



# *Ficus* trees with upregulated or downregulated defence did not impact predation on their neighbours in a tropical rainforest

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## Abstract

Trees can emit volatile organic compounds (VOCs) when under attack by herbivores, and these signals can also be detected by natural enemies and neighbouring trees. There is still limited knowledge of intra- and inter-specific communication in diverse habitats. We studied the effects of induced VOC emissions by three *Ficus* species on predation on the focal *Ficus* trees in a lowland tropical rainforest in Papua New Guinea. Further we assessed predation across a phylogenetically diverse set of neighbouring tree species. Two of the focal tree species, *Ficus pachyrrhachis* and *F. hispidioides*, have strong alkaloid-based constitutive defences while the third one, *F. wassa*, is lower in constitutive chemical defences. We experimentally manipulated the jasmonic acid signalling pathway by spraying the focal individuals with either methyl jasmonate (MeJA) or diethylthiocarbamic acid (DIECA). These treatments induce increases or decreases in VOC emissions, respectively. We tested the possible effects of VOC emissions on each focal *Ficus* tree and two of its neighbours by measuring the predation rate of plasticine caterpillars. We found that predation increased after the MeJA application in only one focal tree species, *F. wassa*, while the DIECA application had no effect on any of the three focal species. Further, we did not detect an effect of our treatments on predation rates across neighbouring trees. Neither the phylogenetic distance of the neighbouring tree from the focal tree nor the physical distance from the focal tree had any effect on predation rates for any of the three focal *Ficus* species. These results suggest that even congeneric tree species vary in their response to the MeJA and DIECA treatment and subsequent response to VOC emissions by predators. Our results also suggest that MeJA effects did not spill over to neighbouring trees in highly diverse tropical rainforest vegetation.

**Keywords** Diethylthiocarbamic acid · Herbivory · Methyl jasmonate · Plant-to-plant communication · Predation · Olfaction · Volatile organic compounds

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## Introduction

Since 1980s, it has become evident that there is both intra- and inter-specific communication among plants, and that animals can detect these cues (Price et al. 1980; Dicke et al. 2003). Plants under herbivore attack alter their volatile profile which can subsequently become attractive to natural enemies, so-called “cries for help” (Turlings et al. 1990). These signals can be also used for the upregulation of defence in other plants (Heil 2014; Karban et al. 2014; Ninkovic et al. 2021). This idea of plant–plant communication has transitioned from scepticism (Fowler and Lawton 1985) via tentative acceptance (Dicke and Bruin 2001) to widespread acceptance (Dicke et al. 2003; Heil and Karban 2010; Ninkovic et al. 2021). Plants can communicate through the air (Farmer and Ryan 1990; Karban et al. 2014)

and below-ground root and mycorrhizal networks (van Dam and Bouwmeester 2016).

The volatile organic compounds (VOCs) released by plants can be constitutive (i.e. always present) or induced by herbivore damage (i.e. activated when needed; reviewed by Orians 2005; Ninkovic et al. 2021). The induced VOCs can deter herbivores (De Moraes et al. 2001), attract their predators and parasitoids (Kessler and Baldwin 2001; Mrazova et al. 2019), convey information relating to herbivore attack to other parts of the same plant (Frost et al. 2007; Li and Blande 2017), and prime neighbouring plants against herbivore attack (Karban et al. 2014). Distress signals from a neighbouring plant can prime recipient plants to upregulate their defences in preparation for future attacks (Hilker and Schmülling 2019).

It has been hypothesized that there is a trade-off between constitutive and induced defences. Plants exposed to high and/or predictable herbivore pressure invest in constitutive defences while plants in environments with low or unpredictable herbivory transfer resources to induced defences (Karban and Myers 1989; but see Pellissier et al. 2016). However, such trade-offs have not been always confirmed empirically (Koricheva et al. 2004; Agrawal and Hastings 2019). Rather than simple univariate trade-offs, suites of complementary traits tend to form defensive syndromes (Agrawal and Fishbein 2006).

Most studies have focused on communication between conspecific plants (e.g. Dolch and Tscharrntke 2000; Karban et al. 2013; Pearse et al. 2013; Kalske et al. 2019), although some studies demonstrated also inter-specific plant communication (Oudejans and Bruin 1995; Karban et al. 2000). Such communication may be more efficient between plants with similar defensive chemistry; more likely among close relatives (Karban et al. 2013). So far, thousands of different plant VOCs have been found (Knudsen et al. 2006). Some of them are universal, such as isoprene, linalool, (*E*)- $\beta$ -ocimene, (*E*)- $\beta$ -caryophyllene, (*E,E*)- $\alpha$ -farnesene and indole. These could facilitate communication even between non-related plants, and may be used by generalist predators to find their prey and underpin interactions among unrelated plants: ‘the mutual benefit hypothesis’ (Meents and Mithöfer 2020, and references therein).

Community diversity can greatly influence intra- and inter-specific communication. Phylogenetically distant plant species may rely on different VOCs in their inter-individual communication. Thus, it is possible that not all communication is detected by all plant species (Loreto and D’Auria 2022). And yet, we know very little about how communication is undertaken in extremely diverse habitats, such as tropical forests. For example, the volatile chemical diversity of the hyper-diverse genus *Piper* in Costa Rica affected herbivory, but in different ways for specialist and generalist herbivores (Salazar et al. 2016). Plant species diversity and

vegetation structure make signalling through VOCs more complex in forests (Douma et al. 2019; Zu et al. 2020). Studies of plant communication are rare in diverse tropical forests, indeed most of the early studies involved temperate tree species in forests or experimental plots (Dolch and Tscharrntke 2000; Pearse et al. 2013). More complex tropical environments, where the species diversity is higher and population density of individual species is lower, may lead to more general communication. Specialist communication using narrowly targeted signals may be lost in the chemical melee (Townsend et al. 2008).

The production of VOCs is partly mediated by the jasmonic acid signalling pathway, especially when damage is inflicted by chewing herbivores (Thaler et al. 1996). The effects of chewing damage can be also stimulated by derivatives of jasmonic acid (Degenhart and Lincoln 2006). These include methyl jasmonate (MeJA), a substance that has been widely used in ecological studies focusing on defence induction in plants (including trees) and its effects on higher trophic levels (Zhang et al. 2009; Mäntylä et al. 2014; Mrazova and Sam 2018, 2019). Upregulation of plant defensive VOCs with MeJA can also spill to neighbouring plants and upregulate their VOC production (Farmer and Ryan 1990; Tang et al. 2013). In contrast, some chemicals, such as diethylthiocarbamic acid (DIECA), can inhibit the jasmonic acid pathway and possibly lead to downregulation of the defences that depend on this pathway (Farmer et al. 1994). Applying DIECA can allow manipulation of VOCs and thus test hypotheses related to chemical communication in plants (Bruinsma et al. 2010).

In this study, we manipulated VOC signalling in order to study the effect on focal trees as well as their neighbouring trees. Specifically, we tested whether the efficacy of inter-specific signalling is related to phylogenetic distance between emitter and receiver. We used *Ficus* trees growing in a highly diverse lowland rainforest in Papua New Guinea for our experiments. The forest provided a wide range of phylogenetically similarity among focal and neighbouring trees. We focused on *F. wassa* (low in constitutive defences), and *F. pachyrrhachis* and *F. hispidooides* (high in constitutive defences such as alkaloid diversity and protease activity; Volf et al. 2018).

## Material and methods

### Study area and tree species

We conducted experiments in tropical lowland primary and secondary forests in Baitabag, Madang province, Papua New Guinea (145° 47" E, 5° 08" S, 150 m asl.) from April to May 2018 during the transition between wet and dry seasons. Primary forest is represented by the Kau Wildlife Conservation

Area, comprising ~ 300 ha of undisturbed forest. The surrounding secondary forest is regrowth in fallow areas following swidden agriculture. We used secondary vegetation of approximately 4 years in age, with a closed canopy at 10 m and higher.

The pantropical genus *Ficus* includes over 750 species, of which over 150 are found in Papua New Guinea (Berg and Corner 2005; Cruaud et al. 2012). Individuals of *Ficus* are numerically abundant in both the primary and secondary lowland forests of Papua New Guinea (Whitfield et al. 2012), and they harbour diverse insect communities (Basset and Novotny 1999; Novotny et al. 2010).

### Study set-up and hypotheses

We approximated predation pressure using plasticine caterpillars (Mäntylä et al. 2008a; Mrazova and Sam 2019). First, we tested if there were differences in (1) VOC emissions and (2) predator attraction among *Ficus* species that differed in their levels of constitutive defence. Furthermore, we hypothesized that predation rate would be higher in trees adjacent to focal *Ficus* trees, (3) if the focal *Ficus* tree was induced with a MeJA treatment, (4) if the focal *Ficus* tree and neighbouring tree were closely related and (5) if the focal *Ficus* tree and neighbouring tree were growing in close proximity (ca. 2 m), no effect was expected in distant (ca. 5 m) trees.

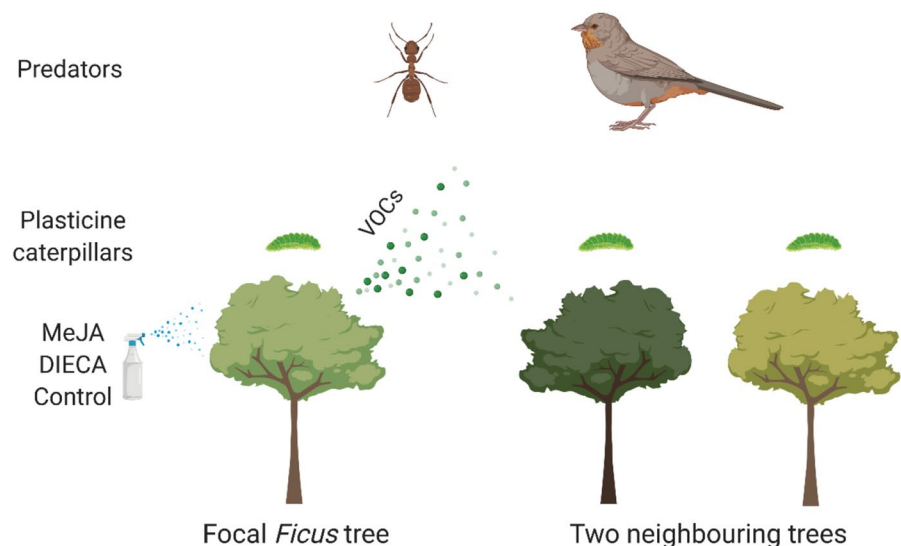
We used three focal species, *Ficus wassa* in the primary forest and *F. pachyrrhachis* and *F. hispidioides* in the secondary forest (Fig. 1). We selected 25 individuals from each of the focal *Ficus* species, at least 3 m from one another. Further, we selected two neighbouring trees of any species for each focal *Ficus* tree (Fig. 1), at ca. 2 m and 5 m distance from the focal tree (Hagiwara et al. 2021). The actual distances of selected neighbouring trees were  $2.9 \pm 1.0$  m (mean  $\pm$  SD) and  $5.5 \pm 1.0$  m from the focal tree. These

two neighbouring trees were always in the same compass direction from the focal *Ficus* tree in order to reduce any among-tree variation caused by wind direction. However, if two focal *Ficus* trees were growing near each other (3–5 m), then their neighbouring trees were selected to be in opposite directions to keep the experimental units as independent as possible. There were never any large trees or any other large obstacles between a focal *Ficus* tree and its two neighbouring trees. There were 73 different species of neighbouring trees in total (Suppl. Fig. 1). We tried to select the focal and neighbouring trees of similar size, between 2.5 and 3.5 m in height and with stem diameter 1.5–2.5 cm (Suppl. Table 1).

### Predation measurement

We placed five plasticine caterpillars on each focal *Ficus* and each of its neighbouring trees to measure the predation rates (Mäntylä et al. 2008a; Roslin et al. 2017). We report the predation rate as the proportion of damaged caterpillars inspected on that tree during the whole experiment. All caterpillars were checked every 2 days, in total six times, and replaced with a new caterpillar if damaged. Thus, the number of caterpillars inspected on each tree during the study was always 30. We made the caterpillars from green, non-drying soft plasticine (Hobby Time®, GLOREX GmbH, Rheinfelder, Germany). They were ca. 2.5 cm long and 0.5 cm in diameter. We made each caterpillar around a thin, brown metal wire, used to attach the caterpillar to branches or leaf petioles (Mäntylä et al. 2008a). In case of replacement, we placed the new caterpillar on the same tree but on a different branch or leaf. A plasticine caterpillar was determined as damaged by predators if it had some marks that were consistent with damage caused by local predators, e.g. birds, ants, spiders (Sam et al. 2014) that could not be explained otherwise (e.g. not a scratch by fingernails

**Fig. 1** Experimental setup of focal *Ficus* tree and two neighbouring trees (ca. 2 and 5 m distance from focal tree). The focal *Ficus* tree was treated to increase VOC emission (MeJA), to decrease VOC emission (DIECA) or untreated as control. The predation rate by arthropods and vertebrates was measured on each tree using artificial plasticine caterpillars



or a nearby branch). We excluded the plasticine caterpillars that had marks caused by non-carnivorous animals. Plasticine caterpillars that had disappeared were excluded from the data ( $n = 5$ ). The potential maximum number of caterpillars inspected during this experiment was 3 tree species  $\times$  25 trees  $\times$  5 caterpillars  $\times$  6 inspections = 2250 for the focal and 4500 for the neighbouring trees. Four neighbouring trees were mistakenly cut down by local villagers during the experiment, so these trees have data for only part of the experiment. One neighbouring tree of *F. hispidioides* (*Macaranga* sp.) was invaded by ants that damaged almost all plasticine caterpillars, and thus it was removed from the dataset as an outlier.

### Predators of plasticine caterpillars

We did bird point counts in both primary and secondary forests. We divided the primary forest into 5 blocks and secondary forest into 6 blocks. The radius of each block was 50 m, and the blocks were not overlapping. The observations were conducted from the midpoint of each block for 15 min during the experiment in early morning when it was not raining. We did not survey arthropod predators, but various species of ant were extremely abundant (Klimeš et al. 2015), especially in the secondary forest.

### Experimental treatments

We used controls and four different treatments for the focal *Ficus* trees, applying: (1) 30 mM MeJA (Sigma-Aldrich); 0.70% MeJA, 0.1% Tween20 (Sigma-Aldrich), 99.20% water, (2) 15 mM MeJA; 0.35% MeJA, 0.1% Tween20, 99.55% water, (3) 50 mM DIECA (Sigma-Aldrich) on 6 leaves, and (4) 50 mM DIECA on 3 leaves. The control trees were not sprayed with any solution. The two levels of MeJA and DIECA were chosen to test optimum doses. We sprayed 20 ml of MeJA solution on leaves of the whole tree every 2 days. We pipetted 1 ml of the DIECA solution per leaf after first puncturing the surface of the leaf with sharp tweezers within ca. 2 cm<sup>2</sup> area, using different leaves for each round of DIECA treatment. We applied the DIECA treatment every 6 days. The MeJA and DIECA concentrations and application schedules were based on earlier studies (Cooper and Rieske 2011; Saavedra and Amo 2018). Both MeJA and DIECA treatments started simultaneously with the plasticine caterpillar predation surveys.

### VOC collection

We collected the emitted VOCs from the focal *Ficus* trees before and after the experiment in order to confirm and quantify induction of possible indirect defences. We passively sampled volatiles from one branch of each focal *Ficus*

tree using polydimethylsiloxane (PDMS) tubes (Carl Roth GmbH, Karlsruhe, Germany; Kallenbach et al. 2014). We placed two cleaned 1.5 cm PDMS cuttings (technical replicates) on a stainless-steel wire, attached it to the measured branch and enclosed it in a PET bag (Toppits® Bratschlauch, Melitta, Minden, Germany). There were 1–7 leaves enclosed in each bag, depending on leaf size. The volatiles were passively adsorbed to the PDMS tubes from the headspace for 24 h.

We used gas chromatography to quantify the sampled VOCs. The PDMS cuttings were analysed by a thermal desorption–gas chromatograph–mass spectrometer (TD–GC–MS) consisting of a thermodesorption unit (MARKES, Unity 2, Llantrisant, United Kingdom) equipped with an autosampler (MARKES, Ultra 50/50). PDMS cuttings were transferred to empty stainless-steel tubes (MARKES) and desorbed with helium as carrier gas and a flow path temperature of 150 °C using the following conditions: dry purge 5 min at 20 ml/min, pre purge 2 min at 20 ml/min, desorption 8 min at 200 °C with 20 ml/min, pre trap fire purge 1 min at 30 ml/min, trap heated to 300 °C and hold for 4 min. The VOCs were separated on a gas chromatograph (Bruker, GC-456, Bremen, Germany) connected to a triple-quad mass spectrometer (Bruker, SCION) equipped with DB-WAX column: (30 m  $\times$  0.25 mm inner diameter  $\times$  0.25  $\mu$ m film thickness, Restek). The temperature program was the following: 60 °C (hold 2 min), 30 °C/min to 150 °C, 10 °C/min to 200 °C and 30 °C/min to 230 °C (hold 5 min). Helium was used as carrier gas at a constant flow rate of 1 ml/min. MS conditions were set at a 40 °C manifold, 240 °C transfer line and 220 °C for the ion source. The scan-range was 33–500 m/z for a full scan and scan-time was 250 ms. We selected the most prominent peaks in the chromatograms (signal to noise ratio > 10). Peaks that were also present in air blanks were regarded as systemic contamination and were excluded from further analysis. VOCs were classified at the compound class level according to their mass spectra. The peak areas of these compounds were calculated using the Bruker Workstation software (v8.0.1).

### Estimating the phylogeny of experimental trees

To estimate the phylogenetic relationships between focal *Ficus* and neighbouring tree species, we used the R package “S.PhyloMaker” (Qian and Jin 2016). We used the updated phylogeny and node ages derived from a sequence-based study by Zanne et al. (2014) as a Megatree. Our tree species were placed within the Megatree where possible and placed to family where not possible. This procedure generates three alternative topologies which differ with respect to the resolution of unplaced taxa. We selected the phylogeny derived from “Scenario 3” as this has been shown to be robust to uncertainty at the higher taxonomic level (Qian

and Jin 2016; Suppl. Fig. 1). Due to the identity of the study species and richness of the clade, the relationship between *Ficus* species was constrained to follow Cruaud et al. (2012).

## Statistical analyses

To assess the effect of all the variables (focal *Ficus* tree species, treatment, total VOC emission, VOC composition, predation rate of caterpillars, neighbouring tree size, phylogenetic and physical distance) on the predation rate of plasticine caterpillars on neighbouring trees, we built a series of generalized linear mixed models (GLMMs; R package “lme4”; Bates et al. 2015). Given that the tree species were in different habitats, predation rates were not directly comparable among them. Thus, we conducted the analyses separately for each focal *Ficus* tree species. We used a binomial distribution with logit link function, with the predation rate of plasticine caterpillars as the response variable. For all models, we used the individual focal *Ficus* tree as a random factor, to account for the blocked design of our study. We used the same block structure as in the bird point counts (5 blocks in primary forest and 6 in secondary forest) in all analyses as a random variable to account for the possible different microclimates inside the forests. The analysed variability of predation rate between the blocks was minimal. We grouped the predictor variables into three classes, based on their ecological meaning: (A) focal *Ficus* tree variables: treatment, VOC composition (we used the first two axes of a principal components analysis of the standardized abundances of the different VOCs present in each *Ficus* species), predation rate of plasticine caterpillars; (B) neighbouring tree variable: tree size measured as the first axis of a PCA on the height of the tree and stem width; (C) variables related to the relationship between the focal and neighbouring tree: phylogenetic distance (square-root transformed), and physical distance in meters.

For each of these variable groups, we conducted model selection to test which variables drive predation rates in each focal *Ficus* species. We compared models using the corrected Akaike information criterion (AICc; Burnham and Anderson 2002). For each group, we included models with all possible combinations of variables, without considering interactions. These models were also compared with a null model including only a fixed intercept and the random factor. We did these analyses separately for all predated plasticine caterpillars, and for caterpillars predated by birds and by ants. There were some differences in the predation rates by birds or ants between the tree species (Suppl. Table 2) but there were no differences in the results of the model selections, so we will here only report results of the analyses of all predated caterpillars. All analyses were done with R (version 3.6.3; R Core Team 2020).

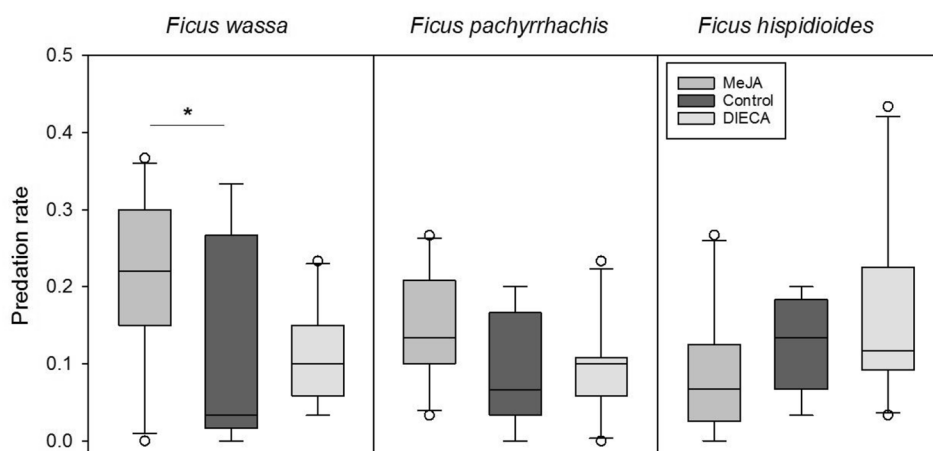
## Results

There were no differences among the focal *Ficus* trees in terms of predation rate of plasticine caterpillars between the high and low MeJA [high:  $15.0 \pm 7.5\%$  (*mean*  $\pm$  *SD*); low:  $14.9 \pm 12.0\%$ ;  $S = -1$ ,  $p = 0.97$ ], or high and low DIECA (high:  $12.4 \pm 10.2\%$ ; low:  $12.2 \pm 8.1\%$ ;  $S = -4$ ,  $p = 0.81$ ) treatments. Due to a lack of significant difference between ‘high MeJA’ and ‘low MeJA’ those treatments are henceforth combined as ‘MeJA’, and similarly ‘high DIECA’ and ‘low DIECA’ are combined as ‘DIECA’.

In focal *Ficus* trees, the treatments had an effect on the predation rate of plasticine caterpillars only in one species: *F. wassa*, where the predation rate was significantly higher in MeJA treated trees than in control trees ( $S = 18.5$ ,  $p = 0.031$ ). There was no difference between control and DIECA treated trees ( $S = 0$ ,  $p = 1.00$ ). In *F. pachyrrhachis* and *F. hispidioides* there were no differences between the treatments (Fig. 2).

During this experiment, we checked a total of 2246 plasticine caterpillars across the focal *Ficus* trees and 4429 plasticine caterpillars across neighbouring trees. In total, 296 (13.2%) caterpillars on the focal *Ficus* trees were predated and 449 (10.1%) on the neighbouring trees. There were differences in the predation rate of the plasticine caterpillars between the focal *Ficus* species (*F. wassa*  $15.2 \pm 1.5\%$ ; *F. pachyrrhachis*  $11.6 \pm 1.0\%$ ; *F. hispidioides*  $13.1 \pm 1.4\%$ ; *mean*  $\pm$  *SE*) as well as their neighbouring trees (*F. wassa*  $12.3 \pm 1.2\%$ ; *F. pachyrrhachis*  $8.7 \pm 0.9\%$ ; *F. hispidioides*  $9.5 \pm 1.1\%$ ; *mean*  $\pm$  *SE*).

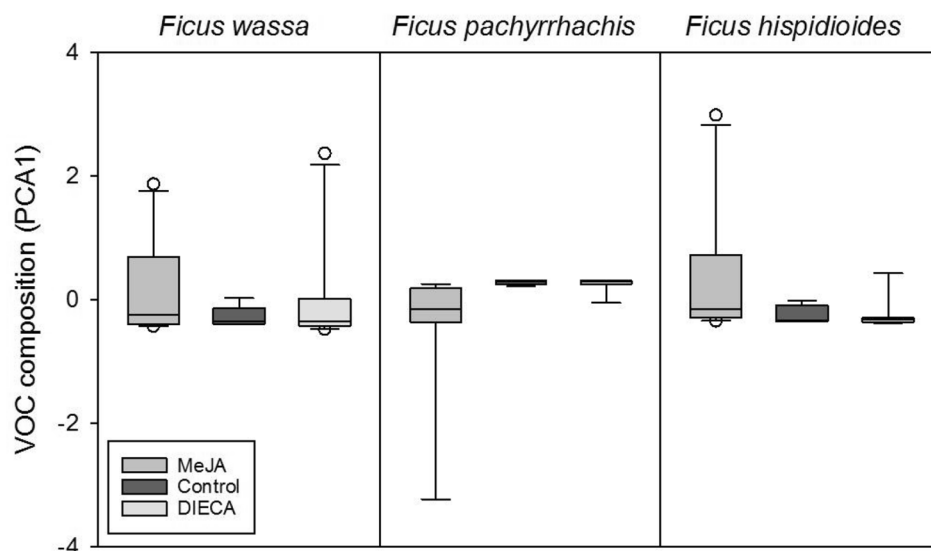
We classified the found VOCs as terpenoids; 12 from *F. wassa* (compound codes: W01–W12), 14 from *F. pachyrrhachis* (P01–P14), and 14 from *F. hispidioides* (H01–H14). Most of the VOCs we recorded in our samples were sesquiterpenes. We also recorded some monoterpenes, such as eucalyptol emitted by *F. pachyrrhachis* (P14) and *F. hispidioides* (H14). The VOC emissions before the experiment showed extensive baseline differences among individuals of the same species (Suppl. Fig. 2). When comparing the baseline and post-treatment changes in VOC emissions, we can see that the MeJA treatment seemed to upregulate the emission of at least some VOCs (such as W08, W10, P08, P10 and H12), while the DIECA treatment did not differ from the control treatment (Suppl. Fig. 3). For further analyses of this study we used post-treatment VOCs as these emissions represent better the amount and identity of VOCs available to predators. There were no differences between the treatments in the VOC composition (the first PCA axis) in any of the focal *Ficus* species (Fig. 3). The VOC composition also did not affect the predation rate in neighbouring trees, except in *F. pachyrrhachis* where we found a positive trend between the



**Fig. 2** The predation rate of artificial plasticine caterpillars in the focal *Ficus* trees, divided by treatment. The box-plot shows: median, 25th and 75th percentiles (box), 10th and 90th percentiles (whiskers), and outliers (circles). Wilcoxon signed rank tests: *F. wassa*; MeJA

vs. control  $S=18.5$ ,  $p=0.031$ , control vs. DIECA  $S=0$ ,  $p=1.00$ ; *F. pachyrrhachis*; MeJA vs. control  $S=14.5$ ,  $p=0.094$ , control vs. DIECA  $S=0$ ,  $p=1.00$ ; *F. hispidooides*; MeJA vs. control  $S=-10.5$ ,  $p=0.31$ , control vs. DIECA  $S=-10.5$ ,  $p=0.33$

**Fig. 3** The VOC composition (the first PCA axis) in the focal *Ficus* trees, divided by treatment. The box-plot shows: median, 25th and 75th percentiles (box), 10th and 90th percentiles (whiskers), and outliers (circles). Paired  $t$ -tests: *F. wassa*; MeJA vs. control  $t=1.73$ ,  $p=0.118$ , DIECA vs. control  $t=-1.02$ ,  $p=0.336$ ; *F. pachyrrhachis*; MeJA vs. control  $t=-1.81$ ,  $p=0.107$ , DIECA vs. control  $t=0.68$ ,  $p=0.514$ ; *F. hispidooides*; MeJA vs. control  $t=1.78$ ,  $p=0.109$ , DIECA vs. control  $t=0.24$ ,  $p=0.820$



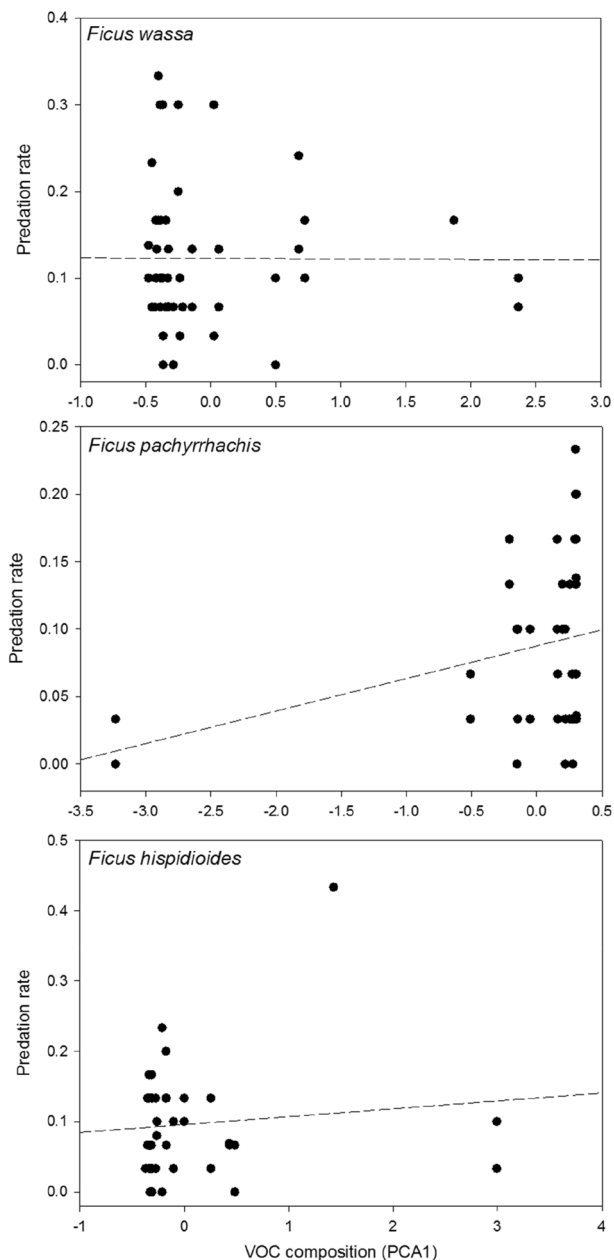
predation rate and VOC emissions (*F. wassa*:  $r=-0.0057$ ,  $p=0.97$ ; *F. pachyrrhachis*:  $r=0.28$ ,  $p=0.058$ ; *F. hispidooides*:  $r=0.10$ ,  $p=0.49$ ; Fig. 4).

Based on AICc model selection, the predation rate of plasticine caterpillars on the neighbouring trees was not affected by any of the measured focal tree variables, neighbouring tree, or the distances between these two trees (Table 1). The only exception was with *F. pachyrrhachis* where the predation rate on its neighbouring trees was higher in smaller neighbouring trees (Table 1). The treatment of the focal tree also did not have an effect (Fig. 5).

When considering individual VOCs emitted after the treatments, there were couple of potentially interesting results. In focal *F. wassa* trees, there was a significant

positive correlation between emission of one compound (W02) and predation rate by birds ( $r=0.43$ ,  $p=0.032$ ). Additionally, in the neighbouring trees of *F. pachyrrhachis* there was a significant negative correlation of emission of four different VOCs and predation rate of caterpillars (P02:  $r=-0.37$ ,  $p=0.013$ ; P03:  $r=-0.42$ ,  $p=0.0038$ ; P08:  $r=-0.31$ ,  $p=0.034$ ; P09:  $r=-0.40$ ,  $p=0.0059$ ).

In the bird point counts, we observed a total of 35 species and 81 individuals of insectivorous birds in the primary forest. In the secondary forest, these numbers were 27 and 93, respectively. In the primary forest from one block, we observed  $11.8 \pm 2.3$  (mean  $\pm$  SD) species and  $15.4 \pm 3.7$  individuals, and in the secondary forest  $10.3 \pm 1.7$  species and  $15.0 \pm 3.1$  individuals of insectivorous birds.



**Fig. 4** Relationship between the VOC composition (first PCA axis) from the focal *Ficus* tree and the predation rate of plasticine caterpillars on the neighbouring trees. (Pearson correlation: *F. wassa*:  $r = -0.0057$ ,  $p = 0.97$ ; *F. pachyrrhachis*:  $r = 0.28$ ,  $p = 0.058$ ; *F. hispidioides*:  $r = 0.10$ ,  $p = 0.49$ )

## Discussion

Here, we studied up and downregulation of defences in focal *Ficus* trees and evaluated if those had impact on predation of plasticine caterpillars on the focal or neighbouring trees. There were large inter- and intra-specific differences among the focal *Ficus* trees in the VOCs they emitted, both in number of compounds and emission level. This large variability

likely masked the possible effects of our treatments. Only in *F. wassa* was the predation rate of plasticine caterpillars higher in MeJA treated trees than in control trees. The treatments with MeJA and DIECA on the focal *Ficus* trees had no significant effects on the predation rate in the neighbouring trees and none of the variables measured here affected the predation rate. Our study design was not optimal, as *F. wassa* grows in primary forest, and *F. pachyrrhachis* and *F. hispidioides* in secondary forest. Thus, we cannot separate the effects of treatments and habitat between the focal *Ficus* species. We discuss the possible reasons for the lack of significant trends in this study.

*F. wassa* emitted a lower amount of VOCs, and also fewer individual compounds, than *F. pachyrrhachis* and *F. hispidioides* but still attracted more predators to both itself and its neighbours. It could also be expected *F. wassa* to rely more on induced defences, such as VOCs, than the other two *Ficus* species, because it has lower level of constitutive defence (Volf et al. 2018), even though the trade-off between constitutive and induced defence is not straightforward (Koricheva et al. 2004; Moreira et al. 2014). One explanation for the differences between *Ficus* species is that the amount of VOCs does not necessarily reflect the composition of the VOC blend and content of the VOCs attractive to predators (Steidle and van Loon 2003). Earlier studies have found that predation rate by birds is higher in trees emitting more specific VOCs, such as (*E*)-DMNT,  $\beta$ -ocimene and linalool (Mäntylä et al. 2008a) or  $\alpha$ -pinene (Mrazova and Sam 2018). We found that one compound (W02) possibly increased the bird predation rate in focal *F. wassa* trees, which would support the theory that individual VOCs are more important to insectivorous birds than total amount of VOC emissions. In contrast, we found that four VOCs emitted by *F. pachyrrhachis* (P02, P03, P08 and P09) seemed to deter predators from neighbouring trees. Ants and other arthropods are important predators in tropical forests while themselves being consumed by birds. These results perhaps hint at the complexity of trophic interactions and intraguild predation in this forest. We would need additional experiments to illuminate these tactics and use of VOC cues important for different predator groups.

Habitat identity and predation pressure by birds may have played an important role. While *F. wassa* grew in primary forest, the other two *Ficus* species were restricted to secondary forest in this study. In disturbed tropical forests, the bird populations are usually smaller than in undisturbed forests which influences the predation rate of herbivorous arthropods (Sam et al. 2014; Morante-Filho et al. 2016). In the bird point counts conducted during this experiment there were no pronounced differences in the number of insectivorous species or individual birds observed in the two forests. This lack of clear difference between the two forest types could be attributed to the fact that the disturbed secondary forest

**Table 1** Three separate AICc models analyse different sets of variables for each of the three focal *Ficus* species to explain the predation rate of plasticine caterpillars on neighbouring trees: (A) focal *Ficus* tree: treatment (MeJA, DIECA or control), VOC composition (the first two axes of a principal components analysis of the stand-

ardized abundances of the different VOCs present in each *Ficus* species), predation rate of plasticine caterpillars; (B) neighbouring tree: PCA of the height of the tree and stem width = tree size; (C) distances between the focal and neighbouring tree: phylogenetic distance in square root millions of years, physical distance in meters

<i>Ficus wassa</i>			<i>Ficus pachyrrhachis</i>			<i>Ficus hispidooides</i>		
<b>A. Focal tree</b>			<b>A. Focal tree</b>			<b>A. Focal tree</b>		
null model	<b>0.0</b>	<b>3</b>	null model	<b>0.0</b>	<b>3</b>	null model	<b>0.0</b>	<b>3</b>
treatment	2.3	5	treatment + VOC composition	3.7	7	treatment	<b>1.6</b>	<b>5</b>
treatment + predation rate	3.4	6	treatment	4.2	5	treatment + predation rate	2.9	6
treatment + VOC composition	7.0	7	treatment + predation rate + VOC composition	5.5	8	treatment + VOC composition	4.7	7
treatment + predation rate + VOC composition	8.4	8	treatment + predation rate	6.8	6	treatment + predation rate + VOC composition	6.8	6
<b>B. Neighbouring tree</b>			<b>B. Neighbouring tree</b>			<b>B. Neighbouring tree</b>		
null model	<b>0.0</b>	<b>3</b>	tree size	<b>0.0</b>	<b>4</b>	null model	<b>0.0</b>	<b>3</b>
tree size	<b>0.7</b>	<b>4</b>	null model	3.1	3	tree size	2.1	4
<b>C. Distances</b>			<b>C. Distances</b>			<b>C. Distances</b>		
null model	<b>0.0</b>	<b>3</b>	null model	<b>0.0</b>	<b>3</b>	phylogeny	<b>0.0</b>	<b>4</b>
phylogeny	<b>1.4</b>	<b>4</b>	phylogeny	<b>0.1</b>	<b>4</b>	null model	<b>0.3</b>	<b>3</b>
physical	<b>2.0</b>	<b>4</b>	physical	<b>2.0</b>	<b>4</b>	phylogeny + physical	<b>0.9</b>	<b>5</b>
phylogeny + physical	3.5	5	phylogeny + physical	2.5	5	physical	<b>0.9</b>	<b>4</b>

The best models and models within 2  $\Delta$ AICc of the best models are in bold

was right next to the much larger undisturbed primary forest. Birds resident to primary forest could also easily visit the secondary forest, and vice versa. But the predation rate by birds was at least three times higher in the primary forest than in the secondary forest, so the primary forest seemed to be a preferred habitat for many bird species responsible for damaging the plasticine caterpillars. With new DNA methods it would be interesting in the future to identify the exact species of the predators of plasticine caterpillars (Röbner et al. 2020).

Sesquiterpenes and monoterpenes have been shown to serve as cues to natural enemies (Mäntylä et al. 2008a; Dudareva et al. 2013; Mrazova and Sam 2018; Volf et al. 2021). Chemical diversity, including emission of constitutive and induced VOCs, of tropical trees has been shown to be extensive, and this also affects the herbivores and their predators (Proffit et al. 2007; Salazar et al. 2016). Our results illustrate that the ecological relevance of indirect defences, such as VOCs, is strongly dependent on factors affecting the abundance of natural enemies and the physical structure and accessibility of the habitat. Our study showed how extensive the differences in VOC emission can be among individual trees, and this would also require the potential predators of herbivores to learn the role of various compounds (Sam et al. 2021) or necessitate the evolution of signal receptors (Schultz 2002). VOCs are also not the only cues predators can use to locate insect-rich plants. For example, predators

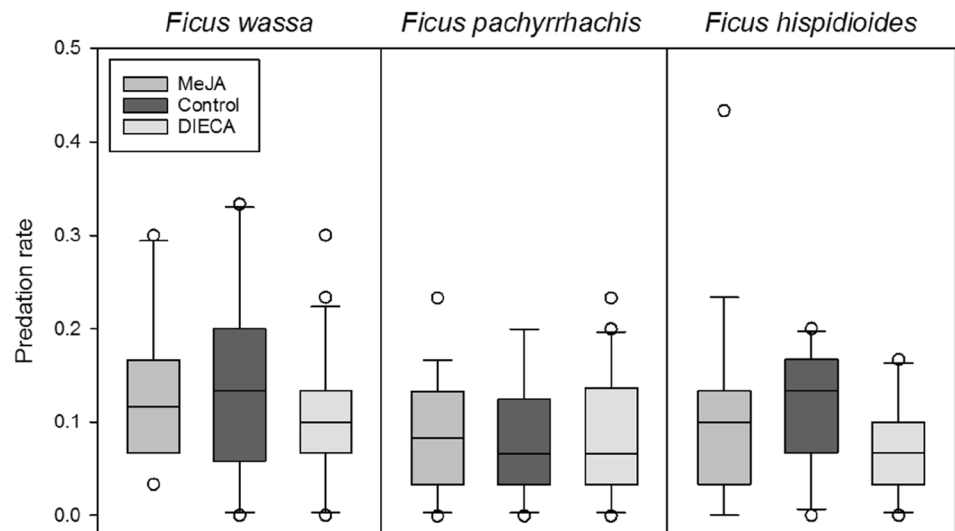
using visual cues can be attracted by changes in the reflectance of leaves in damaged and induced plants (Zangerl et al. 2002; Mäntylä et al. 2017). Day-active birds especially have extensive colour vision that enables them to recognize leaves of herbivore-damaged trees (Cuthill 2006; Mäntylä et al. 2008b, 2020).

Plants growing in the understory of tropical forest are usually shaded by the taller canopy trees. This was the case also in our study, especially in the primary forest. The reduced sunlight can limit both photosynthetic rate and VOC emissions, but there is still a limited number of studies in tropics (Kesselmeier and Staudt 1999). Thus, leaf light reflectance changes due to herbivory might not be clearly visible in shaded environments (Mäntylä et al. 2008b) and/or plant cannot emit as much VOCs as in sunnier conditions (Bertin et al. 1997). These could be also the reasons for the observed variation in the VOC emissions and predation rates of focal *Ficus* trees. On average, it was shadier in the primary than in the secondary forest, but many trees in primary forest grew in light gaps. We tried to include the scale of local sunlight (shaded, partly shaded, sunny) in the analyses, but it did not affect the results. In future studies, it would be useful to measure light reflectance and VOC emissions of tropical tree species growing both in the understory and canopy layer, and in both undisturbed and disturbed forests.

We should also consider how the longevity of VOCs influences how effective communication can be, because VOCs



**Fig. 5** The predation rate of artificial plasticine caterpillars in the neighbouring trees around the focal trees of three *Ficus* species, divided by treatment. The box-plot shows: median, 25th and 75th percentiles (box), 10th and 90th percentiles (whiskers), and outliers (circles). Paired *t*-tests: *F. wassa*; MeJA vs. control  $t = -0.48$ ,  $p = 0.640$ , DIECA vs. control  $t = 0.74$ ,  $p = 0.480$ ; *F. pachyrrhachis*; MeJA vs. control  $t = 0.14$ ,  $p = 0.888$ , DIECA vs. control  $t = -1.05$ ,  $p = 0.319$ ; *F. hispidooides*; MeJA vs. control  $t = -0.29$ ,  $p = 0.775$ , DIECA vs. control  $t = 1.86$ ,  $p = 0.096$



react very easily with other chemicals in the air, they may not be a reliable cue. For example, ozone can disturb VOC communication among plants, herbivores, and their predators (Pinto et al. 2007). Current surface ozone levels are poorly known in tropical forests (Sofen et al. 2016), therefore more research on this topic is needed. Also, atmospheric nitrogen oxides and hydroxyl radicals can change VOCs to new compounds, thus converting the original message of the herbivore-damaged tree (Blande et al. 2014). The reliability of VOC messages can reduce over short distances and times in species-rich tropical forests (Douma et al. 2019). Thus, species-rich tropical vegetation can increase the chemical noise, making it more difficult for the neighbouring trees and predators to correctly detect and respond the message of the original VOC emissions. Herbivore-damaged tropical trees could thus rely on other cues to attract predators, such as the changes in leaf reflectance, that may convey information more reliably in such complex environment.

Neither phylogenetic nor physical distance between the focal *Ficus* tree and neighbouring trees had an effect on the predation rate. Our trees were sampled from > 70 species and from 28 families, ranging from Lamiaceae to Gnetaceae (from Asterids to Tracheophytes). In general, VOCs emitted by a closer relative should be more easily recognized and the transferred information be more reliable (Karban et al. 2013; Kalske et al. 2019). On the other hand, it would be understandable for the trees in species-rich tropical forests to conform to the expectations of the mutual benefit hypothesis (Heil and Karban 2010). In a typical forest, the nearest neighbours are typically of different species, often phylogenetically distant (Janzen 1970; Connell 1971). Therefore, a multi-species signalling network preparing plants for herbivore attack may be beneficial. The signals thus could be expected to be largely universal instead of species specific (Dicke and Bruin 2001; Heil and Karban 2010; Heil 2014).

The results of our study did not support the role of VOCs as a means of communication among tropical trees, or to the potential predators of their herbivores, as the VOC emissions or predation rates did not differ between the treatments. One reason for the non-significant results is that our sample size clearly was too small. A sample size of five focal *Ficus* individuals per treatment was too low number to overcome the extensive differences between individual trees. It is also possible that the message of important VOCs was lost in the noise of all other odours emitted by the species-rich vegetation. There clearly should be more research of the role VOC emissions as communication method in tropical rainforests.

To conclude, we did not show that plant–plant aerial communication would affect the predation rate of herbivores in species-rich tropical forest. The possible reasons include the complexity of networks between and within trophic levels and high variation among conspecific plants we observed. A number of the earlier plant–plant communication studies have been conducted with a limited number of species and in cooler climates, with fewer confounding factors. It would be beneficial in the future to do more experiments in various environmental conditions to see how much the environmental conditions themselves cause differences. Further useful experiments could be with plants of different known ability to emit VOCs, with a large number of plants, or try to separate the aerial and root parts of the communication network. Experiments conducted in settings where plant diversity can be manipulated should also be encouraged. In conclusion, our work identifies a number of fruitful directions of future research and provides a glimpse into the complex multi-trophic networks found in tropical forests.

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**Author contributions** The study was planned by EM, KS, STS, MV and VN. EM and BK did the fieldwork. MV and AW analysed the VOCs. STS did the phylogenetic relationship analyses. LRJ did the statistical analyses. All authors contributed to the writing and commented on the manuscript.

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## Declarations

**Conflict of interest** All authors declare that they have no conflict of interest.

**Ethical approval** Not applicable.

**Consent to participate** All authors agreed to participate in the article.

**Consent for publication** All authors consent to the publication of this article.

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