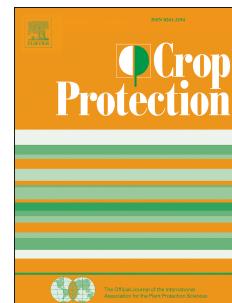


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Contribution of shade trees to wind dynamics and pathogen dispersal on the edge of coffee agroforestry systems: A functional traits approach

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1 **Contribution of shade trees to wind dynamics and pathogen dispersal on the edge of coffee
2 agroforestry systems: a functional traits approach**

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13

14 **Abstract**

15 Through microclimate modifications, coffee agroforestry systems have both facilitative and
16 inhibitory effects on the persistence of *Hemileia vastatrix*, a major fungal pathogen. Wind, a key
17 element in the dispersal of *H. vastatrix* uredospores, is affected by shade tree presence,
18 especially at the edge of agroforestry systems. However, little is known on how shade tree leaf
19 functional and canopy-level architectural traits impact wind dynamics and subsequent airborne
20 uredospore dispersal in this transition zone. In this study, we determine the contribution of shade
21 tree leaf functional and canopy traits to changes in throughflow wind speeds and *H. vastatrix*
22 uredospore dispersal at the edge of coffee agroforests across three size classes of the shade tree
23 *Erythrina poeppigiana* (sparse (pruned shade trees), medium (conventional management) and

24 dense (mature, larger, unpruned shade trees)). As expected, dense shade trees reduced
25 throughflow speeds into the farm more frequently than the other size classes. Shade tree leaf
26 functional traits (*e.g.* specific leaf area, leaf thickness, leaf angle) expressed high variability
27 (coefficient of variations: 13.67% to 89.48%) across the size classes and significantly predicted
28 throughflow speed reductions ($r^2=0.891$, $P=0.002$). Emerging mature uredospore counts were
29 significantly lower ($P<0.001$) on the leeward side of dense shade trees, yet high reductions in
30 throughflow speed into the farm were related to increased airborne uredospore capture across all
31 size classes in these agroforestry systems. Seemingly, trade-offs exist between reduced wind
32 speeds that decrease uredospore dispersal and reduced wind speeds that encourage uredospore
33 settling into the coffee canopy at the edge of farms. This suggests a level of “fluidity” in
34 desirable shade tree traits throughout the agroforestry system design. Our findings highlight the
35 complexity of uredospore movement in agroforestry systems and the important role of shade tree
36 canopy and leaf functional traits in wind dynamics.

37

38 **Keywords:** *Hemileia vastatrix*, *Coffea arabica*, agroforestry, throughflow wind speed, fungal
39 spore dispersal, functional leaf traits

40

41 1. Introduction

42 Coffee is an important international commodity, grown by over 25 million people in more
43 than 60 countries (Jayakumar et al., 2017). Coffee leaf rust (CLR), a disease that results in
44 premature leaf fall and significant yield loss, is present in almost all coffee-growing regions and
45 has become a major concern, especially in Central and South America, after recent intense
46 epidemics that resulted in up to 31% reduction in coffee production (Avelino et al., 2015). CLR

47 is caused by the biotrophic basidiomycete fungus *Hemileia vastatrix* Berkeley and Broome.
48 Mature *H. vastatrix* uredospores emerge from infected coffee leaves in clusters. Wind is the main
49 abiotic driver that releases uredospores from these clusters into the air and disperses them long
50 distances via air currents (Kushalappa and Eskes, 1989). Once the uredospores settle out of the
51 turbulent wind and deposit onto coffee leaf surfaces, uredospores germinate, penetrate into the
52 leaf, and re-emerge from chlorotic lesions in clusters of now mature uredospores, where they are
53 released to regenerate the cycle (Avelino et al., 2004; Kushalappa and Eskes, 1989; Silva et al.,
54 2002; Talhinas et al., 2017; Zambolim, 2016). Given wind's facilitation of long distance
55 uredospore dispersal, wind dynamics play a key role in the onset of CLR epidemics (Avelino et
56 al., 2015).

57 Agroforestry systems, which range from rustic forest plantations to shaded monocultures
58 (Toledo and Moguel, 2012), are the dominant mode of coffee production in most Latin American
59 countries (Jha et al., 2014) and can have inhibitory effects on pathogen lifecycle stages and
60 dispersal mechanisms (Allinne et al., 2016; Boudrot et al., 2016; López-Bravo et al., 2012;
61 Ratnadass et al., 2012). Specifically, shade trees can act as a physical barrier at the edge of
62 agroforestry farms, trapping airborne particles from outside of the plot (Bouvet et al., 2007;
63 Grote et al., 2016; Raupach et al., 2001), and can reduce throughflow wind speeds (Pezzopane et
64 al., 2007, 2011a; Wright et al., 2010), limiting the quantity of spores released from infected leaf
65 surfaces at the interior edge of agroforestry farms (Aylor, 1990; Magyar et al., 2016). The ability
66 of shade trees to restrict the windborne release and dispersal of *H. vastatrix* uredospores
67 highlights their importance in limiting the spread of spores across large landscapes (Vandermeer
68 et al., 2014), which is especially significant in curbing the spread of new pathotypes.

69 This windbreak effect has been studied in relation to various shade tree canopy
70 characteristics, such as canopy geometry, plot-level plant heterogeneity and foliage distribution
71 (Bohrer et al., 2008, 2009; Cleugh, 1998). However, shade tree leaf-level functional traits, such
72 as specific leaf area (SLA) and leaf thickness, and canopy-level architectural traits beyond
73 geometry, have not been operationalized as key predictors of wind dynamics and of the wind
74 dispersal of *H. vastatrix* uredospores in complex coffee agroforestry systems. Taking a plant
75 functional traits lens (see e.g. Garnier and Navas, 2012; Martin and Isaac, 2015, 2018) to
76 describe patterns of wind and disease dynamics is widely absent from studies on complex
77 agroecosystems despite its ability to better inform the design and management of agroforestry
78 systems, especially since farmers often select shade trees based on their understanding of shade
79 tree traits (Cerdán et al., 2012; Isaac et al., 2009, 2018).

80 The main objective of this study is to determine the contribution of shade tree size class,
81 characterized by leaf functional and canopy traits, to changes in wind speeds and subsequent *H.*
82 *vastatrix* uredospore dispersal at the edge of coffee agroforestry systems. We hypothesize that
83 throughflow wind speeds will decrease as wind passes from coffee in monoculture through dense
84 shade tree canopies expressing key leaf functional traits (e.g. high leaf area and leaf thickness) at
85 the edge of coffee in agroforests. This in turn will suppress the release and dispersal of *H.*
86 *vastatrix* uredospores from infected plant surfaces and reduce the quantity of airborne
87 uredospores captured at the interior edge of coffee agroforestry systems.

88

89 **2. Material and Methods**

90 *2.1 Study site*

91 This study was conducted at the international coffee agroforestry research site Centro
92 Agronómico Tropical de Investigación y Enseñanza (CATIE), located in Turrialba, Costa Rica
93 ($09^{\circ}53'44''$ N, $83^{\circ}40'7''$ W) at 685 m.a.s.l, with less than 1% slope (Mora and Beer, 2013). The
94 CATIE experimental farm is over 9 ha and features *Coffea arabica*, an economically important
95 coffee species, accounting for ~65% of internationally exported coffee (FAO, 2015). We only
96 included the cultivated dwarf variety, Caturra, which is susceptible to almost all CLR races
97 (Rodrigues Jr. et al., 1975). This site is characterized by a mean annual temperature of 23.4°C ,
98 annual rainfall of 3200 mm and dominant wind speeds of 0.75 m s^{-1} (Haggar et al., 2011; van
99 Oijen et al., 2010). Sampling for this study occurred at the beginning of the rainy season in this
100 region (May – early July), though still with low daily rainfall amounts averaging less than 9mm.
101 Sampling occurred on days and at times with minimal rainfall.

102 Nine study plots were established at the edge of coffee agroforestry systems with an
103 *Erythrina poeppigiana* tree at the centre, which is the most commonly used shade tree in Costa
104 Rican coffee agroforestry systems (Russo and Budowski, 1986). Plot size, ranging from 9 m^2 to
105 64 m^2 , was based on the height of the central *E. poeppigiana*. The radius of each plot equalled
106 the height of the shade tree (Raupach et al., 2001; see Fig. 1a), resulting in plots with taller *E.*
107 *poeppigiana* trees being larger in size. Each plot was adjacent to coffee in monoculture to
108 capture agroforestry edge effects on wind speeds. The *E. poeppigiana* shade trees within our
109 study plots were categorized into three size classes based on the shade tree canopy openness
110 determined with preliminary canopy image analysis (n= 2 images per individual tree) (Frazer et
111 al. 1999). These three size classes captured the scope of contemporary on-farm shade tree
112 management practices: sparse (shade trees with extensive pruning practices), medium

113 (intermediate pruning practices and average shade tree height), and dense (unpruned shade trees)
 114 (following Yang et al. (2017) classification of wind breaks).

115

116 *2.2 Shade tree characterization*

117 Shade tree canopy-level architectural trait data were collected for each tree, including: tree
 118 height (m), canopy diameter (m), canopy base height (CBH; m), and canopy openness using
 119 hemispherical photographs analyzed with Gap Light Analyzer (Frazer et al., 1999). Five
 120 replicate leaf samples were collected from the edge of the lower canopy of each tree. Since *E.*
 121 *poeppigiana* has large compound leaves, each leaflet was considered as an individual leaf. Each
 122 leaf was measured for the following shade tree leaf functional traits following protocols by
 123 Pérez-Harguindeguy et al. (2013): leaf area (LA; cm²), specific leaf area (SLA; mg mm⁻²), leaf
 124 dry matter content (LDMC; mg g⁻¹), leaf angle (°), and leaf thickness (mm).

125

126 *2.3 Meteorological variables*

127 Based on about two years of meteorological measurements collected every 30 minutes at the
 128 CATIE site, the dominant wind directions were determined to be North and Northeast. At each
 129 plot, portable environmental sensors (Onset Computer Corporation, Bourne, MA), herein
 130 referred to as microstations, were arranged on the windward and leeward side of each study tree
 131 to simultaneously and continuously measure and record wind dynamics every second for four
 132 consecutive days. One microstation, equipped with a wind vane (HOBO wind direction smart
 133 sensor, S-WDA-M003) and wind anemometer (HOBO wind speed smart sensor, S-WSB-M003)
 134 at 2.5 m height, was positioned on the windward side North of the study tree in the adjacent
 135 coffee monoculture plot (Fig. 1b, A). Since there were no obstructions at the windward position,

136 wind from any direction was captured by the 'A' microstation. Three microstations, equipped
 137 with the same wind anemometer model at 2.5 m height, were positioned in a semi-circular
 138 pattern from South (180°) to Southwest (240°) of the study tree on the leeward side (Fig. 1b, B-
 139 D). Microstations 'B', 'C' and 'D' were used to measure wind speed dynamics directed within
 140 30° of their position (*i.e.* we used 'B' microstation for wind originating between 345° and 14.99° ,
 141 'C' microstation for 15° and 44.99° , and 'D' microstation for 45° and 74.99°). Each microstation
 142 was placed at a distance from the shade tree base equal to the height of the shade tree (3 m to 8
 143 m) (Fig. 1a).

144

145 2.4 Uredospore sampling

146 Two SporeWatch electronic spore samplers (Burkard Scientific Ltd., Uxbridge, Middx, UK)
 147 were placed on the windward side of the study tree in the adjacent coffee monoculture plot and
 148 leeward side of the study tree in the coffee agroforestry plot to determine changes in the quantity
 149 of airborne uredospores dispersed. Spore samplers were positioned at a height of 1.5m,
 150 corresponding to the upper-middle stratum of the average coffee tree (Fig. 1b) (Becker et al.,
 151 1975) and collected airborne uredospores for three days for six consecutive hours (11:00 am to
 152 5:00 pm) to correspond with times of peak aerial dispersal of *H. vastatrix* (Boudrot et al., 2016)
 153 and minimal rainfall activity. Airflow was set to 10 L/min to continuously pull in air samples.
 154 Spore sampler tapes were analysed under a compound microscope at 100x magnification and *H.*
 155 *vastatrix* uredospores were counted for the total sampling period.

156 Within 5 m surrounding each spore sampler at the windward and leeward positions, six
 157 randomly selected coffee plants were sampled to quantify the branch-level counts of mature *H.*
 158 *vastatrix* uredospores (spores that previously infected leaves and have re-emerged to regenerate

159 the cycle of infection). Similar to Boudrot et al. (2016), every leaf with sporulating *H. vastatrix*
160 lesions was collected from two branches from three strata (top, middle, bottom) of each sampled
161 coffee plant. These mature uredospore counts were used to quantify the potential number of
162 spores available for release and dispersal in the immediate environment. Uredospores from all
163 sporulating lesions from each branch were collected in microcentrifuge tubes and combined with
164 1 mL of 2.5% Tween. After 5 minutes in an ultrasonifier at 30°C, 10 µL of suspension was
165 placed into a Neubauer chamber and uredospores were counted through a 10x magnification.
166 Counts were repeated 4 times per branch and averaged.

167

168 2.5 Statistical analyses

169 All statistical analyses were performed using RStudio v. 1.1.456 (R Foundation for Statistical
170 Computing, Vienna, Austria). All variables were log-transformed except for canopy openness
171 and LDMC to achieve normality. For each shade tree size class, the mean, standard error and
172 coefficient of variation (CV) was calculated for all measured shade tree leaf functional traits
173 (n=15) and canopy architectural traits (n=3). We used a one-way ANOVA to test if the shade
174 tree traits differed across the size classes.

175 Wind speed analyses included only wind speed measurements when the wind direction was
176 between 345° to 75° and when the wind speed at position A was greater than zero. To
177 demonstrate reductions in wind speeds from the windward to leeward side of all shade trees, a
178 wind rose diagram was created using the OpenAir package (Carslaw and Ropkins, 2012), where
179 wind speed data across the global dataset was separated into four wind speed bins and relative
180 frequencies were plotted.

181 The magnitude of throughflow wind speed reductions was calculated as the leeward wind
 182 speeds subtracted from the windward wind speeds. These magnitudes were separated into three
 183 categories: 1) greater than 2 m s^{-1} reduction; 2) 0 to 2 m s^{-1} reduction; and 3) increase in
 184 throughflow speed. The relative frequency of each of these categories was calculated for each
 185 shade tree size class and a repeated measures ANOVA was used to test if certain classes reduced
 186 throughflow speeds more frequently than others.

187 We then performed a backwards stepwise linear modelling procedure to determine the
 188 functional leaf and canopy architectural traits that best explain frequencies of throughflow speed
 189 reductions. Collinearity among all predictor variables was assessed with correlation analysis and
 190 variables that were colinear were not included in the same model. Models were compared using
 191 Akaike's information criteria (AIC), with the lowest AIC score indicating the most parsimonious
 192 model fit.

193 The percent change in captured airborne uredospores was calculated as the number of
 194 captured spores on the windward side subtracted from those on the leeward side, divided by the
 195 former. These values were normally distributed. Means and standard errors were calculated for
 196 the percent change in captured uredospores ($n=9$) and of mature uredospore counts per coffee
 197 plant stratum ($n=12$). A two-way ANOVA was performed to test for significant differences
 198 between positions (windward and leeward) and across the size classes. A linear model was
 199 developed including throughflow speed reduction frequencies to predict percent change in
 200 captured airborne uredospores across the global dataset with no significant random effects.

201

202 **3. Results:**

203 *3.1 Shade tree trait variation*

204 Specific shade tree leaf functional traits, namely leaf area, thickness and angle, differed
 205 significantly between the shade tree size classes (Table 1). Coefficients of variation (CV) of
 206 functional leaf traits ranged from 13.67 to 89.48% and CVs of canopy architectural traits ranged
 207 from 2.37 to 78.73%. Shade canopy architectural traits were more similar between size classes
 208 except canopy openness, which was significantly greater in the sparse compared to the dense
 209 class ($P=0.034$) (Table 1).

210

211 *3.2 Throughflow wind speeds*

212 Wind speeds decreased as wind passed from the windward to leeward side of the shade tree
 213 canopies by about 0.45 m s^{-1} on average. Fig. 2a highlights the greater relative frequency of high
 214 wind speeds (greater than 1 m s^{-1}) on the windward (A) and the greater relative frequency of
 215 slow wind speeds (less than 1 m s^{-1}) on the leeward (B, C, D) across all sampled shade trees.
 216 Similar patterns were found when data were separated into shade tree size classes. Reductions in
 217 throughflow wind speeds of between 0 to 2 m s^{-1} occurred most frequently with dense shade
 218 trees and least frequently with sparse shade tree canopies ($P=0.005$) (Fig. 2b).

219 To capture the effect of the variability in shade tree functional traits across the size classes,
 220 we modelled the frequency of throughflow speed reductions with two canopy architectural traits
 221 (canopy openness, CBH) and two leaf functional traits (SLA, leaf thickness), excluding all other
 222 variables due to collinearity. The AIC-selected model includes canopy openness, CBH and leaf
 223 thickness ($r^2=0.891$, $P=0.002$), where frequency of throughflow speed reduction was
 224 significantly negatively correlated with CBH ($P<0.001$) and significantly positively correlated
 225 with mean leaf thickness ($P=0.001$; Table 2). In summary, shade trees with lower CBH and

226 greater leaf thickness, regardless of size class, related to greater frequencies in throughflow wind
 227 speed reductions.

228

229 *3.3 Uredospore dispersal*

230 Mean plant-level mature uredospore counts were not significantly different between the
 231 windward and leeward positions across the shade tree size classes, except for the medium size
 232 class, where there were significantly greater mature uredospores at the leeward position
 233 ($P<0.001$; Table 3a). Comparing each coffee plant stratum individually, there were no significant
 234 differences in mature uredospores between the windward and leeward positions. Percent changes
 235 in the airborne uredospores captured with the SporeWatch electronic samplers did not
 236 significantly differ between the shade tree size classes (Table 3b). Within each class, though
 237 there were no significant differences in captured airborne uredospores between the windward and
 238 leeward positions, each class had positive daily percent change values in captured airborne
 239 uredospores, indicating that there were, on average, more captured uredospores on the leeward
 240 compared to the windward positions. Global percent change in captured airborne uredospores
 241 was significantly positively related to greater frequency of high throughflow wind speed
 242 reductions (more than 2 m s^{-1}) ($r^2=0.753$, $P=0.003$), indicating there was an increase in captured
 243 airborne uredospores in plots where high wind speeds were reduced more frequently.

244

245 **4. Discussion**

246 *4.1 Throughflow wind and plant functional traits*

247 We demonstrate that shade tree traits in agroforestry systems display intraspecific variability,
 248 which are linked to differences in management practices. While major canopy traits, such as

249 canopy openness, differed significantly between the size classes as expected (Table 1), shade tree
 250 functional leaf traits also displayed intraspecific plasticity, similar to that observed in tree-crops
 251 in full sun and shaded environments (*e.g.* Matos et al., 2009). For example, denser canopies with
 252 a higher degree of self-shading tended to have larger, more horizontal leaves (Table 1), likely to
 253 maximize photosynthetic rates in the lower canopy (Hikosaka and Hirose, 1997). However,
 254 shade tree leaf thickness, which tends to decrease under dense shade (Björkman, 1981), was
 255 instead lowest in the sparse shade tree canopies (Table 1). Since these canopies had been
 256 extensively pruned, this anomaly may reflect the pruning management, especially since the
 257 expected pattern is evident between the medium and dense shade tree size classes. This plasticity
 258 in shade tree traits is not commonly considered in relation to management practices, despite this
 259 variation's effect on plot-level abiotic processes.

260 Previous research has demonstrated that shade trees reduce wind speeds at the edge of
 261 plantations (Wright et al., 2010), including coffee agroforestry farms (Pezzopane et al., 2011b).
 262 These reductions in wind speeds have previously been linked to pruning practices (Pezzopane et
 263 al., 2007), similar to the differences in throughflow speed reductions we found between dense
 264 and sparse shade trees (Fig. 2b). Our results highlight how wind dynamics are dramatically
 265 impacted by shade tree functional leaf and canopy traits. In particular, the lower the vertical
 266 distribution of vegetation in the canopy, which can restrict sub-canopy wind jets (Dupont and
 267 Brunet, 2008), and thicker leaves, which can prevent leaves from reconfiguring to reduce drag
 268 forces (Vogel, 1989), slowed throughflow speeds more frequently. By using shade tree traits, on-
 269 farm management decisions can be centered on specific traits rather than specific species, to
 270 more effectively understand the influence of shade trees and management practices on wind
 271 dynamics and consequent spore dispersal patterns.

272

273 4.2 Throughflow wind and *H. vastatrix* dispersal

274 Other studies, such as Boudrot et al. (2016) and Avelino et al. (2020), observed greater
275 branch-level mature uredospore counts and captured airborne uredospores than the present study.
276 These discrepancies are attributed to seasonal differences. Our study was conducted at the onset
277 of the rainy season when there is generally lower quantities of *H. vastatrix* uredospores (Boudrot
278 et al., 2016) and still low amounts of daily rainfall (see 2.1 Study site). At this time, wind is still
279 the main abiotic driver of uredospore dispersal, especially for the transport of uredospores across
280 large distances (*i.e.* other coffee farms) (Vandermeer et al., 2014). Once the rainy season
281 develops, as captured in the studies initially mentioned, wind becomes a less significant abiotic
282 driver of dispersal in agroforestry systems, being replaced by rainfall events and the impact of
283 raindrops on coffee leaves that release uredospores in the air (Boudrot et al., 2016).

284 Previous research has linked changes in wind speeds to changes in fungal spore dispersal,
285 due to the vital role of wind speed in the detachment of spores from fungal clusters, notably in
286 drier conditions. Early studies on *H. vastatrix* have estimated wind speeds between 1 and 5.6 m
287 s⁻¹ are required for the release of *H. vastatrix* uredospores (Becker, 1977; Martinez et al., 1977).
288 The role of wind speed in the dispersal of *H. vastatrix* uredospores has been reflected in field
289 studies, where wind gusts encouraged spore dispersal in exposed conditions, yet had limited
290 effect under the protection of shade trees (Boudrot et al., 2016). The objective of this study was
291 to understand the effect of changing wind dynamics on uredospore dispersal at the edge of coffee
292 agroforestry farms. We found that shade trees with a greater frequency of throughflow speed
293 reduction had a greater percent change in captured airborne uredospores. We observed, on
294 average, an increase in captured uredospores at the leeward position (positive percent change

values), which, although unexpected, may be the result of the gravitational settling of spores in the “quiet zone” on the lee side of the shade tree (Cleugh, 1998; Magyar et al., 2016). *H. vastatrix* uredospores are prone to release in clusters, which have greater settling speeds than single uredospores (Bowden et al., 1971). Combined with the greater frequency of still air due to the windbreak effect of shade trees, there is a greater likelihood of airborne uredospores settling out of the turbulent wind and entering the coffee plant canopy space.

Wind-driven release of spores from infected surfaces does not impact the plant profile evenly. Instead, the top stratum is most exposed to high wind speeds and greater turbulence, resulting in greater spore release (Aylor, 1990). However, the microclimate conditions for *H. vastatrix* uredospore germination and sporulation, such as regulated air temperatures, high relative humidity and longer leaf wetness duration (Avelino et al., 2004; López-Bravo et al., 2012), are better near the middle and bottom strata of the coffee plant canopy. Our results reflect these trends, with greater mature uredospore counts in the middle and bottom strata compared to the top stratum, except behind the sparse shade tree size class (Table 3). Comparing the size classes, the dense shade trees at the leeward position had greater mature uredospores only in the bottom stratum and had the least number of mature uredospores in the top stratum (Table 3), reflecting a lower potential for windborne dispersal.

312

313 4.3 Fluidity in desirable shade tree traits

314 Contrary to shelterbelt designs of single windbreak rows, coffee agroforestry systems are
 315 generally characterized by the integration of shade trees throughout the agricultural field.
 316 Previous research suggests that as wind moves through landscapes with multiple windbreaks, as
 317 would be commonly found in coffee agroforestry systems, there is a greater overall windbreak

318 effect (Judd et al., 1996) that depends on distances between trees (Bohrer et al., 2009). This, in
319 turn, can reduce airborne spore dispersal more efficiently (Magyar et al., 2016). While dense
320 shade trees are most effective in slowing the wind-driven dispersal of *H. vastatrix* uredospores at
321 the edge of coffee agroforestry farms, the desirability of such trees can change both spatially and
322 temporally. For example, continuous dense shade cover can reduce coffee yields (DaMatta,
323 2004; DaMatta et al., 2007) and improve conditions for certain pathogens (Avelino et al., 2018).
324 Similarly, shade trees during dry conditions are more effective in interfering with airborne
325 uredospores travelling via wind, and, as our results demonstrate, lead to a settling of uredospores
326 near the interior edge of an agroforestry farm. However, during the rainy season, dense shade can
327 promote the *H. vastatrix* lifecycle and enhance dispersal via rainfall kinetics (Boudrot et al.,
328 2016; López-Bravo et al., 2012), highlighting the temporal variability of shade tree effectiveness
329 in limiting the spread of *H. vastatrix*.

330 These findings reflect a fluidity in the desirable shade tree traits across agroforestry farms,
331 from edge to interior and over time, that should be considered in initial farm design and on-farm
332 management decisions. Coffee farmers recognize the functional traits analysed in this study and
333 already use these traits for shade tree selection during farm design (Cerdán et al., 2012; Isaac et
334 al., 2018; Valencia et al., 2015). For example, coffee farmers in Costa Rica often look at shade
335 tree height and leaf area when deciding on shade tree species to include, due to their perceived
336 influence on microclimate adjustments that affect crop growth and fungal pathogen success and
337 dispersal (Cerdán et al., 2012). Therefore, it is important for research to use these accessible and
338 recognizable techniques to tease out the dynamics of pathogen movement in complex systems so
339 that research can better translate to on-farm crop protection practices.

340

341 **5. Conclusions**

342 Our results suggest that dense shade trees with low CBH and thick leaves are most effective
 343 in slowing throughflow wind speeds at the edge of agroforestry farms. These still air conditions
 344 promoted the settling of airborne *H. vastatrix* uredospores into the coffee canopy space,
 345 essentially trapping these spores at the interior edge of the agroforestry farm. Furthermore, the
 346 leeward side of dense shade trees had a lower potential for wind-driven dispersal of mature
 347 uredospores from the top stratum of infected coffee plants. Findings from our study suggest that
 348 desirable shade tree traits are fluid throughout the farm design, with preferences changing from
 349 edge to interior and between season, tracking with the changing role of the shade tree. We also
 350 highlight a new layer in the complexity of uredospore movement in agroforestry systems through
 351 the important role of shade tree canopy traits and leaf functional traits in moderating abiotic
 352 processes, such as wind dynamics. This research is essential to further our understanding of how
 353 to limit the spread of *H. vastatrix* and its ever-evolving new pathotypes at the plot, farm and
 354 landscape scales.

355

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365

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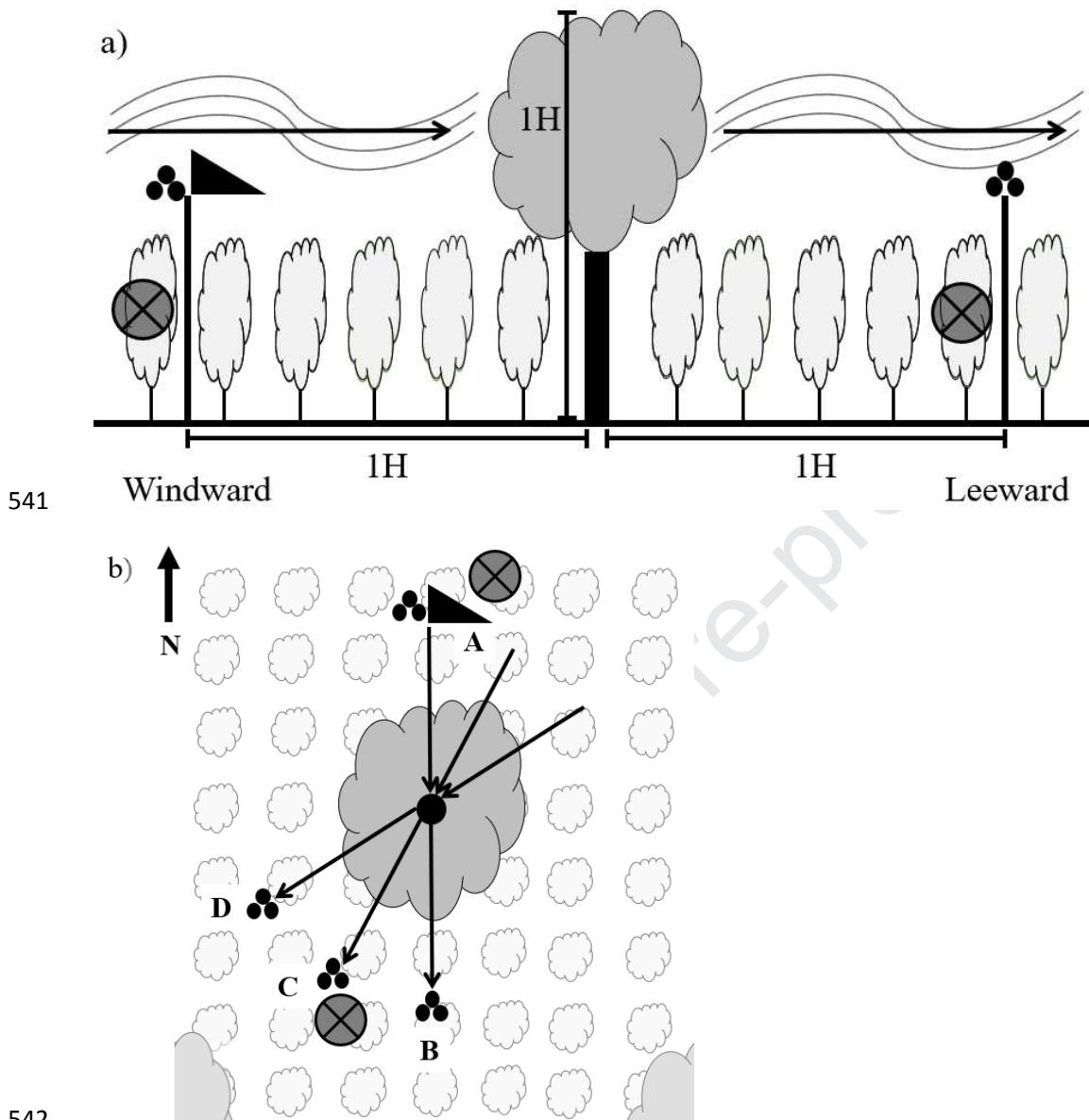
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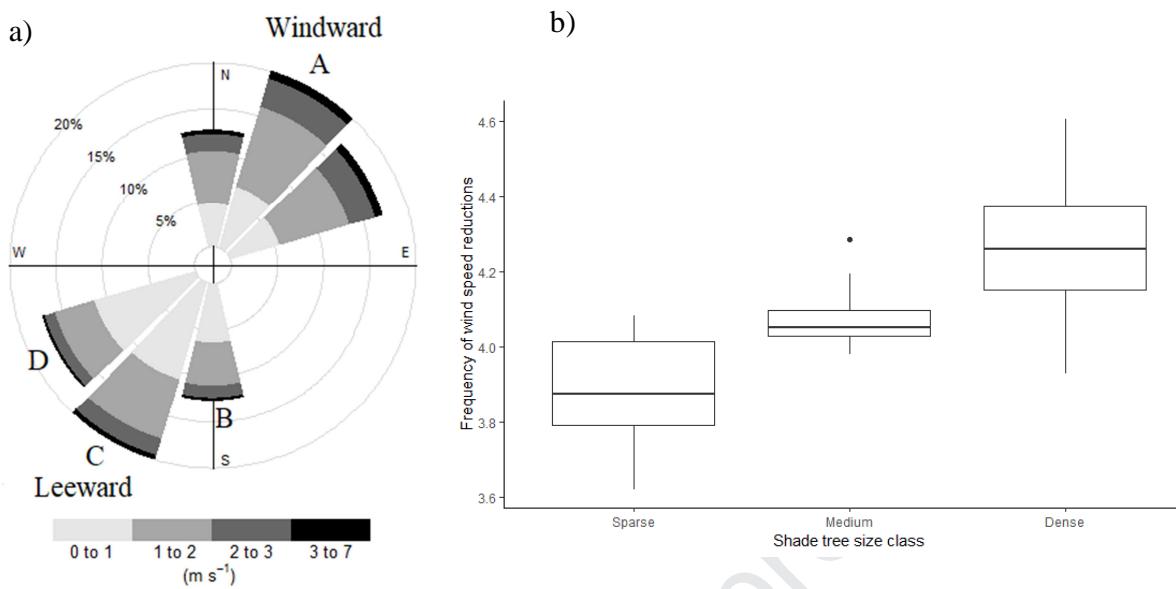
543 **Fig. 1.** a) Planar view of study plot design. All microstations were positioned one tree height
 544 (1H) distance from the base of the shade tree. b) Aerial view of study plot design. The windward
 545 microstation, located in adjacent monocultured coffee, is labelled 'A' equipped with a wind vane
 546 (►) and anemometer (●). The leeward microstations, located inside the agroforest, are labelled
 547 'B', 'C' and 'D' positioned 30° from each other, each equipped with a wind anemometer. At
 548 microstation 'A' and 'C' a SporeWatch sampler (⊗) was placed at 1.5 m height.

549 **Table 1.** Mean, standard error (SE) and coefficient of variation (CV) of *E. poeppigiana*
 550 functional leaf (leaf area (LA); specific leaf area (SLA); leaf dry matter content (LDMC); leaf
 551 thickness; leaf angle) and canopy (canopy openness; total tree height; canopy base height (CBH);
 552 canopy diameter) traits for each of the three shade tree classes (where n=15 for leaf traits and
 553 n=3 for canopy traits). *P*-value results from an ANOVA are shown (significant results are in
 554 bold).

Leaf traits	Units	Shade tree size class						<i>P</i> -value	
		Sparse		Medium		Dense			
		Mean ± SE	CV (%)	Mean ± SE	CV (%)	Mean ± SE	CV (%)		
LA	cm ²	169.2 ^{ab*} ± 11.1	25.44	139.7 ^b ± 10.4	28.89	211.1 ^a ± 24.1	44.30	0.027	
SLA	mg mm ⁻²	21.7 ± 1.4	24.13	22.4 ± 1.5	25.25	21.8 ± 1.2	21.03	0.920	
LDMC	mg g ⁻¹	210.0 ± 11.8	21.71	238.6 ± 9.4	15.24	222.9 ± 7.9	13.67	0.131	
Leaf thickness	mm	0.17 ^b ± 0.01	18.46	0.21 ^a ± 0.01	14.50	0.19 ^{ab} ± 0.01	20.22	0.004	
Leaf angle	°	51.7 ^a ± 5.1	38.40	24.6 ^b ± 5.6	88.47	29.5 ^b ± 6.8	89.48	0.007	
Canopy traits									
Canopy openness	%	41.5 ^a ± 1.8	7.69	37.3 ^{ab} ± 0.5	2.37	29.6 ^b ± 3.7	21.68	0.034	
Total tree height	m	4.8 ± 1.6	56.97	4.7 ± 0.8	30.46	5.2 ± 1.5	49.66	0.974	
CBH	m	1.9 ± 0.4	34.44	1.9 ± 0.2	14.04	1.8 ± 0.8	78.73	0.838	
Canopy diameter	m	7.5 ± 2.1	48.10	7.7 ± 1.9	41.92	8.9 ± 2.2	43.39	0.856	

* Different letters beside mean values denote significant differences between size classes.

555



556

557 **Fig. 2.** a) Windrose with total relative frequency of different wind speed bins for all measured
 558 directions across all plots. ‘A’ represents the wind measurements from 345° to 75° captured on
 559 the windward North side of the shade tree in the coffee monoculture plot. ‘B’, ‘C’ and ‘D’
 560 represent the complementary wind measurements captured on the leeward side of the shade tree.
 561 b) Boxplot of log-transformed relative frequencies of throughflow speed reductions of 0 to 2m s⁻¹
 562 for each shade tree size class.

563 **Table 2.** Stepwise and multiple regression model analysis of the relationship between leaf functional and canopy traits with
 564 throughflow wind speed reduction frequency. The most parsimonious model fit (based on AIC values) is highlighted in bold and the
 565 ΔAIC value represents the comparison to the full model, where wind speed reduction frequency is predicted as a function of specific
 566 leaf area (SLA), canopy openness (O), canopy base height (CBH) and leaf thickness (Th). Estimates of the slope term for each
 567 predictor variable and explained variance for each model with associated *P*-values in parentheses are presented.

Predictor variables	Step-wise regression		Multiple regression model terms					Model r^2 (<i>P</i> -value)
	Model AIC	Δ AIC	Intercept	Th	CBH	O	SLA	
SLA + O + CBH + Th	-59.198	--	4.830 (<0.001)	0.405 (0.008)	-0.228 (0.003)	0.002 (0.389)	0.099 (0.433)	0.885 (0.010)
O + CBH + Th	-59.637	-0.439	5.172 (<0.001)	0.433 (0.002)	-0.237 (0.001)	0.002 (0.268)	--	0.891 (0.002)

568 **Table 3.** Means and standard errors of (a) mature uredospore counts at the branch-level at
 569 windward and leeward positions for each coffee stratum (top, middle, bottom) and the whole
 570 coffee plant for each shade tree size class; and (b) captured airborne uredospore counts per
 571 sampling day at each position with percent changes in paired daily captured airborne uredospore
 572 counts for each shade tree size class [(leeward – windward) / windward] . Within each size class,
 573 capital letters denote significant differences between positions; within each position, small letters
 574 denote significant differences between size classes ($P \leq 0.05$). The absence of a letter indicates no
 575 significant difference.

a)	Position	Shade tree size class		
		Sparse	Medium	Dense
		Mature uredospore counts (per branch)		
Top coffee stratum	Windward	6609 ^a ± 1460.6	1336 ^b ± 309.2	1825 ^b ± 694.7
	Leeward	5254 ^a ± 988.6	3156 ^a ± 678.2	1482 ^b ± 423.1
Middle coffee stratum	Windward	5069 ^a ± 947.7	3417 ^b ± 1397.9	1871 ^b ± 409.3
Bottom coffee stratum	Windward	6548 ^a ± 959.8	2616 ^b ± 740.2	2209 ^b ± 416.8
Whole coffee plant	Windward	6075 ^a ± 660.1	2456 ^{Bb} ± 538.6	1969 ^b ± 300.2
	Leeward	4556 ^a ± 544.0	3867 ^{Aa} ± 550.4	2891 ^b ± 446.8
b)				
Captured airborne uredospores (per 3.6 m ³)				
SporeWatch sampler	Windward	5.00 ± 0.73	13.11 ± 3.12	7.38 ± 3.85
	Leeward	6.67 ± 0.53	10.44 ± 2.12	9.25 ± 3.11
Daily percent change		42.33 ± 8.51	20.78 ± 42.97	50.91 ± 22.77

576

Highlights

- We study shade tree traits and effects on wind dynamics and pathogen dispersal.
- Shade trees with low canopy base height and thick leaves significantly slow wind speed.
- Reduced wind speeds decrease uredospore dispersal and possibly encourage uredospore settling.
- Trade-offs in shade tree functional traits are key to pathogen dynamics at the farm edge.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

