during the dry season (62 s⁻¹; missing OH reactivity of up to 79%), suggesting that more unknown reactive compounds are present in the atmosphere during the dry season (Nölscher et al., 2016; Yang et al., 2016). Lower reactivity leads to a more oxidative atmosphere in the wet season, with high deposition of oxidation products onto wet surfaces and possible enhanced microbial activity on foliar surfaces that could influence the OH reactivity budget (Nölscher et al., 2016).

The gas-phase oxidation of BVOCs can form new particles by nucleation (Kirkby et al., 2016), or the oxidized BVOCs can condense onto pre-existing particles, undergo heterogeneous reactions on particle surfaces, be processed in clouds or undergo further atmospheric degradation and deposition. Photochemistry is an important Amazonian source of oxygenated VOCs (Yáñez-Serrano et al., 2015), particularly for short-chain compounds (Seco, Peñuelas, & Filella, 2007). A recent study has demonstrated the strong role of isoprene oxidation, which contributes ca. 20% of the organic aerosols (OAs) produced in Amazonia (Schulz et al., 2018). The contribution of other BVOCs to aerosol formation in the tropical rainforest is more difficult to estimate, but SQTs have been estimated to contribute 0.4%–5% to submicron OAs (Yee et al., 2018). Shrivastava et al. (2019) recently reported that isoprene and terpenes can contribute almost half of the Amazonian biogenic secondary organic aerosols (SOAs).

Aerosols have profound implications on the radiation balance locally, regionally and globally, either directly by scattering (Artaxo et al., 2013; Kulmala et al., 2013) or by absorbing solar radiation

(Boucher et al., 2013) or indirectly by impacting cloud and rain formation processes. Furthermore, they can boost global primary production up to 25% for Amazonian ecosystems via diffuse radiation fertilization (Cirino, Souza, Adams, & Artaxo, 2014; Koren et al., 2012; Rap et al., 2018). Therefore, the presence of BVOCs influences the associated albedo by modifying the number and size of cloud condensation nuclei (CCN) and cloud droplets, affecting how the clouds reflect and absorb light (Boucher et al., 2013) and thus the radiation balance (Andreae & Crutzen, 1997; Artaxo et al., 2009; Sena, Artaxo, & Correia, 2013) and hydrological cycle (Sheil, 2018). BVOCs and their role in SOAs, dominant type the fine-mode aerosol mass (Martin et al., 2010), could ultimately affect the radiative cooling of the Earth (Ehn et al., 2014), particularly in Amazonia where sulphur compounds are at low concentrations (Kirkby et al., 2016) and the radiation balance is driven by organic aerosols (Artaxo et al., 2013). A significant fraction of SOAs can act as CCN formed from BVOCs in the Amazonian wet season (Pöschl et al., 2010). The low CCN particle concentrations lead to larger cloud droplets producing clouds at lower altitudes that have higher rain efficiency (Rosenfeld, 1999), intensifying the role of BVOCs in aerosol and cloud dynamics. The formation of new particles at the planetary boundary layer has not been observed in Amazonia. BVOC species are instead elevated by deep convection and converted into condensable species in the upper troposphere, forming new aerosol particles and increasing the loading of OAs, which can then be transported down to the planetary boundary layer (Andreae et al., 2018; Schulz et al., 2018; Figure 2).

Biogenic volatile organic compounds can also affect radiative forcing by their degradation in the atmosphere (with CO₂ as an end product) and by their perturbation of the lifetime of other greenhouse gases such as methane, ozone (Guenther, 2002) and further reactive gases such as CO (Collins, Derwent, Johnson, & Stevenson, 2002). This is estimated to add 0.16 Pg C/year to the amount of global atmospheric CO₂ (Suntharalingam, Randerson, Krakauer, Logan, & Jacob, 2005), which can increase CO₂ levels by 0.07 ppm/year, and can have a significant impact on the results of inverse model investigations of CO₂ sources. Because BVOCs deplete OH faster than methane (for which the primary sink is OH), methane will have a longer lifetime in the atmosphere (Collins et al., 2002). Alternatively, tropospheric ozone is formed via BVOC oxidation when sufficient NO_x is available, adding to the radiative forcing of greenhouse gases.

NO_x levels are low (ca. 0.4 ppb) in the atmosphere over the undisturbed Amazonian rainforest (Liu et al., 2016), particularly during the wet season when air masses arrive predominantly from the north-east over mostly pristine rainforest (Pöhlker et al., 2019). NO from soils that reacts with O₃ to form NO₂ inside the canopy is the main source of NO_x. This NO₂ is deposited on the leaves of the very dense rainforest canopy, reducing the contribution of soil NO emissions to the levels of NO_x above the canopy (Jacob & Wofsy, 1990). The direct loss by reaction of O₃ with BVOCs outcompetes O₃ formation under these pristine conditions, thereby leading to a decrease in O₃ (Jacob & Wofsy, 1990; Scott et al., 2018). O₃ budgets are thus mainly controlled by transport from above (downdrafts from convective

storms Dias-Júnior et al., 2017; Gerken et al., 2016) and deposition to the canopy, with little net effect from photochemistry (Jacob & Wofsy, 1990).

NO_x levels increase significantly during the dry season due to changes in wind direction from the easterly and southeasterly fetch regions, transporting considerable amounts of pollution from burning biomass and human activities (Bela et al., 2015; Pacifico et al., 2015). Consequently, O₃ levels also increase during this season (8–15 ppb in the wet season, 15–50 ppb in the dry season at midday; Andreae et al., 2015; Artaxo et al., 2013; Figure 5). The concentrations of trace gases and particles are thus strongly seasonal. In fact, an increase in NO_x mixing ratios (to >1 ppb) can affect the oxidative pathways (i.e. HO₂ or NO pathway; Liu et al., 2016) of BVOC peroxy radicals, thus altering photochemistry, even in this region where NO_x levels are generally low. The central Amazonia plume has been reported to significantly increase O₃ levels by 35% at 70 km downwind of Manaus, whereas NO_x levels increased by <20% relative to remote areas, indicating the strong role of BVOC oxidation in forming O₃, in areas where NO_x levels have increased due to pollution (maxima of up to 6 ppb; Wei et al., 2019). Enhanced urban

pollution and plumes from burning biomass alter BVOC emissions by inducing further emissions of highly reactive BVOCs (Bolsoni, de Oliveira, da Silva Pedrosa, & de Souza, 2018) and thus, altering the dynamics of natural aerosols, with an increase in SOAs formed by BVOC oxidation (Shrivastava et al., 2019). The burning of biomass can profoundly alter SOA composition, although increases in organic submicron particulate matter during the dry season are also due to increased BVOC emissions combined with reduced deposition (de Sá et al., 2019; Williams et al., 2016).

Canopy structure is another very important parameter in determining the impact of BVOCs in the atmosphere. The dense and tall canopy of the Amazonian rainforest can stratify air masses, with an intermittent coupling of the upper canopy and the atmosphere above. Air is poorly mixed within the canopy, particularly at night when conditions are stable, with occasional exceptions of periods with bursts of intermittent turbulence (Freire et al., 2017). The lower part of the canopy is characterized by a thermal inversion, hindering mixing between the canopy and the forest floor (Nölscher et al., 2016; Santana et al., 2018). This feature can affect the residence times of emitted BVOCs and their turbulent transport out

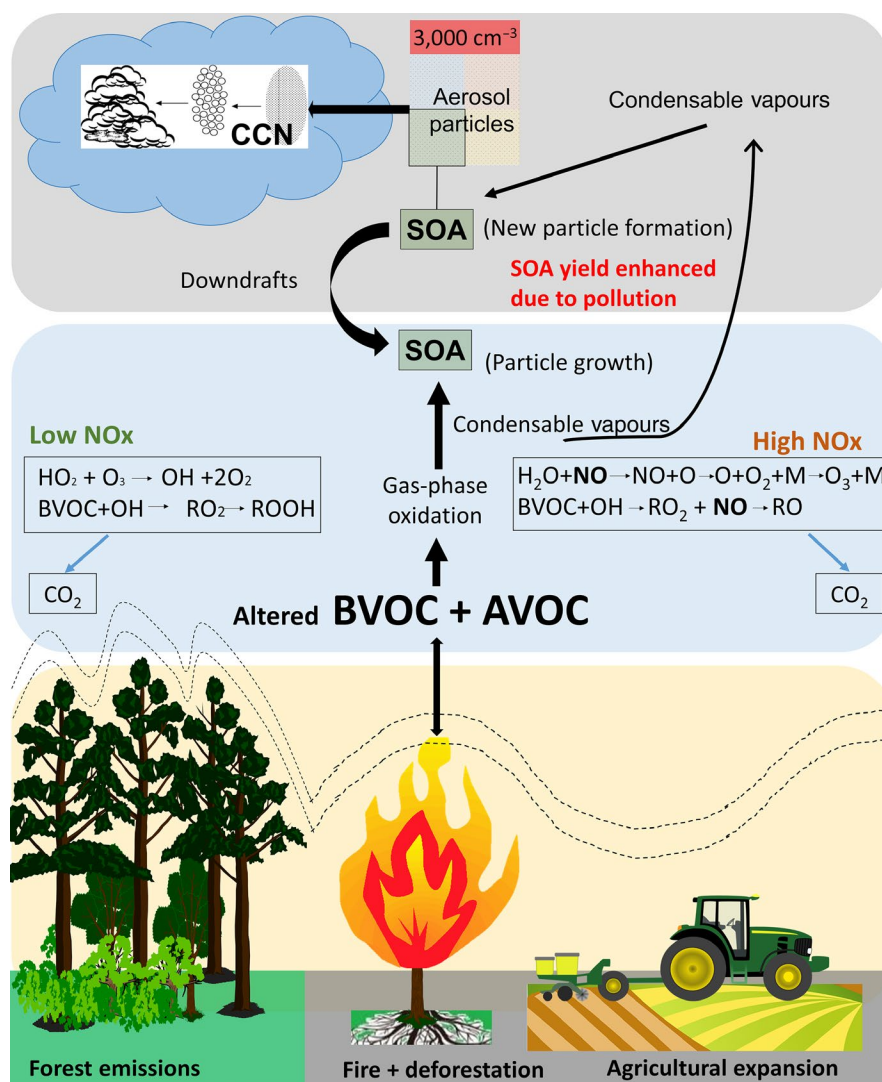


FIGURE 5 Schematic showing biogenic volatile organic compound (BVOC) dynamics in a polluted Amazonian atmosphere, including BVOC sources and interactions, interaction with anthropogenic volatile organic compounds (AVOCs), BVOC oxidation in the atmosphere, and subsequent aerosol and cloud dynamics. CCN, cloud condensation nuclei; SOA, secondary organic aerosol [Colour figure can be viewed at wileyonlinelibrary.com]

of the forest canopy (Bakwin et al., 1990; Fitzjarrald, Stormwind, Fisch, & Cabral, 1988; Gerken, Chamecki, & Fuentes, 2017). BVOCs can thus remain trapped within the canopy, becoming oxidized before reaching the atmosphere above. For example, 50%–70% of O_3 reactivity within the canopy has been attributed to the ozonolysis of highly reactive SQTs (Bourtsoukidis et al., 2018; Jardine, Yañez Serrano, Arneth, Abrell, Jardine, van Haren, et al., 2011; Yee et al., 2018).

Isoprene oxidation by OH produces, among many other products, isoprene peroxide radicals. These radicals can react with HO_2 to form ISOPOOH or with nitric oxide (NO) to produce mostly methyl vinyl ketone and methacrolein. Both pathways (HO_2 and NO) are important in Amazonia, despite their strong seasonality (Liu et al., 2016). The formation of isoprene epoxydiols can lead to the growth/formation of SOAs, mostly in the upper troposphere (Schulz et al., 2018). ISOPOOH levels can nevertheless decrease in polluted conditions (Liu et al., 2016), with implications for OA levels, because higher NO_x levels can suppress the production of SOAs derived from isoprene epoxydiols (IEPOX; de Sá et al., 2017; Schulz et al., 2018). Isoprene was previously thought to yield very low quantities of condensable material under low NO_x levels (Pandis, Paulson, Seinfeld, & Flagan, 1991). More recently, gas-phase IEPOX, second-generation products of isoprene oxidation under $RO_2 + HO_2$ chemistry (Surratt et al., 2010), and reactive uptake have been proposed as an additional pathway. The IEPOX may be responsible for the production of observed SOA isoprene tracers, such as 2-methyltetrols found in the particle phase of Amazonian samples (Carlton, Wiedinmyer, & Kroll, 2009; Claeys et al., 2004; Kroll, Ng, Murphy, Flagan, & Seinfeld, 2005).

In summary, BVOCs can have very strong impacts on the atmospheric chemistry over Amazonia. BVOC emissions determine oxidant regimes, as they modulate the major atmospheric oxidant, OH, and they can lead to pollutant production (e.g. tropospheric ozone) when the pristine Amazonian conditions are altered.

6 | DEPOSITIONAL PROCESSES

Deposition of BVOCs can be divided into wet and dry deposition onto surfaces, biological uptake and physicochemical processes at the leaf–atmosphere interface (Figure 2). In Amazonia, wet deposition can be an important sink for trace gases. Polar compounds are particularly well washed off by rain. Moreover, BVOC oxidation products can be formed in the water layer of leaves and other surfaces. This process is especially important during the wet season and periods of rain and contributes to the observed general decrease in the concentrations of trace gases. For example, organic acids such as formic and acetic acid can contribute up to 90% of rain acidity in Amazonia (Andreae & Andreae, 1988; Jardine, Yañez Serrano, Arneth, Abrell, Jardine, Artaxo, et al., 2011). Dry deposition depends on the movement of air, the vertical stability of the boundary layer, the chemical properties of the species and the nature of the depositional surface (Stickler et al., 2007), which may be important in

Amazonia, particularly at night with 78% of isoprene lost to surface deposition (Wei et al., 2018). Further information is needed to understand dry deposition in Amazonian ecosystems, which may have been underestimated as has been demonstrated over a dense tropical rainforest in Costa Rica (Karl et al., 2004).

Vegetation takes up compounds via stomatal or non-stomatal processes, where re-metabolization can occur (Matsui, 2016). The ambient mixing ratio of a compound regulates its uptake or emission depending on the compensation point. Compensation points for Amazonian ecosystems have been reported to be <0.6 ppb for acetaldehyde and formaldehyde (Rottenberger et al., 2004) and <0.3 for formic and acetic acid (Kuhn, Rottenberger, Biesenthal, Ammann, et al., 2002) based on leaf-level measurements. Data estimated on an ecosystem level were found to range around 1.4 and 2.1 ppb for formic and acetic acid respectively (Jardine, Yañez Serrano, Arneth, Abrell, Jardine, Artaxo, et al., 2011). In view of the possible bio-facilitation for plant VOC uptake (Matsui, 2016), more information is needed to understand the function of bi-directional BVOC exchange by Amazonian ecosystems.

Bacteria are another sink or source for BVOCs. They can take up BVOCs as a source of carbon (Ginkel, Jong, Tilanus, & Bont, 1987) when levels are not toxic and can detoxify BVOCs above toxic levels (Marmulla & Harder, 2014). For example, isoprene can be taken up by tropical soils (Cleveland & Yavitt, 1997), depending on the atmospheric mixing ratio of isoprene and with decreasing rates of uptake under drought conditions (Pegoraro et al., 2005). Bacterial communities in the phyllosphere may also be a BVOC sink (Farré-Armengol, Filella, et al., 2016). Phenol degradation has been observed in phyllospheric communities elsewhere (Sandhu, Halverson, & Beattie, 2007). All these phyllospheric sink processes for BVOCs could be especially important in Amazonia, given its abundant phyllospheric communities.

Processes taking place at the leaf surface such as oxidation and adsorption/desorption are important for ecological interactions, plant physiology and accounting for gross and net BVOC emissions. Oxidation can occur in the stomatal cavity or at the leaf surface as it serves to quench ROS damage in vegetation. Examples have been reported for monoterpenes (Loreto et al., 2004), by semi-volatile organic compounds exuded by glandular trichomes (Jud et al., 2016), and specifically in Amazonia for isoprene (Jardine, Monson, et al., 2011). This oxidation can lead to the production of oxygenated BVOCs such as ketones and aldehydes (Jardine, Monson, et al., 2011; Jud et al., 2016; Pinto et al., 2010). This within-leaf oxidation process is of particular importance for dry deposition estimates worldwide. When fast metabolic conversion of oxygenated BVOCs was incorporated into a global chemistry transport model, Amazonia showed an increased annual dry deposition flux of 75% (Karl et al., 2010).

Adsorption/desorption can occur on surfaces, such as plant cuticles (Müller & Riederer, 2005) and water films and may be important in humid places such as Amazonia, even though their functioning is not yet fully understood. Water layers on the upper surfaces of leaves may strongly influence the absorption of water by leaves, stomatal conductance, pathogenic infection, nutrient leaching

and adsorption of pollutants (Aryal & Neuner, 2010). Oxygenated BVOCs may thus be adsorbed onto water films and are then released upon the evaporation of the films. This process may occur in wet environments such as Amazonia.

In summary, BVOC deposition is dependent on many factors, including the nature and concentration of the compound and the existent meteorology. Despite high uncertainties, in an attempt to quantify the magnitude of BVOC deposition, we used approximations from literature. Dry deposition has been estimated to occur onto leaf surfaces as well as to soil surfaces with shares of 70% and 30% respectively (Karl et al., 2010). These estimates are expected to be higher for leaf surfaces in Amazonia due its larger leaf area. In contrast, in Amazonia, rain wet deposition occurs 90% to soil surfaces, with only 10% being intercepted by vegetation (Czikowsky & Fitzjarrald, 2009). In addition, fog wet deposition is expected to occur at high percentage values (Shimadera, Kondo, Shrestha, Kaga, & Inoue, 2011), although no estimates have been found so far for Amazonia. A proper characterization of Amazonian BVOC deposition flux could result in higher estimates of gross BVOC production, larger than previously thought. The aforementioned processes may account for active and partly unexplored sinks, which have to be considered in regional and global modelling exercises.

7 | CLIMATE CHANGE, LAND-USE CHANGE AND FEEDBACKS

Amazonian ecosystems may be moving towards tipping points. For example, a temperature increase of 4°C or deforestation exceeding 40% of the forested area (Nobre et al., 2016) due to human intervention as land-use change possibly lead to savannization (Marengo, Nobre, Sampaio, Salazar, & Borma, 2011) and limit rainfall in synergistic interactions with the impacts of climate change.

Climate change is expected to alter Amazonian ecosystems, since increased warming will be combined with decreased precipitation (IPCC, 2013). Accompanying effects are drought associated with El Niño–Southern Oscillation (ENSO) anomalies and changes in the surface temperature of the Atlantic Ocean (Leitold et al., 2018), increased frequency and intensity of heat waves (Perkins-Kirkpatrick & Gibson, 2017), and increased duration and intensity of dry (Adams et al., 2017) and intensity of wet (Leite-Filho, Costa, & Fu, 2019; Mori & Becker, 1991) seasons. Increasing temperatures and drought (Aragão et al., 2018; Feldpausch et al., 2016; Leitold et al., 2018; Li, Fu, Juárez, & Fernandes, 2008; Marengo, Williams, Alves, Soares, & Rodriguez, 2016; Pfannerstill et al., 2018; Yang et al., 2018) and intensified dry seasons (Sena et al., 2018), which are slowly drying Amazonia (Esquivel-Muelbert et al., 2018), have already been observed.

These conditions of thermal and drought stress have multiple effects in Amazonian ecosystems. An intensified dry season can particularly increase the frequency of fires (Silva Junior et al., 2019), reduce net primary productivity and accelerate canopy turnover

(Leitold et al., 2018). Drier conditions can lead to an overall decrease in BVOC production (although drought may induce transient GLV emission (Jardine, Chambers, et al., 2015; Figure 6). Other effects are higher irradiance due to lower cloud cover (Sena et al., 2018) and higher temperatures, which ultimately lead to a net increase in BVOC production (Jardine et al., 2017; Pfannerstill et al., 2018) of both BVOCs associated with stress (Jardine, Chambers, et al., 2015) and other unknown highly reactive compounds (Pfannerstill et al., 2018). If threshold limits for heat and radiation are exceeded, increased tree mortality will naturally reduce BVOC emissions. Altered ecological interactions (e.g. insect outbreaks or altered floral compositions) and increasing pollution can modify BVOC emissions, with unforeseen consequences. However, an intensified wet season could lead to stronger storms (Nelson, Kapos, Adams, Oliveira, & Braun, 1994) and floods (Barichivich et al., 2018), increasing BVOC production associated with root anoxia. Tree mortality associated with storms (Aleixo et al., 2019) have potential implications for atmospheric chemistry because of increased BVOC emission associated with anoxia from floods.

These effects ultimately lead to increased tree mortality (Aleixo et al., 2019; Brando et al., 2019) aggravated by deforestation, and, therefore, to decreased BVOC production due to biomass reduction, which further feeds back on a changing climate by altering ecological interactions and aerosol dynamics. Additionally, the loss of biodiversity (Nobre et al., 2016) caused by climate change (Chapin et al., 2000) and deforestation (Barlow et al., 2007) can alter ecological interactions and associated BVOC emissions.

Agricultural practices, including but not limited to biomass burning, and urbanization are the two main impacts of land-use change affecting Amazonia. Twenty percent of the original forest in the Brazilian Amazonia has been cleared in the last three decades (Bullock, Woodcock, Souza, & Olofsson, 2020; Davidson et al., 2012), particularly from the so-called arc of deforestation in southern and southwestern Amazonia (Leite-Filho et al., 2019; Pöhlker et al., 2019), with a sharply increasing trend during the past several years. Deforestation has implied substantial environmental changes (Davidson et al., 2012) and forest disturbance (Bullock et al., 2020), such as water stress due to shallower roots (Huete et al., 2006) that causes an energy imbalance, loss of biodiversity, changes to carbon storage (Huete et al., 2006) and an overall decrease in BVOC emissions due to the loss of biomass (Scott et al., 2018). Biomass burning also profoundly affects the oxidation pathways of BVOCs and increases emissions of air pollutants (Bulbovas et al., 2014) by clearing land mainly for soy production (Bulbovas, de Souza, de Moraes, Luizão, & Artaxo, 2007), oil palm production (Jardine, Gimenez, et al., 2016) and cattle ranching (Figure 5). Soy crops are very sensitive to tropospheric ozone (Bulbovas et al., 2007), so higher ozone mixing ratios will feed back to more deforestation to counteract decreased soy productivity (Pimentel, 2011).

Increasing urbanization (Richards & VanWey, 2015) and rural development (Nobre et al., 2016) are also the drivers of land-use change in Amazonia. The urban population of the region has increased from about 1 to 11 million in the last 50 years (1960–2010; Medeiros

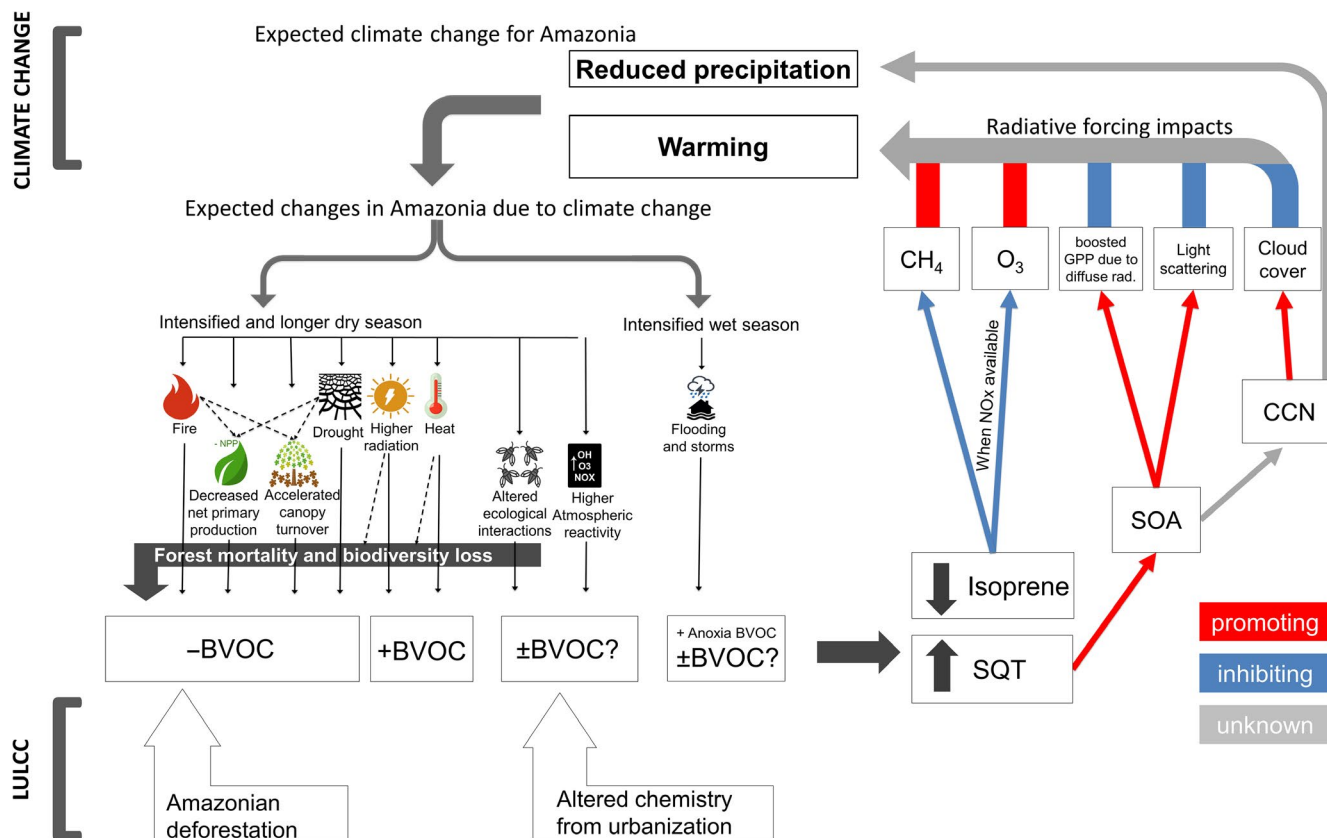


FIGURE 6 Proposed feedback loops for the impacts of climate and land-use changes in Amazonian biogenic volatile organic compounds (BVOCs) and how these impacts will feed back into the system. The dashed arrows represent the situation where threshold limits are reached (i.e. heat can stimulate BVOC emissions until the point where heat is detrimental to plant fitness, thereby decreasing BVOC emissions). Red colour denotes promoting and blue colour denotes inhibiting. Grey arrows indicate inconclusive/unknown effects. LULCC, land use land cover change [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2017). In central Amazonia, the city of Manaus has 2 million inhabitants, and pollution sources include vehicular emissions, refinery operations and electricity generation. Even though anthropogenic emissions are lower than for other regions around the world, Amazonian air chemistry is highly sensitive, amplified by the high solar irradiance and concentrations of water vapour in an environment with plentiful BVOC emissions. NO_x and ozone production are much higher in urban plumes (Kuhn et al., 2010; Trebs et al., 2012; Wei et al., 2019) and have profound impacts on atmospheric chemistry and physics by increasing biogenic SOA production by 60%–200% (Shrivastava et al., 2019) and altering gaseous (Liu et al., 2016) and particle (de Sá et al., 2017) chemical pathways. A programmed change from fuel oil and diesel to natural gas is nevertheless projected to improve urban air quality (Medeiros et al., 2017).

At a global scale, BVOC emissions may increase in a warmer climate (Peñuelas & Staudt, 2010) due to higher plant metabolism and diffusion, but in Amazonia, the effects of climate could increase the emission of stress-related BVOCs and the effects of land-use change could lead to a decrease in BVOCs due to loss in biomass. An increase of BVOCs due to warmer temperatures would lead to more SOA having a cooling impact through the direct light scattering or indirectly by the increase in cloud cover. This would lead to a negative radiative forcing. Additionally, more SOA would lead to more diffuse

radiation, boosting GPP (Rap et al., 2018) and thus the uptake of atmospheric CO₂. On the other hand, an increase in BVOCs would lead to an increase of the CH₄ lifetime. In the presence of sufficient NO_x, an increase in tropospheric ozone could be a consequence resulting in a warming effect. A decrease in BVOC emissions, however, would have opposite effects on the radiative balance. Moreover, the net effects of altered ecological interactions (Niederbacher, Winkler, & Schnitzler, 2015), higher atmospheric reactivity, changes in species composition and increased flooding on BVOC responses remain unknown for Amazonian ecosystems. Unfortunately, there is almost no information about the impact of BVOCs in the Amazonian hydrological cycle, with effects for the rest of the South American continent (Boers et al., 2017; Rocha et al., 2018). Thus, a substantial change in Amazonian BVOC emission may have strong climatic impacts at a regional and even at global levels, but there are large uncertainties in current estimates.

8 | RECENT EVOLUTION OF ISOPRENE EMISSIONS IN AMAZONIA

We investigated the evolution of isoprene fluxes in Amazonia using modelled isoprene emissions from the CAMS-GLOB-BIO

dataset (Granier et al., 2019), and satellite-based estimates (Bauwens et al., 2016) for 2005–2014. The CAMS-GLOB-BIO global dataset is based on the Model of Emissions of Gases and Aerosols from Nature (MEGANv2.10; Guenther et al., 2012) and includes monthly isoprene emissions at $0.5^\circ \times 0.5^\circ$ resolution. The MEGAN model was driven by re-analysed ERA-Interim meteorological fields (Dee et al., 2011). Global annual land cover was provided by the ESA-CCI dataset (Climate Change Initiative of the European Space Agency, ESA, 2017), processed in order to be consistent with plant functional types used in the MEGAN model (see Supporting Information 3). In contrast, for the satellite data we used formaldehyde columns from the OMI satellite sensor and an inverse modelling framework (see Supporting Information 4). Both techniques were used successfully for estimating isoprene fluxes in this region in the past (Barkley et al., 2009; Pacifico et al., 2011). Seasonal and inter-annual variations of the modelled and satellite-based isoprene fluxes over the Amazonian region (5°N – 13°S , 46 – 77°W) are shown in Figure 7. Both approaches display similar magnitudes and seasonal patterns, with slightly higher fluxes for modelled isoprene. The decrease of isoprene

fluxes during the wet season is observed in the complete time series of modelled isoprene (1992–2015; Figure S.I.2). Since biomass burning during the dry season affects the formaldehyde columns, only wet season data are used for the trend calculation, but it has to be noted that both modelled and satellite isoprene fluxes show a decrease for the reported period. The decrease of isoprene fluxes during the wet season can be partly attributed to large and rapid changes in land cover (Acosta Navarro et al., 2014). Even though the rate of deforestation decreased in the period of 2005–2014 (Artaxo et al., 2013), studies point out that drought-related fires may have increased during this period (Aragão et al., 2018). In fact, satellite observations suggest a widespread forest degradation due to deforestation (Bullock et al., 2020).

The modelled isoprene flux indicates an increase of isoprene emissions during the dry season for 1992–2015, with peaking fluxes in El Niño years (1997, 2015; Figure S.I.2). Given that SQTs are temperature-dependent and emitted as a plant response to environmental stresses (Zhao et al., 2017), we have calculated the SQT to isoprene ratio as a proxy of environmental stress (Figure 8). The ratio

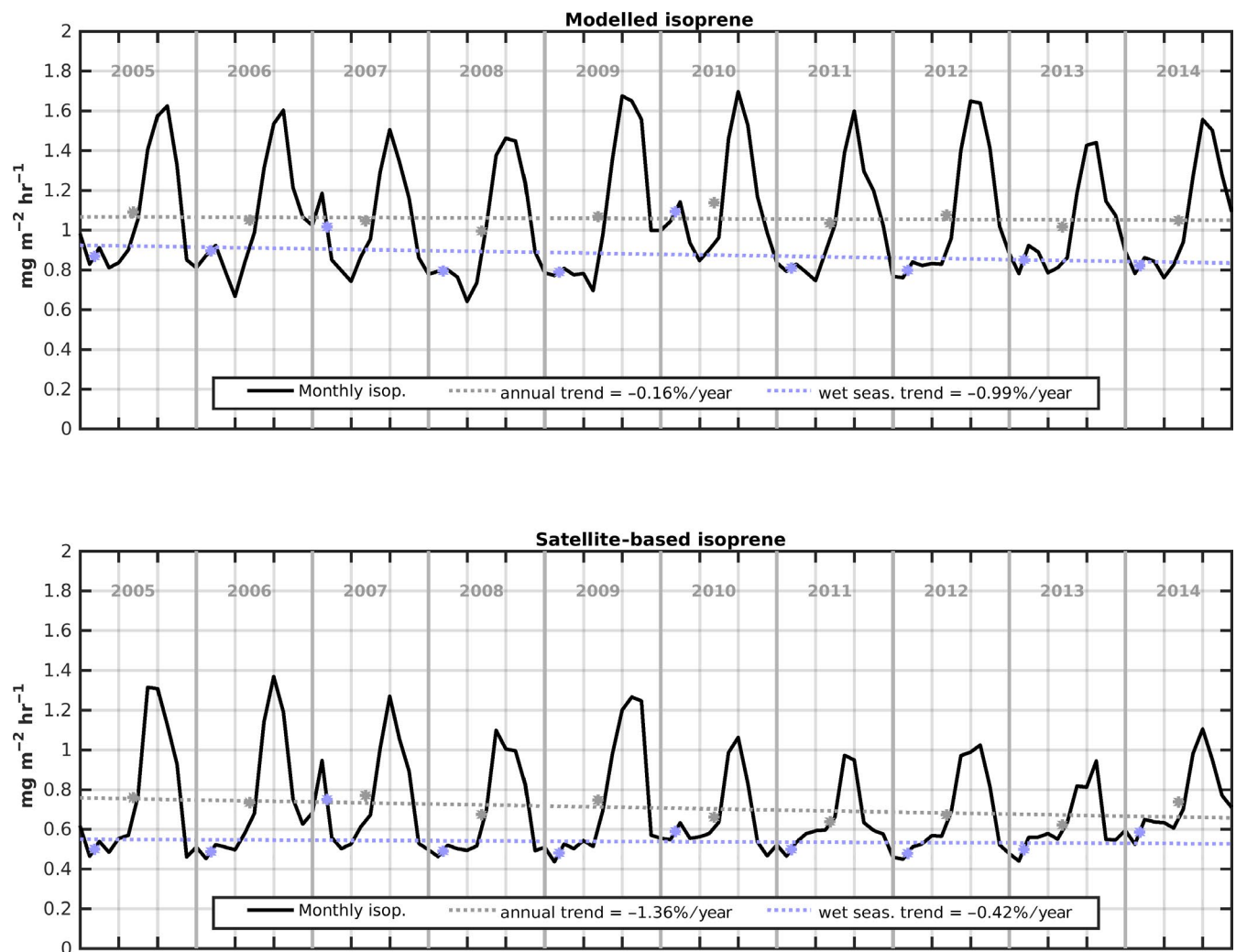


FIGURE 7 Monthly top-down isoprene flux estimates based on global model simulations using MEGAN (top) and based on the OMI satellite formaldehyde columns (bottom) over 2005–2014 averaged over the Amazon region. Grey dots represent yearly averages, whereas the blue dots represent the wet season average [Colour figure can be viewed at wileyonlinelibrary.com]

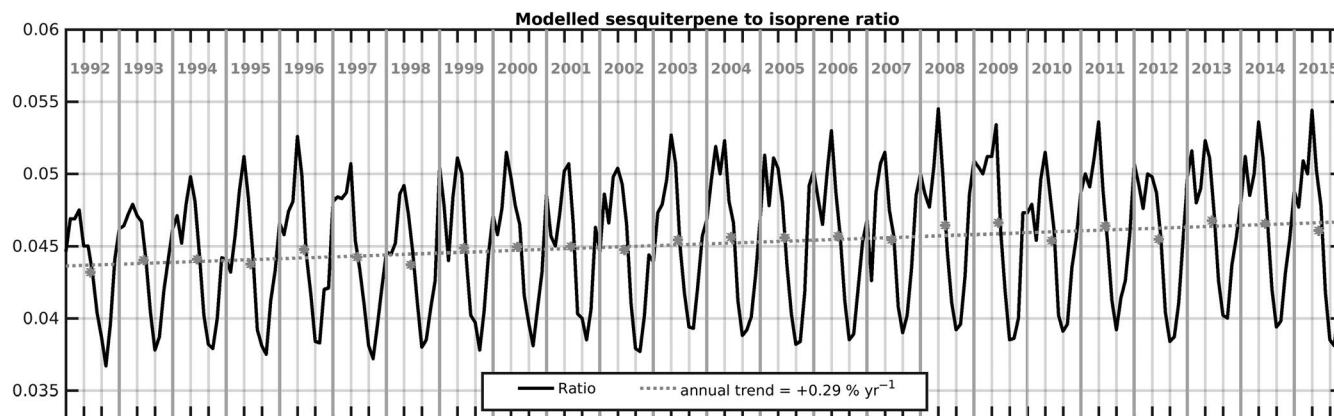


FIGURE 8 Time series of the sesquiterpene to isoprene ratio fluxes from model simulations. Dots represent yearly averages from which the trend is calculated. Grey dots represent yearly averages [Colour figure can be viewed at wileyonlinelibrary.com]

significantly increases over time, suggesting that Amazonian forest is undergoing increased heat stress due to climate warming.

These results underline the combined effect of climate change and land-use change affecting BVOC fluxes. During the dry season, strong environmental stresses to Amazonian vegetation occur at higher intensity and frequency over time. This view is supported by the increasing ratio of SQT to isoprene fluxes. During the wet season, the decrease in isoprene emissions may be partly explained by the rainforest loss due to deforestation, although further analysis is needed to prove this hypothesis.

9 | RESEARCH PRIORITIES

Kesselmeier et al. (2009) identified several research priorities that need to be addressed to better understand BVOC dynamics in Amazonia. However, some of them remain unaddressed even one decade later. Intensive efforts towards integrated investigations of emissions, chemistry, transport and cloud processes, with campaigns such as Brazilian-Air 2010, GOAMAZON (2014–2015), ACRIDICON (2014) and ATTO (2012–present), which comprised observations from tower-based measurements (at TT34, K34, ATTO) and aircraft-based studies (ACRIDICON and GOAMAZON) have been made or planned for the near future (CAFÉ-Brazil 2020). These studies provided essential information, particularly in understanding the fate of emitted isoprene in the atmosphere. Many studies have now addressed a wide range of biogenic VOCs, including oxygenated BVOCs, aromatic compounds, sulphurous compounds and oxidation products (Alves et al., 2016; Bourtsoukidis et al., 2018; Jardine, Chambers, et al., 2015; Jardine, Jardine, et al., 2015; Jardine, Monson, et al., 2011; Jardine, Yáñez Serrano, Arneth, Abrell, Jardine, Artaxo, et al., 2011; Jardine et al., 2014, 2017; Liu et al., 2016; Paralovo et al., 2015; Yáñez-Serrano, Nölscher, et al., 2018; Yáñez-Serrano et al., 2015, 2016; Yee et al., 2018), although new studies should aim to characterize unknown reactive compounds to better understand atmospheric reactivity, particularly in the dry season (Nölscher et al., 2016; Pfannerstill et al., 2018). Progress has been

made in understanding of the impact of BVOCs on oxidant and aerosol distributions (Andreae et al., 2018; de Sá et al., 2017, 2019; Liu et al., 2016; Nölscher et al., 2016; Pfannerstill et al., 2018; Schulz et al., 2018; Shrivastava et al., 2019), the processes controlling the seasonal (Alves et al., 2016, 2018; Wei et al., 2018; Yáñez-Serrano, Fasbender, et al., 2018; Yáñez-Serrano et al., 2015) and spatial (Barkley et al., 2009, 2011; Bauwens et al., 2016; Salazar et al., 2018; Taylor et al., 2018; Taylor, Smith, Slot, & Feeley, 2019) variations of BVOCs, flooding (Bracho-Nunez et al., 2012) and ecological interactions (Salazar et al., 2018). However, more process-based studies are essential, such as those using laboratory and enclosure methods, to understand mechanistically what is happening at foliar surfaces, including phyllospheric processes, BVOC sink processes, relationships between BVOCs and the carbon and water cycles, ecological interactions and the response of BVOCs to climate change and deforestation in Amazonia. Model simulations could thus become more process-based, reducing the uncertainty of predictions. For example, strong efforts are currently being made to understand BVOC variation across plant populations beyond plant functional type, which is too broad to represent variability in Amazonian ecosystems (Taylor et al., 2018).

Understanding how BVOC emissions would affect CCN and rain formation, including rain acidity (Jardine, Yáñez Serrano, Arneth, Abrell, Jardine, Artaxo, et al., 2011), is important as clouds can have an effect on the radiative forcing by reflecting radiation and by increasing diffuse radiation thereby increasing GPP, as well as having impacts on the hydrological cycle (Koren et al., 2012). But the effect of increased flooding, as a response to climate change, must also be understood at an ecosystem level, particularly the role of anoxia BVOCs in CH₄ and CO₂ cycles in flooded ecosystems. More effort is needed to obtain a more regional and long-term vision of BVOCs in Amazonia, which can only be approached with synergistic investigations of different Amazonian ecosystems, to understand the timing and duration of the response dependency of BVOC dynamics. This review demonstrates the necessity of understanding the signals of BVOC feedback loops in response to climate and land-use changes in Amazonia, for which understanding the potential

impacts of the role of BVOCs in ecological interactions is crucial, a subject rarely studied in Amazonia despite its enormous biological productivity and biodiversity. Understanding how these interactions can be modulated by climate change is also critical. Some ecological theories have been proposed to account for hyperdominant species in Amazonia (ter Steege et al., 2013), which study the evolution and distribution of defensive compounds as a function of species composition. For example, *Protium* genus produces large quantities of phenolics, which may increase the colonization of its species (Salazar et al., 2018). This approach may be used to study the ecological interactions of BVOCs in Amazonia. Climate change and pollution increase the reactivity of the Amazonian atmosphere (Nölscher et al., 2016; Pfannerstill et al., 2018; Yáñez-Serrano et al., 2015), but the signals of the BVOC responses in the feedback loops remain unknown. Similarly, the signal of the BVOC response to an intensified wet season remains unknown. The responses of BVOCs to global change in Amazonia, either as a direct response to stress (e.g. increase drought, increase in UVB or nutrient availability) or as an indirect response due to the extinction of BVOC sources (e.g. tree mortality or agricultural expansion), are key research priorities for understanding how Amazonian ecosystems function and how they will be modified in the future. This review suggests that warming and associated drying, combined with the rate of deforestation, deforestation and associated drying is and will be the most determinant in the fate of BVOCs in Amazonia (both for chemistry and physics), impacting the radiative forcing of the atmosphere and the hydrological cycle. Deforestation is a major threat to Amazonia, with >10,000 km² between August 2018 and July 2019, the highest annual loss since 2008 (Barlow, Berenguer, Carmenta, & França, 2020). Even the most optimistic climatic scenarios where forest protection policies are implemented predict substantial deforestation in Amazonia (Pöhlker et al., 2019; Soares-Filho et al., 2006). This trend indicates a major loss of forest biomass, potentially reaching threshold levels with difficult recovery. This loss will affect not only the tropical and extra tropical carbon and water cycles, but also the BVOC exchange between the surface and the atmosphere. Actions such as large-scale forest restoration (Bastin et al., 2019) and the promotion of services (Šimpraga et al., 2019) provided by Amazonian ecosystems may therefore help to mitigate these impacts of deforestation. Human action will thus delineate also the future of BVOCs in Amazonia.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data are available upon request to the corresponding author.

ORCID

Ana M. Yáñez-Serrano  <https://orcid.org/0000-0001-6408-5961>

Eliane G. Alves  <https://orcid.org/0000-0001-5245-1952>

Josep Peñuelas  <https://orcid.org/0000-0002-7215-0150>

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SUPPORTING INFORMATION

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