




# Contrasting patterns of fig wasp communities along Mt. Wilhelm, Papua New Guinea



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## Abstract

The fig (Moraceae) and pollinating fig wasp (Agaonidae) mutualism is best known as a model system for the study of coevolution in plant–pollinator interactions and its central role in shaping vertebrate communities in tropical forests. Figs also host myriad antagonistic parasitic fig wasps which impose costs on both partners threatening mutualism stability. Spatiotemporal variation in parasitic wasp abundance is a key factor in mitigating these effects. Because fig wasps are temperature sensitive and likely vary in their ability to traverse environmental gradients, we expect community assemblages and abundance of both pollinating and non-pollinating fig wasps to respond to changes along an elevational gradient. In the present study, we compare the fig wasp communities and abundance of three fig species growing along the slopes of the Mount Wilhelm altitudinal gradient in Papua New Guinea. We quantified wasps from over 100 male fig trees and calculated seed set for 55 female trees along each of the species' distribution on the transect. Our results show that the abundance of both pollinating and non-pollinating fig wasps follow a mid-elevation peak, consistent with fig species richness found in the same transect. The patterns, however, are different according to the host's species distribution. Seed set remained relatively constant along the gradient for all species with some decrease along higher elevations, potentially affecting connectivity along the gradient. As suggested for insects in general, temperature and habitat diversity appear to play a fundamental role in the species richness and abundance of fig wasps.

## KEYWORDS

altitudinal gradient, *Ficus*, non-pollinating fig wasps, pollination, seed set

## 1 | INTRODUCTION

Insect species richness and composition along altitudinal gradients are known to vary with elevation. These patterns, however, are different among different taxonomic groups (Maunsell, Kitching,

Burwell, & Morris, 2015; McCoy, 1990; Peck, Banko, Schwarzfeld, Euaparadorn, & Brinck, 2008; Warren, Harper, & Booth, 1988). As insects are ectothermic, they are particularly sensitive to temperature (Arroyo, Primack, & Armesto, 1982; García-Robledo, Kuprewicz, Staines, Erwin, & Kress, 2016) and correspondingly less diverse at higher elevations and lower latitudes. The vast majority of

angiosperms are pollinated by insects which inextricably links plant and insect fitness (Ellstrand, 2014; Lowry, Modliszewski, Wright, Wu, & Willis, 2008; Ollerton, Winfree, & Tarrant, 2011). The abundance of wasps and beetles tends to decrease with increasing elevation and instead, more abundant dipteran communities pollinate flowers at higher elevations, implying a shift in pollinator composition which influences plant reproductive strategies and success (Warren et al., 1988). Also affected by elevation is parasitoid wasp abundance and species richness. Both are highest at mid-elevations, due in part to the abundance of potential hosts. This distribution likely influences

structure and function of food webs by affecting plant herbivore and/or pollinator interactions (Maunsell et al., 2015; Peck et al., 2008).

Obligate pollination mutualisms offer a tractable and relatively simple model for measuring fitness-related traits along environmental gradients (Souto-Vilarós et al., 2018) because species specificity is high and traits can be easily quantified. Parasites and parasitoids of mutualisms add an extra layer of complexity because direct and indirect costs on mutualistic partners can influence the stability of such mutualisms (Bronstein, 2001), and in some cases, abiotic factors may even shift mutualists into parasites and vice versa (Kawakita,

**TABLE 1** Summary of collections per species including name of collection sites. (A) Female figs only. (B) Male figs only

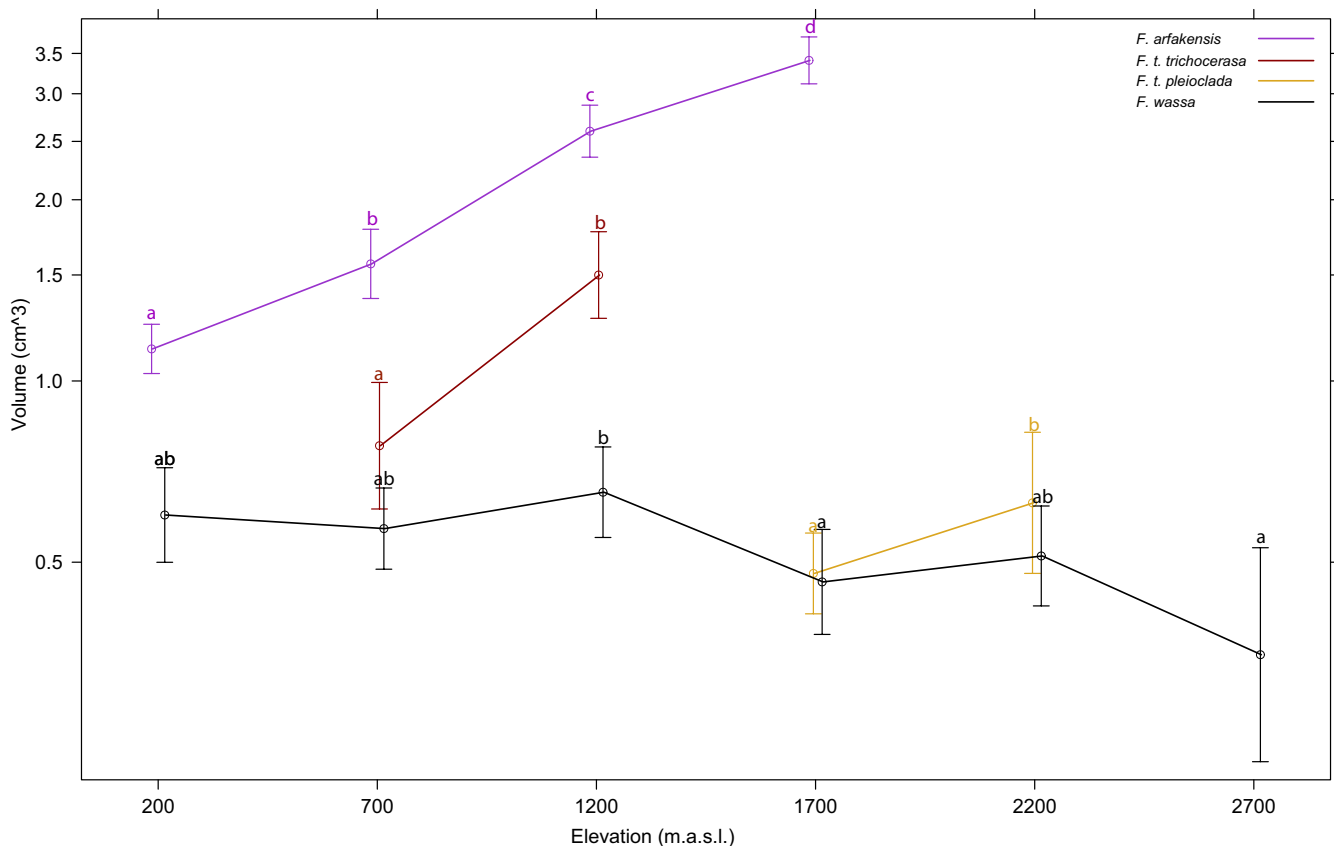
(A)							
<i>Ficus</i> species	Collection Site	Elevation (m)	Female figs (dissected) (total trees = 55)	Fig volume ( $\pm$ SE)	Seed set ( $\pm$ SE)		
<i>F. arfakensis</i>	Kausi	200	6	1.13 $\pm$ 0.049	0.739 $\pm$ 0.058		
	Numba	700	6	1.565 $\pm$ 0.063	0.758 $\pm$ 0.028		
	Memeku	1,200	4	2.599 $\pm$ 0.311	0.91 $\pm$ 0.031		
	Degenumbu	1,700	6	3.408 $\pm$ 0.114	0.794 $\pm$ 0.039		
<i>F. t. trichocerasa</i>	Numba	700	9	0.781 $\pm$ 0.051	0.98 $\pm$ 0.008		
	Memeku	1,200	10	1.5 $\pm$ 0.219	0.975 $\pm$ 0.007		
<i>F. t. pleioclada</i>	Degenumbu	1,700	9	0.479 $\pm$ 0.017	0.7 $\pm$ 0.087		
	Snowpass	2,200	8	0.627 $\pm$ 0.064	0.796 $\pm$ 0.092		
<i>F. wassa</i>	Kausi	200	12	0.599 $\pm$ 0.059	0.748 $\pm$ 0.053		
	Numba	700	12	0.569 $\pm$ 0.03	0.786 $\pm$ 0.035		
	Memeku	1,200	10	0.653 $\pm$ 0.054	0.79 $\pm$ 0.047		
	Degenumbu	1,700	12	0.464 $\pm$ 0.037	0.546 $\pm$ 0.071		
	Snowpass	2,200	8	0.512 $\pm$ 0.05	0.795 $\pm$ 0.112		
	Bruno Sawmill	2,700	na	0.351 $\pm$ 0.026	na		
(B)							
<i>Ficus</i> species	Collection site	Elevation (m)	Male figs <sup>a</sup> (trees = 103)	Infested figs (%)	Number of pollinators ( $\pm$ SE)	Number of NPFW ( $\pm$ SE)	Percentage parasitism ( $\pm$ SE)
<i>F. arfakensis</i>	Kausi	200	35 (8)	96	116.571 $\pm$ 8.152	22.677 $\pm$ 3.489	0.173 $\pm$ 0.031
	Numba	700	9 (7)	88	247.222 $\pm$ 34.29	23.222 $\pm$ 9.212	0.098 $\pm$ 0.037
	Memeku	1,200	12 (8)	100	475.833 $\pm$ 63.768	98.833 $\pm$ 16.692	0.172 $\pm$ 0.036
	Degenumbu	1,700	9 (7)	25	526.556 $\pm$ 82.802	0.75 $\pm$ 0.496	0.002 $\pm$ 0.001
<i>F. t. trichocerasa</i>	Numba	700	8 (8)	100	136.875 $\pm$ 23.394	33.125 $\pm$ 9.48	0.225 $\pm$ 0.074
	Memeku	1,200	10 (10)	100	89 $\pm$ 5.55	14.889 $\pm$ 2.939	0.138 $\pm$ 0.027
<i>F. t. pleioclada</i>	Degenumbu	1,700	27 (13)	95	65.296 $\pm$ 8.552	14.792 $\pm$ 1.689	0.245 $\pm$ 0.018
	Snowpass	2,200	12 (11)	91	64.667 $\pm$ 18.915	20.917 $\pm$ 3.487	0.377 $\pm$ 0.074
<i>F. wassa</i>	Kausi	200	15 (6)	75	126.2 $\pm$ 20.018	10.417 $\pm$ 3.306	0.082 $\pm$ 0.03
	Numba	700	27 (10)	95	176.556 $\pm$ 36.166	29.792 $\pm$ 5.08	0.31 $\pm$ 0.071
	Memeku	1,200	15 (4)	73	344.467 $\pm$ 42.177	8.8 $\pm$ 4.018	0.037 $\pm$ 0.022
	Degenumbu	1,700	10 (6)	75	77.9 $\pm$ 17.805	7.625 $\pm$ 2.656	0.073 $\pm$ 0.026
	Snowpass	2,200	27 (13)	75	31.074 $\pm$ 6.403	17.826 $\pm$ 3.258	0.323 $\pm$ 0.059
	Bruno Sawmill	2,700	7 (2)	50	63.571 $\pm$ 31.742	3.333 $\pm$ 1.846	0.083 $\pm$ 0.039

<sup>a</sup>Numbers within parenthesis indicate the number of figs which were sorted from emerged wasps. Total numbers include sorted and dissected fig samples.

Mochizuki, & Kato, 2015). Studies focusing on the response of trophic interactions with increasing elevation have found that while there is a general trend for insect predation and parasitism rates to decline, the predators and parasitoids involved do not necessarily respond in the same manner and in many cases depend on host distribution, as well as their density and temporal overlap during key life stages (Corcos et al., 2018; Maunsell et al., 2015; Péré, Jactel, & Kenis, 2013).

For this study, we focus on the fig (Moraceae) and fig wasp (Agaonidae) mutualism, one of the most specialized nursery pollination systems (Cook & Rasplus, 2003), where the reproductive success of both parties depends on species-specific encounters. Briefly summarizing, female wasps emerge from the figs (called syconia) and are guided by volatile signals as they search for a receptive fig of the same host species. Upon landing, mated and pollen-loaded wasps enter the floral cavity through a narrow passage (ostiole) and pollinate the flowers within. While approximately half of described fig species are monoecious, having both male and female flowers within the same fig, the remainder are functionally dioecious meaning that sexual function is segregated between trees (though they are anatomically gynodioecious; Bronstein, 1988; Corlett, Boudville, & Seet, 1990). Monoecious figs contain both long-styled flowers (which frequently develop as seeds) and short-styled flowers that are more

accessible for wasps to oviposit, thus housing the next generation of wasps. In dioecious species, male figs contain flowers suitable for oviposition and produce only wasps becoming nurseries while female fig trees deceive the wasps to enter and pollinate, but wasps are unable to oviposit in the long-styled flowers inside and so female fig trees produce only seeds (Galil & Eisikowitch, 1968; Kjellberg, Jouselin, Hossaert-McKey, & Rasplus, 2005). Some fig wasps are known for long distance pollen dispersal as these minute insects (1–2 mm) appear to be transported by wind over wide distances of up to 160 km (Ahmed, Compton, Butlin, & Gilmartin, 2009; Kobmoo, Hossaert-McKey, Rasplus, & Kjellberg, 2010; Liu, Compton, Peng, Zhang, & Chen, 2015). Thus far, these findings have been restricted mostly to large monoecious trees which occur at naturally low densities. In contrast there is evidence that dioecious and under-canopy fig trees are clustered into dense local populations and so pollinating fig wasps do not disperse over such long distances (Dev, Kjellberg, Hossaert-McKey, & Borges, 2011). Figs house a large number of non-pollinating fig wasps (NPFW) which parasitize pollinator larvae or compete for seed resources thus significantly affecting pollinator populations and consequentially fig pollen dispersal (Kerdelhué & Rasplus, 1996; Weiblen, 2002; Weiblen, Yu, & West, 2001). NPFW have a fascinating ecology of their own: ranging from galls which enter the syconia alongside pollinators to kleptoparasites which



**FIGURE 1** Effect of elevation on fig volume for all (sub)species. Effect was calculated using generalized linear model with volume as the response variable to elevation and (sub)species interaction. The interaction of elevation and (sub)species identity is highly significant ( $\chi^2 = 104.90$ ,  $df = 5$ ,  $p < .001$ ). Pairwise differences between elevations were tested using Tukey HSD post hoc test. Different letters indicate significant differences between comparisons ( $p < .05$ )

oviposit into pre-existing galls or parasitoids. Many parasitoids oviposit from the outside of the fig, the ovipositor length correlated with the fig developmental stage at which these wasps oviposit (Borges, 2015; Cook & Segar, 2010; Weiblen, 2002).

Some authors have suggested that the negative effect of parasitism is stabilized through temporal and spatial heterogeneity in non-pollinator occurrence and abundance, as well as variation in the availability of figs at the right developmental stage for them to invade.

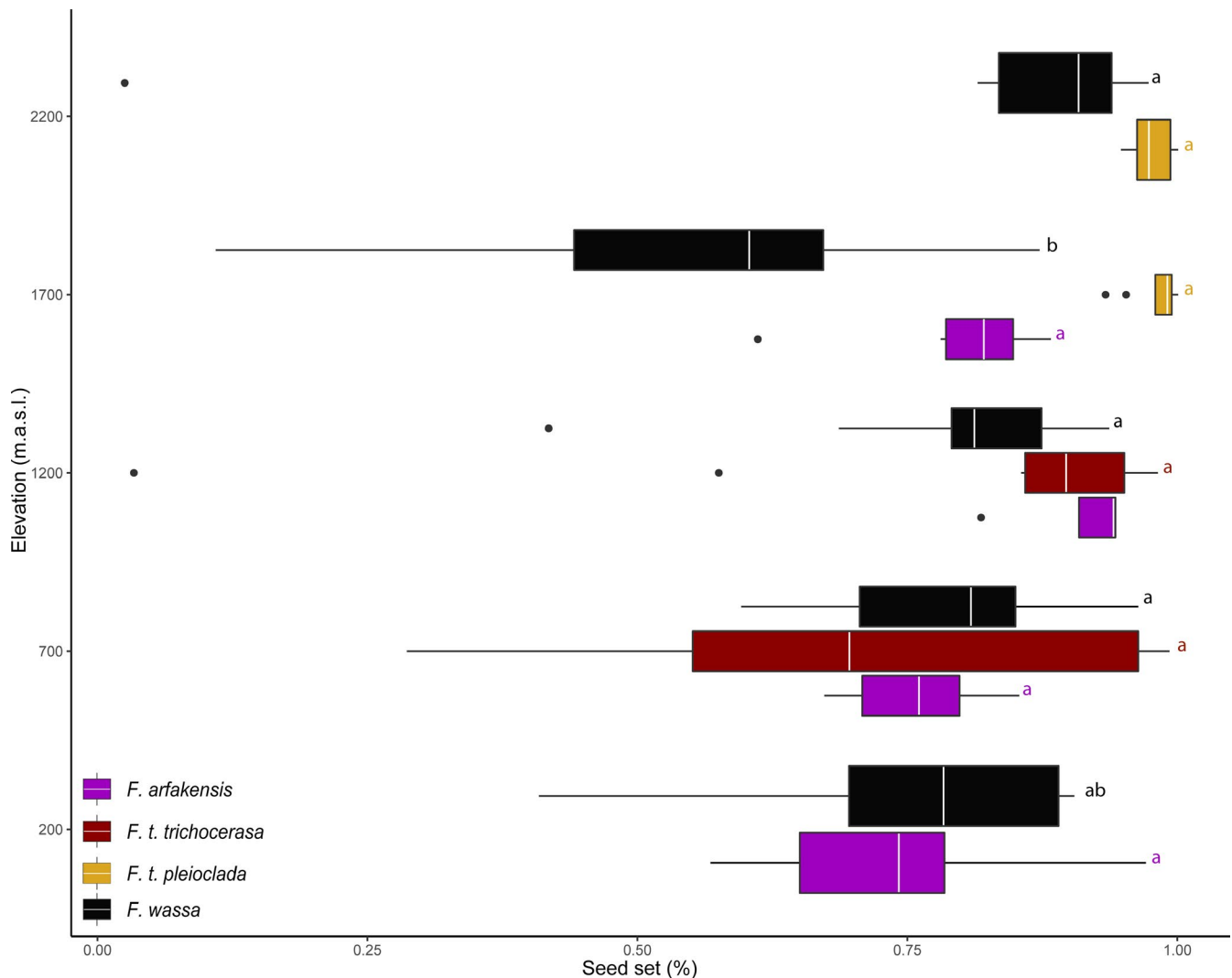
So far, the distribution and abundance of NPFW along environmental gradients have not been well studied, despite the knowledge that parasitism varies with both phenotypic and environmental variation (Maunsell et al., 2015; Yu, Liang, Tian, Zheng, & Kjellberg, 2018). We suggest that elevational gradients, which to some extent control for species-pool effects, make excellent systems to study environmentally mediated variation in fitness traits and parasite loads. Such gradients

provide natural spatial structure and environmental clines which mimic more wide scale variation across the range of a given resource species.

Specifically, we test the hypotheses that (1) pollinating wasp abundance decreases with elevation, (2) non-pollinator diversity and abundance have a mid-elevation peak due to mixing between lowland and highland communities, (3) seed set is highly dependent on pollinator abundance and so will follow the same trend as (1); finally, (4) because fig size limits the amount of seeds or developing wasps that can fit within them, we also test whether or not fig size (volume) varies along the gradient.

## 2 | METHODS

The study was conducted along an elevational gradient in the central range of New Guinea. The continuously forested Mount



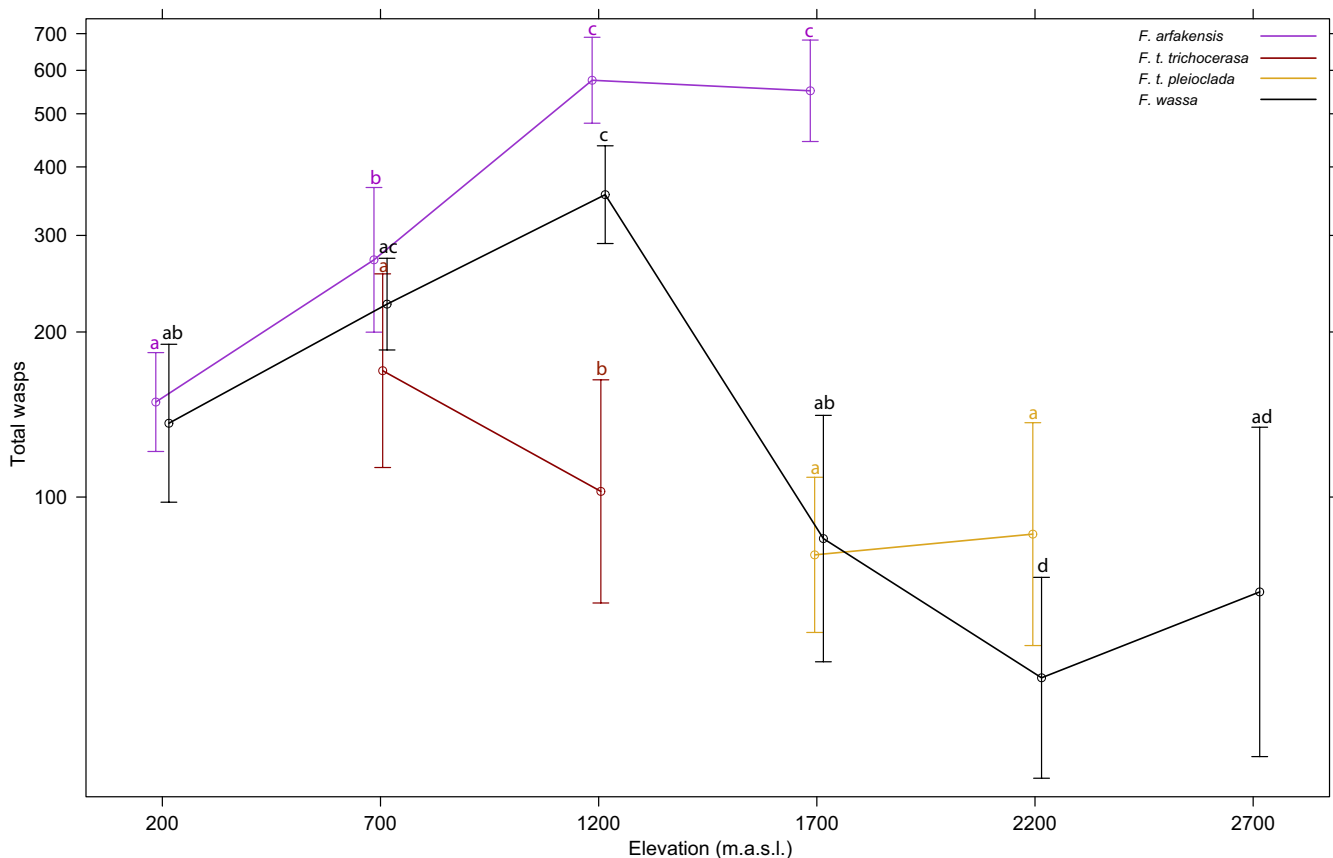
**FIGURE 2** Boxplots showing seed set per (sub)species and elevation. Effect was calculated using generalized linear model with seed set as the response variable to elevation and (sub)species interaction. The interaction of elevation and (sub)species identity was not significant and so removed from the model through backwards elimination. The effect of elevation and (sub)species is significant (Elevation  $\chi^2 = 9.393$ ,  $df = 4$ ,  $p < .051$ ; (sub)species  $\chi^2 = 24.580$ ,  $df = 3$ ,  $p < .001$ ). Pairwise differences between elevations were tested using Tukey HSD post hoc test. Different letters indicate significant difference between comparisons ( $p < .05$ )

Wilhelm (5.7800°S, 145.0297°E) gradient ranges from lowland alluvial forest up to lower montane forest and has been previously described in detail elsewhere (Marki et al., 2016; Robillard, Legendre,

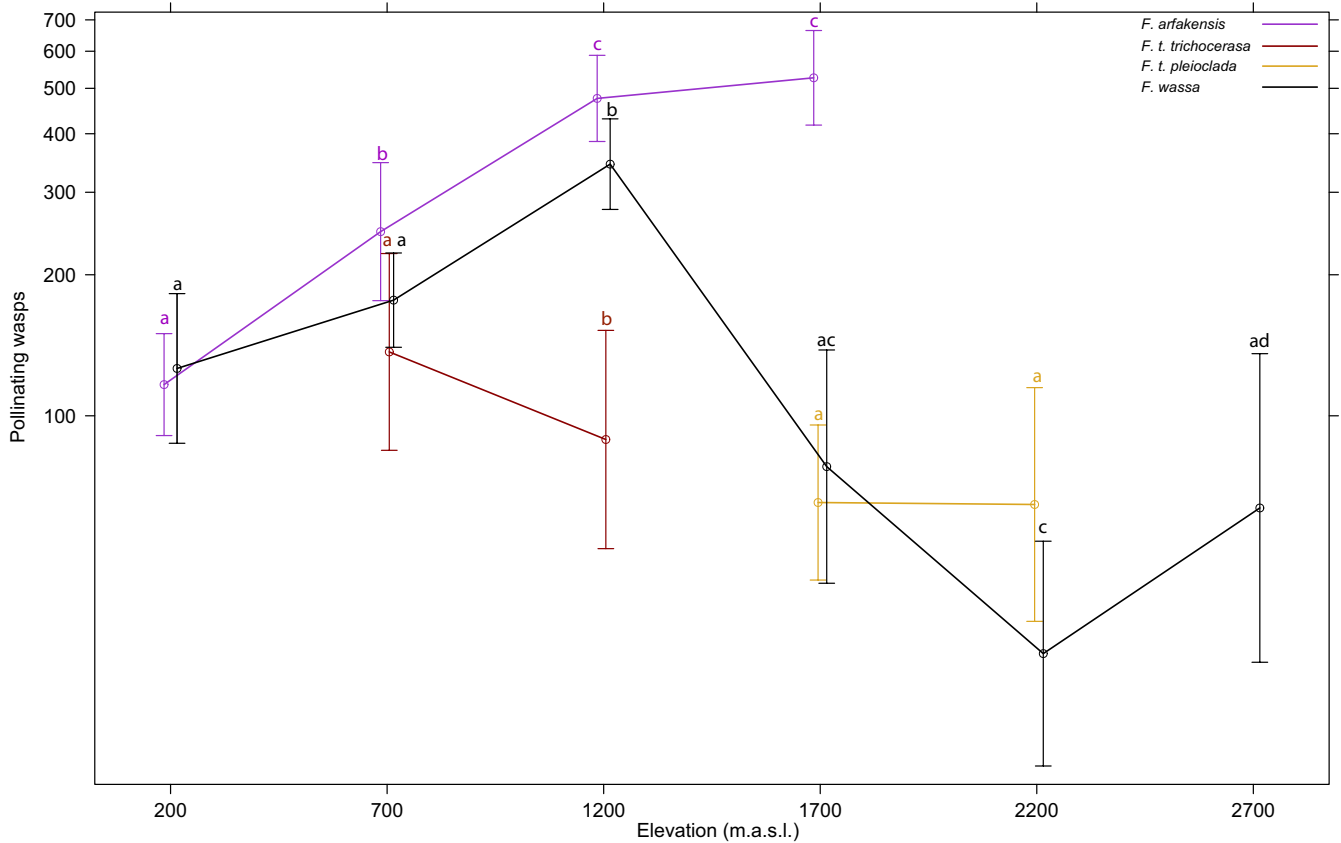
**TABLE 2** Summary of generalized linear model results and Analysis of Variance for each model tested. Values in bold indicate significant effect of the predictive term on the response variable

Response	Interaction	$\chi^2$	df	p
Volume	Elevation	253.01	5	<.001
	Species	941.88	3	<.001
	Species: elevation	104.90	5	<.001
Seed set	Elevation	9.393	4	.051
	Species	24.580	3	<.001
Total wasps	Elevation	185.835	5	<.001
	Species	128.351	3	<.001
	Elevation: species	66.865	5	<.001
Total pollinators	Elevation	163.735	5	<.001
	Species	105.359	3	<.001
	Elevation: species	59.101	5	<.001
Total NPFW	Elevation	66.61	5	<.001
	Species	41.273	3	<.001
	Elevation: species	60.474	5	<.001

Villemant, & Leponce, 2016; Toussaint et al., 2014). Our study was conducted at six sites each with approximately 500 meter elevational intervals from 200 to 2,700 m (all elevations stated as above sea level; Table 1). Approximately half of the 150 *Ficus* (Moraceae) species recorded for the island occur there along the transect (Berg & Corner, 2005) and previous fig species surveys along the transect reveal that some of these species have wide elevational ranges (Novotny et al., 2005; Segar et al., 2017). For the present study, we focused on three dioecious species endemic to New Guinea and adjacent islands selected on the basis of their distribution along the transect: *Ficus wassa* Roxb. is a botanically recognized species abundant throughout the gradient with a wide distributional range occurring between 200 and 2,700 m pollinated by the fig wasp *Kradibia wassae*; *Ficus arfakensis* King distributed between 200 and 700 m and pollinated by *Ceratosolen solitarius*; *Ficus trichocerasa* Diels is represented by lowland and a highland subspecies with the nominate *F. t. trichocerasa* distributed between 700 and 1,200 m and the highland *F. t. pleioclada* distributed between 1,200 and 2,600 m, and these subspecies appear to be pollinated by undescribed species of *Ceratosolen* wasps. Recent genomic analyses have revealed that these species are pollinated by three, four, and two species complexes, respectively (Souto-Vilarós et al., 2019a), distributed in parapatry along the gradient.



**FIGURE 3** Effect of elevation on total wasp production for all (sub)species. Effect was calculated using generalized linear model with total wasp as the response variable to elevation and (sub)species interaction. The interaction of elevation and (sub)species identity is highly significant ( $\chi^2 = 66.865$ ,  $df = 5$ ,  $p < .001$ ). Pairwise differences between elevations were tested using Tukey HSD post hoc test. Different letters indicate significant difference between comparisons ( $p < .05$ )



**FIGURE 4** Effect of elevation on pollinating wasp production for all (sub)species. Effect was calculated using generalized linear model with total pollinating wasps as the response variable to elevation and (sub)species interaction. The interaction of elevation and (sub)species identity is highly significant ( $\chi^2 = 59.101$ ,  $df = 5$ ,  $p < .001$ ). Pairwise differences between elevations were tested using Tukey HSD post hoc test. Different letters indicate significant difference between comparisons ( $p < .05$ )

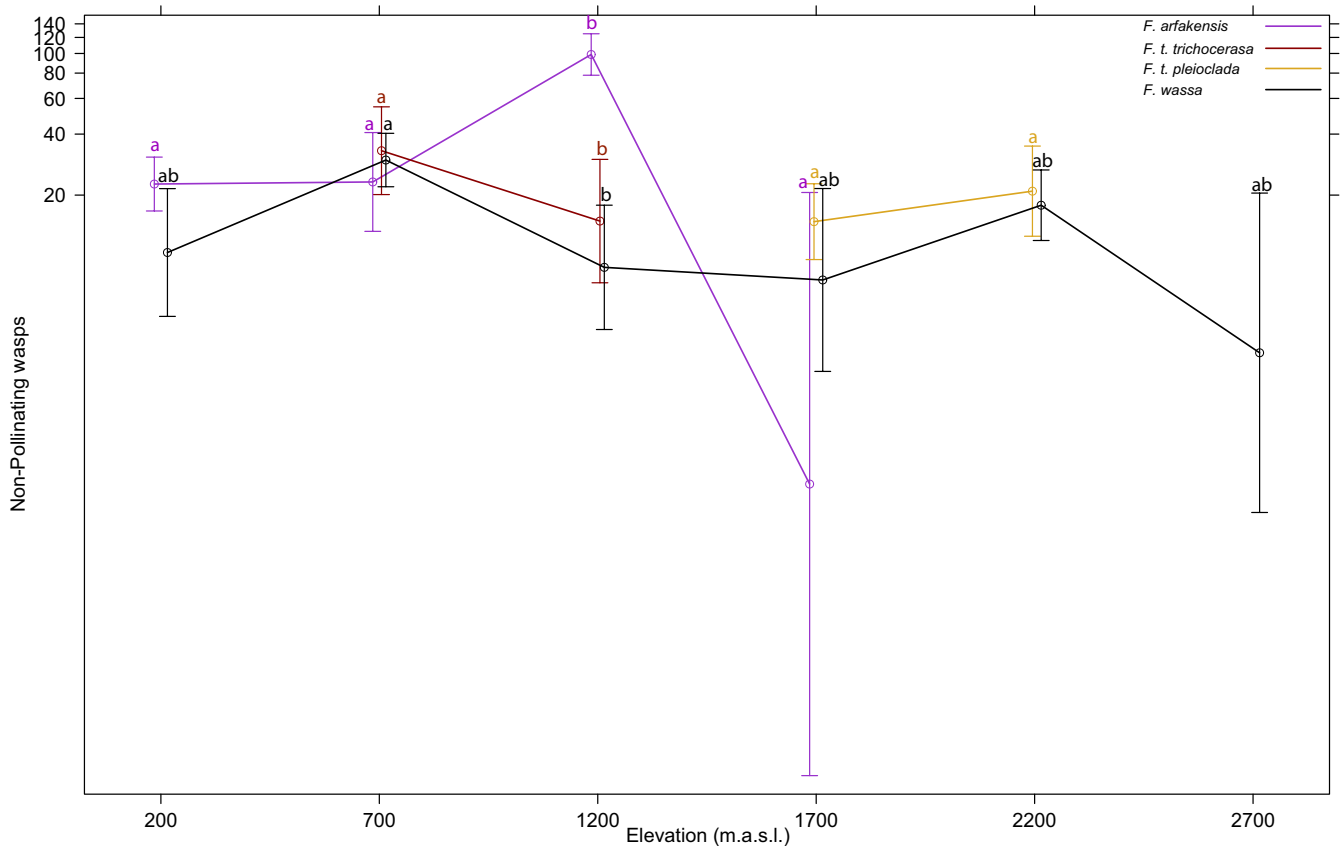
Sampling was conducted between August 2015 and November 2016. At each of six sites along the transect, we tagged several male and female trees of each locally available focal species and monitored them during the duration of the sampling. For each of the focal trees, we collected up to five ripe figs for each female tagged tree, stored them in plastic pots in a 70% ethanol solution and exported to the University of South Bohemia, Czech Republic, for later dissection. Using a microscope, up to two figs selected haphazardly from each pot were dissected ( $n = 112$ ) and all fully developed seeds and all available ovules were counted, and seed set was calculated as the number of seeds divided by the number of ovules.

For each male tree, figs were sampled either through emergence or dissection methods (Segar, Dunn, Darwell, & Cook, 2014). For the emergence method, we collected up to five D-stage figs (Galil & Eisikowitch, 1968), the stage when wasps are already hatched from the galls and are clustered within the fig cavity, and stored them in individual plastic pots covered with fine mesh. Wasps were allowed to emerge naturally from the figs ( $n = 113$ ) and were immediately collected and stored in 100% ethanol. Wasp individuals were sorted to at least genus and morphospecies level. For the dissection method, a second set of D-stage figs was directly stored in 70% ethanol solution. All collections were sent to the University of South Bohemia for

later dissection of figs and sorting and identification of wasps. Up to two figs per tree ( $n = 110$ ) were selected haphazardly and dissected under a microscope and the total number of wasps recorded. Width and height were measured to the nearest 0.01 mm using Vernier calipers to calculate fig volume following the standard cone volume formula (as per Segar et al., 2017):

$$V = \pi r^2 \frac{h}{3}$$

To test the influence of elevation and fig species on fig volume, seed set, and total number of wasps produced, we performed generalized linear models (GLMs) separately using collection site (as elevation) and fig species as explanatory variables. Minimal models were retained using standard backward selection by removing non-significant higher-level interactions. We used Welch Two Sample  $t$  test to compare fig volume between male and female figs, as there was no significant difference according to sex (see results), volume analyses combined both sexes. Analyses on seed set and wasp numbers were conducted separately for female and male figs. The full models run were as follows: (a) fig volume as a response to elevation and species, (b) seed set as a response to elevation and species, (c) total wasps number per fig as a response to elevation and species; further,



**FIGURE 5** Effect of elevation on parasitic wasp production for all (sub)species. Effect was calculated using generalized linear model with total parasitic wasps as the response variable to elevation and (sub)species interaction. The interaction of elevation and (sub)species identity is highly significant ( $\chi^2 = 60.474$ ,  $df = 5$ ,  $p < .001$ ). Pairwise differences between elevations were tested using Tukey HSD post hoc test. Different letters indicate significant differences between comparisons ( $p < .05$ )

we separated analyses on wasps to include, (d) number of pollinating wasps as a response to elevation and species, and (e) number of non-pollinating wasps as a response to elevation and species. For all models, we fitted a quasipoisson error structure, except for seed set for which we used a Gaussian distribution. Finally, multiple comparisons between elevations were tested for significance using Tukey's test of main effects as implemented in the General Linear Hypothesis function *glht* in the R package "multcomp" v.1.10 (Hothorn, Bretz, & Westfall, 2008). All analyses were conducted in R version 3.5.1 (R Core team, 2015).

### 3 | RESULTS

#### 3.1 | Fig volume variation between species and elevation

We measured volume for a total of 222 figs (female  $n = 112$ , male  $n = 110$ ) for each species separately (details summarized in Table 1). We initially tested fig volume separately according to tree sex but found no significant difference between them ( $t = -1.048$ ,  $df = 266.7$ ,  $p = .295$ ) and so we analyzed the effect

elevation has on fig volume for both sexes combined. Elevation affected fig volume; however, the strength and direction varied according to species (Figure 1): There was a positive effect of altitude for *F. arfakensis* while fig volume remains almost constant for *F. wassa* with declines at the 1,700 and the 2,700 m sites. In the case of *F. trichocerasa*, volume increased with elevation for both subspecies (Table 2).

#### 3.2 | Seed set variation between fig species and elevation

The effect of fig volume and seed set was analyzed for female figs only using a total of 112 dissected figs and shows that in general, larger figs have higher seed set. Overall, seed production remains constant for all species along the transect (Figure 2b) with the exception of a significant decrease of seed set for *F. wassa* at the 1,700 m site (Tukey HSD test shows significant difference between this site and all other  $p < .04$  except at 200 m). Important to note is that for this species, most mature female figs found at the highest elevation (2,700 m) were infested by maggots or decaying on the tree and so we were unable to calculate seed set (Table 2).





### 3.3 | Wasp abundance and variation between fig species across elevations

All analyses pertaining to wasp numbers (both pollinators and parasites) were conducted on data from male figs only. Elevation played a significant role on the total number of wasps produced per fig with a distinct mid-elevation peak; however, the effect varies according to fig species (Figure 3; Table 2). Wasp numbers steadily increased with elevation in *F. arfakensis* and *F. wassa* up to the 1,200 m site where the former appears to plateau at its range limit (1,700 m) and the latter sharply decreases beyond this point (Figure 3). In the case of *F. trichocerasa*, there is a significant decrease of total number of wasps per fig in subsp. *Trichocerasa* while the total number of wasps for *F. t. pleioclada* remains constant between both elevations (Fig 3).

Separating the data into pollinator and non-pollinator numbers reveals a similar pattern. Pollinator numbers vary in response to elevation with a sharp increase at the mid-elevation peak (between 1,200 and 1,700 m) followed by a decrease in pollinator numbers in the highlands (Figure 4; Table 2). In the case of NPFWs, the total number of wasps was affected by elevation but the effect varied among species (Figure 5). For both pollinating and non-pollinating wasps associated with *F. arfakensis*, elevation had a positive effect on the total number of wasps; however, in the case of NPFWs, there is a sharp decline at the species range limit (1,700 m) where very few NPFWs were found (mean =  $0.75 \pm 0.49$ ; Table 1); however, inter-sample variation was high. The effect of elevation for both pollinating and non-pollinating wasps from *F. trichocerasa* was similar for both subspecies. There was a general decline of wasp numbers in *F. t. trichocerasa* and no significant changes in wasp numbers from *F. t. pleioclada*. For *F. wassa*, elevation played a significant role on the total number of pollinators per fig with an increase up to the 1,200 m site followed by a sharp decline increasing again at the highest elevation site. NPFW numbers remained relatively constant with significant differences between the 700 and 1,200 m sites. Notably, the increase of parasitic wasp loads at the 700 m site is due to a considerable increase in non-pollinating wasp species richness, rather than exclusively numbers, as at this site we found most figs to host up to six different morphospecies of NPFW (Table 3).

In terms of community composition (Table 3), the most diverse community was found in the figs of *F. wassa* with up to eight different genera at the 700 m site. Overall, the diversity of NPFW of *F. wassa* remains between one and two genera at each site, with *Philotrypesis* and an Otitellinae being the most abundant NPFWs found in these figs commonly found throughout *F. wassa*'s range. In the case of *F. arfakensis*, we found two very abundant species from the genus *Apocrypta*, and *Sycophaga*, in nearly all of the figs sampled. The lowland populations (200 and 700 m) supported up to three genera while in the highest elevation of this species (1,700 m) we only found five individuals of *Apocrypta*. The NPFW community of *F. trichocerasa* is similar in both subspecies with up to six different genera with individuals from *Sycophaga* being the most abundant in both subspecies. Nevertheless, the genera between subspecies varied; for instance, in *F. t. trichocerasa*

we found one species of *Apocrypta* while in *F. t. pleioclada* we found wasps from the subfamily Otitellinae (possibly *Micranisa*) and *Megastigmus*, the latter only known from figs in the section *Malvanthera* (Cook & Segar, 2010).

## 4 | DISCUSSION

The present study is, to our knowledge, the first to offer insight on fig seed set and wasp load variation along an elevational gradient. We found that elevation substantially affected the variables studied here (fig size, seed set, and wasp production). However, the direction of the effect varies between species. As with other taxa (García-Robledo et al., 2016; Peters et al., 2016; Robillard et al., 2016), altitude plays an important role in abundance of both pollinating and NPFWs as well as species richness of the latter. Climatic changes that occur with increasing elevation have been shown to be some of the major factors affecting the distribution and survival of insect species (García-Robledo et al., 2016; Jevanandam, Goh, & Corlett, 2013). Temperature decreases with elevation while precipitation tends to increase at higher altitudes directly affecting insect development and survival while the same factors influence the surrounding vegetation, similarly affecting links along the trophic chain (i.e., herbivores and parasitoids). The results presented herein follow the *Ficus*-wide species trends presented by Segar et al. (2017) where fig species richness decreases with increasing elevation after a mid-elevation peak. We find wasp production follows this trend with a clear increase with elevation up to between 1,200 and 1,700 m followed by a sharp decrease at higher elevations.

Fig female fitness, measured as seed set, remains relatively stable for all species (Figure 2) throughout the transect, similar to findings from Weiblen, Flick, and Spencer (1995) in *F. variegata* (69% seed set), a dioecious species distributed through most of South East Asia; however, there is seed set variation between the different sites (Table 1). It is known that reduced seed set in figs is explained by the number wasps entering figs at receptivity (Corlett et al., 1990), but is also limited by the amount of pollen they carry, which is often related to emergence times (with early emerging wasps generally carrying more pollen than late emerging ones; Kjellberg et al., 2014). Our results show that even at the range limits of *F. t. pleioclada* (2,200 m), nearly every available ovule in female figs produced a seed suggesting little pollen limitation occurring when a fig is entered. There is evidence suggesting that seed set increases with foundress wasps entering receptive figs (Moore & Greeff, 2003; Nefdt & Compton, 1996), as well as more wasps entering bigger figs (Anstett, Bronstein, & Hossaert-McKey, 1996). We did find variation in the size of figs along the gradient for some species. However, although the size of figs of *F. arfakensis* steadily increased with increasing elevation, seed set remained constant throughout the elevational range occupied by this species. We did not record the number of foundress wasps entering figs. It was hard to assess the occurrence of multiple foundress wasps in the dissected figs and so we were unable to relate seed set to the number of wasps entering receptive figs.

Contrastingly, at the range limits of *F. wassa* (2,700 m), we were unable to find figs with seeds. It is known that fig trees abort figs if there are no available pollinators or if there is a mismatch between receptivity of figs and pollinator arrival (Suleman, Raja, Zhang, & Compton, 2011). The variation in seed set of *F. wassa* could be attributed to the lack of pollinators available at the highland sites (above 1,700 m), where fig trees can survive the colder temperatures, but wasp survival may be limited (Chen, Zhang, Peng, & Corlett, 2018).

We found variation in the total number of wasps in the studied species with increasing elevation having a significant effect (Figure 3). Studies on the monoecious *F. petiolaris* in northern Mexico concluded that foundress wasp distribution likely affects pollinator and non-pollinator abundances as well as overall seed production on the landscape (Duthie & Nason, 2016). Duthie and Nason (2016) suggest that seed set and non-pollinator production are negatively affected by pollinator abundance which is in turn positively affected by the number of foundress wasps. Foundress arrival appears to be associated with tree aggregation suggesting that habitat connectivity plays an important role in the overall mutualism. Studies on *F. racemosa* along a disturbance gradient also found that production of non-pollinating fig wasps was higher in highly fragmented habitat (Wang, Yang, Zhao, & Yang, 2005). The Mount Wilhelm elevational gradient is continuously forested from the lowland up to the treeline. Souto-Vilarós et al. (2019b) found that these fig species do form highland and lowland populations often with a distinct mid-elevation “contact-zone,” and however, connectivity between these populations is high (Souto-Vilarós et al., 2019a) suggesting that variation in wasp abundances may be related to varying conditions along the gradient instead of tree connectivity.

The ecology and life history strategies of these NPFWs are beyond the scope of this study; however, placing these wasps along the various trophic levels would greatly contribute to our as of yet limited understanding of NPFW communities. Species richness and abundance of galling wasps influence the diversity of parasitoids and hyperparasitoids. Larger figs have greater number of flowers, which in turn offer more opportunities for wasp colonization (Borges, 2015). Indeed, the largest figs in this study, *F. arfakensis*, supported the largest number of pollinating and non-pollinating fig wasps, but not the most diverse communities. Due to our limited taxonomic identification, we cannot rule out the ability of some of these NPFWs to use multiple host species. Although host specificity for NPFW may be less constrained than that of pollinators, it has been suggested that some degree of specificity is still frequent (Duthie & Nason, 2016; Joussetin et al., 2008; McLeish, Beukman, Van Noort, & Wossler, 2012). Ecological and/or morphological requirements for NPFW development such as synchrony with fig development, volatile cues for host recognition, fig wall thickness, and/or the presence of other wasps either as hosts, competitors, or parasitoids may promote species specificity and/or invasion (Borges, 2015; Farache et al., 2018; Marussich & Machado, 2007; McLeish et al., 2012; Weiblen et al., 2001). The co-occurrence of specific genera in different fig species at the same elevation may be of great interest from a community network perspective. Similarly, under-sampling individual trees may

be a constraint in our results. It is known that NPFWs do not colonize all available figs within a patch due to asynchrony of developing fig. Furthermore, the available species pool is likely to vary over time and space, and hence wasp communities in a given fig crop depend on a multitude of factors (McLeish et al., 2012). Molecular approaches would help greatly in determining species turnover and population connectivity between the NPFW groups identified herein. Of particular interest are some of the uncommon associations reported, particularly the occurrence of Otitesellinae wasps and *Megastigmus* in *F. t. pleioclada* figs: both occur alongside *Sycophaga* in the same figs on the same tree. One of the main challenges of describing NPFW assemblages is the variability in their abundance and distribution across fig sections. *Megastigmus* species, for instance, are only known from fig species in section *Malvanthera* (Cook & Segar, 2010); however, this genus is known to be associated with a wide range of host plants both as seed feeders and parasitoids of gall-makers (Auger-Rozenberg et al., 2006). Otitesellinae on the other hand are well known to parasitize sympatric figs from section *Urostigma* (Joussetin, Van Noort, Rasplus, & Greeff, 2006). Within our sampling, we found at least two instances of *Megastigmus* and Otitesellinae wasps within reared figs of *F. t. pleioclada* both coming from different elevations. Wider sampling at both inter- and intraspecific levels would help reveal whether these associations were frequent or a mistake on our part, or by the wasps themselves. Indeed, unusual associations in communities at the range edge of figs are more common.

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#### CONFLICT OF INTEREST

The corresponding authors confirm on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated. We report no potential conflict of interest.

#### AUTHOR CONTRIBUTION

V.N., S.T.S., and D.S.V. planned the research and provided input at all stages. G.D.W. and B.I. suggested suitable species for the study. D.S.V., M.S., and T.K. conducted and managed all fieldwork aspects with initial assistance of S.T.S. J.M. assisted with data analysis and management of fig dissections. D.S.V. and M.H. analyzed the data

and interpreted the results. D.S.V. wrote the manuscript with substantial help from all authors. All authors contributed and approved the final version of the manuscript.

#### DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pvmcndngv> (Souto-Vilarós et al., 2019b).

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